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Marine conservation across political borders

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

Doctor of Philosophy

in

Marine Biology

by

Juan Arturo Ramírez-Valdez

Committee in charge:

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Edward P. Parnell

2020

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University of California San Diego

2020

DEDICATION

I dedicate this dissertation to my parents, Eduardo and Yolanda.

The beginning of everything is a loving family.

EPIGRAPH

For love of domination we must substitute equality;

for love of victory we must substitute justice;

for brutality we must substitute intelligence;

for competition we must substitute cooperation.

We must learn to think of the human race as one family.

Bertrand Russell

TABLE OF CONTENTS

Signature page.....	iii
Dedication.....	iv
Epigraph.....	v
Table of Contents.....	vi
List of Tables.....	vii
List of Figures.....	viii
Acknowledgments.....	xi
Vita.....	xv
Abstract of the Dissertation.....	18
Introduction.....	20
Chapter 1: The nearshore fishes of the Cedros Archipelago (North-Eastern Pacific) and their biogeographic affinities.....	33
Chapter 2: Asymmetry across political borders: research, management, and economic value of the critically endangered giant sea bass (<i>Stereoleopis gigas</i>).....	60
Chapter 3: The economic value of the giant kelp (<i>Macrocystis pyrifera</i>) forest ecosystem services across political boundaries: an approach with commercial fishery ex-vessel value.....	121
Chapter 4: Mexico-California binational initiative of kelp forest ecosystems and fisheries.....	161
Conclusions.....	203

LIST OF TABLES

Table 1.1: Study sites and habitat in the Cedros Archipelago.....	36
Table 1.2: Systematic list of fishes of Cedros Archipelago, Mexico, Northeastern Pacific.....	39
Table 1.3: Fish species that present range extension in their distribution in Cedros Archipelago...58	
Table 2.1: Management policies, conservation categorizations, and government regulations that impacted in the GSB management across the U.S. and Mexico territories.....	97
Table 2.2: Scientific knowledge on Giant sea bass in peer-reviewed papers. WS= ISI Web of Science; GS= Google Scholar. GSB-listed= Papers that mention GSB. GSB-centric Paper= Papers that are focused on GSB.....	98
Table 3.1: Economically important species of invertebrate and fish closely associated with the kelp forest ecosystem.....	147
Table 3.2: Fishery Management Areas (FMA) for commercial fisheries in both geographic regions; 10 × 10-minute grid blocks by California Department Fish and Wildlife (U.S.) and fishery concession areas by Mexican Fisheries Management Agency-CONAPESCA (Mexico).....	148
Table 3.3: Summary of regression analyses on 10-year mean fishery production (kg/km ²) and percentage of giant kelp cover within the Fishery Management Areas (FMA).....	149

LIST OF FIGURES

Figure 1.1: Locations of field surveys at the Cedros Archipelago, Mexico.....	39
Figure 1.2: Non-metric Multidimensional Scaling analysis (nMDS) for fish species recorded in the subtidal field surveys at Cedros, Natividad and San Benito, and eight islands in the Pacific coast of Baja California and California.....	43
Figure 1.3: Distribution ranges (bars) in the Eastern Pacific of 262 species included in Table 2...43	
Figure 1.4: Distribution patterns of fish species of the Cedros Archipelago.....	58
Figure 2.1: Study area and the spatial management of the fishery in both geographic regions; 10 × 10-minute grid blocks by California Department Fish and Wildlife (U.S.) and fishery concession areas by Mexican Government Fisheries Agency - CONAPESCA (Mexico).....	99
Figure 2.2: Spatial representation of the literature review (blue), and the biological monitoring program (orange). Peer-reviewed papers data not associated with a specific study site is included as general southern California, general Baja or general Gulf of California.....	100
Figure 2.3: Synthesis of the literature review of the knowledge of the giant sea bass across its entire distribution. A) Giant sea bass research has recently increased, especially in Mexico. B) Most papers on giant sea bass are focused on the distribution and fishery of the species, C) The majority of papers focus on adult giant sea bass.....	101
Figure 2.4: Management of the GSB across the U.S.-Mexico border is highly asymmetric. Despite little economic or scientific input Mexican fishery catches and revenue is high, a trend that is reversed in the United States. GSB ecotourism revenues after (Guerra et al., 2017).....	102
Figure 2.5: Historic and contemporary fishery landings of giant sea bass in the U.S. and Mexico show strong variability over time. Historical data on commercial fisheries. Despite the perceived collapse of Mexican GSB populations, U.S. recreational catches indicate that political legislation (rather than population collapse) was truly limiting catches before 1980.....	103
Figure 2.6: Giant sea bass contemporary catches (2000-2016) are highest in the summer, in both the U.S. and Mexico. In Mexico, this corresponds in part to the closure of the lobster fishery from April to September. Data source: Mexico = CONAPESCA-SEPESCA official landings; U.S.= CDFW fishery Landings.....	104
Figure 2.7: A) Box plot indicating the GSB body weight (kg) sampled through the Mexican fishery monitoring program. Median weight of 210 samples (12 kg) in red dotted line. Locations have been divided into one of three biogeographic regions: San Diegoan province, Cortez province, and a transitional zone.....	105

Figure 2.8: Spatial representation of the contemporary 2000-2016 annual average fishery landings of giant sea bass from the U.S. and Mexico commercial fleets shows much higher landings in Mexico. When divided into biogeographic regions, the transitional zone between the San Diego and Cortez provinces has the highest proportion of total landings.....106

Figure 3.1: 2000-2015 Fishery landings (tons/yr) for three of the Giant Kelp forest-associated species California spiny lobster (*Panulirus interruptus*), red sea urchin (*Mesocentrotus franciscanus*), purple sea urchin (*Strongylocentrotus purpuratus*) by country, Mexico and the U.S.....150

Figure 3.2: 2000-2015 Fishery sales (Millions USD/yr¹) for three of the giant kelp forest-associated species California spiny lobster (*Panulirus interruptus*), red sea urchin (*Mesocentrotus franciscanus*), purple sea urchin (*Strongylocentrotus purpuratus*) by country, Mexico and the U.S.....151

Figure 3.3: Fishery Management Areas (FMA) for commercial fisheries in both geographic regions; 10x10-minute grid blocks by California Department Fish and Wildlife (U.S.) and fishery concession areas by Mexican Fisheries Management Agency-CONAPESCA (Mexico).....152

Figure 3.4: Landsat 5 Thematic Mapper image displaying the kelp cover in a small section of the study area; south of Bahia Todos Santos, Ensenada, Mexico (Fall 2008).....153

Figure 3.5: Percentage of kelp cover categories within the Fishery Management Areas (FMA); High (> 1.0%), Medium (0.1 – 1.0), Low (< 0.1%).....154

Figure 3.6: 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA; California spiny lobster (*Panulirus interruptus*), purple sea urchin (*Strongylocentrotus purpuratus*), red sea urchin (*Mesocentrotus franciscanus*), and abalone species (*Haliotis* spp.).....155

Figure 3.7: 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA; California sheephead (*Semicossiphus pulcher*), giant sea bass (*Stereolepis gigas*).....156

Figure 3.8: California spiny lobster (*Panulirus interruptus*) 10-year (2008-2017) average fishing production (kg/km²) according to the Giant Kelp cover size within the FMA by country, the U.S. and Mexico. Data are presented as mean ±S.E.M. where bars sharing letter are not significantly different from one another; first letter= within country, second letter= between countries.....157

Figure 3.9: Purple sea urchin (*Strongylocentrotus purpuratus*) 10-year (2008-2017) average fishing production (kg/km²) according to the Giant Kelp cover size within the FMA by country, the U.S. and Mexico. Data are presented as mean ±S.E.M.....158

Figure 3.10: Red sea urchin (*Mesocentrotus franciscanus*) 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA by country, the U.S. and Mexico. Data are presented as mean ±S.E.M. where bars sharing letter are not significantly different from one another; first letter= within country, second letter= between countries.....159

Figure 3.11: Relationship between economic value (USD/yr⁻¹) of 10-year average fishery production (2008-2017) considering fishery sales alone and the percentage of giant kelp cover within the FMA by country, the U.S. and Mexico.....160

Figure 4.1: Geographic localization and main oceanographic features in the California Current System, including study sites and study effort in number of peer-reviewed papers of the kelp forest ecosystem across the California (U.S.) and Baja California (Mexico) coast.....165

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FIELD OF STUDY

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ABSTRACT OF THE DISSERTATION

Marine conservation across political borders

by

Juan Arturo Ramírez-Valdez

Doctor of Philosophy in Marine Biology

University of California San Diego, 2020

Marco Octavio Aburto Oropeza, Chair
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In the marine environment, political borders are essentially imaginary lines that often divide well-connected populations, communities and habitats. Scientific evidence shows that collaboration among nations can improve the effectiveness of program management, and cost efficiency. Despite the evidence that the marine region between California (U.S.) and Baja California (Mexico) constitutes a single ecoregion, our research revealed a lack of binational collaboration and differences in knowledge, and management of trans-boundary marine species.

