

MARINE RESERVES, COMMUNITY-BASED MANAGEMENT,
AND SMALL-SCALE BENTHIC FISHERIES
IN THE GULF OF CALIFORNIA, MEXICO

By

Richard Cudney-Bueno

A Dissertation submitted to the Faculty of the
SCHOOL OF NATURAL RESOURCES

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN RENEWABLE NATURAL RESOURCES STUDIES

In the Graduate College

THE UNIVERSITY OF ARIZONA

2007

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Dissertation Committee, we certify that we have read the dissertation prepared by Richard Cudney-Bueno

entitled: Marine Reserves, Community-Based Management, and Small-Scale Benthic Fisheries in the Gulf of California, Mexico

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

_____ Date 12/11/06
Dr. James B. Greenberg

_____ Date 12/11/06
Dr. Stephen Lansing

_____ Date 12/11/06
Dr. Peter T. Raimondi

_____ Date 12/11/06
Dr. William W. Shaw

_____ Date 12/11/06
Dr. Robert J. Steidl

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

_____ Date 12/11/06
Dissertation Director: Dr. William W. Shaw

STATEMENT BY AUTHOR

This dissertation has been submitted in partial fulfillment of requirements for an advanced degree at The University of Arizona and is deposited in the University of Arizona Library to be made available to borrowers under rules of the Library.

Brief quotations from this dissertation are allowable without special permission, provided that accurate acknowledgement of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the Graduate College when in his or her judgement the proposed use of the material is in the interests of scholarship. In all other instances, however, permission must be granted from the author.

SIGNED: Richard Cudney-Bueno

ACKNOWLEDGEMENTS

My dissertation research is truly the product of the aggregated support of numerous people and institutions. First, I would like to thank Dr. William “Bill” Shaw for taking me as his graduate student. Bill was always available when I needed him and advised me not only as his student, but also as a colleague and friend. To my other committee members, Jim Greenberg, Steve Lansing, Pete Raimondi, and Bob Steidl, thank you for believing in my work and enriching it. I am profoundly indebted to those organizations that trusted me enough to essentially keep my research, family, and me alive all these years: The David and Lucile Packard Foundation, Consejo Nacional de Ciencia y Tecnología (CONACYT), Inter American Foundation (IAF), Environmental Leadership Program (ELP), PADI Project AWARE Foundation, Wallace Research Foundation, Graduate College of the University of Arizona, World Wildlife Fund-Gulf of California Program, Tinker Foundation, Sandler Foundation, and last, but certainly not least, the Intercultural Center for the Study of Deserts and Oceans (CEDO). CEDO was a pillar in the work with Puerto Peñasco divers, the stage for countless memories, and a home, literally and figuratively, for many years. A heart-felt thanks to Peggy Turk-Boyer, Director of CEDO, and Olegario Morales, CEDO’s field research technician at the time I conducted my studies. To the commercial divers of Puerto Peñasco, who opened the doors to their life, work, and knowledge. Our learning transcends the realms of natural history and science: friendship, laughter, sorrow, love, good ceviche, mourning, singing, music, dancing, story telling, distant lights in the night, climbing summits, diving to bottoms, dehydration, scorching nights, chilling waters, warm waters... together we have learned about life. Gracias Cuco, Angelillo, Tacho, Pin, Botete, Don Nacho, Pelón, Cándido, Tele, Chilo, Marcano Viejo, Marcanillo, Badachi, Valente, Manichi, Lalo, Güero, Pony, Chito, Bambocho, Chavira, Zurdo... gracias por compartir y navegar conmigo los repuntes y bajadas de marea. To my friends and colleagues: Mariana Altrichter, Xavier Basurto, Luis Bourillón, Rocío Covarrubias, Josh Donlan, Bete Jones, Tad Pfister, Kirsten Rowell, Peter Sherman, Jorge Torre, Hudson Weaver. Our relationship and conversations have more than enriched my work. Thanks also to all *PANGUEROS*, particularly Ana Cinti, Jennie Duberstein, Marcia Moreno, Martín Rivera, and Gaspar Soria for all your hard work and patience while we got this “little” project going in the midst of finishing a PhD. I am honored to have the privilege of working with you all. And to Lindsey Haskin, Osvel Hinojosa, Emily Omana, Rebecca Prescott, Jen Rupnow... it was a pleasure to share “the field” with you. Thank you. Lastly, to the most important people in my life: my parents, Roger and Eloisa; my brothers and sister, Roger, Robert, and Kathy; my beautiful boys, Ian and Santiago, and my wife and best friend Tiffany. You all ground me and have made the essence of who I am. Ian and Santi, you have made me read *Moby Dick* and dress up like a pirate again. Each of your smiles hits me to the core, even when I have been distracted. This is for you asking why I was so often working on the computer. And Tiff... from a night in April 13 years ago to another April night as I write this. It has been an incredible ride, and you have been there through all its turns. Your patience, integrity, and love are as real and humbling as they get. Here’s to you, us, exploration, and the songs I learn and compose in my new banjo.

DEDICATION

For Jorge Hernández Bueno, my cousin and friend.

Your gypsy soul will continue to build castles
and live in our hearts and dreams.

TABLE OF CONTENTS

LIST OF FIGURES	8
LIST OF TABLES	15
ABSTRACT.....	17
INTRODUCTION	19
The Problem and its Global Context.....	19
State of the world’s fisheries, importance of small-scale fisheries, and management challenges	19
The “tragedy of the commons”: the main management problem?	21
Community-based management and the use of marine reserves	22
Small-Scale benthic fisheries and the use of marine reserves	24
Summary: research needs.....	27
This Dissertation	28
Explanation of Dissertation Format	33
PRESENT STUDY.....	38
Study Area.....	38
Life History of Rock Scallop and Black Murex	39
Puerto Peñasco Benthic Fishery Case Study	47
A Regional Perspective on the Emergence and Governance of Marine Reserves in the Gulf of California	51
Implications of this Study for the Establishment and Governance of Community-Based Reserves	57

APPENDIX A. ESTABLISHING A BASELINE: GROWTH AND REPRODUCTION OF THE ROCK SCALLOP (<i>SPONDYLUS CALCIFER</i>) IN THE UPPER GULF OF CALIFORNIA, MEXICO.....	61
APPENDIX B. GROWTH, LONGEVITY, AND MORPHOLOGICAL VARIATIONS OF THE BLACK MUREX SNAIL (<i>HEXAPLEX NIGRITUS</i>): IMPLICATIONS FOR MANAGEMENT OF A RAPIDLY DECLINING FISHERY	95
APPENDIX C. BREEDING AGGREGATIONS AND REPRODUCTIVE ECOLOGY OF THE BLACK MUREX SNAIL (<i>HEXAPLEX NIGRITUS</i>) IN THE NORTHERN GULF OF CALIFORNIA, MEXICO	125
APPENDIX D. RAPID EFFECTS OF MARINE RESERVES AND THE RISE AND FALL OF COOPERATION IN A YOUNG FISHERY.....	159
APPENDIX E. ONLINE SUPPORTING MATERIALS FOR APPENDIX D.....	198
APPENDIX F. GOVERNANCE AND EFFECTS OF MARINE RESERVES IN THE GULF OF CALIFORNIA, MEXICO	220
APPENDIX G. PLAN DE MANEJO REGIONAL PARA EL APROVECHAMIENTO Y LA RECUPERACION DEL CALLO DE ESCARLOPA, <i>SPONDYLUS CALCIFER</i>	266
APPENDIX H. SUBTIDAL TEMPERATURES IN ISLA SAN JORGE, OCTOBER 2003 – OCTOBER 2004	300
APPENDIX I. PHOTOGRAPHS OF ROCK SCALLOP, BLACK MUREX, AND COMMERCIAL DIVING	307
APPENDIX J. GLOSSARY OF TERMS AND ABBREVIATIONS.....	316
REFERENCES	317

LIST OF FIGURES

APPENDIX A. ESTABLISHING A BASELINE: GROWTH AND REPRODUCTION OF THE ROCK SCALLOP (*SPONDYLUS CALCIFER*) IN THE UPPER GULF OF CALIFORNIA, MEXICO.

Figure A.1. Rock scallop (<i>Spondylus calcifer</i>) study areas in the upper Gulf of California, Mexico.....	81
Figure A.2. Cross-section of rock scallop (<i>Spondylus calcifer</i>) specimen A collected in the upper Gulf of California, Mexico	82
Figure A.3. Example of cross-section of rock scallop, <i>Spondylus calcifer</i> , (specimen D) collected in the upper Gulf of California, Mexico	83
Figure A.4. Isotopic profiles of the last growth increments of rock scallop specimens A, B, and C.....	84
Figure A.5. $d^{18}O$ profiles of rock scallop, <i>Spondylus calcifer</i> , specimens D, E, and F which fall within the minimum reproductive size range (shell height 86 mm - 113 mm)	85
Figure A.6. $d^{18}O$ profiles of rock scallop, <i>Spondylus calcifer</i> , specimens G and H collected in the upper Gulf of California, Mexico.....	86
Figure A.7. Seasonal representation of the relationship between shell height and adductor muscle length for <i>Spondylus calcifer</i> in the Upper Gulf of California, Mexico	87
Figure A.8. Seasonal representation of the relationship between shell height and adductor muscle weight for <i>Spondylus calcifer</i> in the Upper Gulf of California, Mexico.....	88
APPENDIX B. GROWTH, LONGEVITY, AND MORPHOLOGICAL VARIATIONS OF THE BLACK MUREX SNAIL (<i>HEXAPLEX NIGRITUS</i>): IMPLICATIONS FOR MANAGEMENT OF A RAPIDLY DECLINING FISHERY	
Figure B.1. Study area and collecting sites of black murex (<i>Hexaplex (Muricanthus) nigritus</i>) breeding aggregations in the upper Gulf of California, Mexico	117
Figure B.2. Schematic representation of black murex morphological nomenclature and measurements taken.....	118

Figure B.3. Cross section of body whorl of the largest black murex specimen sampled for stable oxygen isotope analyses	119
Figure B.4. Cross sections and protoconch of youngest black murex specimen sampled for oxygen isotope analysis	120
Figure B.5. Length-weight relationship of black murex snails (<i>Hexaplex (Muricanthus) nigritus</i>) from four areas in the upper Gulf of California, Mexico	121
Figure B.6. Relationship between snail size and one year growth in TL (A) and whorl (B) of black murex snail, <i>Hexaplex (Muricanthus) nigritus</i> , in the upper Gulf of California, Mexico	122
Figure B.7. $d^{18}O$ VPBD profiles from <i>Hexaplex (Muricanthus) nigritus</i> shells, collected from La Cholla, upper Gulf of California, Mexico	123

APPENDIX C. BREEDING AGGREGATIONS AND REPRODUCTIVE ECOLOGY OF THE BLACK MUREX SNAIL (*HEXAPLEX NIGRITUS*) IN THE NORTHERN GULF OF CALIFORNIA, MEXICO

Figure C.1. Study area and collecting sites of black murex (<i>Hexaplex nigritus</i>) aggregations in the northern Gulf of California, Mexico	148
Figure C.2. Egg capsule measurements of the Black murex snail, <i>Hexaplex nigritus</i>	149
Figure C.3. Breeding aggregations, egg capsules, and larvae of black murex snail, <i>Hexaplex nigritus</i>	150
Figure C.4. Relationship between egg capsule size and number of larvae of the black murex snail, <i>Hexaplex nigritus</i> , in the northern Gulf of California, Mexico	151
Figure C.5. Relationship between snail size and size of egg capsules of the black murex snail, <i>Hexaplex nigritus</i> , in the northern Gulf of California, Mexico	152

APPENDIX D. RAPID EFFECTS OF MARINE RESERVES AND THE RISE AND FALL OF COOPERATION IN A YOUNG FISHERY

Figure D.1. Location of Puerto Peñasco community-based reserves and monitored fishing areas	187
Figure D.2. Density (number of individuals per 100 m ²) of observed juvenile black murex (<i>Hexaplex nigritus</i>) and rock scallops (<i>Spondylus calcifer</i>) in marine reserves and fishing sites combined (mean ± S.E.).....	188
Figure D.3a. Differences in spatial signatures of the effects of marine reserves on the density of juvenile rock scallops (<i>Spondylus calcifer</i>) in the northern Gulf of California, Mexico (mean ± S.E.).....	189
Figure D.3b. Differences in spatial signatures of the effects of marine reserves on the density of juvenile black murex (<i>Hexaplex nigritus</i>) in the northern Gulf of California, Mexico (mean ± S.E.)	190
Figure D.4. Final position of particles 2 and 4 weeks after having been released in (a) the nearest rocky reef located south of the marine reserve network, and (b) its southern boundary	191
Figure D.5. Trajectory of satellite-tracked drifters released near San Jorge Island, July 2006	192
Figure D.6a. Comparison of the average adductor muscle weight and length of rock scallops (<i>Spondylus calcifer</i>) from fishing areas in the northern Gulf of California between 2002-2004	193
Figure D.6b. Comparison of the average live weight of black murex snails (<i>Hexaplex nigritus</i>) from reserve and fishing areas in the northern Gulf of California between 1999 (pre-establishment of reserves) and 2003-2004 (post-establishment of reserves).....	194

APPENDIX E. ONLINE SUPPORTING MATERIALS

Figure E.1. Changes in density of observed juvenile rock scallop in marine reserves and fishing sites in the northern Gulf of California	209
Figure E.2. Changes in density of observed juvenile black murex in marine reserves and fishing sites in the northern Gulf of California	210
Figure E.3. Comparison of the average total length of black murex snails from reserve and fishing areas in the northern Gulf of California	

before and after establishment of reserves	211
Figure E.4. Progressive vector diagram of data obtained from an ADCP (Accoustic Doppler Current Profiler).....	212
APPENDIX F. GOVERNANCE OF MARINE RESERVES IN THE GULF OF CALIFORNIA, MEXICO	
Figure F.1. Location of the Puerto Peñasco, San Pedro Mártir, and Loreto Bay marine reserves	262
Figure F.2. Loreto Bay National Park and location of el Bajo del Murciélago and Bajo el Cochi no-take marine reserves	263
Figure F.3. Marine reserve network of Puerto Peñasco, Sonora, Mexico	264
Figure F.4. San Pedro Mártir Island Biosphere Reserve	265
APPENDIX G. PLAN DE MANEJO REGIONAL PARA EL APROVECHAMIENTO Y LA RECUPERACION DEL CALLO DE ESCARLOPA, SPONDYLUS CALCIFER	
Figure G.1. Corte de una concha adulta de callo de escarlopa, <i>Spondylus calcifer</i> , mostrando los anillos de crecimiento	271
Figure G.2. Relación entre altura de la concha y longitud del músculo aductor del callo de escarlopa, <i>Spondylus calcifer</i>	272
Figure G.3. Relación entre altura de la concha y el peso del músculo aductor del callo de escarlopa, <i>Spondylus calcifer</i>	272
Figure G.4. Perfil de valores isotópicos de oxígeno obtenidos para tres organismos reproductores	273
Figure G.5. Distribución de sitios arqueológicos Mesoamericanos donde se han encontrado ejemplares de <i>Spondylus spp</i>	278
Figure G.6. Zonas de pesca de callo de escarlopa utilizadas por buzos comerciales de Puerto Penasco	282
Figure G.7. Propuesta de zona de pesca permitida para buzos comerciales de Puerto Peñasco organizados en la Sociedad Cooperativa Buzos de Puerto Punta Peñasco.....	289

Figure G.8. Zonas de refugio pesquero aledañas a la Isla San Jorge	291
Figure G.9. Zonas de refugio pesquero en los arrecifes aledaños a Puerto Penasco, Sonora, México	292

APPENDIX H. SUBTIDAL TEMPERATURES IN ISLA SAN JORGE, OCTOBER 2003 – OCTOBER 2004

Figure H.1. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. October 1 2003-October 1 2004	300
Figure H.2. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. October 1 2003-November 1 2003	301
Figure H.3. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. November 1 2003-December 1 2003	301
Figure H.4. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. December 1 2003-January 1 2004	302
Figure H.5. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. January 1 2004-February 1 2004	302
Figure H.6. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. February 1 2004-March 1 2004	303
Figure H.7. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. March 1 2004-April 1 2004	303
Figure H.8. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. April 1 2004-May 1 2004	304
Figure H.9. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. May 1 2004-June 1 2004	304
Figure H.10. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. June 1 2004-July 1 2004	305
Figure H.11. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. July 1 2004-August 1 2004	305
Figure H.12. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. August 1 2004-September 1 2004	306

Figure H.13. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. September 1 2004-October 1 2004	306
---	-----

APPENDIX I. PHOTOGRAPHS OF ROCK SCALLOP, BLACK MUREX, AND COMMERCIAL DIVING.

Figure I.1. Left and right valves of a juvenile rock scallop (shell height = 45 mm, ~1 year old).....	307
Figure I.2. Recently harvested rock scallop, <i>Spondylus calcifer</i> , and mother of pearl, <i>Pinctada mazatlanica</i>	307
Figure I.3. Harvested rock scallop, <i>Spondylus calcifer</i> , adductor Muscles	308
Figure I.4. Juvenile and adult rock scallop scallops, <i>Spondylus calcifer</i> , with mark tags	308
Figure I.5. Adult rock scallop shells, <i>Spondylus calcifer</i> , showing marked differences in morphology	309
Figure I.6. Sliced shell of an adult rock scallop, <i>Spondylus calcifer</i> , showing heavy infestation of burrowing organism.....	309
Figure I.7. Various sizes and age classes of black murex, <i>Hexaplex Nigrinus</i>	310
Figure I.8. Adult black murex, <i>Hexaplex nigrinus</i> , of different sizes and their corresponding egg capsule sizes	310
Figure I.9. Small breeding aggregation of black murex snails	311
Figure I.10. Black murex <i>Hexaplex nigrinus</i> , laying egg capsules on another snail	311
Figure I.11. Marked black murex snails from a breeding aggregation.....	312
Figure I.12. Recently harvested female (left) and male (right) black murex snails	312
Figure I.13. A) hauling bag full with black murex; B) boat filled with black murex; C) commercial diver entering the water.....	313

Figure I.14. Commercial diver breaking black murex snail shells to sell the meat.....	313
Figure I.15. Commercial diver harvesting rock scallop, <i>Spondylus calcifer</i> , in rocky reefs of northeastern Gulf of California, Mexico	314
Figure I.16. Commercial diver counting rock scallop, <i>Spondylus calcifer</i> , and black murex, <i>Hexaplex nigritus</i> , in subtidal monitoring Quadrants	314
Figure I.17. Virgen de Guadalupe depicted on a rock scallop shell held by a commercial diver of Puerto Peñasco, Sonora, Mexico	315
Figure I.18. Hohokam black murex shell midden found approximately 20 km north of Puerto Peñasco, Sonora, Mexico.....	315

LIST OF TABLES

APPENDIX A. ESTABLISHING A BASELINE: GROWTH AND REPRODUCTION OF THE ROCK SCALLOP (*SPONDYLUS CALCIFER*) IN THE UPPER GULF OF CALIFORNIA, MEXICO

Table A.1. Collection scheme, reproductive season, and percentage of male and female <i>Spondylus calcifer</i> in the Upper Gulf of California, Mexico.....	89
---	----

APPENDIX B. GROWTH, LONGEVITY, AND MORPHOLOGICAL VARIATIONS OF THE BLACK MUREX SNAIL (*HEXAPLEX NIGRITUS*): IMPLICATIONS FOR MANAGEMENT OF A RAPIDLY DECLINING FISHERY

Table B.1. Length/weight and length/aperture ratios and mean length and weight of reproductive black murex snails found in four areas of the Upper Gulf of California, Mexico.....	124
--	-----

APPENDIX C. BREEDING AGGREGATIONS AND REPRODUCTIVE ECOLOGY OF THE BLACK MUREX SNAIL (*HEXAPLEX NIGRITUS*) IN THE NORTHERN GULF OF CALIFORNIA, MEXICO

Table C.1. Distribution of egg mass sizes and egg mass-laying times for 10 black murex snails (<i>Hexaplex nigritus</i>) maintained in aquaria	153
--	-----

APPENDIX D. RAPID EFFECTS OF MARINE RESERVES AND THE RISE AND FALL OF COOPERATION IN A YOUNG FISHERY

Table D.1. Fishers' opinions and attitudes towards their community-based reserves	195
---	-----

Table D.2. Rules developed, <i>de facto</i> (<i>df</i>) and formal (<i>f</i>) sanction types, and levels of rule compliance before and after entrance of outsiders into the Puerto Peñasco marine reserve network.....	196
--	-----

Table D.3. Example of fishers' responses to the open-ended question "In what way does breaking an agreement of the Cooperative affect you?"	197
---	-----

APPENDIX E. ONLINE SUPPORTING MATERIALS FOR APPENDIX D

Table E.1. Univariate and multivariate tests for the analysis of temporal changes in density of juvenile rock scallops found within monitored reserve and fishing sites.....	207
Table E.2. Univariate and multivariate tests for the analysis of temporal changes in density of juvenile black murex found within monitored reserve and fishing sites.....	208
APPENDIX G. PLAN DE MANEJO REGIONAL PARA EL APROVECHAMIENTO Y LA RECUPERACION DEL CALLO DE ESCARLOPA, SPONDYLUS CALCIFER	
Table G.1. Resumen de datos de muestra de colecta de especímenes de callo de escarlopa para la determinación de su período reproductivo en el alto Golfo de California, México	274
Table G.2. Cronograma de actividad reproductiva, reclutamiento, y período principal de aprovechamiento del callo de escarlopa en el alto Golfo de California, México	274
Table G.3. Relación de tallas y pesos de organismos completos y del músculo aductor (“callo”) del callo de escarlopa, <i>Spondylus calcifer</i> , en el alto Golfo de California, México	275
Table G.4. Relación de pesos promedio mensuales del músculo aductor (“callo”) del callo de escarlopa, <i>Spondylus calcifer</i> , en el alto Golfo de California, México	275
Table G.5. Desglose de estimación de densidades poblacionales de callo de escarlopa, <i>Spondylus calcifer</i> , en los arrecifes aledaños a Puerto Peñasco, Sonora.....	282
Table G.6. Captura promedio y relación del número y porcentaje de viajes de pesca realizados para la captura del callo de escarlopa, <i>Spondylus calcifer</i> , por un pescador típico de Puerto Peñasco, Sonora, México	285

ABSTRACT

I address the emergence, governance, and effects of marine reserve efforts in the Gulf of California, Mexico, emphasizing a community-based marine reserve network established by the commercial diving sector of Puerto Peñasco, Sonora. This network emerged as a means to manage benthic resources in rocky reefs, primarily rock scallop (*Spondylus calcifer*) and black murex snail (*Hexaplex nigritus*). My study also provides an analysis of growth, reproductive ecology, and management of both species.

I show that local cooperation to manage fisheries commons incorporating the use of marine reserves can emerge rapidly. Furthermore, this cooperation can be sustained in a fishery spanning no more than two generations, effectively avoiding a local “tragedy of the commons”. A blend of social group characteristics, fishers’ ecological knowledge and participation in monitoring, and relatively rapid ecological response of the system can play key roles in reinforcing cooperation.

I provide evidence of rapid effects of reserves on adjacent fisheries via larvae dispersal. Visual censuses revealed that density of young rock scallop (individuals recruited since reserve establishment) had increased by up to 40.7% within coastal reserves and by 20.6% in fished sites in only two years. Changes were also evident for black murex, with more than a three-fold increase in the density of juveniles within fished sites. These effects, however, were spatially-constricted, evident only for the northern portion of the reserve network. These empirical findings are more indicative of a reserve effect rather than other confounding factors and are consistent with field

oceanography data (release of satellite-tracked drifters) and outputs from larvae dispersal models.

Finally, I show that just as cooperation can emerge, it can rapidly fall with cascading effects to the system's resilience, particularly amidst threats to social capital and pressure from outside the community. I conclude that even when community-based reserves are effective within the biophysical and local social context, their long-term efficacy will rely on the system's capacity to control access and will demand the institutional capacity to do so. In Mexico this implies, at the least, the government's formal recognition of community-based initiatives and a means to give viability to these efforts.

INTRODUCTION

The Problem and its Global Context

State of the world's fisheries, importance of small-scale fisheries, and management challenges

Most natural resource management textbooks include a section that addresses the overexploitation of fishery resources as one of the biggest management failures of the 20th century. In 1995 the Food and Agriculture Organization reported that “69% of the world’s fisheries were fully to heavily exploited, depleted... and therefore are in need of urgent conservation and management measures” (United Nations Food and Agriculture Organization 1995). From an ecological perspective, historical catch composition data suggest we have increasingly fished down marine food webs, with a gradual transition in landings from long-lived, high trophic level piscivorous fish to short lived invertebrates and planktivorous fish (Pauly 1998). The problem is further exacerbated as we increasingly operate in a global economy with fishery stock depletions occurring at a rate that exceeds the response abilities of local regulatory institutions (Berkes et al. 2006). Long-term global marine fisheries prospects also suggest declining global catches, serious impacts on biodiversity, and expansion of bottom fisheries into deeper waters (Pauly et al. 2003). Not surprisingly, one of the only resolutions agreed upon in the 2002 World Summit on Sustainable Development was to halt over fishing worldwide. In essence, many fisheries throughout the world and the people who depend on them are in a state of crisis (McGoodwin 1990).

Within the fishery management realm, the complex nature of “small-scale” fisheries (also referred to as “artisanal”, “inshore”, or “folk” fisheries) represents a particular challenge for fishery managers. Management of small-scale fisheries has become of increasing concern as fishery scientists and governments have realized the social and economic importance of this economic sector.

For historical and logistical reasons, small-scale fisheries have been largely neglected in the formulation of fisheries policies (McGoodwin 1990). They involve little capital investment and per capita production is low, producing primarily for household subsistence, community food needs, and local markets (McGoodwin 1990). Individual fishers also usually have little economic impacts on a regional and national scale. Collectively, however, their ecological, cultural, and economic impact is quite substantial. It is estimated that small-scale fisheries employ 50 of the world’s 51 million fishers and produce more than half of the world’s annual marine fish catch (Berkes et al. 2001). They are particularly important in developing countries, providing the bulk of the domestic food for many communities and numerous employment opportunities. In Latin America alone there exist over 2,200 small-scale fishing communities involving well over one million people directly engaged in this economic activity (Bermudez and Agüero 1994).

Traditionally, most of the resources available and harvested by this sector have been species usually found close to shore. As resources have become increasingly scarce and technology improved, however, venturing into offshore waters has become less of an obstacle for small-scale fishers (Castilla and Fernández 1998). As a result,

overexploitation has certainly not been immune to small-scale fishing activities. Furthermore, contrary to large-scale industrial fishing, which is often capable of maintaining profits amidst overexploitation by transferring fishing effort to other areas, small-scale fishers are generally restricted to a specific geographic region. Local overharvest can therefore have rampant effects on the social dynamics and economy of small-scale fishing communities.

The “tragedy of the commons”: the main management problem?

The blame for failures in fishery management cannot be easily addressed. Most often, however, politicians and scholars have pointed to the *commons* dilemma as the root of the overexploitation of fishery and other natural resources. Since Garret Hardin popularized “the tragedy of the commons” 30 years ago, his ideas about common property regimes have become the most widely accepted explanation for overexploitation of commonly held resources (Feeny et al. 1990).

Hardin’s theory stated that any resource held in common is subject to degradation... “freedom in a commons brings ruin to all” (Hardin 1968). To avoid overexploitation of these resources, Hardin concluded that they should be privatized or controlled by the government (Hardin 1968). However, the “tragedy of the commons” theory fails to distinguish between common property and open access, and does not take into account the self-regulating capability of users (McCay and Acheson 1987). As a result, this theory has simplified and overlooked the complexity of the various issues at play in the overexploitation of natural resources. However, it has largely remained as the

blueprint to cope with various natural resource management settings and has been commonly used as a means to justify top-down management approaches, government coercion, and privatization of natural resources (Ostrom et al. 1999). This has often led to disastrous consequences and the dismantling of existing and efficient local forms of governance (see Ostrom et al. 1999, McCay and Acheson 1987).

Community-based management and the use of marine reserves

As a response to this emphasis on government regulation, the late 70's and beginning of the 80's saw rising scholarly efforts that challenged a "tragedy of the commons" fatalistic approach and proved that in many cases the commons was not the root of the problem. In contrast, numerous case studies showed that communities had developed governance structures leading to apparent sustainable harvest practices of common pool resources (McCay and Acheson 1987, Ostrom 1990, Dyer and McGoodwin 1994). These efforts, coupled with the drastic decline of various fisheries under traditional top-down management approaches led conservation and development agencies (non governmental as well as governmental) to make "local" governance and empowerment a top priority in their environmental agendas, most often under the banners of "community-based management" (CBM) and/or "co-management".

CBM of small-scale fisheries is appealing in developing countries because the financial and human resources for implementing and enforcing management decisions are usually lacking at a federal level (Agrawal and Gibson 1999). Almost unquestionably, a community-based approach is believed to reduce costs and increase management

efficiency and long-term sustainability. It is also usually assumed that users and stakeholders will benefit from participation and will always want to be involved in such processes; that regulations established with community input will have more credibility among users, and that a community-based approach will increase the willingness and incentives to respect management guidelines.

Coupled to the rise in CBM of fisheries, the use of marine protected areas (MPA's) in the form of marine reserves or "no take zones" as fishery management tools increased in the 1990's. This approach emerged largely as a frustration over failure of many marine fisheries management practices (Agardy 1997) and acknowledgement of the uncertainty and complexity of marine systems (Wilson et al. 1994). Essentially, marine reserves are seen as a potentially effective strategy for dealing with the uncertainties and volatility inherent to marine fisheries (Carr and Reed 1993, Agardy 1997, Roberts and Hawkins 2000, National Research Council 2001), and for protecting ecosystems and ecological processes while also enhancing fisheries via density-dependent spillover of juveniles and adults into fishing areas and through larvae dispersal on ocean currents (Roberts et al. 2001).

Marine reserves established under a community-based umbrella could have the potential of providing lasting benefits under "win-win" situations, serving not only conservation and fisheries needs, but mitigating social and political conflicts as well. Nevertheless, evidence supporting this is still sparse. Although there is little debate that reserves meet important conservation needs (Roberts and Hawkins 2000), there is insufficient empirical data supporting their role as tools to enhance fisheries, particularly

by means of larvae dispersal. Previous analyses have focused mainly on the benefits to adjacent fisheries via density-dependent spillover of fish (NRC 2001, Russ et al. 2004) or have been based primarily on hypothetical models (Gaines et al. 2003, Hastings and Botsforth 2003). In addition, studies of the social and institutional efficacy of CBM of fisheries have largely focused on geographically isolated fishing communities with long-standing fishing traditions. These communities have often been able to acquire vast ecological knowledge and develop effective compliance and customary management practices through multiple generations of fishing and trial and error processes (Johannes 1978). Nevertheless, many if not most of today's coastal communities and/or their fisheries are far from what could be considered multi-generational or traditional, are experiencing a rapid turnover of species targeted, and are increasingly exposed to outside pressure (Berkes et al. 2006). This leaves little room or time to develop the local ecological knowledge and robust institutional arrangements that could potentially facilitate CBM (see Ostrom 1990, Agrawal 2002).

Small-scale benthic fisheries and the use of marine reserves

Contrary to terrestrial reserves where limits can be relatively easy to trace, the fluid and open nature of marine systems makes the boundaries of a marine reserve difficult to demarcate and these boundaries may have to be adjusted in response to changes in annual patterns of currents. This is especially true when defining reserves targeting mobile resources like fish. Ironically, however, most reserve efforts have

focused on monitoring and protecting fish stocks, whereas sessile or semi-sessile benthic benthic resources have received less attention (Castilla and Defeo 2001).

Nevertheless, benthic fisheries, particularly of sessile or semi sessile mollusks, can provide a useful setting to address the effects of marine reserves via larvae dispersal by reducing (or eliminating) possibilities of adult movement. Many temperate and tropical shellfish are also prone to have rapid growth rates, facilitating measures of reserve effects in short time frames. In addition, given their sessile nature, they facilitate the definition of clear protection boundaries as well as monitoring of population parameters. A higher sense of stewardship towards the resources harvested may exist as well, as they are always found in the same area. In contrast, other fisheries requiring constant movement of fishing fleets according to the movement patterns of resources will tend to hinder development of marine tenure systems or, if forms of tenure do emerge, these will likely be highly contested as the fishery will be shared by other communities or sectors.

However, the same characteristics of benthic fisheries that can facilitate establishment, management, and monitoring of marine reserves can also be detrimental to these efforts and to the fishery as a whole. Limited resource mobility allows fishers to easily target the same exploitable stocks repeatedly. For these same reasons, small-scale benthic fisheries can potentially inflict considerable pressure on resources exploited in a relatively short time frame and without necessarily having a large number of users participating in the fishery. Without adequate regulations and enforcement concerning access to commercial stocks, complications rather than benefits of coping with sedentary

resources can take over, as fishers will strive to maximize production with the least amount of effort possible. In addition, marine invertebrate populations, particularly those of broadcast spawning species like rock scallop, can be particularly susceptible to an Allee density effect, with sudden collapse when gradually increasing habitat destruction or fishing pressure drop populations below densities necessary for adequate fertilization and subsequent recruitment (Karlson and Levitan 1990).

The above issues, both the benefits and the costs, are manifested in history. Some of the most successful small-scale fisheries have been attributed to benthic resources, such as the Chilean Loco, *Concholepas concholepas* (Castilla and Defeo 2001), various bivalve mollusks, and lobster fisheries (McCay and Acheson 1987). These cases are characterized by the emergence of *de facto* or *de jure* forms of marine tenure, strong community-based efforts, and the use of forms of MPAs. However, history is also filled with examples of rapid overexploitation of sessile and semi-sessile benthic resources, from pearl industries worldwide (Donkin 1998) to abalones (Caddy 1989) and conch snails (Stoner et al. 1998).

Another important characteristic of small-scale benthic fisheries is that the pace of exploitation often exceeds the pace of knowledge generation about resources harvested. Essentially, whether because of oceanographic and productivity changes (which mollusk populations are particularly susceptible to) or shifts in the market, small-scale benthic fisheries typically undergo a rapid boom and bust pattern. By the time resource users or managers begin to understand the system and apply management interventions, it may simply be too late to ensure conservation and sustainable harvest. Addressing this issue is

of particular importance, particularly given worldwide tendencies to fish down the food webs (Pauly et al. 1998).

Summary: research needs

Undoubtedly, CBM and marine reserves have become important and promising tools in many places of the world. These issues warrant more research providing empirical evidence of factors leading to and affecting successful CBM of marine reserves, particularly for young and highly exposed fishing societies and of the overall effects of reserves on adjacent fisheries. In particular, we need to address the following questions: What role can reserves play in maintaining or enhancing fisheries via larvae dispersal? Can CBM of marine reserves **emerge and be sustained** in recently developed fishing societies (i.e. 1-2 generations) with no or minimal government intervention? What factors can maintain or dismantle cooperation for CBM of marine reserves?

In terms of benthic fisheries, we need more empirical evidence testing the effects of marine reserves as tools for their management. We also need better understanding of key life history parameters of species harvested and require incorporating this information into appropriate management guidelines before exploitation takes a toll on harvestable stocks.

This Dissertation

My dissertation addresses the overarching topics outlined above using the Gulf of California, Mexico (herein “the Gulf”), as a case study. This region provides a particularly appealing setting to study small-scale benthic fisheries and the emergence, governance, and effects of community-based marine reserves.

The Gulf is a unique body of water, being the only sea that may be considered “the exclusive property” of a single nation (Sarukhán 2001). This geographic characteristic facilitates analyses of local processes by eliminating confounding governance boundaries with other nations.

As with other marine conservation hot spots in the world, the Gulf has also seen a rise in marine conservation efforts since the early 1990’s, which have included the establishment of various MPAs. Although attempts of using MPAs as management tools in the Gulf began in 1993 with the creation of the Upper Gulf of California and Colorado River Delta Biosphere Reserve – primarily for the protection of the endangered and endemic large croaker *totoaba* (*Totoaba macdonaldi*) and vaquita porpoise (*Phocoena sinus*) - it is only since 2000 that efforts have focused specifically on defining no-take marine reserves as a means to manage and enhance small-scale fisheries while conserving marine ecosystems. These reserves are located in Puerto Peñasco (PP) – in the upper Northern Gulf -, the Loreto Bay National Park (LBNP) - adjacent to the Baja California Peninsula -, and San Pedro Mártir Island (SPMI) – in the Midriff Island Region.

These reserves have emerged within various governance settings, ranging from significant to practically no government intervention. In all three cases, community

participation has been a core component in the establishment and subsequent operation of the reserves. They have also emerged within relatively young commercial fishing communities, spanning no more than four generations.

History of resource exploitation by small-scale fishers in the Gulf has been marked by various “boom and bust” cycles and a tendency towards a higher diversification of species targeted, with over 100 species commercially harvested in the northern Gulf alone (www.pangas.arizona.edu). Within the small-scale fishing realm, possibly no other activity exemplifies fishery diversification and these boom and bust patterns as benthic commercial diving. Exploitation of benthic resources by small-scale fishers is highly and increasingly prevalent, particularly given what some would label a tendency for the Gulf’s fishing activities to “fish down the food webs” (Sala et al. 2004). However, adequate knowledge for management of numerous benthic resources targeted is largely lacking.

Using an air compressor and 50-100 m hoses, present-day commercial divers have been harvesting benthic resources, primarily mollusks, since the 1970’s (Cudney-Bueno 2000)¹. Within this timeframe alone, resource exploitation has followed a clear and rapid pattern in which harvest of each species rises and then falls dramatically. For instance, the Pacific conch (*Strombus galeatus*), once abundant throughout the Gulf, was depleted by the early 1990’s. Today, it is rare to find this species unless one dives in deep waters of offshore islands (pers. obs.). Likewise, the “hay day” of the sea cucumber industry that

¹ This is not to be confused with the lucrative and highly impacting pearl diving fishery that developed in the Gulf of California From the 16th through the 18th Century. This industry was largely constricted to the Southern Gulf and was conducted primarily by Yaqui Indian slaves free diving (Bowen 2000).

developed in the early 1990's for the Asian market only lasted 6 years and prompted a special protection status by the Mexican Government. Finally, breeding aggregations of the black murex snail (*Hexaplex nigritus*) were heavily targeted in the Puerto Peñasco area during the early 1990's, leading to a marked decline in catch per unit of effort and total landings by 1999 (Cudney-Bueno 2000).

Despite these tendencies, it is within commercial diving benthic fisheries that various encouraging community-based management efforts have also emerged. For instance, the Seri or Comcaác indigenous community has devised various means to control access to their pen shell fishery in the Infiernillo Channel and maintain a productive fishery (Basurto 2005). Commercial divers of Bahía de Kino are organizing to establish various community-based management schemes for their pen shell fishery (Moreno et al. 2005). Finally, Puerto Peñasco divers have established various management guidelines, including season and area closures, and have participated in monitoring and research of their benthic resources since 1999 (this dissertation). These efforts prompted their recognition at a National level and led to their selection to receive Mexico's National Conservation Award in 2003 (this dissertation).

My dissertation addresses the emergence and governance of the three marine reserve efforts of Puerto Peñasco, San Pedro Mártir, and Bahía de Loreto. However, most of my detailed research embodies an analysis of the community-based marine reserve network established by the PP commercial diving sector. This network was established as a means to manage their benthic resources, primarily rock scallop (*Spondylus calcifer*) and black murex snail (*Hexaplex nigritus*). Given the importance of these species and yet

previous lack of information for management, this study also provides an analysis of key growth and reproduction parameters.

The PP system is of particular relevance for various reasons. It exemplifies the current development of many small-scale fisheries world wide in that the fishing sector and its resource harvesting history are quite young, characteristics that are prone to hinder evolution of cooperation for local fisheries management. Yet, the system also shares characteristics that could facilitate evolution and maintenance of cooperation and that are usually present in more “traditional” societies. Specifically, the diving fishery of PP developed largely isolated and buffered from outside pressures, the social group is small (between 12-15 boats), and is characterized by strong social capital².

“Hookah” or air hose divers from Puerto Peñasco have been harvesting benthic shellfish from rocky reefs for approximately 30 years (Cudney-Bueno 2000). Today, these habitats are partly within the boundaries of the Upper Gulf of California and Colorado River Delta Biosphere Reserve, and extend eastwards to San Jorge Island, part of Mexico’s Gulf of California Island Reserve.

Preliminary studies had suggested that these commercial divers have practiced a *de facto* rotation of fishing zones, essentially establishing forms of temporary harvest refugia (Cudney-Bueno 2000). This rotation, however, appeared to have been tacitly carried out as a cost-benefit individual fisherman’s response to the accessibility of the resource, and not as a collective active management decision (Cudney-Bueno 2000).

² Social capital refers to the institutions, networks, stocks of social trust, and norms that shape the quality and quantity of a community’s social interactions and that people can draw upon to solve common problems (World Bank 2002).

However, in 2002, PP divers established a network of three marine reserves, the first network of marine reserves in the Gulf of California. Having worked with this fishing sector since 1998, conducted community-based research, and seen first hand the establishment of these reserves, I hypothesized that the emergence of these reserves occurred without having had previous experience implementing other collective management decisions. I had also built extensive rapport with fishers, which allowed me to assess the effects of their community-based efforts from various social and ecological angles.

Goals of dissertation

The goals of this research were to:

1. Understand the main factors leading to the emergence of marine reserve establishment in the Gulf of California and the main factors that have governed their performance.
2. Determine if CBM of reserves can evolve and be sustained in young fisheries with limited experience implementing collective management decisions.
3. Determine the main factors leading to the evolution of cooperation for the establishment of a community-based marine reserve network in the Puerto Peñasco benthic fishery and the main mechanisms governing the system.
4. Determine the effects of marine reserves on recruitment of juvenile commercial mollusks in the Puerto Peñasco reserve network system.

5. Determine key life history information of the black murex snail (*Hexaplex nigrinus*) and rock scallop (*Spondylus calcifer*) - particularly in terms of growth, longevity, and reproduction – to facilitate future management of these species.

Explanation of Dissertation Format

The results of this dissertation are presented as six separate appended manuscripts (Appendix A, B, C, D, E, and F). Each presents a detailed account of specific research questions addressed, methodology, results, and discussion. Various colleagues appear as co-authors based on our mutual collaboration through the development of my doctoral research and subsequent dissertation. However, the responsibility for data collection, analysis, and writing these manuscripts is entirely my own and the dissertation as a whole represents my original and independent research.

Appendix A “*Establishing a Baseline: Growth and Reproduction of the Rock Scallop, Spondylus calcifer (Carpenter 1857), in the Upper Gulf of California, Mexico*” is a manuscript submitted to the *Journal of Shellfish Research*. The paper addresses growth and reproduction of the rock scallop via the use of stable oxygen isotopes as well as field observations and analyses of fishers’ catches. I wrote it in collaboration with Kirsten Rowell, previously a graduate student at the Geosciences Department of the University of Arizona and now a researcher at the University of Washington. Kirsten collaborated with me in the use of stable oxygen isotopes as a tool for age estimation as well as in revisions of the manuscript.

Appendix B “*Growth, longevity, and morphological variations of the black murex snail, Hexaplex (Muricanthus) nigritus: Implications for Management of a Rapidly Declining Fishery*” will be submitted to the journal *Fishery Bulletin*. The paper provides an analysis of growth, longevity, reproductive age, and morphological variations of the black murex. This information provides basic and key information for any future management of this species, which has been heavily fished since the early 1990’s. As with the rock scallop work, I co-author this paper with Kirsten Rowell, who collaborated with me in the use of stable oxygen isotopes as a tool for age estimation as well as in revisions of the manuscript.

Appendix C “*Breeding Aggregations and Reproductive Ecology of the Black Murex Snail, Hexaplex nigritus (Philippi, 1845) in the Northern Gulf of California, Mexico*” will be submitted to the journal *Marine Biology*. It provides an extensive description of the reproductive biology and ecology of the black murex in the northern Gulf of California. It includes data extending back to 1999 when I began working extensively with Puerto Peñasco commercial divers and conducted field research for my Masters Thesis. This data was obtained through field observations on 42 breeding aggregations, mark-recapture, laboratory analyses, and snail rearing in aquaria.

Participating as co-author is Rebecca Prescott, a masters student from the School of Natural Resources of the University of Arizona who collaborated with me as part of her Masters work on the epifauna associated with breeding aggregations of black murex in the northern Gulf of California.

Appendix D “*Rapid Effects of Marine Reserves and the Rise and Fall of Cooperation in a Young Fishery*” is a manuscript prepared for the journal *Proceedings of the National Academy of Sciences* (PNAS). Results of this research have been presented in various invited meetings and seminars. It provides an analysis of rapid ecological and social effects of the Puerto Peñasco community-based marine reserve network, as well as of the factors leading to the evolution of cooperation and establishment of marine reserves in a young fishery and of the locally-devised means to avoid a local tragedy of the commons. I focus my analysis on the two main species harvested by small-scale commercial divers: the black murex snail (*Hexaplex nigritus*) and rock scallop (*Spondylus calcifer*). Given the specific format of the journal, I provide supporting material, including methodology, as a separate Appendix (Appendix E). In addition, support information on the biology and ecology of both species is provided in Appendix A, B, and C as independent research articles.

Participating as co-authors are Miguel Lavín, Guido Marinone, and William W. Shaw. Both Lavín and Marinone, from the *Centro de Investigación Científica y de Educación Superior de Ensenada* (CICESE), were instrumental in the development of oceanographic models used to model hypothetical larvae flows in the northern Gulf of California. William W. Shaw acted as my academic advisor and provided important feedback through the development of the manuscript.

Appendix E “*Supporting Materials for Appendix D*” provides support materials for the PNAS manuscript (Appendix D), including methodology used, additional statistics, tables, and figures.

Appendix F “*Governance and Effects of Marine Reserves in the Gulf of California, Mexico*” is a manuscript submitted to the journal *Ocean and Coastal Management*. A portion of it was originally presented at the American Anthropological Association 101st annual meeting in New Orleans on November 2002 and the 9TH biennial conference of the International Association for the Study of Common Property, held in Zimbabwe June 2002. It encompasses an analysis of the evolution of efforts to establish, govern, and monitor no-take marine reserves in the Gulf of California, using as case studies Bahía de Loreto National Park, San Pedro Mártir Biosphere Reserve, and the Puerto Peñasco network of community-based reserves. I wrote this manuscript in collaboration with Drs. Jorge Torre, Luis Bourillón, and Andrea Sáenz, colleagues whom I have been collaborating with in various degrees since 1994. My colleagues were instrumental in the establishment and monitoring of the marine reserves in Loreto Bay National Park and the San Pedro Mártir Island Biosphere Reserve as researchers from the NGO *Comunidad y Biodiversidad* (COBI). Also participating as co-author is Peggy Turk-Boyer, Director of the Intercultural Center for the Study of Deserts and Oceans (CEDO). Peggy, through CEDO, facilitated much of the work with Puerto Peñasco divers and helped obtain funding to conduct an analysis of the Puerto Peñasco, Bahía de Loreto, and San Pedro Mártir Island reserves.

In addition to these research articles, in Appendices G through I I have included information that could be useful for anyone studying benthic fisheries in the northern Gulf, particularly rock scallop and black murex. Appendix G is a Regional Management Plan for Rock Scallop (in Spanish). I developed this Plan at the request of the *Dirección General de Aprovechamiento de Vida Silvestre* of Mexico's Ministry of the Environment and Natural Resources (*Secretaría del Medio Ambiente y Recursos Naturales, SEMARNAT*). Using the commercial diving fishery of Puerto Peñasco as a pilot study, this Plan will act as the blueprint for anyone seeking a permit to harvest rock scallop in the Gulf of California. The other appendices include additional data, photographs, subtidal temperatures from San Jorge Island, and a glossary of terms used throughout the dissertation.

PRESENT STUDY

The methods, results, and conclusions of this study are presented in the papers appended to this dissertation. However, the following is a summary of the most important findings of my research.

Study Area

Gulf of California

The Gulf of California is located in Northwest Mexico between the mainland and the Baja California Peninsula. It is a large marine basin stretching over 1000 miles and embracing an array of marine environments, from deep-water trenches and coastal and island rocky reefs to the sandy and shallow waters of the Colorado River delta. It also constitutes one of the most productive seas in the world (Brusca et al. 2005). Fed by constant tidal and wind-driven upwelling systems, tidal currents, and variations in sea surface temperature, the productive machinery of the Gulf allows a large accumulation of biomass on a year-round basis (Álvarez-Borrego 2002). This sea provides 70% of Mexico's National fisheries' value (Carvajal et al. 2004).

Puerto Peñasco and its marine reserve network

Puerto Peñasco is the largest community of the northern Gulf of California. It is a fishing and tourism hub of 40,000 people located on the outskirts of the Upper Gulf of California and Colorado River Delta Biosphere Reserve (31°18', 113°32'). Its surrounding waters are marked by intense tidal and water temperature fluctuations (up to

10 m and 20°C, respectively), strong currents, predominance of low visibility, and the presence of extended beach-rock (coquina) and granite reefs separated by mussel, rodolith, and shell/sandy patches.

The reserve network established by commercial divers includes an offshore reserve surrounding San Jorge Island, the region's most productive fishing ground in terms of density and size of species harvested by commercial divers, and two coastal reserves ("Las Conchas" and "Sandy"). This network provides protection to roughly 30% of the fishing sector's entire fishing grounds and covers approximately 18 km of coastline primarily encompassed by flat reefs known locally as *tepetates*. These environments support the largest diversity of benthic invertebrates in the Gulf (Brusca 2005) and some of the largest populations of black murex and rock scallop. To the North and South, Puerto Peñasco diving grounds are flanked by long stretches of sand, with the nearest substantial (>1000 m²) rocky reef located 150 km South of the reserve network.

Life History of Rock Scallop and Black Murex

Rock scallop growth and longevity

The rock scallop, *Spondylus calcifer*, is the largest member of any Panamic Province *Spondylus* and has played important economic, political, and cultural roles in coastal communities of the Eastern Tropical Pacific for thousands of years. Despite its economic and historical importance, however, very little is known about the biology of this species.

I assessed seasonal variations of shell and adductor muscle growth, longevity, reproductive age and period, and population sex ratios of *S. calcifer* in the upper Gulf of California, Mexico, the northernmost distribution of this species. Information on shell growth and age was obtained via the use of stable oxygen isotope profiles of shell aragonite cross-referenced with mark recapture data. I also visually assessed sex ratios and reproductive period by looking at coloration, size characteristics, and texture of the gonads of specimens harvested by fishers. To address if there were seasonal variations in the size of adductor muscles (the part of the organism that is commercialized), I took length/weight measures of the muscle of 2725 individuals harvested by fishers. In addition, I assessed the relationship between muscle length/weight and shell height by haphazardly collecting approximately 30 complete adult specimens during fishing trips in winter-spring (4 trips, n = 172 individuals) and summer-fall (5 trips, n = 175 individuals) 2003-2004 and measured shell height and adductor muscle size and weight for each. I obtained the best regression model fit for both seasonal periods.

Rock scallop shells form white growth bands. Stable oxygen isotope readings revealed that these bands are deposited during colder winter and spring months and can therefore facilitate a visual assessment of growth. Shell growth accelerates during warmer months and diminishes during colder months, likely as a result of energetic shifts related to resource allocation pre and post reproduction. This is evidenced by variations in seasonal adductor muscle growth. The adductor muscle tends to increase both in size and weight during colder months as it accumulates glycogen in preparation for reproduction, which takes place in July- August as water temperatures reach 28-30°C.

The species reaches sexual maturity between 2.5-3 years of age and can live to at least 10-12 years. However, even though I used the largest specimen encountered in five years of fieldwork (160.7 mm) to assess longevity, a maximum length of 250 mm has been reported for this species, suggesting *S. calcifer* could live much longer. Finally, overall sex ratios consisted of 1 male/1 female, a population structure in accordance with previous reports for the southern Gulf of California.

Management implications for rock scallop

Although the species has official protective status in Mexico, it is still widely harvested throughout its geographic range in Latin America whether for local consumption or as a formally and legally recognized commercial fishery. Currently, there is also interest and pressure from the commercial fishery sector of the Gulf of California to formally open the fishery with adequate management guidelines. Given this evident commercial interest, I provide the following management and conservation recommendations.

Harvest should be limited to winter and spring and restricted most of the summer and fall, particularly during July, August, and September, when water temperatures reach 28-30° C. Aside from assuring spawning events, this would also avoid unnecessary commercial losses due to a decrease in weight and size of the adductor muscle resulting from the species' energetic allocation during and post reproduction.

Management of the species must also pay particular attention to the establishment of size limits. Only individuals with a shell height of 130 mm or higher (equivalent to an

adductor muscle length of 39.6 mm during winter/spring and 35 mm during summer/fall) should be allowed to be harvested. This measure would assure that young individuals reproduce at least once, allow for new individuals to be recruited to the fishery, and avoid population collapses due to an Allee density effect.

Rock scallop populations as well as those of other benthic sessile and semi-sessile species have the potential of being enhanced through the use of networks of permanent and temporary harvest refugia. Source and sink populations should be identified, and refugia networks established in accordance to physical oceanographic processes, population densities, and known population connectivity. Areas with low densities that have clear signs of having been over-harvested should be closed for a minimum of 4 years to allow for newly settled individuals to reach first reproductive age and spawn at least once. Likewise, the closure of source populations should be considered in order to facilitate population enhancement in adjacent areas via larvae dispersal. Rotation schemes should be implemented particularly for “sink” populations, conducting fishing alternations between reefs to assure local recoveries in the year or years following harvest.

Finally, given that *S. calcifer* is found throughout an extensive geographical range with marked variations in biological and physical gradients, my results should be interpreted with caution outside the more temperate waters of the Gulf of California. Management schemes should be designed and implemented according to the bio-physical and social realities of the region where the species is harvested.

Black murex growth, longevity, and morphological variations

I assessed longevity, seasonal growth variations, age of reproductive maturity, and geographic variations in morphology of the black murex snail, *Hexaplex (Muricanthus) nigritus*, in the northern Gulf of California, Mexico. My methods relied on a combination of field (mark recapture) and laboratory (use of stable oxygen isotopes) approaches, as well as five years of field observations.

Black murex reaches reproductive maturity between 2-3 years of age and has a life span of at least 8 years. Its growth is considerably accelerated during the first year, reaching ~60 mm in total length, and slows down markedly after the first year. Growth is accelerated during the summer and fall and largely stunted during winter, particularly January-March.

Finally, I found evidence of variation in the species' morphology, with marked region-specific variations in length-weight relationships. These variations are likely related to environmental factors and phenoplasticity rather than expressions of genotype.

Black murex reproductive ecology

The black murex is dioecious and highly gregarious during reproduction. It forms large breeding aggregations with 1:1 sex ratios in subtidal waters between April and September, with the earliest aggregations in the season forming closer to shore.

I located 42 breeding aggregations, all in waters with temperatures of 22° C to 31° C and varying markedly in size. The largest aggregation comprised an area of 900 m² and provided a catch of 3 metric tons. However, 60% were between 100-200 m² and had no

more than 1000 individuals. Egg masses were laid primarily on the shells of both male and female conspecific snails and often included the clutch of more than one female. Some egg masses were comprised of more than 1000 capsules, but the average number of egg capsules/snail varied between 230-350 capsules depending on the area the aggregation was found.

Seventy-eight percent of aggregations formed over substrates composed primarily of broken and complete mollusk shells, rhodoliths and other encrusting coralline algae, and large grain sand. However, 73.8% of aggregations were also found in areas adjacent or within 25 m of a rocky, coquina (beach rock) or mussel bed reef. Towards the latter part of the breeding season, they were also usually found adjacent to pink murex (*Phyllonotus erythrostomus*) breeding aggregations. I also found evidence of reproductive site fidelity. Breeding aggregations tended to form on or near (<10 m) breeding aggregation sites of the preceding year. Similarly, recaptured marked individuals aggregated in the same sites as the year before.

Aggregation time can last at least 40 days, with embryos incubating in the capsule between 18-31 days, at which time egg capsules hatch veliger larvae. The number of larvae/capsule varied between 150-20,189 with a mean range of 2932-3248. I found a marked correlation between snail length and capsule length, with larger snails tending to produce larger capsules and more embryos.

During winter, snails tended to burrow into the sand and emerge on early spring to feed. While aggregated, all snails stopped feeding but engaged in feeding behavior prior and after aggregating, preying on at least 10 different mollusks, primarily on mussel

beds of *Modiolus capax*. Although I am unaware of other species preying on adult snails, I documented fish, sea turtles, and other gastropods feeding on black murex egg capsules.

Although the reproductive ecology and behavior of black murex fits some general patterns documented for other muricid snails, it also shows some unusual characteristics. In particular, the species' high reproductive output, the formation of some of the largest breeding aggregations registered for neogastropod snails, and the presence of reproductive site fidelity.

Management implications for black murex

Life history traits of the black murex have the potential to facilitate a sustainable and well-managed fishery. These characteristics reside primarily in the species' high reproductive output, longevity (capable of reproducing at least 5 times in consecutive years), and relatively rapid growth rate. If managed correctly, the predictability of formation of breeding aggregations in roughly the same areas can also allow for spatially explicit forms of management.

To the species' detriment, however, aggregating behavior has facilitated the development of highly impacting fishing practices that remove much of the reproductive biomass by targeting aggregation areas repeatedly. Given the evidence of reproductive site fidelity, it is possible that genetic structure exists within the PP fishing area and that fishing practices could be exerting pressure on different genetic stocks. Furthermore, regional variation in snail morphology, particularly in terms of length-weight relationships, suggests that there may be artificial selection favoring certain stocks less

targeted by the fishing industry. Given this, an assessment of genetic structure within and between breeding aggregations should be conducted and coupled with population viability analyses of the existent stocks.

Given the massive removal of the reproductive biomass during peak reproductive periods, a formal season closure should also be established from May through the end of July as a first step towards a recovery of the fishery and conservation of the species. This measure would allow for most individuals to reproduce and would protect in-shore populations, which aggregate sooner and are the ones in need of more urgent conservation measures. Temporary season closures alone, however, may not provide adequate protection and enhancement of heavily harvested and overexploited areas. For these areas, the establishment of harvest refugia should be considered.

Finally, management efforts should be coupled with future studies and long-term monitoring of both the fishery as well as of the benthic ecosystem associated with black murex. A better understanding of early life history (including pre and post-settlement processes), adult movement patterns, genetic population structure, as well as of the species' role in the ecosystem will be of particular importance to allow for a more comprehensive management and conservation of black murex and the subtidal benthic ecosystem of the northern Gulf of California.

Puerto Peñasco Benthic Fishery Case Study

Emergence and governance of community-based marine reserves

I show that local cooperation to manage fisheries commons, of which marine reserves form a core component, can emerge and evolve rapidly in a young, modern fishery with a limited history for collective action. The marine reserve network of Puerto Peñasco emerged exclusively from the grass-roots level, with no influence by top-down government processes.

There were two main incentives that triggered cooperation for the development of collective management decisions: 1) a decline in the availability of the main species targeted, and 2) year-round dependence on their fishery resources. Cooperation for the establishment of reserves was largely facilitated by an inherent belief in the resilience of their fishing system, and the effects of refugia through previous tacit experimentation with fishing area rotation schemes.

Governance relied primarily on a set of simple rules and means of enforcement, meeting venues that allowed for feedback between the social and ecological subsystems, fishers' participation in monitoring, and the leadership role of key members of the group. The evolution of rules and sanctions built primarily on foundations of trust and reciprocity and concerns for the group's well being. Hence, the most effective and usual form of enforcement relied on variations of peer pressure and public shame that could ultimately threaten the individual's reputation and his place within the group's social capital base. These were *de facto* sanctions with no legal standing under any statutes of

the Cooperative. While other formal sanction types were developed, they were largely avoided, often changed, or were applied as a last resource.

Rapid effects of marine reserves

Through the PP case study I provide evidence of rapid effects of marine reserve networks on fishery recruitment via larvae dispersal. Only two years after the establishment of the network, the overall population of juveniles (< 2 years old) of rock scallop and black murex snail (individuals born and recruited since the establishment of the reserves) had increased in coastal reserves and fishing areas. Visual censuses revealed that density of young rock scallop had increased by up to 40.7% within coastal reserves and by 20.6% in fished sites. Changes were also evident for black murex, with more than a three-fold increase in the density of juveniles within fished sites. However, while an increased density of juveniles of both of these species was evident, I also found strong spatial signatures in the reserve effect. Essentially, increase in juvenile recruitment was evident for the northernmost reserve and its paired fishing site monitored, but not for other reserves and fishing areas monitored. These spatial signatures were consistent with regional oceanographic circulation and larvae dispersal models.

Effects of reserves were also evident to fishers. In interviews conducted prior to providing results on the monitoring efforts, over 85% of fishers reported benefits from the reserves and that they would continue having reserves in the future. Seventy-eight percent also stated that they had seen more rock scallop in areas that had been previously depleted. Similarly, 89% reported seeing an increase in juvenile rock scallop.

Sustainability of the Puerto Peñasco community-based reserves

While the social dynamics of the system remained bound to its local realities, the system undoubtedly worked to effectively manage the local fisheries commons. Not only were reserves largely respected and community-based rules established and enforced, but fishers also regularly participated in underwater monitoring activities. However, I show that social capital, which allowed for effective local governance in the first place, became an obstacle for collective action and cooperation once rule breaking hit a threshold, instigated primarily by external factors.

While I was conducting my research, leadership of local fishery officials changed drastically, instating personnel from outside the region that were overall unknowledgeable and less supportive of CBM practices. Coupled with this, news about the PP management efforts and perceived positive effect of the reserves spread quickly at a regional scale. What followed was a wave of fishers from other communities coming to fish in the area, a lack of support from local authorities, and the impossibility of local fishers to control access. This led to a cascade effect in local compliance of all tacit and formal rules previously respected and a temporary threat to the social system's resilience. This occurred even after foreign fishers had returned to their communities.

While for two years local cheating events had been limited and easily accounted for, the system was maintained in check without necessarily threatening its social capital base. However, by this point everyone was to blame in some way or another. Accountability was no longer as obvious, and it was easier to fall into forms of apathy

and lack of cooperation than to confront the problem, which meant confronting practically everyone in the group. There were simply too many social ties to lose if this was done. The most revealing evidence of this was that key members of the Cooperative stopped attending Cooperative meetings in order to avoid encounters with specific people, at times family related.

Broader theoretical implications of the Puerto Peñasco case study

This case provides important insights concerning theory and practice surrounding local governance of the commons in young fishing societies and the effects of marine reserves. The tragedy of the commons, as coined by Hardin in his seminal essay (Hardin 1968) and addressed by others before him (see Gordon 1954, Scott 1955), suggests that rational choice of individuals will tend towards maximizing profits from resources held in common before others do. It is most often argued, then, that the aggregated outcome of these individual decisions ultimately leads to inevitable overexploitation of natural resources unless privatization or government control are put into effect (Hardin 1968). This study, however, shows that local cooperation for governance of the commons in order to avoid overexploitation can emerge rapidly and that the realities and outcomes of commons situations can be much more complex and scale-dependent.

There have been various well-studied cases where communities have devised necessary rules and norms to avoid local overexploitation of natural resources (for reviews see McCay and Acheson 1987, Ostrom 1990, Agrawal 2002). There is evidence

that this has occurred even within large-scale complex landscape systems (Lansing 1991). However, the particular relevance of the PP case is three-fold.