Chapter 1 asks what the fish composition of the Cedros archipelago is, and if the affinity of the species would allow us to recognize the biogeographic break between temperate and subtropical systems. We found that the Cedros archipelago fish community is a species-rich assemblage, with a fairly even blend of temperate and tropic-subtropical species. Nineteen new species occurrences were recorded in the archipelago, and limited sampling effort south of the U.S.-Mexico border may be the most likely reason. Chapter 2 asks whether the management of the giant sea bass (*Stereolepis gigas*) across political borders could result in loss of economic opportunities and threaten populations through overfishing. We found that extremely strong asymmetry management exists across the border, political regulations have both hidden and created illusions of false historical population collapses, and the total population size is likely higher than previously estimated. Chapter 3 seek to estimate the economic value of the giant kelp forest ecosystems across the Northeastern Pacific, based on some of the most important fisheries in the region. We found a positive relationship between kelp forest cover and the fisheries production, the higher the kelp cover, the higher the fishery production. Chapter 4 aims to analyze the effects of climate change in the giant kelp forest ecosystem across the U.S.-Mexico border and what the future scenario would be in the face of the current climatic trends. Our literature review showed that the giant kelp and the biological communities it supports will likely react to climatic and non-climatic changes in complex ways, likely by contracting their southern extent due to warming waters, reductions in nutrient availability, increasing wave disturbance, and grazing by warm-water herbivores. As a result, the best strategy in the long run is transboundary cooperation through sharing cross-border marine resources and acknowledging the actions taken by one of the invariable parties affects the other. Our results highlight the need for greater cross-border cooperation in marine resources management and generate research political-borderless.

INTRODUCTION

Marine conservation strategies are commonly aimed at limiting human-induced impacts, restoring damaged marine ecosystems, and preserving vulnerable species (Duarte et al., 2020; Knowlton, 2020; Worm, 2017). For this reason, the design and implementation of marine conservation strategies require multi-factor analysis, which can be even more complicated when considering the resources being shared by nations. In marine ecosystems, cooperation and coordination between countries are especially important because of ocean currents and the natural flow of material in the sea, the high mobility and dispersion of species, the maintenance of genetic flow in the populations, the common use of marine resources, and marine sovereignty (Levin et al., 2013).

In marine environments, political borders are intangible lines that often divide well-connected populations, communities, and habitats (Block et al., 2011; Selkoe et al., 2010). While biogeographic boundaries are the result of the natural distribution of species, political boundaries are artifacts of human organization that tend to delineate the limits of decision-making processes (Dallimer and Strange, 2015). When nations share species and ecosystems, they also share the ecosystem services that maintain human life (López-Hoffman et al., 2010). The identification of the spatial areas of species and ecosystems is relevant for the establishment of adequate and representative conservation strategies, especially in ecosystems shared across nations.

Additionally, scientific evidence shows that collaboration among nations can improve management and conservation program effectiveness and cost efficiency by developing a fully coordinated plan that encompasses protected area and conservation goals (Kark et al., 2009).

Despite the evidence that the marine region between California, United States (U.S.), and Baja California, Mexico, constitutes a single marine ecoregion (Horn et al., 2006; Pondella et al., 2005), research efforts have revealed a lack of binational collaboration and differences in knowledge, conservation, and management of trans-boundary marine species (Aburto-Oropeza et al., 2018; Wilder, 2013). The U.S. and Mexico together account for more than 2,600 km of coastline in the temperate sea of the Northeastern Pacific, which hosts a huge diversity of species ranging from local resident populations important for sustaining food webs, such as Giant Kelp (*Macrocystis pyrifera*) (Edwards and Hernandez-Carmona, 2005), to large predators and other mobile organisms that cross the national border regularly, such as sharks and Giant sea bass (*Stereolepis gigas*) (Block et al., 2011; Chabot et al., 2015). In the Northeastern Pacific, Giant Kelp forms dense forests from Santa Cruz, California (U.S.) to Bahia Asuncion, Baja California Sur (Mexico). Giant Kelp forests can be considered the submerged counterparts of rain forests and are among the most species-rich communities (Schiel and Foster, 2015) and productive ecosystems on earth (Reed et al., 2015). Giant kelp is an ecosystem engineer that creates biogenic habitats that provide refuge for numerous species, including many that are often economically important for fisheries (Parnell et al., 2010; Schiel and Foster, 2015).

The kelp forest communities of the Northeastern Pacific have experienced two very different histories. Along the coast of California, a long history of fishing pressure (Tegner and Dayton, 2000a), continuous long-term scientific monitoring programs (Foster et al., 2013; Schiel and Foster, 2015; Tegner and Dayton, 1987), and networks of marine reserves (Murray and Hee,

2019) all highlight the high quantity of coastal human impacts both positive and negative for the ecosystem. Contrastingly, the kelp forests off the coast of the Baja California Peninsula lack a marine reserve network established along the coastline and have received much less attention from both large-scale fisheries and research and monitoring initiatives (Arafeh-Dalmau et al., 2017). Along the Baja California Peninsula and Southern California, the presence and abundance of kelp is very dynamic in space and time as a result of grazing, storms, episodic oceanographic events, and climate change (Arafeh-Dalmau et al., 2017; Cavanaugh et al., 2019; Parnell et al., 2010). In addition to natural and anthropic stressors, coastal marine ecosystems around the world and the human communities that depend on them are facing the challenge of an increasingly variable climate. (Doney et al., 2012; Hoegh-Guldberg and Bruno, 2010). The pressure that these stressors pose to the marine ecosystem has generated habitat alteration and an increase of species vulnerability (Hoegh-Guldberg and Bruno, 2010).

The existence of four research pathways has been suggested (Dallimer and Strange, 2015), which may enhance our ability to address the adverse effects of socio-political borders on conservation: (i) scale-matching, (ii) quantification of the mutual economic benefits of conservation across boundaries, (iii) determining transboundary societal values, and (iv) acknowledging the importance of stakeholder behavior and incentives. This work addresses these research pathways, involving marine resources of ecological importance and economic value in the California (U.S.) and Baja California Peninsula (Mexico) region, and incorporating a wide range of stakeholders.

Building upon existing information and generating new evidence, my research incorporates different sources of observational data to develop and propose new conservation strategies in the management of marine resources from a transboundary perspective. The following specific

questions guide each chapter of this thesis: *How do socio-political barriers operate to restrict the knowledge we have of marine resources? What are the ecological and economic implications as a result of differential use and management of marine resources across socio-political boundaries? How does climate change impact the conservation and management of trans-boundary marine resources?*

The goals of this dissertation were to assess the asymmetry in knowledge and management of marine resources across the U.S.-Mexico political border, using the distribution of fish species, the differential management of the giant sea bass (*Stereolepis gigas*), the economic value of the giant kelp (*Macrocystis pyrifera*) forest ecosystem, and the implications of climate change for the future scenario of kelp forests across the border as indicators. Using fish distributions as a case study, the objectives for Chapter 1 were to analyze the implications of the uncertainty of the species distribution in the transition between the warm-temperate and subtropical real. The objectives of Chapter 2 were to evaluate the ecological and economic implications of the differential management of marine resources across socio-political boundaries. To that end, I developed two case studies. For the first case study, I analyzed the asymmetry in the management of a critically endangered fish species across the political border between the U.S. and Mexico. For the second case study, I examined the ecological and economic value of the kelp forest ecosystem and the services it provides using commercially important species that rely on this ecosystem. The objectives of Chapter 3 were to analyze the effects of climate change in the giant kelp forest ecosystem across the U.S.-Mexico border and what the future scenario would be in the face of the current climatic trends. To do this, I developed a literature review to compile the existing knowledge about the giant kelp forest ecosystems in California (U.S.) and Baja California (Mexico). The collection of research identifies the importance of how political boundaries can

represent a challenge for some marine resources, in the same way as it has been documented with the terrestrial system (López-Hoffman et al., 2010; Wilder, 2013).

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CHAPTER 1:

The nearshore fishes of the Cedros Archipelago (North-Eastern Pacific)

and their biogeographic affinities

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THE NEARSHORE FISHES OF THE CEDROS ARCHIPELAGO (NORTH-EASTERN PACIFIC) AND THEIR BIOGEOGRAPHIC AFFINITIES

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ABSTRACT

Located in the central region of the west coast of Baja California Peninsula, the Cedros Archipelago consists of five continental islands (Cedros Island, Natividad, San Benito Este, Medio, and Oeste), with Cedros being the largest island in the Mexican Pacific. This archipelago represents the biogeographic transition zone between the temperate and subtropical region and hence, the end of the geographic distribution of a large number of species. Based on field surveys, literature, and scientific collection records, an exhaustive species list of fishes associated with the archipelago and their biogeographic relationships is presented. The checklist includes 269 species belonging to 191 genera, 97 families, 31 orders, and 4 classes. Of the total species, 105 species were recorded in the field, 57 were the result of the literature review, and 218 species of the records were obtained from collections. A total of 14 biogeographic affinities are presented, where 51% of the species have warm-temperate or cold-temperate affinity and 37% have tropical-subtropical affinity. This work highlights the fish diversity present in a transition zone within the temperate and subtropical marine areas of the Northeastern Pacific. More importantly, it reveals a biogeographic region where a great number of species converge, and may be related with the evolutionary history of different taxa and the geological history of the region.

INTRODUCTION

The Cedros Archipelago (CEA) includes five continental islands, and is located 10 km off the coast in the east-central region of the Baja California Penin-

sula (fig. 1). Cedros is the largest island in the Mexican Pacific, and along with San Benito Oeste, Medio, Este, and Natividad Island, represent a land territory of 360.7 km². The polygon formed between all of these islands accounts for a marine region of 3,928.9 km².

The CEA forms a group of northwestward-trending islands that are considered an extension of the Vizcaino Desert; therefore a subregion of the Sonoran Desert (Oberbauer 1985). The area was separated from the coast of Baja California by a submersion process in the last glacial period (Busby-Spera 1988), resulting in a 200 m deep channel called the Kellet Channel. The archipelago has a complex geologic history, beginning with rock material accumulated in a deep trough in the late Jurassic period, forming the Jurassic Grand Canyon. During the Cretaceous, the formations were folded, faulted, and overlaid by marine deposits. Finally, uplift occurred as recently as the late Pleistocene (Oberbauer 1985; Busby-Spera 1988).

The Pacific islands of the Baja California Peninsula can be considered as among the least degraded ecosystems in continental islands (Littler 1980; Richards 2000; Pondella et al. 2005; Aguirre-Munoz et al. 2008), however unlike their terrestrial biodiversity (Huey 1942; Oberbauer 1985; Mellink 1993; Aguirre-Munoz et al. 2008), the marine diversity has been poorly documented. This contrasts with ecological interest on the central region of the Baja California Peninsula, which represents a transition zone between the San Diegan and the Cortez biogeographic provinces (sensu Horn et al. 2006; Ruiz-Campos et al. 2010). South of the CEA the cold waters from the California Current system converge

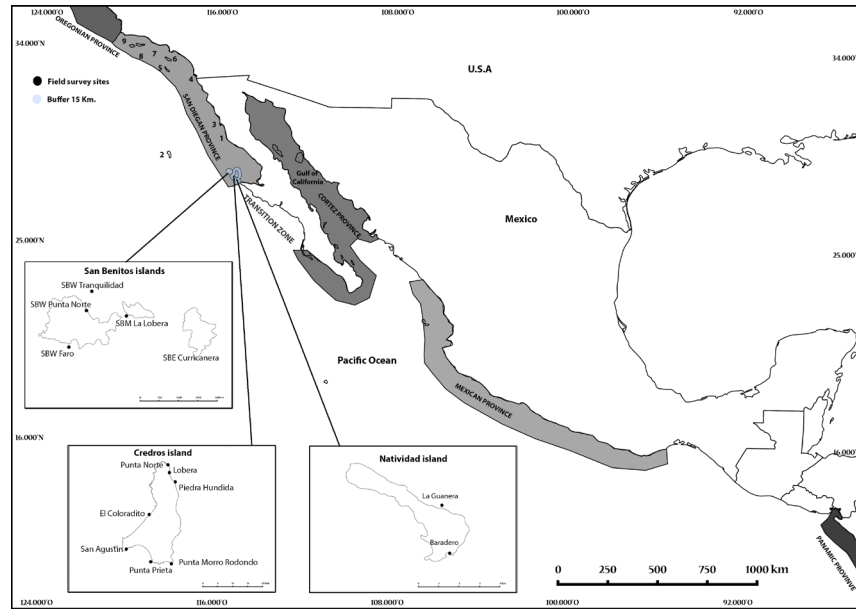


Figure 1. Locations of field surveys at the Cedros Archipelago, México

with the subtropical current system from the south, West Mexican Current (Hubbs 1960; Hickey 1979; Kessler 2006; Taylor et al. 2007), and recently documented intricate eddy motions of ocean water masses in the region contribute to the complexity of the coastal upwelling regime (Miller et al. 1999).

To the north of the CEA, temperate species associated with rocky reefs and kelp forests begin to be dominant until Point Conception, California (Horn et al. 2006). To the south of the CEA, species associated with the tropical Cortez and Mexican provinces begin to appear, mainly associated with mangrove ecosystems in estuaries and bays located in Bahía Magdalena (24°47.6'N, 112°18.2'W). While some species associated with the San Diegan faunistic province can be found as far south as Bahía Magdalena, the transition begins sharply at Punta Eugenia (27°50.7'N, 115°4.84'W), a major mainland landmark in front of the archipelago. Kelp forests do not persist farther south than Punta Eugenia and tropical marine species become more common (Taylor et al. 2007).

The CEA region has been historically relevant for extractive purposes, as archaeological investigations have documented an intensive pre-Hispanic use of marine resources (Des Lauriers 2010), and currently there are fisheries that target on spiny lobster (*Panulirus interruptus*; Randall 1840), green abalone (*Haliotis fulgens*; Philippi 1854), and pink abalone (*H. corrugata*; Gray 1828). Although the finfish fishery has less relevance, some taxa are of artisanal importance (e.g., *Paralabrax nebulifer* [Girard 1854]; *P. clathratus* [Girard 1854]; *Semicossyphus pulcher* [Ayres 1854]; and *Seriola lalandi* [Valenciennes 1833; Rodríguez-Valencia et al. 2004]).

Despite the ecological and economical importance of this region, there is scarce information about the species that inhabit it. In fact, most published species lists of marine groups contain only information from occasional visits or literature reviews (e.g., Hubbs 1960; Miller and Lea 1972; Love et al. 2005). The few studies that have specifically targeted any of the islands of the CEA are focused on particular fish families (Clinidae: Stepien and Rosenblatt 1991), species (*Sardinops* spp.: Felix-Uraga et al. 1996; Quiñonez-Velazquez et al. 2002) or habitats (reef fishes: Pondella et al. 2005; intertidal fishes: Carpizo-Ituarte et al. 2012).

Baseline studies for the CEA are a priority because the region has begun to show signs of environmental decay related to anthropogenic impacts. Among them the overexploitation of the fishing resources, overpopulation of Cedros Island, and the Mitsubishi/Mexican government-owned salt-transshipment facility, which is a source of introduction for exotic species (Mellink 1993; Des Lauriers 2009; Aguilar-Rosas et al. 2011). The lack of a detailed fish checklist hinders the efforts of decision-makers, who require comprehensive baseline data to set adequate protocols for monitoring temporal changes in community composition caused either by anthropogenic or natural forces (Reyes-Bonilla et al. 2010). Furthermore, without a thorough inventory of fish species, any biogeographic analysis of the CEA will be limited in its relevance and outcomes.

The main objective of this work is to provide the first comprehensive, systematic checklist of marine ichthyofauna of the CEA. We performed an overview of the composition of fish community and an analysis of zoo-

TABLE 1

Study sites and habitat in the Cedros Archipelago.
 *I=Intertidal, S=Subtidal; **T=Tidepools, K=Kelp forest, R=Rocky reefs, S=Soft bottom.

Site	Coordinates	Date	Sampled zone*	Habitat**	Temp C	
Cedros Island	Punta Norte	28°21'48.7 N, 115°11'50.7 W	17-May-12	I, S	T, K	14
	Lobera	28°20'12.1 N, 115°11'43.9 W	18-May-12	S	K, R	14
	San Agustin	28°4'48.9 N, 115°20'27.3 W	19-May-12	I, S	T, K	14
	El Coloradito	28°11'54.5 N, 115°15'45.7 W	I	T		
	Punta Prieta	28°2'14.6 N, 115°15'11.9 W	I	T		
	Punta Morro Redondo	28°1'56.7 N, 115°11'18.1 W	I	T		
	Piedra Garropa	28°18'17.5 N, 115°10'19.1 W	18-May-12	S	S, R	14
San Benito	SBE Curricanaera	28°17'38.5 N - 115°32'28.1 W	20-May-12	I, S	T, K	15
	SBE Tranquilidad	28°19.0' N - 115°35.0' W	22-May-12	I, S	T, K	14
	SBM La Lobera	28°18'25 N - 115°34'11 W	21-May-12	S	T, K, R	16
	SBW Punta Norte	28°18'29.6 N, 115°35'9.5 W	22-May-12	I	T	
	SBW Faro	28°17'40.7 N - 115°35'31.1 W	21-May-12	S	R	15
Natividad	Baradero	27°52'31.4 N - 115°10'16.8 W		I, S	T, K	15
	La Guanera	27°51'5.8 N - 115°10'2.6 W		S	T, K	15

geographic affinity of the species using field surveys, fish collection records, and a full literature review. The results highlight that the relatively high local fish diversity is a result of physical and biological factors determining the transition between warm temperate and subtropical communities in the northeastern Pacific.