First, it shows that cooperation for management of the commons, in which marine reserves form a core component of the system, can emerge and evolve rapidly in a young fishery with limited or no experience in collective action. Secondly, I provide evidence of rapid effects of reserve networks on adjacent fisheries via larvae dispersal and that these effects are not necessarily evident for an entire reserve network but can rather be markedly constricted in space. Thirdly, as robust and effective a CBM system with marine reserves may be, my research shows that it is likely this effectiveness may only last as long as the system remains bounded to its own local reality and buffered from external forces. Since this isolation is highly unlikely to remain in most setting, granting forms of access rights that recognize local marine tenure systems will be necessary.

A Regional Perspective on the Emergence and Governance of Marine Reserves in the Gulf of California

The Gulf of California is experiencing a rapid evolution of institutional arrangements and the emergence of challenging management actions aimed at conserving biodiversity while also maintaining fishing life-styles and economies and a high productivity of fishery resources. This evolution has been fueled largely by steady downward trends in production per-capita, an increase of people making use of the Gulf's marine resources, and by the direct and indirect influence of NGOs. I show that one manifestation of these changes is the interest in the establishment of different forms of

MPAs. What follows is a summary of some of the main conditions that have led to the emergence of these reserve efforts and the key processes that are governing their performance.

Dependence, scarcity, and resilience

Dependence on and scarcity of natural resources have been key conditions leading to the interests of fishers, NGOs, and Mexico's National Commission of Protected Natural Areas (CONANP) in establishing forms of marine reserves in the Gulf of California. Clearly, the state of the Gulf's fishery resources has declined when compared to what it used to be two or three decades ago (Sala et al. 2004). It is precisely this decrease in fishery resources combined with belief in the ecological resilience of the Gulf that has largely facilitated the emergence of conservation actions with community support. In the three cases here described, fishers depend on their fishery resources year round and they have evidently experienced a decrease in catches. However, the state of their natural resources is not at a level such that it is no longer worth the initial costs associated with the establishment of marine reserves. They have also experienced, in some form or another, positive responses of the system when protected from fishing.

Local ecological knowledge, stakeholder monitoring, and return rates of social-ecological feedbacks

Fishers will unlikely engage in any conscious management effort if they do not believe it will bring some benefit in the future. This requires, at the very least, some

knowledge of the resilience of their system and clear proof of the positive outcome of their management actions. However, in many areas of the world where commercial fishing has been a relatively recent endeavor, insufficient knowledge of the system's response time frames makes sacrifices unaffordable to fishers. In this dissertation I provide evidence where a blend of local ecological knowledge, stakeholder participation in monitoring, and relatively rapid response of the fisheries on which fishers depend on has brought about a reinforcement of their management institutions. Rapid growth rates of resources harvested, coupled with the divers' direct underwater observations of their natural system, has accelerated the accumulation of ecological knowledge and facilitated informal management trial and error processes.

MPAs: negotiation opportunities for access rights

The establishment of MPAs in the Gulf can be seen as negotiation opportunities for stakeholders to acquire access rights to fishery resources and preferential use of fishing grounds. Faced with the government's proposal to establish MPAs, fishers and communities have a better means to demand some form of exclusivity to the fishing areas and resources they have historically depended on. This occurs regardless of whether they are "buying in" to an outside entity's proposal to establish MPAs, or if the proposal emerged from within the fishing sector. The question then arises as to which communities or sectors should be granted these rights and who decides how these rights are granted. This will probably be the single most conflicting issue for the future establishment of MPAs in the Gulf.

In the three cases presented, fishers' adoption of MPAs has unquestionably been used as a means to help petition for exclusive fishing and territorial access rights. Currently, the government has granted access rights to the communities that lie within the LBNP, has established a type of territorial fishing concession for PP commercial divers and, in the case of SPMI, is studying the possibility of granting territorial use rights to the community of Bahía de Kino, which has historically been the primary user of the island.

Distance of reserves

How far away a fishing area is found from shore will largely determine how often it is used. Although SPMI - in the case of Bahía de Kino -, and San Jorge Island - in the case of Puerto Peñasco - are some of the richest fishing grounds for fishers of these communities, their distance from shore makes fishers target other areas that are closer on a more regular basis.

Part of the reason why fishers from these communities have opted to establish these islands as reserves is that historically they have already been treated as forms of temporary refugia. Nevertheless, there is evidently a tradeoff as well. Enforcement costs and effectiveness will likely increase with the distance at which MPAs are found. Areas found closer to shore can be more easily monitored by local fishers during their regular fishing activities or even when on shore. Incidentally, the belief that other fishers within and outside the community will respect near-shore reserves may increase. For areas that are farther away and out of fishers' immediate control, on the other hand, there can always be mistrust whether they are being poached in or not. In this regard, transaction

costs associated to enforcement will likely be the most important challenge for the management of both San Jorge and San Pedro Mártir Islands.

The government's role

The three case studies show different levels and types of involvement of the Mexican government in the design, establishment, and management of reserves. This involvement has been crucial in various ways. Most importantly, the federal government has acted as a means to legitimize some community efforts. Currently, the only clear means to formalize a no-take marine reserve in Mexico is if it forms part of an existent MPA (i.e. LBNP) or if a new MPA is created in which no-take zones can be included as part of its management scheme (SPMI). In essence, then, in order to have any legally recognized no-take marine reserve, it will likely fall within one of two management categories of Mexico's national park system (i.e. National Park or Biosphere Reserve), currently managed through the National Commission of Natural Protected Areas (CONANP).

The government's formalization of an MPA also represents the only legal means to grant exclusive fishing rights to fishing communities while at the same time aim at conserving the marine environment through an ecosystem approach³. This can also support the justification for enforcement of other fishery management guidelines such as season closures and gear restrictions.

³ CONAPESCA, Mexico's Fishery Commission, also grants fishing concessions as a form of exclusive fishing access right within specific areas. However, these concessions are species-specific.

Nevertheless, the government's involvement and/or lack thereof can also destabilize community initiatives and undermine future grassroots efforts. In the three cases presented, community initiatives have operated on very different time frames than those of the government. In addition, the constant restructuring of fishery administration in Mexico - from a Federal Secretariat to a Commission - has led to important consequences in terms of budget reductions, confusion as to which agencies are held accountable for what, and inefficiencies in bureaucratic processes. To exemplify this, with the changes in the Presidential administration that came about in 2000, bureaucratic problems caused many small-scale fishers to lose their fishing permits during their renovation process. Many of these permits were never renewed, forcing fishers to work illegally or under the auspices of other permit holders.

Role of NGOs and academia

The influence of NGOs and academia in accelerating the emergence of institutional arrangements and management and conservation actions for the marine reserves here studies has been significant. NGOs and academia have played an important role in empowering stakeholders, producing data and proposals with scientific backup, facilitating the communication of fishers with local and federal government entities, and working with the government and fishing sectors to establish reserves as management and conservation tools. They have also provided a more neutral forum for discussion of the issues at play and, consequently, some of the scenarios necessary for the evolution of institutions for co-management. Finally, they have taken some of the financial, logistic,

and technical burden off of essential monitoring processes and have helped bridge local ecological knowledge with experimental design, offering a powerful means to validate fishermen's knowledge and actions within higher local, state, and federal entities.

However, these institutions must work in close coordination and communication with environmental and fisheries management government agencies, and some times battle to be perceived as allies rather than enemies in the fulfilling of their institutional mission.

Implications of this Study for the Establishment and Governance of Community-Based Reserves

Governments and the conservation and academic communities alike are investing millions of dollars to foster CBM of coastal fisheries and the establishment of marine reserves, often with major difficulties in stakeholders' appropriation of management guidelines and large investments to a loss. In the specific case of the Gulf of California, a large network of marine reserves has been proposed (Sala et al. 2002). It is also a region where the fate of various small-scale fisheries is largely left to community-based arrangements⁴. Given the worldwide and regional interest in marine reserves and CBM, I provide the following views.

Compliance for community-based establishment of area closures demands a great deal of social group strength. Not only do reserves reduce the total fishing area and

⁴ A review of the legislation showed 22 species specific fishery norms, of which only 6 apply to species harvested by small-scale fishers in the Gulf of California. However, small-scale fishers in the Gulf target more than 100 species (www.pangas.arizona.edu).

initially render an economic cost to fishers, but they also complicate fishers' management of risk by reducing the physical spaces available to choose from in accordance to variations in environmental conditions and the state of their resources.

It is therefore important that community-based efforts are initially implemented in systems where responses can be measured rapidly and where there is an existing social base for their establishment. This can be largely facilitated by a combination of a) the state of natural resources on which there is a high level of livelihood dependence (i.e. having experienced some form of downfall in these resources but not at a level such that it is useless for cooperation to emerge), b) fishers' previous tacit individual experimentation and local knowledge gained on the resources' response rate, c) direct influence of researchers or outside sources with established rapport, credibility, and trust amongst appropriators, and d) strong social capital with high levels of trust within appropriators. Furthermore, stakeholder participation in monitoring where there is a rapid feedback of the system's response can play a key role in reinforcing cooperation.

When a system proves to be promising for establishment of community-based reserve networks, networks need to be designed to enhance or maintain local recruitment and not benefit other communities at the expense of local management initiatives. In some situations, this may not be possible as the oceanographic processes may render larvae export rather than retention within the community-based system. In addition, some areas even within the same regional landscape may respond in different time frames than others. Adaptive management should therefore be implemented so as to incorporate these variations and not assume false expectations.

Nevertheless, even if community-based reserves are effective within the biophysical and local social context, their long-term success will rely on the system's capacity to control access. I argue that even in a small-scale setting like the PP case, with a tight knit, relatively homogenous, and self-enforcing group of fishers, with a *de facto* fishing territory that is markedly isolated from other communities, local cooperation and social capital alone are likely not enough to sustain the efficacy of reserves. Fishers and fishing communities need to be granted, at the least, formal government recognition of territorial access rights and their locally-devised management structures should be given legal weight when they appear to be effective strategies. In essence, threats to the existent social capital base and open access situations with other fishing communities, coupled with insufficient government recognition of community-based initiatives and lags between local and government timeframes and interests are likely to be the main constraint on the long-term success of locally managed marine reserves.

Current calls and efforts to revive and formally recognize customary marine tenure systems are an important step towards this direction (Johannes 2002), but much more remains to be done within a global context. In particular, we need to pay more attention to nascent fisheries or young fishing societies and communities in less isolated areas. This will surely represent a challenge as the concept of community and territorial use rights can be nebulous in these settings. Nevertheless, the costs of not doing so are much greater. In an increasingly globalized world economy, the existence of isolated fishing communities has been largely lost. Yet, as I show, effective community-based structures that include costly decisions like the establishment of marine reserves can

emerge even in these settings. Not granting appropriate forms of territorial use rights nor formally recognizing effective local governance structures, as simple or complex as these may be, could dismantle a community's existing foundations for promising long-term sustainable use of fishery resources.

APPENDIX A
ESTABLISHING A BASELINE: GROWTH AND REPRODUCTION
OF THE ROCK SCALLOP (*SPONDYLUS*
CALCIFER) IN THE UPPER GULF OF CALIFORNIA, MEXICO

Journal of Shellfish Research

Richard Cudney-Bueno^{*†‡} and Kirsten Rowell[§]

* Department of Natural Resources, School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA.

‡ Centro Intercultural de Estudios de Desiertos y Océanos (CEDO). Apartado Postal #53, Puerto Peñasco, Sonora, México.

§ Department of Biology, University of Washington, 528 Kincaid Hall, Box 351800, Seattle, WA 98115.

† Corresponding author: School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA email: cud@ag.arizona.edu, phone: 520-626-5607, fax: 520-621-8801.

Key words : Rock scallop, thorny oyster, *Spondylus calcifer*, Spondylidae, growth, reproduction, Gulf of California, oxygen isotopes, fisheries.

Establishing a Baseline: Growth and Reproduction of the Rock Scallop, *Spondylus calcifer* (Carpenter 1857), in the Upper Gulf of California, Mexico

Richard Cudney-Bueno and Kirsten Rowell

Abstract

The rock scallop, *Spondylus calcifer*, is the largest member of any Panamic Province *Spondylus* and has played important economic, political, and cultural roles in coastal communities of the Eastern Tropical Pacific for thousands of years. Despite its importance, knowledge of its biology is scant. We assessed seasonal variations in shell and adductor muscle growth, longevity, reproductive age and period, and population sex ratios in the upper Gulf of California, Mexico, the northernmost area within the geographic distribution of this species. Information on shell growth and age was obtained via the use of stable oxygen isotope profiles of shell aragonite cross-referenced with mark-recapture data. *Spondylus calcifer* forms white growth bands during winter and spring months. Shell growth accelerates during warmer months and diminishes during colder months, likely as a result of energetic shifts related to resource allocation pre and post reproduction. This is evidenced by variations in seasonal growth of adductor muscles. The adductor muscle increases both in size and weight during colder months in preparation for reproduction, which takes place in July-August as water temperatures reach 28-30°C. The species reaches sexual maturity between 2.5-3 years of age and can live to at least 10-12 years. Overall sex ratios consisted of 1:1 male:female, a population structure in accordance with previous reports for the southern Gulf of California. We discuss our findings in the context of management and conservation of the species.

Introduction

The rock scallop (also known as “donkey thorny oyster”, “spiny oyster”, “thorny oyster”), *Spondylus calcifer* (Carpenter, 1857), is the largest member of the family Spondylidae found in the Americas (Keen 1971, Skoglund and Mulliner 1996). It is distributed throughout a large portion of the Eastern Tropical Pacific from the Gulf of California, Mexico to Ecuador (Keen 1971, Poutiers 1995), but may briefly colonize the coast of Perú during warmer El Niño years (Sandweiss 1992). It is found primarily on subtidal rocky reefs up to 55 m deep (Poutiers 1995). While several species of *Spondylus* are found in the Gulf of California and Mexican Pacific (Skoglund and Mulliner 1996), *S. calcifer* is the only Spondylid commonly found in the upper Gulf of California and appears to be more abundant in this region compared to other areas (Cudney-Bueno 2007).

This bivalve has played an important economic, political, and cultural role in coastal communities of the Eastern Tropical Pacific for thousands of years. Together with its close relative, *Spondylus princeps*, it was highly valued and traded by Mesoamerican cultures since the Pre-ceramic period (12,000-1,800 B.C.), prized for its ornamental value and used in offerings and religious rituals (Pillsbury 1996, Donkin 1998). Although today its cultural and political significance has been lost for most Latin American cultures, the species is still harvested commercially for its colorful shell as well as adductor muscle. In the Gulf of California, Mexico, *S. calcifer* (known locally as *callo de escarlopa* or *almeja burra*) is harvested by commercial divers primarily for its adductor muscle, which is sold at a high price within the local and regional market (\$10-14 dollars/kg) (Cudney-Bueno

2000). Unfortunately *S. calcifer* population sizes are now low throughout Mexico's coastline (Baqueiro et al. 1982), and the species is listed as in need of special protection under Mexican environmental law (Norma Oficial Mexicana 1994). The declines in abundance and its economic importance have also led to community-based efforts for management and conservation of this and other species of mollusks harvested by commercial divers in the upper Gulf of California (Cudney-Bueno 2007).

Despite its importance and conservation status, very little is known about the biology of this species, its population structure or current state of exploitation throughout most of its range. Published life history information is limited to a small study defining the reproductive biology for a population in Bahía de Loreto in southern Baja California (Villalejo-Fuerte et al. 2002).

In this study, we establish baseline demographic information using a suite of traditional and technically innovative methods to determine and validate growth rates, age at sexual maturity, longevity, spawning period, and sex ratios. The demographic parameters documented in this study will help inform population models and size limits for management. We discuss growth, longevity, and reproduction of *S. calcifer* in the upper Gulf of California, the northernmost distribution of the species and the area subject to the most intense fishing pressure in Mexico (Cudney-Bueno 2007).

Methods

Use of oxygen isotopes for growth and age estimations

We use profiles of oxygen isotope ratios obtained from shells to determine growth rates in *S. calcifer* and to validate age. Shells contain excellent records of growth and environmental conditions. The oxygen isotope ratios in shell aragonite provide a seasonal clock (Jones and Quitmyer 1996, Goodwin et al. 2001), as the ratio between ^{16}O and ^{18}O ($d^{18}\text{O}$) of biogenic aragonite is primarily controlled by the temperature and oxygen isotope ratio of the water in which the bivalve lived (Grossman and Ku 1986).

In the marine setting, where the $d^{18}\text{O}$ of seawater is relatively constant, the oxygen isotope ratio precipitated in mollusk shells is primarily influenced by the ambient temperature. As temperature increases, the $d^{18}\text{O}$ of biogenic carbonate decreases: for every 4-5°C increase in temperature, the $d^{18}\text{O}$ decreases by approximately 1‰ (Arthur et al. 1983; Grossman and Ku 1986). Negative $d^{18}\text{O}$ values are associated with summer temperatures and more positive values with cooler temperatures. Therefore, the oxygen isotope profile along a shell's axis of growth reflects a chronology of seasonal variations of temperature that provides a seasonal time scale to measure rate of growth (Allmon et al. 1992). Thus, a year of growth is defined as one complete annual cycle of temperature-driven $d^{18}\text{O}$. This relationship has already been established for biogenic carbonates in the upper Gulf of California (see Goodwin et al. 2001, Rowell et al. 2005).

Growth and longevity

To establish growth rates, age estimates, longevity and validate the periodicity of growth estimates we relied on three approaches: analyses of $d^{18}O$ profiles, counting of “growth scars”, and analyses of mark and recapture growth data. We used eight individuals, specimens A-H, for these estimations. These specimens were from three fishing sites found near Puerto Peñasco, Sonora, the largest fishing town in the upper Gulf of California (UG): San Jorge Island, Los Tanques, and La Cholla (Figure 1). We measured height (mm) of the left (exposed) valve of each specimen. Shells covered a wide size range, the smallest being 51.4 mm in shell height and the largest 160.7 mm.

To determine age and growth, first we tested the hypothesis that increments (scars) in *S. calcifer* were annual. For this we used one of the largest individuals (specimen A, 160.7 mm shell height) collected in three years of fieldwork. We collected a larger specimen (186.6 mm) but extensive damage done to the shell by burrowing animals impeded its use for both isotope and growth scar analysis. We sampled in detail (samples = 1 mm apart) the calcareous material of the last three increments of growth of specimen A (marked by white bands) (Figure 2) to determine if they were indicators of some sort of annual periodicity like that reported by Goodwin et al. (2003), where white bands in the venus clam, *Chione cortezi*, indicate a seasonal (winter) decline in growth. Alternatively, these white scars could represent spawning scars, since they occur at the mature stage of this large individual. To validate our technique for using $d^{18}O$ variation in the shell as a seasonal clock, we collected, measured, marked, and released twenty specimens in November 2003. We retrieved the available specimens (i.e. those found and

alive) one year later, recorded the additional growth and analyzed carbonate samples for $d^{18}\text{O}$ in this last year of growth. We expected that this year of known new growth should have a $d^{18}\text{O}$ profile representative of one-year seasonal temperature-driven variation.

We used standard methods for isotope analysis preparation (Goodwin et al. 2001). All shells were cross-sectioned through the axis of maximum growth, making 5 mm thin-sections using an Isomet low-speed saw equipped with a diamond blade. Shell sections were then polished using a 0.05 μ grit polish and photographed under reflected light. All samples of shell material used for isotope analysis were made using a micromill drill with a 0.3 mm drill bit. Samples, weighing between 30–60 μg , were heated to 180°C in a vacuum oven for one hour to remove volatile material. Oxygen isotope ratios in carbonate values are expressed relative to the Vienna Pee Dee Belemnite (VPDB) standard. These methods for sampling shell carbonate are well established (see Krantz et al. 1987, Jones and Quitmyer 1996). Shell carbonate was analyzed at the Stable Isotope Laboratory of the Department of Geosciences, University of Arizona, using a Finnigan MAT 252 mass spectrometer equipped with a Kiel-III automated carbonate sampling device. Standardization of oxygen isotope ratios was based on normalization to published ratios of NBS19 and NBS 18. Analytical error was ± 0.1 ‰.

Age at reproductive maturity

Following the same isotopic analysis procedure, we sampled five shells (specimens D, E, F, G, H), along a transect from earliest stages of the shell (close to the protoconch) to the terminal year (Figure 3). We measured the distance from the

protoconch to each sampling point. We then estimated age of reproductive maturity by comparing isotope profiles with known first spawning size of *S. calcifer*, 86-113mm (Villalejo-Fuerte et al. 2002).

Seasonal variations in shell and adductor muscle growth

We looked at $d^{18}O$ profiles to determine if there was any difference in shell growth between colder (Winter-Spring) and warmer (Summer-Fall) months. Little or no variation in seasonal growth would be represented by a relatively consistent sinusoid curve, with little differences in crest and valley widths (Goodwin et al 2001). However, seasonal variations in growth are depicted when sharp peaks in the crest or valley are present, representing fewer values that record extreme cold or hot temperatures (Wefer and Killingley 1980). Because we sampled at a constant interval, slow growth or a hiatus in growth during a season will be evident by fewer $d^{18}O$ values representing that warm or cold season.

We assessed seasonal variations in growth and weight of adductor muscles. This information is important for fishery management purposes as the adductor muscle is the part of the organism that is commercialized and fishing effort could be partly mediated by variations in muscle weight (Cudney-Bueno 2007). Variations in adductor muscle length and weight could also be indicative of energy allocation related to reproductive events (Dore 1991). We participated in between 1-4 fishing trips/month for two consecutive years and obtained a random sample of the adductor muscle from fishers' catches (91 fishing trips, $n = 2725$ rock scallops). We measured weight and total length of each

muscle (defined as the length between the base of the muscle - adhered to the right valve - and the top part of the muscle - attached to the left valve) and compared between Summer-Fall and Winter-Spring periods using a Students t-test.

Because only the scallop muscle is brought to the market, enforcement of size limits is difficult. Defining the relationship between muscle and shell size is therefore essential for monitoring the fishery. Here, we assessed the relationship between muscle size and shell height by collecting 347 complete specimens during fishing trips in Winter-Spring (4 trips, n =175 individuals) and Summer-Fall (5 trips, n = 172 individuals) 2003-2004 and measured shell height and adductor muscle length and weight for each. We analyzed our data using regressions and obtained the best fit for both seasonal periods by comparing residual plots and r^2 values. Finally, we used ANCOVA models to assess seasonal differences between shell height-muscle length as well as shell height-muscle weight relationships. Prior to our analysis, we examined the data for homogeneity of variance, excessive skewness, and outliers.

Reproductive period and sex ratios

To assess reproductive period and sex ratios, we used the same complete specimens that were collected for estimation of relationships between shell height and muscle length. Gonadic condition and sex of each collected animal was assessed visually by looking at coloration, size characteristics, and texture of the gonads. Given that *S. calcifer* is gonochoric (Villalejo-Fuerte et al. 2002), sex determination was done visually by differentiating the conspicuous gonads of mature specimens.

Following Strathmann (1987), males were identified by a white to ivory colored gonadic tissue, and females by a bright orange to red colored gonadic tissue. We determined the percentage of males and females for each site in which a sample was taken and in which all gonads were clearly differentiated. We then tested all samples for marginal homogeneity using a Pearson χ^2 test.

We differentiated two different stages for the condition of the sample tissue: (1) presence of sexual activity, and (2) absence of sexual activity or undifferentiated. For (1), individuals included in this category ranged from those who were visibly under a developing stage (gonads differentiated, brightly colored, but not completely swollen) to those that were ripe (gonads brightly colored and swollen, bursting open with minimum contact). For (2), individuals included in this category presented an unidentifiable gonadic tissue. For each sample period/site, we calculated the percentage of individuals for which gonads were maturing/mature or undifferentiated. This field observation method has been used in other studies on commercial bivalves in the Gulf of California (see Basurto 2001).

Results

Growth and longevity

The $d^{18}O$ values from all *S. calcifer* shells show distinct annual cycles (Figures 4 and 5). We recovered two of the twenty specimens marked and released in November 2003 (specimens B and C). Detailed sampling of specimens A (largest individual), and B and C revealed that white growth increments have $d^{18}O$ values that are relatively more

positive, indicating that they were precipitated under colder temperatures (Winter-Spring). Spaces between the white growth increments, in contrast, consistently yielded more negative $d^{18}\text{O}$ values, indicating precipitation under warmer temperatures (Summer-Fall) (Figure 4). In addition, measurements of specimens B and C revealed that they had grown 25.7 mm and 5.9 mm, respectively, during a one-year period. These measurements coincide with the distances encompassed by the last isotopic profile cycle of these shells (Figure 4).

Specimen A had at least ten white growth increments, indicating a minimum age of 10 years. However, because of biological damage (i.e. boring of polychaetes and burrowing clams) done to the oldest part of the shell (the oldest calcareous deposits), we were unable to assess if any other white scars were present and therefore this is a minimum age estimate based on growth increments that were visible.

Age at reproductive maturity

Age estimates from $d^{18}\text{O}$ profiles indicate that specimens D, E and F (minimum reproductive size) were between 2-4 years of age (Figure 5). Individuals D (104.9 mm height) and E (97.1 mm height) have oxygen profiles that indicate at least four years of growth. Specimen F (85.8 mm) had an oxygen profile indicating between 2.5 and 3 years of age. Counting the number of growth increments of individuals B (125.9 mm) and C (126.5 mm), also of reproductive size, indicated that these individuals were at least four years old. The smaller, non-reproductive individuals (G and H; 51.4 mm and 68.3 mm,

respectively), on the other hand, had isotopic profiles indicating that they were = 3 years old (Figure 6).

Seasonal variations in shell and adductor muscle growth

The shape of the oxygen isotopic profiles of all specimens tended to have large valleys and sharp peaks when presented graphically, indicating more growth during warmer months (most negative values) and less during colder months (most positive values).

We found a significant relationship between shell height and adductor muscle length of adult individuals ($P < 0.0001$, $r^2 = 0.26$, $n = 347$, simple linear regression; muscle length = $11.064 + 0.204 \times$ shell height). A similar pattern was observed for adductor muscle weight ($P < 0.0001$, $r^2 = 0.28$, $n = 347$, simple linear regression; muscle weight = $-25.49 + 0.43 \times$ shell height). However, contrary to our analysis of shell height vs length, weight data was better explained, as expected, using a non-linear curve (Figures 7 and 8). ANCOVA analyses also revealed seasonal differences between the shell height-muscle length as well as shell height-muscle weight relationship (ANCOVA effect test for shell height \times season $F_{1,343} = 15.01$, $P < 0.0001$). These differences were much more apparent for younger individuals, becoming progressively less distinct for older individuals (Figures 7 and 8). Overall, muscles tended to be larger ($t_{2721} = -15.15$, $P < 0.0001$; students two-tailed t test) and heavier ($t_{1580} = -9.57$, $P < 0.0001$; students two-tailed t test) during Winter-Spring than Summer-Fall. Mean muscle length and weight for Winter-Spring was 39.55 mm (95% C.I. = 39.25-39.86 mm) and 34.54 g (95% C.I. = 33.76, 35.33)

respectively, whereas for Summer-Fall the mean length was 36.46 mm (95% C.I. = 36.20, 36.72) and weight 29.71 g (95% C.I. = 29.10, 30.32).

Reproductive period and sex ratios

Sexual activity became apparent in mid-March (temp 17°C), when the gonadic tissue of a few individuals began to swell. Nevertheless, it was not until the end of April (temp 21° C) that gonads were clearly differentiated in most specimens. At this time, the sex of each individual was easily determined but gonads were not developed enough to spawn. The presence of spawning activity was not seen until early July (temp 28°C). We were unable to sample during August, but by mid-September the gonads were spent and sex of individuals was again not clearly differentiated (Table 1).

The combined sex ratio of the seven samples for which we were able to determine sex of each specimen did not deviate significantly from the expected 1:1 ratio ($P=0.48$, Pearson's $\chi^2 = 5.48$). However, when analyzing the sampling days/sites independently, two of these samples had double the number of males than females (67%: 33%; 63%: 37%) (Table 1).

Discussion

Rock scallop produces white bands consistent with annual growth cycles. White growth bands are developed during the colder months, a pattern that has also been documented in the Gulf of California for *Chione cortezi* (Goodwin et al. 2001) and for other bivalves elsewhere (Jones et al. 1983, Jones and Quitmyer 1996). When clearly

visible, these growth bands can be used as a rapid and reliable tool to estimate age of an individual. Nevertheless, growth bands are neither always clearly visible nor distinct, especially for younger individuals that have a thin shell or for those that have been heavily infested by burrowing epifauna. Therefore, the use of oxygen isotopes in combination with visual examination of growth increments can provide a robust means to assess age and growth of *S. calcifer*.

Using this combined method, we estimated that our largest specimen (160.7 mm in shell height) was at least 10 years old, although this individual was surely older given that a small section of the umbo of the shell could not be sampled due to heavy biogenic infestation. However, judging from the age of the other younger individuals (of the same size class) analyzed in this study, we are confident that this missing portion of the shell would not add more than two years of growth to our estimate. Keen (1971) reports that the maximum size of *S. calcifer* is approximately 150 mm in shell height. Similarly, Villalejo-Fuerte et al. (2002), never found individuals in the southern Gulf of California larger than 160 mm ($n = 220$). Given this and the fact that we very rarely saw individuals this large during our fieldwork, we are confident that the largest individual sampled in this study is representative of some of the oldest individuals currently found in the region. Nevertheless, as noted earlier, we did find a larger specimen (186.6 mm) that couldn't be sampled due to heavy burrowing throughout the shell. Poutiers (1995) and Skoglund and Mulliner (1996) reported that *S. calcifer* can get to be ~ 250 mm, but don't provide the region where these specimens were found. Elder divers in Puerto Peñasco also state that

larger individuals used to be found more regularly 20-30 years ago (Cudney-Bueno 2007). This suggests that rock scallop could grow to be much older than 12 years.

The only study on the reproductive biology of *S. calcifer* that we are aware of was conducted by Villalejo-Fuerte et al. (2002) in the southern Gulf of California. This study showed that spawning was restricted to Summer and that the size at spawning of a population of *S. calcifer* (smallest shell height at which 50% of females and males are spawning (Somerton 1980) was 113 mm, although individuals could begin spawning at 86 mm in shell height. Using these estimates for the minimum reproductive population size of *S. calcifer* in the Gulf of California our results indicate that *S. calcifer* reaches reproductive maturity between 3-4 years of age.

S. calcifer grows considerably faster during the warmer months than during the colder season. The fact that colder months also correspond with a significant increase in length and weight of the adductor muscle suggests that variations in shell growth are related to resource allocation pre- and post-reproduction. As with other bivalves (Dore 1991), *S. calcifer* may be allocating most of its energy during the colder months (Winter and Spring) into the storage of glycogen on the adductor muscle in preparation for reproduction, therefore limiting its shell growth.

Our results also suggest that variations in growth could take place even within a localized area. Specimens B and C, for instance, showed marked variations in one-year growth (25.7 and 5.9 mm respectively.) Although this could be attributed to initial differences in the size of both specimens (100.8 and 120.6 mm in shell height, respectively) leading to subsequent variations in growth rates, it could also be an

indication of a high degree of growth variability in the population. Factors such as temperature fluctuations, food availability, substrate type, and influence of parasitic organisms, among others, are known to be important determinants of the rate of growth of various species of mollusks (Hyman 1967, Breen 1980, Kemp and Bertness 1984, Berg and Olsen 1989). Further research with larger sample sizes and translocation experiments would be needed to assess the degree of growth variations.

Our reproductive data indicates that *S. calcifer* in the upper Gulf of California has a relatively short spawning period between July and August when the water reaches its highest temperatures (28-30°C), similar to the pattern reported in Bahía de Loreto, Southern Baja California (Villalejo-Fuerte et al. 2002). During spawning in the Summer and post reproduction (first few months of Fall) size of the adductor muscle is considerably reduced when compared with Winter and Spring. As stated before, this reduction is likely attributed to the increased use of glycogen stored in the muscle as a response to high-energy costs associated with reproduction (Dore 1991). Variation in muscle size is also consistent with fishing practices. Local commercial divers historically have preferred harvesting rock scallops in the colder months because at this time the muscle is larger, weighs more, and has a firmer consistency than during late summer and early fall (Cudney-Bueno 2000).

The sex ratio of all combined samples taken in our study area did not differ from the expected 1:1 ratio. A similar pattern has been documented in the southern Gulf of California (Villalejo-Fuerte et al. 2002). However, two of our samples were skewed towards males. This could be attributed to possible lags in the timing of gonadic

maturation between males and females, with males beginning to mature earlier on in the season when these samples were obtained. However, further studies would be needed to address this more conclusively.

Management implications and recommendations

Although the species has an official protection status in Mexico, it is still widely harvested throughout its geographic range in Latin America. It is both a subsistence and commercial fishery, with little management or oversight of fishing practices. There is however, a growing interest within the commercial fishery sector of the Gulf of California to legitimately open the rock scallop fishery and establish formal management with sustainability as one of its top priorities (Cudney-Bueno 2007). Given this evident commercial interest, we provide the following management and conservation recommendations.

Results of this study should be incorporated into population viability analyses (PVA) of the fishery. We recommend that PVAs are conducted prior to the allowance of any harvest in order to determine long-term risks of the population(s) and the most appropriate harvesting scenarios. If harvest does take place, it should be limited to Winter and Spring and restricted most of the Summer and Fall, particularly during July, August, and September, when water temperatures reach 28-30° C. Aside from assuring spawning events, this would also avoid unnecessary commercial losses due to a decrease in weight and size of the adductor muscle.

Management of the species must also rely on size limits, quotas, and spatial control of fishing in accordance to adult densities. Only individuals with a shell height of 130 mm or higher (equivalent to an adductor muscle length of 39.6 mm during Winter/Spring and 35 mm during Summer/Fall) should be allowed to be harvested. This measure would assure that young individuals reproduce at least once and allow for younger individuals to be recruited to the fishery. In addition, areas showing adult densities of ≈ 5 individuals/m² should be protected and harvesting should never go beyond this density (Baqueiro et al. 1982). When established, quotas should be highly precautionary, recommended at no more than 10% of the adult population (Cudney-Bueno 2007). These measures would help avoid population collapses due to an Allee density effect. Marine invertebrate populations, particularly those of broadcast spawning species like rock scallop, can be particularly susceptible to sudden collapse when gradually increasing habitat destruction or fishing pressure drop populations below densities necessary for adequate fertilization and subsequent recruitment (Karlson and Levitan 1990). Examples of this are the collapse of various pearl industries worldwide (Donkin 1998) and of the white abalone in California (Hobday et al. 2001).

Rock scallop populations as well as those of other benthic sessile and semi-sessile species have the potential of being enhanced through the use of networks of permanent and temporary harvest refugia (Quinn et al. 1993, Cudney-Bueno 2007). Refugia networks should be established in accordance to physical oceanographic processes, population densities, and known population connectivity. Areas with low densities that have clear signs of having been over-harvested should be closed for a minimum of 4

years to allow for newly settled individuals to reach first reproductive age and spawn at least once. Likewise, closure of source populations should be considered in order to facilitate population enhancement to adjacent areas via larvae dispersal. Rotation schemes should be implemented particularly for “sink” populations, conducting fishing alternations between reefs to assure local recoveries in the year or years following harvest.

Finally, given that *S. calcifer* is found throughout an extensive geographical range with marked variations in biological and physical gradients, our results should be interpreted with caution outside the more temperate waters of the Gulf of California. Management schemes should be designed and implemented according to the bio-physical and social realities of the region where the species is harvested.

Acknowledgements

We thank the Sociedad Cooperativa Buzos de Puerto Punta Peñasco, Olegario Morales, and the Intercultural Center for the Study of Deserts and Oceans (CEDO) for their invaluable logistical support and help in the field. Isotopic lab assistance and space was kindly provided by Drs. Karl Flessa and David Dettman of the Stable Isotope Laboratory of the Geosciences Department at the University of Arizona. This study has been conducted thanks to financial contributions from the Tinker Foundation, the David and Lucile Packard Foundation, as well as fellowships and scholarships to Cudney-Bueno from the Consejo Nacional de Ciencia y Tecnología (CONACYT), The Inter American Foundation, the Wallace Research Foundation, and the Environmental Leadership

Program. Research was conducted under permit # SGPA/DGVS/13159 of the *Dirección General de Vida Silvestre; Secretaría de Medio Ambiente y Recursos Naturales* (SEMARNAT) of Mexico. This is contribution # 2 of Project PANGAS, www.pangas.arizona.edu.

Figures and Tables

Figure A1. Rock scallop (*Spondylus calcifer*) study areas in the upper Gulf of California, Mexico.

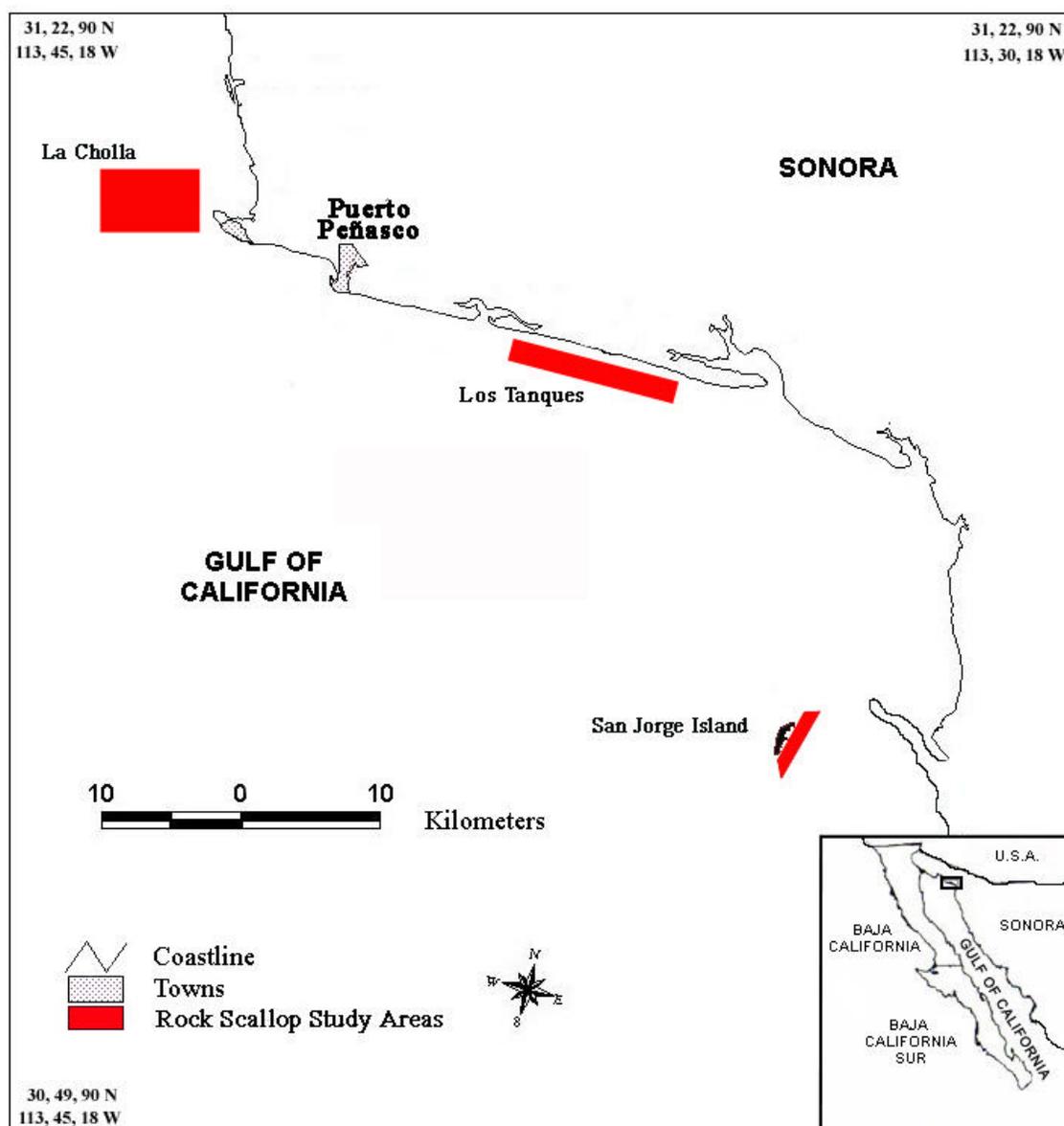


Figure A2. Cross-section of rock scallop (*Spondylus calcifer*) specimen A collected in the upper Gulf of California, Mexico. Scale in cm. Black dots illustrate the $d^{18}O$ sampling scheme for the last three increments of growth.

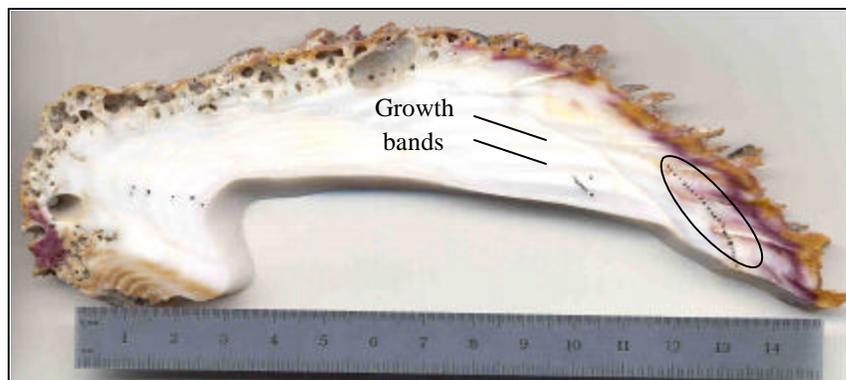


Figure A3. Example of cross-section of rock scallop, *Spondylus calcifer*, (specimen D) collected in the upper Gulf of California, Mexico. Black dots illustrate the $d^{18}\text{O}$ sampling scheme along the axis of the shell.



Figure A4. Isotopic profiles of the last growth increments of rock scallop specimens A, B, and C (A= last three increments, B=last increment, C=last two increments).

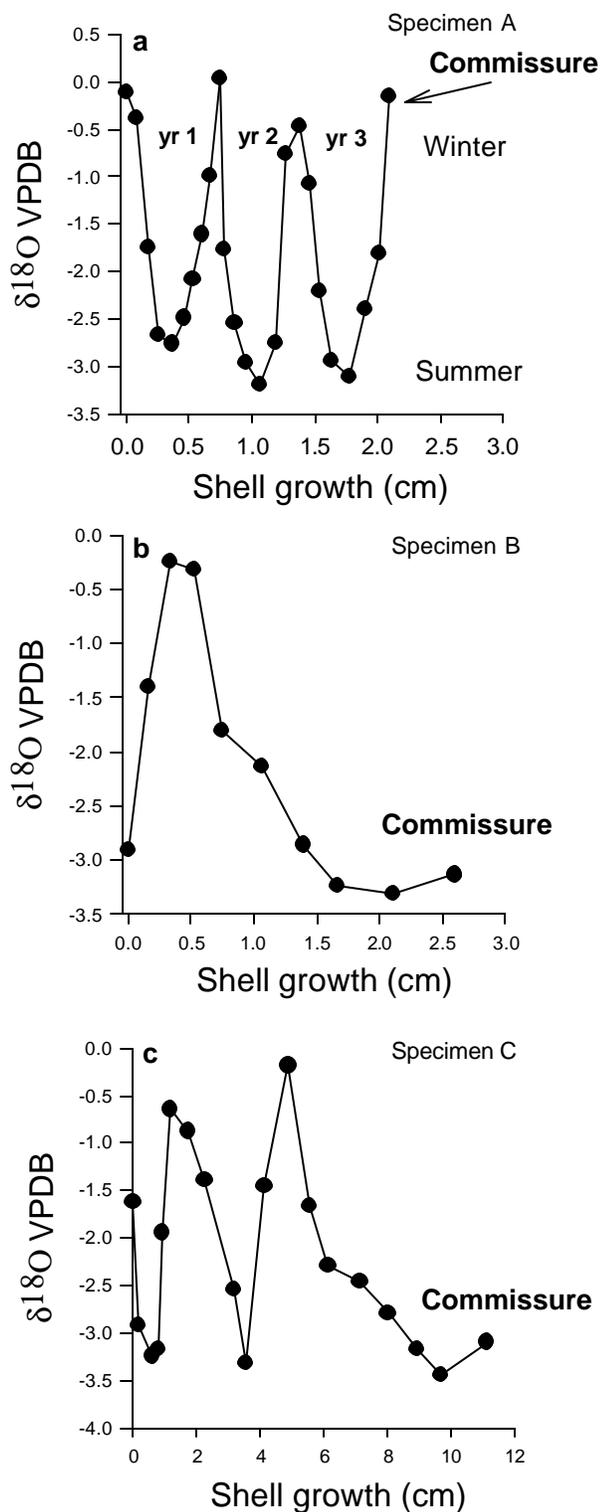


Figure A5. $\delta^{18}\text{O}$ profiles of rock scallop, *Spondylus calcifer*, specimens D, E, and F which fall within the minimum reproductive size range (shell height 86 mm - 113 mm). The isotopic signatures of these individuals indicate that they lived to be between 2-4 years old.

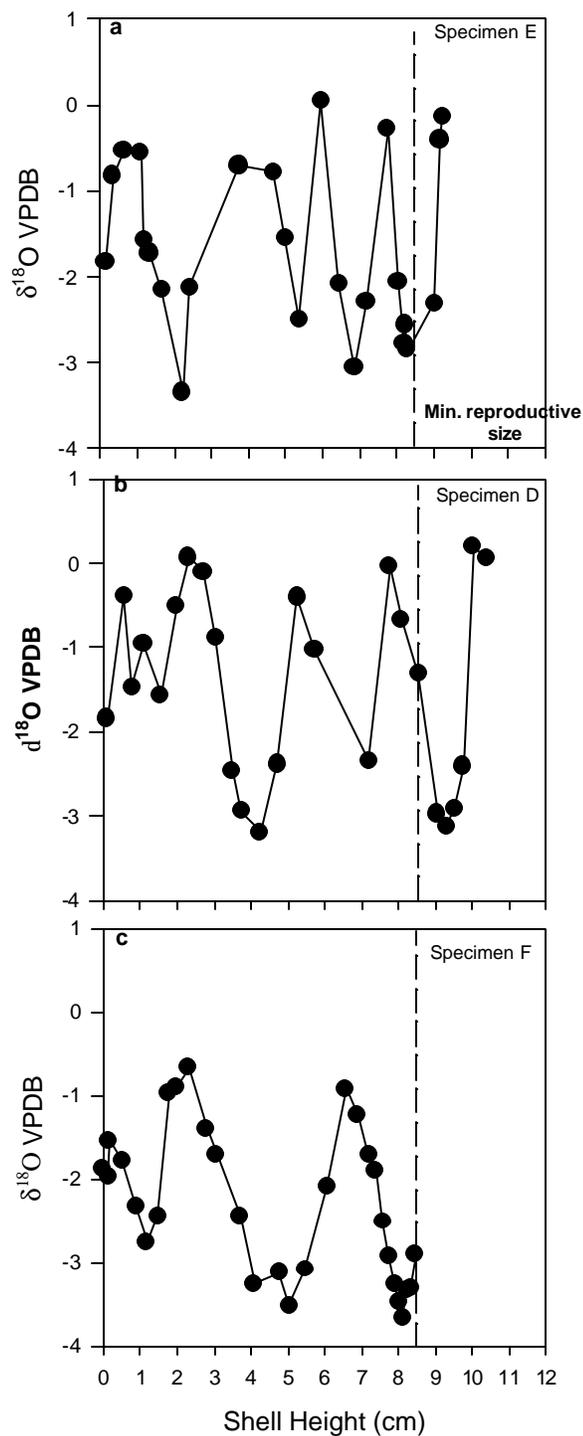


Figure A6. $d^{18}\text{O}$ profiles of rock scallop, *Spondylus calcifer*, specimens G and H collected in the upper Gulf of California, Mexico.

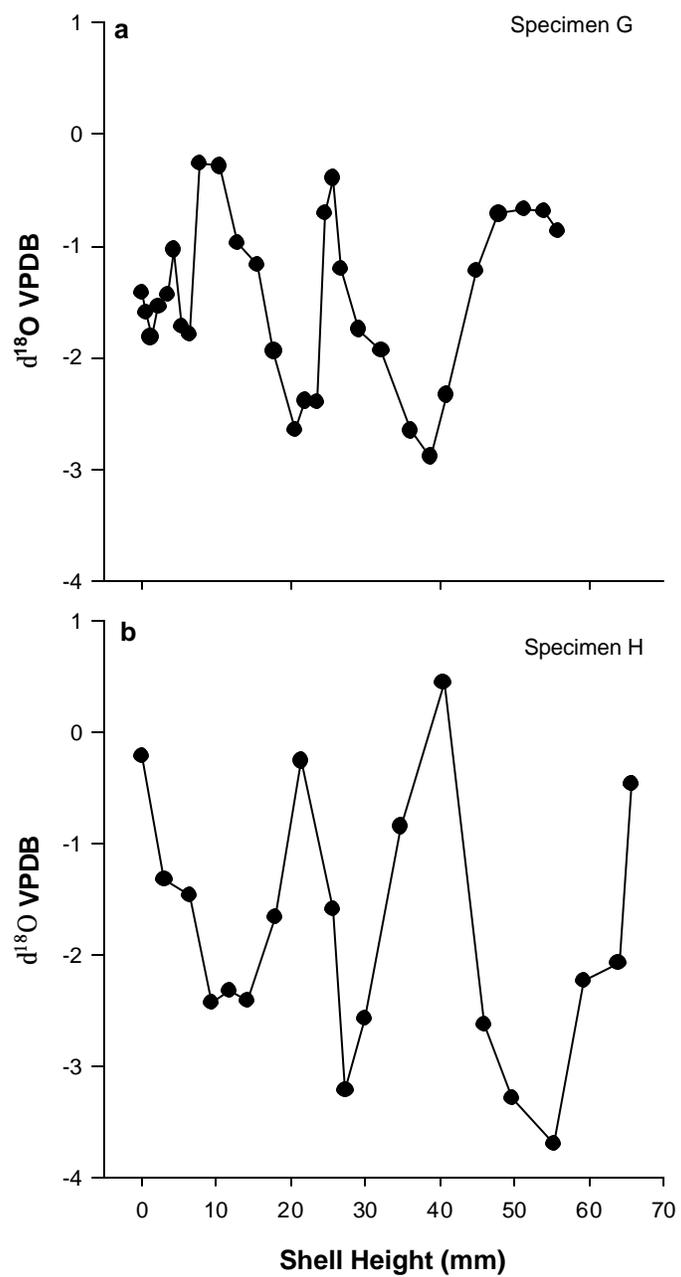


Figure A7. Seasonal representation of the relationship between shell height and adductor muscle length for *Spondylus calcifer* in the Upper Gulf of California, Mexico.

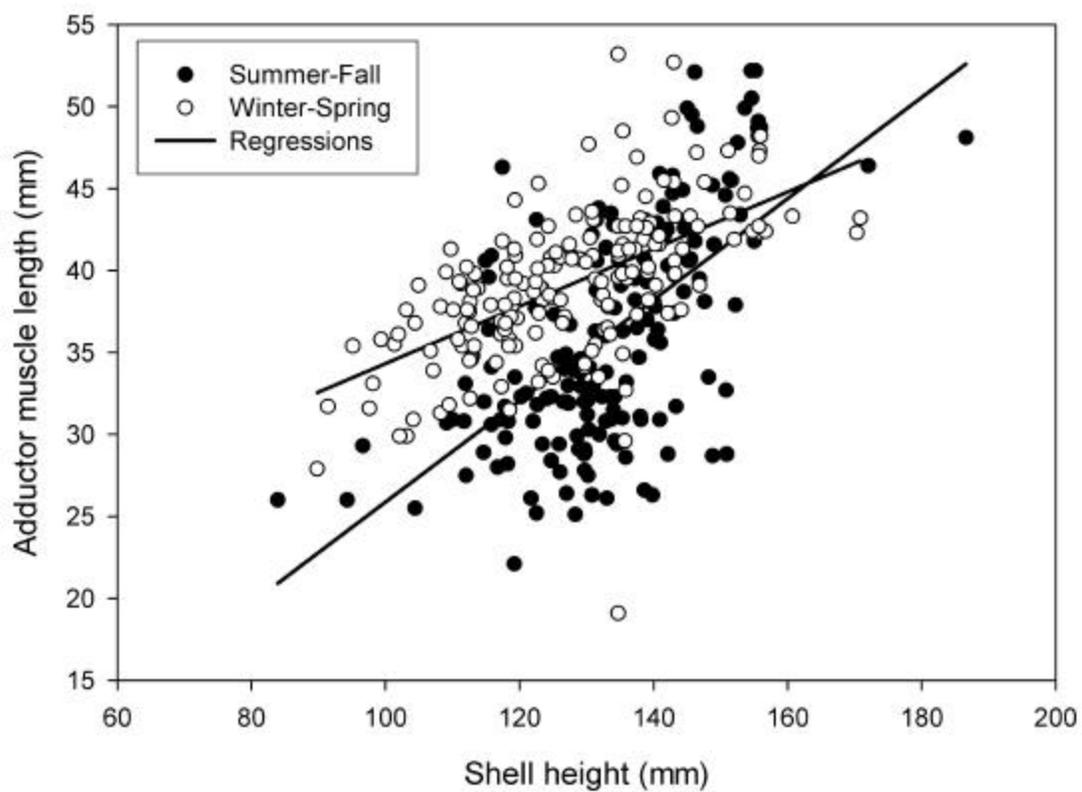


Figure A8. Seasonal representation of the relationship between shell height and adductor muscle weight for *Spondylus calcifer* in the Upper Gulf of California, Mexico.

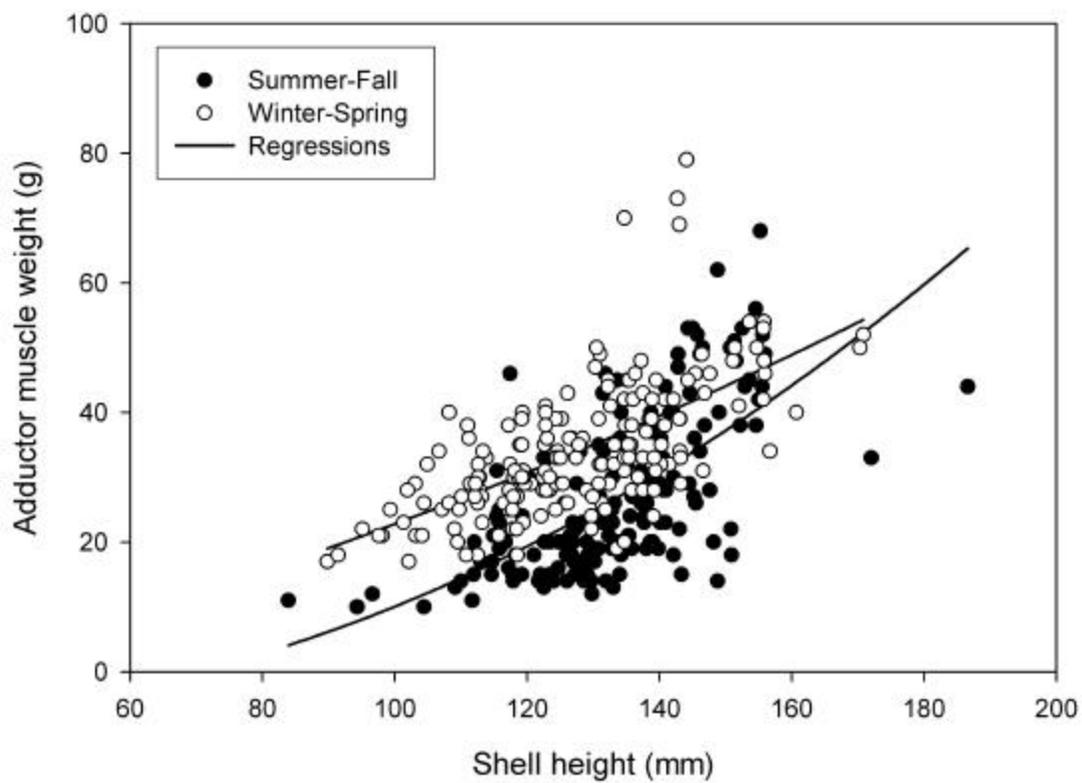


Table A1. Collection scheme, reproductive season, and percentage of male and female *Spondylus calcifer* in the Upper Gulf of California, Mexico. Notation: NA= Not assessed since the gonads of all individuals were not ripe enough to visually differentiate sex.

Collection Day	Temp (°C)	Depth (m)	N	% Mature	Individuals Spawning	% Males	% Females
11-20-03	22	11	30	0	No	NA	NA
11-21-03	21	13	30	0	No	NA	NA
03-12-04	17	9	30	13	No	NA	NA
03-26-04	18	9	30	16	No	NA	NA
03-28-04	21	6	30	27	No	NA	NA
04-28-04	21	13	30	100	No	63	37
05-07-04	22	12	30	100	No	67	33
05-28-04	23	14	30	100	No	57	43
06-12-04	25	27	30	100	No	50	50
07-09-04	28	9	30	100	Yes	50	50
07-16-04	28	13	30	100	Yes	43	57
07-26-04	30	9	30	100	Yes	47	53
09-21-04	29	13	30	36	No	NA	NA
09-22-04	28	13	22	27	No	NA	NA

References

- Allmon, W. D., D. S. Jones and N. Vaughan. 1992. Observations on the biology of *Turritella gonostoma* Valenciennes (Prosobranchia: Turritellidae) from the Gulf of California. *The Veliger* 35(1):52-63
- Arthur, M. A., D. F. Williams and D.S. Jones. 1983. Seasonal temperature salinity changes and thermocline development in the mid-Atlantic Bight as recorded by the isotopic composition of bivalves. *Geology* 11:655-659
- Baqueiro, C. E., J. A. Masso, H. B. Guajardo. 1982. Distribución y abundancia de moluscos de importancia commercial en Baja California Sur, México. *Inst. Nal. De la Pesca, México, Serie de Divulgación*. 11:1-32
- Basurto, X. 2001. Community-Based Conservation of the *Callo de Hacha* fishery by the Comcáac Indians, Sonora, Mexico. Ms. Thesis. University of Arizona. Tucson, Arizona, U.S.A. 187 pp.
- Berg, C. J. and D. A. Olsen. 1989. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. In: J. F. Caddy, editor. *Marine invertebrate fisheries: their assessment and management*. U.S.A.: John Wiley and Sons. pp. 421-442.
- Breen, P. A. 1980. Measuring fishing intensity and annual production in the abalone fishery of British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* 947:1-49
- Cudney-Bueno, R. 2000. Management and conservation of benthic resources harvested by small-scale hookah divers in the northern Gulf of California, Mexico: the black

- murex snail fishery. Ms. Thesis. University of Arizona. Tucson, Arizona, U.S.A. 177 pp.
- Cudney-Bueno, R. 2007. Marine reserves, community-based management, and small-scale benthic fisheries in the Gulf of California, Mexico. PhD Dissertation. University of Arizona. Tucson, Arizona, U.S.A.
- Donkin, R. A. 1998. Beyond price: pearls and pearl fishing: origins to the age of discoveries. Philadelphia: American Philosophical Society. 448 pp.
- Dore, I. 1991. Shellfish: a guide to oysters, mussells, scallops, clams and similar products for the commercial user. New York, NY: Van Nostrand Reinhold. 240 pp.
- Goodwin, D. H., B. R. Schöne and D. L. Dettman. 2003. Resolution and fidelity of oxygen isotopes as paleotemperature proxies in bivalve mollusk shells: models and observations. *Palaios* 18:110-125.
- Goodwin, D. H., K. W. Flessa, B. R. Schöne and D. L. Dettman. 2001. Cross- calibration of daily growth increments, stable isotope variation, and temperature in the Gulf of California bivalve mollusk *Chione cortezi*: implications for paleoenvironmental analysis. *Palaios* 16:387-398.
- Grossman, E. L. and Teh-Lung Ku. 1986. Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effects. *Chemical Geology* 59: 59-74.
- Hobday, A. L., M. J. Tegner, and P. L. Haaker. 2001. Over-exploitation of a broadcast spawning invertebrate: decline of the white abalone. *Reviews in Fish Biology and Fisheries* 10:493-514.
- Hyman, L.H. 1967. The invertebrates: mollusca I. U.S.A.: McGraw-Hill. 792 pp.

- Jones, D. S. and I. R. Quitmyer. 1996. Marking time with bivalve shells: oxygen isotopes and season of annual increment formation. *Palaios* 11:340-346.
- Jones, D.S., D.F. Williams, and M.A. Arthur. 1983. Growth history and ecology of the Atlantic surf clam, *Spisula solidissima* (Dillwyn), as revealed by stable isotopes and annual shell increments. *J. Exp. Ma. Biol. Ecol.* 73:225-242.
- Karlson, R. H. and D. R. Levitan. 1990. Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. *Oecologia* 82:40-44.
- Keen, A. M. 1971. Sea shells of tropical West America. 2nd ed. Stanford, CA: Stanford University Press. 1064 pp.
- Kemp, P. and M. D. Bertness. 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proc. Natl. Acad. Sci.* 81:811-813.
- Krantz, D. E., D. F. Williams and D.S. Jones. 1987. Ecological and paleoenvironmental information using stable isotope profiles from living and fossil mollusks. *Palaeogeography, Palaeoclimatology, Palaeoecology* 58:249-266
- Norma Oficial Mexicana 1994. Determinación de las especies y subespecies de flora y fauna silvestre terrestres y acuáticas en peligro de extinción, amenazadas, raras y las sujetas a protección especial, y que establece especificaciones para su protección. NOM-059-ECOL-1994, *Diario Oficial de la Federación*, México, pp. 2-59
- Pillsbury, J. 1996. The thorny oyster and the origins of empire: implications of recently uncovered *Spondylus* imagery from Chan Chan, Perú. *Latin American Antiquity* 7(4): 313-340

- Poutiers, J. M. 1995. Moluscos. In: W. Fischer, F. Krupp, W. Schneider, C. Sommer, K. E. Carpenter, and V. H. Niem, editors. Guía FAO para la identificación de especies para los fines de la pesca: Pacífico Centro-Oriental Vol. 1: Invertebrados. Rome: Food and Agriculture Organization. 646 pp.
- Quinn, J.F., S.R. Wing, and L.W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Amer. Zool.* 33:537-550.
- Rowell, K., K. W. Flessa, D.L. Dettman, and M. Román. 2005. The importance of Colorado River flow to nursery habitats of the Gulf corvina (*Cynoscion othonopterus*). *Can. J. Fish. Aquat. Sci.* 62:2874-2885.
- Sandweiss, D. H. 1992. The archaeology of Chincha fishermen: specialization and status in Inka Perú. *Bulletin of Carnegie Museum of Natural History* 29 pp.
- Skoglund, C. and D. K. Mulliner. 1996. The genus *Spondylus* (Bivalvia: Spondylidae) of the Panamic Province. *The Festivus* 28(9):93-107
- Somerton, D. A. 1980. A computer technique for estimating the size of sexual maturity in crabs. *Can J. Fish. Aquat. Sci.* 47:1488-1494.
- Strathmann, M. F. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast: Data and methods for the study of eggs, embryos, and larvae. Seattle, WA: University of Washington Press. 670 pp.
- Villalejo-Fuerte, M. M. Arellano-Martinez, B. P. Ceballos-Vázquez, F. García-Domínguez. 2002. Reproductive cycle of *Spondylus calcifer* Carpenter, 1857

- (Bivalvia : Spondylidae) in the “Bahía de Loreto” National Park, Gulf of California, Mexico. *Journal of Shellfish Research* 21(1):103-108.
- Wefer, G. and J. S. Killingley. 1980. Growth histories of strombid snails from Bermuda recorded in their O-18 and C-13 Profiles. *Marine Biology* 60:129-135.

APPENDIX B
GROWTH, LONGEVITY, AND MORPHOLOGICAL VARIATIONS
OF THE BLACK MUREX SNAIL (*HEXAPLEX NIGRITUS*):
IMPLICATIONS FOR MANAGEMENT OF A RAPIDLY DECLINING FISHERY

Fishery Bulletin

Richard Cudney-Bueno^{*‡†} and Kirsten Rowell[§]

* Department of Natural Resources, School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA.

‡ Centro Intercultural de Estudios de Desiertos y Océanos (CEDO). Apartado Postal #53, Puerto Peñasco, Sonora, México.

§ Department of Biology, University of Washington, 528 Kincaid Hall, Box 351800, Seattle, WA 98115.

† To whom correspondence should be addressed: School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA email: cud@ag.arizona.edu, phone: 520-626-5607, fax: 520-621-8801.

Key words : Black murex, *Hexaplex nigritus*, muricidae, growth, oxygen isotopes, phenoplasticity, Gulf of California, fisheries.

Growth, Longevity, and Morphological Variations of the Black Murex Snail,

Hexaplex (Muricanthus) nigritus:

Implications for Management of a Rapidly Declining Fishery

Richard Cudney-Bueno and Kirsten Rowell

Abstract

We assessed longevity, seasonal growth variation, age of reproductive maturity, and geographic variations in morphology of the black murex snail, *Hexaplex (Muricanthus) nigritus*, in the northern Gulf of California, Mexico. Our methods relied on a combination of mark recapture, use of stable oxygen isotopes, and five years of field observations. Black murex reaches reproductive maturity between 2-3 years of age and has a life span of at least 8 years. Its growth is highest during the first year, reaching ~60 mm in total length, then slows down markedly after the first year. Growth is accelerated during the summer and fall and largely stunted during winter, particularly January-March. We found evidence of marked region-specific variations in the species' morphology. These variations affect fishing practices and have likely forced an artificial selection of stocks. We discuss our findings in the context of comparison of this species with other muricid snails and of the management implications and long-term viability of the fishery.

Introduction

The speed at which many invertebrate fisheries evolve often out-paces our knowledge of the species being harvested (Hobday et al. 2001). There are numerous examples of even large conspicuous marine mollusks that have been the target of a rapidly developed fishery lacking proper knowledge on the species' life history and subsequently leading to their rapid demise, from pearl industries worldwide (Donkin, 1998) to abalones (Caddy, 1989) and conch snails (Stoner et al., 1998). Addressing this lag in knowledge in marine invertebrate fisheries is of particular relevance today given increasing evidence of worldwide tendencies to fish down marine food webs (Pauly et al., 1998, Sala et al., 2004). In this paper, we describe basic demographic information for a heavily-exploited mollusk in the Gulf of California, Mexico the black murex snail, *Hexaplex (Muricanthus) nigritus*.

The black murex is a muricid gastropod endemic to the Gulf of California, Mexico ⁵ (Poutiers, 1995) that has been subject to intense fishing by commercial divers since the early 1990's largely for the Asian market (López-Reyes, 1992; Cudney-Bueno and Turk-Boyer, 1998). Historically, adult *H. nigritus* inhabited intertidal and subtidal waters (primarily sand and gravel substrate) up to 60 m deep (Poutiers, 1995; Brusca et al., 2004). Today, they are rarely found intertidally (Cudney-Bueno, 2007). Thus, fishing has turned to targeting their large-subtitle summer breeding aggregations. Targeting breeding aggregation has likely resulted in the observed declines in catch of ~ 88% (600-71 metric tons) in less than a decade (Cudney-Bueno, 2007). This rapid exploitation not

⁵ A few specimens have been reported from the Pacific coast in San Diego, California (Farmer, 1987; Trego, 1996). However, these rare sightings have been likely a result of anthropogenic introductions (Trego, 1996).

only may have consequences on the long-term viability of the fishery, but on the benthic ecosystem as well. Like other muricids, *H. nigritus* plays important ecological roles. It is a top predator of benthic communities (Paine, 1966), preying upon various species of mollusks (Keen, 1971; Brusca, 1973; Cudney-Bueno, 2007). Recent studies also suggest that black murex breeding aggregations act as living temporary reefs and refugia for numerous species of juvenile invertebrates, including other commercial species (Prescott and Cudney-Bueno, *in review*).

Given the fishery's susceptibility to rapid decline, it has been the object of community-based management efforts in the upper Gulf of California since 2001, including establishment of spatial and temporal harvest refugia (Cudney-Bueno, 2007). These efforts, however, need to be supported and complemented with information that can inform population demographic models and allow for a long-term assessment of the species' conservation status.

Despite the state of the resource, as well as its ecological and economic importance, our knowledge of the species is limited, in particular in terms of reproductive behavior and growth. Furthermore, given the phenotypic and ontogenic plasticity of mollusks (Kemp and Bertness, 1984; Jones, 1988), application of other species' life history information for management of black murex can be highly risky (see Radwin and D'Attilio, 1976; Hobday et al. 2001). This plasticity may also render a need for region-specific management schemes. For instance, fishers' local ecological knowledge suggests that there are marked regional variations in the morphology of black murex, variations

that may affect fishing patterns and market value of the species (Cudney-Bueno, 2000). These variations, however, have never been tested.

In this study we provide much needed life history information on the species' growth to better inform management decisions. We assess area-specific morphological variations, longevity, age at reproductive maturity, and seasonal growth variations of black murex in the northern Gulf of California, where most of the harvest takes place. We use both field and laboratory (stable oxygen isotopes) approaches, as well as five years of field observations. This study is part of a larger effort to define the life history and ecology of black murex (Cudney-Bueno, 2007; Prescott and Cudney-Bueno, *in review*) and to monitor the effects of established management guidelines (Cudney-Bueno, 2007). Our findings not only extend our knowledge of one of the most diverse families of mollusks, but also provide critical information for long-term management and conservation of the black murex fishery.

Materials and Methods

We collected snails from four fishing zones located off the coast of Puerto Peñasco, Sonora, Mexico, in the upper Gulf of California (Figure 1): La Cholla, Sandy Beach, Los Tanques-Conchas, and San Jorge Island. Fieldwork took place in years 1999-2001 and 2003-2004, between May and August. During this time, we participated in fishing trips with commercial divers and obtained random samples from their catches, totaling 792 snails from 20 distinct black murex breeding aggregations.

Shell morphology

We tested the null hypothesis that there are no variations in snail morphology between fishing zones. Testing this is of particular importance for management. Local fishers believe there are marked differences in morphology and in overall sizes and yield of snails between fishing zones, and this belief likely plays an important role in the spatial distribution of their fishing effort (Cudney-Bueno 2000). We sampled a minimum of 30 adults from each breeding aggregation. We recorded total length (TL, measured from apex to anterior tip of siphon canal), aperture length (AL, measured from tip of aperture notch to posterior tip of siphonal canal), and total wet weight (WW) (Figure 2). We calculated the length/weight and length/aperture ratios, and compared these ratios across zones using a one-way ANOVA and Tukey's HSD test. We then plotted TL by WW of all snails, obtained the best length-weight equation fit using regression models, and compared TL-WW and TL-AL relationships across the various zones using ANCOVA models. Prior to our analysis, we examined the data for homogeneity of variance, excessive skewness, and outliers. We applied log transformations ($\log_{10} X$) to improve homogeneity of variance.

Growth

We used two means to estimate growth: mark-recapture data and stable oxygen isotopes ratios. We marked 180 breeding adults from San Jorge Island in July 2003. We weighed each snail (wet weight, WW_1), and measured its total length (TL_1) and the distance from the tip of the marked spine to the tip of the newest spine (SL_1). We

attached stainless steel (0.5 cm) number tags to the largest spine on the second-to-last or third-to-last most posterior varix (thickness-dependent) of each snail. Tags were secured with zip ties that laced through a drilled hole on the spine. In July 2004, 32 of the 180 tagged snails were recaptured, weighed (WW_2), re-measured (TL_2), and any new varices were counted. We also measured whorl growth (WG), defined as the distance from the edge of the tip of the most posterior and last (newest) spine found in 2003 with the edge of the tip of the newest spine developed since snails were tagged (1 year whorl growth). We plotted the difference in total length ($\Delta TL = TL_2 - TL_1$), whorl growth ($\Delta WG = WG_2 - WG_1$) and weight ($\Delta W = W_2 - W_1$) and tested for variations in relation to TL_1 using regression models.

The daily deposition of shell material makes mollusk shells excellent biological recorders (Goodwin et al. 2001). The oxygen isotope ratio ($d^{18}O$) in their shells records the environmental conditions, such as temperature, during growing periods (Jones and Quitmyer, 1996, Goodwin et al. 2001). By coupling seasonal temperature and shell growth, we are able to validate annual growth and to back-calculate age of an individual. Variation in oxygen isotope ratios is inversely related to temperature. For every $\sim 4^\circ C$ increase in ambient water, there is a 1‰ decrease in shell $d^{18}O$ (Grossman and Ku, 1986). In marine gastropods, the oxygen isotope profile along the whorls (from the body whorl to the apex/protoconch) provides a seasonal time scale to measure rate of growth (Wefer and Killingley, 1980; Allmon et al., 1992). We use this valuable tool to reconstruct maximum age for black murex, since large individuals are now rarely found. We determine age and document growth using oxygen isotope profiles along the axis of

growth for two shells from La Cholla: Specimen Ch01 – one of the largest and heaviest specimen we found in 5 years of work, 180 mm TL - and specimen Ch02, the smallest reproductive individual we observed depositing an egg mass, 93 mm long.

Because black murex tend to be infested with calcareous epiphytes on the exterior portion of the shell, we cut both specimens in sections parallel to each whorl suture (perpendicular to growth increments) and sampled the shell between the exterior/exposed portion and the interior cavity of the snail. In a previous study (Todd-Pearson et al., 2005) of the larger specimen (Ch01), the last three varices of the body whorl were estimated to represent two years of growth. In this study, we obtained the remaining samples for Ch01 (Figure 3). Because much of the oldest portion of the shell was heavily burrowed and reworked, we were unable to sample the rest of this specimen. However, for the smaller individual (representing approximately the same size class for which we were unable to sample on Ch01), the entire shell was sampled, giving us a good estimate of growth during these earliest stages (Figure 4).

We obtained and analyzed all samples of shell material following well-established procedures (see Krantz et al., 1987; Jones and Quitmyer, 1996, Goodwin et al. 2001). Oxygen isotope ratios ($\delta^{18}\text{O}$) in carbonate values are expressed relative to the Vienna Pee Dee Belemnite (VPDB) standard. Shell carbonate was analyzed at the Stable Isotope Laboratory of the Department of Geosciences, University of Arizona, using a Finnigan MAT 252 mass spectrometer equipped with a Kiel-III automated carbonate sampling device. Standardization of oxygen isotope ratios was based on normalization to published ratios of NBS19 and NBS 18. Analytical error was ± 0.1 ‰.

We plotted the isotopic profiles of each snail in relation to distance from protoconch/apex (cm). Distance was measured between each sample and summed to get the accumulated growth of the snail. It should be noted that the distance from the protoconch associated with $d^{18}\text{O}$ values should not be confused with the total length measurement. We analyzed the $d^{18}\text{O}$ profiles for differences in growth between colder (winter-spring) and warmer (summer-fall) months. Using this method, little or no differences in seasonal growth are represented by a relatively consistent sinusoid curve, with crests mirroring valleys in length. Difference in growth between seasons are evident when sharp peaks in the crest or valley are present (Wefer and Killingley, 1980; Goodwin et al., 2001). These “peaks” represent slowed growth or a hiatus in growth (Goodwin et al., 2001).

Results

When pooling TL and WW measurement data of all reproductive snails sampled, we found a power equation fit for the increase of weight as a function of increased TL ($P < 0.0001$; $r^2 = 0.77$; $W = 0.0009 \times \text{TL}^{2.6721}$) (Figure 5). However, length-weight and length-aperture ratios varied between the various zones (TL/WW: $F_{3, 731} = 107.15$; $P < 0.0001$, 1-way ANOVA; TL/AL: $F_{3, 236} = 40.81$, $P < 0.0001$, 1-way ANOVA) (Table 1). In general, snails from Los Tanques-Conchas were markedly smaller than snails from all other areas. They also tended to have greater buildup of calcareous material, often covering the spines, making them duller and less conspicuous than snails from all other study areas. Snails from La Cholla and San Jorge, in contrast, tended to have thinner shells, even though, on average, the snails were considerably larger than those of Los

Tanques-Conchas. We also found marked differences among sites in the length-weight relationship (ANCOVA effect test for site $F_{3, 731} = 11.13$; $P < 0.0001$). However, we did not find any site differences in the length-aperture relationship (ANCOVA effect test for site $F_{3, 236} = 0.379$, $P = 0.768$).

Based on the recaptured individuals ($n = 30$), we found a significant relationship between snail size and growth rate of adult (reproductive) snails. Total length growth rate decreased as a function of increased snail size ($P = 0.0048$, $r^2 = 0.29$; $\Delta TL = -0.469 \times TL_1 + 70.446$). We observed a similar pattern for whorl growth (WG) ($P = 0.013$, $r^2 = 0.27$; $\Delta WG = -0.792 \times TL_1 + 122.17$) and wet weight gain ($P = 0.015$, $r^2 = 0.22$; $\Delta WW = -5.441 \times TL_1 + 836.08$) (Figure 6). Our data also showed considerable variation in 1 year TL growth, ranging between no growth to 29.6 mm. Similarly, ΔWG and ΔWW were also quite variable (0 to 34.6 mm and 0-340 g, respectively). Half of the snails ($n = 30$) added 1 spine/varice along the body whorl while the other 50% did not add any.

Isotope profiles of the small reproductive individual suggest that it was between 2-3 years old, with two distinct peaks (colder water temperatures) and valleys (warmer temperatures) and what appears to be the beginning of a third year of growth (Figure 7). The larger specimen had a similar seasonal growth pattern (Figure 7). The isotopic profile documents at least 3 years of growth and no more than 4. If we add this to the profile obtained by Todd-Pearson et al. (2005) (last three varices of body whorl), estimated to represent 2.5 years of growth, we can say with certainty that it took at least 5 years and no more than 6 for this specimen to complete its last body whorl. Although we were unable to sample the remainder of this large specimen (the spire), the width of that

section was roughly equivalent to that of the young reproductive individual we sampled. Given this, we estimate that the lifespan of a black murex is at least 8 years.

Discussion

We provide evidence of geographic variations in snail morphology. In biological terms, these variations could be attributed either to genetic differences (Gould, 1966) or to environmental influences acting on the phenotypic expression of the genotype (Kemp and Bertness, 1984). Although no genetic studies have been conducted on this species, it is very likely that black murex presents morphological plasticity that is environmentally mediated, as has been shown for other gastropods (Kemp and Bertness, 1984; Berg and Olsen, 1989; Stoner et al., 1998). For instance, maximum size of abalone is determined by both quantity and species composition of local food availability (Breen, 1980), and stunted individuals can retain the potential for adequate growth when moved to more favorable habitat (Breen, 1986). Similarly, shell variation among genetically undifferentiated gastropods can be a function of variations in snail growth rates predicted by differences in snail densities in a resource-limited environment (Kemp and Bertness, 1984). The consistently larger individuals in our study came from San Jorge Island and La Cholla, where we observed a high abundance and density of black murex prey species, such as mussels (*Modiolus capax*) and callista clams (*Megapitaria* spp.).

Some gastropods can also grow more rapidly in agitated water than in quiet water (Hyman, 1967). This is consistent with our findings. Both San Jorge Island and La Cholla experience intense daily tidal currents, whereas the currents of Lo s Tanques-Conchas,

where stunted individuals are found, are usually mild (Cudney-Bueno, 2007). These snails also tended to have more silt and calcareous deposits than other snails, and much of the characteristically irregular surface of the species was concealed by these deposits or worn out, suggesting older individuals.

Another explanation for some of these differences could involve differences in fishing pressure, with smaller individuals expected in heavily fished areas. However, this is unlikely since the area that has traditionally been fished the most, La Cholla, is one of the areas with larger snails (Cudney-Bueno, 2000). Our analyses also coincide with local knowledge regarding snail quality classification according to zone and size (Cudney-Bueno, 2000). This is not to suggest that fishing activity has had no effect on local populations. Fishers did mention that they have seen more “newer” snails in La Cholla than in previous years. “New” snails are those that have a thinner shell, are cleaner, and have less calcareous deposits. In addition, although all of the aggregations were found in subtidal waters, fishers mention they used to harvest murex intertidally during the lowest tides of spring (Cudney-Bueno, 2000). Poutiers (1995) also reports that murex can be found in intertidal waters; and Paine (1966) mentions black murex as an apex predator, together with *Heliaster kubiniji*, in the intertidal zone of the Upper Gulf. These accounts indicate that intense fishing in the 1990s could have removed older individuals from the commercial stock and over-harvested populations found closer to shore (Cudney-Bueno, 2007).

In terms of growth and longevity, we provide evidence that black murex can reach reproductive maturity between 2-3 years of age and can live for at least 8 years. Growth

in length is considerably slowed down after first reproduction, adding more shell thickness and overall body weight. Based on the relationship between size class and growth rate obtained from recaptured individuals, black murex from San Jorge Island grow rapidly during year one, approximately 60 mm in TL, and their growth slows down markedly after the second or third year, once they reach a length consistent with early reproductive maturity, approximately 85-95 mm (Cudney-Bueno, 2007). Although our recapture data were for individuals that ranged from 123.6 to 150 mm (mature individuals), limiting our predictions on growth of smaller individuals, estimates of growth are consistent with results obtained through our isotope data. These results are also similar to those reported for other large gastropods such as *Strombus gigas* and *Strombus costatus* (Wefer and Killingley, 1980). In contrast, pink murex (*Phyllonotus erythrostomus*) in the Gulf of California can reach sexual maturity in less than a year (Baqueiro et al., 1983).

The isotopic profiles of both specimens show differences in seasonal growth rates. The wide valleys indicate that that these snails grew rapidly during the warmer months (April-October), illustrated by more negative $\delta^{18}\text{O}$ values. The abrupt “peaks” suggest growth rate is reduced considerably during the colder months, with possibly no growth during the coldest months, January and February. This growth pattern is consistent with that reported by Todd-Pearson et al. (2005) and could be related to the species’ reproductive strategy and behavior in the months preceding and following reproduction. Black murex have distinct seasonal behavior centered around spawning. In March-May, before aggregation peaks, snails feed extensively on nearby mollusk beds and then cease

to feed while aggregated in the summer months (Cudney-Bueno, 2007), a behavior that has also been documented for other muricid snails (Tompa et al., 1984). At this time, much of the stored energy could be allocated to reproduction and growth. Immediately after aggregating, snails disperse and again feed, which also coincides with the time they appear to be growing most. As water temperatures become colder, snails stop feeding and between December and early March they tend to be buried in the sand (Cudney-Bueno, 2007), possibly accounting for the slowed to no growth in the cold months.

Management implications

Our findings have important implications for management of the black murex fishery. Length-weight ratios and shell variation likely forces artificial selection of harvestable stocks. Snail buyers in Puerto Peñasco have always avoided buying snails from Los Tanques because they obtain a much lower yield than snails from other zones, since the shell is much heavier in relation to the amount of meat they can commercialize (Cudney-Bueno, 2000). Given evidence of reproductive site fidelity for this species (Cudney-Bueno, 2007), it is possible that genetic structure exists and that fishing practices could be exerting more pressure on specific genetic stocks. An assessment of genetic structure within and between breeding aggregations should therefore soon be conducted.

We now know that black murex can reach sexual maturity in 2-3 years and it can live at least 8 years, therefore capable of reproducing a minimum of five times in its lifetime. This information is key for the development of future population viability

analyses of the species and stock recruitment models. Rapid early growth of black murex also offers an opportunity for detecting responses in stock recruitment soon after management and conservation actions. This is of particular importance for maintenance of cooperation of local stakeholders in management. Nevertheless, as pointed above, black murex growth is slower than that of the pink murex (*Phyllonotus erythrostomus*). To our knowledge, this is the closest taxonomic relative of black murex on which growth studies have been conducted in the Gulf of California. Our results therefore only corroborate the risks of using life history information of similar species as proxies for the development of management guidelines.

Finally, given the evidence of site-specific morphological variations, we caution the interpretation of our growth and longevity results beyond the areas of La Cholla and San Jorge island, where we obtained our specimens for this component of the analysis. Similar lengths do not necessarily imply similar ages, especially with larger individuals, as gastropods have a tendency towards determinate growth (Berg and Olsen, 1989). Further studies should address growth and age from other sites and areas in the Gulf of California and this information be incorporated to spatially-explicit management approaches.

Acknowledgements

We thank the divers of the Sociedad Cooperativa Buzos de Puerto Punta Peñasco for their friendship, unconditional support in the field, and their knowledge sharing. The Intercultural Center for the Study of Deserts and Oceans (CEDO) provided invaluable

logistical assistance and support throughout this study. Olegario Morales, Osvel Hinojosa, Jennifer Rupnow, and Rebecca Prescott collaborated in field and laboratory work. We thank Tiffany Ash-Cudney, who provided editorial comments and the black murex shell drawing. Isotopic lab assistance and space was kindly provided by Drs. Karl W. Flessa and David L. Dettman, of the Stable Isotope Laboratory of the Geosciences Department at the University of Arizona. This study was conducted via financial contributions from the Tinker Foundation, the David and Lucile Packard Foundation, as well as fellowships and scholarships to Cudney-Bueno from the Consejo Nacional de Ciencia y Tecnología (CONACYT), the Inter American Foundation, the Wallace Research Foundation, and the Environmental Leadership Program. Research was conducted under permit # DGOPA.04693.150506.1832 from the *Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación* (SAGARPA) of Mexico. This is contribution # 3 of Project PANGAS, www.pangas.arizona.edu.

Literature cited

Allmon, W. D., D. S. Jones and N. Vaughan.

1992. Observations on the biology of *Turritella gonostoma* Valenciennes (Prosobranchia: Turritellidae) from the Gulf of California. *The Veliger* 35(1):52-63.

Baqueiro, E., J. A. Massó, A. Vélez.

1983. Crecimiento y reproducción de una población de caracol chino *Hexaplex erythrostomus* (Swainson, 1831), de Bahía Concepción, B.C.S. *Ciencia Pesquera* (4):19-31.

Berg, C. J. and D. A. Olsen.

1989. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. *In* Marine invertebrate fisheries: their assessment and management (Caddy, J.F., ed.) 421-442 p. John Wiley and Sons. U.S.A.

Breen, P. A.

1980. Measuring fishing intensity and annual production in the abalone fishery of British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* 947:1-49.

Breen, P. A.

1986. Management of the British Columbia fishery for northern abalone (*Haliotis kamtschatkan*). *Can. Tech. Rep. Fish. Aquat. Sci.* 92:300.

Brusca, R. C., E. Kimrey, and W. Moore.

2004. A seashore guide to the northern Gulf of California, 203 p. Arizona-Sonora Desert Museum, Tucson, Arizona, U.S.A.

Brusca, R. C.

1973. A handbook to the common intertidal invertebrates of the Gulf of California, 427 p. The University of Arizona Press, Tucson, Arizona, U.S.A.

Caddy, J. F.

1989. Marine invertebrate fisheries: their assessment and management, 752 p. John Wiley and Sons, U.S.A.

Cudney-Bueno R. and P. J. Turk-Boyer.

1998. Pescando entre mareas del alto Golfo de California: una guía sobre la pesca artesanal, su gente, y sus propuestas de manejo, 166 p. Technical Series # 1. CEDO-Intercultural, Puerto Peñasco, Sonora, México.

Cudney-Bueno, R.

2000. Management and conservation of benthic resources harvested by small-scale hookah divers in the northern Gulf of California, Mexico: the black murex snail fishery. M.Sc. thesis, 177 p. Univ. Arizona, Tucson, AZ.

Cudney-Bueno, R.

2007. Marine reserves, community based management, and small-scale benthic fisheries in the Gulf of California, Mexico. PhD diss., 301 p. Univ. Arizona, Tucson, AZ.

Donkin, R. A.

1998. Beyond price: pearls and pearl fishing: origins to the age of discoveries, 448 p. American Philosophical Society, Philadelphia, U.S.A.

Farmer, W. M.

1987. The black murex, *Muricanthus nigrinus*, from Bird Rock, La Jolla, California: fact or fiction? *The Festivus* 19(5):42.

Gould, S. J.

1966. Allometry in Pleistocene land snails from Bermuda: the influence of size upon shape. *J. Paleontol* 40:1131-1141.

Goodwin, D. H., K. Flessa, B.R. Schöne and D.L. Dettman.

2001. Cross-calibration of daily growth increments, stable isotope variation, and temperature in the Gulf of California bivalve mollusk *Chione cortezi*: Implications for paleoenvironmental analysis. *Palaios* 16:387-398.

Grossman, E.L. and L.T. Ku.

1986. Oxygen and carbon fractionation in biogenic aragonite: temperature effects. *Chemical Geology* 59:59-74.

Hobday, A.L., M.J. Tegner and P.L. Haaker.

2001. Over-exploitation of a broadcast spawning invertebrate: decline of the white abalone. *Reviews in Fish Biology and Fisheries* 10:493-514.

Hyman, L. H.

1967. *The invertebrates: Mollusca I*, 792 p. McGraw-Hill, U.S.A.

Jones, D. S.

1988. Schlerochronology and the size versus age problem. *In Heterochrony in evolution: a multidisciplinary approach* (McKinney, M.L., ed.) 348 p. Plenum Press, NY.

Jones, D. S. and I. R. Quitmyer.

1996. Marking time with bivalve shells: oxygen isotopes and season of annual increment formation. *Palaios* 11:340-346.

Keen, A. M.

1971. Sea shells of tropical West America, 1064 p. 2nd ed. Stanford University Press, Stanford, CA.

Kemp, P. and M. D. Bertness.

1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proc. Natl. Acad. Sci.* 81:811-813.

Krantz, D. E., D. F. Williams and D. S. Jones.

1987. Ecological and paleoenvironmental information using stable isotope profiles from living and fossil mollusks. *Palaeogeog. Palaeoclim. Palaeoecol.* 58:249-266.

López-Reyes, E.

1992. Análisis y diagnóstico de la pesquería del caracol chino *Muricanthus nigrinus* y *Hexaplex erithrostomus* en Bahía la Choya, Sonora: pregunta problema para obtener el título de Oceanólogo, 29 p. Universidad Autónoma de Baja California. Ensenada, Baja California, México.

Paine, R.

1966. Food web complexity and species diversity. *Amer. Nat.* 100:65-75.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese and F. Torres.

1998. Fishing down marine food webs. *Science* 279:860-863.

Poutiers, J. M.

1995. Moluscos *In* Guía FAO para la identificación de especies para los fines de la pesca: Pacífico Centro-Oriental: invertebrados (Fischer, W., F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter, and V.H. Niem, eds.) 646 p. Food and Agriculture Organization, Rome, Italy.

Prescott, R. and R. Cudney-Bueno.

In review. Living reefs in the upper Gulf of California: aggregations of Black Murex snails (*Hexaplex nigritus*) as habitat for juvenile and adult invertebrates. Marine Ecology Progress Series.

Radwin, G. E. and A. D'Attilio.

1976. Murex shells of the world, 284 p. Stanford University Press Stanford, CA.

Sala, E., O. Aburto-Oropeza, M. Reza, G. Paredes, and L. López-Lemus.

2004. Fishing down coastal food webs in the Gulf of California. *Fisheries* 29(3):19-25.

Stoner, A. W., M. Ray-Culp, and S. M. O'Connell.

1998. Settlement and recruitment of queen conch, *Strombus gigas*, in seagrass meadows: associations with habitat and micropredators. *Fish. Bull.* 96:885-899.

Todd-Pearson, S., K. W. Flessa, R. Cudney-Bueno, D. L. Dettman, and K. Rowell.

2005. Stable isotope variation in black murex shells, Gulf of California, Mexico: rapid assessment of growth rates for community-based fishery management. Book of Abstracts, 19th Annual Meeting of the Society for Conservation Biology, 245 p. Brasilia, Brasil.

Tompa, A. S., N. H. Verdonk, and J. A. M. Van Den Biggelaar.

1984. *The Mollusca: reproduction*, 486 p. Academic Press, Orlando, FL.

Trego, K. D.

1996. A second record of the muricid *Hexaplex nigrinus* (Gastropoda: Muricidae) at Bird Rock, La Jolla, California. *The Festivus* 28(4):46-47.

Wefer, G. and J. S. Killingley.

1980. Growth histories of strombid snails from Bermuda recorded in their O-18 and C-13 Profiles. *Mar. Biol.* 60:129-135.

Figures and Tables

Figure B1. Study area and collecting sites of black murex (*Hexaplex (Muricanthus) nigritus*) breeding aggregations in the upper Gulf of California, Mexico.

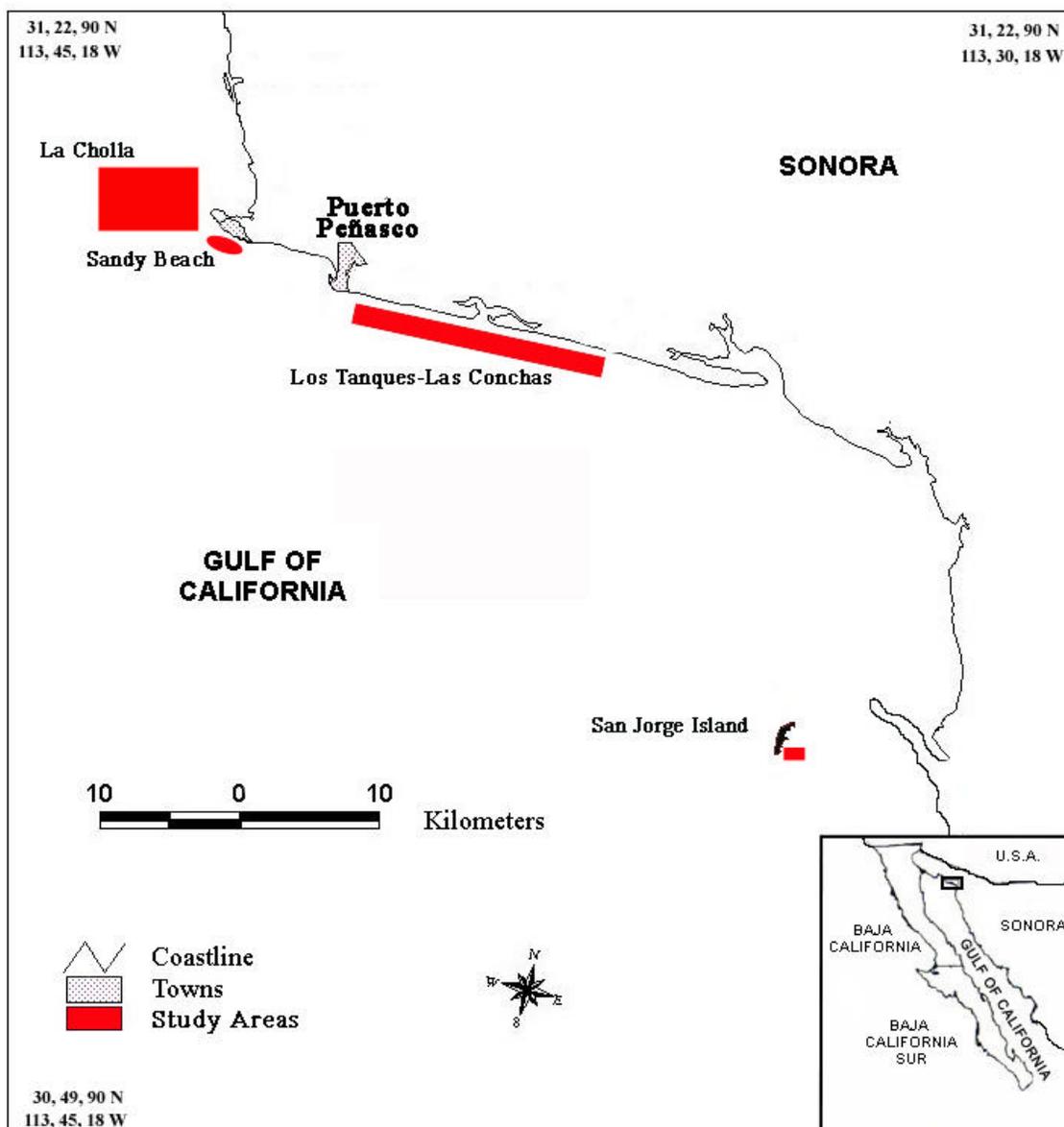


Figure B2. Schematic representation of black murex morphological nomenclature and measurements taken.

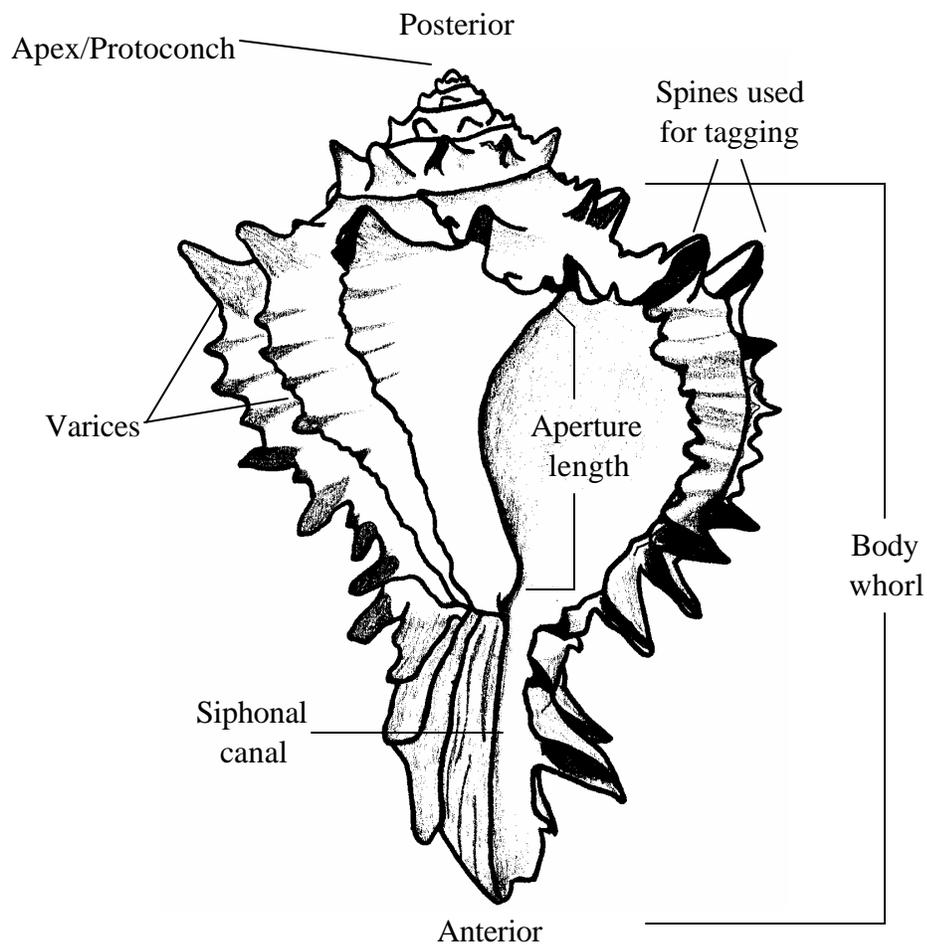


Figure B3. Cross section of body whorl of the largest black murex specimen sampled for oxygen isotope analyses (specimen Ch01). Carbonate samples points taken along the whorl can be seen as small drill holes. The arrows indicate the direction of growth and area sampled in this study. The last three varices (35 samples) were sampled in a previous study (Todd-Pearson et al. 2005). Scale units in centimeters.

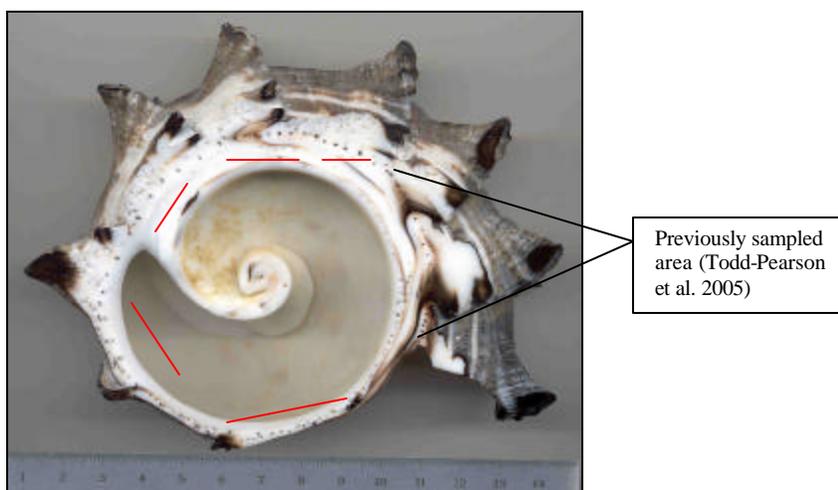


Figure B4. Cross sections and protoconch of youngest black murex specimen sampled for oxygen isotope analysis (specimen Ch02), with “A” being most recent whorl (body whorl), “B” second whorl, “C” last (oldest) whorl, and “D” protoconch. Shell material sampling points marked in black. Scale units in centimeters.

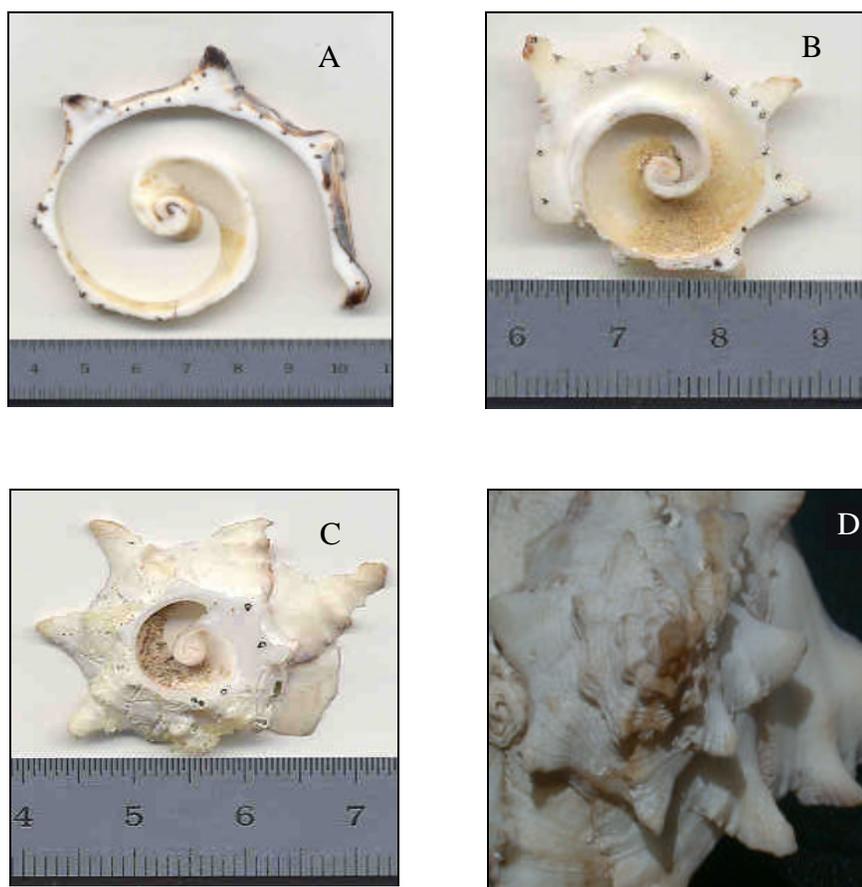


Figure B5. Length-weight relationship of black murex snails (*Hexaplex (Muricanthus) nigritus*) from four areas in the upper Gulf of California, Mexico.

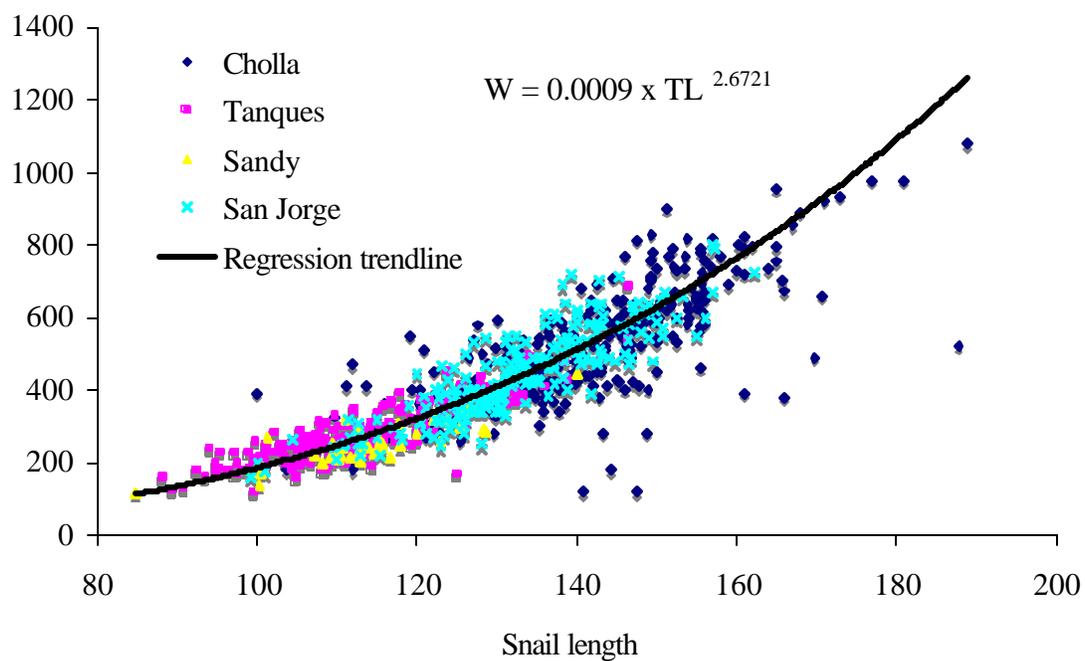


Figure B6. Relationship between snail size and one year growth in total length (A) and whorl (B) of black murex snail, *Hexaplex (Muricanthus) nigritus*, in the upper Gulf of California, Mexico.

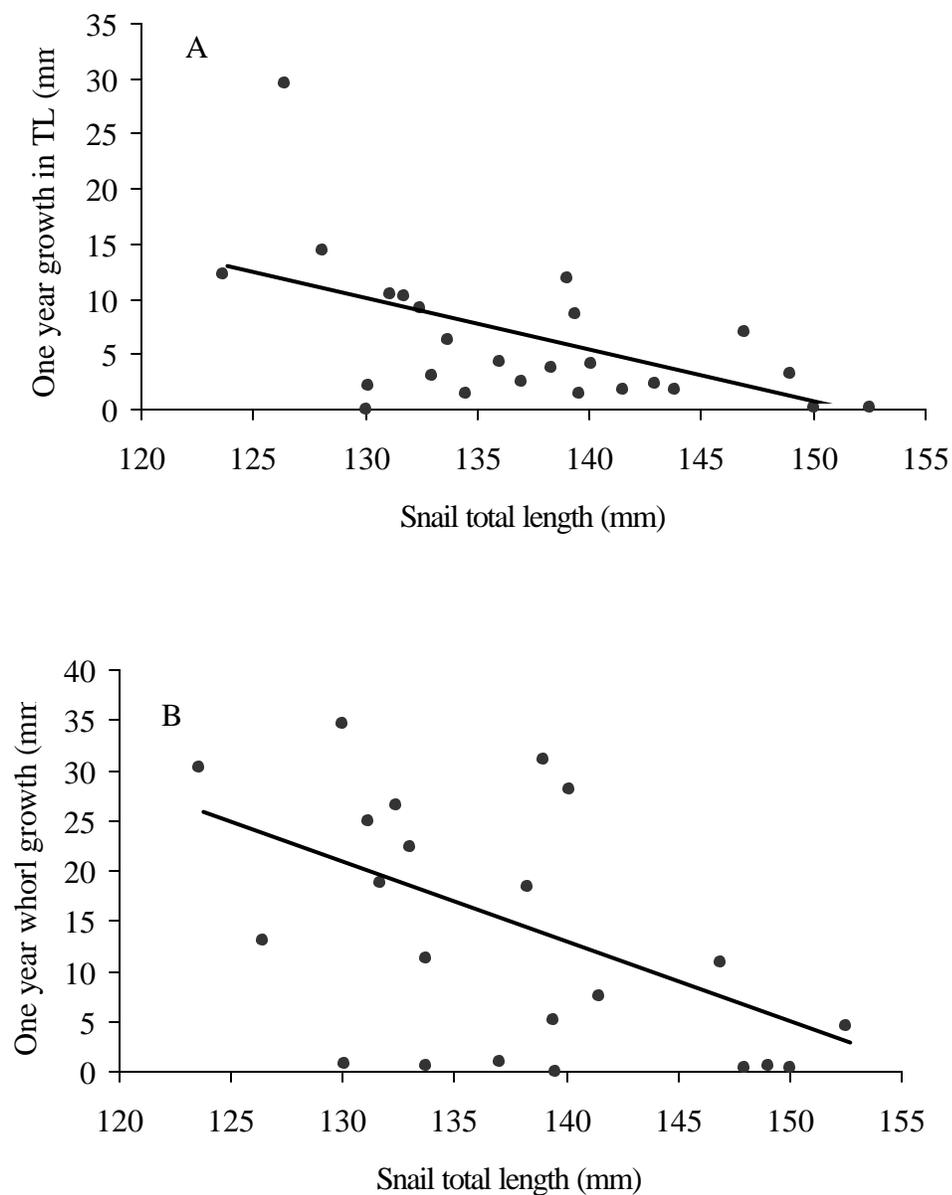


Figure B7. $\delta^{18}\text{O}$ VPBD profiles from *Hexaplex (Muricanthus) nigritus* shells, collected from La Cholla, upper Gulf of California, Mexico. Negative $\delta^{18}\text{O}$ values represent warmer temperatures (shaded area). Distance (cm) is measured from protoconch to outer lip for specimen Ch02 (small reproductive individual) and from the point that is the equivalent size (~25cm whorl length) of specimen Ch01 (largest specimen) toward the lip. In addition, Todd-Pearson et al. (2005) determined that there are two and a half years of growth represented in the last three varices of specimen Ch01 (not shown here).

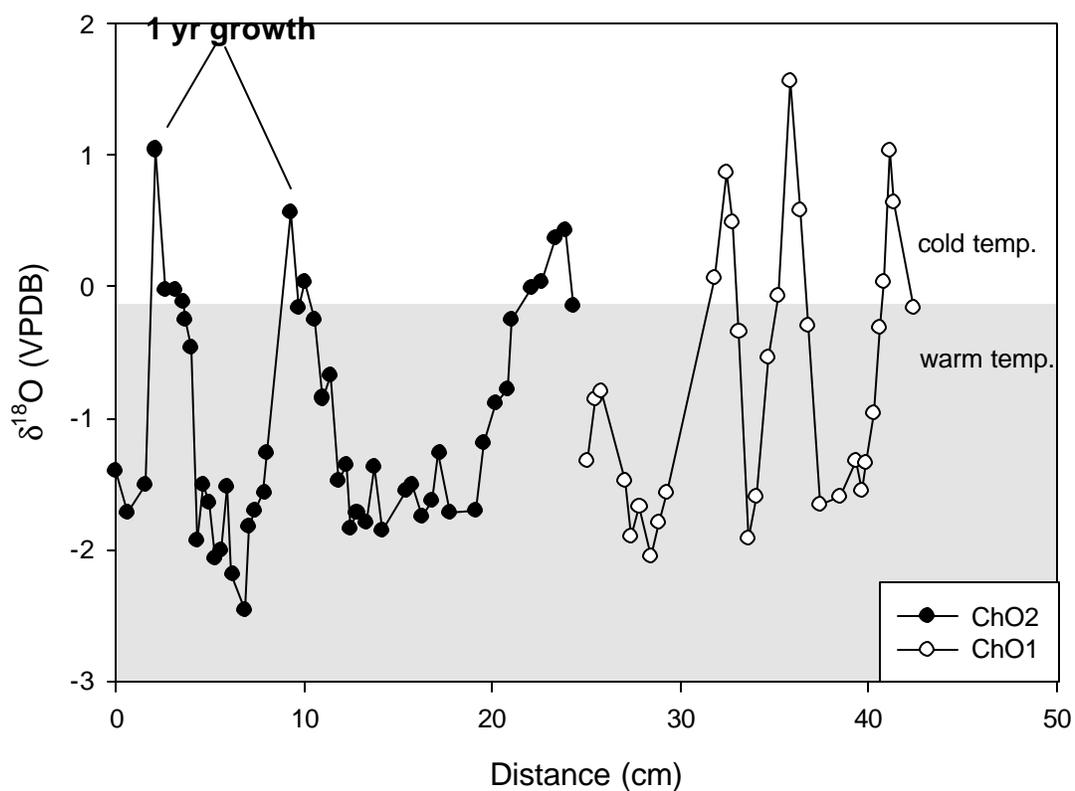


Table B1. Length/weight and length/aperture ratios and mean length and weight of reproductive black murex snails found in four areas of the upper Gulf of California, Mexico.

Zone	<i>n</i> TL/WW	Mean TL/WW (95% C.I.)	<i>n</i> TL/AL	Mean TL/AL (95% C.I.)	<i>n</i> TL	Mean TL (95% C.I.)	<i>n</i> WW	Mean WW (95% C.I.)
Cholla	283	0.29 (0.28,0.30)	95	0.50 (0.49,0.50)	283	142.14 (140.7,143.5)	283	533.0 (517.8,548.1)
Sandy Beach	40	0.47 (0.44,0.50)	40	0.47 (0.46,0.48)	40	114.17 (110.4,117.9)	40	250.12 (209.8,290.4)
Los Tanques - Conchas	183	0.42 (0.41,0.43)	72	0.46 (0.45,0.46)	198	112.95 (111.2,114.6)	183	280.53 (261.6,299.3)
San Jorge Island	226	0.31 (0.30,0.32)	31	0.52 (0.50,0.52)	271	133.48 (132.0,134.9)	226	451.49 (434.5,468.4)

APPENDIX C
BREEDING AGGREGATIONS AND REPRODUCTIVE ECOLOGY
OF THE BLACK MUREX SNAIL (*HEXAPLEX NIGRITUS*)
IN THE NORTHERN GULF OF CALIFORNIA, MEXICO

Marine Biology

Richard Cudney-Bueno^{*†‡}, Rebecca Prescott^{*}

* Department of Natural Resources, School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA.

‡ Centro Intercultural de Estudios de Desiertos y Océanos (CEDO). Apartado Postal #53, Puerto Peñasco, Sonora, México.

† Corresponding author: School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA email: cud@ag.arizona.edu, phone: 520-626-5607, fax: 520-621-8801.

Key words : Black murex, *Hexaplex nigritus*, muricidae, reproductive ecology, breeding aggregations, Gulf of California, fisheries.

**Breeding Aggregations and Reproductive Ecology of the Black Murex Snail,
Hexaplex nigritus (Philippi, 1845), in the Northern Gulf of California, Mexico**

Richard Cudney-Bueno and Rebecca Prescott

Abstract

We studied the reproductive ecology and behavior of the black murex snail, (*Hexaplex nigritus* = *Muricanthus nigritus*), a heavily harvested species endemic to the Gulf of California, Mexico. Specifically, we examined formation and habitat of breeding aggregations, sex ratios, egg laying and hatching, fidelity to reproductive sites, and snail behavior before, during, and after the formation of breeding aggregations. We relied on both fishery independent and fishery dependent data, studying 42 breeding aggregations and fishers' catches between summer 1999 and 2004. We found that the black murex is dioecious and highly gregarious, forming large breeding aggregations in subtidal waters between April and September when water temperatures range from 22° C to 31° C. The largest aggregation we observed was 900 m² and provided a catch of 3 metric tons. However, 60% of aggregations were between 100-200 m². We determined that sex ratios in aggregations were 1:1 and snails laid egg masses primarily on the shells of both male and female conspecifics. Egg masses on any one snail could be from multiple females and contain > 1000 capsules, but the average number of egg capsules/snail varied between 230-350. Eggs incubate in capsules between 18-31 days, at which time they hatch as veliger larvae (mean = 3,603; 95% CI 3,382-3,825 larvae per capsule). Seventy-four percent of aggregations formed adjacent to or within 25 m of a rocky, coquina

(beach rock) or mussel bed reef. During winter, snails tended to bury in the sand and emerge in early spring to feed. While aggregated, all snails ceased feeding but fed prior and after aggregating. We found evidence of fidelity to reproductive sites, as breeding aggregations with marked individuals formed on or near (<10 m) sites used the preceding year. The species' aggregating behavior has facilitated development of fishing practices that remove much of the reproductive biomass by targeting aggregation areas repeatedly. We discuss the implications of our findings for management and conservation of the black murex fishery.

Introduction

The black murex (*Hexaplex nigritus* = *Muricanthus nigritus*) is a muricid gastropod endemic to the Gulf of California, Mexico (Poutiers 1995) that has been subject to intense fishing since the early 1990's (López-Reyes 1992, Cudney-Bueno and Turk-Boyer 1998). Adults are found in intertidal and subtidal waters living primarily on sand and gravel bottoms in waters up to 60 m deep (Poutiers 1995, Brusca et al. 2004). Like other muricids, *H. nigritus* is a predator occupying an important niche in food webs of subtidal benthic communities (Paine 1966), preying upon various species of mollusks (Keen 1971, Brusca 1973).

The first written description of the reproductive behavior of *H. nigritus* was that of Barber (1961), who observed spawning in the northern Gulf of California in early August and suggested a communal event including deposition of egg capsules on conspecific shells. Based on morphological characteristics of capsules, D'Asaro (1991) also suggested the hatching of embryos as planktotrophic veliger larvae.

Other than these brief findings, there have been no other published studies conducted on the reproductive biology and ecology of the black murex that we are aware of. However, a better understanding of its reproductive life history is needed as the species has been heavily fished during reproduction and is showing signs of a rapid decline (Cudney-Bueno 2007). Furthermore, given the phenotypic and ontogenic plasticity of mollusks (Kemp and Bertness 1983, Jones 1988), extrapolation of data from other similar species even within the same genera is risky (Radwin and D'Attilio 1976), particularly if we want to establish appropriate management and conservation guidelines.

In this paper, we identify key aspects of the reproductive ecology and behavior of black murex based on five years of field and laboratory research. Specifically, we describe 1) formation and habitat of breeding aggregations, 2) sex ratios of breeding aggregations, 3) egg laying and hatching, 4) reproductive output of individuals, and 5) site fidelity of aggregations. We also describe behavior of snails before and after reproduction and aggregation formation. These findings not only extend our knowledge of one of the most diverse families of mollusks, but also provide information critical for management of the black murex fishery in the Gulf of California.

Methods

Study Site

Between 1999 and 2004, we completed fieldwork from May to October near Puerto Peñasco, Sonora, Mexico, one of the largest fishing enterprises for Black Murex snails in the Gulf of California. We collected data on aggregations within four distinct fishing zones located near Puerto Peñasco: La Cholla, Sandy Beach, Los Tanques-Conchas, and San Jorge Island (Figure 1).

Formation of Breeding Aggregations and Site Fidelity Assessment

We participated in 53 fishing trips during snail fishing season (May-August), to assess 1) timing, location, size of breeding aggregations, and habitat where aggregations were formed, and 2) fidelity to reproductive sites and snail behavior before, during, and after the formation of breeding aggregations. During these trips, we dove with fishers

until an aggregation was found. We defined an aggregation as a group of at least 10 snails in close proximity, engaged in reproductive behavior, and separated by at least 10 m from another aggregation. Once found, we recorded depth, temperature, and approximated the size of the aggregation by measuring its width and length. We also qualitatively described the habitat where the aggregation was found and swam around the aggregation up to 25 m away to search for non-aggregated snails.

To assess snail fidelity to reproductive sites and behavior before, during, and after reproduction, in summer 2000 we set a colored concrete block in the center of three breeding aggregations (one each from Los Tanques-Conchas, Sandy Beach, and San Jorge Island), and color-marked between 50-100 snails from each aggregation. We returned to these sites in summer 2001, 2002, and 2003 to see if aggregations had formed near blocks, and we searched for marked snails within a 20 m radius. In addition, in 2001 we worked with local fishers to set aside a temporary refuge around San Jorge Island, allowing us to follow the entire formation of breeding aggregations without the disturbance of fishing activities. We marked 180 breeding adults from San Jorge Island in July 2003, attaching circular (0.5 cm) number tags of stainless steel to the largest spine on the second-to-last or third-to-last most posterior varix (thickness-dependent). Tags were secured to snails with zip ties that laced through a drilled hole on the spine. We took mass and length measurements of each snail and returned the snails to the breeding aggregation. We returned to this site every two months for one year after the snails were tagged. During each visit, we swam around the concrete block at 5, 10, 15, and 20 m intervals and counted the number of snails, noted whether they were feeding, mating, or

buried in the sand, their direction of movement (moving away/towards the concrete block), and registered the number of tagged snails.

Sex Ratio of Breeding Aggregations

We obtained a random sample from two breeding aggregations at La Cholla: June, 1999 (n = 36 snails) and July, 1999 (n = 32 snails). We returned snails to a local laboratory, sexed each individual snail, and evaluated the sex ratio of both samples using a Pearson χ^2 test.

Egg Laying and Hatching

We maintained 47 live snails in aquaria from mid-June to mid-August, 1999, feeding them live clams (*Chione* sp.) and mussels (*Modiolus capax*). We placed between 5-10 snails in 75-L and 189-L aquariums filled with seawater and maintained ambient water temperature and salinity levels (28.0-29.0°C and 37-38 ‰ respectively).

We recorded behavior of snails throughout these two months. When egg-laying occurred, we recorded laying time and counted the total number of egg capsules laid. We defined successful egg-laying as a snail laying an egg mass of >10 capsules with \leq 24 hr interruption between each capsule laid.

To assess egg laying and reproductive output in the natural environment, we took random samples of snails from divers' catches at the beginning and end of the 1999 fishing season. We ensured each sample came from one breeding aggregation only by participating in the fishing trip and collecting the sample once the aggregation was found.

We assessed if there was any variation in number of capsules laid on aggregated snails through time and if there was any relationship between sex and the presence or absence of egg capsules on snails. Samples contained snails with and without egg cases. For snails with egg cases, we counted all capsules on each snail and then compared the mean number of capsules/snail for La Cholla (three sample periods, June 6 n = 24, June 23 n = 19, and July 10 n = 19, 1999) and Los Tanques-Conchas (two sample periods, June 14 n = 21, and July 14 n = 61, 1999). For Los Tanques-Conchas, we used a Student's t-test to compare the mean number of egg capsules/snail between both sample periods. For La Cholla samples, we analyzed the data using a 1-way ANOVA and performed a Tukey's HSD multiple comparison test to determine pairwise relationships.

We assessed if there was any effect of the sex of snails on deposition of egg capsules. For this, we analyzed the same snails that were used to assess sex ratios of breeding aggregations by registering presence and absence of egg capsules on male and female snails. We calculated percentage of presence/absence of egg clutches for males and females and tested both sexes for marginal homogeneity with a Pearson χ^2 test.

We determined if egg capsules were laid on substrates other than snails. We searched for other substrates with egg capsules within 25 m of the perimeters of the aggregations. We also dove along the border of the Las Conchas rocky reefs and around San Jorge Island, covering a combined transect approximately 6 km long, and consulted key fishers regarding past and/or present experiences of finding egg masses on substrates other than snails.

Finally, we monitored egg masses laid in the aquariums throughout their development until individual capsules began hatching. We recorded the incubation time, defined as days of incubation from the first day a snail began laying an egg mass to the first hatching day. To determine the developmental stage at which offspring hatch from the capsules, we maintained 30 ready-to-hatch capsules in small 20-ml vials with seawater at 28.0-29.0°C; 37-38 ‰. Once hatched, we took a 1-ml sample and observed the embryos under a 10x dissecting microscope.

Determining Reproductive Output

To address reproductive output, we determined: 1) the relationship between egg capsule length and number of offspring produced, and 2) the relationship between snail length and capsule length. We collected ready-to-hatch individual egg capsules ($n = 454$) from La Cholla ($n = 131$, yrs. 1999, 2003, 2004), Las Conchas ($n = 107$, yrs. 2003, 2004), Los Tanques ($n = 136$, yrs. 1999, 2003), and San Jorge Island ($n = 81$, yrs. 2003, 2004). We collected each capsule from individual snails found within a given aggregation as separate as possible from each other to minimize the possibility of repeatedly obtaining egg capsules laid by the same snail. We measured the length and width of each capsule. Length of capsule was defined as the distance between the basal membrane and the apical plate with an escape aperture, and width was defined as the greatest dimension at right angles to length (D'Asaro 1970, 1986) (Figure 2). After measuring the capsule, we cut it open and emptied its contents into a small vial with seawater, assuring a total water level of 10 ml. Immediately after stirring, we took a 1 ml sample from the middle of the water

column and counted the embryos under a 10x dissecting microscope. We used a 1:10 conversion to calculate the number of embryos contained in each capsule and tested the null hypothesis that there is no relationship between capsule size and number of larvae using linear regression.

To assess if there was any relationship between snail length and capsule length, we collected 84 snails from three aggregations (La Cholla $n = 30$, San Jorge Island $n = 24$, Las Conchas $n = 30$) and 2 egg capsules from each snail as they were laid. We measured snail total length (TL) as well as length of each pair of capsules, obtaining an average capsule length for each snail. We used linear regression to test for the null hypothesis that there is no relationship between snail and capsule size.

Results

Formation of Breeding Aggregations and Site Fidelity

Breeding aggregations formed from early April through September. Between April-June aggregations were usually found closer to shore in shallow waters (= 15 m deep). We located aggregations in waters with temperatures of 22°C - 31°C and depths of 4 m - 25 m. In San Jorge Island, where we observed a breeding aggregation site for an entire year, an aggregation of 120 m² formed and dispersed completely in a period of 40 days. Breeding snails did not feed, but in the months immediately preceding (April-May) and following the formation of the aggregation (September-November), snails preyed primarily on mussels (*Modiolus capax*) from an adjacent mussel bed, leaving conspicuous trails of open shells. As the water temperature dropped, it became

increasingly difficult to locate snails, and those found were usually buried, exposing only part of their spines.

The largest aggregation was found in La Cholla. It covered an area of approximately 900 m² and provided a total fishing catch of 3 metric tons. However, the majority of aggregations (60%) were between 100-200 m².