MATERIALS AND METHODS

The Cedros Archipelago (CEA) is composed of five islands. Cedros is the dominant topographic feature of a 400 km long submerged ridge, with a maximum height of 1,204 m, encompassing an area of 348.2 km² and laying approximately 22 km from the nearest point on the central coast of the Baja California Peninsula (fig. 1). San Benito Archipelago has three small islands situated 31.5 km west of Cedros, encompassing an area of 6 km² and with a highest altitude of 212 m. Finally, Natividad is located 7.5 km west of Punta Eugenia and measures 6 km in length and 2.5 km at its maximum width, accounting an area of 7.28 km².

In order to compile the fish checklist of the CEA, we followed three steps. First, we gathered information from electronic and in-house scientific collections from institutions in México, the United States, and Canada, encompassing records between 1934 and 2001. In the case of museum data, we reviewed records from thirty collections, either electronically or by direct visits, obtaining records of the following eleven institutions: Universidad Autónoma de Baja California (UABC; Ensenada); Centro Interdisciplinario de Ciencias Marinas (CICIMAR; La Paz); Instituto de Biología de la Universidad Nacional Autónoma de México (México, DF); Scripps Institution of Oceanography (La Jolla); Los Angeles County Natural History Museum (Los Angeles); California Academy of Sciences (San Francisco);

National Museum of Natural History, Smithsonian Institution (Washington, DC); American Museum of Natural History (New York); University of Kansas Natural History Museum (Kansas City); University of Florida (Gainesville); and Canadian Museum of Nature Fish Collection (Dartmouth).

Second, we conducted an extensive literature review of the species reported in peer reviewed articles and technical reports from libraries at UABC (Ensenada, México), CICIMAR (La Paz, México), Centro de Investigaciones Biológicas del Noroeste (La Paz, México), Centro de Investigación Científica y de Educación Superior de Ensenada (Ensenada, México), and Scripps Institution of Oceanography (La Jolla, CA).

Finally, we conducted field surveys around the islands between 2010 and 2012 (table 1). Field surveys included intertidal and subtidal samplings. Intertidal fishes were sampled during eight sampling campaigns, carried out between February 2010 to April 2012 in the rocky tidepools of five sites at Cedros Island, two at San Benito, and two at Natividad (fig. 1, table 1). Tidepools were sprayed using manual aspersion pumps containing a solution of 10% eugenol (clove oil) dissolved in ethanol. After 10 minutes, the tidepools were thoroughly checked using dip and hand nets (Ruiz-Campos et al. 2010).

Subtidal fishes were sampled in May 2012 through underwater visual censuses performed by trained scuba divers. Using 30 × 2 m belt transects, we dove at three different depths (10, 15, and 20 m) and three main habitats (kelp forest, rocky reef, and soft-bottom). We carried out a total of 66 transects in four sites at Cedros, four sites at San Benito and two at Natividad. The total surveyed area with visual censuses was 3,960 m². Subtidal species were also recorded using the roving dive technique and underwater photography. Voucher specimens

of all recorded species in tidepools were kept in the Fish Collection at UABC, while most of the species recorded in the subtidal had in situ photographs taken.

In order to establish which records would be considered as valid for purposes of the study, in a geographical information system (QGIS 2.8) we traced a buffer area of 15 km around the archipelago. The records with coordinates inside the buffer area were considered part of the checklist, independently of the collection method or year of collection.

The taxonomic identification was performed using descriptions by Miller and Lea (1972), Fischer et al. (1995), and Robertson and Allen (2015). A specialized bibliography was also used for some groups (e.g., clingfishes [Briggs 1955]; gobies [Hoese and Reader 2001]; labrisomid blennies [Hubbs 1953]; rays [Castro-Aguirre and Espinoza-Pérez 1996]; sharks [Espinoza-Pérez et al. 2004]; tube blennies [Stephens 1963 and Stephens et al. 1996]). The final checklist follows a systematics order according to Eschmeyer (2015), with modifications by Wiley and Johnson (2010). Genera and species names are presented alphabetically. To eliminate synonyms and generate a systematic list consisting only of valid names, each taxonomic name was corroborated in the Catalog of Fishes of the California Academy of Sciences (Eschmeyer 2015) and common names in Page et al. (2013).

The biogeographic analysis followed three approaches.

- 1) We created a species presence/absence matrix using the species recorded in our subtidal field surveys at Cedros, San Benito and Natividad Islands, and field records from eight Northeastern Pacific islands gathered from peer review journals (Guadalupe Island, México [Reyes-Bonilla et al. 2010]; San Martin and North Coronado from México; and San Clemente, Santa Catalina, Santa Cruz, Santa Barbara, and San Nicolas from USA [Pondella et al. 2005]). Then, we performed a non-metric multidimensional scaling analysis (nMDS) (Kruskal & Wish, 1978) using the unweighted paired group method and arithmetic averages (UPGMA), based on a Bray-Curtis similarity matrix. SIMPER analysis was used to determine which species contributed with the largest dissimilarity patterns, using the statistical package PRIMER 6.1 (Primer-E Ltd: Plymouth; Clarke and Gorley 2006).
- 2) Species distributions were plotted using the available information for northern and southern endpoints following Love et al. (2005), and Robertson and Allen (2015). If a species had not been reported at CEA but was observed during field surveys, endpoints were updated with such information. We developed a MATLAB routine to generate latitudinal distribution for the 262 species with known distribution. We defined species with wide distribution those that have a full geographic range covering at least 60 degrees

in latitude and which occurred beyond 30 degrees of latitude in both hemispheres.

- 3) Finally, we assessed the regionalization of the fish species recorded at CEA. The zoogeographic affinity of the ichthyofauna was achieved following Horn et al. (2006) for the North Pacific region, and Hastings (2000) for the Tropical Eastern Pacific, with modifications from Robertson and Cramer (2009). Considering their distribution range, the species were grouped into eight biogeographic provinces from the Eastern Pacific (Briggs 1974), one realm (North Pacific), and three distribution patterns (AmphiAmerican, Circumtropical, and Circumglobal).

RESULTS

The field surveys, museum records, and literature review, taken together helped to construct a list of 269 species of marine fishes of the CEA, from 191 genera, 97 families, 31 orders, and 4 classes (table 2). Perciformes was the most commonly represented order, with 33 families and 106 species in total. Almost half of the families (48) are represented by a single species. The most speciose families were Sebastidae (22 spp.), Myctophidae (16 spp.), and Embiotocidae (10 spp.). The genera with the highest number of species were *Sebastes* (22 spp.) and loosely followed by *Citharichthys* (5 spp.), and *Apogon*, *Halichoeres*, *Paralabrax*, *Icelinus*, *Lepophidium*, and *Pleuronichthys* with 4 species each.

The nMDS ordination plot based on presence/absence data clearly shows a separation of the CEA from the other eight northern islands, located in the California Current system (fig. 2). The fish assemblages from Cedros, Natividad, and San Benito are tightly grouped, indicating high similarities (>50%), while the Channel Islands, North Coronado, and Guadalupe Islands constitute a more spread group with equivalent similarity between fish assemblages (<50%), and San Martin island is separated from the rest.

According to the geographic distribution, 135 species have a temperate affinity (warm-temperate to cold-temperate) and 92 species have a tropical affinity (tropical-subtropical). A third group of 35 species are widely distributed in tropical and subtropical seas, and a geographic distribution was not assigned to seven taxa that were not identified to specific level (fig. 3).

A total of 170 species comes from a single source (field record, scientific collections and literature review) and 100 species came from multiple sources (table 2). Considering all records, 105 species were seen or collected in the field, 57 taxa were cited in the literature review and 218 species had specimens from the CEA housed in scientific collections. Based on our field records, 90 species were recorded in the subtidal (soft bottom [9 spp.]; kelp forest and rocky reefs [84 spp.],

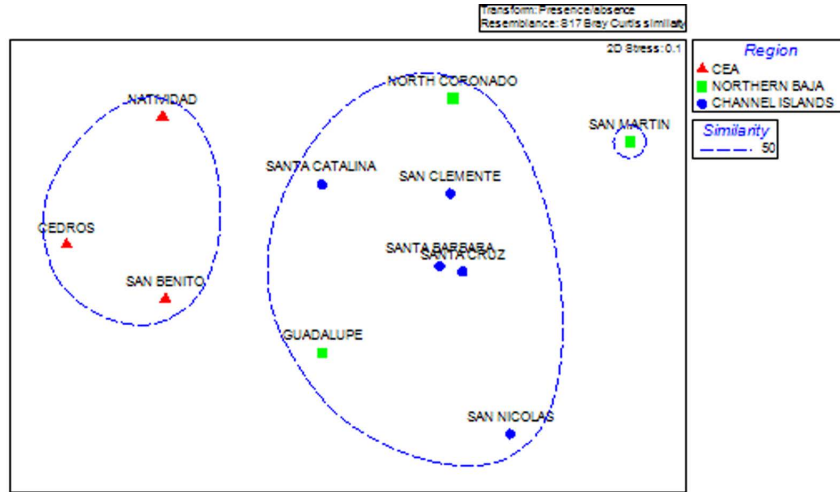


Figure 2. Non-metric Multidimensional Scaling analysis (nMDS) for fish species recorded in the subtidal field surveys at Cedros, Natividad and San Benito, and eight islands in the Pacific coast of Baja California and California [data from Pondella et al. (2005), Reyes-Bonilla et al. (2010) and present study].

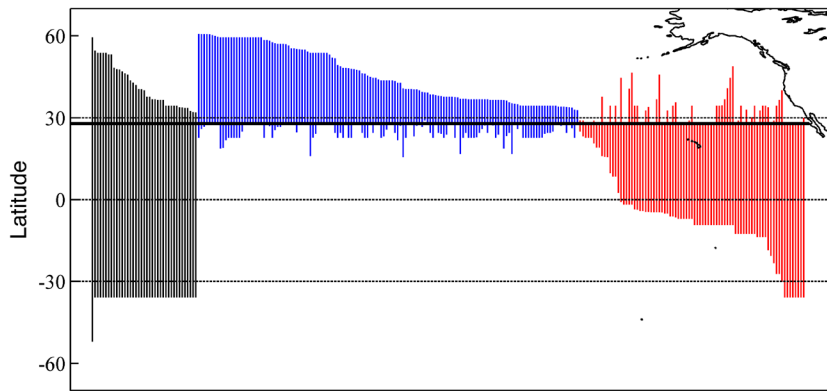


Figure 3. Distribution ranges (bars) in the eastern Pacific of 262 species included in Table 1. Black lines: species widely distributed in the EP surpassing the 30 degrees Latitude in both hemispheres. Blue lines: species with temperate affinity. Red lines: fishes with tropical-subtropical affinity. Black line: Latitude in where CEA archipelago is located.

3 species were present in both habitats). The intertidal fieldwork contributed with 24 species to the checklist.

Analyzing separately the species richness for each of the islands, Cedros had more than twice the number of taxa as San Benito (224 and 107, respectively) and four times that for Natividad Island (63 spp.). The differences are largely reduced when considering only the field surveys; in Cedros 78 species were seen or collected, 54 and 56 species at San Benito and Natividad, respectively.

The CEA represents the limit of geographical distribution for 104 species; 38% of the total species checklist. For 35 species the archipelago is the northern limit, and for 47 species it is the southernmost point of distribution (fig. 3). From the listing, we have range extensions for 19 species. For 9 species, this represents the northernmost documented record, and for 10 species the southernmost record (table 3).

According to the geographic distribution information of all the species, we found 14 distribution patterns; these included one or more biogeographic provinces (fig. 4). The distribution ranges of 95% of the species comprise two or more biogeographic provinces. The best-represented distribution in number of species was the Oregonian-San Diegan, with 46 species. The distribution pattern Aleutian-San Diegan was represented with 25 species.

The presence of 10 endemic species to the San Diegan province was recorded (fig. 4), including: the lined clingfish (*Gobiesox eugrammus*), the yellowchin sculpin (*Icelinus quadriseriatus*), the southern clingfish (*Rimicola dimorpha*), the Guadalupe blenny (*Starksia guadalupae*) the chocolate pipefish (*Syngnathus euchrous*), the tripefin poacher (*Xeneretmus ritteri*), the island kelpfish (*Alloclinus holderi*), the California moray (*Gymnothorax mordax*), the

TABLE 2

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015).

*Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum record, 3 = Literature; **Data from field surveys;

***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province,

CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province,

POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific,

EP = Eastern Pacific, AA = Amphianmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
MYXINI											
MYXINIFORMES											
MYXINIDAE											
			<i>Eptatretus deani</i> (Evermann & Goldsborough 1907)	Black hagfish	2	2		LACM, SIO		Southern limit	AL-SD
			<i>Eptatretus mcconnaugheyi</i> (Wisner & McMillan 1990)	Shorthead hagfish	3	3				Southern limit	SD-CZ
			<i>Eptatretus stoutii</i> (Lockington 1878)	Pacific hagfish	2	2		LACM, SIO			OR-SD
CHONDRICHTHYES											
HEXANCHIFORMES											
HEXANCHIDAE											
			<i>Notorynchus cepedianus</i> (Péron 1807)	Broadnose sevengill shark			1		S		CG
HETERODONTIFORMES											
HETERODONTIDAE											
			<i>Heterodontus francisci</i> (Girard 1855)	Horn shark	1, 2	1	1	CICIMAR, LACM	S		OR-CZ
			<i>Heterodontus mexicanus</i> (Taylor & Castro-Aguirre 1972)	Mexican horn shark	1, 3	3	1		S		MX-PA
LAMNIFORMES											
LAMNIDAE											
			<i>Isurus oxyrinchus</i> (Rafinesque 1810)	Shortfin mako			1		S		CG
CARCHARINIFORMES											
SCYLIORHINIDAE											
			<i>Cephaloscyllium ventriosum</i> (Garman 1880)	Swell shark		2		SIO			OR-CH
TRIAKIDAE											
			<i>Galeorhinus galeus</i> (Linnaeus 1758)	Tope		2		IGUNAM, SIO			CG
			<i>Mustelus californicus</i> (Gill 1864)	Gray smoothhound	2			CICIMAR			OR-CZ
			<i>Mustelus lunulatus</i> (Jordan & Gilbert 1882)	Sicklefin smoothhound		2		SIO			SD-CH
			<i>Triakis semifasciata</i> (Girard 1855)	Leopard shark		2		CICIMAR, SIO			OR-MX
CARCHARHINIDAE											
			<i>Carcharhinus brachyurus</i> (Günther 1870)	Narrowtooth shark		2		IGUNAM, SIO			CG
SPHYRNIDAE											
			<i>Sphyrna zygaena</i> (Linnaeus 1758)	Smooth hammerhead	3						CT
			<i>Sphyrna</i> sp.				1		S		
SQUATINIFORMES											
SQUATINIDAE											
			<i>Squatina californica</i> (Ayres 1859)	Pacific angelshark	1		1		S		EP

(continued)

TABLE 2 (Continued)

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CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
CHONDRICHTHYES (continued)											
RAJIFORMES											
RAJIDAE											
			<i>Raja inornata</i> (Jordan & Gilbert 1881)	California skate	2			CAS, LACM			AL-CZ
			<i>Raja stellulata</i> (Jordan & Gilbert 1880)	Starry skate	3					Southern limit	NEP
RHINOBATIDAE											
			<i>Rhinobatos productus</i> (Ayres 1854)	Shovelnose guitarfish	2			LACM			OR-MX
			<i>Zapteryx exasperata</i> (Jordan & Gilbert 1880)	Banded guitarfish	1	1	1		S		SD-PA
MYLIOBATIFORMES											
MYLIOBATIDAE											
			<i>Myliobatis californica</i> (Gill 1865)	Bat ray	1				S		OR-MX- POI
UROLOPHIDAE											
			<i>Urobatis concentricus</i> (Osburn & Nichols 1916)	Reef stingray	1, 3				S	Northern limit	CZ-MX
			<i>Urobatis halleri</i> (Cooper 1863)	Round stingray	1, 2		1	SIO	S		OR-PA
HOLOCEPHALI											
CHIMAERIFORMES											
CHIMAERIDAE											
			<i>Hydrolagus collieri</i> (Lay & Bennett 1839)	Spotted ratfish	2, 3			CICIMAR			AL-CZ
ACTINOPTERI											
ANGUILLIFORMES											
MURAENIDAE											
			<i>Gymnothorax mordax</i> (Ayres 1859)	California moray	1, 2	1, 2		UABC, LACM, SIO	I, S		SD
CONGRIDAE											
			<i>Gnathophis cinctus</i> (Garman 1899)	Hardtail conger		2		SIO			SD-CH
NEMICHTHYIDAE											
			<i>Nemichthys scolopaceus</i> (Richardson 1848)	Slender snipe eel	2			LACM			CT
NETTASTOMATIDAE											
			<i>Facciolella equatorialis</i> (Gilbert 1891)	Dogface witch eel	2	2		SIO			SD-PA
CLUPEIFORMES											
CLUPEIDAE											
			<i>Etrumeus teres</i> (DeKay 1842)	Round herring	2, 3			CICIMAR, CMN, CAS			CG
			<i>Sardinops sagax</i> (Jenyns 1842)	Pacific sardine	1, 2, 3		1, 2		S		AL-CZ
ENGRAULIDAE											
			<i>Engraulis mordax</i> (Girard 1854)	Northern anchovy	2			CICIMAR, LACM, SIO			AL-CZ