Of the 42 aggregations found, 30 were located within the fishing area of La Cholla. In addition, 78.5% of aggregations formed on top of substrates comprised primarily of broken and complete mollusk shells, rhodoliths and other encrusting coralline algae, and large grain sand (Figure 3). All others were located on sandy bottoms and 73.8% were found in areas adjacent or within 25 m of a rocky, coquina (beach rock) or mussel bed reef. Towards the end of the breeding season (July-September) aggregations of another muricid snail, the pink murex (*Phylonotus erythrostomus*), were found adjacent and sometimes intermingled with those of black murex. Contrary to the black murex aggregations which are extended in area yet only comprise one layer of individuals, pink murex aggregations consisted of large mounds, up to 2.5 m tall and 15 m in circumference, covering one single colonial egg mass.

Of the 180 snails tagged in San Jorge Island in summer 2003, we recovered 31 in summer 2004, and all were aggregated within 10 m of the original aggregation location. We did not find tagged snails in another aggregation located 35 m away. Similarly, for the three consecutive years that we monitored the breeding aggregation sites in Sandy Beach, Los Tanques-Conchas, and San Jorge marked in 2000, we observed aggregations forming on or within 10 m of locations used in previous years. We also found marked

snails in these aggregations after the first year they were marked, with a maximum recapture success of 22% at San Jorge Island and a minimum of 10% at Sandy Beach.

Sex Ratios of Breeding Aggregations

The percentages of male and female snails was 56%:44% respectively for the first sample period (n = 36, La Cholla, June 23 1999) and 50%:50% for the second sample period (n = 32, La Cholla, July 5 1999). The percentage of males and females of both samples combined was 53%:47%. We found no significant differences to the expected 1:1 ratio when comparing sex distributions of both sample periods ($\chi^2 = 0.21$, $P = 0.646$).

Egg Laying and Hatching

Nine snails held in aquaria laid ten egg masses. The number of capsules per egg mass varied from 27 to 337 ($\bar{x} = 137$, 95% CI = 66, 208). The number of capsules laid per day per snail also varied from 5 to 87 ($\bar{x} = 20$, 95% CI = 10, 41) (Table 1).

Incubation time for snails maintained in aquaria ranged from 18 to 31 days ($\bar{x} = 23$, 95% CI = 19, 27) (Table 1) and all capsules released veliger larvae (Figure 3).

Eight egg masses were laid on the glass surface of the aquariums (Figure 3), and two on top of other snails. At least nine other laying attempts were made. However, we did not consider these since the number of capsules laid was less than 10, our chosen standard. Subtidal scuba observations revealed the presence of 45 egg masses laid on substrates other than conspecific snails, including loose shells of clams and other snails,

small granite boulders, some crevices within coquina reefs, and our three permanent concrete marking blocks.

We found no differences when comparing the mean number of capsules/snail for the three sample periods of La Cholla ($F_{2,57} = 1.7$, $P = 0.191$; 1-way ANOVA after square root transformation). For this zone, the mean number of capsules on individual snails was 285 ($n = 62$, 95% CI = 228, 342). Similarly, mean number of capsules/snail did not differ for the two sample periods from Los Tanques ($t = -0.89$, two-sided $P = 0.37$). Here, the mean number of capsules on individual snails was 421 ($n = 82$, 95% CI = 355, 487). However, both La Cholla and Los Tanques samples contained snails carrying more than 1000 capsules (Figure 3). When analyzing the two samples from La Cholla collected on June 26 and July 5 1999 ($n = 68$ combined), both male and female snails carried egg cases. The percentage of male and female snails with egg cases was similar, 63.89% and 65.63% respectively ($\chi^2 = 0.022$, $P = 0.881$).

It was common to find snails within one aggregation with most of their egg capsules hatched and others with the majority of the capsules recently laid. Likewise, individual snails often had a patch or patches of hatched capsules and others of recently laid capsules. These patches could easily be identified at a glance by a variation in color, structure, and/or size of the capsules, with some snails having up to four of these patches (Figure 3).

Reproductive Output

We found a strong relationship between capsule size and number of larvae present in the capsule ($F_{1,455} = 85.87$, $P < 0.0001$ simple linear regression) (Figure 4). The number of larvae/capsule for capsules collected in the four study sites ($n = 456$) varied considerably, from 150 (capsule length = 15 mm) to 20,189 (capsule length = 21.84 mm). The mean number of larvae/capsule was 3,603 (95% CI = 3,382-3,825). As with the number of larvae, we also found a marked relationship between snail length and capsule length ($F_{1,81} = 123.41$, $P < 0.0001$, simple linear regression) (Figure 5).

Other Observations: Feeding and Predation

Diet of black murex varied markedly depending on the area where the snails were found. We observed black murex preying on at least 10 species of mollusks, usually mussels (*Modiolus capax*), callista clams (*Megapitaria* spp.), and venus clams (*Chione* spp.). We never witnessed other species preying on adult black murex. However, we did record predation on snail egg masses by other animals. Wrasses and rock sea bass (*Paralabrax maculatufasciatus*) were observed biting egg masses on aggregations (Figure 3). On one occasion, we found the intestines of a recently poached sea turtle (*Chelonia mydas*) 200 km south of Puerto Peñasco filled with hundreds of fresh murex egg capsules. In addition, black murex shells, together with those of the pink murex (*Phylonotus erythrostomus*) were the main shells used by the giant hermit crab (*Petrochirus californiensis*) and octopus (*Octopus* spp.).

Discussion

In the Gulf of California, mollusk species may spawn year-round or seasonally (Ceballos-Vázquez et al. 2000). The black murex is an example of the latter, reproducing only as water temperature rises, with reproductive peaks in June and July. This pattern is consistent with spawning and reproduction of various other invertebrates in the Gulf of California such as *Spondylus calcifer* (Villalejo-Fuerte et al. 2002), *Dosinia ponderosa* (Arreola-Hernández 1997) and *Chione undatella* (Baqueiro and Massó 1988) as well as numerous elasmobranches (Cudney-Bueno and Turk-Boyer 1998). For black murex, a rise in temperature is likely the main cue triggering reproduction, which could explain why the earliest aggregations tend to form in shallow waters near-shore, and as the season progressed, they are found in deeper waters offshore. Rise of temperature in spring induces spawning in many species of prosobranchs (Hyman 1967), and spawning has been shown to occur as a result of temperature increase for other mollusks in the Gulf of California (Villalejo-Fuerte et al. 2002). However, reproduction could also be the product of temporal variations of environmental factors such as food availability and/or photoperiod (Ceballos-Vázquez et al. 2000). Controlled experiments will be needed to determine the role that various biological, physical, and/or chemical factors could play in triggering reproduction of black murex. Furthermore, because of diving constraints, we were only able to obtain samples from depths = 30 m, so it is possible that black murex found in deeper and colder waters could reproduce at different times.

The black murex is highly gregarious during reproduction. Although breeding aggregations are reported for other gastropods (Tompa et al. 1984, D'Asaro 1986), we are

unaware of any gastropod that can form aggregations as large as those of black murex. We confirmed the presence of an aggregation of 900 m² providing a catch of 3 metric tons. We estimate that this aggregation contained between 5400-5800 snails based on the average weight of 533 g/snail reported for that area (Cudney-Bueno 2007). Interviews with fishermen and local buyers strongly suggest that aggregations used to be even larger during the initial stages of the fishery in the early 1990's, with catches between 3-6 metric tons sometimes obtained from one aggregation (Cudney-Bueno 2007). Based on weight data (Cudney-Bueno 2007), catches of this magnitude could comprise up to 12,000 animals.

We observed 42 breeding aggregation sites in five years of study, with the majority in La Cholla. This area is the most heavily fished during snail fishing season, providing over 70% of snail catches (Cudney-Bueno 2000). Cudney-Bueno (2000) recorded 139 snail fishing trips in summer 1999. This suggests that in that year there were at least 139 aggregations present in the vicinities of Puerto Peñasco, as our participation in 53 fishing trips showed that fishers harvest the entire aggregation once it's found and often target more than one aggregation in one day. Similarly, a total catch of 600 metric tons of snail was reported for La Cholla in 1992 (López-Reyes 1992). Using the average snail weight of 533g/snail for this area (Cudney-Bueno 2007) this catch would entail at least 1,125,700 snails. In addition, given an average density of 31 snails per m² (Prescott and Cudney-Bueno *in review*) this amount of snails would be equivalent to a total breeding aggregation surface area of approximately 36,313 m² or 3.63 hectares. As far as we know, snail captures anywhere close to these amounts in such

a small area (approximately 25 km²) and short amount of time (three months) have not been reported for any other region of the Gulf of California or for any other area in the world.

Black murex shows some level of fidelity to reproductive sites. Individuals return to the same breeding locations during consecutive years and breeding aggregations form in the same general areas. Although the reasons for this are unclear, communal reproductive behavior in specific areas could conceivably have biological and evolutionary advantages. The location of reproductive sites, for instance, is an important factor determining the dispersal and settlement of planktonic veliger larvae (Stoner et al. 1998). In this case, aggregations could play a crucial role in the settlement process by being located on or close to settlement and feeding habitat such as mussel and clam beds. Metamorphic and settlement cues of mollusks often arise from a plant or animal on which adults of the metamorphosing species feed (Hadfield 1978, Disalvo and Carriker 1994). Similarly, forming large breeding aggregations could extend the surface area where egg masses are laid by laying them on the shells of conspecifics. Although we observed egg masses laid on substrates other than snails, those were minimal compared to those laid on conspecifics.

Snails were usually found aggregated on sandy or broken shell substrates and close to rocky reef fouled with algae or other epibionts. Egg-laying on conspecifics could therefore have evolved as a strategy to cope with insufficient or lack of unfouled hard substrates for egg mass attachment. Prosobranchs requiring unfouled, solid substrata for oviposition have limited choices and can aggregate to spawn on available substrata, often

in multispecific populations, including exuviae of arthropods, plastic and aluminum debris, and shells of other spawners (D'Asaro 1986). Similarly, snails living on soft substrates can construct their holdfast from a few empty capsules or take advantage of any available firm surface for deposition (Tompa et al. 1984).

Carrying of egg masses on conspecifics within large breeding aggregations could also enhance survival of offspring and their subsequent dispersal as snails leave the aggregation. Preliminary observations showed a prevalent presence of black murex snail protoconchs found within the spaces between egg capsules. Although capsules can also hatch once snails disperse from the aggregation, most hatching takes place while snails are aggregated (Cudney-Bueno 2000). The presence of protoconchs suggest that some larvae could be settling on top of snails themselves where they may be protected from predation by remaining above ground and hidden between egg capsules. Similarly, as snails leave the aggregation, they could enhance dispersal of any offspring they carry and reduce local competition for food. Although early life history was not the focus of our study, in the laboratory we observed that larvae could remain in a veliger stage without feeding as long as ten days. However, we also observed that, although not metamorphosing, the majority of larvae tended to remain in the bottom of vials and appeared to be competent to settle soon after hatching (<10 days). The duration of a veliger stage is highly variable among gastropod species (Hyman 1967, Young et al. 2002). This duration also varies within a species according to environmental conditions in which the larvae are found. For example, some species delay metamorphosis for long periods of time in the absence of appropriate settlement cues (Hadfield 1978, Scheltema

1986). These long periods may have significant consequences over the dispersal range of a species, as the larval stage is the most important mode of dispersal for sedentary and semi-sedentary marine invertebrates (Olson 1985, Scheltema 1986).

Large breeding aggregations and the laying of egg masses on conspecifics could also have wider ecosystem effects. Black murex aggregations act as temporary reefs and play an important role in the subtidal benthic ecology of the northern Gulf of California (Prescott and Cudney-Bueno *in review*). A high number of juvenile species of mollusks, arthropods, echinoderms, annelids, and fish are associated with black murex breeding aggregations, finding cryptic protection within the egg masses and between aggregated snails. In this study, we also confirmed the existence of other species feeding on egg capsules, including green turtles (*Chelonia mydas*).

We found no snails breeding prior to the formation of aggregations. This, along with the equal ratio of male to female snails, suggests that breeding takes place while snails are aggregated. Whether all individuals are aggregating with the purpose of reproducing is not known. Non-spawning females and males have been reported in aggregations of *Murex fulvescens* studied in northwest Florida (D'Asaro 1986).

Aggregations grow throughout the season but reproduction begins early in their formation. While aggregated, females may lay egg cases on one snail and/or on more than one snail at different times. As the season progresses, new snails are recruited into the aggregation and old ones begin leaving after copulation and egg-laying. These observations are consistent with those reported for *Murex fulvescens* (D'Asaro 1986). Individuals of *M. fulvescens* gather in protected areas and begin spawning almost

simultaneously, while late arrivals add capsules on the periphery, on the shells of other spawners or on previously deposited capsules. This explanation is also consistent with fishers' observations and their fishing methods. At the beginning of the season, commercial divers usually follow the direction of the anterior canal of individual snails to lead them towards the aggregation. By the end of the season, they rely on the opposite direction to lead them towards the aggregation the snails are leaving (Cudney-Bueno 2000). Fishers also rely on the conspicuous visible evidence of feeding left by snails immediately preceding the formation of a breeding aggregation or as they begin dispersing from it.

It is impossible to conclude how many capsules a snail usually lays during one reproductive season as only ten female snails successfully reproduced and laid egg masses in the laboratory. However, based on these, we can infer that the reproductive output of this species is likely to be very high, with more than 1,000,000 larvae present in one egg mass of 300-400 capsules. Evidently, a large number of egg capsules (>1000) can be laid on an individual snail as well, and these can be laid at different times and by at least four different females while aggregated. We can also conclude that there is a marked "snail size-capsule size" and "capsule size-number of larvae" relationship, suggesting larger or older individuals have a higher reproductive output. A relationship between size and/or age and reproductive output has been found not only in gastropods, but other mollusks as well (see Spight 1979, Dame 1996). Smaller individuals seem to put more effort into somatic growth and older individuals put more effort into reproduction (Dame 1996). However, younger individuals as a group may contribute as

many or more offspring because their numbers are often greater than those of larger individuals in the population (Dame 1996). It is also important to consider that geographic variation in reproductive output could be present, mediated either by environmental constraints or variations in the genotype.

Management Implications

There is evidence that harvestable stocks of black murex have declined rapidly since the early 1990's when the species began to be fished intensely in Puerto Peñasco, from 600 to 71 metric tons in only seven years since the fishery began in 1992, with catch per unit of effort decreasing by 30% (Cudney-Bueno 2007). Fishers also state that the frequency of formation of breeding aggregations close to shore and the overall size of individual aggregations has decreased considerably (Cudney-Bueno 2000).

Because aggregation areas are targeted repeatedly, year after year, the species is particularly vulnerable to overharvest. As the fishery developed throughout the 1990's, snails were being harvested as they were beginning to aggregate, while fully aggregated, and as they began to disperse. This practice not only led to a loss of much of the reproductive biomass, but also likely increased early mortality by removing juveniles newly settled within aggregation sites and not allowing for adequate parturition. In addition, since they were easily found, were less costly to target, and formed early in the season when anticipation for the fishery is at its highest, aggregations found closer to shore were ultimately harvested the most and soon depleted. Throughout our fieldwork

we never found black murex in the intertidal zone, even though it was reported as a key intertidal predator in the same region during the 1960's (Paine 1966).

Although community-based management efforts for black murex and other benthic mollusks have taken place in Puerto Peñasco in recent years, these initiatives cannot stand alone (Cudney-Bueno 2007). Regional demand and pressures override local management initiatives, calling for a need for government support and the establishment of future comprehensive management structures (Cudney-Bueno 2007).

Given the biology and behavior of black murex, we suggest that harvest be restricted from May through the end of July as a first step towards a recovery of the fishery. This measure would allow for most individuals to reproduce (Cudney-Bueno 2000) and would protect in-shore populations, which aggregate sooner and are the ones in need of more urgent conservation measures. Seasonal closures alone, however, may not provide adequate protection and enhancement of heavily harvested and overexploited areas. Areas with low densities that have clear signs of having been over-harvested should be closed for a minimum of 2 years to allow for newly settled individuals to reach first reproductive age and reproduce at least once (Cudney-Bueno 2007). We also suggest the establishment of networks of harvest refugia that include heavily harvested areas as well as source populations as a tool to enhance recruitment and protect overharvested populations via larvae dispersal (Carr and Reed 1993).

Finally, management efforts should be coupled with future studies and long-term monitoring of both the fishery as well as of the benthic ecosystem associated with black murex. A better understanding of early life history (including larvae dispersal and post-

settlement processes), adult movement patterns, genetic population structure, as well as of the species' role in the ecosystem will be of particular importance to allow for a more comprehensive management and conservation of black murex and the subtidal benthic ecosystem of the northern Gulf of California.

Acknowledgements

We thank the members of the Sociedad Cooperativa Buzos de Puerto Punta Peñasco and the Intercultural Center for the Study of Deserts and Oceans (CEDO) for their friendship and unconditional logistical and field support. We are thankful for the field and laboratory assistance of Lindsey Haskin, Osvel Hinojosa, Darrin Kelly, Olegario Morales, Emily Omana, Katie Penke, and Jennifer Rupnow. Egg capsule drawings, as well as breeding aggregation and murex larvae photographs were kindly provided by Tiffany Ash-Cudney, J. Rupnow and Doug Moon, respectively. This study was completed thanks to financial contributions from the Tinker Foundation, the David and Lucile Packard Foundation, as well as fellowships and scholarships to Cudney-Bueno from the Consejo Nacional de Ciencia y Tecnología (CONACYT), the Inter American Foundation, the Wallace Research Foundation, and the Environmental Leadership Program. Research was conducted under permit # DGOPA - 04693 -150506 - 1832 from the *Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación* (SAGARPA) of Mexico. This is contribution # 4 of Project PANGAS, www.pangas.arizona.edu.

Figures and Tables

Figure C1. Study area and collecting sites of black murex (*Hexaplex nigritus*) aggregations in the northern Gulf of California, Mexico.

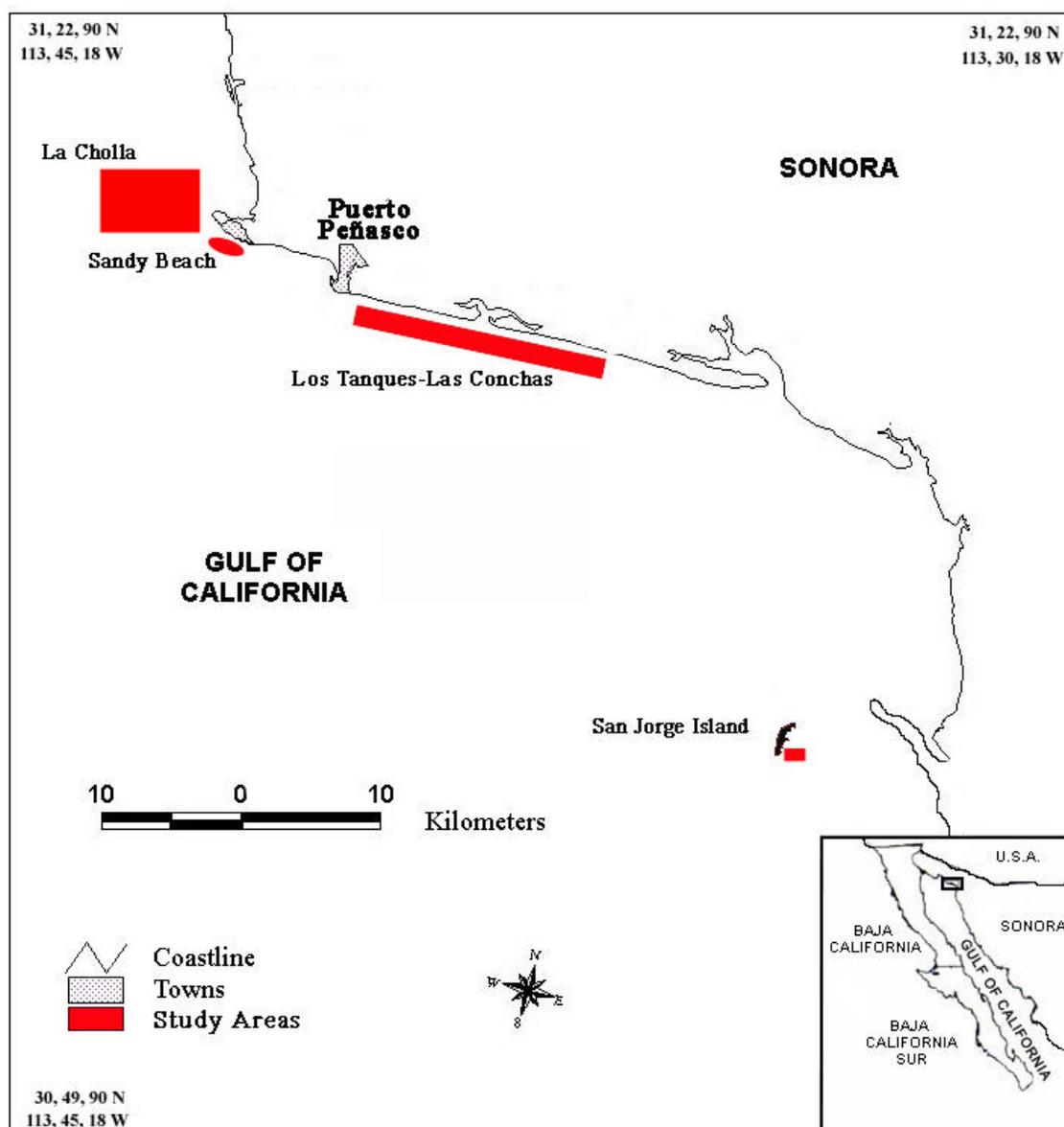


Figure C2. Egg capsule measurements of the black murex snail, *Hexaplex nigritus*.

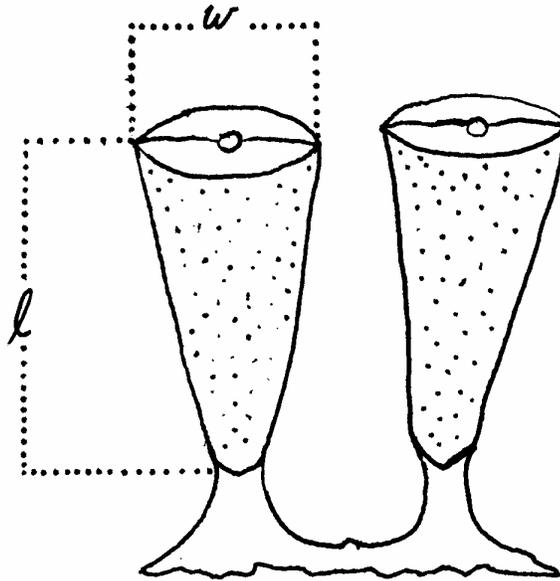


Figure C3. Breeding aggregations, egg capsules, and larvae of black murex snail, *Hexaplex nigritus*. (A) Portion of a breeding aggregation with numerous egg masses laid on top of conspecific snails; (B) a rock sea bass, *Paralabrax maculatufasciatus*, next to a black murex egg mass and over typical black murex breeding aggregation habitat comprised of broken shells, sand, and calcareous algae/rhodoliths; (C) black murex snail with an egg mass of >1000 capsules; (D) black murex snail showing patches of egg masses laid by different snails; (E) female snail with foot extended while laying egg capsules on glass of aquaria. Individual eggs within the egg capsules can be observed; (F) black murex veliger larvae.

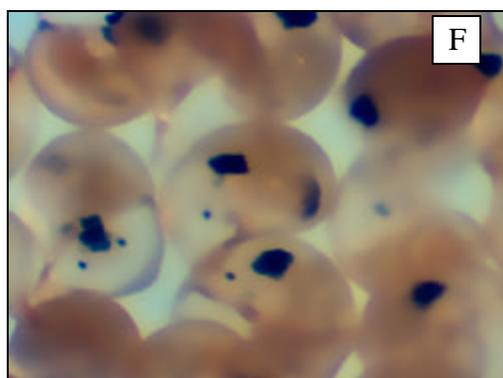
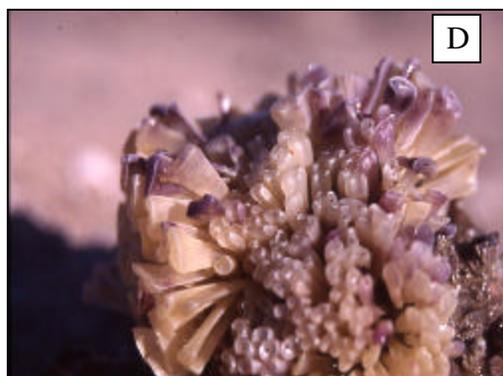
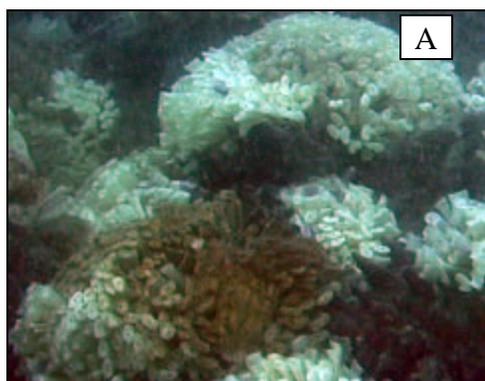


Figure C4. Relationship between egg capsule size and number of larvae of the black murex snail, *Hexaplex nigrinus*, in the northern Gulf of California, Mexico.

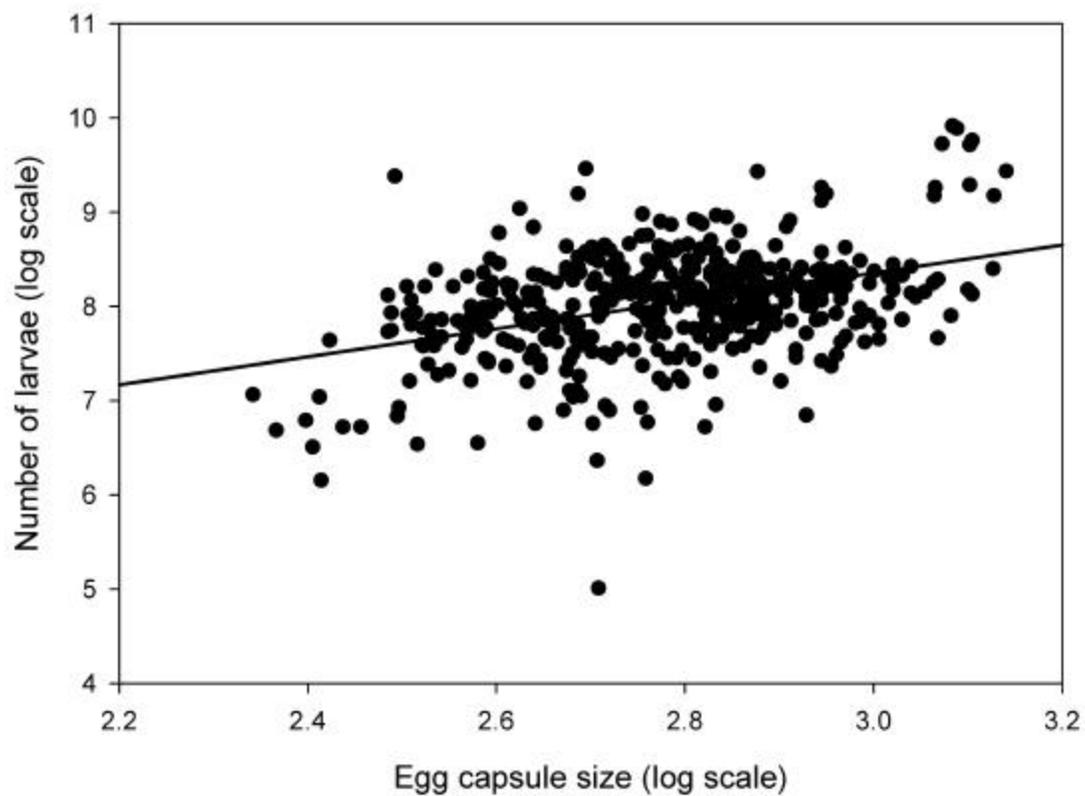


Figure C5. Relationship between snail size and size of egg capsules of the black murex snail, *Hexaplex nigritus*, in the northern Gulf of California, Mexico.

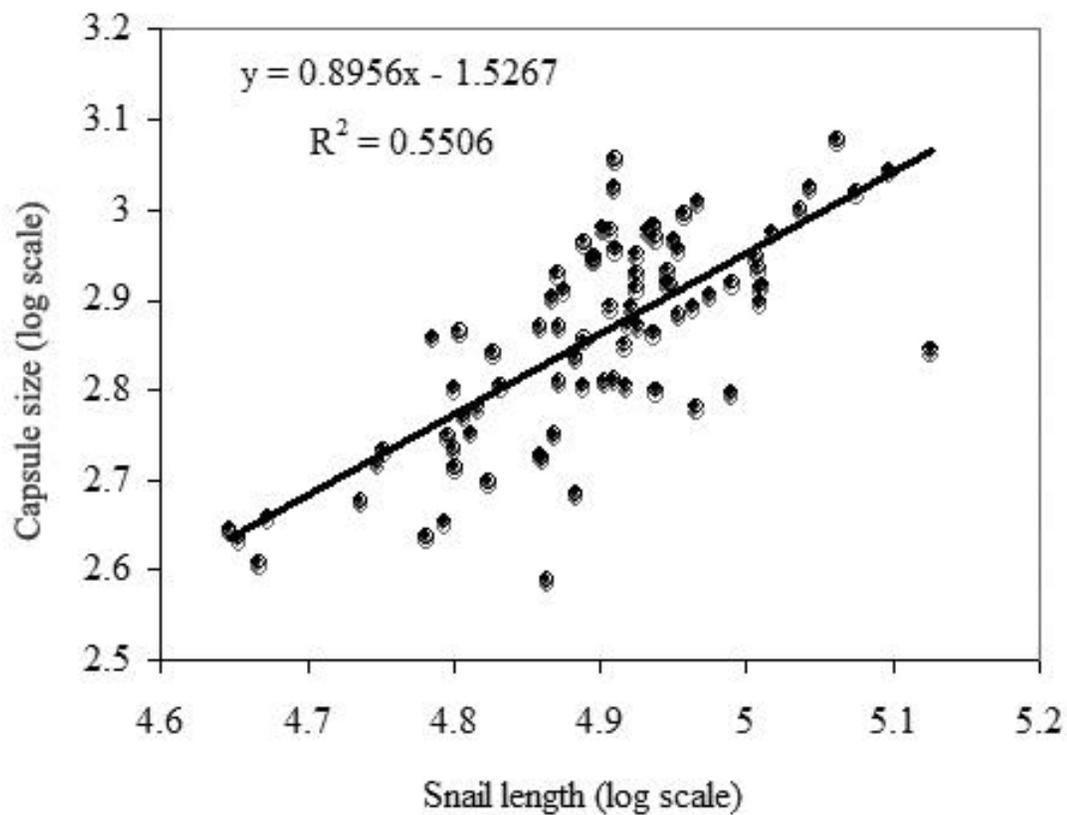


Table C1. Distribution of egg mass sizes and egg mass-laying times for 10 black murex snails (*Hexaplex nigritus*) maintained in aquaria.

Snail TL (mm)	Snail weight (g)	Capsules laid per egg mass	Days laying	# of capsules laid/day
110.2	290	69	3	23
110.2	290	186	9	21
118.3	330	337	14	24
120.4	340	161	2	81
120.8	290	117	6	20
122.8	310	27	6	5
127.2	340	261	8	33
141.5	440	63	10	6
146.0	500	62	7	9
146.0	500	87	1	87
mean = 123.34 SE = 4.3	mean = 363 SE = 26.7	mean = 137 SE = 31.4	mean = 6.6 SE = 1.2	mean = 30.9 SE = 9.2

Literature Cited

- Arreola-Hernández, F. 1997. Aspectos reproductivos de *Dosinia ponderosa*, Gray, 1838 (Bivalvia: Veneridae) en Punta Arena, Bahía Concepción, B.C.S., México. M.S. Thesis. Instituto Politécnico Nacional CICIMAR, La Paz, México. 85 pp.
- Baqueiro, E. and J.A. Masso. 1988. Variaciones poblacionales y reproducción de dos poblaciones de *Chione undatella* (Sowerby, 1835) bajo diferentes regímenes de pesca en la Bahía de La Paz, B.C.S., México. *Cienc. Pesq. Inst. Nal. De la Pesca. México.* 6:51-67
- Barber, W.E. 1961. Murex spawning. News of the Association of Shell Clubs of California. *Pacific Shell Club* 1(4): 1-2
- Brusca, R. C., E. Kimrey, and W. Moore. 2004. A Seashore Guide to the Northern Gulf of California. Arizona-Sonora Desert Museum. Tucson, Arizona 203 pp.
- Brusca, R.C. 1973. A Handbook to the Common Intertidal Invertebrates of the Gulf of California. The University of Arizona Press. Arizona, U.S.A. 427 pp.
- Carr, M.H. and D.C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* 50: 2019-2028.
- Ceballos-Vázquez, B.P., M. Arellano-Martínez, F. García-Domínguez, M. Villalejo-Fuerte. 2000. Reproductive cycle of the rugose pen shell, *Pinna rugosa* Sowerby, 1835 (Mollusca: Bivalvia) from Bahía Concepción, Gulf of California and its relation to temperature and photoperiod. *Journal of Shellfish Research* 19(1):95-99

- Cudney-Bueno R. and P.J. Turk-Boyer. 1998. Pescando Entre Mareas del Alto Golfo de California: Una Guía Sobre la Pesca Artesanal, su Gente, y sus Propuestas de Manejo. Technical Series # 1. CEDO-Intercultural. Puerto Peñasco, Sonora, México. 166 pp.
- Cudney-Bueno, R. 2000. Management and Conservation of Benthic Resources Harvested by Small-Scale Hookah Divers in the Northern Gulf of California, Mexico: The Black Murex Snail Fishery. Ms. Thesis. University of Arizona. Tucson, Arizona, U.S.A. 177 pp.
- Cudney-Bueno, R. 2007. Marine Reserves, Community Based Management, and Small-Scale Benthic Fisheries in the Gulf of California, Mexico. PhD Dissertation. University of Arizona. Tucson, Arizona, U.S.A.
- D'Asaro, C.N. 1970. Egg capsules of prosobranch mollusks from south Florida and the Bahamas and notes on spawning in the laboratory. *Bulletin of Marine Science* 20(2): 414-440
- D'Asaro, C.N. 1986. Egg capsules of eleven marine prosobranchs from northwest Florida. *Bulletin of Marine Science* 39(1): 76-91
- D'Asaro, C.N. 1991. Gunnar Thorson's worldwide collection of prosobranch egg capsules: Muricidae. *Ophelia* 35(1): 1-101
- Dame, R.F. 1996. Ecology of Marine Bivalves: An Ecosystem Approach. CRC Press. Florida, U.S.A. 254 pp.
- Disalvo, L.H. and M.R. Carriker. 1994. Planktonic, metamorphic, and early benthic behavior of the Chilean loco *Concholepas concholepas* (Muricidae, Gastropoda, Mollusca). *Journal of Shellfish Research* 13(1): 57-66

- Hadfield, M.G. 1978. Metamorphosis in marine invertebrate larvae: an analysis of stimulus and response. In: Chia, F. and M.E. Rice (Eds.). Settlement and Metamorphosis of Marine Invertebrate Larvae. 290 pp.
- Hyman, L.H. 1967. The Invertebrates: Mollusca I. McGraw-Hill. U.S.A. 792 pp.
- Jones, D.S. 1988. Schlerochronology and the Size versus Age Problem. In: McKinney, M.L. Heterochrony in Evolution: A Multidisciplinary Approach. Plenum Press, NY. 348 pp
- Keen, A.M. 1971. Sea Shells of Tropical West America. 2nd ed. Stanford University Press. Stanford, California, U.S.A.
- Kemp, P. and M.D. Bertness. 1984. Snail shape and growth rates: Evidence for plastic shell allometry in *Littorina littorea*. *Proc. Natl. Acad. Sci.* 81: 811-813
- López-Reyes, E. 1992. Análisis y diagnóstico de la pesquería del caracol chino *Muricanthus nigritus* y *Hexaplex erithrostomus* en Bahía la Choya, Sonora. Pregunta problema para obtener el título de Oceanólogo. Universidad Autónoma de Baja California. Ensenada, Baja California, México. 29 pp.
- Olson, R.R. 1985. The consequences of short-distance larval dispersal in a sessile marine invertebrate. *Ecology* 66(1): 30-39
- Paine R. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-75
- Poutiers, J.M. 1995. Moluscos. In: Fischer, W., F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter, and V.H. Niem (Eds.). Guía FAO para la Identificación de Especies Para los Fines de la Pesca: Pacífico Centro-Oriental: Invertebrados. Food and Agriculture Organization. Rome, Italy. 1: 646 pp.

- Prescott, R. and R. Cudney-Bueno. *In review*. Living reefs in the upper Gulf of California: aggregations of Black Murex snails (*Hexaplex nigritus*) as habitat for juvenile and adult invertebrates. *Marine Ecology Progress Series*.
- Radwin, G.E. and A. D'Attilio. 1976. Murex Shells of the World. Stanford University Press. Stanford, California U.S.A. 284 pp.
- Rawlings, T.A. 1995. Direct observation of encapsulated development in muricid gastropods. *The Veliger* 38(1): 54-60
- Scheltema, R.S. 1986. Long-distance dispersal by planktonic larvae of shallow-water benthic invertebrates among central Pacific islands. *Bulletin of Marine Science* 39(2): 241-256
- Spight, T.M. 1979. Environment and life history: the case of two marine snails. In: Stancyk, S.E. (Ed.). Reproductive Ecology of Marine Invertebrates. University of South Carolina Press. South Carolina, U.S.A. 283 pp.
- Stoner, A.W., M. Ray-Culp, and S.M. O'Connell. 1998. Settlement and recruitment of queen conch, *Strombus gigas*, in seagrass meadows: Associations with habitat and micropredators. *Fishery Bulletin* 96: 885-899
- Tompa, A.S., N.H. Verdonk, and J.A.M. Van Den Biggelaar. 1984. The Mollusca: Reproduction. Academic Press. Orlando, Florida, U.S.A. 486 pp.
- Villalejo-Fuerte, M. M. Arellano-Martinez, B. P. Ceballos-Vázquez, F. García-Domínguez. 2002. Reproductive Cycle of *Spondylus calcifer* Carpenter, 1857 (Bivalvia : Spondylidae) in the "Bahía de Loreto" National Park, Gulf of California, Mexico. *Journal of Shellfish Research* 21(1): 103-108

Young, C.M., M.A. Sewell, M.E. Rice. 2002. Atlas of Marine Invertebrate Larvae.

Academia Press. San Diego, California, U.S.A.

APPENDIX D

RAPID EFFECTS OF MARINE RESERVES AND THE
RISE AND FALL OF COOPERATION IN A YOUNG FISHERY

Proceedings of the National Academy of Sciences

R. Cudney-Bueno^{*†‡}, M. F. Lavín[§], S.G. Marinone[§], W. W. Shaw^{*}

* Department of Natural Resources, School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA.

† Centro Intercultural de Estudios de Desiertos y Océanos (CEDO). Apartado Postal #53, Puerto Peñasco, Sonora, México.

§ Departamento de Oceanografía Física, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE). Carretera a Tijuana, Ensenada, Baja California, México.

‡ To whom correspondence should be addressed: School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA email: cud@ag.arizona.edu, phone: 520-626-5607, fax: 520-621-8801.

**Rapid Effects of Marine Reserves and the
Rise and Fall of Cooperation in a Young Fishery**

R. Cudney-Bueno, M. F. Lavín, S.G. Marinone, W. W. Shaw

Abstract

We show that local cooperation to manage fisheries commons incorporating the use of marine reserves can emerge rapidly. Furthermore, this cooperation can be sustained in a fishery spanning no more than two generations, effectively avoiding a local “tragedy of the commons”. A blend of social group characteristics, fishers’ ecological knowledge and participation in monitoring, and relatively rapid ecological response of the system can play key roles in reinforcing cooperation. We also provide evidence of rapid (2yrs) spatially-constricted effects of reserves on adjacent fisheries via larvae dispersal. However, just as cooperation can emerge, it can rapidly fall with cascading effects to the social system and resources harvested, particularly amidst threats to social capital and pressure from outside the community. Even if community based reserves are effective within the biophysical and local social context, their long-term success will rely on the system’s capacity to control access and will demand the institutional capacity to do so.

Introduction

In response to numerous failures under single species management and command-and-control approaches, marine reserve and community-based management (CBM) programs have been advocated as means to achieving a more sustainable use of marine resources (1,2). Marine reserves established under a CBM approach could potentially provide lasting returns, serving not only conservation and fisheries needs, but mitigating social and political conflicts. An effective CBM approach should precipitate regulations with more credibility among users and more cost-effective management processes, taking much of the financial burden off of state and federal government agencies with regards to guideline definition, implementation, and enforcement (3).

However, CMB approaches are often viewed as dubious with little utility. For example, most of fisheries today result in overexploitation and operate under dynamic global markets. Fishing communities are experiencing a rapid turnover of species targeted and are increasingly exposed to externalities (4). Indeed, studies of the social and institutional efficacy of CBM of fisheries are largely confined to geographically isolated fishing communities with long-standing traditions (5). In contrast to most fisheries today, these communities have often been able to acquire the ecological knowledge to develop customary, effective management practices through multiple generations of fishing, meeting prerequisite conditions of effective CBM (6,7). Thus, empirical evidence of the efficacy of CBM in modern fisheries remains sparse.

Similarly, proof of the effectiveness of marine reserves is scant. The rationale behind their use lies primarily in the dual opportunity they offer to protect ecosystems

and ecological processes while also enhancing fisheries via density-dependent spillover of target species and larvae dispersal into fishing areas (8). While it is evident marine reserves can meet conservation targets (9), it is unclear whether they can enhance fisheries, particularly by means of larvae dispersal. Previous analyses of reserve effects have focused mainly on the benefits to adjacent fisheries via density-dependent spillover of fish (8, 10) or have been based primarily on hypothetical models (11,12).

Here, we provide evidence that cooperation for the management of a commons, of which marine reserves form a core component, can emerge and evolve rapidly in a young, modern fishery with a limited history for collective action. We also provide evidence of rapid effects of marine reserve networks on adjacent fisheries via larval dispersal. The marine reserve network emerged exclusively from the grass-roots level, with no influence by top-down processes. We analyze the social-ecological feedbacks leading to this genesis, the biological and social effects of the community-based reserves, and the eventual downfall of the system.

The Puerto Peñasco Community-Based Reserves

The Puerto Peñasco (PP) reserve network was the first of its kind to be established in Mexican waters. Reserves were created, monitored, and enforced by commercial divers of PP in collaboration with a local non-governmental conservation organization and an academic institution. This was done without waiting for official government recognition at a time when other efforts for the establishment of marine reserves in the region have been highly contentious. The network was established primarily as a means

to protect declining stocks of the two most important species harvested by PP commercial divers: rock scallop (*Spondylus calcifer*) and black murex snail (*Hexaplex nigritus*).

The network includes an offshore reserve surrounding San Jorge Island, the region's most productive fishing ground in terms of density and size of species harvested, and two coastal reserves (Las Conchas and Sandy), providing protection to roughly 30% of an entire fishing sector's fishing grounds (Figure 1). It covers approximately 18 km of coastline primarily encompassed by extended beach-rock (coquina) and granite reefs separated by mussel, rodolith, and shell/sandy patches.

Pre - Marine Reserves: *De Facto* Management and Resource Declines

“Hookah” or air hose divers from Puerto Peñasco have been harvesting benthic shellfish from rocky reefs and adjacent sandy areas for approximately 30 years (13), with some of these species beginning to be harvested only within the last ten years. The fishing sector is comprised of no more than two generations of divers who arrived from communities south of Puerto Peñasco in the late 1970's to dive primarily for rock scallop in the rocky reefs of the upper Gulf of California. Today, the fishing fleet of 12 boats is organized in one cooperative comprised of the same divers who arrived in the late 70's, their descendants, and people with close ties to the network.

The fishery developed within a unique bioregion, marked primarily by intense tidal fluctuations and currents, water temperature fluctuations of more than 20°C, predominance of low visibility, and isolated reefs. To the North and South, PP diving

grounds are flanked by long stretches of sand, with the nearest substantial (>1000 m²) rocky reef located 150 km South of the reserve network.

These characteristics served two key purposes. They helped form a strong sense of pride among divers as a fishery sector that distinguished itself from any other in the community and even from other divers elsewhere in the Gulf of California. Locally, they are referred to as “*Los Buzos*” (The Divers) and not fishermen. Environmental conditions and the landscape layout also helped maintain a relatively constant fishing effort throughout the years. The region acts as a natural fishing entry filter as it demands specific commercial diving skills and strong determination to settle permanently as a diver. Except for occasional recreational line fishing and rare surface gillnet fishing for mackerel (*Scomberomorus sierra*) and corvinas (*Cynoscion parvipinnins*), at the time when the reserves were established these areas were commercially fished only by PP divers and were largely buffered from outside encroachment.

Rotation of fishing zones and species targeted, as well as size selection of reproductively mature individuals represented the only resource-based management structures that developed. For instance, studies of rock scallop catches of each diver showed that 95% constituted individuals that had reproduced at least once. When asked how long it took for rock scallops to reach commercial size, 83% replied one year or less. This understanding was largely fostered by individual divers observing an increase in the number of rock scallop when returning to sections of reefs or areas that they had not fished in for some time, particularly areas farther from shore such as San Jorge Island.

Rotation and size selection, however, were largely *de facto* practices. They were mediated by environmental and market factors and resulted from a cost-benefit individual response to the accessibility and availability of the resource in question, rather than from a conscious management-intended group decision. When asked if they “recalled any time in the past when divers talked about or decided to collectively establish means to assure a better fishery”, 98% could not think of any situation that came close to such thoughts or actions. Similarly, when asked if in the past they had “personally done anything with the intention of helping maintain a healthy fishery in the future”, 95% did not recall any specific action. The reasons given as to why - whether individually or collectively - there had been a lack of consciously driven decisions and actions to manage their resources were varied but most expressed no perceived need to organize or implement management decisions given the abundance of resources.

Rotation, size selection, and maintenance of relatively constant fishing effort likely played an important role in the maintenance of the fishery throughout the years[†]. However, these practices were not robust and effective enough. Interviews with older fishermen indicate that overall catch per unit of effort of rock scallop decreased considerably after the beginning of diving enterprises in the early 80's, even though fishing effort remained relatively constant. A good day's catch during the beginning of

[†] Since the early 1990's, black murex catches of PP have consistently surpassed catches of all commercial species of snail combined for all other states in the Gulf of California (14). Similarly, rock scallop has become regionally endangered in the Southern Gulf, with densities of 1 individual per 100 m² (15). However, rock scallop densities in the PP area are, on average, 24 individuals/100 m², in some areas densities surpassing 100 individuals/100 m².

the fishery was considered to be, on average, 59.16 kg/day (95% C.I. 48.5- 69.8; median 60kg/day; range = 30-100 kg/day). In contrast, the average good day's catch at present is 19.94 kg/day (95% C.I. 17.8-22.0 kg/day; median 20 kg/day; range = 10-30 kg/day). Similarly, overall catches of black murex snail fell from 600 metric tons to 71 tons in only 7 years since the fishery began in 1992, with a CPUE decrease of 30% (13).

As evidenced above, when the reserve network was established by the PP diving cooperative in 2002 it was done so with no previous experience in collective management decisions. Nevertheless, existent *de facto* forms of management, the system's rapid feedbacks (that fostered accelerated accumulation of key local ecological knowledge by the fishers), as well as the recent experience in a decline of fishery resources played key roles in the subsequent emergence of collective management agreements, including the definition of reserves.

Emergence of Cooperation and Establishment of Reserves

Interviews with all fishermen indicate that there were two main incentives that triggered cooperation for the development of collective management decisions: 1) a decline in the availability of the main species targeted, and 2) year-round dependence on their fishery resources. Cooperation for the establishment of reserves was facilitated by an inherent belief in the resilience of their fishing system and the effects of refugia through previous tacit experimentation with rotation schemes. Rock scallops actually take between 3-4 years to grow to commercial size, and not <1 year as was believed by fishers. Nevertheless, for management purposes fishers' observations were essentially

correct, as it takes 1 year for juveniles 50-80 mm long to reach commercial size. Essentially, divers had been harvesting cohorts of reproductively mature individuals dismissing the existence of young specimens, which are more cryptic and harder to find. This is evidenced by fishers' surprise at the amount rock scallops once monitoring efforts targeting young individuals began.

The initiative to establish marine reserves was community-based driven in the sense that fishers directly petitioned the support from research and conservation institutions with a presence in the region. Establishment of the marine reserve network came after a) three years of interactions with NGO and academic institutions, facilitating community-based research for long-term monitoring and assessment of the diving fishery, b) one year of having experimented with a temporary closure of San Jorge Island, evidencing an increase in density of rock scallop, c) at least 20 meetings between cooperative members to assess local management options.

Effects of Reserves

Only two years after the establishment of the network, the overall population of juveniles (< 2 years old) of rock scallop and black murex snail (individuals born and recruited since the establishment of the reserves) had increased in coastal reserves and fishing areas (Figure 2). Visual censuses revealed that density of young rock scallop had increased by up to 40.7% within coastal reserves and by 20.6% in fished sites (Repeated measures two-way MANOVA, time X protection from fishing, $F_{4, 41} = 2.67$, $P=0.04$). Changes were also evident for black murex, with more than a three-fold increase in the

density of juveniles within fished sites (Repeated measures two-way MANOVA, time X protection from fishing, $F_{4, 41} = 3.28$, $P=0.01$)[‡].

The increase in juveniles, however, was spatially explicit, evident only for the northern portion of the network (Figure 3). Density of both species increased markedly in the reserve/fishing zone treatment of Sandy/La Cholla, particularly during the last year. However, on the Las Conchas-Los Tanques reserve/fishing zone treatment, densities remained relatively constant throughout (Rock scallop: repeated measures three-way MANOVA, time X protection from fishing X treatment, $F_{4, 41} = 2.535$, $P=0.05$; black murex: repeated measures three-way MANOVA, time X protection from fishing X treatment, $F_{4, 41}=3.028$, $P<0.05$). Furthermore, analysis of San Jorge Island, the offshore reserve in the network, revealed that overall density of juvenile rock scallops actually decreased since reserve establishment (1-way ANOVA; $F_{4, 45} = 4.46$, $P<0.01$) and those of black murex remained relatively constant (1-way ANOVA; $F_{4, 45} = 0.615$, $P=0.65$).

Rapid buildup of juveniles in the northernmost part of our study area is consistent with the circulation pattern for summer (the spawning season), which is cyclonic overall (16), with northwestward flow in the area where the reserve network is located. To test if the network could be influenced by southern sources of larvae, we used a three-dimensional baroclinic numerical model to track passive particles (see online material)

[‡] Increase of juveniles is even more pronounced if we take into consideration that both species showed a drop during the first monitoring season following reserve establishment. This initial drop may be attributed to a lag in the detection of juveniles recruited since reserve establishment in summer 2002 coupled with the growth of juveniles that were present at the time of protection (i.e. individuals recruited prior to reserve establishment).

released (a) in the rocky reef nearest to the reserve network (~150 km south), and (b) in San Jorge Island. In case (a) the particles showed a mean south-north travel distance of 53 km in two weeks and 147 km in four weeks (Figure 4a). Larvae of both species, however, are competent to settle in less than 20 days, which makes it highly unlikely that there could have been a direct influence from southern reefs in such a short time frame. Furthermore, our modeling results are likely to be an overestimation of true dispersal distances, as we only used passive particles. Recent studies have shown that larvae dispersal can be much more constrained than previously thought as a result of behavior and environmental factors (17). Finally, influence from western sources (Baja California peninsula) is discarded as previous studies have shown a clear cyclonic movement of the water during the summer (16), when both of these species reproduce (18). On the eastern side of the Gulf, the water mass has a northbound movement while on the western side the water moves towards the south and doesn't reach the eastern coastline (16).

Particles released in the area surrounding San Jorge Island (Case b), showed a marked flow towards the northwest, with a mean travel distance of 32 km in two weeks (Figure 4b), which would put the larvae within the northern reserve sites. Direct evidence of this flow pattern is provided by the tracks of the surface drifters released near San Jorge Island (Figure 5), and the progressive vector diagrams from concurrent Acoustic Doppler Current Profilers (see online material). Drifter tracks show the tidal ellipses plus a residual flow toward the reserve sites.

These results are more indicative of a reserve effect than of overall good regional recruitment years or wider oceanographic processes, as effects of these processes would

have been manifested throughout the study area and not spatially constricted to the northern portion of the reserve network. Similarly, monitoring efforts in at least two other regions of the Gulf of California did not show an increase in density or biomass for these species within the last 5 years (19) and we are unaware of fishers from PP or other communities shifting their spatial distribution of fishing as a result of increases elsewhere[‡].

Our modeling and current observations also suggest that San Jorge Island could be acting as a key component of the network system, providing a source for larval export to adjacent coastal reserves and fishing areas. Although numbers of juveniles decreased on the island, even the lowest average densities were 80% higher than those of coastal reserves. Overall densities there (adults and juveniles) were also 6 times higher than all coastal reserves and fishing sites combined, reaching up to 106 individuals in 100 m². These numbers exceed any others reported for the Gulf of California (15, 20). Given these high densities, we hypothesize that a decrease in juveniles in San Jorge Island could be related to inherent density-dependent processes. However, further targeted experimental studies on San Jorge will be needed to provide a more conclusive understanding of recruitment patterns seen within the island.

We also saw an increase in the average weight of rock scallops and black murex snail. Data from fishers' catches of the adductor muscle of *S. calcifer*, the part of the animal that is commercialized, show that their weight in fished areas increased by 19.9 %

[‡] While we are unaware of regional divers shifting their efforts to other areas, divers from communities south of Puerto Peñasco, some as far as 1000 km, reached PP diving grounds as a result of local increase in benthic resources after reserve establishment.

($F_{2, 897} = 10.78$; $P < 0.0001$, 1-way ANOVA) in the two years since the reserves were established (Figure 6a). Similarly, average weight of black murex increased by 74.74 % in reserves ($F_{2, 220} = 77.75$; $P < 0.001$, 1-way ANOVA) and by 35% in fishing areas ($F_{2, 421} = 23.80$; $P < 0.001$, 1-way ANOVA) (Figure 6b). This overall increase could not only have a direct effect on fishers' catches (i.e. more weight with less animals), but could have a positive effect on future recruitment given a marked increase in reproductive output as a function of snail size and weight (18).

Effects of reserves were also evident to fishers. In interviews conducted prior to providing results on the monitoring efforts, over 85% of fishers reported benefits from the reserves and that they would continue having reserves in the future (Table 1). Seventy-eight percent also stated that they had seen more rock scallop in areas that had been previously depleted. Similarly, 89% reported seeing an increase in juvenile rock scallop.

Social Capital[§] and Local Management of the Commons

The system's governance relied primarily on a suite of simple rules and means of enforcement (Table 2), meeting venues that allowed for feedback between the social and ecological subsystems, and the leadership role of key members of the group.

The evolution of rules and sanctions built primarily on foundations of trust and reciprocity and concerns for the group's well being. To exemplify this, 100% of fishers

[§] Social capital refers to the institutions, networks, stocks of social trust, and norms that shape the quality and quantity of a community's social interactions and that people can draw upon to solve common problems.

said that they trusted that other fellow fishers for the most part respected the reserves. Similarly, when asked the open ended question “In what way would breaking Cooperative rules affect you?” all answers fell into three categories: 1) personal guilt and sense of betrayal to the group, 2) concern of the rest of the group’s opinion about one’s actions, and 3) concern over the possibility of losing trust and friendship (Table 3).

Hence, the most effective and usual form of enforcement relied on variations of peer pressure and public shame that could ultimately threaten the individual’s reputation and his place within the group’s social capital base (Table 2). These were *de facto* sanctions with no legal standing under any statutes of the Cooperative. While other formal sanction types were developed, they were either largely avoided, often changed, or were applied as a last resource.

In essence, if someone within the group cheated, the first approach was to tap into the personal guilt associated with the event. Often, it was only necessary to bring the case to the attention of the group without singling out specific people. “Cheaters” assumed that at least someone else likely knew who the culprit was. This way, the informer’s reputation was also protected and he would not be labeled as an accuser. “Accuser” is one of the worst labels a diver can have, largely because it can undermine his network ties and his reliance on these ties when in need of any help. During interviews, when given a choice to express what would be worse, for the group to label you as an accuser or as a cheater, practically all fishers found it impossible to make a choice. They were both seen as equally detrimental.

When direct accusations in front of the group did take place, however, these were carried out by the more elder or experienced fishers who had already gained high levels of respect within the group. These individuals played a pivotal role during meetings. They gave credibility to agreements and helped maintain, although often contentious, a respectful meeting atmosphere. They were also the main players involved in confronting cheaters directly on site when found breaking any given rule.

Cooperative meetings encompassed a key component for the evolution of the system. Between summer 2002 and summer 2004, 15 meetings were held, all with an attendance of at least 80% of members. More than acting as a means to discuss various issues pertaining to administration, these meetings provided the main venue to maintain the checks and balances of the system and its functionality. They provided a forum for the evolution of cooperation, the generation of rules and sanctions, and allowed for collective feedbacks from biological knowledge gained while commercial diving and/or monitoring. This, in turn, reinforced among the group the perceived benefits of the reserves and played a key role in dismissing poaching allegations and re-enforcing group strength. For instance, it was common for rumors of poaching to develop and quickly spread within the group. However, these rumors were usually dismissed during Cooperative meetings. Given that fishers were directly involved in the monitoring process, with the same designated individuals repeatedly monitoring the same areas jointly with academic researchers, there was a strong sense of individual appropriation towards each monitored site and of other group members' respect towards the reports or opinions of these individuals. Knowing that poaching allegations were often false and

that resources were in good health would in turn re-enforce the unity and strength of the group and trust in its members. In short, burden of proof regarding the state of reserves and fishing areas fell largely on fishers themselves.

Knowing if, when, and where a poaching event took place was facilitated by the social, topographical, and environmental layouts of the system. It is simple to know where a diver fishes on a daily basis. The group is small and highly communicative, allowing for the quick spread of rumors. Coastal reserves are found close to port and fishing activities within them can be easily detected either from shore or from fishing areas. In addition, the diving patterns within any given month are largely constrained by environmental factors, particularly tidal currents and visibility. For instance, during monthly spring tides, when tidal currents are strongest, fishers are largely constrained to dive within the reefs south of port. During neap tides, divers target offshore areas and the reefs north of port.

In the case of San Jorge Island, which is found farther offshore and is harder to patrol, enforcement relied on more active means. These, however, were geared towards patrolling entrance of outsiders and not of members of the group. It is quickly known when a diver from PP goes to the island as this trip demands extra preparation and usually involves overnight stays. Members of the group would sometimes carry out trips to the island during neap tides with the sole purpose of seeing if anyone was there. However, on three occasions when credible rumors emerged about outsiders poaching, PP divers also gained the support of the local Navy and fisheries offices to assist in patrolling and enforcement operations. This collaboration was based on the rapport built

between divers and local government officials throughout the years rather than as a mandate, as reserves were yet to be formalized at a federal level.

The unique environmental characteristics of the region also facilitated local divers' efforts to discourage settlement of outsiders. A case in point is when a prominent PP buyer hired divers from another region to work for him at low wages and increase his revenues. Local divers told them to fish in areas and times marked by intense currents and low visibility. These fishers never developed the skills to dive in the region and left soon after.

This simple and somewhat informal governance system was highly effective. Regular underwater monitoring visits to reserve sites revealed minimal evidence of fishing activity within reserves[¶]. Similarly, we confirmed only 13 poaching events in at least 2,000 individual fishing trips conducted between Summer 2002-Summer 2004. Of these, 4 took place on the edge of the reserves. In addition, only the crew of one boat repeated poaching events. However, this crew also became the most active enforcer of the reserves against outsiders as the system evolved, largely as a way of redeeming their reputation with the rest of the group.

Hence, while the system remained largely bounded within the community of PP, reserves and other local rules were highly respected. This respect was accomplished not through heavy policing, but primarily through means of social pressures, local

[¶] Finding evidence of rock scallop fishing is facilitated by the fact that the right valve remains attached to the rock after the scallop muscle has been removed and its bright white color contrasts with the rest of the reef. In the case of black murex snails, these are only harvested when they form large summer breeding aggregation mounds. We saw the same aggregations repeatedly in reserve sites.

institutional arrangements, and an inherent belief in the future benefits of the group's various initiatives.

The Fall of Cooperation: External Pressures and Social Capital

Concurrently with the community-based establishment of reserves, PP divers in coordination with conservation and academic institutions lobbied to obtain formal government recognition of their management initiatives. In November 2003, Mexico's federal government awarded the Cooperative with the National Conservation Recognition award, one of the highest environmental distinctions bestowed annually by the Secretariat of the Environment. Soon after, Mexico's National Commission of Fisheries and Aquaculture (CONAPESCA) granted the Cooperative some, albeit not all, of the fishing permits that it had lost during a National fisheries restructuring process that took place in 2000⁷. More than acting as a positive incentive, however, the incomplete granting of permits caused strife within the cooperative. On one hand, contentious decisions had to be made to allocate permits. On the other, fishers clearly expected much more from the government given their management efforts.

In this same vein, the directorship of the local fisheries office changed drastically, bringing in foreign personnel unaware of existing local institutional arrangements and overall less supportive of community-based management initiatives. This made it impossible for divers to gain local government support for enforcing San Jorge island as a reserve, which by then had become a particularly productive fishing ground for rock

⁷ Irregularities in the granting (by the government) and maintenance (by fishers) of fishing permits are a common occurrence in Mexican fisheries.

scallop, with a 23% increase in density since the establishment of the reserves and densities almost 6 times higher than in all coastal reserve and non reserve monitored quadrants combined.

News about management efforts and the state of the reserves spread quickly at a regional scale. What followed was marked not only by uncontrolled exploitation, but also by a cascade effect in the compliance of all tacit and formal rules (Table 2) and a temporary threat to the social system's resilience. Two boats from communities more than 500 km south of PP began fishing at San Jorge Island. After various confrontations with interlopers and unable to deter poaching, divers convened and opted to collectively fish at the island before others continued free-riding on their efforts. The island quickly became a free for all. In one month, benthic mollusk populations had been reduced by half. While this occurred, some members of the group began fishing in coastal reserves as well and soon the effects cascaded to the entire system. Once fishers from other communities had left the region, most PP divers fished within the coastal reserves, collectively breaking local rules even without much direct pressure from outsiders. A second wave of people, from communities as far as 1000 km south of Puerto Peñasco came to the region to harvest newly found pen shell beds only 5 km north of the reserve network, doubling the fishing effort for over a month. Since none of these fishers had fishing permits, local fishery officials illegally established financial quotas to allow them to fish, further increasing discontent among local fishers.

Changes were also manifested in other organizational matters. Participation in Cooperative meetings fell markedly. Between summer 2004 and December 2005, of 6

meetings only 1 had the minimum quorum necessary (50%+1) to make decisions recognized under the Cooperative's statutes. Learning about the results of monitoring efforts as well as of studies on the life histories of key commercial species also clearly lost priority within the Cooperative. Four members opted to leave and work under other permit holders or illegally. In addition, dive-related accidents increased as some divers ventured into deeper waters and extended their overall work hours.

More importantly, social ties that allowed for a rapid evolution of cooperation and local governance now facilitated overexploitation and rule breaking. As mentioned before, while cheating events were limited and easily accounted for, the system was maintained in check without necessarily threatening its social capital base. However, by this point everyone was to blame in some way or another. Accountability was no longer as obvious, and it was easier to fall into forms of apathy and lack of cooperation than to confront the problem. There were simply too many social ties to lose by confronting the problem since, by this point, everyone had broken a rule in some way or another. Key members of the group, for instance, stopped attending meetings in order to avoid encounters with specific people, at times family related.

The aftermath of what occurred in PP provides a different scenario. In summer, 2006, the Mexican government granted a fishing concession to the PP Cooperative, providing exclusive access rights to fishing grounds. There is a clear belief among fishers regarding the benefits of their reserves. These will be re-established by January 2007 coupled with other spatial-temporal management schemes after new ecosystem-based and

population assessments are implemented. Nevertheless, lessons that transcend this particular case study were already clear.

The Commons and Community-Based Marine Reserves

This case provides important insights to theory and practice surrounding local governance of the commons in young fishing societies and the effects of marine reserves. The tragedy of the commons, as coined by Hardin in his seminal essay (21) and addressed by others before him (see 22, 23), suggests that rational choice of individuals will tend towards maximizing profits from resources held in common before others do. It is most often argued, then, that the aggregated outcome of these individual decisions ultimately leads to inevitable overexploitation of natural resources unless privatization or government control are put into effect (21). However, here we show that local cooperation for governance of the commons in order to avoid overexploitation can emerge rapidly and that the realities and outcomes of commons situations can be much more complex and scale-dependent.

There have been various well-studied cases where communities have devised necessary rules and norms to avoid local overexploitation of natural resources (for reviews see 24, 11, 12). There is evidence that this has occurred even within large-scale complex landscape systems (25). However, the particular relevance of the PP case is three-fold.

First, it shows that cooperation for management of the commons, in which marine reserves form a core component of the system, can emerge and evolve rapidly in a young

fishery with limited or no experience in collective action. Secondly, we provide evidence of rapid effects of reserve networks on adjacent fisheries via larvae dispersal. However, we also show that reserve effects are not necessarily evident for an entire reserve network but can rather be markedly constricted in space. Thirdly, as robust and effective a CBM system with marine reserves may be, it is likely that this effectiveness may only last as long as the system remains bounded to its own local reality and buffered from external forces.

Governments and the conservation and academic communities alike are investing millions of dollars to foster CBM of coastal fisheries and the establishment of marine reserves, often with major difficulties in stakeholders' appropriation of management guidelines and large investments to a loss. In the specific case of the Gulf of California, a large network of marine reserves has been proposed (26). It is also a region where the fate of various small-scale fisheries is largely left to community-based arrangements^{**}. Given the worldwide and regional interest in marine reserves and CBM, we provide the following views.

Compliance for community-based establishment of area closures demands a great deal of social group strength. Not only do reserves reduce the total fishing area and initially render an economic cost to fishers, but they also complicate fishers' management of risk by reducing the physical spaces available to choose from in accordance to variations in environmental conditions and the state of their resources.

^{**} A review of the legislation showed 22 species-specific fishery norms, of which only 6 apply to species harvested by small-scale fishers in the Gulf of California. However, small-scale fishers in the Gulf target more than 100 species (www.pangas.arizona.edu).

It is therefore important that community-based efforts are initially implemented in systems where responses can be measured rapidly and where there is an existing social base for their establishment. This can be largely facilitated by a combination of a) the state of natural resources on which there is a high level of livelihood dependence (i.e. having experienced some form of downfall in these resources but not at a level such that it is useless for cooperation to emerge), b) fishers' previous tacit individual experimentation and local knowledge gained on the resources' response rate, c) direct influence of researchers or outside sources with established rapport, credibility, and trust amongst appropriators, and d) strong social capital and high levels of trust within appropriators. Furthermore, stakeholder participation in monitoring where there is a rapid feedback of the system's response can play a key role in reinforcing cooperation.

When a system proves to be promising for establishment of reserves, networks need to be designed so as to enhance or maintain local recruitment and not benefit other communities at the expense of local management initiatives and initial costly decisions. In some situations, this may not be possible as the oceanographic processes may render larvae export rather than retention within the community-based system. In addition, some areas even within the same regional landscape may respond in different time frames than others. Adaptive management structures should be implemented so as to incorporate these variations and not assume false expectations.

Nevertheless, even if community based reserves are effective within the biophysical and local context, their long-term success will rely on the system's capacity to control access. We argue that even in a small-scale setting like the one presented here,

with a tight knit, relatively homogenous, and self-enforcing group of fishermen, with a *de facto* fishing territory that is markedly isolated from other communities, local cooperation and social capital alone are likely not enough to sustain the efficacy of reserves. Fishers and fishing communities need to be granted, at the least, formal government recognition of territorial access rights and their locally-devised management structures should be given legal weight when they appear to be effective strategies. In essence, threats to the existent social capital base and open access situations with other fishing communities, coupled with insufficient government recognition of community-based initiatives and lags between local and government timeframes and interests are likely to be the main constraints for long-term success of locally managed marine reserves.

In this regard, current calls and efforts to revive and formally recognize customary marine tenure systems are an important step towards this direction (2), but much more remains to be done within a global context. In particular, we need to pay more attention to nascent fisheries or young fishing societies and communities in less isolated areas. This will surely represent a challenge as the concept of community and territorial use rights can be nebulous in these settings. Nevertheless, the costs of not doing so are much greater. In an increasingly globalized world economy, the existence of isolated and buffered fishing communities has been largely lost. Yet, as we show, effective community-based structures that include costly decisions like the establishment of marine reserves can emerge even in these settings. Not granting appropriate forms of territorial use rights nor formally recognizing effective local management structures and institutional arrangements, as simple or complex as these may be, could dismantle a

community's existing foundations for promising long-term sustainable use of fishery resources.

Acknowledgements

We thank the members of the *Sociedad Cooperativa Buzos de Puerto Punta Peñasco*, the Intercultural Center for the Study of Deserts and Oceans (CEDO), Olegario Morales, and Jennifer Rupnow for their invaluable assistance and participation in monitoring. Ana Cinti, Jennifer Duberstein, Victor Godínez, René Loaiza, Marcia Moreno, Arturo Ocampo, Martín Rivera, Refugio Salazar, and Gaspar Soria assisted in field oceanography work. This study was completed thanks to financial contributions from the Tinker Foundation, the David and Lucile Packard Foundation, as well as fellowships and scholarships to Cudney-Bueno from the Consejo Nacional de Ciencia y Tecnología (CONACYT), the Inter American Foundation, the Wallace Research Foundation, and the Environmental Leadership Program. Research was conducted under permits # DGOPA - 04693 - 150506 - 1832 from the *Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación* (SAGARPA), and SGPA/DGVS/13159 of the *Dirección General de Vida Silvestre; Secretaría de Medio Ambiente y Recursos Naturales* (SEMARNAT). This is contribution # 5 of Project PANGAS, www.pangas.arizona.edu.

References

1. National Research Council (2001) *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems* (National Academy Press, Washington, DC).
2. Johannes, R.E. (2002). *Annu. Rev. Ecol. Syst.* **33**, 317-340.
3. Agrawal, A. & Gibson, C.C. (1999) *World Development* **27**, 629-649.
4. Berkes, F., Hughes, T. P., Steneck, R. S., Wilson, J. A., Bellwood, D. R., Crona, B., Folke, C., Gunderson, L. H., Leslie, H. M., Norberg, J., Nyström, M., Olsson, P., Österblom, H., Scheffer, M. & Worm, B. (2006) *Science* **311**, 1557-1558.
5. Johannes, R.E. (1978) *Annu. Rev. Ecol. Syst.* **9**, 349-64.
6. Ostrom, E. (1990) *Governing the Commons: The Evolution of Institutions for Collective Action* (Cambridge University Press, New York, NY).
7. Agrawal, A. (2002) in *The Drama of the Commons*, Ostrom, E., Dietz, T., Dolsak, N., Stern, P.C., Stonich, S. & Weber, E. U. (National Academy Press, Washington, DC).
8. Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P. & Goodridge, R. (2001) *Science* **294**, 1920-1923.
9. Roberts, C. & Hawkins, J. P. (2000) *Fully-protected Marine Reserves: A Guide*. WWF Endangered Seas Campaign, 1250 24th Street, NW, Washington D.C., 20037, USA and Environment Department, University of York, York, YO105DD, UK.
10. Russ, G.R., Alcalá, A.C., Maypa, A.P., Calumpans, H.P. & White, A.T (2004). *Ecological Applications* **14**: 597-606.
11. Gaines, S.D., Gaylord, B. & Largier, J. L. (2003) *Ecological Applications* **13**, S32-S46.

12. Hastings, A. & Botsforth, L. W. (2003) *Ecological Applications* **13**, S65-S70.
13. Cudney-Bueno, R. (2000). *Management and conservation of benthic resources harvested by small-scale hookah divers in the northern Gulf of California, Mexico: The black murex snail fishery* (MS Thesis, School of Renewable Natural Resources, The University of Arizona, Tucson, AZ).
14. Instituto Nacional de la Pesca (2004) *Carta Nacional Pesquera* (Instituto Nacional de la Pesca, México).
15. Baqueiro, E., Massó, J.A., & Guajardo, H. (1988). *Distribución y Abundancia de Moluscos de Importancia Comercial en Baja California Sur* (Instituto Nacional de la Pesca, México).
16. Marinone, S. G., Gutiérrez, O. Q. & Parés-Sierra, A. (2004) *Estuarine, Coastal, Shelf Sciences* **60**: 611-617.
17. Cowen, R.K., Paris, C.B. & Srinivasan, A. (2006) *Science* **311**, 522-527.
18. Cudney-Bueno, R. 2007. PhD Dissertation, University of Arizona, Tucson, Arizona.
19. Torre, J. Director of Operations, Comunidad y Biodiversidad A.C. www.cobi.org.mx.
Personal communication.
20. Villalejo-Fuerte, Arellano-Martinez, M., Ceballos-Vázquez B.P. & García-Domínguez, F. (2002) *Jornal of Shellfish Research* 21: 103-108.
21. Hardin, G. (1968) *Science* **162**, 1243-1248.
22. Gordon, H.S. (1954) *Journal of Political Economy* **62**, 124-142.
23. Scott, A. D. (1955) *Journal of Political Economy*. **63**,116-124.

24. McCay, B. & Acheson, J. (1987) *The Question of the Commons: The Culture and Ecology of Communal Resources*, eds. McCay, B. & Acheson, J.M. (The University of Arizona Press, Tucson, AZ).
25. Lansing, J. S. (1991) *Priests and Programmers: Technologies of Power in the Engineered Landscape of Bali* (Princeton University Press).
26. Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J. C., & Dayton, P. K. (2002) *Science* **298**, 1991-1993.

Figure D1. Location of Puerto Peñasco community-based reserves and monitored fishing areas.

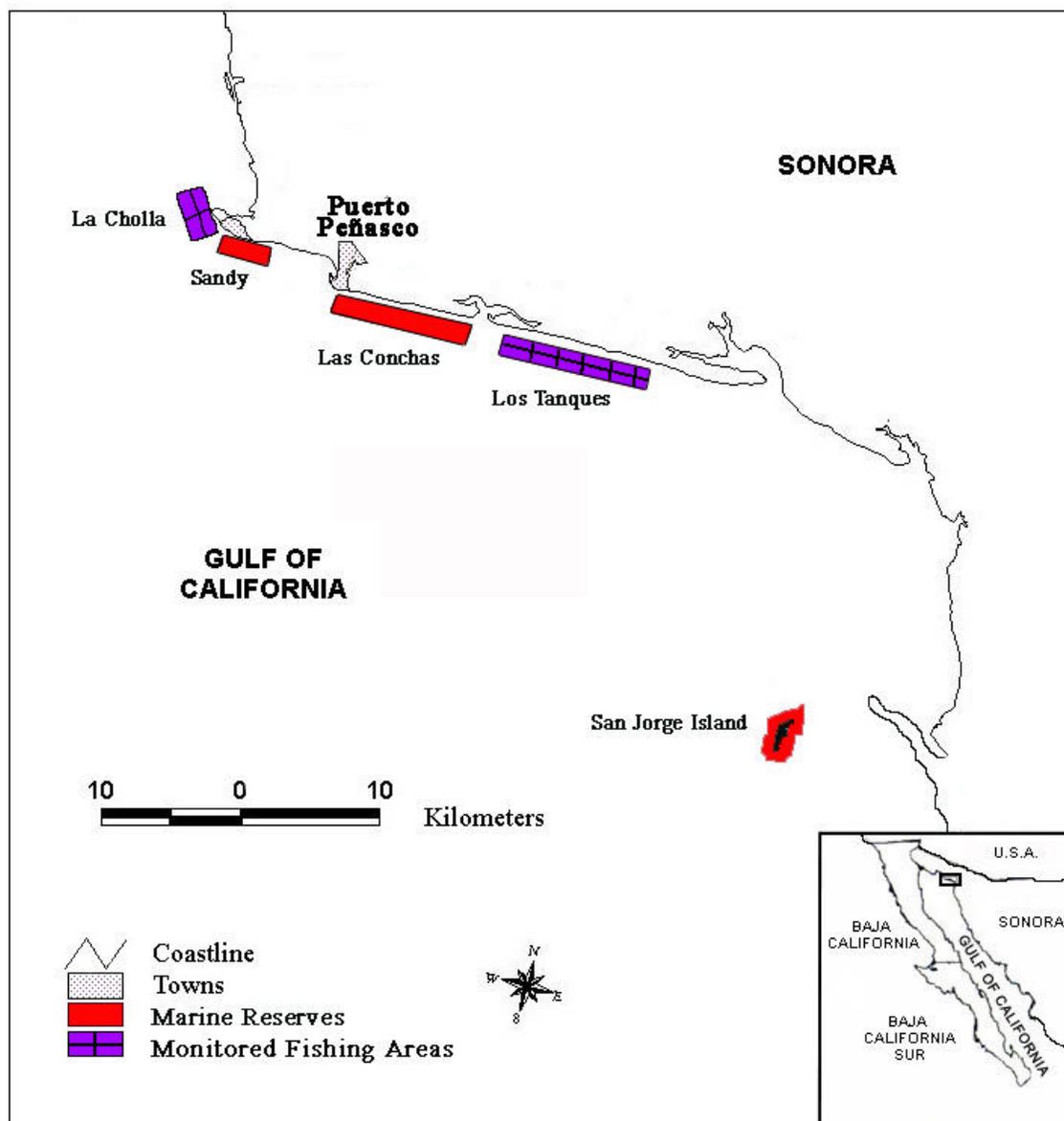


Figure D2. Density (number of individuals per 100 m²) of observed juvenile black murex (*Hexaplex nigritus*) and rock scallops (*Spondylus calcifer*) in marine reserves and fishing sites combined (mean \pm S.E.).

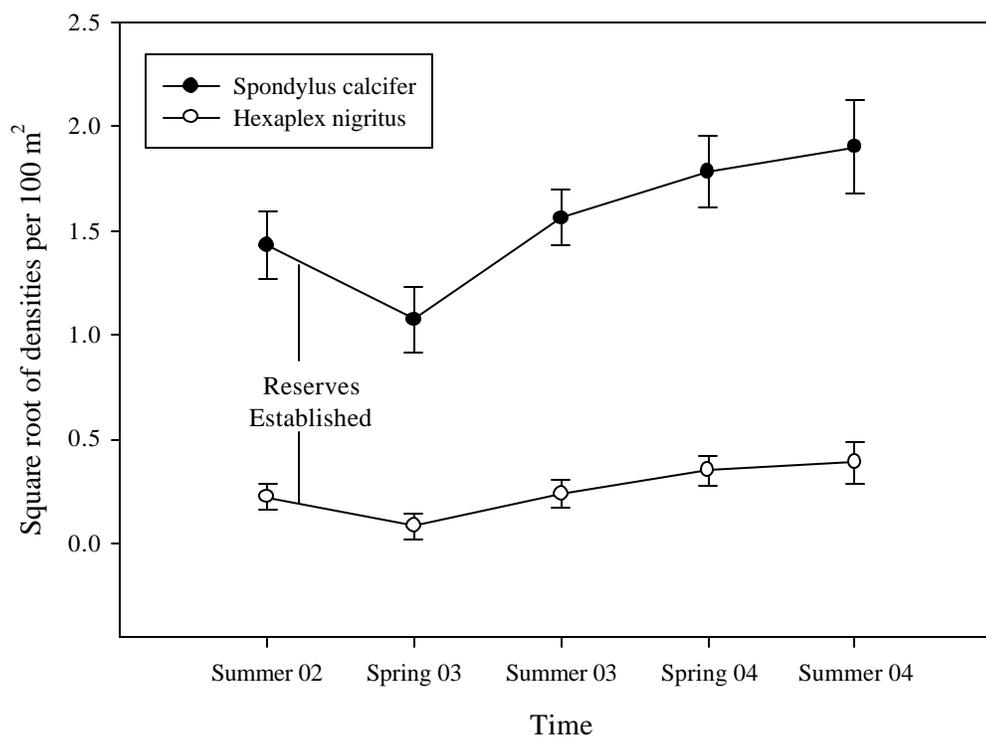


Figure D3a. Differences in spatial signatures of the effects of marine reserves on the density of juvenile rock scallops (*Spondylus calcifer*) in the northern Gulf of California, Mexico (mean \pm within treatment S.E.)

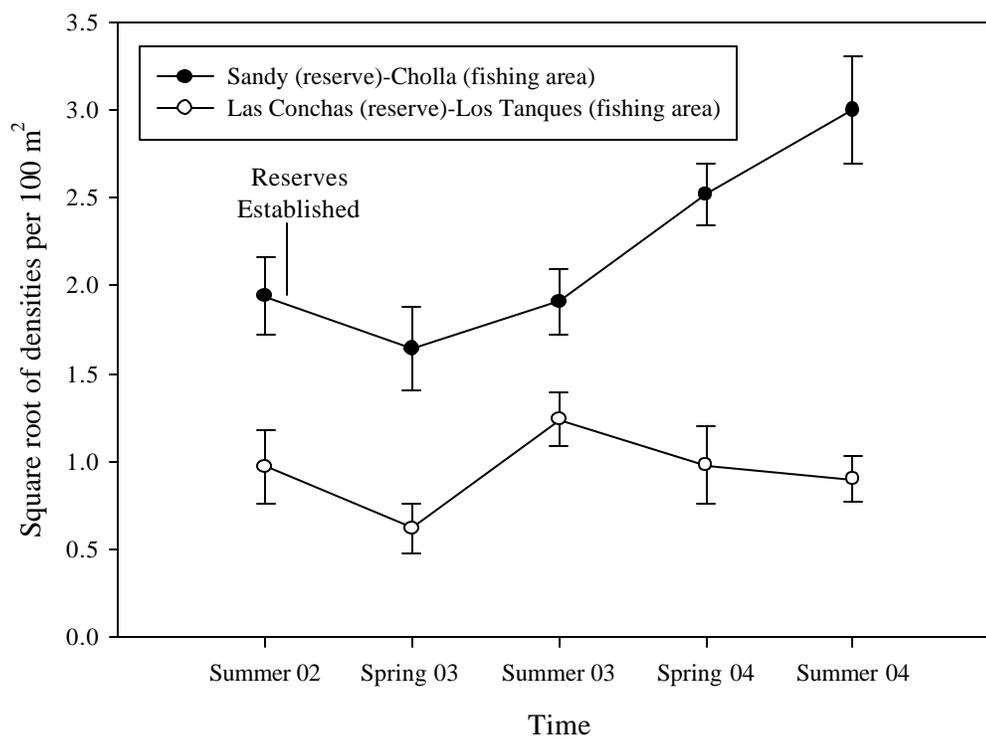


Figure D3b. Differences in spatial signatures of the effects of marine reserves on the density of juvenile black murex (*Hexaplex nigritus*) in the northern Gulf of California, Mexico (mean \pm within treatment S.E.)

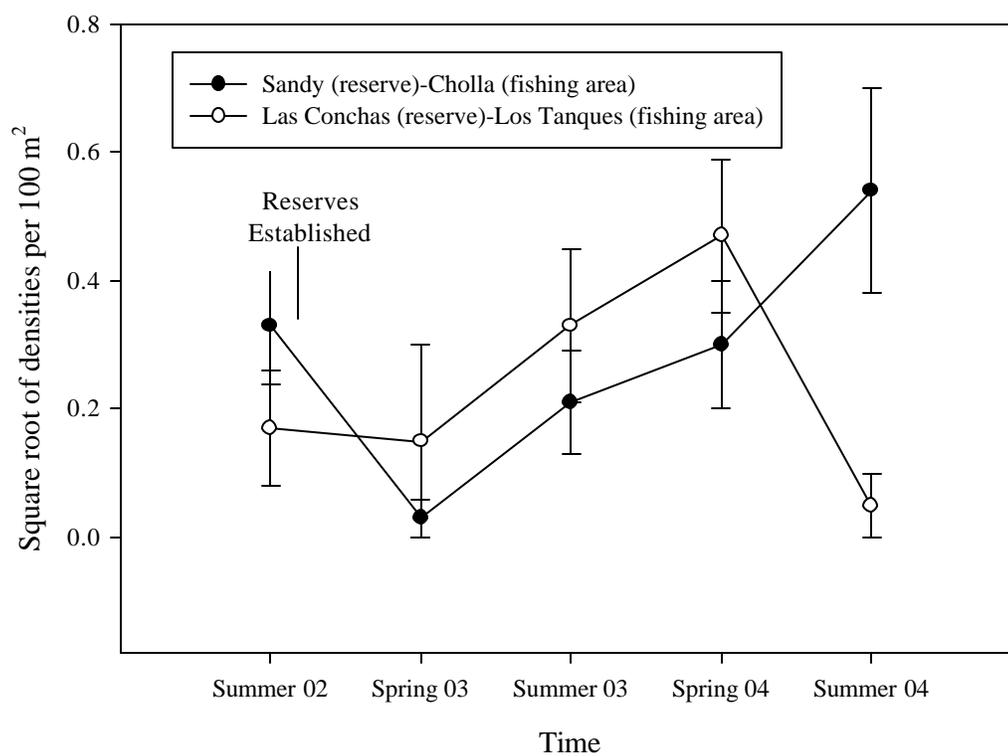


Figure D4. Final position of particles 2 and 4 weeks after having been released in (a) the nearest rocky reef located south of the marine reserve network, and (b) the network's southern boundary.

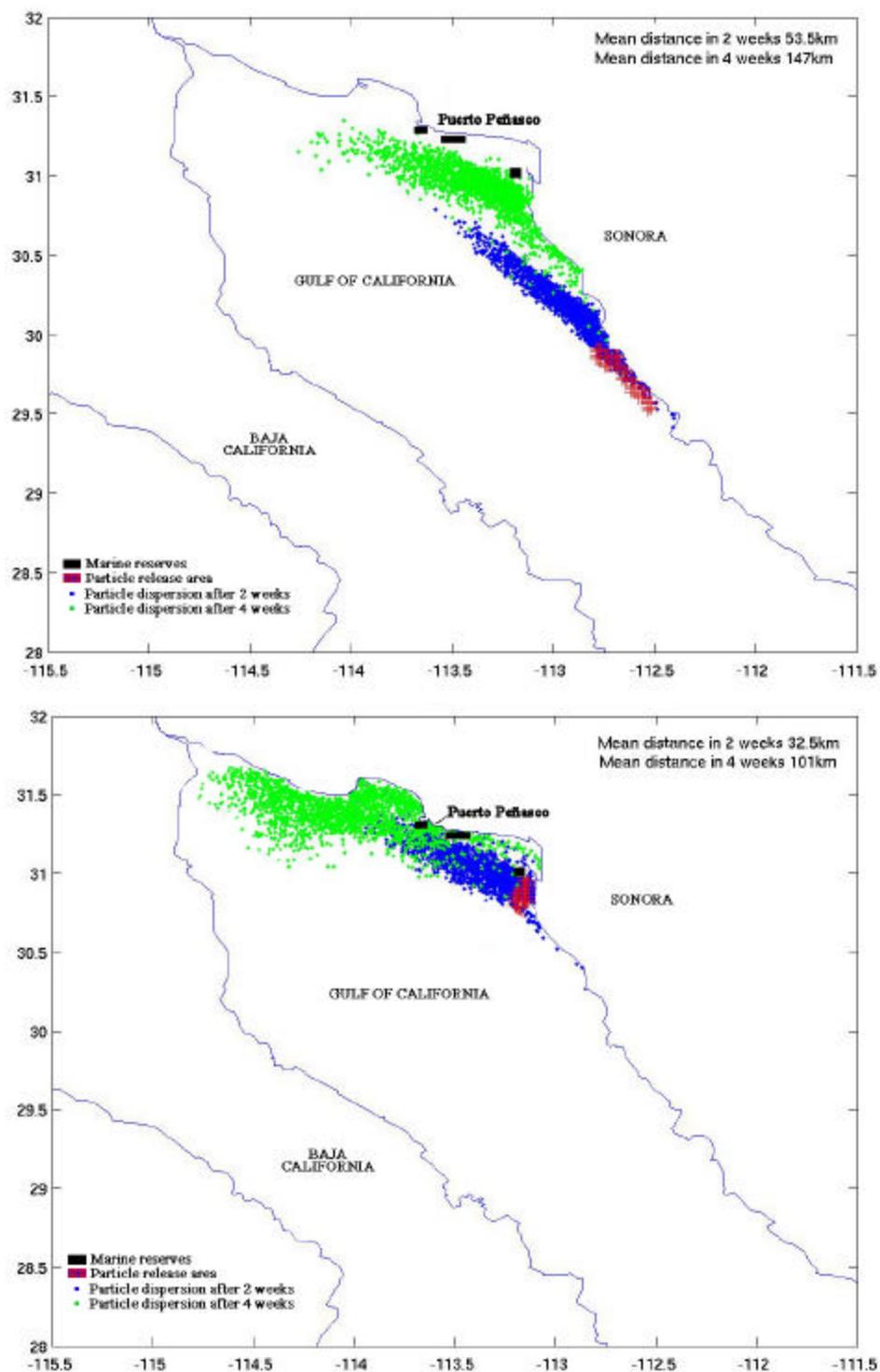


Figure D5. Trajectory of satellite-tracked drifters released near San Jorge Island, July 12-14 2006. Note tidal ellipses and Northwest direction of residual current. Coastal reserves begin ~35 km Northwest of the drifters. Color gradients represent depth range (0-60 m).

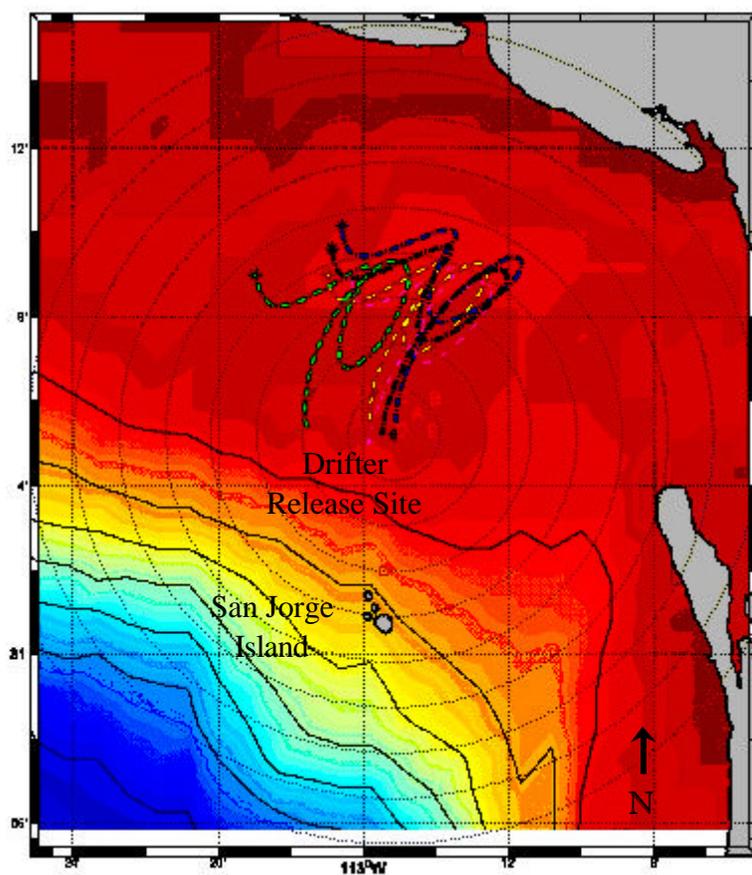


Figure D6a. Comparison of the average adductor muscle weight and length of rock scallops (*Spondylus calcifer*) from fishing areas in the northern Gulf of California between 2002-2004. Data from reserves was not obtained as animals would need to be sacrificed.

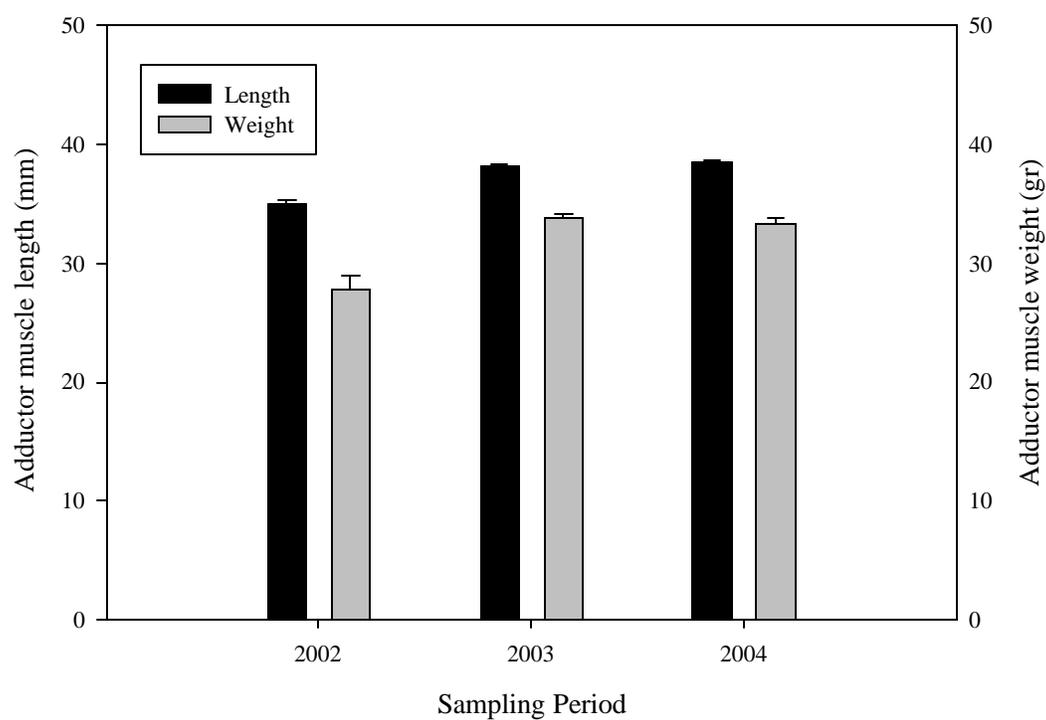


Figure D6b. Comparison of the average live weight of black murex snails (*Hexaplex nigritus*) from reserve and fishing areas in the northern Gulf of California between 1999 (pre-establishment of reserves) and 2003-2004 (post-establishment of reserves).

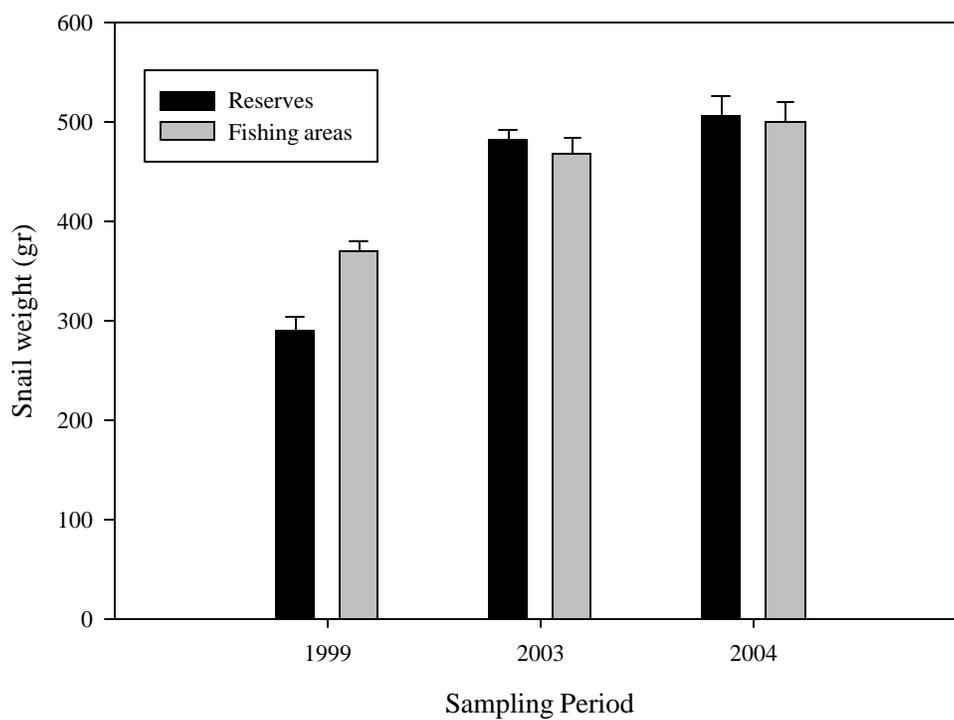


Table D1. Fishers' opinions and attitudes towards their community-based reserves.

Interviews made one year and a half after the establishment of reserves to 95% of fishers.

Opinions on the Effects of Reserves	Yes (%)	No (%)	Don't Know
Are your reserves giving you good results?	100	0	0
Will reserves increase production in fishing areas?	89	11	0
Will reserves bring you more financial gains?	94	6	0
Would you continue having reserves?	94	0	6

Table D2. Rules developed, *de facto* (*df*) and formal (*f*) sanction types, and levels of rule compliance before and after entrance of outsiders into the Puerto Peñasco marine reserve network. Time A= summer 2001-summer 2004, Time B = first six months after entrance of outsiders. Compliance levels based on percentage of fishers known to have broken the rule at least once. 1 = very low (<10%), 2 = low (10-40%), 3 = moderate (41-60%), 4 = high (61-90%), 5 = very high (>90%).

Rule Type	Sanction Types	Compliance Time A	Compliance Time B
<i>Resource-based Rules</i>			
Snail fishing banned May-July	On site personal warnings (<i>df</i>) Peer pressure/public shame during meetings (<i>df</i>)	1	5
Fishing banned within marine reserve network	On site verbal confrontations (<i>df</i>) On site warnings and verbal confrontations (<i>df</i>) Peer pressure/public shame during meetings (<i>df</i>)	1	5
Harvest octopus once it reaches large size/higher value	Threats of temporary confiscation of boat (<i>f</i>) Threats of expulsion from the cooperative (<i>f</i>) Peer pressure/public shame during meetings (<i>df</i>)	3	4
<i>Dive Safety Rules</i>			
Reduce air compressor emissions	N/A: Individual choice	3	4
Increase air intake tube height	N/A: Individual choice	3	4
Establish safety decompression stops	N/A: Individual choice	2	4
<i>Monitoring</i>			
Participation in monitoring	Peer pressure/public shame during meetings (<i>df</i>) Extend rule breaker's monitoring responsibilities (<i>f</i>)	1	5
Financial support for monitoring	Peer pressure/public shame during meetings (<i>f</i>)	1	5
<i>Administrative Rules</i>			
Participation in all meetings	Peer pressure/public shame during meetings (<i>df</i>) Threat of expulsion from cooperative after 3 faults (<i>f</i>) Temporary confiscation of boat (<i>f</i>)	1	4
Monthly financial contribution	Peer pressure/public shame during meetings (<i>df</i>) Threat of expulsion from cooperative (<i>f</i>)	2	5
Providing paperwork necessary for the Cooperative	Peer pressure/public shame during meetings (<i>df</i>) Threat of expulsion from the Cooperative (<i>f</i>) Expulsion from the Cooperative (<i>f</i>)	2	2

Table D3. Example of fishers' responses to the open-ended question "*In what way does breaking an agreement of the Cooperative affect you?*"

-
- Fisher 1.** I would make enemies and loose help from others.
- Fisher 2.** The reserves would soon be terminated. There would be a chain reaction and nothing would be left for our future.
- Fisher 3.** I would feel guilty. I would be stealing. It would affect me morally. I would feel bad morally.
- Fisher 4.** I would be hurting myself and harming my own future.
- Fisher 5.** The group would be disappointed in me and I would harm my future.
- Fisher 6.** I would harm myself and the word that I gave.
- Fisher 7.** I would disappoint my friends.
- Fisher 8.** I would loose friends.
- Fisher 9.** The other members of the group would stop trusting me.
- Fisher 10.** I would be harming everyone else.
- Fisher 11.** I would just feel bad.
- Fisher 12.** It would affect me in the moral sense because I broke my word.
- Fisher 13.** It would affect me morally.
- Fisher 14.** It harms me morally. I would feel guilty.
- Fisher 15.** It would affect me morally.
- Fisher 16.** I would be pressured by the group wherever I'm seen.
-

APPENDIX E

ONLINE SUPPORTING MATERIALS FOR APPENDIX D

Manuscript: Rapid Effects of Marine Reserves and the Rise and Fall of Cooperation in a Young Fishery

Authors: R. Cudney-Bueno, M. F. Lavín, S. G. Marinone, W. W. Shaw

I. Summary of Methods Used for Analysis of Marine Reserves

Our research followed a mixed method approach that combined qualitative and quantitative field research in the social and biophysical sciences as well as development of numerical oceanographic models. At the broadest level, our findings build on social and ecological research with commercial divers of Puerto Peñasco (Conducted by Cudney-Bueno) before (1997-2001), during (2002) and after (2003-2004) the establishment of locally-defined marine reserves. This timeframe entails more than 600 days living in PP, participation in 147 commercial diving trips, and attending 30 meetings of the *Sociedad Cooperativa Buzos de Puerto Punta Peñasco*, Puerto Peñasco's divers' fishing cooperative.

Research was based on principles of participatory research (PR) (1), where stakeholders are actively involved in research and decision-making. Fishers formed part of the research process by having designed and established their marine reserves and monitored the state of their fishery resources within these. Before monitoring began, commercial divers were trained by R. Cudney-Bueno. All monitoring was conducted by

divers in collaboration with academic researchers. Monitoring results were presented to fishers through group meetings and at an individual level in order to obtain their feedback and contrast quantitative findings with fishers' observations.

Following is a detailed description of some of the methods used to address the effects and evolution of the Puerto Peñasco community-based marine reserve initiative.

1.1 Social Research

Having had the time to build sufficient rapport and trust with local fishers, research built on standard long-term ethnographic approaches. It relied heavily on participant observation, informal and semi-structured interviews, community mapping, and oral histories with fishers. It also relied on underwater monitoring of benthic resources, monitoring of fishery catches, and studies on the reproductive ecology and natural history of the main species targeted.

We were regularly engaged in participant observation, participated in 147 fishing trips, helped fishers in their day-to-day activities, and attended social gatherings and 30 cooperative meetings. This allowed us to obtain a comprehensive understanding of the diving fishery, how divers define and enforce rules and regulations, record the presence or absence of free-riding (poaching) events, and note if conflict resolution and consensus-building processes were facilitated or halted.

Ethnographic research on the Puerto Peñasco diving fishery began 5 years before the establishment of marine reserves, which allowed us to understand the system's social dynamics prior to and after the establishment of reserves. Between Summer 2003-2004,

we conducted fieldwork specifically targeted to address a) if current collective action for the establishment of marine reserves indeed developed quickly and with no or very limited previous experience to define and/or establish collective management decisions, and b) the conditions that facilitated and led to the establishment of community-based management efforts.

We complemented our qualitative research with structured interviews.

Throughout March and at the beginning of April 2004, we conducted structured interviews with 95% of the members of the diving cooperative of Peñasco. These interviews addressed various issues related to the effect of marine reserves and changes in social capital among fishers such as:

- Changes in spatial-temporal distribution of commercial diving activities.
- Changes in catch per unit of effort (production/boat/fishing trip).
- Fishers' perceptions on the efficacy of their management efforts.
- Factors affecting the evolution of cooperation among the cooperative.
- Level of trust between cooperative members.

Interviews also addressed issues related to fishers' local ecological knowledge, personal histories, and dive decompression-related problems. We conducted all interviews at fishers' homes. We supplemented this information through oral histories, through which we searched for previous cooperative efforts and key past events or situations that could have shaped fishers' interests in adopting more conservation-oriented measures. Oral histories also allowed us to single out and understand relevant

issues that may not be as clearly or obviously identified with the use of directed questions.

1.2 Estimation of Population Parameters

We estimated changes in density of black murex snail (*Hexaplex nigritus*) and rock scallop (*Spondylus calcifer*) in reserve and fishing sites for two consecutive years beginning in Summer 2002, the moment reserves were established. These species were selected for being the main species targeted by the commercial diving fishery and representing the main reason leading to the establishment of the community-based reserves.

Sampling Frame and Strategy

The area monitored encompassed the reefs of San Jorge Island and those found near the fishing town of Puerto Peñasco (within 3km from highest tide line) in the eastern part of the northern Gulf of California, Mexico. This area extends from 31,22,18.1 N; 113,39,09.4 W to 31,15,03.8 N; 113,20,48.1 W.

We subdivided the area into 5 sampling sites: a) two coastal reserves (replicates), Las Conchas and Sandy Beach; b) two coastal comparison sites (“controls”), Los Tanques and La Cholla-Cerro Prieto; c) one offshore island reserve, San Jorge Island (Figure 1). For analysis purposes, we paired the coastal reserves with appropriate comparison sites (Sandy Beach with La Cholla-Cerro Prieto and Las Conchas with Los Tanques). Each of these pairs is referred to as a “treatment”. Given the lack of adequate

comparison sites for San Jorge island, we analyzed the response of this off-shore reserve independently.

To reduce heterogeneity associated with depth, we restricted all sampling to depths ranging from 40-65 ft. This also reduced health risks associated with diving and facilitated overall monitoring as we were able to remain underwater for longer periods of time. In all cases except San Jorge Island, this depth as well as the established constrained distance from the tide line covers the entire extension of the reefs. We restricted sampling in San Jorge Island to the reefs found on the eastern part of the island, as these are shallower and more similar to those found on the mainland coast.

Plot Design and Sample Unit Selection

We selected plots from within these constricted areas through simple random sampling. In the event that a specific plot selected happened to fall in an area where at least 50% of sand was present, that plot was replaced by another one by swimming underwater in a straight line along the reef until reaching sufficient (>50%) rocky substrate. Once selected, all plots were permanently marked underwater.

Use of 10 x 10 m plots subdivided into 16 quadrants of 2.5 x 2.5 m (for ease of observation) is the best choice for sampling these reefs. Testing other sampling methods such as the use of 5 x 50 m or 5 x 30 m transects, distance sampling or others typically used for sessile organisms did not prove adequate for the study area given the highly variable visibility of the region, the strong currents, and the overall patchiness of the reefs (i.e. patches of reef typically separated by patches of sand).

We counted all individuals visible within each 2.5 x 2.5 m quadrant (subplot). For rock scallop, size of each individual was estimated to fall within one of three categories: small juveniles (up to 5 cm of height), medium-sized juveniles and young adults (>5 and <10 cm of height), and large adults (>10 cm of height). For black murex, sizes fell into two categories: pre-adults and reproductively mature adults. To reduce variation in detectability, the same person counted organisms on each sampling occasion and in the same designated plots while another diver assisted setting and maintaining the plot lines in place. To support this work, ten commercial divers with extensive experience searching for benthic mollusks (>5 years) were trained to participate in the monitoring process. We calculated variations in the detection of monitored species ($s = 3$ individuals/plot) and incorporated this variation to calculate statistical power of our sampling design (see below).

Sampling Frequency, Sample Sizes, and Allocation of Samples

We established a total of 58 sampling plots: San Jorge = 10, Las Conchas = 10, Los Tanques = 10, Sandy = 10, La Cholla-Cerro Prieto = 18. Power analysis from baseline data on density of rock scallops found on these 58 plots gave us a high probability of detecting at least a 10% increase in their density (Power > 95 % for each reserve and fishing zone, $\alpha = 0.05$ and $s = 3$ individuals/plot). Given that rock scallops are harder to detect than black murex (when closed they look like rocks), we assume an even higher statistical power for detection of changes in population densities of black murex.

We monitored each plot twice every year (Spring and Summer) for two consecutive years (Summer 2002, Spring 03, Summer 03, Spring 04, Summer 04). These months provide some of the best visibility underwater and are also usually devoid of algae beds covering the rocky reefs, which reduce detectability of species monitored.

This is a longitudinal study with a repeated measures research design and various levels of analysis. We first generated profile plots of baseline data and applied square root transformations to improve homogeneity of variance. We then addressed “between subject” and “within subject” variability of baseline data graphically, determined the coefficient of variation, and tested for independence of plots and sampling sites in order to avoid pseudoreplication scenarios. We used multivariate analyses of variance (MANOVA) and relied on Multivariate Pillai’s Trace P values to help assess time, site, and protection effects independently as well as combined factors. Univariate estimates were also obtained and analyzed to further understand observed patterns.

1.3 Estimating Changes in Size and Weight of Harvested Commercial Species

We estimated changes in the size and weight of adult (harvested) black murex and rock scallop. For black murex, we collected specimens (n=244) from breeding aggregations of reserve and fishing sites before the establishment of reserves (Summer 1999) and after their establishment (Summer 2003 and 2004). All snails from reserves were returned to the collecting site, whereas snails from fishing sites were obtained from fishers’ catches.

For rock scallop, we estimated changes in average size and weight of the adductor muscle, the part of the animal that is commercialized and that fishers return to port. Since the only way of obtaining samples of the adductor muscle is by killing the animal, we limited our samples and analyses to fishing sites. All samples were constricted to Spring (post reproduction) to avoid variations in weight and size caused by glycogen accumulation in the muscle pre and post reproduction. We obtained a total of 1081 samples of rock scallop from Spring 2002-2004. Both black murex and rock scallop data were analyzed using 1-way ANOVAs and Tukey's HSD multiple comparison test to determine pairwise relationships.

1.4 Particle Tracking from a Three Dimensional Oceanographic Numerical Model

We calculated connectivity matrices in the northern Gulf of California from currents produced by a three-dimensional baroclinic numerical model and a random walk process to simulate turbulent motions. We released 2000 hypothetical passive particles in each of 2 areas (between 0-60 m deep): San Jorge Island, and the nearest substantial rocky reef south of the Puerto Peñasco marine reserve network. We chose to use 2000 particles after having run the model with larger numbers of particles and concluding that the connectivity matrices were very similar.

We tracked each set of particles for up to two and four weeks. The field of currents used to conduct particle tracking was obtained from a 3D baroclinic numerical model (2). The temporal scales resolved by the model (due to forcing) were tidal and seasonal.

Particle trajectories were obtained by time-integrating the velocity field from a three-dimensional baroclinic Hamburg Shelf Ocean Model (HAMSOM) (3). The model is described in detail for the Gulf of California by Marinone (2) and Mateos et al. (4), and in general references therein. The model domain has a mesh size of 2.5' x 2.5' (~3.9 x 4.6 km) in the horizontal and 12 layers in the vertical with nominal lower levels at 10, 20, 30, 60, 100, 150, 200, 250, 350, 600, 1000 and 4000 m. The model equations are solved semi-implicitly with fully prognostic temperature and salinity fields, thus allowing time-dependent baroclinic motions.

The model is started from rest with a time step of 300 s; it is forced with tides, climatological winds, climatological hydrography at the mouth of the gulf of California, and climatological heat and fresh water fluxes at the air-sea interface. It becomes periodically stable after three years and the results for this study were obtained from the fourth year of the model. As shown by Marinone (2), the model adequately reproduces the main seasonal signals of surface temperature, heat balance, tidal elevation and surface circulation in the NGC as reported by Lavín et al. (5).

To help test model outputs, we deployed 6 satellite-tracked surface drifters between San Jorge Island and the coastline. Several deployments were made between July 12-23, 2006. In addition, we submerged an Acoustic Current Profiler (ADCP) at 24 m in the same site where drifters were released. The ADCP gave us information on speed and direction of the current at various depth intervals for June 2-July 4 and July 6-August 18, 2006. We constructed Progressive Vector Diagrams (PVD) by calculating the vector displacement that a water parcel would experience during each sampling interval.

II. Additional Statistics and Figures

Table E1. Univariate and multivariate tests for the analysis of temporal changes in density of juvenile rock scallops found within monitored reserve and fishing sites.

Tests	Value	F	Num DF	Den DF	P
Time					
Univariate unadjusted Epsilon	1	6.85	4	171	<.0001
Univariate G-G Epsilon	0.80	6.85	3.20	140.98	0.0002
Univariate H-F Epsilon	0.93	6.85	3.72	163.71	<.0001
Multivariate Pillai's Trace	0.59	6.07	4	41	0.0006
Time X Treatment					
Univariate unadjusted Epsilon	1	6.13	4	171	0.0001
Univariate G-G Epsilon	0.80	6.13	3.20	140.98	0.0004
Univariate H-F Epsilon	0.93	6.13	3.72	163.71	0.0002
Multivariate Pillai's Trace	0.69	7.09	4	41	0.0002
Time X Protection					
Univariate unadjusted Epsilon	1	2.35	4	171	0.05
Univariate G-G Epsilon	0.80	2.35	3.20	140.98	0.07
Univariate H-F Epsilon	0.93	2.35	3.72	163.71	0.06
Multivariate Pillai's Trace	0.26	2.67	4	41	0.04
Time X Treatment X Protection					
Univariate unadjusted Epsilon	1	2.99	4	171	0.02
Univariate G-G Epsilon	0.80	2.99	3.20	140.98	0.02
Univariate H-F Epsilon	0.93	2.99	3.72	163.71	0.02
Multivariate Pillai's Trace	0.24	2.53	4	41	0.05

Table E2. Univariate and multivariate tests for the analysis of temporal changes in density of juvenile black murex found within monitored reserve and fishing sites.

Tests	Value	F	Num DF	Den DF	P
Time					
Univariate unadjusted Epsilon	1	2.03	4	176	0.09
Univariate G-G Epsilon	0.86	2.03	4	151.89	0.10
Univariate H-F Epsilon	1	2.03	3.45	176	0.09
Multivariate Pillai's Trace	0.18	1.91	4	41	0.12
Time X Treatment					
Univariate unadjusted Epsilon	1	3.42	4	176	0.01
Univariate G-G Epsilon	0.86	3.42	4	151.89	0.01
Univariate H-F Epsilon	1	3.42	3.45	176	0.01
Multivariate Pillai's Trace	0.28	2.95	4	41	0.03
Time X Protection					
Univariate unadjusted Epsilon	1	2.79	4	176	0.02
Univariate G-G Epsilon	0.86	2.79	4	151.89	0.03
Univariate H-F Epsilon	1	2.79	3.45	176	0.02
Multivariate Pillai's Trace	0.32	3.28	4	41	0.01
Time X Treatment X Protection					
Univariate unadjusted Epsilon	1	3.34	4	176	0.01
Univariate G-G Epsilon	0.86	3.34	4	151.89	0.01
Univariate H-F Epsilon	1	3.34	3.45	176	0.01
Multivariate Pillai's Trace	0.29	3.02	4	41	0.02

Figure E1. Changes in density of observed juvenile rock scallop (*Spondylus calcifer*) in marine reserves and fishing sites in the northern Gulf of California, Mexico (mean \pm S.E.)

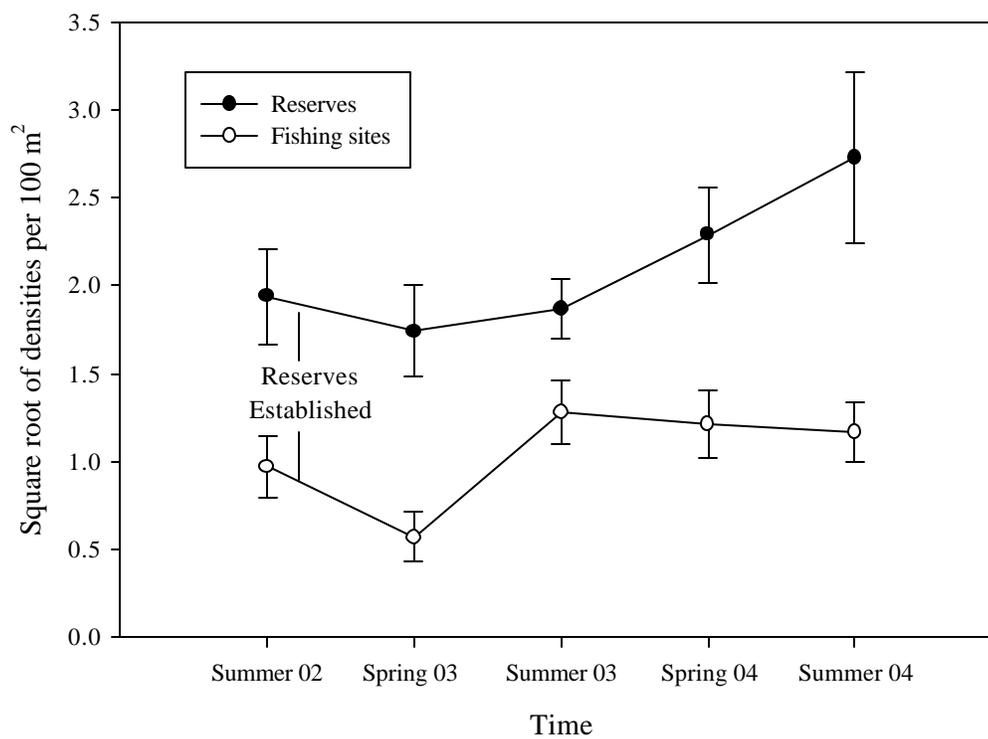


Figure E2. Changes in density of observed juvenile black murex (*Hexaplex nigrinus*) in marine reserves and fishing sites of the northern Gulf of California, Mexico (mean \pm S.E.)

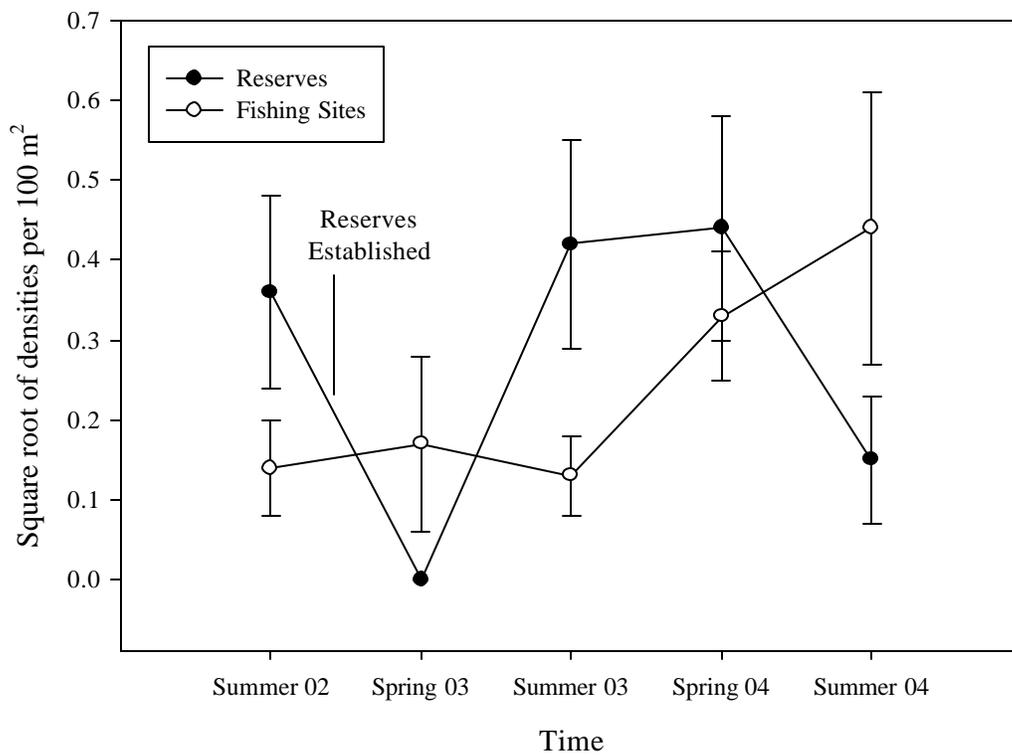


Figure E3. Comparison of the average total length of black murex snails (*Hexaplex nigritus*) from reserve and fishing areas in the northern Gulf of California before and after establishment of reserves.

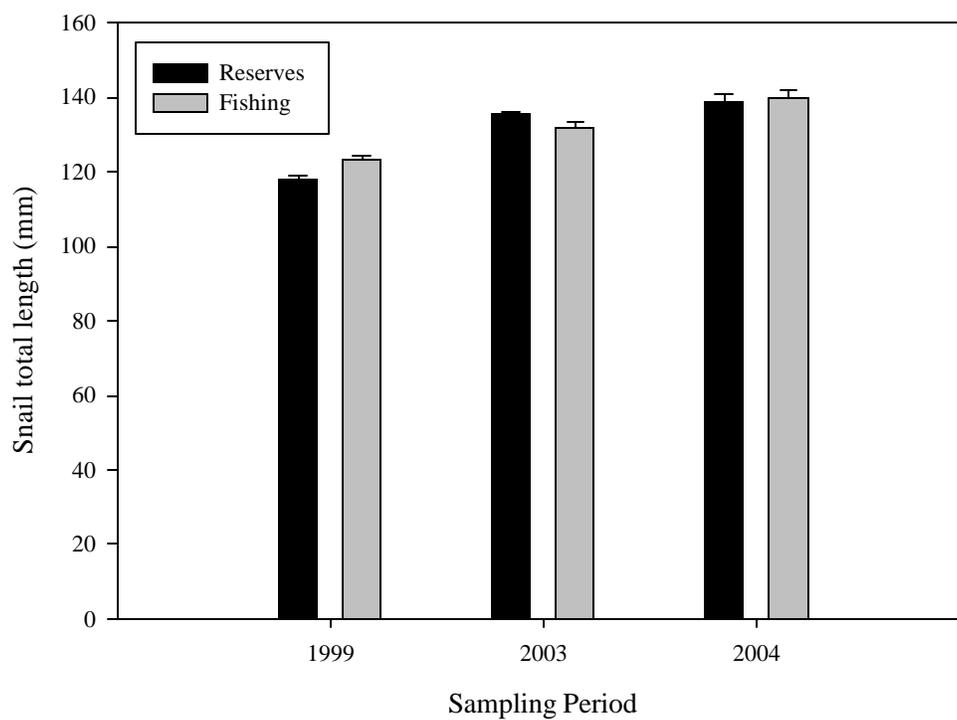
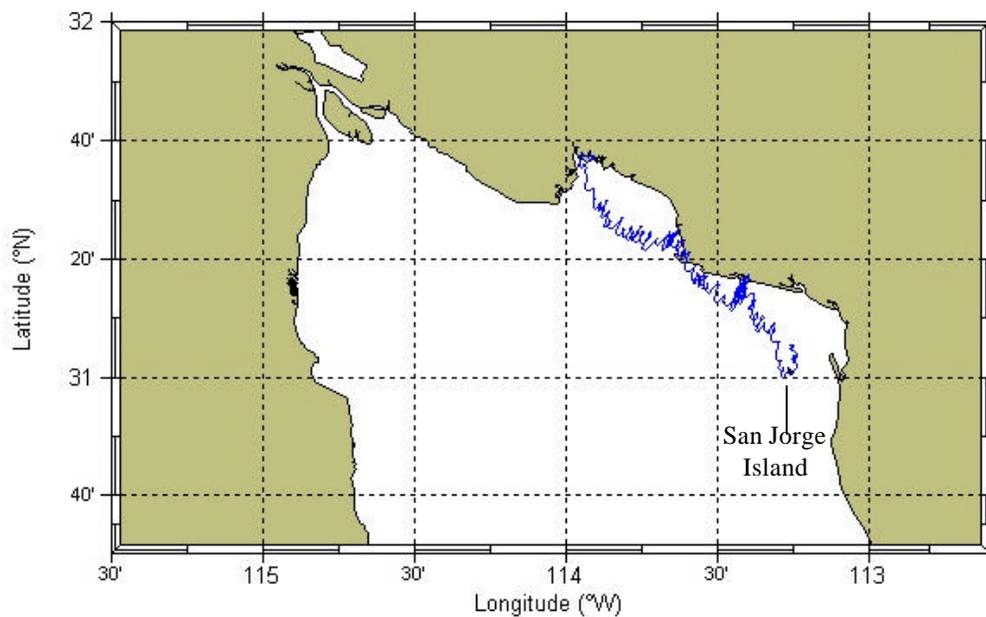


Figure E4. Progressive vector diagram of data obtained from an ADCP (Acoustic Doppler Current Profiler). The ADCP was maintained submerged in the area where drifters were released. Data is from the first 10 m interval and progression follows the period of June 2 – August 18 2006 (except July 5).



III. Summary of the History of Development of Diving Fisheries in Puerto Peñasco

The community of Puerto Peñasco lies in the northeastern portion of the Gulf of California, Mexico. It lies within one of the most productive bodies of water in Mexico (5) and borders the Upper Gulf of California and Colorado River Delta Biosphere Reserve.

Although harvesting of coastal resources for local consumption and trading amongst indigenous tribes took place for hundreds of years, commercial fishing as an organized endeavor did not develop in the upper Gulf of California until the advent of the early 20th Century. In the early 1920's and 30's, Mexican fishers from southern states migrated to the upper Gulf's rich waters primarily for the harvest of totoaba (*Totoaba macdonaldi*), an endemic species of large croaker that spawns in the Colorado River Delta. In only 70 years, however, commercial fishing in the region has been markedly transformed. This is particularly true for the small-scale fishery sector, which practices have shifted drastically as a result of government policies, market changes, and the region's state of natural resources. In this time frame, small-scale fisheries have evolved from being a relatively mono-specific (targeting a few species) endeavor, using a low diversity of gear types and methods, to enterprises that target over 100 species, with a high diversity of gear types and methods.

Possibly no other small-scale fishery sector exemplifies this diversity and rapid change as the commercial diving sector of PP. Using a hookah rig – a modified paint-spraying machine as an air compressor, 100m long hoses and diving regulators - PP divers have been harvesting benthic resources since the late 1970's and early 80's (6).

Most of this activity takes place within relatively flat and patchy rocky and coquina (beach rock) reefs that are unique to this region. Added up, these reefs cover a vast area that harbors some of the most productive grounds of commercial mollusks and reef fish in the Gulf of California.

The beginnings of diving in PP can be traced back to the late 1960's and the early 1970's in the fishing town of Bahía de Kino, Sonora, ~400 km south of PP along the coast with the advent of the development of the aqualung system*. The numerous islands offshore from Bahía de Kino, known as the Midriff islands, supported a rich ecosystem ideal for the harvest of benthic resources such as lobster (*Panulirus* spp.), octopus (*Octopus* spp.), lion's paw scallop (*Lyropecten subnodosus*), rock scallop (*Spondylus* spp.), and pen shells (*Pinna rugosa*, *Pinna tuberculosa*, and *Atrina maura*). Bahía de Kino, being the gateway to the Midriff island region, acted as a magnet for the development of diving fisheries and became one of the source points for the expansion of this activity throughout middle and northern Sonora.