(continued)

TABLE 2 (Continued)

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ACTINOPTERI (continued)											
OSMERIFORMES											
ARGENTINIDAE											
			<i>Argentina sialis</i> (Gilbert 1890)	Pacific argentine	2	2		CICIMAR, IBUNAM, LACM, SIO			OR-SD
MICROSTOMATIDAE											
			<i>Nansenia crassa</i> (Lavenberg 1965)	Stout argentine	2			CICIMAR		Southern limit	OR-SD
BATHYLAGIDAE											
			<i>Bathylagoides wesethi</i> (Bolin 1938)	Snubnose blacksmelt	2			CICIMAR			OR-SD
			<i>Leuroglossus stilbius</i> (Gilbert 1890)	California smoothtongue	2			CICIMAR			OR-PA
STOMIIFORMES											
GONOSTOMATIDAE											
			<i>Cyclothone acclinidens</i> (Garman 1899)	Benttooth bristlemouth	2			CICIMAR			CG
			<i>Cyclothone signata</i> (Garman 1899)	Showy bristlemouth	2			CICIMAR			EP
			<i>Diplophos taenia</i> (Günther 1873)	Pacific portholefish	2			CICIMAR			CG
STERNOPTYCHIDAE											
			<i>Argyropelecus sladeni</i> (Regan 1908)	Sladen's hatchet fish	2			CICIMAR			CG
PHOSICHTHYIDAE											
			<i>Ichthyococcus irregularis</i> (Rechnitzer & Böhlke 1958)	Bulldog lightfish	2			CICIMAR			NEP
			<i>Vinciguerra lucetia</i> (Garman 1899)	Panama lightfish	2			IBUNAM, CICIMAR			OR-CH
STOMIIDAE											
			<i>Idiacanthus antrostomus</i> (Gilbert 1890)	Pacific blackdragon	2			CICIMAR			TEP
			<i>Stomias atriventer</i> (Garman 1899)	Blackbelly dragonfish	2			CICIMAR		Northern limit	SD-CH
AULOPIIFORMES											
SCOPELARCHIDAE											
			<i>Scopelarchus guentheri</i> (Alcock 1896)	Staring pearleye	2			CICIMAR			CT
			<i>Scopelarchoides nicholsi</i> (Parr 1929)	Pearleye	3					Northern limit	SD-CH
SYNODONTIDAE											
			<i>Synodus lacertinus</i> (Gilbert 1890)	Calico lizardfish	3						SD-CH- POI
			<i>Synodus lucioceps</i> (Ayes 1855)	California lizardfish	2	2		IBUNAM, CICIMAR, LACM, SIO		Southern limit	OR-CZ
PARALEPIDIDAE											
			<i>Actozenus risso</i> (Bonaparte 1840)	White barracudina	2			CICIMAR		Southern limit	CG
			<i>Lestidiops ringens</i> (Jordan & Gilbert 1880)	Slender barracudina	2			CICIMAR, LACM		Southern limit	OR-SD

(continued)

TABLE 2 (Continued)

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ACTINOPTERI (continued)											
MYCTOPHIFORMES											
MYCTOPHIDAE											
			<i>Ceratoscopelus townsendi</i> (Eigenmann & Eigenmann 1889)	Dogtooth lampfish	2			CICIMAR			CG
			<i>Diogenichthys atlanticus</i> (Tåning 1928)	Longfin lanternfish	2			CICIMAR			CG
			<i>Diogenichthys laternatus</i> (Garman 1899)	Diogenes lanternfish	2			CICIMAR			SD-CH
			<i>Electrona risso</i> (Cocco 1829)	Electric lanternfish	2			CICIMAR			CG
			<i>Gonichthys tenuiculus</i> (Garman 1899)	Slendertail lanternfish	2			CICIMAR			SD-CH
			<i>Hygophum atratum</i> (Garman 1899)	Thickhead flashlightfish	2			CICIMAR			CZ
			<i>Hygophum reinhardtii</i> (Lütken 1892)	Reinhardt's lanternfish	2			CICIMAR			AA
			<i>Lampadena urophaos</i> (Paxton 1963)	Sunbeam lampfish	2, 3			CICIMAR			AA
			<i>Loweina rara</i> (Lütken 1892)	Laura's lanternfish	2			CICIMAR			CG
			<i>Myctophum nitidulum</i> (Garman 1899)	Pearly lanternfish	2			CICIMAR			CG
			<i>Nannobranchium idostigma</i> (Parr 1931)	Lanternfish	2			CICIMAR		Range extension North	TEP
			<i>Nannobranchium ritteri</i> (Gilbert 1915)	Broadfin lampfish	2			CICIMAR		Southern limit	NEP
			<i>Notolychnus valdiviae</i> (Brauer 1904)	Topside lampfish	2			CICIMAR			CT
			<i>Protomyctophum crockeri</i> (Bolin 1939)	California flashlightfish	2			CICIMAR			NP
			<i>Symbolophorus californiensis</i> (Eigenmann & Eigenmann 1889)	Bigfin lanternfish	2, 3			CICIMAR		Southern limit	NP
			<i>Triphoturus mexicanus</i> (Gilbert 1890)	Mexican lampfish	2			CICIMAR			AL-MX
LAMPRIFORMES											
TRACHIPTERIDAE											
			<i>Zu cristatus</i> (Bonelli 1820)	Scalloped ribbonfish	2			SIO			CG
GADIFORMES											
MORIDAE											
			<i>Physiculus rastrelliger</i> (Gilbert 1890)	Hundred-fathom codling	2			SIO			OR-PA
MERLUCCIIDAE											
			<i>Merluccius productus</i> (Ayres 1855)	Pacific hake	2			CICIMAR, SIO			AL-MX

(continued)

TABLE 2 (Continued)

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ACTINOPTERI (continued)											
OPHIDIIFORMES											
OPHIDIIDAE											
			<i>Chilara taylori</i> (Girard 1858)	Spotted cusk-eel	2			LACM, SIO			OR-PA
			<i>Lepophidium negropinna</i> (Hildebrand & Barton 1949)	Specklefin cusk-eel	2			CICIMAR, SIO		Northern limit	TEP
			<i>Lepophidium prorates</i> (Jordan & Bollman 1890)	Prowspine cusk-eel	2			LACM		Range extension North	TEP
			<i>Lepophidium stigmatistium</i> (Gilbert 1890)	Mexican cusk-eel	3					Northern limit	SD-CZ
			<i>Lepophidium</i> sp.		2			LACM			
			<i>Ophidion galeoides</i> (Gilbert 1890)	Spotfin cusk-eel	3					Northern limit	SD-PA
			<i>Ophidion scrippsae</i> (Hubbs 1916)	Basketweave cusk-eel	2			CICIMAR, CAS, LACM, SIO			OR-SD
BATRACHOIDIFORMES											
BATRACHOIDIDAE											
			<i>Porichthys myriaster</i> (Hubbs & Schultz 1939)	Specklefin midshipman	2			CICIMAR, SIO			OR-PA
			<i>Porichthys notatus</i> (Girard 1854)	Plainfin midshipman	2			CAS, IBUNAM, LACM, SIO			OR-SD
GOBIESOCIFORMES											
GOBIESOCIDAE											
			<i>Gobiesox eugrammus</i> (Briggs 1955)	Lined clingfish		2		SIO		Southern limit	SD
			<i>Gobiesox thessodon</i> (Smith 1881)	California clingfish	1, 2	1, 2	1	UABC, LACM, SIO	I		OR-SD
			<i>Rimicola dimorpha</i> (Briggs 1955)	Southern clingfish		2		SIO		Southern limit	SD
			<i>Rimicola eigenmanni</i> (Gilbert 1890)	Slender clingfish	1, 2			UABC, LACM	I		SD
ATHERINIFORMES											
ATHERINIDAE											
			<i>Leuresthes tenuis</i> (Ayres 1860)	California grunion	1, 2			UABC, SIO	I, S		OR-SD
ATHERINOPSIDAE											
			<i>Atherinops affinis</i> (Ayres 1860)	Topsmelt	1, 2	1, 2	1	UABC, CAS, LACM, SIO	I, S		AL-CZ
			<i>Atherinopsis californiensis</i> (Girard 1854)	Jacksmelt	1, 2	2		UABC, CAS, LACM, SIO	I		OR-CZ

(continued)