Diving activities in those days occurred mainly from May to August, during the annual season closure of shrimp. Since the shrimp fishery was particularly profitable, many divers actively participated in the shrimp fishery throughout most of the year. Once the season ended, about 9 trawler boats were used as mother ships, traveling around the islands

* From the 16th through the 18th Century a lucrative pearl diving fishery developed in the Gulf of California (7). Nevertheless, this industry was largely constricted to the Southern Gulf and was conducted primarily by Yaqui Indian slaves free diving (8). There is no evidence that commercial hookah diving developed as a continuation of early free diving enterprises and there are no indications of any commercial diving enterprises (whether free diving or using some form of air-supplied system) developing in the northern Gulf throughout the 19th and first half of the 20th Century.

and along the Baja California coastline searching for productive diving grounds. These boats would pull 4-7 *pangas*, and each *panga* was equipped with a hookah system usually employed by two divers at a time. By the late 1970's, diving trips, whether based from mother ships or camps on islands and the mainland, were exploiting benthic resources throughout the upper reaches of the Gulf of California.

Elder fishers state that diving in the upper Gulf came as a result of a decrease in the scallop beds of the Midriff region and in light of the rich rock scallop (*Spondylus calcifer*) beds and shallow waters of the upper Gulf †. Although some of the species harvested in the Midriff region were not found or were found in small quantities in the upper Gulf (particularly lobster, lion's paw scallop, and pen shells), rock scallop beds were rich and could provide sufficient income for fishers through a complete fishing year cycle. In addition, the upper Gulf was particularly attractive to divers because of its shallow waters, which reduced the possibilities of suffering from decompression problems. However, diving in this region had its tradeoffs as well. Given the lack of rocky outcrops and islands, finding the patchy reefs was never an easy task ‡. Furthermore, to dive in the upper Gulf demands special skills, determination, and a great deal of strength and good physical condition. The region is home to some of the strongest tidal currents in the Gulf of California, forcing shifts in the spatial and temporal fishing dynamics and rendering it practically impossible to fish during the spring tides of particular times of the year. To complicate things even further, the

† In the midridges there are three large bivalves often referred to as scallops: lion's paw (*Lyropecten subnodosus*), rock scallop (*Spondylus calcifer*), and the thorny oyster (*Spondylus princeps*), but only *L. subnodosus* is a true scallop.

‡ Reefs continue to be found to this day. Special scouting trips are at times made to find new rocky areas. Divers refer to these new locations as *nuevos terrenos* (new terrains).

blessing of the region's productivity also acts as a curse. Constant tidal mixing make diving in murky waters more the norm rather than the exception.

Given these harsh conditions, only a few divers settled permanently in Puerto Peñasco, and their diving activities herein evolved within a very distinct and relatively isolated cultural and ecological region. To the North and South, PP diving grounds are flanked by long stretches of sand, with the nearest substantial ($>1000\text{ m}^2$) rocky reef located 150 km South of the reserve network. North of the PP diving grounds there are no rocky reefs as the region reaches the sand and silt dominated Colorado River Delta.

By the beginning of the 1980's most of the divers who fish in the upper Gulf today were already living in this port, fishing mainly on the distinct flat reefs adjacent to PP. Very rarely, however, divers continued making sporadic fishing trips to the Midriff region aboard mother ships. In addition, the northern most archipelago in the Gulf of California, an area known as the *Islas Encantadas* (Enchanted Islands), began to be used intensely around this time. This area was used both by divers from Puerto Peñasco and Bahía de Kino, Sonora, as well as by divers from San Felipe, Puertecitos, and Bahía de los Angeles, Baja California. By 1994, however, offshore diving trips whether to the Encantadas or the Midriff islands had stopped completely.

Throughout the eighties, diving activities in the upper Gulf were focused on the harvest of rock scallop and octopus, with rock scallop being by far the most important resource in terms of capital gains and its year-round availability. Although other species were harvested as well, these were minimal in comparison. Essentially, rock scallop was the key element that attracted locals to become hookah divers and remain as such. After

shrimp, rock scallop was and has been one of the most profitable marine resources in the region, its price often exceeding that of shrimp [§].

While rock scallops were the initial catalyst for the development of hookah fisheries in the upper Gulf, snails, particularly black murex (*Hexaplex (Muricanthus) nigritus*) and pink murex (*Phyllonotus erythrostomus*) became the primary target for the second growth stage of this activity. Hookah divers in the upper Gulf have harvested four different species of snail since the late 1970's: Pacific melongena (*Melongena patula*), giant Eastern Pacific conch (*Strombus galeatus*), black murex, and pink murex. Until the 1990's, however, their harvest had been a small endeavor since their demand was exclusively local. It was not until 1992, with the interest of Korean buyers, that murex snails began to be harvested in an industrial manner by divers from Puerto Peñasco (6). Murex snails were not only found in great quantities close to shore [¶], but they were also found during the summer months when rock scallop yield is much smaller and fishing in general is slow. In PP, summer months historically have been coined as “*los meses del piojillo*” (the months of lice), referring to the early days when there were heavy summer infestations of lice and, given that fishing was slow for most species and temperatures elevated, fishers would just have to “sit back and pick lice off their hair”. In addition, the early 1990's were particularly bad years for the fishing industry of the UG. Shrimp fishing, the main economic machinery of the entire UG region, had reached all-time lows and was in a state of crisis (9). Therefore, besides emerging as a great alternative fishery

[§] Rock scallop beach price can range anywhere between \$9.00 and \$13.00 dollars/kg. Their price is only surpassed by pen shells.

[¶] Between may-September, murex snails form large (>5000 individuals) breeding aggregations that facilitate the harvest of large quantities in one fishing trip.

for divers, black murex also produced an influx of new fishermen. In 1993, the number of divers doubled with fishers who alternated their usual fishing practices (e.g. gillnetting, long lining, shrimp trawling) with that of diving during the summer. Year-round divers name these seasonal divers *caracoleros* (“snailers”).

Today, commercial diving is more diverse than in its beginnings. Using hookah equipment, divers harvest at least 18 species of invertebrates and 8 species of fish. Of these, rock scallop continues to provide most of a diver’s yearly income. Fishing activities are characterized by a year-round harvest of rock scallop with seasonal targets of all other species. There are twenty year-round divers, all of whom are members of the *Sociedad Cooperativa Buzos de Puerto Punta Peñasco*. Of these, the majority are the same people who arrived to PP in the early 1980’s or related to them in some way or another.

IV. References Cited in Online Supporting Materials

1. Rocheleau, D. (1991) *Agroforestry Systems* **15**, 111-137
2. Marinone, S. G. (2003) *Journal of Geophysical Research* **108**, 3325-
3. Backhaus, J. O., (1985) *Deutsche Hydrographische Zeitschrift* **38**, 165-187.
4. Mateos, E., Marinone, S.G. & Lavín, M.F. (in press) *Deep Sea Res. II*.
5. Lavín, M. F., Durazo, R., Palacios, E., Argote, M. L. & Carrillo, L. (1997) *Journal of Physical Oceanography* **27**, 2298-2305.
6. Cudney-Bueno, R. (2000) *Management and Conservation of Benthic Resources Harvested by Small Scale Hookah Divers in the Northern Gulf of California, Mexico: The Black Murex Snail Fishery* (MSc Thesis, University of Arizona, Tucson, Arizona).
7. Donkin, R.A. (1998) *Beyond Price: Pearls and Pearl Fishing: Origins to the Age of Discoveries* (American Philosophical Society, Philadelphia, USA).
8. Bowen, T. (2000) *Unknown Island: Seri Indians, Europeans, and San Esteban Island in the Gulf of California* (University of New Mexico Press, Albuquerque, New Mexico, USA).
9. McGuire, T. and Greenberg, J.B. (1993) *Maritime Community and Biosphere Reserve: Crisis and Response in the Upper Gulf of California* (Occasional Paper no. 2. Bureau of Applied Research in Anthropology, The University of Arizona, Tucson, Arizona, USA).

APPENDIX F
GOVERNANCE AND EFFECTS OF MARINE
RESERVES IN THE GULF OF CALIFORNIA, MEXICO

Ocean and Coastal Management

R. Cudney-Bueno ^{*†‡}, L. Bourillón[§], A. Sáenz-Arroyo[§], J. Torre-Cosío[§], P. Turk-Boyer[†]

* Department of Natural Resources, School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA.

† Centro Intercultural de Estudios de Desiertos y Océanos. Apartado Postal #53. Puerto Peñasco, Sonora, México.

§ Comunidad y Biodiversidad A.C., Blvd. Agua Marina # 297, entre Jaiba y Tiburón, Colonia Delicias, Guaymas, Sonora, México 85420.

‡ Corresponding author: School of Natural Resources, University of Arizona, Biological Sciences East Room #325, Tucson, Arizona, 85721 USA. Email: cud@ag.arizona.edu, phone: 520-626-5607, fax: 520-621-8801.

Governance and Effects of Marine Reserves in the Gulf of California, Mexico

R. Cudney-Bueno, L. Bourillón, A. Sáenz-Arroyo, J. Torre-Cosío, P. Turk-Boyer

Abstract

We trace the evolution and effects of three marine reserve initiatives in the Gulf of California, Mexico: Loreto Bay National Park (LBNP), San Pedro Mártir Island (SPMI), and Puerto Peñasco (PP), and shed light on their governing institutional and ecological feedbacks. The interest to establish these reserves has arisen within various governance settings, ranging from significant to practically null government intervention. Fishers have petitioned their establishment (PP, LBNP), were key participants in their design (LBNP, SPMI, PP) and are participating in an ecological monitoring process (PP, SPMI). Preliminary monitoring results are encouraging and fishers appear to support their establishment, believing reserves can recover and/or enhance local fisheries. However, open access situations and differing conceptions among local stakeholders and government concerning access rights to fishing grounds, coupled with limited support for surveillance, and lags between local and government institutional arrangements and interests, are the main constraints for the success of these and future reserves in the region.

Key words: Marine protected areas, marine reserves, governance, co-management, small-scale fisheries, Gulf of California, Mexico.

1. Introduction

Since the 1980's, management and conservation of marine resources has seen a global movement towards "local" governance and empowerment, making community-based management and co-management a top priority in non-governmental conservation organizations' and at times government agencies' environmental agendas. Coupled to the rise in the transferability of management responsibilities these strategies entail, the 1990's saw a marked advocacy for the use of marine protected areas (MPA's) in the form of marine reserves or "no-take zones" (areas fully protected from fishing) as fishery management tools [1, 2]. This came in response to the frustration over the evident failure of many traditional "top-down" and single species management practices [3] and the need to implement strategies for protecting and/or enhancing harvestable stocks while promoting marine conservation [4, 1, 2].

Although the coupled establishment of marine reserves and locally-based governance structures is promising as a conservation and development tool, insufficient research has been conducted to assess the conditions that may lead to its successful implementation and their effects on the resilience of social and ecological systems. This requires an analysis of existing cases of the evolution of cooperative management efforts leading to the establishment of reserves, where we trace the outcomes of these efforts both from a social as well as bio-physical perspective.

We present and discuss some of the preliminary outcomes of three emerging efforts to establish marine reserve MPAs in the Gulf of California, Mexico. These efforts are in three areas: Loreto Bay National Park, Puerto Peñasco, and San Pedro Mártir

Island Biosphere Reserve (herein LBNP, PP, and SPMI). These different cases were established and operated under various degrees of local involvement and governance. In all three cases, the involvement of fishers and the participation of conservation NGO's has been integral for the creation and governance of the reserves. Fishers have petitioned their establishment (PP, LBNP), were key actors in designing of the zoning of the reserves (LBNP, SPMI, PP) and have taken a leadership role in the ecological monitoring process (PP, SPMI).

The purpose of this paper is three-fold. First, we trace the evolution of these management and conservation efforts. Second, we shed light on the institutional and ecological feedbacks governing their outcomes. Third, we provide recommendations for future use and implementation of marine reserves in the Gulf of California. Our analysis is based on our collective personal experiences, having been involved in these marine reserves as academic advisors and non-governmental organization (NGO) practitioners and researchers since their inception or during important phases of zoning and implementation. Our involvement in these efforts has led to over 200 days of underwater surveys, participation in more than 50 meetings with the fishing sector, and semi-structured and structured interviews with over 150 people including fishers, government officials, and NGO representatives.

2. The physical setting: the Gulf of California and its fisheries

Apart from being the only sea that may be considered “the exclusive property” of a single nation [5], the Gulf of California or Sea of Cortés (herein “the Gulf”) is unusual

in a global perspective. In a relatively small area, it embraces an array of marine environments, from deep-water trenches and coastal and island rocky reefs to the sandy and shallow waters of the Colorado River delta. It also constitutes one of the most productive seas in the world [6]. Fed by constant tidal and wind-driven upwelling systems, tidal currents, and variations in sea surface temperature, the productive machinery of the Gulf allows a large accumulation of biomass on a year-round basis [7]. This sea provides 70% of Mexico's National fisheries' value [8] and a fishing industry that has molded the communities surrounding the Gulf and crafted most of the complex social-ecological feedbacks of this region.

The development of fisheries in the Gulf has been immersed in a complex political ecology from its onset [9]. Although subsistence fishing has existed for millennia among the various indigenous peoples living in the region [10, 11], commercial fishing did not come into play until the 1920's and 1930's [12] following Mexico's Revolution and President Cárdenas' appropriation politics and institutionalization of fishing cooperatives [9]. In recent decades, fishing in the Gulf has changed dramatically both in terms of production of fishery resources and diversity of species harvested as well as in the evolution of territorial conflicts, institutional arrangements, and increasing presence and interest of conservation NGOs working in the region since the early 1990's.

Possibly no other fishing sector has seen such a rate of development and change as the small-scale fishing sector. In the past 50 years, small-scale fishing has changed from being a relatively low-impact and mono-specific endeavor - targeting a handful of commercial species primarily for the domestic market -, to a multi-specific and,

collectively, highly impacting (ecologically and economically) activity [13, 14, 15]. Depending on the season, anywhere between 10,000 and 24,000 small-scale fishing boats operate in the Gulf on a daily basis and target over 70 different species of fish and shellfish, much of which is destined for the international market in the U.S. and Asia [8,13].

From the political and economic arena, the rapid development of fisheries in the Gulf has been fueled by waves of national and international market demands, tourism growth, maximization and development government policies [9], and the existence of increasingly weak fisheries management institutions. From an ecological perspective, the overall productivity of the Gulf has attracted fishers from various parts of Mexico in wave cycles [13]. However, the brief history of commercial fishing in the Gulf has already experienced a boom-and-bust pattern of various fisheries, with evidence pointing towards an overall decline in ecological complexity and a tendency to fish down the food webs [16, 17].

3. Fishery decline, conservation agendas, and the emergence of MPAs

Given the state of Mexico's fishery resources, the National Institute of Fisheries (*Instituto Nacional de la Pesca*, INP), the scientific backbone of Mexico's fishery management agency, has declared that 60% of fisheries in Mexico are being exploited to their capacity or overexploited, and therefore has advised to stop issuing new fishing permits for most fisheries [18]. However, corruption and inefficiency within the fishery sector and the government, as well as growing immigration rates to the coast, has

managed to overturn precautionary regulations. The result is that many fisheries in the Gulf have operated in near open-access conditions and have seen a marked decline in catch per unit of effort (CPUE) or in total production over their short history [19]. This has given rise to an increase in territorial conflicts among fishers, displacement of fishers to search for productive areas farther away from their home ports, and as one solution the emergence of community-based efforts aimed at controlling access to fisheries and better management of local fishery resources [see 20, 21]. In addition, the rapid increase and influence of conservation NGOs in the 1990's, as well as Mexico's commitments for environmental compliance as part of the North American Free Trade Agreement and other international biodiversity conservation agreements [22] has brought about pressure for the adoption of biodiversity conservation interests in fisheries management and the implementation of various co-management practices.

Parallel to downward trends in catch in the fishing industry, the administration of fisheries at a national level has also gone through dramatic changes. In the past two decades, the management body for fisheries in Mexico has shifted from being a Federal Secretariat solely devoted to fisheries (*Secretaría de Pesca*) to a subsecretariat of the Secretariat of the Environment, Natural Resources, and Fisheries (SEMARNAP) and, currently, a National Commission (*Comisión Nacional de Acuacultura y Pesca*, CONAPESCA) managed independently of environmental issues under the Secretariat of Agriculture created during President Vicente Fox's administration (*Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación*, SAGARPA). These

changes have occurred with the subsequent budget and personnel reductions as well as diminishing authority and weight in national government policies [23].

It is within this political and ecological setting that the emergence of MPAs as management and conservation tools has taken place in the Gulf. Managed under the recently created National Commission of Protected Natural Areas (*Comisión Nacional de Áreas Naturales Protegidas*, CONANP), there are currently eight MPAs in the Gulf. These fall in two general management categories: National Parks and Biosphere Reserves. In addition to the inception of such protected areas, Mexico's National Institute of Ecology, together with prominent Mexican and international academic institutions and conservation NGOs, recently started crafting priorities for conservation [see 24, 25] and for the establishment of a network of marine reserves in the Gulf [see 26].

Although attempts of using MPAs as a management tool in the Gulf began in 1993 with the creation of the Upper Gulf of California and Colorado River Delta Biosphere Reserve – primarily for the protection of the endangered and endemic large croaker *totoaba* (*Totoaba macdonaldi*) and the vaquita porpoise (*Phocoena sinus*) - it is only since 2000 that efforts have focused specifically on defining fully protected (no-take) marine reserves as a means to manage and enhance small-scale fisheries while conserving marine ecosystems. The oldest of these reserve initiatives are located in the Loreto Bay National Park (LBNP) - adjacent to the Baja California Peninsula -, Puerto Peñasco – in the upper Northern Gulf (PP)-, and San Pedro Mártir Island (SPMI) – in the Midriff Island Region - (Figure 1). Following we describe the evolution of these initiatives and their preliminary outcomes.

4. Loreto Bay National Park

The Loreto Bay National Park (LBNP) is located adjacent to the East coast of central Baja California Peninsula in the northern portion of the state of Baja California Sur. It covers an area of 206,580 ha (2,065 km²), including a large marine portion (~1840 km², 89% of the Park's total area) and five islands adjacent to the city of Loreto, a fishing and tourism community of *ca.* 10,000 people (Figure 2). Six other small fishing communities are found within the Park's boundaries, and approximately 330 small-scale fishers make use of the Park [27].

The Park encompasses numerous marine environments such as rocky reefs, silt and sand seabeds, algal prairies, calcareous algae (rodolith) beds, small mangrove estuaries, and pelagic waters. It harbors more than 700 species of macroinvertebrates and vertebrates, of which at least 43 have an official protection status under Mexico's law [28] and/or are listed under the IUCN's Red List of threatened and endangered species and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

In the last fifty years of human use, the main users of the marine area of the LBNP have been small-scale fishers that reside within the Park as well as sport fishers, mainly from the U.S., who permanently reside in the community of Loreto or who visit the region primarily during winter and spring. In addition, occasional large-scale bottom shrimp and fish trawlers, sardine purse seine boats, as well as squid fishing boats and long line anglers from various and far reaching areas of the Gulf and Pacific coast of Mexico had also made use of these waters before the park was created. Historical

research also shows that before persistent commercial extraction took place, the marine ecosystem might have been vastly different to what is acknowledged today. Large pearl oyster reef beds and top predators, commonly found in the past, have been practically eliminated from today's seascape [14, 15, 16].

4.1 Creation of the Park

The Park was officially decreed on July 19, 1996, four years after the community of Loreto and its government officials began lobbying with the Executive Branch of the Federal Government for the creation of a protected area in its surrounding waters. This initiative came primarily as a result of the community of Loreto's interest to close the entry of shrimp and fish trawlers and sardine purse seine boats operating in the waters adjacent to Loreto [29].

More than six years after it was officially decreed, the Park's management plan was established [29]. The Park includes three general management zones: Zones of Restricted Use (*Zonas de Uso Restringido*), Zones for the Sustainable Use of Resources (*Zonas de Aprovechamiento Sustentable de los Recursos*), and Protection Zones (*Zonas de Protección*). In all of these areas, large-scale fishing activities (shrimp and fish trawling, sardine purse-seining) have been prohibited. Each management zone has other specific restrictions, such as spatial-temporal control of sport fishing, commercial diving, and of the use of gillnets and longlines. As part of the Protection Zones' specific restrictions, In 2002 the Park added to its

management structure two no-take marine reserves: The *Bajo del Murciélago* and *Bajo del Cochi* sea mounts.

4.2 *Bajo del Murciélago and Bajo del Cochi Reserves*

In July 2001 the Park directorship, based on the petition of local fishers, set out a notice to revise the Park's existent Management Program, a program that had been operating informally as it had yet to be recognized and published by the Federal Government. This notice was in part a response to concerns of small-scale fishers over some of the restrictions on the use of gillnets in the Park.

Parallel to this process, *Comunidad y Biodiversidad (COBI)*, a marine conservation and community development NGO operating in northwestern Mexico, had been working for a year in the Park, locating large predator (groupers, snappers, sharks), critical habitats and obtaining baseline biological data on some of these sites. Also, COBI had conducted semi-structured interviews with fishers to assess their attitudes and perceptions towards the establishment of marine reserves as tools for fishery management in the Gulf. In a meeting shortly after the call for a revision of the Program had been presented, representatives of local fishing cooperatives and the tourism sector re-negotiated the zoning of the Park as well as other management guidelines. By the time the meeting took place, fishers came with a proposal to establish the *Bajo del Murciélago* and *Bajo del Cochi* as no-take zones (Figure 2). These seamounts are important aggregation sites for large groupers and sharks and, according to fishers, had provided some of the best catches in the past. However, they only comprise less than 1% of the

Park's marine area (1.4 km²). Because of their small size, they cannot be considered effective management or conservation measures beyond a localized scale. This is clearly understood both by fishers as well as by the Parks' personnel. Rather, they are being treated as management and conservation experiments.

Interviews with Loreto fishers and the Park's management team indicate that the interest to propose the establishment of no-take marine reserves had two primary purposes: a) provide a baseline for comparison and to test the use of no-take marine reserves as a means to restore declining fish stocks in these sites and, b) use this initiative as a leverage tool to negotiate the softening of gillnet restrictions and obtaining new fishing permits.

4.3 The current status of the LBNP and its marine reserves

Undoubtedly, the initial conception of the LBNP had strong support from the tourism and small-scale fishing sector, particularly because it granted some form of exclusive access rights to fishers from the municipality of Loreto and managed to keep large-scale boats away from the areas used by small-scale fishers. However, there are currently mixed attitudes towards the restrictions the Park has established on existing fisheries. This has been accentuated by an accumulated disbelief in the government's seriousness to respond to and formalize the petitions that have been crafted at a local level. As mentioned before, it took four years for the government to formalize the initiative for the establishment of the Park. Even after this, for six years practically all of

the Park's rules and regulations lacked any legal weight, as no management plan had been formalized.

Underwater censuses indicate that since 2002 overall reef fish diversity has decreased significantly outside reserve boundaries but not within [30]. In addition, while abundance of commercial species such as leopard grouper (*Mycteroperca rosacea*) and yellow snappers (*Lutjanus argentivestris*) remained stable inside both no-take zones, their numbers decreased drastically in fishing areas monitored. Reserves have also shown to be more "stable" places than fishing sites; while in the no-take reserves twelve species showed significant variations in abundance within reserves, 26 species showed significant variations (decrease and/or increase) within fishing sites [30].

An important limitation of the LBNP monitoring program is that it has little power to assess the strict restrictions that have been set for trawling on the Park's soft bottoms. We know little about how populations and habitat complexity of soft bottoms have responded after more than ten years of protection from trawling. Nevertheless, preliminary interview data revealed that up to 33% of fishers consider that soft-bottom species have recovered since the Park's official closure of shrimp trawling [31].

Finally, one obvious concern for the Park is its current insufficient enforcement capability. Certainly, LBNP is not alone when it comes to difficulty in accessing resources for enforcement, as protected areas in Mexico are largely under-budgeted and enforcement capabilities are still in their infancy [32]. The existent enforcement structure of the Park is clearly insufficient to monitor an area of such magnitude. Furthermore, there are inconsistencies as to the designation and overseeing of enforcement

responsibilities. The Park does not have the political authority for enforcement, needing to orchestrate enforcement operations with other governmental agencies such as CONAPESCA, Mexico's Federal Environmental Protection Agency (*Procuraduría Federal de Protección del Medio Ambiente*, PROFEPA), and the Navy. Although increasingly effective, the need for this constant coordination comes at the expense of significant transaction costs to the Park.

5. Community-based reserve network in Puerto Peñasco

The community of Puerto Peñasco (PP) is located in the state of Sonora, bordering the Upper Gulf of California and Colorado River Delta Biosphere Reserve. It is the largest community in the Northern Gulf (~40,000 people) and one of the most important commercial ports in the Gulf, with an active fleet of 120 shrimp trawler boats capable of working throughout the Gulf [13] and 230 small-scale fishing boats [33].

In the Northern Gulf, possibly no other fishing sector better exemplifies the rapid evolution of community-based management practices as the small-scale hookah diving sector of PP. Using a modified paint-spraying machine as an air compressor and long (50-100 m) hoses, divers have been harvesting benthic shellfish (snails, pen shells, scallops, clams, octopus) and reef fish (large groupers and snappers) in the rocky reefs and adjacent sand flats of this region for the past 30 years. Today, these habitats are partly within the boundaries of the Biosphere Reserve and extend eastwards to San Jorge Island, one of the northernmost rocky islands of the Gulf of California located ~ 30 km southwest of PP.

5.1 Dependence, scarcity, and the emergence of collective action

Through the fishery's brief existence, the region saw an evident decline in the availability of these resources, primarily black murex snail (*Hexaplex nigritus*) and rock scallop (*Spondylus calcifer*). Concerns about this decrease led these divers collectively to adopt a more precautionary behavior [21]. In 1998, they approached the Intercultural Center for the Study of Deserts and Oceans, CEDO (*Centro Intercultural de Estudios de Desiertos y Océanos*), a community-based conservation and research NGO based out of Puerto Peñasco, to help conduct an ecological assessment of their benthic resources.

After the first two years of work, in 2000 the divers convened to discuss future management guidelines. From this meeting, they petitioned the federal government to establish a season closure for black murex snail, a petition that was granted in the summer of 2001 by the National Institute of Fisheries. In addition, without waiting for government recognition, in October of 2000 the divers defined and established a temporary harvest refugia MPA surrounding San Jorge Island (3 km coastline) to provide a refuge and a site for larval recruitment and dispersal of commercial benthic organisms, primarily black murex and rock scallop.

In October 2001, the divers participated in an extensive survey of the density and age class distribution of various commercial species. The outcomes of this participatory monitoring process were two-fold: not only were the results encouraging (i.e. larger sizes of individuals, increased density), but also the diving sector perceived first-hand positive products of their efforts and were collectively empowered to continue with similar initiatives [21].

5.2 Poaching and the reinforcement of cooperative institutions

Information about PP reserves traveled fast among small-scale fishers. Divers from the community of Bahía de Kino, located by road approximately 600 km south of PP and eight hours away by boat, harvested rock scallops on San Jorge Island soon after PP divers had conducted their monitoring efforts. Given the lack of any formal governmental recognition of the island as an MPA, local fishers could not count on the government for enforcement support. After several attempts to deter interloping, what followed was a textbook “tragedy of the commons” pulse of events. As soon as the first neap tides arrived, PP divers headed to the island in frenzy and joined the Bahia Kino divers to harvest as much rock scallops as possible, enough to saturate the local market.

Another incident of snail poaching also took place soon after the San Jorge events. On this occasion, however, Puerto Peñasco divers believed they had the legal means to denounce this activity and approached the then local natural resource enforcement agency (*Procuraduría Federal de Protección al Ambiente*, PROFEPA). Nevertheless PROFEPA did not provide any assistance since the season closure had not been published in the *Diario Oficial de la Federación*, Mexico’s Federal Register. In essence, the agency established that it did not have any means to enforce locally based decisions, even if backed up by the National Institute of Fisheries. The process, however, to get a law published through the *Diario Oficial de la Federación* is lengthy and highly politicized, involving time frames, resources, and efforts that are seldom afforded by fishers and the state of their natural resources.

Interestingly, events that seemed to have undermined any future management efforts appear to have reinforced the evolution of cooperative institutions. In spite of the lack of government support, in early 2002 the PP divers convened to discuss the past set of events and define future management guidelines, the main ones being the use of marine reserves as a management and conservation tool parallel with the establishment of exclusive fishing access rights.

5.3 Puerto Peñasco's network of reserves

Having seen what was perceived as a positive and rapid ecological response of the short-lived San Jorge experiment, PP divers opted to establish a network of three reserves, including San Jorge Island and two coastal areas (Figure 3). The entire network covers 18 km of coastline and gives protection to approximately 30% of the divers' historical fishing grounds. The divers' interests behind the establishment of these reserves was three-fold: a) to see if overexploited areas could recover, b) to increase the number and density of commercial species within all closed areas, and c) to test if the reserves not only increase recruitment within the closed areas but in actively fished sites as well. Divers agreed to close off these areas for a period of three years, at the end of which they would re-assess future management efforts. In the meantime, they also lobbied to obtain legal recognition of their initiatives, including the granting of an exclusive fishing zone for the harvest of benthic mollusks.

To test the efficacy of reserves, PP divers began monitoring commercial species, measuring density and age-class distribution of benthic mollusks within reserve areas and

control sites (areas open for fishing). As part of this effort, they began a Cooperative fund for monitoring their fishery resources, anchoring marking buoys, and traveling to the State and federal fishery offices to lobby their petitions. CEDO, in collaboration with the University of Arizona, facilitated obtaining funds for this monitoring effort, designed with fishers the means to monitor reserves, analyzed the results, and trained divers for ecological data acquisition. Once the decision to establish these reserves had been made, fishers convened a meeting with the Mexican Navy, the Chief of the Puerto Peñasco Fisheries Office, the Director of the Upper Gulf Biosphere Reserve, local buyers, and representatives of NGOs. Divers presented their proposals and discussed ways in which their efforts could be supported by the government at a local level.

5.4 A brief aftermath

Almost three years after their establishment, the reserve efforts in Peñasco have provided mixed outcomes both from an ecological as well as institutional perspective. Monitoring of reserves and fished sites showed that San Jorge's rock scallop population had recovered since the last major harvest took place three years before, with densities at least four times higher than those in all the coastal areas monitored [21]. Density of juveniles of commercial mollusks both within refugia sites and fished sites were significantly higher than prior to their establishment (more than 100% increase in one site), suggesting a direct benefit of the reserve network by means of larvae dispersal [21]. In addition, average size of harvested snails and breeding aggregations increased significantly, and aggregations were found in shallower waters in areas previously

overexploited. These results were consistent with fishers' overall opinion about the efficacy of their closures, expressed both through interviews with all Cooperative members as well as during Cooperative meetings [21].

The divers' example led local and federal government agencies to be more actively engaged in the support and implementation of their management initiatives. The Navy and local fisheries office, for instance, initially participated in several patrolling and enforcement operations of the reserves and snail season closure. These supportive actions were based primarily on the rapport built between the divers and local government officials, as the reserves were yet to be formalized at a federal level.

In November 2003, Mexico's federal government awarded the Puerto Peñasco diving Cooperative with Mexico's National Conservation Recognition, one of the highest environmental distinctions bestowed annually by the Secretariat of the Environment. Soon after, CONAPESCA granted the Cooperative some, albeit not all, of the fishing permits that fishers had lost during a National fisheries restructuring process that took place in 2000. Rather than acting as a positive incentive, however, the incomplete granting of permits caused strife within the cooperative and forced divers to work under other permit holders or illegally. There was a high expectation that all permits would be granted, especially given their efforts to manage their fisheries in a more sustainable manner, the recent National Recognition, and the fact that these permits had been paid for during four consecutive years with all investment lost⁶. Concurrently, the directorship of

⁶ It is not uncommon for the Mexican fisheries permitting process to be tied down in bureaucratic discrepancies, and for fishers to unsuccessfully invest time and money to obtain and/or renovate their fishing permits.

the local fisheries office changed drastically, bringing in personnel from outside the region who were unaware of existing local institutional arrangements and overall less supportive of fisher's management initiatives. This made it impossible for divers to gain local government support for enforcing San Jorge island as a reserve, which by then had become a highly productive fishing ground [21]. After various confrontations with interlopers and unable to deter fishing, the divers convened and opted to collectively fish on the island before others would continue free-riding on their efforts.

The aftermath of what occurred in PP provides a different scenario. In summer, 2006, the Mexican government granted a fishing concession to the PP Cooperative, providing exclusive access rights to rock scallop fishing grounds. There is a clear belief among fishers regarding the benefits of their reserves. These will be re-established by 2008 coupled with other spatial-temporal management schemes after new ecosystem-based and population assessments are implemented.

6. San Pedro Mártir Island: the creation of a biosphere reserve

San Pedro Mártir is the most oceanic island in the Gulf of California, located in the Midriff Island region more than 60 km away from both the states of Baja California (Baja Peninsula) and Sonora (mainland México) (Figure 4). This small island (2.89 km²) was decreed a Biosphere Reserve in 2002 after two years of lobbying from the Sonora State Offices of the Area of Protection of Flora and Fauna (*Área de Protección de Flora y*

Fauna)⁷ - Gulf of California Islands, and two conservation organizations: *Comunidad y Biodiversidad* (COBI) and the World Wildlife Fund (WWF) Gulf of California Program. The reserve has an area of 302 km² - including 3 km² of the island and 299 km² of surrounding marine area. The marine area is divided into 9 km² of a no-take core zone and a remaining 290 km² buffer zone [34].

The island serves as one of the world's most important breeding grounds for blue-footed boobies (*Sula nebouxi*), brown boobies (*S. Leucogaster*) and for six other seabirds [35]. Its adjacent waters harbor a high diversity of fish, and act as an important feeding and reproductive ground for large commercial species (i.e. groupers and snappers) and marine mammals. Regarding commercial fishing, the marine area of the Reserve is used almost entirely by small-scale fishers from the community of Bahía de Kino [35], a small fishing community of 5000 people in the state of Sonora. Small-scale fishing from other communities in Sonora and Baja California, as well as large-scale shark fishing and shrimp and fish trawling also occasionally take place in the island's surrounding waters. In addition, sport fishers mainly from the U.S. target the island to fish for large groupers and pelagic species such as yellowtail jack (*Seriola lalandi*) and dorado (*Coryphaena hippurus*).

6.1 Creation of the San Pedro Mártir Biosphere Reserve

The conditions under which this MPA was created were very different from the other two cases previously discussed. Here, the initiative to begin a discussion with the

⁷ This office belongs to the National Commission of Protected Areas (CONANP), the agency of the Federal Government in charge of managing all of Mexico's protected areas.

fishing community of Bahía de Kino to establish the biosphere reserve emerged from the Federal Government. The regional offices of the Gulf of California Islands Protected Area became interested in re-categorizing San Pedro Mártir as a biosphere reserve and adding the marine environment to the overall management and protection of the island⁸.

In 2000 *Comunidad y Biodiversidad* (COBI) was selected in an open contest and hired to conduct a feasibility study for the establishment of a new protected area by facilitating a negotiation forum between fishers and the government. As part of the assessment, a series of workshops were conducted in the community of Bahía de Kino after having obtained baseline information regarding fishers' and local government officials' perceptions towards the establishment of marine reserves and their interest in protecting the island's marine resources. The initial workshops included talks about the use of marine reserves as fishery management and conservation tools. These were followed by a negotiation workshop with stakeholders, including fishers and government officials, to design the final zoning of the new reserve.

From this negotiation, a formal proposal was presented in late 2000 to the federal government to re-categorize the island as a Biosphere Reserve, a proposal that took two years to be formalized and published in the Federal Register. The proposal included a core zone that, although only comprising approximately 3% of the marine area of the entire MPA, protected approximately 30% of the island's coastline and its adjacent fishing grounds.

⁸ In 1978, San Pedro Mártir, like most other islands in the Gulf of California, was decreed a *Zona de Reserva y Refugio de Aves Migratorias y de la Fauna Silvestre*. However, this protection only included the terrestrial component of islands.

There are several reasons why fishers agreed to establish a large portion of the island as a no-take area. The most important, however, was that the island has always been seen as a temporary refuge. Given its location (more than 60 km offshore from both Gulf's coasts), the island is not an area that is regularly used by individual fishers. Even more so, it is only used by a select group of them. The island is essentially seen as a backup area where fishers can get good catches when having the time, money, and willingness to make the trip. A visit to the island usually requires fishers to camp 3-4 nights. These short trips however, are often enough to take a heavy toll on the island's isolated populations of reef fish. Much of the fishing is carried out at night illegally using diving equipment, fish hooks, and spear guns when fish are most vulnerable. There is a prevalent general belief, however, that the island's populations quickly "bounce back" if there is not much more pressure from other fishers.

Given this, when the government proposed to establish a core zone in the Reserve, fishers agreed to its establishment since they did not have much to lose and conceivably had more to gain by testing it as a management tool. This came after considerable debate over the exact location of the core zone and its size. To illustrate part of this negotiation, when a fisher proposed protecting an area that was evidently a very poor one for fishery purposes, another fisher replied:

Para qué ese lugar?... es como tener un gallinero sin gallinas / "Why that place?... it's like having a chicken farm without chickens".

In addition to the island's far reaching location, part of the attraction to establish a biosphere reserve with a core no-take zone was that Bahía de Kino fishers would be given preferential access to the area and the Reserve would give a legal means to control access of highly impacting fishing activities such as bottom fish trawling. Mexico's environmental law states that communities within and/or near reserves have special access rights to these areas [36]. However, these conditions have not been formalized and enforced, as an official management program for the SPMI Biosphere Reserve is yet to be published.

6.2 *San Pedro Mártir today*

Six years after the establishment of SPMI as a biosphere reserve, it is still lacking enough personnel specifically dedicated to its management, monitoring, and enforcement. To date, most of the basic operational tasks have been conducted by the Director of this MPA, who is also the Director of the regional office of the *Area de Protección de Flora y Fauna Islas del Golfo de California* of CONANP, working in collaboration with NGO's such as COBI, the *Grupo de Ecología y Conservación de Islas* (GECI), and the Prescott College Field Station for Cultural and Ecological Studies, a field station that has been working in education and research in the region for over 20 years. The official management program has been written by these institutions, presented in public hearings, and will become operational by the end of 2007.

Between January 2003 and March 2005, researchers from these institutions conducted "surprise" visits on 43 separate occasions to register human activities. On 45%

of these visits both commercial and sport fishers were seen fishing within the core zone, even after an extensive public education campaign. In May 2004, a large sport fishing derby took place on the island in which indiscriminate fishing was conducted for over a week, targeting rare species such as gulf grouper (*Mycteroperca jordani*) and giant sea bass (*Stereolepis gigas*) as well as leopard groupers and jacks. Given this, more efforts are being invested on monitoring human activities and enforcement. The reserve staff and COBI are conducting 4 monthly visits to the island and have solicited formal enforcement from PROFEPA, Mexico's Federal environmental protection agency.

COBI has been conducting underwater monitoring of commercial species and of overall diversity of fish and invertebrates. As part of this monitoring effort, this institution has engaged the participation of members of the commercial diving union of Bahía de Kino. This has largely come about as a result of the example set by the Puerto Peñasco initiative. However, because of the lack of effective enforcement, these data are only being treated as baseline for future comparisons of fishing and no-take areas.

Finally, in 2006 the reserve staff, COBI, Prescott College and WWF developed a strategic plan that ultimately aims at making of SPMI a marine reserve model. This includes working with local stakeholders and international partners to design the most suitable option for managing resources outside the reserve and implement a plan for the long-term financial sustainability of the reserve.

7. Discussion and conclusions

As evidenced throughout this paper, the Gulf of California is experiencing a rapid evolution of institutional arrangements and the emergence of challenging management actions aimed at conserving biodiversity while also maintaining fishing life-styles and economies and a high productivity of fishery resources. This evolution has been fueled largely by steady downward trends in production per-capita, an increase of people making use of the Gulf's marine resources, and by the direct and indirect influence of NGOs. One manifestation of these changes is the interest in the establishment of different forms of MPAs.

Here we have presented a general overview of some of the first efforts to establish no-take marine reserves for management and enhancement of small-scale fisheries and conservation of marine ecosystems in northwestern Mexico. Although it is certainly too early to give any conclusive remarks as to the long term efficacy of these reserves, we can shed some light on the main conditions that have led to the emergence of these efforts and the key processes that are governing their performance.

7.1 Dependence, scarcity, and resilience

Dependence on and scarcity of natural resources have been identified by various scholars in common pool resource (CPR) theory as two of the main factors leading to the emergence of cooperation and self-governing institutions [see 37, 38]. In this particular case, these factors have been key conditions leading to the interests of fishers, NGOs, and Mexico's National Commission of Protected Natural Areas (CONANP) in establishing

marine reserves. Clearly, the state of the Gulf's fishery resources has declined when compared to what it used to be 100 or even 20 years ago (16, 17). We believe that it is precisely this decrease in fishery resources combined with belief in the ecological resilience of the Gulf that has largely facilitated the emergence of conservation actions. In the three cases here described, fishers have evidently experienced a decrease in catches and depend on their fishery resources year round. However, the state of their natural resources is not at a level such that it is no longer worth the initial costs associated with the establishment of MPAs. They have also experienced, in some form or another, positive responses of the system when protected from fishing.

7.2 Local ecological knowledge, stakeholder monitoring, and return rates of social-ecological feedbacks

Fishers will unlikely engage in any conscious management effort if they do not believe it will bring some benefit in the future. This requires, at the very least, some knowledge of the resilience of their system and clear proof of the positive outcome of their management actions. Some marine systems, however, may take many years to show any sign of recovery. In areas of the world where commercial fishing has been the *modus operandi* for centuries, sufficient empirical knowledge regarding response rates of the marine environment may have been gained and passed on through generations, making long-term sacrifices more justifiable. However, in many areas of the world where commercial fishing has been a relatively recent endeavor, insufficient knowledge of the system's response time frames makes sacrifices seldom affordable to fishers. Here we

have provided evidence where a blend of local ecological knowledge, stakeholder participation in monitoring, and relatively rapid response of the fisheries on which fishers depend on has brought about a reinforcement of their institutions. This is particularly true in the PP case. We hypothesize that the growth rate of resources harvested, coupled with the divers' direct underwater observations of their natural system, has accelerated the accumulation of ecological knowledge and facilitated informal trial and error processes. The ultimate reinforcement and collective social-ecological feedback, however, has come with fishers' participation in fishery monitoring programs.

7.3 MPAs as negotiation opportunities for access rights

The establishment of MPAs can be seen as negotiation opportunities for stakeholders to acquire access rights to fishery resources and preferential use of fishing grounds. Faced with the government's proposal to establish MPAs, fishers and communities have a better means to demand some form of exclusivity to the fishing areas and resources they have historically depended on. This is regardless of whether they are "buying in" to an outside entity's proposal to establish MPAs, or if the proposal emerged from within the fishing sector. The question then arises as to which communities or sectors should be granted these rights and who decides how these rights are granted.

Granting access rights will probably be the single most conflicting issue for the future establishment of MPAs in the Gulf. An example of this conflict of interest can be seen by recent events taking place in the Upper Gulf of California Biosphere Reserve. After a series of protests following the government's decision to enforce zoning rules that

ban trawling within the Biosphere Reserve's buffer area, the government stepped back from its initial decision and gave exclusive access rights to trawlers from the communities of Puerto Peñasco and San Felipe, the two communities found on the edge of the Biosphere Reserve, to fish within the buffer zone with some seasonal and gear restrictions. This decision automatically excluded trawlers from the rest of Mexico's Pacific fleet. What followed was a heated response from other members of the industrial fishing sector, a series of lawsuits, removal of federal fishery employees, and state and federal politicians' adoption of the conflict for their personal election agendas.

In the three cases we have presented, fishers' adoption of MPAs has been used as a means to help petition exclusivity of fishing and territorial access rights, or to negotiate management restrictions to fishing. Currently, the government has granted access rights to the communities that lie within the LBNP, has established a territorial fishing concession for PP commercial divers and, in the case of SPMI, is in the process of evaluating the granting of territorial access rights to the community of Bahía de Kino, which has historically been the primary user of the island.

7.4 Distance of reserves

How far away a fishing area is found from shore will largely determine how often it is used. Although SPMI - in the case of Bahía de Kino -, and San Jorge Island - in the case of Puerto Peñasco - are some of the richest fishing grounds for fishers of these communities, their distance from shore makes fishers target other areas that are closer on a more regular basis. Part of the reason why fishers from these communities have opted

to establish these islands as reserves is that historically they have already been treated as forms of temporary refugia. Nevertheless, there is evidently a tradeoff as well.

Enforcement costs and effectiveness will likely increase with the distance at which MPAs are found. Areas found closer to shore can be more easily monitored by local fishers during their regular fishing activities or even when on shore. Incidentally, the belief that other fishers within and outside the community will respect near-shore reserves may increase. For areas that are farther away and out of fishers' immediate control, on the other hand, there can always be mistrust whether they are being poached in or not. In this regard, transaction costs associated to enforcement will likely be the most important challenge for management of both San Jorge and San Pedro Mártir islands.

7.5 The Government's role

Our three case studies show different levels and types of involvement of the Mexican government in the design, establishment, and management of reserves. This involvement has been crucial in various ways. Most importantly, the federal government has acted as a means to both legitimize as well as de-stabilize some community efforts.

Currently, there are four means to operationalize a no-take reserve in Mexico: 1) if it forms part of an existent MPA (i.e. LBNP), 2) if a new MPA is created in which no-take zones can be included as part of its management scheme (SPMI), 3) if an indigenous community is granted territorial use rights and opts to establish a no-take zone within this territory [see 39], and 4) if an organized group (e.g. a fishing cooperative) is able to amass various species-specific fishing concessions that grant exclusive fishing rights over

those resources within a specified area and the group decides to close a portion of this area to all fishing of the resources over which it holds exclusive fishing rights⁹. In essence, then, in order to have any legally recognized no-take marine reserve, it will likely fall within one of the management categories of Mexico's national park system (i.e. National Park, Biosphere Reserve), currently overseen by the National Commission of Natural Protected Areas, or via grassroots decisions operating within government-granted forms of exclusive fishing access rights (i.e. marine territories of indigenous communities or species-specific fishing concessions). The government's formalization of an MPA, however, represents the only legal means to grant exclusive fishing rights to fishing communities while at the same time aim at conserving the marine environment through a comprehensive ecosystem approach. This can also support the justification for reinforcing official enforcement of other fishery management guidelines such as season closures and gear restrictions.

Nevertheless, the government's involvement and/or lack thereof can also destabilize community initiatives and undermine future grassroots efforts. In the three cases presented, community initiatives have operated on very different time frames than those of the government. In addition, the constant restructuring of fishery administration in Mexico - from a Federal Secretariat to a Commission - has led to important consequences in terms of budget reductions, confusion as to which agencies are held accountable for what, and inefficiencies in bureaucratic processes. To exemplify this,

⁹ CONAPESCA, Mexico's Fishery Commission, grants fishing concessions as a form of exclusive fishing access right within specific areas. However, these concessions are species-specific, and a group will need to have several concession titles to have control over the most important resources in order to have meaningful exclusivity rights.

with the changes in the Presidential Administration that came about in 2000, bureaucratic problems caused many small-scale fishers to lose their fishing permits during their renovation process. Many of these permits were never renewed, forcing fishers to work illegally or under the auspices of other permit holders.

7.6 Role of NGOs and academia

The influence of NGOs and academia in accelerating the emergence of institutional arrangements and management and conservation actions cannot be overlooked. NGOs and academia have played an important role in empowering stakeholders, producing data and proposals with scientific backup, facilitating the communication of fishers with local and federal government entities, and working with the government and fishing sectors to establish reserves as management and conservation tools. They have also provided a more neutral forum for discussion of the issues at play and, consequently, some of the scenarios necessary for the evolution of institutions for co-management. At the same time, they have taken some of the financial, logistic, and technical burden off of essential monitoring processes and have helped bridge local ecological knowledge with experimental design, offering a powerful means to validate fishermen's knowledge and actions within higher local, state, and federal entities.

However, these institutions must work in close coordination and communication with environmental and fisheries management government agencies, and some times battle to be perceived as allies rather than enemies in the fulfilling of their institutional mission.

8. Recommendations

The Gulf of California is an appealing place to establish and test the use of marine reserve networks as management and conservation tools for various reasons. Its productivity could facilitate measuring tangible outcomes for some species in short and affordable time frames. In addition, the current deteriorating condition of the Gulf's fishery resources and the existing drive to establish forms of territorial use rights, particularly in the case of benthic resources, could facilitate the establishment of marine reserves. However, blindly considering reserves as the optimal marine fisheries management and conservation tool could lead to more problems than solutions. Given the interest of NGOs and government officials to establish reserve networks in the Gulf [26, 8] and the fact that reserves could increase in number in the years to come, we provide the following viewpoints and recommendations.

Part of the difficulty with the establishment of marine reserves worldwide is that, often, fishers do not believe they are established in their best interest and there is seldom tangible proof to show if they are, indeed, effective. Therefore, we must pay particular attention to communities or fishing sectors that are already showing signs of interest in their establishment, and to systems in which we can measure results in relatively short (i.e. 2-5 years) time frames. One good point of departure may be the establishment of refugia for benthic sessile or semi sessile fishery resources. The fact that these resources are more generally constrained within a geographical area than other resources (i.e. most fin fish) may facilitate monitoring and assessment of basic population parameters and of the spatial distribution of fishing activities [13]. This characteristic can also lead to a

well-defined management zones of reserves and facilitate access control to exploitable stocks [13]. These systems also lend themselves to facilitate the involvement of stakeholders in the ecological monitoring process. Although it may represent a logistical challenge, stakeholder involvement in research can be a critical component for the success of any future or existing marine reserve, as the burden of proof on their efficacy falls primarily on stakeholders themselves and not necessarily on an external entity.

Nevertheless, even if the majority of fishers believe in the purpose and benefits of reserves, problems with poaching will likely arise when legal fishing and territorial access rights to communities investing in reserves are lacking. As stocks within a refuge become richer, they can act as magnets to outside fishermen. This eventually may result in not only more damage to the harvestable stocks than if a reserve had not been established, but it may also give way to territorial and social conflicts between users. Given this imminent threat, the Mexican Government will need to designate more resources for enforcement and, where appropriate, ease a legal structure in which fishers can control access to fishing grounds. It is also evident that there is a substantial lag between the government's actions and the petitions of fishing communities. Community management petitions that the government is interested in supporting will require a more efficient formalization. Slow responses cause stakeholders to stop believing in the seriousness of their government and undermine their efforts to continue establishing encouraging management and conservation schemes.

In addition, because no legal harvesting occurs in reserves, establishing a reserve - at least temporarily - will reduce the size of the harvestable stock. Increasing harvests of

unprotected stocks often compensates for this reduction. It is important, therefore, to assess the spatial-temporal changes in fishing effort and species targeted after the establishment of reserves. Furthermore, simply prohibiting harvest in a reserve does not ensure that populations of all target species will recover to pre-harvest conditions within the reserve and begin to replenish adjacent populations [4]. Responses will likely be species specific and expressed at differing spatial and temporal scales.

Finally, the ecological and social-political processes operating in the Gulf of California must not be treated as separate entities, but rather as a unit with two components giving feedback to and influencing each other. When established, we must rigorously address the effects of reserves not only on the ecological resilience of the marine system and the economic well-being of fishing communities, but also on the existing social institutions, networks, stocks of social trust, and norms that shape these communities. In a region where enforcement capabilities are insufficient and will likely never be enough, this social capital could ultimately act as a pillar for long-term sustainability if backed up by a more robust legal framework that gives appropriate recognition of ad hoc local and regional management initiatives.

Acknowledgements

This study was made possible via financial contributions from The David and Lucile Packard Foundation, the Wallace Research Foundation, World Wildlife Fund, the Tinker Foundation, Fondo Mexicano para la Conservación de la Naturaleza, the Sandler Family Foundation, International Community Foundation, the Environmental Leadership Program, Marisla, and the PADI Project AWARE Foundation.

We thank the Mexican Government, particularly the National Commission for Protected Areas (CONANP), for its support throughout this work. Marcia Moreno kindly assisted in the development of all figures, and Tiffany Ash-Cudney, Jennifer Duberstein, and William W. Shaw provided insightful comments and editorial reviews. Finally, we thank the fishers of Loreto, Bahía de Kino, and Puerto Peñasco for their friendship, assistance, and support through the years.

References

- [1] Agardy TS. Marine protected areas and ocean conservation. Texas: Landes Company and Academic Press, 1997 (244 pp).
- [2] Roberts C, JP Hawkins. Fully-protected marine reserves: a guide. WWF Endangered Seas Campaign, 1250 24th Street, NW, Washington D.C., 20037, USA and Environment Department, University of York, York, YO105DD, UK. 2000.
- [3] National Research Council. Marine protected areas: tools for sustaining ocean ecosystems. Washington, D.C.: National Academy Press, 2001 (272 pp).
- [4] Carr MH, Reed DC. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* 1993;50:2019-2028.
- [5] Sarukhán J. Introduction. In: Robles Gil P, Ezcurra E, Mellink E, editors. *The Gulf of California: a world apart*. México D.F.: Agrupación Sierra Madre, 2001.
- [6] Brusca RC, Findley LT, Hastings PA, Hendrickx ME, Torre J, van der Heiden AM. Macrofaunal biodiversity in the Gulf of California. In: Cartron JLE, Cevallos G, editors. *Biodiversity, ecosystems and conservation in northern Mexico*. Oxford: Oxford University Press; 2005.
- [7] Álvarez-Borrego S. Physical oceanography. In: Case TJ, Cody ML, Ezcurra E, editors. *A new island biogeography of the Sea of Cortés*. New York: Oxford University Press, 2002. p.41-59.

- [8] Carvajal MA, Ezcurra E, Robles A. The Gulf of California: natural resource concerns and the pursuit of a vision. In: Glover LK, Earl SA, editors. *Defying ocean's end: an agenda for action* Washington, D.C.: Island Press; 2004. p.105-123.
- [9] Greenberg JB. The political ecology of fishing in the Upper Gulf of California. In: A Biersack, JB Greenberg, editors. *Reimagining political ecology*. Durham: Duke University Press, 2006 (419 pp).
- [10] Cariño M. *Historia de las relaciones hombre naturaleza en Baja California Sur: 1500-1940*. Baja California Sur: Universidad Autónoma de Baja California Sur, 1996 (229 pp).
- [11] Bowen T. *Unknown island: Seri Indians, Europeans, and San Esteban Island in the Gulf of California*. New Mexico: University of New Mexico Press, 2000 (548 pp).
- [12] Bahre CJ, Bourillón L, Torre J. The Seri and commercial totoaba fishing (1930-1950). *Journal of the Southwest* 2000;42(3):559-575.
- [13] Cudney-Bueno R. *Management and conservation of benthic resources harvested by small-scale hookah divers in the northern Gulf of California, Mexico: the black murex snail fishery*. MS Thesis. Tucson: University of Arizona; 2000.
- [14] Sáenz-Arroyo A, CM Roberts, Torre J, Cariño-Olvera M. Using fishers' anecdotes, naturalists' observations and grey literature to reassess marine species at risk: the case of the Gulf grouper in the Gulf of California, México. *Fish and Fisheries* 2005;6:1-13.

- [15] Sáenz-Arroyo A, CM Roberts, J Torre, M Cariño-Olvera, JP Hawkins. The value of evidence about past abundance: marine fauna of the Gulf of California through the eyes of 16th to 19th century travelers. *Fish and Fisheries* 2006;7(2):128-146.
- [16] Sala E, Aburto-Oropeza O, Reza M, Paredes G, López-Lemus L. Fishing down coastal food webs in the Gulf of California. *Fisheries* 2004;29(3): 19-25.
- [17] Sáenz-Arroyo A, Roberts CM, Torre J, Cariño-Olvera M, Enríquez-Andrade RR.. Rapid environmental shifting baseline among fishers from the Sea of Cortez. *Proceedings of the Royal Society*; 2005b 272:1957-1962.
- [18] Carta Nacional Pesquera. México: Instituto Nacional de la Pesca; 2004.
- [19] Knudson T. 1999. Return to a dying sea. *The Sacramento Bee*. July 3-4. Available at: <http://www.sacbee.com/static/archive/news/projects/dyingsea/> [21 March 2004].
- [20] Bourillón-Moreno L. Exclusive fishing zone as a strategy for managing fishery resources by the Seri Indians, Gulf of California, Mexico. PhD Dissertation. Tucson: University of Arizona; 2002.
- [21] Cudney-Bueno R. Marine reserves, community-based management, and small-scale benthic fisheries in the Gulf of California, Mexico. PhD Dissertation. Tucson: University of Arizona; 2007.
- [22] McGuire TR, GC Valdez-Gardea. Endangered species and precarious lives in the Upper Gulf of California. *Culture and Agriculture* 1997;19(3):101-107.

- [23] Hernández A, W Kempton. Changes in fisheries management in Mexico: Effects of increasing scientific input and public participation. *Ocean & Coastal Management* 2003;46(6-7):507-526.
- [24] Enríquez-Andrade RR, Anaya-Reyna G, Barrera-Guevara JC, Carvajal-Moreno M, Martínez-Delgado ME, Vaca-Rodríguez JG, Valdés-Casillas C. 2005. An analysis of critical areas for biodiversity conservation in the Gulf of California region. *Ocean & Coastal Management* 2005;48(1):31-50.
- [25] Ulloa R, Torre J, Bourillón L, Alcantar N. Planeación ecoregional para la conservación marina : Golfo de California y costa occidental de Baja California Sur. Final Report to The Nature Conservancy. Guaymas, Mexico: Comunidad y Biodiversidad, 2006. Available at:
<http://www.cobi.org.mx/publicaciones/Reporte_final_EGCYPBCS_mayo_2006.pdf> [January 1 2007].
- [26] Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK. A general model for designing networks of marine reserves. *Science* 2002;298(5600):1991-1993.
- [27] Gutierrez-Barreras JA. Reporte marino y costero del municipio de Loreto, B.C.S., México. Grupo Ecologista Antares, A.C. (GEA) y Parque Nacional Bahía de Loreto (PNBL), 2001.
- [28] Poder Ejecutivo Federal. 2002. Norma Oficial Mexicana NOM-059-ECOL-2001. Protección ambiental-Especies nativas de México de flora y fauna silvestres:

Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio- Lista de especies en riesgo. Diario Oficial de la Federación March 6:1-85.

- [29] Programa de Manejo Parque Nacional Bahía de Loreto. 2002. Instituto Nacional de Ecología (INE). México D.F., México.
- [30] Sáenz-Arroyo A, Torre T, Bourillón L, Kleiberg M. A community-based marine reserve network in North-western Mexico. In: American Commission for Environmental Cooperation: Proceedings of the Symposium and Workshop of the North American Marine Protected Areas Network, Loreto, Baja California Sur, México, 2005c. Available at: <www.cec.org> [January 1 2007].
- [31] Torre J. Pilot project of the draft of “How is your MPA doing?”, Report to WCPA/NOAA, 2004.
- [32] Bezaury-Creel JE. Protected areas and coastal and ocean management in Mexico. *Ocean & Coastal Management* 2005;48:1016-1046.
- [33] http://pangas.arizona.edu/research/research_index.html [January 1 2007]
- [34] Estudio Justificativo Para Redelimitar y Recategorizar Isla San Pedro Mártir. 2000. Documento presentado a la Secretaría del Medio Ambiente, Recursos Naturales y Pesca – Instituto Nacional de Ecología. Comunidad y Biodiversidad, A.C.
- [35] Tershy BR, Breese D, Croll D. Human perturbations and conservation strategies for San Pedro Mártir Island, Islas del Golfo de California Reserve, México. *Environmental Conservation* 1997;24(3):261-270.

- [36] Poder Ejecutivo Federal. Ley General de Equilibrio Ecológico y la Protección al Ambiente. Diario Oficial de la Federación January 28 1998. Available at: <http://www.semarnat.gob.mx/leyesynormas/Leyes%20del%20sector/lgeepa_.pdf> [February 8 2007].
- [37] Gibson CK. Forest resources: institutions for local governance in Guatemala. In: Burger J, Ostrom E, Norgaard RB, Policansky D, Goldstein BD, editors. Protecting the commons: a framework for research management in the Americas. Washington: Island Press, 2001 (360 pp).
- [38] Agrawal A. Common resources and institutional sustainability. In: Ostrom E, Dietz T, Dolsak N, Stern PC, Stonich S. Weber E, editors. The drama of the commons. Washington: National Academy Press, 2002 (521 pp).
- [39] Basurto-Guillermo X. Community-based conservation of the *callo de hacha* fishery by the Comcáac Indians, Sonora, Mexico. MSc. Thesis. Tucson: University of Arizona; 2002.

Figure F1. Location of the Puerto Peñasco, San Pedro Mártir Island, and Loreto Bay marine reserves.