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ACTINOPTERI (continued)											
BELONIFORMES											
SCOMBERESOCIDAE											
			<i>Cololabis saira</i> (Brevoort 1856)	Pacific saury	2	2		CICIMAR, CAS, LACM, SIO			NP
BELONIDAE											
			<i>Platybelone argalus</i> (Lesueur 1821)	Keeltail needlefish		2		SIO		Range extension North	CT
			<i>Strongylura exilis</i> (Girard 1854)	California needlefish	2, 3			LACM, SIO			OR-CH
			<i>Tylosurus crocodilus</i> (Péron & Lesueur 1821)	Hound needlefish	1, 2		1	UABCS	S	Northern limit	CG
HEMIRAMPHIDAE											
			<i>Euleptorhamphus viridis</i> (van Hasselt 1823)	Ribbon halfbeak	2	2		SIO			TR
			<i>Hemiramphus saltator</i> (Gilbert & Starks 1904)	Longfin halfbeak	2			LACM		Range extension North	TEP
EXOCOETIDAE											
			<i>Cheilopogon heterurus</i> (Rafinesque 1810)	Blotchwing flyingfish	2		2	CICIMAR, SIO			CT
			<i>Cheilopogon pinnatibarbatus</i> (Bennett 1831)	Smallhead flyingfish	2	2	2	CAS, LACM, SIO			OR-CZ
			<i>Cypselurus</i> sp.		2			LACM			
STEPHANOBERYCIFORMES											
MELAMPHAIDAE											
			<i>Melamphaes lugubris</i> (Gilbert 1890)	Highsnout melamphid	2			CICIMAR		Southern limit	NEP
BERYCIFORMES											
HOLOCENTRIDAE											
			<i>Myripristis leiognathus</i> (Valenciennes 1846)	Panamic soldierfish	1, 2			SIO	S	Northern limit	TEP
SYNGNATHIFORMES											
CENTRISCIDAE											
			<i>Macroramphosus gracilis</i> (Lowe 1839)	Slender snipefish		2		IBUNAM, CICIMAR, LACM, SIO			CG
SYNGNATHIDAE											
			<i>Syngnathus euchrous</i> (Fritzsche 1980)	Chocolate pipefish	2			CAS, SIO		Southern limit	SD
			<i>Syngnathus exilis</i> (Osburn & Nichols 1916)	Barcheek pipefish	2, 3	2		CAS, SIO		Southern limit	OR-SD

(continued)

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ACTINOPTERI (continued)											
SCORPAENIFORMES											
SEBASTIDAE											
			<i>Sebastes atrovirens</i> (Jordan & Gilbert 1880)	Kelp rockfish	1, 2	1, 2		LACM, SIO	S	Southern limit	OR-SD
			<i>Sebastes auriculatus</i> (Girard 1854)	Brown rockfish	1	1			S		NEP
			<i>Sebastes aurora</i> (Gilbert 1890)	Aurora rockfish	3					Southern limit	NEP
			<i>Sebastes carnatus</i> (Jordan & Gilbert 1880)	Gopher rockfish			2	LACM			OR-SD
			<i>Sebastes caurinus</i> (Richardson 1844)	Copper rockfish		1, 2, 3		LACM	S	Southern limit	NEP
			<i>Sebastes chrysomelas</i> (Jordan & Gilbert 1881)	Black-and-yellow rockfish			2	LACM			OR-SD
			<i>Sebastes diploproa</i> (Gilbert 1890)	Splitnose rockfish	2, 3			SIO		Southern limit	NEP
			<i>Sebastes elongatus</i> (Ayres 1859)	Greenstriped rockfish	1, 3				S	Southern limit	NEP
			<i>Sebastes flavidus</i> (Ayres 1862)	Yellowtail rockfish	1				S	Range extension South	AL-SD
			<i>Sebastes hopkinsi</i> (Cramer 1895)	Squarespot rockfish	1	1			S	Range extension South	OR-SD
			<i>Sebastes lentiginosus</i> (Chen 1971)	Freckled rockfish	2			LACM		Southern limit	OR-SD
			<i>Sebastes macdonaldi</i> (Eigenmann & Beeson 1893)	Mexican rockfish	2			CICIMAR, LACM			SD-CZ
			<i>Sebastes melanostomus</i> (Eigenmann & Eigenmann 1890)	Blackgill rockfish	3					Southern limit	OR-SD
			<i>Sebastes miniatus</i> (Jordan & Gilbert 1880)	Vermilion rockfish		1, 2, 3		LACM	S	Southern limit	AL-SD
			<i>Sebastes paucispinis</i> (Ayres 1854)	Bocaccio rockfish	2			SIO		Range extension South	NEP
			<i>Sebastes rosaceus</i> (Girard 1854)	Rosy rockfish	2			SIO		Southern limit	OR-SD
			<i>Sebastes saxicola</i> (Gilbert 1890)	Stripetail rockfish	2			SIO			NEP
			<i>Sebastes semicinctus</i> (Gilbert 1897)	Halfbanded rockfish	2			SIO		Range extension South	OR-SD
			<i>Sebastes serranoides</i> (Eigenmann & Eigenmann 1890)	Olive rockfish		1, 2, 3		SIO	S	Southern limit	OR-SD
			<i>Sebastes serriceps</i> (Jordan & Gilbert 1880)	Treefish	1, 2, 3			LACM	S	Southern limit	OR-SD
			<i>Sebastes</i> sp.	Rockfish	1	1			S		
			<i>Sebastes umbrosus</i> (Jordan & Gilbert 1882)	Honeycomb rockfish		2		LACM		Southern limit	OR-SD

(continued)

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CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
SCORPAENIFORMES (continued)											
SCORPAENIDAE											
			<i>Pontinus vaughani</i> (Barnhart & Hubbs 1946)	Spotback scorpionfish	1, 2			SIO	S	Range extension North	CZ-POI
			<i>Scorpaena guttata</i> (Girard 1854)	California scorpionfish	1, 2			UABC, CICIMAR, LACM, SIO	I, S		SD-CZ
			<i>Scorpaenodes xyris</i> (Jordan & Gilbert 1882)	Rainbow scorpionfish	2	2		LACM, SIO			SD-PA-POI
EPINEPHELIDAE											
			<i>Mycteroperca rosacea</i> (Streets 1877)	Leopard grouper			1		S		SD-MX
TRIGLIDAE											
			<i>Prionotus rusarius</i> (Gilbert & Starks 1904)	Rough searobin	2			CICIMAR		Range extension North	SD-CH
			<i>Prionotus stephanophrys</i> (Lockington 1881)	Lumptail searobin	2			CAS, LACM			OR-CH
PERCIFORMES											
POLYPRIONIDAE											
			<i>Stereolepis gigas</i> (Ayres 1859)	Giant seabass			1		S		SD-CZ
SERRANIDAE											
			<i>Alphestes immaculatus</i> (Breder 1936)	Pacific mutton hamlet		1	1			Northern limit	TEP
			<i>Epinephelus labriformis</i> (Jenyns 1840)	Flag cabrilla	1, 3	1, 3			S		SD-PA-POI
			<i>Paralabrax auroguttatus</i> (Walford 1936)	Goldspotted sand bass	1, 2, 3			LACM	S	Northern limit	CZ
			<i>Paralabrax clathratus</i> (Girard 1854)	Kelp bass	1, 2	1, 2	1, 2	CICIMAR, LACM, SIO	S		OR-SD
			<i>Paralabrax maculatofasciatus</i> (Steindachner 1868)	Spotted sand bass	2			CICIMAR			OR-CZ
			<i>Paralabrax nebulifer</i> (Girard 1854)	Barred sand bass	1, 2	1, 2	1	CICIMAR, LACM, SIO	S		OR-MX
			<i>Paranthias colonus</i> (Valenciennes 1846)	Pacific creolefish		2	1	LACM	S	Northern limit	TEP
			<i>Pronotogrammus multifasciatus</i> (Gill 1863)	Threadfin bass	2			CICIMAR			SD-PA-POI
			<i>Serranus psittacinus</i> (Valenciennes 1846)	Barred serrano	1, 3				S	Northern limit	TEP

(continued)

TABLE 2 (Continued)