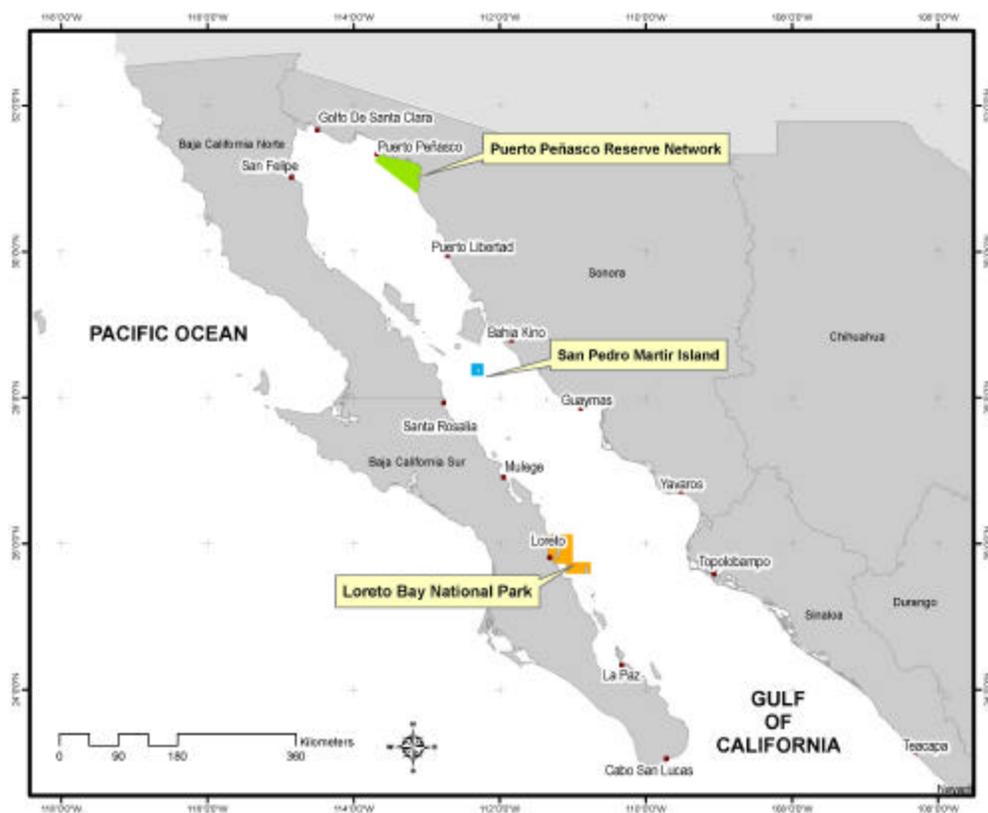


Figure F2. Loreto Bay National Park and location of el Bajo del Murciélago and Bajo el Cochi no-take zones

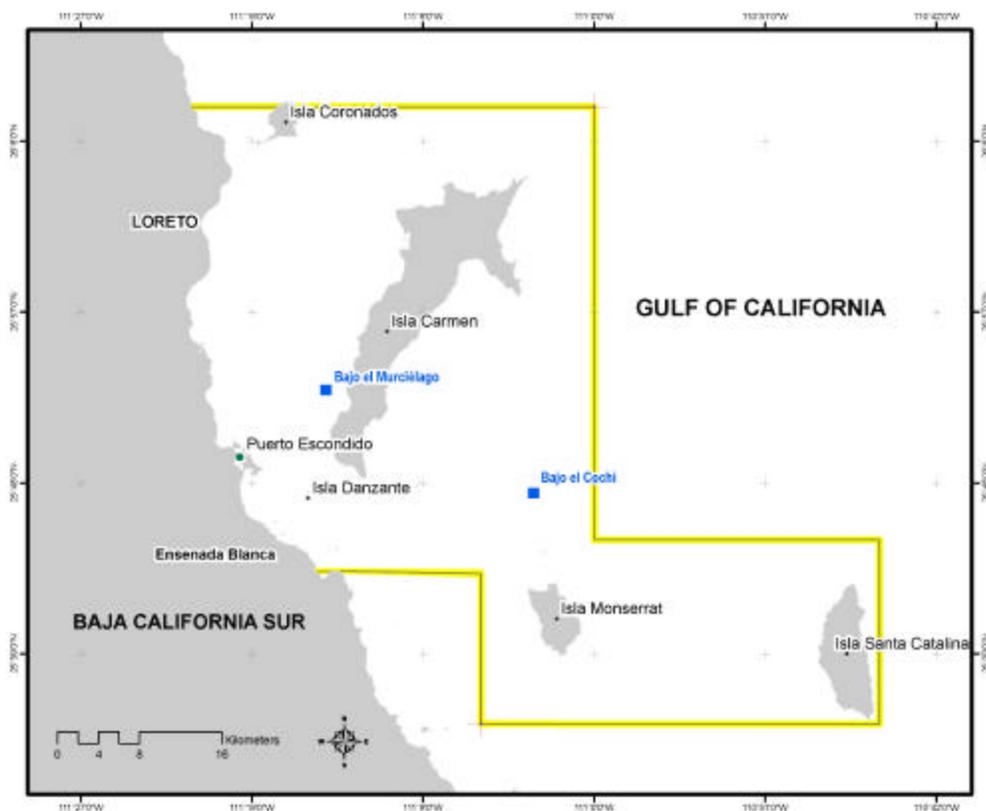


Figure F3. Marine reserve network of Puerto Peñasco, Sonora, Mexico.

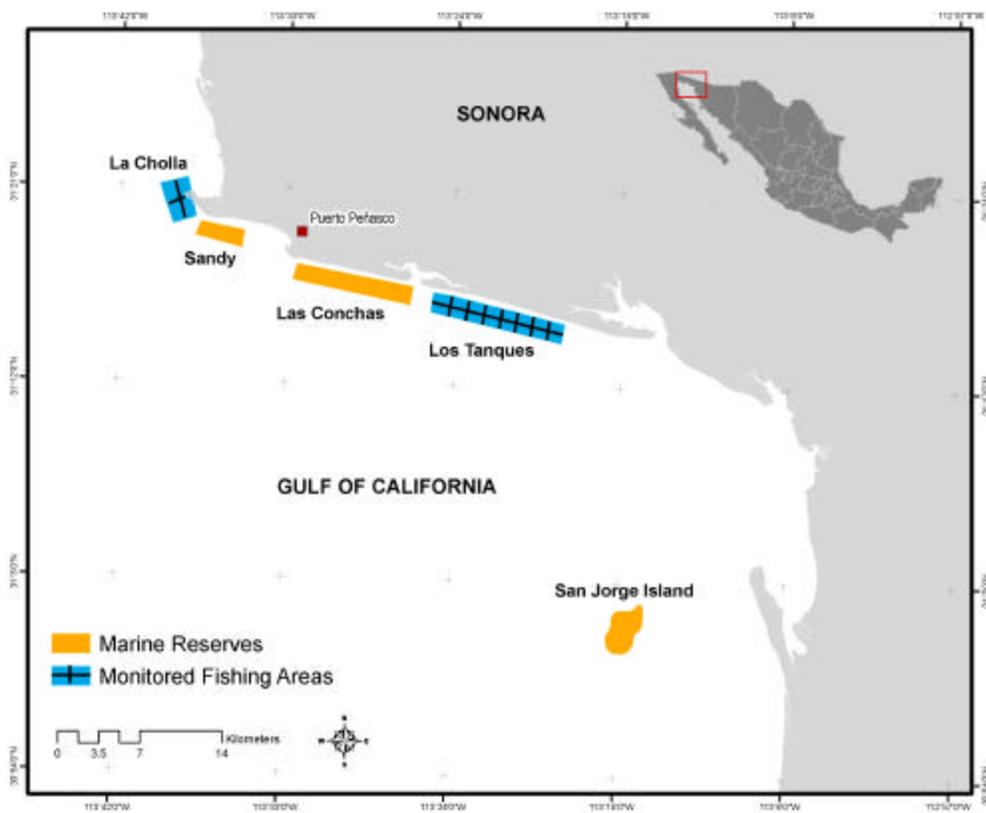
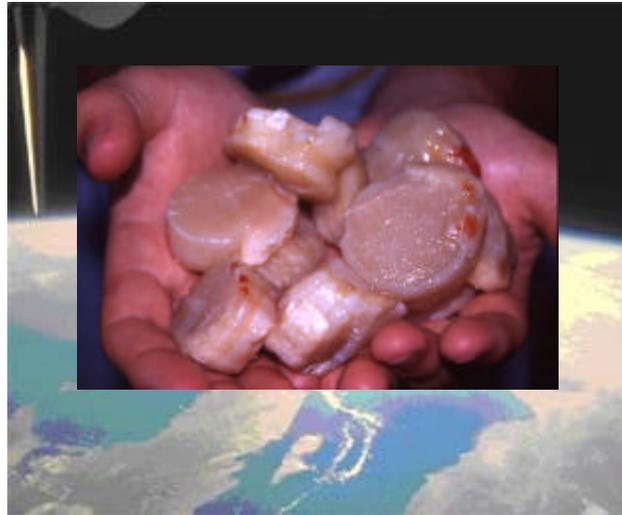


Figure F4. San Pedro Mártir Island Biosphere Reserve.



APPENDIX G

PLAN DE MANEJO REGIONAL PARA EL APROVECHAMIENTO Y LA
RECUPERACION DEL CALLO DE ESCARLOPA, SPONDYLUS CALCIFER



Documento Presentado a la Dirección General de Aprovechamiento de Vida Silvestre

Centro Intercultural de Estudios de Desiertos y Océanos

En colaboración con

Departamento de Recursos Naturales de la Universidad de Arizona

Elaboración de Documento

Richard Cudney-Bueno

Departamento de Recursos Naturales, Universidad de Arizona

Investigador Asociado, CEDO

Con el apoyo financiero de :

Comunidad y Biodiversidad: “Fondo Pescador”

The Tinker Foundation

The David and Lucile Packard Foundation

Citar como : Cudney-Bueno, R. 2007. Plan de manejo regional para el aprovechamiento y la recuperación del callo de escarlopa, *Spondylus calcifer*. Documento preparado para la Dirección General de Aprovechamiento de Vida Silvestre. Centro Intercultural de Estudios de Desierto y Océanos. Puerto Peñasco, Sonora, México.

**Plan de Manejo Regional para el Aprovechamiento y la Recuperación del
Callo de Escarlopa, *Spondylus calcifer*
Proyecto Piloto para el Alto Golfo de California, México**

Introducción

El callo de escarlopa, *Spondylus calcifer*, es un molusco que ha sido capturado a lo largo del Pacífico Centro Oriental, incluyendo las costas mexicanas, por cientos de años. Ha pasado de ser un recurso altamente valuado por su carácter ornamental y usado en ofrendas y rituales religiosos de diversas culturas mesoamericanas, a uno de los recursos pesqueros con mayor valor comercial para fines de consumo. Sin embargo, en México la captura regular de esta especie se ha desarrollado bajo un marco ilegal ya que el callo de escarlopa se encuentra sujeto a protección especial bajo los términos de la NOM-059.

Reconociendo la realidad de extracción histórica así como el potencial de aprovechamiento sustentable de algunos recursos bentónicos listados en la NOM-059, en años recientes la Dirección General de Vida Silvestre del Gobierno Mexicano ha establecido iniciativas que permitan el aprovechamiento regulado y estrictamente fundamentado de algunas de estas especies. Este aprovechamiento se establece bajo los términos de Planes de Manejo Regionales de Aprovechamiento. Tal es el caso del pepino de mar (*Isostichopus fuscus*) y la almeja pismo (*Tivela stultorum*).

Dada la evidente extracción del callo de escarlopa y el potencial de que esta extracción pueda realizarse bajo marcos sustentables y con un enfoque de recuperación de las poblaciones existentes, la Dirección General de Vida Silvestre, en colaboración con el Centro Intercultural de Estudios de Desiertos y Océanos y la Universidad de Arizona, ha tomado la iniciativa de desarrollar el presente Plan de Manejo de Aprovechamiento y Recuperación del Callo de Escarlopa. Dicho Plan tiene como propósito establecer los lineamientos generales estrictos que deben seguirse para establecer la factibilidad y los términos de aprovechamiento del callo de escarlopa. Bajo esta premisa, cualquier marco de aprovechamiento del callo de escarlopa deberá no solo asegurar una pesquería sustentable, pero también la recuperación a largo plazo de los bancos pesqueros de esta especie.

El presente Plan de Manejo de Aprovechamiento y Recuperación del Callo de Escarlopa establece como proyecto piloto al alto Golfo de California, en particular la zona de los arrecifes rocosos aledaños a Puerto Peñasco, Sonora. Esta región actualmente cuenta con los estudios más extensos que se han realizado en torno a la biología y dinámica poblacional de esta especie y cuenta con esquemas alentadores de manejo comunitario para el callo de escarlopa y diversas otras especies de recursos bentónicos. Dichos esquemas han incluido el establecimiento de corredores de reservas marinas, vedas temporales, y la participación activa de buzos comerciales en el monitoreo de recursos bentónicos a largo plazo. Sin embargo, se espera que este proyecto piloto pueda ser utilizado como base para el desarrollo de cualquier esquema de aprovechamiento y manejo del callo de escarlopa en otras regiones del país.

I. Clasificación Taxonómica

Phylum: Mollusca

Clase: Bivalvia

Subclase: Lamellibranchia

Superorden: Filibranchia

Orden: Veneroidea

Familia: Spondylidae

Genero: Spondylus

Especie: calcifer

Sinónimos científicos: *Spondylus limbatus* (Sowerby); *Spondylus radula* (Reeve, 1856); *Spondylus smithi* (Fulton, 1915).

II. Biología

2.1 Descripción

El callo de escarlopa (también conocido como almeja burra o callo margarita), *Spondylus calcifer* Carpenter, 1857, es la especie más grande de la familia Spondylidae que se encuentra en el continente Americano (Keen 1971). En la etapa adulta cuenta con una concha muy gruesa, comúnmente llena de orificios ocasionados por poliquetos y almejas taladreras (*Lithophaga* spp). Una banda ancha color rojo-morado oscuro marca el margen interior de la concha de la mayoría de los especímenes.



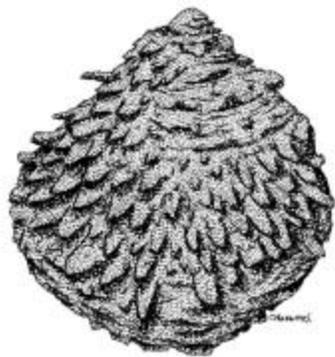
2.2 Identificación

Junto con *Spondylus princeps* (sinónimo *Spondylus leucacanthus*, Broderip 1833), la otra especie de la familia Spondylidae encontrada en las costas del Pacífico Mexicano, el callo de escarlopa comparte con miembros de la familia Pectinidae un ligamento en la parte central de la charnela. Sin embargo, ambas especies difieren de los pectínidos por la ausencia de una apertura bisal en la valva derecha, el grosor de la

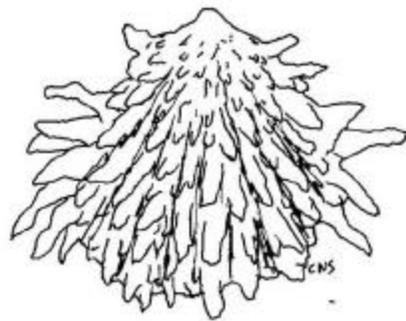
concha, y por la irregularidad de la concha causada por su adhesión a superficies duras (rocas, tepetates, conchas de otros bivalvos).

La concha de *S. calcifer* es irregularmente redondeada, cambiando con el crecimiento a tosca, pesada y muy distorsionada, con valvas fuertemente desiguales en tamaño y escultura. El área de adhesión es grande, extendiéndose sobre gran parte de la valva derecha (inferior). La superficie restante de la valva a menudo está cubierta de excrescencias foliáceas concéntricas. La valva izquierda (superior) comúnmente horadada por organismos perforadores, su escultura formada por costillas radiales toscas, con hileras radiales de espinas relativamente cortas y, entre éstas, numerosos hilos radiales finos a gruesos y rugosos. El color de la superficie externa de la concha es púrpura a pardusca, mientras que la superficie interna es blanco-porcelana con una franja marginal ancha, intensamente coloreada (por lo general púrpura) y a menudo con manchas café en los dientes de la charnela (Poutiers 1995).

Se distingue de *Spondylus princeps* porque las espinas de la concha por lo general son redondeadas, la concha es mucho más distorsionada, las valvas son fuertemente desiguales en forma y escultura, y el área de adhesión es mucho más extensa, cubriendo gran parte de la valva derecha. Sin embargo, durante la etapa juvenil es difícil poder distinguir una especie de otra ya que ambas especies son similares en color y tienen espinas bastante conspicuas.



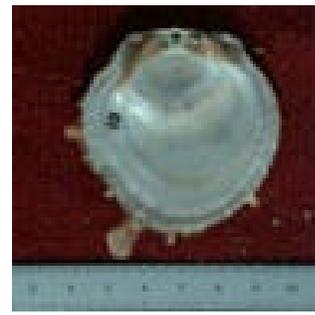
Callo de escarlopa, *Spondylus calcifer*.
Organismo adulto



Almeja mechuda, *Spondylus princeps*.
Organismo adulto



Exterior de la valva derecha de
juvenil de callo de escarlopa



Interior de la valva derecha de
juvenil de callo de escarlopa

Distribución

La especie se distribuye a lo largo de una gran parte del Pacífico Centro Oriental, desde el Golfo de California, México hasta Ecuador (Keen 1971, Poutiers 1995). Sandweiss (1992) reporta que la especie también puede colonizar las costas de Perú hasta la zona de Callao (Puerto de Lima) como resultado de aguas más cálidas durante años Niño.

Se han hecho pocos estudios relacionados a la abundancia y distribución de *Spondylus calcifer* en el Golfo de California. Sin embargo, sabemos que actualmente gran parte de la población se encuentra en la región noroeste del Golfo, particularmente en la zona que comprende desde la región de las Grandes Islas en ambos litorales del Golfo hasta el Borrasco, dentro de la Reserva de la Biosfera Alto Golfo de California y Delta del Río Colorado (Cudney-Bueno 2007).

2.3 Hábitat

El callo de escarlopa normalmente se encuentra en hábitats rocosos en los que predominan epífitas como algas calcáreas. También es común encontrarlo entre mezclado en bancos de mejillón, principalmente *Modiolus capax*. En el alto Golfo de California predomina en arrecifes planos conocidos localmente como *tepetates*, mismos que se constituyen de coquina y/o granito. En ocasiones también se llegan a encontrar organismos sueltos, adheridos a alguna concha o roca pequeña.

A lo largo de su distribución, se encuentra primordialmente en los arrecifes rocosos de la zona submareal hasta aproximadamente los 55 m de profundidad (Poutiers 1995).

2.4 Ciclo de vida y reproducción

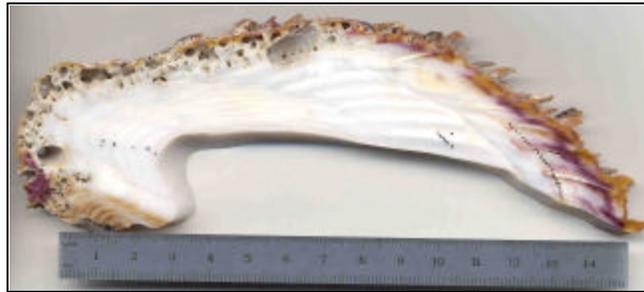
2.4.1 Edad y Crecimiento

Estudios recientes basados en técnicas de estimación de edad y crecimiento mediante isótopos de oxígeno de la concha del callo de escarlopa muestran que esta especie, al menos en la región norte del Golfo de California, tiene una longevidad mínima de 10 años (Cudney-Bueno 2007). Sin embargo, es muy posible que la especie llegue a alcanzar una longevidad aún mayor (Cudney-Bueno 2007). Los estudios hechos para estimar la edad máxima fueron basados en la concha del organismo más grande (160 mm de alto) capturado en el alto Golfo desde el verano del 2001. Sin duda hoy en día es sumamente raro poder encontrar organismos más grandes que éste en el Golfo de California. Villalejo Fuerte et al. (2002), por ejemplo, después de coleccionar más de 200 ejemplares en el sur del Golfo de California, nunca encontraron organismos mayores de 160 mm. Sin embargo, Poutiers (1995) reporta que *Spondylus calcifer* puede llegar a medir hasta 250 mm de alto (aunque Keen 1971 reporta longitudes máximas de 150 mm). De igual forma, pescadores viejos del área de Puerto Peñasco mencionan que hace 20 años regularmente se encontraban organismos con longitudes máximas mayores a los que

se encuentran en la actualidad. De ser cierto, la especie indudablemente podría llegar a tener una longevidad mayor a los 10 años. Así mismo, es importante recalcar que pueden existir variaciones regionales en el crecimiento de la concha. Como muchos otros moluscos, el crecimiento del callo de escarlopa puede estar influenciado considerablemente por patrones de corriente y el tipo de hábitat en que se encuentre.

En términos generales, la especie muestra un crecimiento más acelerado de la concha durante los meses de verano y principios de otoño que durante el invierno y primavera, mismo que se encuentra representado por anillos de crecimiento marcados en el interior de la concha (Cudney-Bueno 2007) (Figura 1).

Figura G1. Corte de una concha adulta de callo de escarlopa, *Spondylus calcifer*, mostrando los anillos de crecimiento.



Este crecimiento es inversamente proporcional al crecimiento del músculo aductor o *callo*. Los meses de aguas frías coinciden con un incremento significativo del músculo aductor (en peso y tamaño, Figuras 2 y 3), lo que sugiere que las variaciones en el crecimiento de la concha se encuentran relacionadas a la distribución de recursos energéticos antes y después del período reproductivo. Al igual que en algunos otros bivalvos, *S. calcifer* podría estar proveyendo la mayoría de sus recursos energéticos durante los meses fríos (invierno-primavera) al almacenamiento de glicógeno en el músculo aductor en preparación a la reproducción (ver sección de “reproducción”) y, por lo mismo, limitando el crecimiento de la concha (Cudney-Bueno 2007)

Figura G2. Relación entre altura de la concha y longitud del músculo aductor del callo de escarropa, *Spondylus calcifer*, diferenciando la relación entre invierno/primavera y verano/otoño.

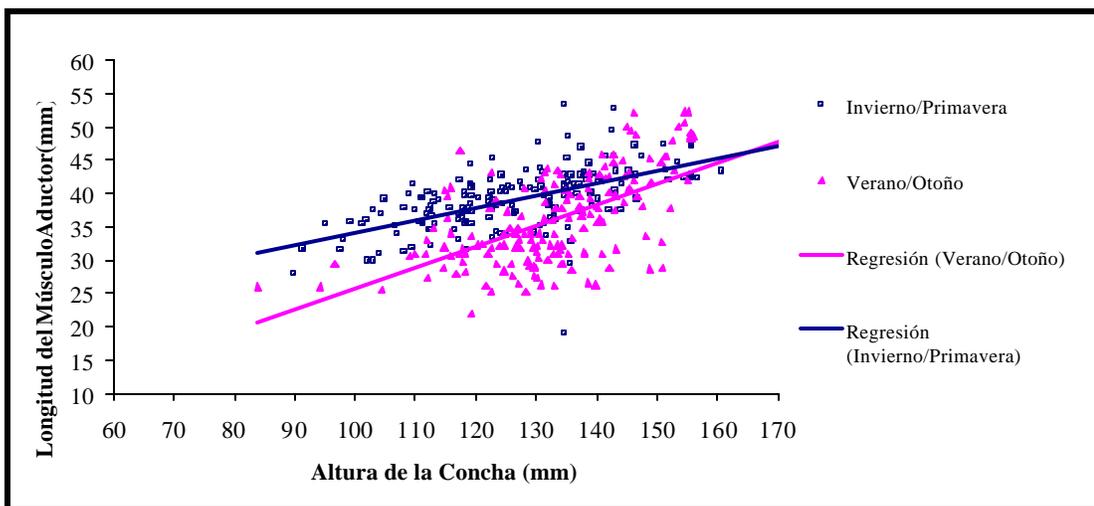
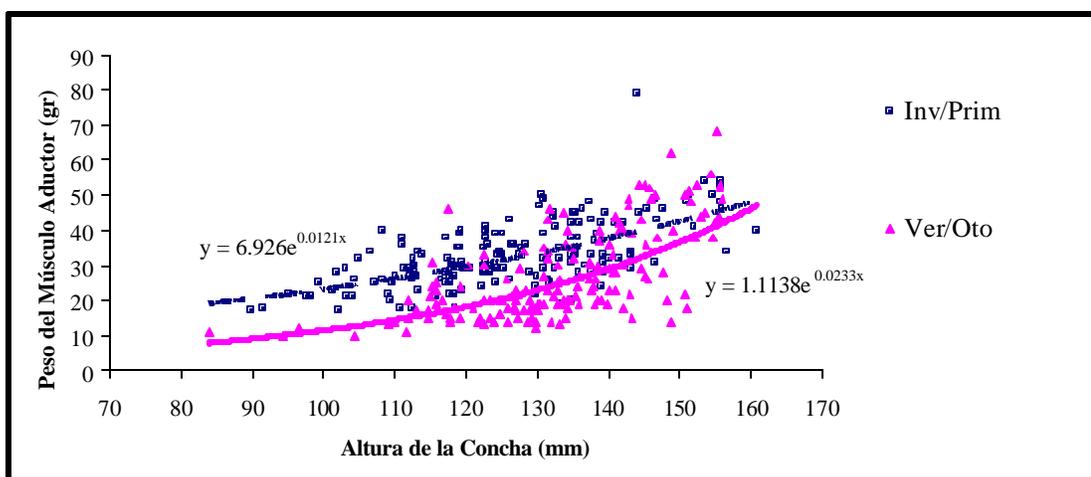


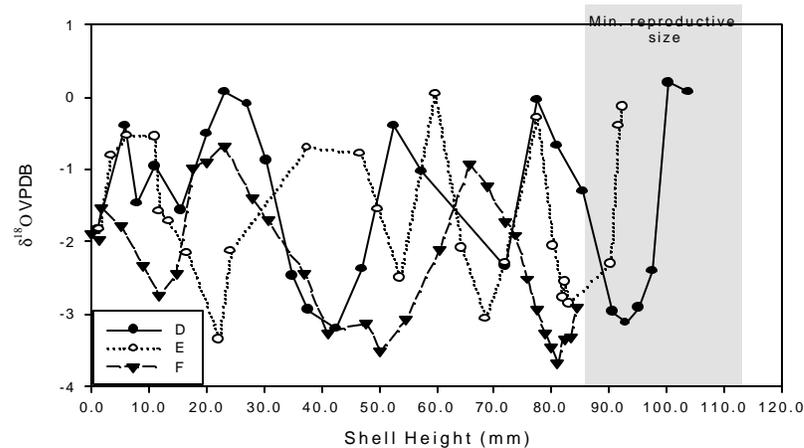
Figura G3. Relación entre altura de la concha y el peso del músculo aductor del callo de escarropa, *Spondylus calcifer*, diferenciando la relación entre invierno/primavera y verano/otoño.



2.4.2 Reproducción

Villalejo-Fuerte et al. (2002), trabajando en el sur del Golfo de California, reportan individuos de 86 mm de alto de la concha habiendo alcanzado la primera madurez sexual. Sin embargo, también concluyen que el 50% de la población no alcanza la madurez sexual sino hasta los 113 mm de altura de la concha. Basándose en esta información, se ha determinado que la mayor parte de la población de *Spondylus calcifer* alcanza la primera edad de madurez sexual entre los 3-4 años (Cudney-Bueno 2007 (Figura 4).

Figura G4. Perfil de valores isotópicos de oxígeno obtenidos para tres organismos reproductores. Un ciclo completo representa un año de crecimiento (Fuente: Cudney-Bueno 2007).



La especie es gonocórica (no hermafrodita), con una distribución de la población de machos y hembras equivalente a 1:1 (un macho por cada hembra) (Villalejo-Fuerte et al. 2002, Cudney-Bueno 2007). El período reproductivo se limita a los meses de verano, normalmente desovando desde Julio a Octubre cuando el agua alcanza una temperatura de 29⁰ C. Este período es seguido por un largo período inactivo desde noviembre a febrero. El incremento en la temperatura del agua a principios de primavera inicia el proceso de maduración gonadal, mientras que la disminución de la temperatura en otoño inhibe la gametogénesis. El reclutamiento se da principalmente entre agosto y septiembre (Tablas 1 y 2).

Tabla G1. Resumen de datos de muestra de colecta de especímenes de callo de escarlopa para la determinación de su período reproductivo en el alto Golfo de California, México. NA = “No Aplica”, ya que las gónadas no se encontraban maduras para poder determinar el sexo de los organismos.

Día de Colecta	Temp (°C)	Prof. (m)	N	% Maduros	Desove	% Machos	% Hembras
11-20-03	22	11	30	0	No	NA	NA
11-21-03	21	13	30	0	No	NA	NA
03-12-04	17	9	30	13	No	NA	NA
03-26-04	18	9	30	16	No	NA	NA
03-28-04	21	6	30	27	No	NA	NA
04-28-04	21	13	30	100	No	63	37
05-07-04	22	12	30	100	No	67	33
05-28-04	23	14	30	100	No	57	43
06-12-04	25	27	30	100	No	50	50
07-09-04	28	9	30	100	Sí	50	50
07-16-04	28	13	30	100	Sí	43	57
07-26-04	30	9	30	100	Sí	47	53
09-21-04	29	13	30	36	No	NA	NA
09-22-04	28	13	22	27	No	NA	NA

Tabla G2. Cronograma de actividad reproductiva, reclutamiento, y período principal de aprovechamiento del callo de escarlopa en el alto Golfo de California, México.

Evento	E	F	M	A	M	J	J	A	S	O	N	D
Reproducción						■	■	■	■			
Desove							■	■	■			
Reclutamiento								■	■	■		
Realización de censos	■	■	■	■	■	■	■	■	■	■	■	■
Aprovechamiento	■	■	■	■	■	■				■	■	■

2.5 Longitud y Peso

Tabla G3. Relación de tallas y pesos de organismos completos y del músculo aductor (“callo”) del callo de escarlopa, *Spondylus calcifer*, en el alto Golfo de California, México.

Parámetro	Valor/Intervalo Organismo Completo	Valor/Intervalo Músculo Aductor
Talla mejor representada	130.8 mm altitud	37.4 mm alto
Talla mínima (captura comercial)	83.9 mm altitud	21.1 mm alto
Talla máxima	Reportada: 220 mm Registrada: 186.6 mm	69.6 mm alto
Talla media anual	130.2 mm	37.76 mm alto
Peso mayor representado	Desconocido	30 g
Peso mínimo (captura comercial)	Desconocido	10 g
Peso máximo	2.0 kg	200 g
Peso promedio anual	Desconocido	31.79 g

Tabla G4. Relación de pesos promedio mensuales del músculo aductor (“callo”) del callo de escarlopa, *Spondylus calcifer*, en el alto Golfo de California, México

Mes	Peso Promedio (g)	95% I.C.	Talla Promedio (g)	95% I.C.
Enero	31.30	29.94; 32.67	37.54	36.88; 38.21
Febrero	37.04	35.68; 38.40	38.69	38.03; 39.36
Marzo	36.07	34.24; 37.90	38.31	37.51; 39.10
Abril	48.53	45.99; 51.08	42.29	41.78; 42.80
Mayo	34.33	32.23; 36.42	39.56	38.54; 40.58
Junio	35.36	33.28; 37.44	39.83	38.81; 40.84
Julio	25.00	23.79; 26.20	34.58	33.99; 35.17
Agosto	23.21	21.41; 25.01	32.66	31.87; 33.44
Septiembre	32.14	31.24; 33.05	38.57	38.13; 39.01
Octubre	31.23	27.63; 34.84	36.10	35.62; 36.59
Noviembre	29.83	28.02; 31.63	36.00	35.34; 36.67
Diciembre	30.83	29.04; 32.63	38.18	37.31; 39.05

2.6 Abundancia

El único trabajo previo al que aquí se presenta en el que se ha estimado la abundancia de esta especie en el Golfo de California es el de Baqueiro et al (1982). En este trabajo, calculan densidades muy bajas en Baja California Sur, de tan solo 1

organismo por 100 m². Así mismo, Villalejo-Fuerte et al. (2002) reportan densidades similares para el área de Loreto en años recientes, aunque no proveen estimaciones de densidad poblacional ya que el enfoque de su estudio fue sobre el ciclo reproductivo de la especie.

Fuera de estos trabajos y de anécdotas de pescadores y observaciones históricas, aparentemente no se ha hecho ningún otro esfuerzo por estimar la densidad de esta especie en otras regiones del Golfo de California ni existen estimaciones de abundancia para otras regiones del Pacífico Mexicano. Aún más importante, no existen trabajos de base para poder realizar comparaciones sobre el estado de las poblaciones actuales con las poblaciones “naturales” o previas al desarrollo de una pesca más intensiva. Por lo mismo, es imposible establecer el grado en el que las poblaciones de *S. Calcifer* han sido explotadas ni las poblaciones óptimas o la capacidad de carga de esta especie. Sin embargo, para años recientes, se cuenta con un mayor conocimiento de las poblaciones de esta especie en el alto Golfo de California, en particular en los arrecifes aledaños a Puerto Peñasco, Sonora.

En términos generales y comparado con lo poco que se conoce sobre las densidades poblacionales del callo de escarlopa en el resto del Golfo de California, las poblaciones de esta especie en el alto Golfo muestran ser mucho más saludables. En la sección 4.4 se provee un desglose de las densidades poblacionales estimadas para distintas zonas de captura.

2.7 Estado de Conservación

El callo de escarlopa actualmente se encuentra listado como especie sujeta a protección especial en la NOM-059-SEMARNAT-2001 del Gobierno Mexicano. No tiene ningún estatus de riesgo atribuido por IUCN o CITES. Sin embargo, Baqueiro et al. (1982) y Villalejo Fuerte et al. (2002) ambos mencionan a la especie como amenazada en el área de Baja California Sur, con densidades comúnmente de tan sólo 1 individuo por 100 m². Así mismo, es importante recalcar que la legislación limitada que protege a la especie a la fecha realmente no ha tenido peso alguno ni ha sido ejercida. Buzos comerciales del Golfo de California han capturado el callo de escarlopa por más de tres décadas consecutivas. En el caso de los arrecifes del alto Golfo, las densidades poblacionales son mucho mayores a cualquier otra registrada en el Golfo, en algunas zonas altamente elevadas, dando soporte a una pesquería anual estable. Sin embargo, estas densidades seguramente no representan las densidades que la especie llegó a tener en su estado “natural” previo a la explotación comercial de este siglo (ver sección de “La Pesquería”). Desgraciadamente no se cuenta con datos previos a esta captura, pero entrevistas con los buzos más veteranos, algunos presentes cuando la pesquería tomó auge a finales de los 70’s, indican que las poblaciones a lo largo de la región del norte del Golfo de California, incluyendo las Islas de la Cintura, eran considerablemente mayores cuando la especie comenzó a ser capturada con técnicas de buceo.

III. Legislación Nacional e Internacional

El callo de escarlopa actualmente se encuentra listado como especie sujeta a protección especial en la NOM-059-SEMARNAT-2001 del Gobierno Mexicano (Poder Ejecutivo Federal 2002). Esto significa que la especie puede ser aprovechada, aunque bajo condiciones distintas a las de otras especies pesqueras. El aprovechamiento y manejo de esta especie se debe llevar a cabo de acuerdo con lo establecido en la Ley General del Equilibrio Ecológico y la Protección al Ambiente (LGEEPA) (Poder Ejecutivo Federal 1988), y la Ley General de Vida Silvestre (LGVS) (Poder Ejecutivo Federal 2000). No tiene ningún estatus de riesgo atribuido por IUCN o CITES.

IV. La Pesquería

4.1 Historia

El callo de escarlopa ha jugado un papel muy importante en términos económicos, políticos, culturales y religiosos en las comunidades costeras de Latinoamérica por cientos de años. Junto con la almeja mechuda, también conocida como “viejita” o “concha china” (*Spondylus princeps*), era intercambiado por culturas mesoamericanas desde el período pre-cerámico (12,000-1,800 A.C.), altamente valuado por su carácter ornamental y usado en ofrendas y rituales religiosos (Pillsbury 1996). Gobernantes de la cultura Chimú, en Perú, financiaban una red de intercambio a larga distancia durante un estadio temprano de la expansión del imperio, particularmente con la concha de *Spondylus*. Los beneficios de esa red comercial constituyeron un elemento de suma importancia en la formación y mantenimiento de las bases económicas y rituales del poder sobre el que se sustentaba la expansión del estado (Pillsbury 1996). La evidencia arqueológica, combinada con reportes tempranos de los españoles, indica que la clase alta de todas las civilizaciones dominantes del Nuevo Mundo en el tiempo de la conquista española, así como varias otras que para entonces habían declinado o desaparecido, invertían grandes recursos y esfuerzos para obtener las conchas de *Spondylus* (Donkin 1998). La presencia de conchas de *Spondylus* spp. en sitios arqueológicos sugiere que el intercambio de estos bivalvos se extendía desde la frontera con los Estados Unidos hasta el sur de Perú (Figura 5) (Donkin 1998).

Figura G5. Distribución de sitios arqueológicos Mesoamericanos donde se han encontrado ejemplares de *Spondylus* spp. (Fuente: Donkin 1998)



En el Valle de México, *Spondylus*, posiblemente tanto del Pacífico como del Caribe, fue importado por la metrópolis de Teotihuacán y representado en varios murales. Así mismo, según algunas leyendas Aztecas, Quetzalcóatl le dio a la ciudad de Tula conchas rojas y blancas (*Spondylus*), las cuales se usaron en la edificación de cuatro palacios. De acuerdo a la Matrícula de Tributos en el Código Mendoza (ca. 1540), Moctezuma II demandaba 1600 especímenes anualmente de varios pueblos en la costa del Pacífico entre Cihuatlán (Jalisco) y Coyucac (Guerrero).

A la llegada de los españoles, la concha de *Spondylus* adquirió un valor más comercial. El nombre *calcifer* (“Proveedor de Calcio”) refiere al uso extensivo que los Españoles le dieron a la concha de esta especie, pulverizándolas para obtener materia prima usada en la elaboración de cemento.

Desde tiempos prehispánicos hasta finales de los años 60’s del siglo XX, la recolección del callo de escarlopa estaba limitada a zonas relativamente someras. Sin embargo, con el desarrollo del sistema de buceo con toma de aire, su recolección pudo extenderse a zonas más profundas.



Buzo colectando conchas de *Spondylus* y colocándolas en su bolsa atada al cuello (Fuente: Donkin 1998)

Hoy en día, el aprovechamiento de *Spondylus* ha pasado de ser un uso prácticamente exclusivo de la concha a uno de comercialización del músculo aductor o “callo” como producto alimenticio.

Adivino Mesoamericano con conchas de *Spondylus* (Fuente: Donkin 1998)



La Pesquería en el Norte del Golfo de California y el Área de Puerto Peñasco

En el norte del Golfo de California, la pesca del callo de escarlopa, al igual que otras pesquerías de buceo, se inició principalmente en la comunidad de Bahía de Kino. A finales de los 70's y principios de los 80's, durante la temporada de veda del camarón, barcos camaroneros nodriza hacían viajes de buceo desde Bahía de Kino a las Islas de La Cintura y las Islas Encantadas (Cudney-Bueno 2000). A raíz de estos viajes se descubrieron los bancos extensos de callo de escarlopa y otros moluscos que se encuentran en las zonas aledañas a Puerto Peñasco (Cudney-Bueno 2000). Aunque los arrecifes extensos de esta región representaban un gran incentivo para el desarrollo de actividades de buceo, las fuertes corrientes de marea y la poca visibilidad también actuaron como un filtro de acceso. Pocos buzos se quedaron en la zona de Peñasco, y muchos de los buzos que hoy en día pescan en la región son los mismos que llegaron en los 70's-80's o la segunda generación de éstos (Cudney-Bueno 2007).

Cabe mencionar que en el verano del 2002, a raíz del interés de la Sociedad Cooperativa Buzos de Puerto Punta Peñasco por mantener una pesca sustentable de los recursos bentónicos de la región, se establecieron diversas medidas de manejo comunitarias, incluyendo el primer corredor de reservas pesqueras (zonas de repoblamiento/refugio pesquero) establecido en el Golfo de California. Junto con el Centro Intercultural de Estudios de Desiertos y Océanos (CEDO) y la Universidad de Arizona, se inició un programa de monitoreo intensivo de los diversos recursos pesqueros capturados por los buzos de Puerto Peñasco. Dicho monitoreo cuenta con la participación activa de los buzos de la Cooperativa. Estos esfuerzos no solo dieron pie a que la Cooperativa fuera receptora del reconocimiento Nacional de la Conservación de la

Naturaleza 2003, pero también dieron inicio a una nueva etapa en el manejo de recursos bentónicos de la región y han sentado un ejemplo para otras comunidades pesqueras del Golfo de California. Sin embargo, estas medidas de manejo y conservación no cuentan con un soporte legal gubernamental y se ven complicadas aún más dado que no existen permisos para la captura legal del callo de escarlopa (ver siguiente sección, “Captura Ilegal”). Irónicamente, el caso de la pesca de buceo en Puerto Peñasco es una de las pesquerías artesanales del Golfo de California con los mejores esquemas de manejo a nivel ecosistema pero que desafortunadamente se encuentra fuertemente debilitada al no contar con una estructura de respaldo gubernamental adecuada.

4.2 Captura Ilegal

Técnicamente en todos los sitios de México donde el callo de escarlopa es y ha sido capturado a partir de 2001 se ha hecho en forma ilegal ya que la especie se encuentra en la NOM-059 y a la fecha no existen permisos de pesca para su captura. Sin embargo, es importante recalcar que contrario a otras especies que se encuentran en la NOM-059 como la totoaba, tortugas marinas, y otras, la mayoría de los pescadores desconocen que el callo de escarlopa está sujeto a algún tipo de protección. Si lo saben, desconocen qué lineamientos existen para su estatus de riesgo.

Dado que la historia ha mostrado que esta especie no se ha dejado de pescar, que no ha contado con lineamientos adecuados de vigilancia y de seguimiento de la Ley, y que su estado de protección es altamente desconocido entre el sector pesquero, es de suma importancia que esta realidad se reconozca y que **su extracción sólo se realice bajo marcos de manejo regionales adecuados y estrictamente implementados**. Estos esquemas de aprovechamiento **deben incorporar medidas para la recuperación de la especie a largo plazo**. Así mismo, **la ley debe de ser aplicada para prohibir su captura en los sitios que muestren estar sobreexplotados y donde no se hayan extendido permisos de aprovechamiento** bajo los lineamientos de un Plan Regional de Aprovechamiento.

4.3 Métodos de Pesca

El callo de escarlopa se captura primordialmente mediante el buceo tipo “hookah”, en el que el buzo recibe aire de una manguera conectada a un compresor en la embarcación. Dependiendo de la región donde se capture, las mangueras y el tipo de compresor pueden variar de tamaño y tipo. Por lo general se utilizan compresores de pintura con mangueras de 100 metros de largo a las que se les adapta un regulador de aire con boquilla.



Normalmente participan dos buzos y un motorista por panga en un viaje de pesca. Sin embargo, dependiendo principalmente de la fuerza de las corrientes de marea en ocasiones solo participa un buzo para facilitar el trabajo del motorista (Cudney-Bueno 2007). Un viaje típico de pesca de callo comienza entre las 7-8 de la mañana. En promedio, los buzos permanecen debajo del agua 4.36 horas, por lo general divididas en 2-4 inmersiones dependiendo del éxito de búsqueda de callo y de la profundidad a la que se esté trabajando. La selección del sitio de pesca es marcada por tres factores principales: a) éxito de captura obtenido en el viaje previo, b) grado de visibilidad y presencia de corrientes de marea, c) disponibilidad de recursos monetarios y del capitán de la panga por invertir tiempo, esfuerzo y recursos para realizar un viaje de pesca alejado (Cudney-Bueno 2007).

4.4 Áreas y Volúmenes de Aprovechamiento

El callo de escarlopa se captura desde el Golfo de California a lo largo del Pacífico Centro Oriental hasta las costas de Ecuador. Debido a que los estudios existentes sobre esta pesquería a lo largo del rango de distribución de la especie son muy limitados, se desconoce a ciencia cierta en qué sitios se ha desarrollado una pesca formal para el callo de escarlopa. Sin embargo, ya sea como pesquería formal comercial o en forma de recolección artesanal, se puede decir que el callo de escarlopa muy probablemente está sujeto a algún nivel de presión antropogénica en cualquier sitio donde existan buzos comerciales y hábitat adecuado para sostener poblaciones a profundidades accesibles para el buceo. En la actualidad se están realizando estudios extensivos sobre las actividades pesqueras en la región del Norte del Golfo de California bajo la Iniciativa *PANGAS* (www.pangas.arizona.edu). Dichos estudios indudablemente darán una visión más extensa sobre la realidad de uso de este recurso desde la zona de las Grandes Islas hasta el delta del Río Colorado.

Conocimiento Existente para el Alto Golfo de California

Historias orales de pescadores viejos de Puerto Peñasco que han trabajado en otras regiones del Golfo, principalmente la zona de las Grandes Islas y en los estados de Jalisco y Nayarit, sugieren que las densidades en los arrecifes del alto Golfo siempre han sido mayores que en otras zonas del Golfo. Esto concuerda con patrones de corriente en el verano, cuando la especie se reproduce. En el verano predominan corrientes de sur a norte en la costa oriental del Golfo de California (Marinone et al. en revisión). Sin embargo, es imposible corroborar a ciencia cierta si las densidades poblacionales siempre han sido mayores en el área de Puerto Peñasco ya que no existen estudios base para otras regiones.

Las densidades poblacionales en el alto Golfo varían considerablemente entre una zona y otra. Estas variaciones indudablemente son producto de aspectos naturales (e.g. variaciones en corrientes y dispersión de larvas, tipo y cantidad de sustrato adecuado para la fijación de larvas) así como del nivel de presión de pesca histórica y presente. En términos generales, existen ocho zonas principales de uso. Cada una de estas zonas cuenta con densidades poblacionales marcadamente distintas (Figura 6). En la Tabla 5 se resumen las densidades poblacionales de cada una de estas zonas estimadas para el **verano**

del 2004, período en el que se realizó la estimación de densidad poblacional regional más reciente.

Figura G6. Zonas de pesca de callo de escaropa utilizadas por buzos comerciales de Puerto Peñasco.



Tabla G5. Desglose de estimación de densidades poblacionales de callo de escaropa, *Spondylus calcifer*, en los arrecifes aledaños a Puerto Peñasco, Sonora.

Zona de Pesca	Densidad (# individuos/100m ²)	Intervalo de confianza (95%, alpha 0.05)	Número de sitios de muestreo
El Borrascoso	Desconocida	---	---
Cerro Prieto	9.47	6.73-12.21	17
La Cholla	12.72	9.9-15.51	25
Sandy Beach	37	26-47.96	10
Las Conchas	12.6	7.3-17.8	10
Los Tanques	3	2.17-3.82	10
Isla San Jorge	76.5	61.6-91.3	10
San Francisquito	Desconocida	---	---

El Borrascoso

El Borrascoso es el arrecife rocoso sustancial más norteño del Golfo de California¹⁰ y un sitio clave de reproducción de numerosas especies comerciales, tanto peces como invertebrados. Se encuentra dentro de la zona de amortiguamiento de la Reserva de La Biosfera Alto Golfo de California y Delta del Río Colorado y ha sido identificado en varios esfuerzos como un sitio clave de conservación marina. Aunque no se han realizado estimaciones de densidad poblacional, entrevistas con pescadores y las capturas por unidad de esfuerzo (CPUE) de este arrecife (ver tabla 6) sugieren que cuenta con una de las densidades de callo de escarlopa más grandes de la región y una población sustancial de organismos reproductores adultos. Así mismo, cuenta con uno de los bancos de mejillón más grandes del norte del Golfo de California. Debido a su distancia y a las fuertes corrientes de marea, la zona no es utilizada con tanta regularidad como las otras zonas costeras aledañas a Peñasco. Cuando se utiliza, los pescadores por lo general establecen campo por 2-5 días.

Cerro Prieto

El área conocida como *Cerro Prieto* cuenta con “parches” de arrecifes que se extienden desde la parte norte de la península de la Cholla hasta Bahía Adaír. Los arrecifes de esta zona aparentemente están conformados por el mismo complejo arrecifal de La Cholla.

La Cholla

Esta es la zona más utilizada por los buzos de Puerto Peñasco. Contiene los arrecifes más extensos de la región. Debido a sus fuertes corrientes de marea, la zona es utilizada primordialmente durante las mareas muertas de cada mes. Existe mucha variabilidad en las densidades poblacionales de esta zona, en gran medida atribuida a su extensión y a las variaciones de uso de los numerosos “parches” arrecifales existentes en esta zona. Es común que año con año buzos encuentren nuevos tepetates o piedras donde pescar.

Sandy Beach

Zona de menor extensión pero con las densidades más elevadas de la zona costera adyacente a Puerto Peñasco. Dicha densidad elevada es atribuida al establecimiento de reservas marinas comunitarias en el verano del 2002 y al flujo de corrientes en la zona (Cudney-Bueno 2007).

Las Conchas

Como en el caso de *Los Tanques*, el arrecife de las Conchas es un sitio importante de captura durante mareas muertas debido a su poca intensidad de corrientes. El arrecife está conformado por coquina que se extiende desde la base del Cerro de Peñasco hasta la boca del estero Morúa. Durante los 80's, esta zona contaba con densidades elevadas de callo de escarlopa. Sin embargo, la sobre explotación de los bancos de callo ha reducido las poblaciones en forma sustancial. Al igual que en el caso de Los Tanques, la tasa de

¹⁰ Existen otras zonas rocosas al norte del Borrascoso. Sin embargo, el área de estas zonas es mínima, no están conformadas por un arrecife continuo, y predominan aguas turbias. Por estas razones, estas zonas prácticamente nunca son utilizadas para actividades de buceo.

recuperación de los bancos de callo en Las Conchas es considerablemente menor al de otras zonas de pesca. En el verano del 2002, esta zona fue establecida como reserva marina por la Sociedad Cooperativa Buzos de Puerto Punta Peñasco.

Los Tanques

El arrecife de Los Tanques se extiende desde el límite sur del estero Morúa hasta el límite norte del estero La Pinta. Es una zona importante de captura durante las mareas vivas, ya que, junto con el arrecife de Las Conchas, las corrientes a lo largo de este arrecife son considerablemente menores que aquellas de cualquier otra zona de la región. Las densidades poblacionales de callo de escarlopa en Los Tanques incrementan a medida que el arrecife se extiende hacia el sur, principalmente en la zona conocida como “Los Huesos”. Sin embargo, este arrecife cuenta con algunas de las densidades más bajas en la región. Así mismo, estudios preliminares de monitoreo sugieren que la tasa de recuperación en esta zona es menor a la de las otras zonas de captura.

Isla San Jorge

La Isla San Jorge cuenta con las densidades más elevadas de moluscos comerciales capturados por los buzos de Puerto Peñasco. Es un sitio clave de reproducción del callo de escarlopa, caracol chino (*Hexaplex nigritus*), así como de otras especies comerciales, incluyendo las bayas (*Mycteroperca jordani*), principalmente en la punta norte conocida como “Los Anegados”. Debido a su distancia (~50 km de Peñasco), la isla no es utilizada con tanta frecuencia como las zonas aledañas a Peñasco e históricamente ha actuado como un refugio natural del callo de escarlopa y otras especies. Sin embargo, debido a su área relativamente pequeña, puede ser fácilmente sobreexplotada si se realizan actividades pesqueras en forma regular. Estudios preliminares con modelos oceanográficos sugieren que la Isla San Jorge puede actuar como un sitio importante de dispersión larvaria hacia la zona costera. La isla fue protegida (declarada como zona de no-pesca total) por los buzos comerciales de Puerto Peñasco entre el verano del 2001 al verano del 2004. Sin embargo, debido a una falta de soporte legal de estas iniciativas, incluyendo medidas formales para controlar acceso a pescadores foráneos, la protección de la isla ha sido interrumpida desde el verano del 2004.

San Francisquito

Debido a su distancia y aislamiento, es la zona menos utilizada por los buzos de Peñasco. Por lo mismo, también es uno de los arrecifes que menos se conocen en términos de su caracterización de biodiversidad y de las densidades de callo de escarlopa y otras especies comerciales. Sin embargo, basándose en las capturas que provienen de esta zona así como en entrevistas con pescadores, la zona de San Francisquito debe de ser una de las zonas con mayor densidad de organismos reproductores en la región.

En términos de volúmenes de captura, nunca se ha llevado un control de éstos y desgraciadamente no existen datos que especifiquen las capturas o el esfuerzo pesquero desde que la pesquería mediante el buceo comenzó en los años 70's. Sin embargo, sí se cuenta con historial de capturas agrupadas - ver ficha “Almejas: Océano Pacífico”, Carta

Nacional Pesquera 2000. Además, a lo largo del Golfo de California, el callo de escarlopa comúnmente se comercializa junto con el callo de hacha y de riñón (*Pinna* spp, *Atrina* spp), de madreperla (*Pinctada mazatlanica*), y de árbol (*Pteria sterna*), lo cual dificulta aún más el conocer los patrones y las cantidades de su captura real.

Sin embargo, se conoce el patrón de uso de los diversos arrecifes aledaños a Puerto Peñasco, así como la captura por unidad de esfuerzo aproximada para estas zonas. En este caso, se estima que la **captura anual** del callo de escarlopa en Puerto Peñasco, donde operan 12 pangas, equivale aproximadamente a unas **15 toneladas métricas**. La Tabla 6 muestra un resumen del número y porcentaje de viajes de pesca realizados para capturar callo de escarlopa por un pescador típico de Puerto Peñasco, así como la captura promedio para cada una de estas zonas.

Tabla G6. Captura promedio y relación del número y porcentaje de viajes de pesca realizados para la captura del callo de escarlopa, *Spondylus calcifer*, por un pescador típico de Puerto Peñasco, Sonora, México. Datos basados en 298 viajes de pesca realizados en tres años.

Zona de Pesca	Número de Viajes	% de Viajes	Captura Promedio Diaria (Kg)	95% I.C.
La Cholla	103	34.5	6.43	4.79; 8.00
Cerro Prieto	67	22.5	9.96	7.93; 12.00
Los Tanques	26	8.7	8.36	5.09; 11.63
Las Conchas	25	8.3	10.5	7.16; 13.83
Sandy Beach	21	7.0	8.11	4.48; 11.75
Isla San Jorge	17	5.7	38.04	34.00; 42.09
Los Huesos ¹¹	15	5.0	11.4	7.09; 15.70
El Borrascoso	13	4.3	21.9	17.27; 26.52
San Francisquito	11	3.7	35.86	30.83; 40.89
TOTAL	298	100	16.73	8.69; 24.76

4.6 Valor económico y comercialización

En la actualidad, el callo de escarlopa capturado en el Golfo de California tiene un mercado local y regional, primordialmente para la comercialización del “callo” o músculo aductor. El callo se compra primordialmente como producto alimenticio y se consume, al igual que el callo de riñón y de hacha, en forma de ceviche, empanizado, o frito en mantequilla y al mojo de ajo.

Después del callo de riñón y el camarón, el callo de escarlopa es uno de los recursos pesqueros mejor pagados en el Golfo de California. Su precio de playa (precio

¹¹ El área conocida como *Los Huesos* forma parte del mismo complejo arrecifal de *Los Tanques*. Sin embargo, aquí se ha separado para ilustrar las densidades más elevadas de este sitio en comparación con el resto del arrecife.

de venta del pescador) varía entre ~\$80.00 y \$110.00 pesos/kg de callo dependiendo de la temporada y la demanda. Se vende al consumidor en \$180.00 pesos/kg.

4.7 Acuicultura

No existen trabajos documentados para el desarrollo de técnicas de cultivo del callo de escarlopa o de otras especies de la familia Spondylidae. A diferencia de otros bivalvos de cultivo cuyo crecimiento es bastante acelerado (alcanzando tamaños y edades reproductivas en 1-2 años), el callo de escarlopa seguramente no se presta a ser cultivado tan fácilmente. Sin embargo, estudios recientes sobre su biología reproductiva (Villalejo-Fuerte 2002, Cudney-Bueno 2007), edad y crecimiento (Cudney-Bueno 2007), así como del período larvario y técnicas de inducción de desove de otras especies del género *Spondylus* (Parnell 2002) aportan un avance considerable en el conocimiento de esta especie el cual podría facilitar el establecimiento de experimentos futuros de cultivo. Así mismo, se debe estudiar el potencial para realizar transplantes de semilla a los arrecifes naturales con el fin de recuperar zonas sobreexplotadas.

V. Lineamientos Para el Manejo

Debido a la poca información existente sobre el callo de escarlopa en otras regiones del Golfo de California y del Pacífico Mexicano, a la fecha es imposible poder estructurar un Plan de Manejo para el aprovechamiento y recuperación de este recurso que abarque más allá de la región del alto Golfo, donde se han hecho trabajos considerables en torno a la biología, dinámica poblacional, y la pesquería de esta especie. Cabe recalcar que, como se mencionó anteriormente, en esta región también ya se han definido esquemas comunitarios de manejo, conservación, y monitoreo de ésta y otras especies bentónicas, mismos que han dado resultados alentadores y llevaron a los buzos comerciales de Puerto Peñasco a ser receptores del Reconocimiento Nacional de la Conservación de la Naturaleza, 2003.

Sin embargo, con el propósito de que el ejemplo presentado para el alto Golfo pueda ser estudiado e incorporado a otras regiones, a continuación se presentan lineamientos generales a considerarse en la definición de cualquier esquema de manejo regional para esta especie.

5.1 Consideraciones Generales

El callo de escarlopa tiene el potencial de ser una de las pesquerías mejor manejadas en el Golfo de California. Siendo que la especie se captura mediante el buceo, su recolección puede ser altamente selectiva hacia tallas adecuadas. Así mismo, la misma actividad de buceo y el hecho de que ésta es una especie bentónica sésil propician el monitoreo participativo de la pesquería a largo plazo. De igual forma, su presencia en áreas claramente delimitadas facilita un sistema de manejo mediante la definición de usos

preferenciales de territorios de pesca definidos para sectores de pesca o comunidades específicas. La especie también cuenta con un alto potencial reproductivo, lo cual puede facilitar el repoblamiento de zonas explotadas mediante el establecimiento de vedas estacionales y zonas de refugio pesquero. Finalmente, el callo de escarlopa es una de las especies pesqueras con mayor valor agregado en México y con alto potencial de contar con un mercado internacional. Estas características son altamente propicias para buscar la certificación pesquera internacional bajo los estatutos del Marine Stewardship Council (MSC). Actualmente México se encuentra a la vanguardia de la certificación pesquera para el sector pesquero “artesanal” o de “pequeña escala”, habiendo certificado la langosta del Pacífico Mexicano.

Es importante recalcar que aunque forme parte de las especies sujetas a Protección Especial de la NOM-059, el callo de escarlopa actualmente es sujeto a diversos niveles de explotación a lo largo de su distribución geográfica. Es imperativo que esta realidad se reconozca y que se apliquen medidas de manejo adecuadas y estrictas para asegurar la existencia de poblaciones saludables de esta especie en los años venideros y su recuperación en áreas explotadas. Estas medidas deben estar en acorde a las realidades bio-físicas y sociales de las diversas regiones donde se realice la pesquería. Deben de incluir herramientas mixtas de manejo que incluyan, pero no se limiten a, la asignación de usos territoriales preferenciales, el establecimiento de áreas de refugio, esquemas de rotación de los bancos pesqueros, vedas temporales, tallas de captura y tasas de aprovechamiento. Dicho esto, se deben de implementar estudios de factibilidad de captura en las diversas regiones donde actualmente se capture esta especie (ilegalmente) o donde exista interés por capturarla. Basándose en estos estudios, se debe de prohibir estrictamente su captura en zonas que muestren haber sido sobreexplotadas. De la misma forma, la apertura formal y adecuadamente regulada de esta pesquería podría ser considerada para sitios que muestren una alta factibilidad biológica y social de contar con un manejo sustentable a largo plazo y de asegurar la recuperación de la especie en zonas que lo requieran.

5.2 Acceso al Aprovechamiento del Recurso

Uno de los beneficios más importantes y sobresalientes del desarrollo de un Plan de Manejo Regional para el aprovechamiento de cualquier recurso bentónico es la facilidad y oportunidad de establecer sistemas de uso preferencial territorial a cooperativas pesqueras. Cabe recalcar que los mejores ejemplos de manejo pesquero exitoso en nuestro país se han dado en sitios donde existe un sistema de concesiones pesqueras para recursos bentónicos, como en el caso de la langosta en el Caribe y Baja California, así como el abulón comercializado por la Federación de Cooperativas del Pacífico Norte en Baja California.

Cualquier permiso otorgado para el aprovechamiento del callo de escarlopa debe de estipular claramente **polígonos de aprovechamiento exclusivo para cooperativas específicas que ameriten su captura**. Dichas cooperativas deben de cumplir con lo siguiente:

- Seguir los estatutos establecidos por la Ley General de Cooperativas.
- Mostrar un compromiso por la recuperación de la especie y el aprovechamiento sustentable y la conservación de recursos marinos en su región.
- Todos los buzos de la cooperativa deben comprobar su residencia en la localidad de base de la cooperativa.
- Todos los buzos de la cooperativa deben haber pasado por un programa de certificación de buceo.
- Todos los buzos deben mostrar, mediante un examen médico anual, estar en buena salud física para poder desempeñar actividades de buceo.
- Todos los capitanes de panga deben mostrar haber estado buceando en la región al menos los últimos 5 años previos al momento en que se considere otorgar permisos de aprovechamiento.

Puerto Peñasco

Sólo se considerará extender un permiso de aprovechamiento del callo de escarlopa a la Sociedad Cooperativa Buzos de Puerto Punta Peñasco. Esta es la única cooperativa de buceo legalmente constituida y su área geográfica de ingerencia no infringe sobre otras cooperativas.

Los miembros de la SSCP Buzos de Puerto Punta Peñasco han estado trabajando recursos bentónicos en el área de Puerto Peñasco desde principios de los años 80's. Así mismo, los socios pescadores de la cooperativa, junto con el Centro Intercultural de Estudios de Desiertos y Océanos (CEDO), establecieron en el 2003 el primer Programa Piloto de Certificación de Buzos Comerciales en México a través de doctores e instructores de DAN-México (Divers Alert Network) y el Hospital Ángeles del Pedregal. Cuentan actualmente con entrenamiento en teoría del buceo y en la evasión de accidentes asociados a actividades subacuáticas.

5.3 Área de Explotación

El área asignada a la cooperativa para la explotación del recurso deberá estar en acorde a el uso presente de área de explotación y a la distribución y condición de los bancos de callo en la región. De esta forma, y siguiendo el mismo protocolo que se utiliza para la asignación de concesiones de pesca, la cooperativa deberá demostrar un acuerdo de colindancia con otras cooperativas/comunidades y asegurar que en efecto el área propuesta corresponde al territorio *de facto* de esa cooperativa y que no infringirá sobre áreas de pesca de otras cooperativas de buceo.

Por otro lado, dentro de los polígonos asignados, con el fin de reducir riesgos a la salud, las actividades pesqueras estarán restringidas a terrenos ubicados desde la línea de bajar, hasta un **máximo de 13 brazas** de profundidad (**24 metros ó 78 ft**).

Puerto Peñasco

En el caso de Puerto Peñasco, el área de pesca asignada para la SCPP Buzos de Puerto Punta Peñasco comprenderá desde El Borrascoso hasta Punta Jagüey, en la costa de Sonora (Figura 7)

Figura G7. Propuesta de zona de pesca permitida para buzos comerciales de Puerto Peñasco organizados en la Sociedad Cooperativa Buzos de Puerto Punta Peñasco (Fuente: Cudney-Bueno 2000).



5.4 Áreas de Repoblamiento/Refugio Pesquero y Áreas de Rotación

Debido a que es una especie bentónica sésil cuyos gametos son liberados al agua, el éxito reproductivo del callo de escarlopa depende principalmente de una densidad adecuada de organismos reproductores (organismos cuya altitud de concha es de más de 115mm). Así mismo, su reclutamiento depende en gran medida de la naturaleza de las corrientes y de la presencia de hábitats adecuados para la fijación de larvas. Por lo mismo, es de suma importancia que se conozca a ciencia cierta las densidades poblacionales de esta especie y los patrones de corrientes en las diversas regiones donde se encuentre para poder definir medidas adecuadas de manejo. Estas medidas deben

incorporar el establecimiento de corredores de refugios pesqueros que incluyan zonas sobreexplotadas con factibilidad de ser repobladas, y zonas con alta densidad de organismos reproductores que actúen como centros de dispersión de larvas. Así mismo, se recomienda que estas Áreas de Repoblamiento/Refugios Pesqueros se establezcan como zonas de reserva totalmente protegidas a la extracción de cualquier especie con el fin de mantener en forma saludable los procesos ecológicos del ecosistema y que estos procesos beneficien las áreas de pesca.

Puerto Peñasco

Desde el 2002, los buzos de Puerto Peñasco, con el apoyo de la Universidad de Arizona y el Centro Intercultural de Estudios de Desiertos y Océanos (CEDO), han establecido y monitoreado un corredor de refugios para el manejo y conservación de diversos recursos bentónicos de la región, incluyendo el callo de escarlopa y el caracol chino (*Hexaplex nigritus*). Dicha medida ha mostrado un incremento sustancial en las poblaciones de ambas especies, en algunos sitios incrementando la densidad de juveniles en más de un 100% (Cudney-Bueno 2007).

Mediante este Plan Regional, se hace hincapié en la necesidad de continuar con estas medidas de manejo pero también de incorporar un esquema híbrido que incluya la rotación temporal de bancos pesqueros. Basado en los patrones de corriente de verano, este esquema aseguraría un flujo larvario adecuado de sur a norte, ayudando a la repoblación de zonas sobreexplotadas y al incremento de recursos pesqueros en zonas productivas. El esquema que se recomienda seguir es el siguiente:

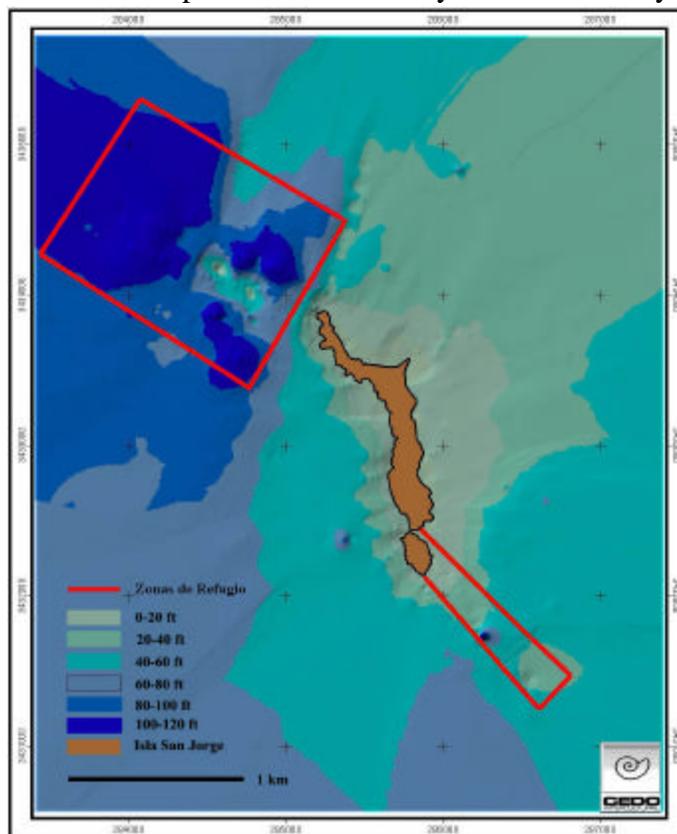
a) Zonas de Repoblamiento y Refugio Pesquero

Se recomienda restringir la pesca de buceo (para todas las especies de peces e invertebrados capturadas mediante este método de pesca) permanentemente o hasta nuevo aviso en los siguientes sitios:

Isla San Jorge: Zona de los Anegados Norte y Piedras del Sur (Figura 8)

La Isla San Jorge cuenta con la mayor densidad de callo de escarlopa en la región de Puerto Peñasco, en algunos sitios contando con densidades de más de 100 organismos/100 m². Las áreas conocidas como “los anegados” y “piedras del sur” actúan como un sitio clave para la dispersión de larvas de ésta y otras especies debido a la existencia de fuertes corrientes y a la alta densidad de organismos reproductores. Así mismo, debido a su profundidad (en algunos sitios más de 40 metros), el buceo en los anegados implica un alto riesgo a la salud. Varios buzos de Puerto Peñasco han sufrido accidentes de descompresión en esta zona.

Figura G8. Zonas de refugio pesquero aledañas a la Isla San Jorge
(Elaboración de mapa: Marcia Moreno y Richard Cudney-Bueno)



Polígono de la Cholla (Figura 9)

Se recomienda establecer como zona de repoblamiento y refugio pesquero a una porción de la zona de pesca de la Cholla (Figura 9). Esta zona cuenta con la presencia de corrientes intensas tanto de marea como de advección y actúa como sitio clave para la dispersión de larvas hacia las zonas de pesca al norte de La Cholla (El Borrascoso y Cerro Prieto). Así mismo, es un sitio importante para las poblaciones de pulpo y caracol chino, así como un sitio donde regularmente se encuentran tortugas marinas.

Sandy Beach

El arrecife de tepetates conocido como Sandy Beach fue protegido entre el verano del 2002 y el 2004. En tan sólo dos años, las densidades poblacionales de callo de escarlopa en este sitio incrementaron en aproximadamente un 30%. Hoy en día es uno de los arrecifes cercanos a Puerto Peñasco que cuenta con mayor densidad poblacional. Sin embargo, esta densidad se encuentra dominada por organismos juveniles. Contando con densidades adecuadas de organismos reproductores, estudios recientes sugieren que el arrecife de Sandy Beach puede estar actuando como sitio clave de dispersión de larvas hacia la zona de la Cholla (Cudney-Bueno 2007), la zona de pesca más importante para los buzos de Puerto Peñasco en términos de su accesibilidad y frecuencia de uso. Así

b) Zonas de Rotación de Bancos Pesqueros

Basándose en experimentos previos de cierre y apertura de zonas de pesca de callo de escarlopa, se recomienda seguir el siguiente esquema de rotación de bancos pesqueros:

- En el momento en que entre en vigor el presente plan de manejo, se recomienda el cierre de las zonas de San Francisquito y la Isla San Jorge por un período mínimo de un año. Transcurridos estos dos años, la apertura a la pesca de una u otra zona estaría sujeta a los resultados de monitoreos subacuáticos (ver sección de monitoreo). La apertura a la pesca subsecuente seguiría un patrón de alternación anual, de forma que cada año una de las zonas esté abierta y una cerrada.
- Este patrón de rotación podrá ser modificado o interrumpido dependiendo de los resultados de los monitoreos subacuáticos.
- La pesca en la zona abierta estará restringida a las mareas muertas del 1 de diciembre a último día del mes de abril.
- La pesca restringida a estos meses asegurará un mayor valor agregado del callo debido a su mayor tamaño y peso durante el invierno y primavera y proveerá un importante ingreso económico para los pescadores durante los festejos Navideños y de Semana Santa.
- La pesca en estas zonas estará sujeta a tasas de captura determinadas anualmente a través de estimaciones de abundancia en los meses de julio-septiembre previos a la apertura de la temporada de pesca.
- **Sólo se permitirá la captura de organismos adultos** cuya longitud de la concha (altura) sea **igual o mayor a 130 mm**. Esta medida asegura la permanencia de individuos reproductores para la temporada de desove de verano y la incorporación de un nuevo cohorte a la población adulta reproductora en el año subsecuente. Esta longitud de la concha corresponde a una longitud promedio del callo equivalente a **35.14 mm** (ver siguiente sección, “tallas de captura”).

5.5 Tallas de Captura

La captura del callo de escarlopa en todo momento estará sujeta a tallas de captura. Sólo se permitirá la captura de individuos cuya longitud de concha (altura) sea **mayor o igual a 130 mm**. Debido a que es imposible que los pescadores carguen con las conchas, el monitoreo de las capturas de los pescadores en playa tendrá que hacerse indirectamente usando la medida del callo. Para el **verano/otoño** la longitud del callo que corresponde a 130 mm de alto de la concha equivale a **35.14 mm** y para **invierno/primavera 39.64 mm**.

5.6 Densidades Mínimas

Por **ningún motivo se permitirá la captura en áreas donde las densidades de organismos adultos reproductores sea igual o menor a 5 individuos x 100 m²**. Esta

medida va en acorde a densidades mínimas establecidas en estudios previos (ver Baqueiro et al. 1982).

5.6 Tasa de Aprovechamiento

Se deberá establecer una tasa de aprovechamiento anual. Estas estimaciones deberán realizarse con una interrupción completa de las actividades pesqueras a manera de que los datos reflejen el estado real de la población disponible a ser aprovechada. Se recomienda que las estimaciones de tasas de aprovechamiento se realicen durante el verano, cuando la pesquería debe de ser vedada temporalmente para asegurar un período reproductivo adecuado. Así mismo, **sólo se permitirá el aprovechamiento de un 10% o menos de la población adulta y se restringirá la captura en aquellas zonas que muestren tener densidades de organismos adultos de 5 o menos individuos por 100 m²**. Por último, se recomienda realizar análisis de viabilidad poblacional a largo plazo que incorporen distintos factores de riesgo, escenarios de captura, y conectividad poblacional.

Puerto Peñasco

Las estimaciones de tasas de aprovechamiento se realizarán en el verano del 2006 entre junio-agosto y anualmente en los mismos meses previo a la expedición de un nuevo permiso de aprovechamiento.

5.7 Métodos de Pesca

La pesca del callo de escarlopa se realizará ya sea en apnea o mediante el buceo con compresor de aire tipo hookah. Las especificaciones para el equipo y método de pesca a utilizarse son las siguientes:

- Tanto el compresor como el regulador (boquilla) deberán estar en buen estado. Cada pescador deberá realizar inspecciones regulares de su equipo, sin que estas inspecciones pasen de seis meses.
- Sólo se utilizará aceite mineral como lubricador del compresor.
- Se deberá utilizar filtro de aire para aquellos compresores que lo requieran.
- Se deberá incorporar un tubo de pvc o de acero inoxidable de 1 m de alto para asegurar que la toma de aire no esté entremezclada con humos de escape del motor del compresor.
- La pesca se realizará por un máximo de 2 buzos por panga.
- Sólo se permitirá la utilización de mangueras de no más de 100 m de largo.
- Sólo se permitirá la pesca nadando en el fondo. El buceo caminando en el fondo queda estrictamente prohibido.
- Todo pescador deberá contar al menos con un reloj contra agua y un profundímetro, haciendo paradas de descompresión adecuadas.

- Cada panga deberá contar con un cabo de vida que cuelgue de la superficie del agua hasta 4-5 metros de profundidad.
- Independientemente de la profundidad en la que se trabajó, cada pescador deberá hacer una **parada obligatoria** de al menos **20 minutos** sujetos al cabo de vida a 4-5 metros de profundidad.
- Todas las actividades de pesca estarán restringidas a profundidades de **13 brazas o menos (24 metros ó 78 ft)**.
- Durante las actividades de pesca del callo de escarlopa, queda **estrictamente prohibida la captura de madreperla (*Pinctada mazatlanica*) y callo de carbol (*Pteria sterna*)**.
- Se prohíbe en todo momento cargar con pistola/arpón.
- Se prohíbe el buceo de noche para el callo o cualquier otra especie capturada mediante el buceo.

5.8 Vedas

Contrario a algunos otros moluscos, el callo de escarlopa tiene un período de desove relativamente corto, restringido a los meses de verano. Por lo mismo, cualquier lineamiento de manejo para esta especie debe incluir una **veda total durante los meses de julio, agosto, y septiembre**. El cierre temporal de la pesquería, combinado con el establecimiento de áreas de repoblamiento y refugio pesquero y áreas de rotación, permitirá el reclutamiento de nuevos organismos a la pesquería. Así mismo, si estos estatutos son seguidos en forma estricta, se espera que la combinación de medidas de manejo espacio-temporales y el empleo de tasas de captura podría dar un incremento en la producción total a largo plazo.

5.9 Entrega del Producto y Comercialización

- La cooperativa deberá contar con un centro de acopio de la producción de callo. El callo de escarlopa deberá ser separado del callo de hacha y de riñón (*Pinna* spp, *Atrina* spp) a la hora de ser entregado en el centro de acopio y comercializado
- La cooperativa llevará un control estricto de las cantidades arribadas **por panga**
- El acopio y procesado del producto deberá seguir estándares nacionales de sanidad
- Se hará todo lo posible por buscar mercados internacionales y precios de compra competitivos que den un mayor valor agregado al producto. En este aspecto, **se buscará la certificación de la pesquería** como una pesquería que muestre ser sustentable bajo los lineamientos del Marine Stewardship Council (MSC)
- En caso de saturación del mercado local, por ningún motivo se seguirá pescando. Esto no sólo causa un desperdicio de producto, pero también la disminución en el precio de compra debido a la relación oferta-demanda

VI. Monitoreo y Adaptación del Plan de Manejo

6.1 Monitoreo y Reportes

a) Monitoreo

La pesca del callo de escarlopa deberá estar respaldada por un programa estricto de monitoreo. Este monitoreo requerirá:

- Llevar un control de las capturas totales diarias y la distinción de capturas arribadas por cada panga.
- El llenado de bitácoras pesqueras (una por panga). Estas bitácoras especificarán: especies capturadas, cantidad, zona de captura, y gastos de gasolina. Así mismo, se especificarán los días en que no se salió a pescar y los motivos (e.g. mucho viento, problemas con el compresor, etc)
- Monitoreos subacuáticos semestrales (julio-Agosto; enero-febrero) donde se estimen densidades poblacionales dentro y fuera de zonas de refugio.
- Toma de muestras aleatorias de cada panga para registrar tallas y pesos promedio

b) Reportes

La cooperativa preparará un reporte anual que incluya, pero no necesariamente esté limitado a, los siguientes puntos:

- Resumen ejecutivo de las actividades de monitoreo y vigilancia realizadas durante el año y de los resultados principales, incluyendo retos y logros
- Estado de las poblaciones de callo de escarlopa. Dicho diagnóstico incluirá la densidad promedio (# organismos/100 m²) e intervalos de confianza (alpha 0.05, 95%) totales así como haciendo distinción de la variación de densidades de acuerdo a zonas, tanto zonas de refugio como zonas permitidas a la pesca.
- Reporte de capturas totales mensuales y anuales. Se distinguirán las capturas de cada zona de aprovechamiento.
- Reporte de distribución de tallas y pesos mensuales de callo de escarlopa. Se distinguirán las longitudes y pesos promedio mensuales de cada zona de aprovechamiento.
- Reporte financiero que incluya los gastos de la cooperativa y los ingresos brutos y netos. Se deberá hacer mención específica sobre los gastos e ingresos atribuidos a la pesca del callo de escarlopa.
- Resumen que indique el número de casos de pesca furtiva (en caso de que los hubiese) y la manera en que dichos casos fueron tratados.
- Reporte de actividades a seguir durante el siguiente año y propuestas de adaptación y cambio al Plan de Manejo en caso de considerarse necesario.

6.2 Inspección y vigilancia

Como en el caso de monitoreo, el aprovechamiento del callo de escarlopa deberá estar respaldado por un estricto programa de inspección y vigilancia. Dicho programa deberá incorporar a miembros de la cooperativa trabajando en colaboración con autoridades competentes (PROFEPA, Sector Naval). El programa deberá contar con, pero no estar limitado a, los siguientes puntos:

a) Visitas regulares a las áreas de refugio/repoblamiento pesquero

Se harán visitas regulares a las áreas de refugio, **particularmente durante mareas muertas**. Dichas visitas se harán bajo un esquema rotativo de la participación de miembros de la cooperativa en conjunto con autoridades competentes cuando se pueda contar con su presencia. La cooperativa definirá el esquema de rotación, asegurando la participación equitativa de sus miembros y la compensación económica para las personas que aportará los recursos económicos y materiales para el seguimiento de dicha actividad. Por lo mismo, se recomienda que la cooperativa dedique parte de sus ingresos brutos para labores de monitoreo y vigilancia. Así mismo, se recomienda que se busquen ingresos adicionales mediante fundaciones y organizaciones no gubernamentales.

b) Recorridos en tiempo de veda (verano)

Se harán recorridos regulares durante el verano con el motivo de asegurar que no se esté capturando callo de escarlopa en ningún sitio de pesca incluido dentro del área de aprovechamiento estipulada por el Plan de Manejo Regional. Como en el punto anterior, la cooperativa definirá el esquema de rotación de personal de vigilancia.

c) Vigilancia de tallas de captura permitidas

En el momento de arribo, se tomará una muestra aleatoria de la captura de callo de cada panga y se registrará la longitud y el peso de cada callo. La longitud promedio del callo capturado por cada panga deberá caer dentro del rango permitido para la temporada específica de captura (invierno/primavera o verano/otoño). En caso de que la longitud promedio esté debajo de este rango, el pescador no recibirá las ganancias de su captura y el ingreso de la venta de ese producto se destinará a fondos de monitoreo, inspección, y vigilancia de la cooperativa.

d) Sanciones

El aprovechamiento del callo de escarlopa deberá contar con la definición de sanciones claras y adecuadas. La autoridad competente establecerá el esquema de sanciones en caso de incumplimiento de cualquiera de los estatutos del Plan de Manejo. Cabe mencionar que la Dirección de Vida Silvestre tendrá la última palabra en la definición de sanciones y podrá revocar la renovación de permisos de aprovechamiento

en caso de que no se cumplan los estatutos establecidos en el Plan de Manejo Regional. **Así mismo, la captura de cualquier especie listada en la NOM-059 por cualquier miembro de la cooperativa será motivo suficiente para negar la expedición de un permiso de aprovechamiento subsiguiente.**

6.3 Esquema de revisión y adaptación del plan de manejo

El manejo del callo de escarlopa seguirá un esquema de manejo adaptativo. Dicho esquema requerirá la revisión anual del Plan de Manejo por parte de la cooperativa y el establecimiento de propuestas de cambio (en caso de que las hubiesen) a la hora de presentar el reporte anual a la Dirección de Vida Silvestre. Dicha instancia gubernamental tendrá la última palabra en la definición de nuevos esquemas de manejo.

VII. Referencias

- Baqueiro, C.E., J.A. Masso, H.B. Guajardo. 1982. Distribución y abundancia de moluscos de importancia comercial en Baja California Sur, México. *Inst. Nal. De la Pesca, México, Serie de Divulgación*. 11:1-32
- Cudney-Bueno, R. 2000. Management and Conservation of Benthic Resources Harvested by Small-Scale Hookah Divers in the Northern Gulf of California, Mexico: The Black Murex Snail Fishery. Ms. Thesis. University of Arizona. Tucson, Arizona, U.S.A. 177 pp.
- Cudney-Bueno, R. 2007. Marine Reserves, Community-Based Management, and Small-Scale Benthic Fisheries in the Gulf of California, Mexico. PhD Dissertation, University of Arizona. Tucson, Arizona,
- Donkin, R.A. 1998. Beyond Price: Pearls and Pearl Fishing: Origins to the Age of Discoveries. American Philosophical Society. Philadelphia, U.S.A. 448 pp.
- Keen, A.M. 1971. Sea Shells of Tropical West America. 2nd ed. Stanford University Press. Stanford, California, U.S.A.
- Marinone S.G., M. J. Ulloa, A. Parés-Sierra, M. F. Lavín, and R. Cudney-Bueno Connectivity in the northern Gulf of California from particle tracking in a three-dimensional numerical model. *J. of Marine Systems (Artículo en revisión)*.
- Poder Ejecutivo Federal 1988. Ley General de Equilibrio Ecológico y Protección Ambiental. Diario Oficial de la Federación, 28 de enero de 1988.
- Poder Ejecutivo Federal 2000. Ley General de Vida Silvestre. Diario Oficial de la Federación, 3 de julio de 2000.
- Poder Ejecutivo Federal 2002. Norma Oficial Mexicana NOM-059-SEMARNAT-2001, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. Diario Oficial de la Federación, 6 de marzo de 2002.
- Parnell, P.E. 2002. Larval development, precompetent period, and a natural spawning event of the pectinacean bivalve *Spondylus tenebrosus* (Reeve, 1856). *The Veliger* 45(1): 58-64
- Pillsbury, J. 1996. The thorny oyster and the origins of empire: Implications of recently uncovered *Spondylus* imagery from Chan Chan, Perú. *Latin American Antiquity* 7(4): 313-340
- Poutiers, J.M. 1995. Moluscos. In: Fischer, W., F. Krupp, W. Schneider, C. Sommer, K.E. Carpenter, and V.H. Niem (Eds.). Guía FAO para la Identificación de Especies Para los Fines de la Pesca: Pacífico Centro-Oriental Vol. 1: Invertebrados. Food and Agriculture Organization. Rome, Italy. 1: 646 pp.
- Sandweiss, D.H. 1992. The archaeology of Chincha fishermen: specialization and status in Inka Perú. *Bulletin of Carnegie Museum of Natural History* 29
- Villalejo-Fuerte, M. M. Arellano-Martínez, B. P. Ceballos-Vázquez, F. García-Domínguez. 2002. Reproductive Cycle of *Spondylus calcifer* Carpenter, 1857 (Bivalvia : Spondylidae) in the “Bahía de Loreto” National Park, Gulf of California, Mexico. *Journal of Shellfish Research* 21(1):103-10

APPENDIX H
SUBTIDAL TEMPERATURES IN ISLA SAN JORGE,
OCTOBER 2003 – OCTOBER 2004

Figure H1. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. October 1 2003 - October 1 2004.

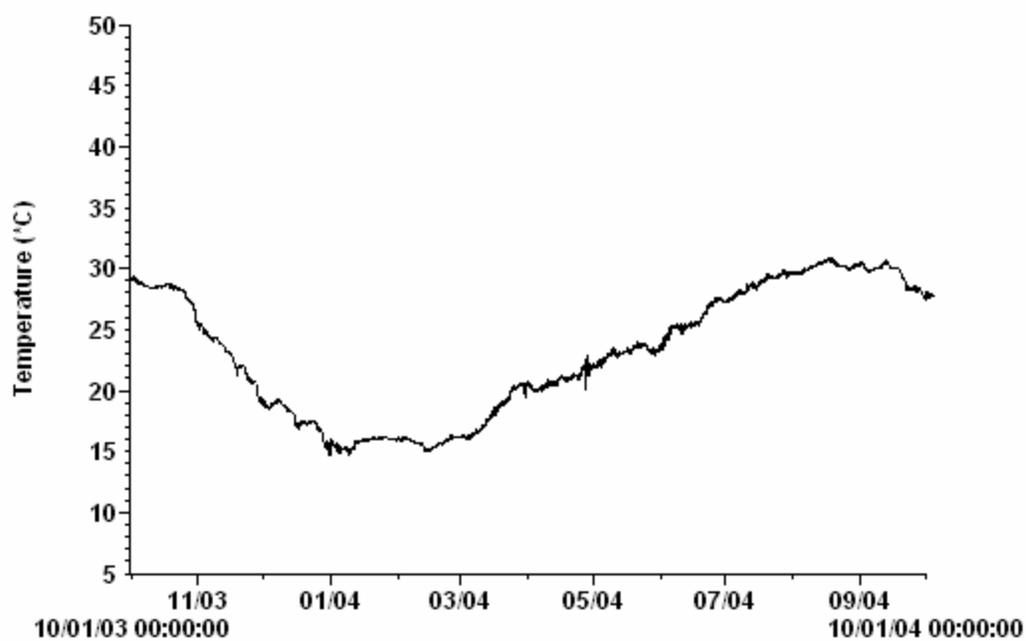


Figure H2. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. October 1 2003 - November 1 2003.

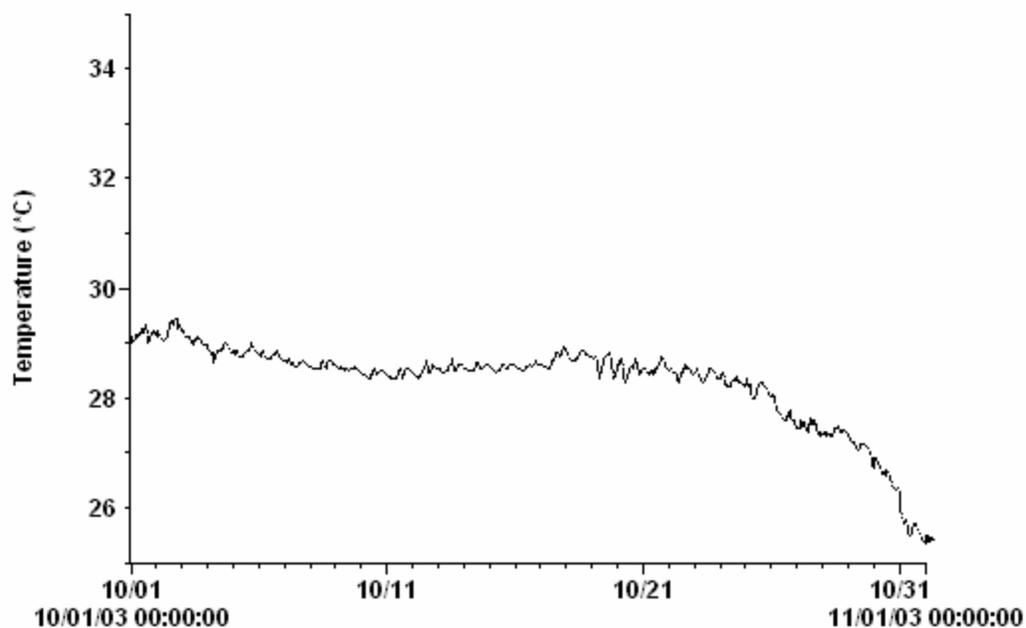


Figure H3. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. November 1 2003 - December 1 2003.

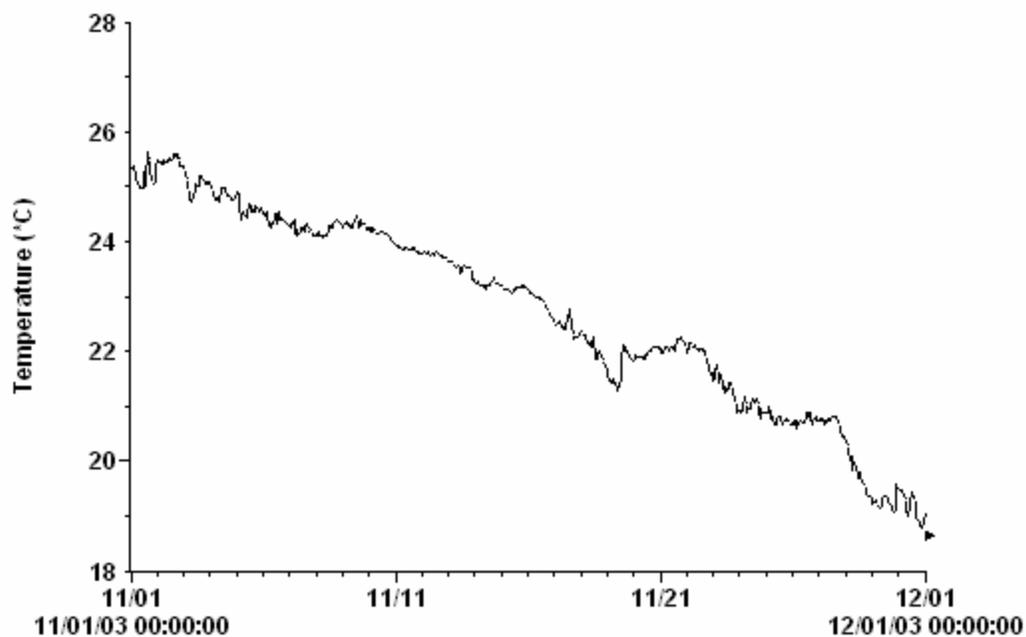


Figure H4. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. December 1 2003 - January 1 2004

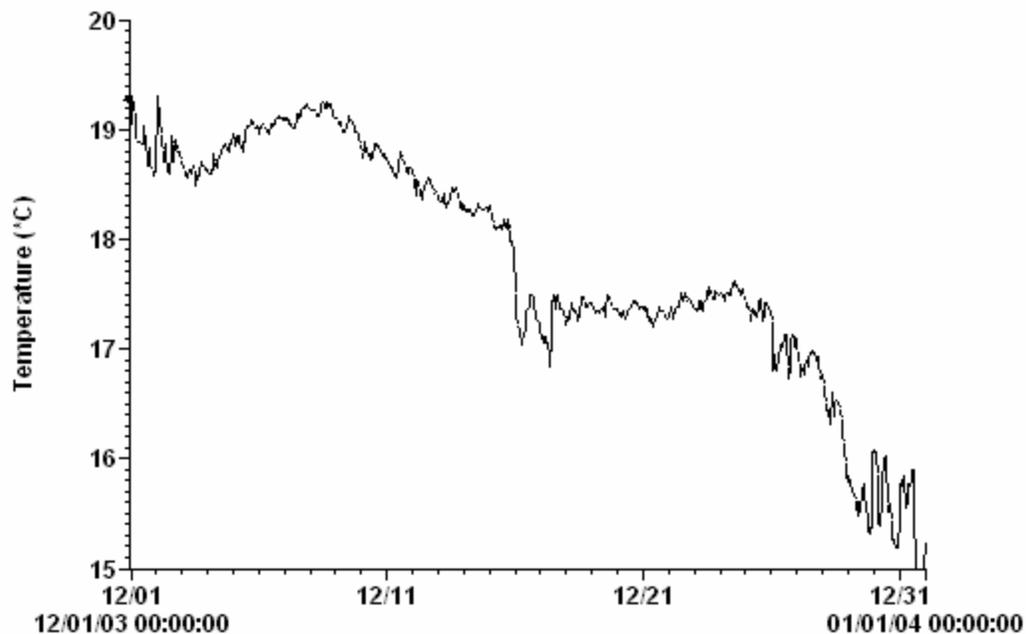


Figure H5. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. January 1 2004 – February 1 2004.

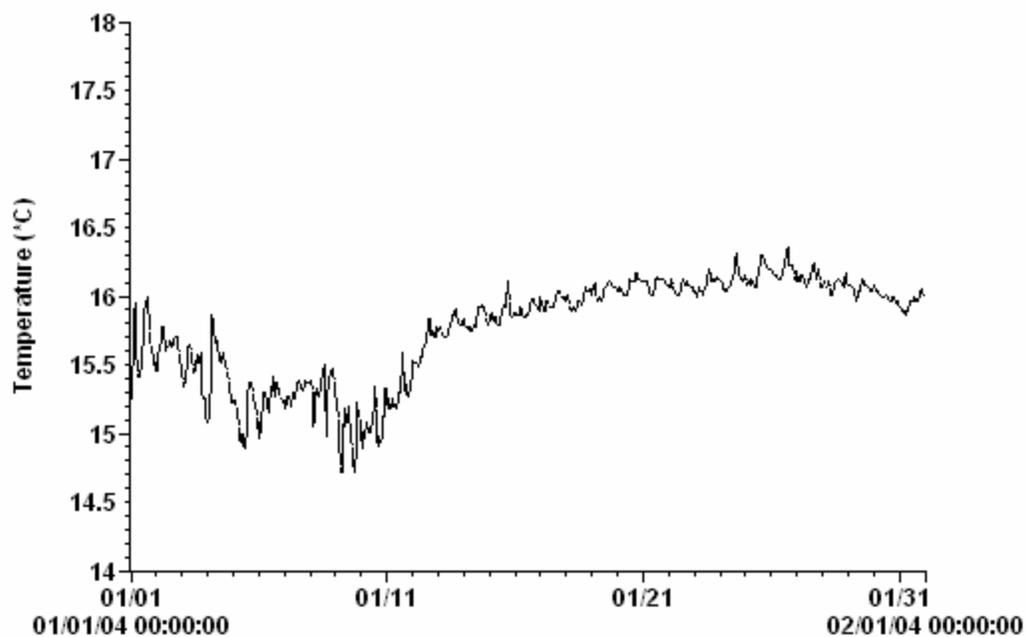


Figure H6. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. February 1 2004 – March 1 2004.

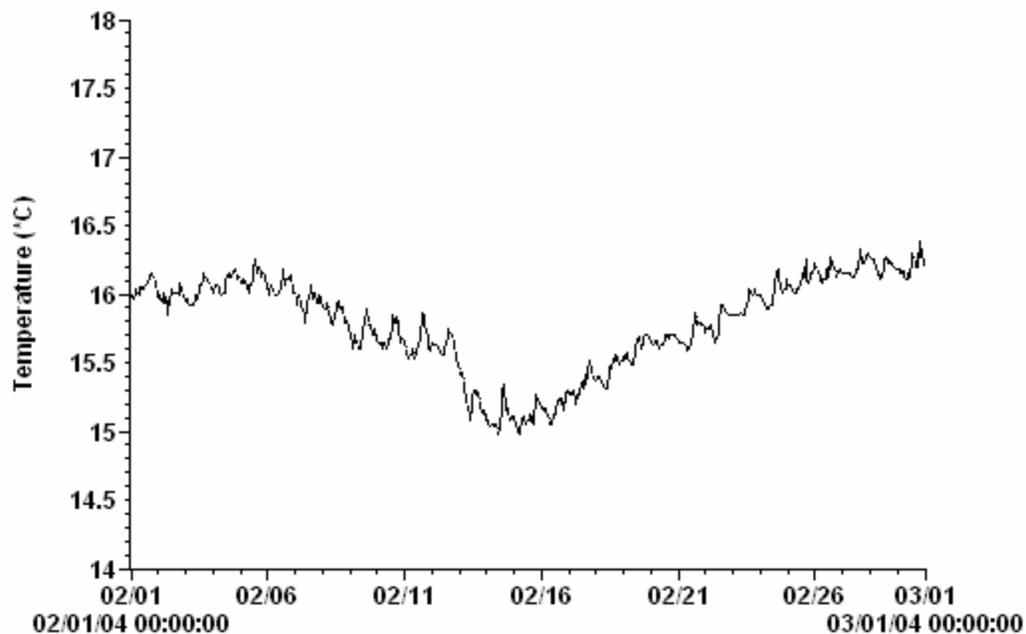


Figure H7. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. March 1 2004 – April 1 2004

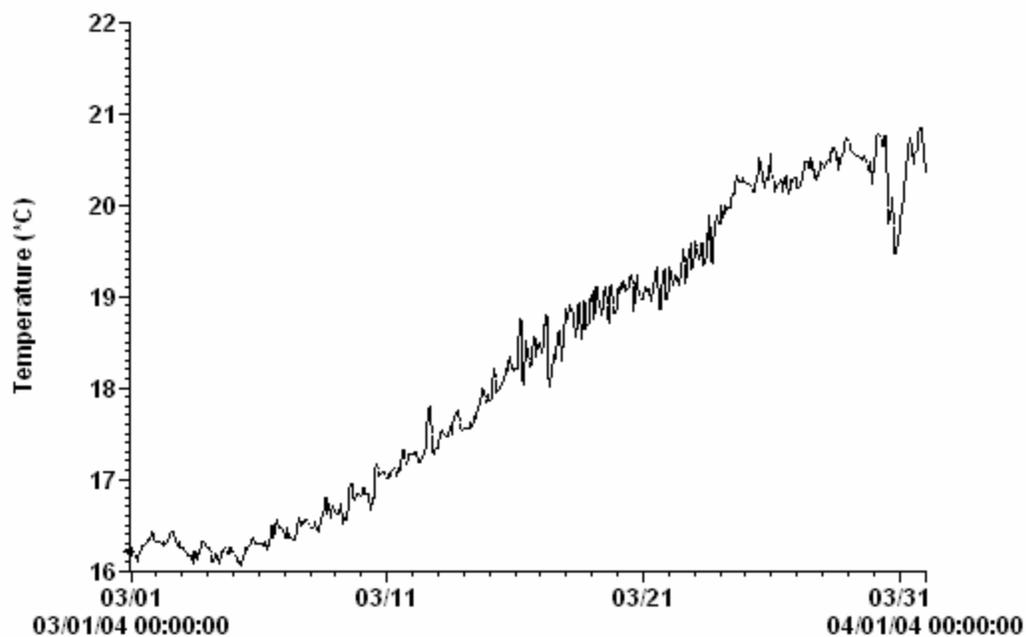


Figure H8. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. April 1 2004 – May 1 2004.

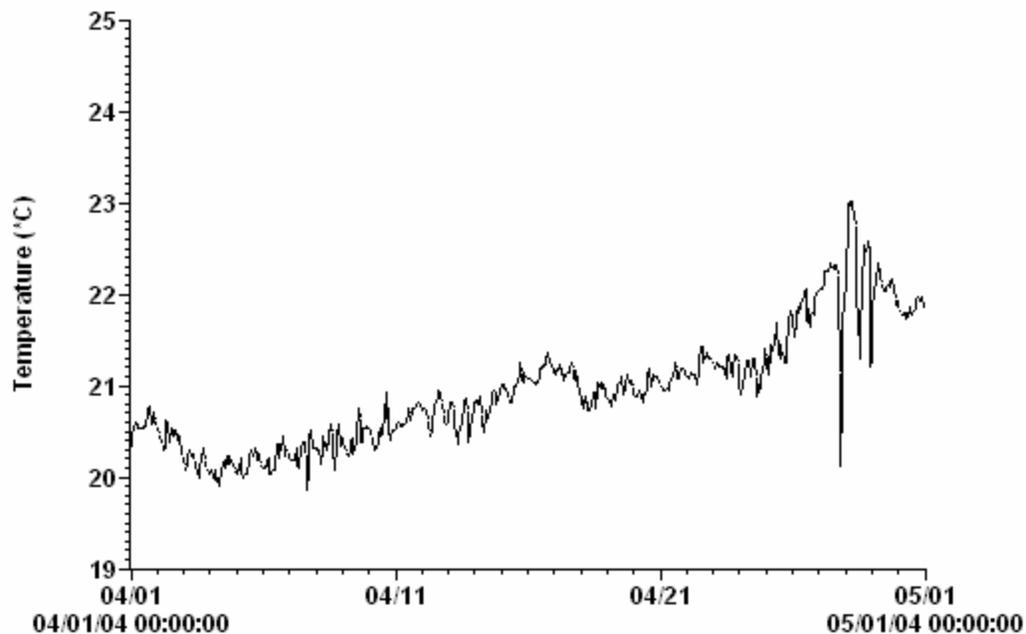


Figure H9. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. May 1 2004 – June 1 2004.

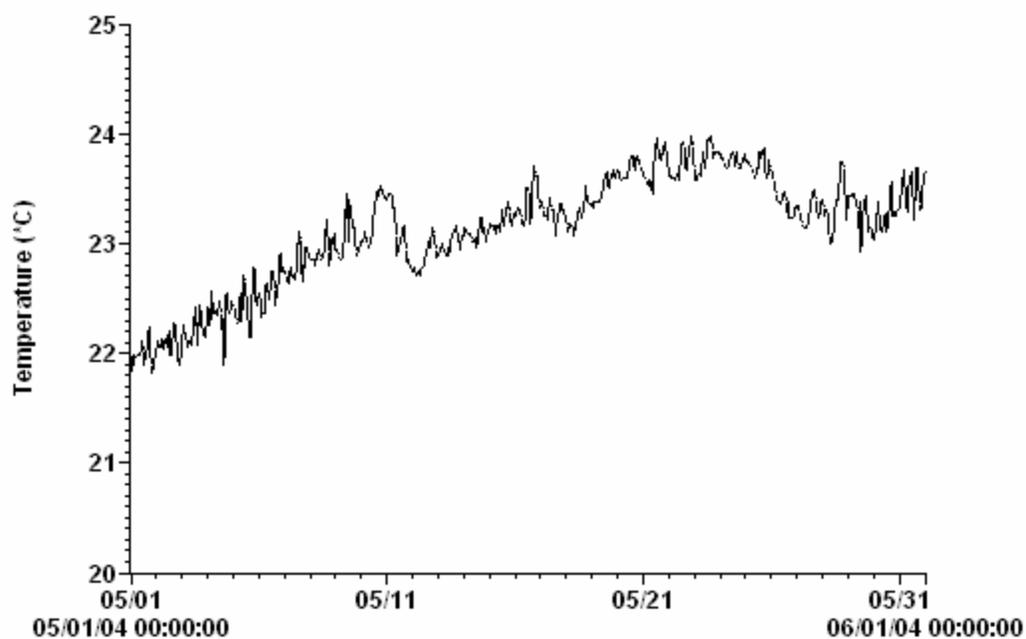


Figure H10. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. June 1 2004 – July 1 2004.

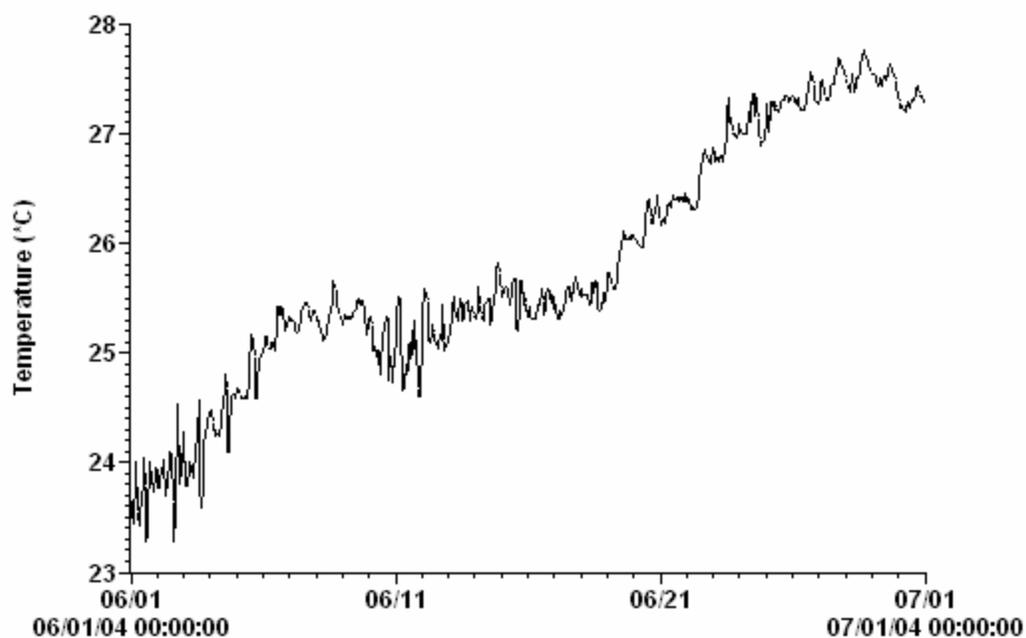


Figure H11. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. July 1 2004 – August 1 2004.

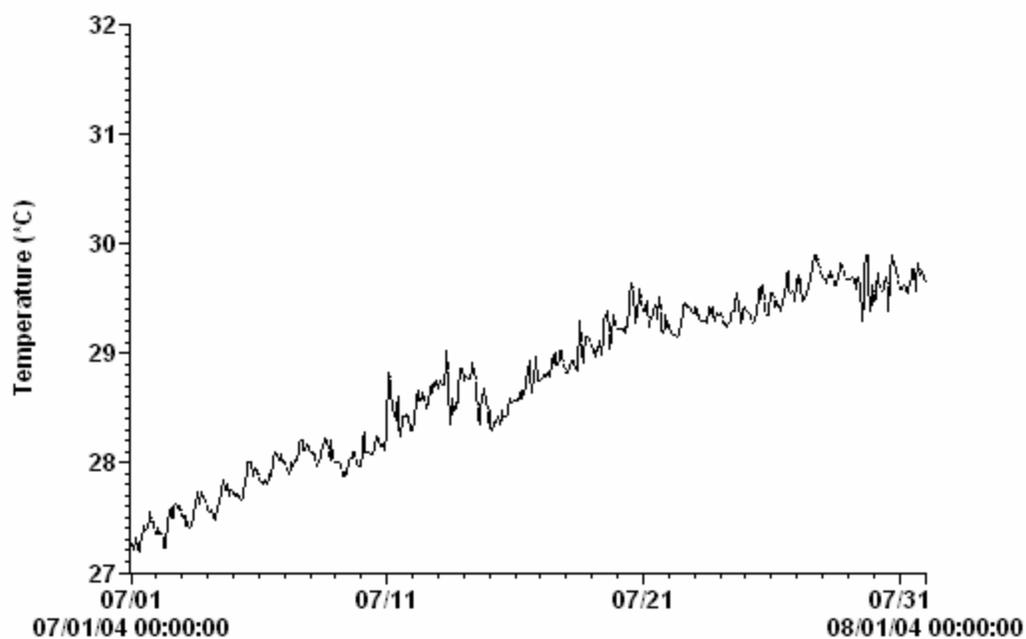


Figure H12. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. August 1 2004 – September 1 2004.

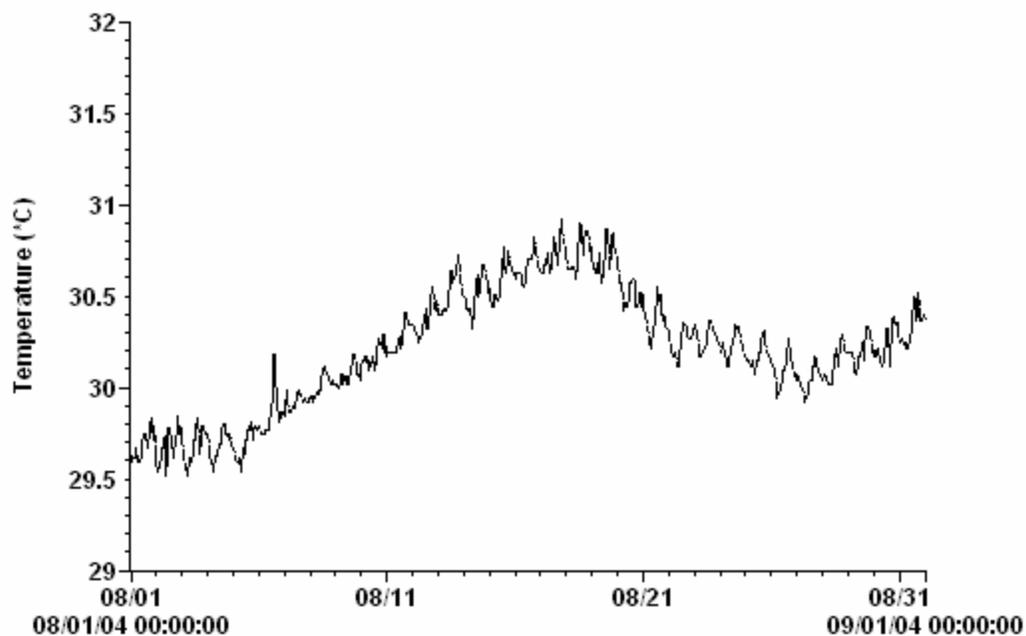
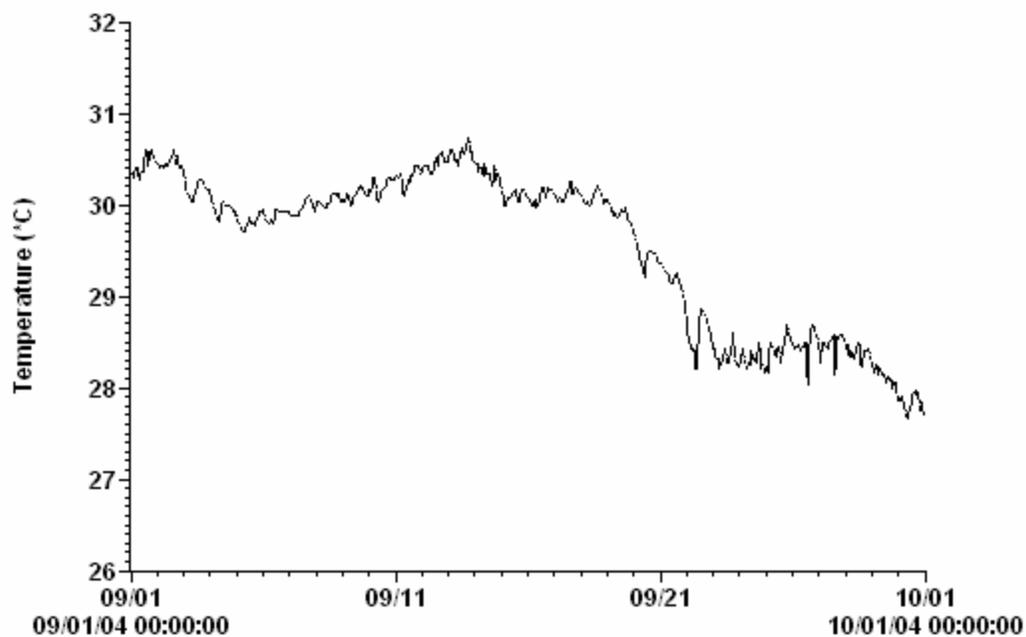


Figure H13. Water temperature at 10 m depth at Isla San Jorge, Gulf of California, Mexico. September 1 2004 – October 1 2004.



APPENDIX I
PHOTOGRAPHS OF ROCK SCALLOP, BLACK MUREX,
AND COMMERCIAL DIVING

Rock Scallop Photographs



Figure I1. Left and right valves of a juvenile rock scallop (shell height = 45 mm, ~1 year old).



Figure I2. Recently harvested rock scallop, *Spondylus calcifer*, and mother of pearl, *Pinctada mazatlanica*.



Figure I3. Harvested rock scallop, *Spondylus calcifer*, adductor muscles.



Figure I4. Juvenile and adult rock scallops, *Spondylus calcifer*, with mark tags.



Figure I5. Adult rock scallop shells, *Spondylus calcifer*, showing marked differences in morphology.



Figure I6. Sliced shell of an adult rock scallop, *Spondylus calcifer*, showing heavy infestation of burrowing organisms, including large burrowing mussel, *Lithophaga* sp. Notice heavy shell deposits as a result of burrowing.

Black Murex Photographs



Figure 17. Various sizes and age classes of black murex, *Hexaplex nigritus*.



Figure 18. Adult black murex, *Hexaplex nigritus*, of different sizes and their corresponding egg capsule sizes.

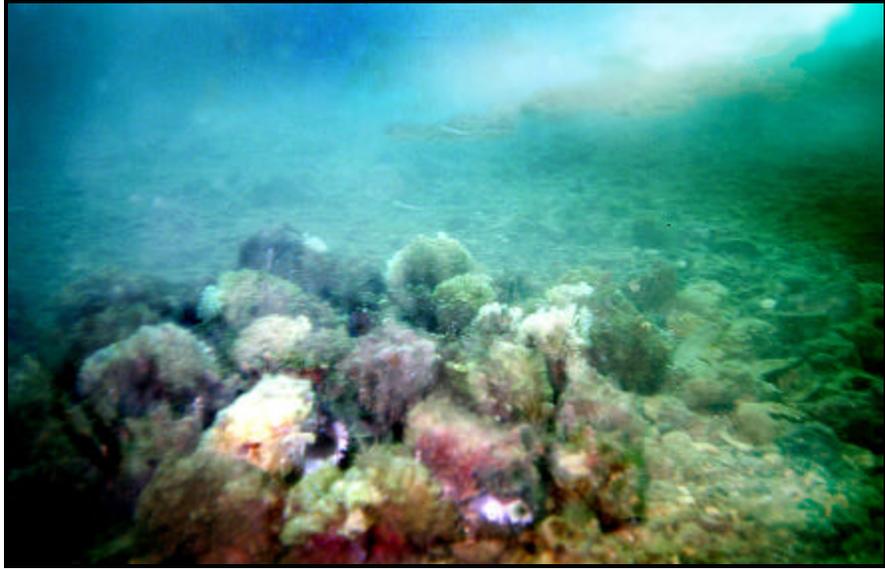


Figure I9. Small breeding aggregation of black murex snails, *Hexaplex nigrinus*.



Figure I10. Black murex, *Hexaplex nigrinus*, laying egg capsules on another snail.



Figure I11. Marked black murex snails, *Hexaplex nigritus*, from a breeding aggregation.



Figure I12. Recently harvested female (left) and male (right) black murex snails. Notice curled penis in the mid portion of the male individual.

Commercial Diving Photographs



Figure I13. A) hauling bag full with black murex; B) boat filled with black murex; C) commercial diver entering the water.



Figure I14. Commercial diver breaking black murex snail shells to sell the meat. All snails came from one breeding aggregation.



Figure I15. Commercial diver harvesting rock scallop, *Spondylus calcifer*, in rocky reefs of northeastern Gulf of California, Mexico (photo: Lindsey Haskin).

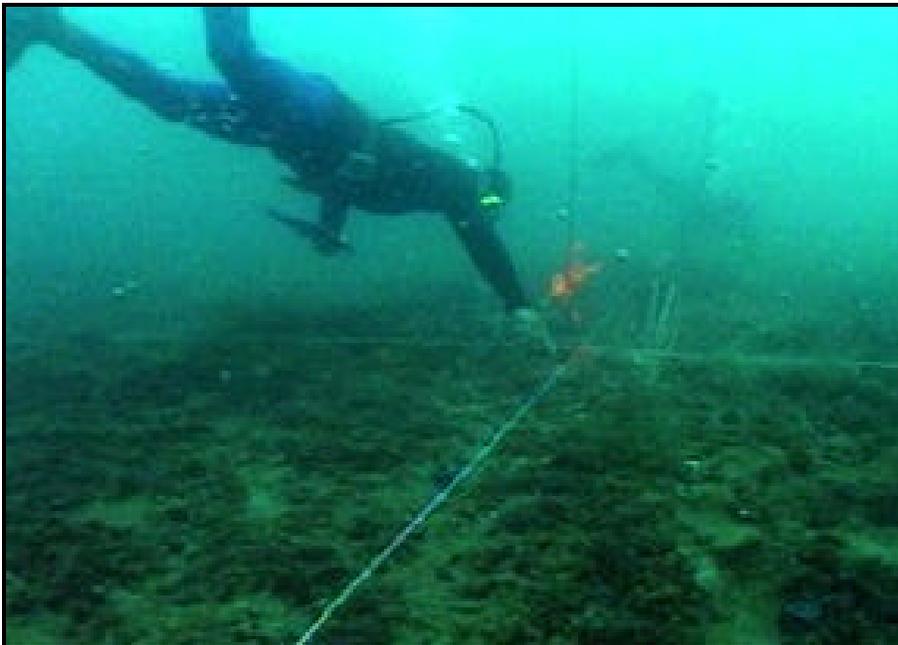


Figure I16. Commercial diver counting rock scallop, *Spondylus calcifer*, and black murex, *Hexaplex nigrinus*, in subtidal monitoring quadrants (photo: Lindsey Haskin).



Figure I17. Virgen de Guadalupe depicted on a rock scallop shell held by a commercial diver of Puerto Peñasco, Sonora, Mexico.



Figure I18. Hohokam black murex shell midden found approximately 20 km north of Puerto Peñasco, Sonora, Mexico.

APPENDIX J

GLOSSARY OF TERMS AND ABBREVIATIONS

Callo de Escarlopa: Rock scallop, *Spondylus calcifer*

Callo de Hacha: Pen shell, *Atrina* spp.

Callo de Riñón: Rugose pen shell, *Pinna tuberculosa*

Caracol Chino: Black murex

CBM: Community-based management

CEDO: *Centro Intercultural de Estudios de Desiertos y Océanos* (research and conservation non governmental organization based in Puerto Peñasco, Sonora).

CICESE: *Centro de Investigación Científica y de Educación Superior de Ensenada*

COBI: *Comunidad y Biodiversidad* (research and conservation non governmental organization based in Guaymas, Sonora).

CONANP: *Comisión Nacional de Áreas Naturales Protegidas*

CONAPESCA: *Comisión Nacional de Pesca y Acuacultura*

INE: *Instituto Nacional de Ecología*

INP: *Instituto Nacional de la Pesca*

LBNP: Loreto Bay National Park

MPA: Marine protected area

NGO: Non governmental organization

PP: *Puerto Peñasco*

SAGARPA: *Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación*

SEMARNAT: *Secretaría del Medio Ambiente y Recursos Naturales*

SPMI: San Pedro Mártir Island

REFERENCES

- Agardy, T.S. 1997. Marine Protected Areas and Ocean Conservation. Landes Company and Academic Press. Texas, U.S.A.
- Agrawal, A. and C.C. Gibson. 1999. Enchantment and disenchantment: the role of community in natural resource conservation. *World Development* 27(4): 629-649.
- Agrawal, A. 2002. Common Resources and Institutional Sustainability. In: Ostrom, E. T. Dietz, N. Dolsak, P.C. Stern, S. Stonich, and E. U. Weber (eds). *The Drama of the Commons*. National Academy Press. Washington, DC.
- Álvarez-Borrego, S. 2002. Physical Oceanography. In: Case, T.J., M.L. Cody, and E. Ezcurra (eds). *A New Island Biogeography of the Sea of Cortés*. Oxford University Press. New York, New York.
- Basurto, X. 2005. How locally designed access and use controls can prevent the tragedy of the commons in a Mexican small-scale fishing community. *Society and Natural Resources* 18: 643-659
- Berkes, F., R. Mahon, P. McConney, R. Pollnac, R. Pomeroy. 2001. *Managing Small-Scale Fisheries: Alternative Directions and Methods*. IDRC. Canada.
- Berkes, F., T. P. Hughes, R. S. Steneck, J. A. Wilson, D. R. Bellwood, B. Crona, C. Folke, L. H. Gunderson, H. M. Leslie, J. Norberg, M. Nyström, P. Olsson, H. Österblom, M. Scheffer, B. Worm. 2006. Globalization, roving bandits, and marine resources. *Science* 311 (5767): 1557-1558
- Bermudez and Agüero. 1994. Socioeconomic Research on Fisheries and Aquaculture in Latin America. In: Charles A.T., T.R. Brainerd, A. Bermudez, H.M. Montalvo, R.S. Pomeroy (eds.) *Fisheries Socioeconomics in the Developing World: Regional Assessments and Annotated Bibliography*. Ottawa, Ontario.
- Bowen, T. 2000. *Unknown Island: Seri Indians, Europeans, and San Esteban Island in the Gulf of California*. University of New Mexico Press, Albuquerque, New Mexico.
- Brusca, R. C., L. T. Findley, P. A. Hastings, M. E. Hendrickx, J. Torre-Cosío, and A.M. van der Heiden. 2005. Macrofaunal biodiversity in the Gulf of California. In: J.-L. E. Cartron and G. Cevallos (eds). *Biodiversity, Ecosystems and Conservation in Northern Mexico*. Oxford University Press. U.K.
- Caddy, J.F. (ed.). 1989. *Marine Invertebrate Fisheries: Their Assessment and Management*. John Wiley and Sons. U.S.A.

- Carr, M.H. and D.C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* 50: 2019-2028.
- Carvajal, M.A., E. Ezcurra, and A. Robles. 2004. The Gulf of California: Natural Resource Concerns and the Pursuit of a Vision. In: *Defying Ocean's End: An Agenda for Action*. Glover, L.K. and S.A. Earl (eds). Island Press. U.S.A.
- Castilla J.C. and M. Fernández. 1998. Small-scale fisheries in Chile: On co-management and sustainable use of benthic fisheries. *Ecological Applications* 8(1): 124-132.
- Castilla, J.C. and O. Defeo. 2001. Latin American benthic shellfisheries: emphasis on co-management and experimental practices. *Reviews in Fish Biology and Fisheries* 11: 1-30
- Cudney-Bueno, R. 2000. Management and conservation of benthic resources harvested by small-scale hookah divers in the northern Gulf of California, Mexico: The black murex snail fishery. MS Thesis, School of Renewable Natural Resources, The University of Arizona, Tucson, Arizona, U.S.A.
- Donkin, R.A. 1998. *Beyond Price: Pearls and Pearl Fishing: Origins to the Age of Discoveries*. American Philosophical Society. Philadelphia, U.S.A.
- Dyer, C.L., and J.R. McGoodwin. 1994. *Folk Management in the World's Fisheries*. University Press of Colorado. Niwot, CO, U.S.A.
- Feeny, D., F. Berkes, B. J. McCay, and J.M. Acheson. 1990. The tragedy of the commons: Twenty-two years later. *Human Ecology* 18:1-19.
- Gaines, S.D., B. Gaylord, and J. L. Largier. 2003. Avoiding current oversights in marine reserve design. *Ecological Applications* 13(1): S32-S46.
- Gordon, H.S. 1954. The economic theory of a common property resource: The fishery. *Journal of Political Economy* 62: 124-142.
- Hardin, G. 1968. The tragedy of the commons. *Science* 162: 1243-1248.
- Hastings, A. and L. W. Botsforth. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. *Ecological Applications* 13(1): S65-S70.
- Johannes, R.E. 1978. Traditional marine conservation methods in Oceania and their demise. *Annu. Rev. Ecol. Syst.* 9: 349-64.
- Johannes, R.E. 2002. The renaissance of community-based marine resource management in Oceania. *Annu. Rev. Ecol. Syst.* 33: 317-340.

- Karlson, R.H. and D.R. Levitan. 1990. Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. *Oecologia* 82: 40-44.
- Lansing, J. S. 1991. *Priests and Programmers: Technologies of Power in the Engineered Landscape of Bali*. Princeton University Press.
- McCay, B.J. and J.M. Acheson, editors. 1987. *The Question of the Commons: The Culture and Ecology of Communal Resources*. The University of Arizona Press, Tucson, Arizona, USA.
- McGoodwin, J.R. 1990. *Crisis in the World's Fisheries: People, Problems, and Policies*. Stanford University Press. California, U.S.A.
- Moreno, C., J. Torre, L. Bourillón, M. Durazo, A. H. Weaver, R. Barraza, and R. Castro. 2005. Estudio y Evaluación de la Pesquería de Callo de Hacha (*Atrina tuberculosa*) en la Región de Bahía de Kino, Sonora y Recomendaciones Para su Manejo. Internal Report, Comunidad y Biodiversidad, A.C. (www.cobi.org.mx/index.php?pag=publicaciones&idioma=esp) [accessed September 2006].
- National Research Council. 2001. *Marine Protected Areas. Tools for Sustaining Ocean Ecosystems*. National Academy Press, Washington, D.C.
- Ostrom, E. 1990. *Governing the Commons: The Evolution of Institutions for Collective Action*. Cambridge University Press, New York, U.S.A.
- Ostrom, E., J. Burger, C.B. Field, R.B. Norgaard, and D. Policansky. 1999. Revisiting the commons: local lessons, global challenges. *Science* 284: 278-282.
- Pauly, D. J. Alder, E. Bennett, V. Christenses, P. Tyedmers, R. Watson. 2003. The future for fisheries. *Science* 302: 1359-1361.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese and F. Torres. 1998. Fishing down marine food webs. *Science* 279:860-863.
- Roberts, C. and J. P. Hawkins. 2000. Fully-protected marine reserves: a guide. WWF Endangered Seas Campaign, 1250 24th Street, NW, Washington D.C., 20037, USA and Environment Department, University of York, York, YO105DD, UK.
- Roberts, C. M., J. A. Bohnsack, F. Gell, J. P. Hawkins, R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. *Science* 294(5548): 1920-1923
- Russ, G.R. A.C. Alcalá, A.P. Maypa, H.P. Calumpans, A.T. White. 2004. Marine reserve benefits local fisheries. *Ecological Applications* 14(2): 597-606

- Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J. C. Barrera, P. K. Dayton 2002. A general model for designing networks of marine reserves. *Science* 298(5600): 1991-1993.
- Sala, E., O. Aburto-Oropeza, M. Reza, G. Paredes and L. López-Lemus. 2004. Fishing down coastal foodwebs in the Gulf of California. *Fisheries* 29(3): 19-25.
- Sarukhán, J. 2001. Introduction. *In: The Gulf of California: A World Apart*. Robles Gil, P., E. Ezcurra, E. Mellink. Agrupación Sierra Madre. México D.F.
- Scott, A. D. 1955. The fishery: The objectives of sole ownership. *Journal of Political Economy*. 63: 116-124.
- Stoner, A.W., M. Ray-Culp, and S.M. O'Connell. 1998. Settlement and recruitment of queen conch, *Strombus gigas*, in seagrass meadows: Associations with habitat and micropredators. *Fishery Bulletin* 96: 885-899.
- United Nations Food and Agriculture Organization. 1995. Marine Fisheries and the Law of the Sea: a decade of change. U.N. Food and Agriculture Organization Fisheries Circular Number 853, Rome, Italy.
- Wilson, J.A., J.M. Acheson, M. Metcalfe, and P. Kleban. 1994. Chaos, complexity and community management of fisheries. *Marine Policy* 18(4): 291-305.
- World Bank (www.worldbank.org/poverty/scapital) [accessed May 21 2002].