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CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
PERCIFORMES (continued)											
APOGONIDAE											
			<i>Apogon atricaudus</i> (Jordan & McGregor 1898)	Plain cardinalfish	2, 3			CICIMAR			SD-CZ
			<i>Apogon guadalupensis</i> (Osburn & Nichols 1916)	Guadalupe cardinalfish		2		LACM, SIO			SD-CZ
			<i>Apogon pacificus</i> (Herre 1935)	Pink cardinalfish		1, 2, 3		SIO	S		SD-CH-POI
			<i>Apogon retrosella</i> (Gill 1862)	Barspot cardinalfish	1, 2, 3	1, 2, 3	1	LACM, SIO	S	Northern limit	TEP
MALACANTHIDAE											
			<i>Caulolatilus princeps</i> (Jenyns 1840)	Ocean whitefish	1, 2	1, 2	1, 2	LACM, SIO	S		EP
CARANGIDAE											
			<i>Caranx caballus</i> (Günther 1868)	Green jack			1		S		SD-CH
			<i>Chloroscombrus orqueta</i> (Jordan & Gilbert 1883)	Pacific bumper	2			CICIMAR			SD-CH
			<i>Decapterus muroadsi</i> (Temminck & Schlegel 1844)	Amberstripe scad	2	2		LACM		Northern limit	TR
			<i>Seriola lalandi</i> (Valenciennes 1833)	Yellowtail jack	1, 2	1	1, 2	CICIMAR, LACM, SIO	S		CT
			<i>Trachurus symmetricus</i> (Ayres 1855)	Pacific jack mackerel	1	1, 2		CICIMAR, LACM, SIO	S		AL-CZ
			<i>Uraspis secunda</i> (Poey 1860)	Whitemouth jack		2		SIO			CG
CORYPHAENIDAE											
			<i>Coryphaena hippurus</i> (Linnaeus 1758)	Dolphinfish	2		1	CICIMAR, SIO	S		CT
CARISTIIDAE											
			<i>Caristius macropus</i> (Bellotti 1903)	Bigmouth manefish	3					Southern limit	NEP
GERREIDAE											
			<i>Euclinostomus dowii</i> (Gill 1863)	Pacific spotfin mojarra		2		SIO			SD-CH
HAEMULIDAE											
			<i>Anisotremus davidsonii</i> (Steindachner 1876)	Sargo	1, 2	1, 2	1	CICIMAR, LACM, SIO	S		SD-CZ
			<i>Anisotremus interruptus</i> (Gill 1862)	Burrito grunt	1				S	Northern limit	TEP
			<i>Orthopristis reddingi</i> (Jordan & Richardson 1895)	Bronzestriped grunt	2, 3			CAS		Northern limit	SD-MX
			<i>Xenistius californiensis</i> (Steindachner 1876)	Salema	1	1			S		OR-PA

(continued)

TABLE 2 (Continued)

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ACTINOPTERI (continued)											
PERCIFORMES (continued)											
SPARIDAE											
			<i>Calamus brachysomus</i> (Lockington 1880)	Pacific porgy		2	1	SIO	S		SD-CH
SCIAENIDAE											
			<i>Cheilotrema saturnum</i> (Girard 1858)	Black croaker		2		SIO			SD-CZ
			<i>Genyonemus lineatus</i> (Ayres 1855)	White croaker	2			SIO			OR-SD
			<i>Larimus acclivis</i> (Jordan & Bristol 1898)	Steeplined drum	3					Northern limit	TEP
			<i>Pareques</i> sp.	Croaker	1	1, 2			S		
			<i>Seriphus politus</i> (Ayres 1860)	Queenfish	2			SIO			OR-CZ
			<i>Umbrina roncadorensis</i> (Jordan & Gilbert 1882)	Yellowfin croaker	2			SIO			SD-CZ
KYPHOSIDAE											
			<i>Girella nigricans</i> (Ayres 1860)	Opaleye	1, 2	1, 2	1, 2	UABC, LACM, SIO	I, S		SD-CZ
			<i>Kyphosus azureus</i> (Jenkins & Evermann 1889)	Zebra perch	1, 2		1, 2	UABC, CICIMAR	I, S		OR-CZ
			<i>Medialuna californiensis</i> (Steindachner 1876)	Halfmoon	1, 2	1, 2	1, 2	IBUNAM, CICIMAR, LACM, SIO	S		AL-CZ
CHAETODONTIDAE											
			<i>Chaetodon humeralis</i> (Günther 1860)	Threebanded butterflyfish		2		SIO		Northern limit	SD-CH
			<i>Johndrandallia nigrirostris</i> (Gill 1862)	Barberfish	1, 3	3			S	Northern limit	TEP
			<i>Prognathodes falcifer</i> (Hubbs & Rehnitz 1958)	Scythe butterflyfish	2	1, 2		LACM, SIO	S		SD-CZ
MUGILIDAE											
			<i>Mugil curema</i> (Valenciennes 1836)	White mullet			1, 2	UABC	I		CT
POMACANTHIDAE											
			<i>Pomacanthus zonipectus</i> (Gill 1862)	Cortez angelfish		2		SIO			TEP

(continued)

TABLE 2 (Continued)

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ACTINOPTERI (continued)											
PERCIFORMES (continued)											
EMBIOTOCIDAE											
			<i>Brachyistius frenatus</i> (Gill 1862)	Kelp surfperch	1, 2	1, 2	1	SIO	S	Southern limit	AL-SD
			<i>Embiotoca jacksoni</i> (Agassiz 1853)	Black perch	1, 2	1, 2	1, 2	CICIMAR, SIO	S		OR-SD
			<i>Embiotoca</i> sp.		2			SIO			
			<i>Hyperprosopon argenteum</i> (Gibbons 1854)	Walleye surfperch	2			SIO		Southern limit	OR-SD
			<i>Micrometrus minimus</i> (Gibbons 1854)	Dwarf perch	2			SIO		Southern limit	OR-SD
			<i>Phanerodon atripes</i> (Jordan & Gilbert 1880)	Sharpnose seaperch	1	1, 2		SIO	S	Southern limit	OR-SD
			<i>Phanerodon furcatus</i> (Girard 1854)	White seaperch	1	1			S	Range extension South	AL-SD
			<i>Rhacochilus toxotes</i> (Agassiz 1854)	Rubberlip seaperch	1, 2	1, 2		LACM, SIO	S	Southern limit	OR-SD
			<i>Rhacochilus vacca</i> (Girard 1855)	Pile perch	2		1	LACM	S	Range extension South	NEP
			<i>Zalemnius rosaceus</i> (Jordan & Gilbert 1880)	Pink seaperch	2			CAS, LACM, SIO		Range extension South	OR-CZ
POMACENTRIDAE											
			<i>Abudefduf troschelii</i> (Gill 1862)	Panamic sergeant major	1, 2	1	1	UABC	I, S	Northern limit	SD-CH-POI
			<i>Azurina hirundo</i> (Jordan & McGregor 1898)	Swallow damselfish		2, 3		KU, SIO			SD-CZ
			<i>Chromis alta</i> (Greenfield & Woods 1980)	Silverstripe chromis	1, 2	1, 2		KU, SIO	S		SD-CH-POI
			<i>Chromis atrilobata</i> (Gill 1862)	Scissortail chromis	1, 2	2		SIO	S	Northern limit	TEP
			<i>Chromis punctipinnis</i> (Cooper 1863)	Blacksmith	1, 2	1, 2	1, 2	CICIMAR, KU, LACM, SIO	S		OR-SD
			<i>Hypsypops rubicundus</i> (Girard 1854)	Garibaldi	1, 2	1, 2	1, 2	UABC, CICIMAR, LACM, SIO	I, S		SD-CZ
			<i>Stegastes flavilatus</i> (Gill 1862)	Beaubrummel	1, 3				S	Northern limit	TEP
			<i>Stegastes leucorus</i> (Gilbert 1892)	Whitetail damselfish		1, 2		SIO	S		CZ-MX
			<i>Stegastes rectifraenum</i> (Gill 1862)	Cortez damselfish		2		LACM, SIO			SD-MX

(continued)

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ACTINOPTERI (continued)											
PERCIFORMES (continued)											
LABRIDAE											
			<i>Bodianus diplotaenia</i> (Gill 1862)	Mexican hogfish	1, 2, 3	2		LACM	S	Northern limit	SD-CH-POI
			<i>Halichoeres dispilus</i> (Günther 1864)	Chameleon wrasse	1	1, 2		SIO	S	Northern limit	TEP
			<i>Halichoeres melanotis</i> (Gilbert 1890)	Golden wrasse	3	1, 3			S	Northern limit	TEP
			<i>Halichoeres notospilus</i> (Günther 1864)	Banded wrasse	1, 2		1	UABC	I, S	Range extension North	TEP
			<i>Halichoeres semicinctus</i> (Ayres 1859)	Rock wrasse	1, 2	1, 2	1, 2	UABC, CICIMAR, CAS, LACM, SIO	I, S		SD-CZ
			<i>Oxyjulis californica</i> (Günther 1861)	Señorita	1	1, 2	1	SIO	S		OR-SD
			<i>Semicossyphus pulcher</i> (Ayres 1854)	California sheephead	1, 2	1, 2	1, 2	LACM, SIO	S		OR-CZ
			<i>Thalassoma lucasanum</i> (Gill 1862)	Cortez rainbow wrasse	1	1			S	Northern limit	TEP
			SCARIDAE								
			<i>Nicholsina denticulata</i> (Evermann & Radcliffe 1917)	Loosetooth parrotfish	1, 3	1, 3			S		SD-PA-POI
			ZOARCIDAE								
			<i>Lycanema barbatum</i> (Gilbert 1896)	Bearded eelpout	2	2		SIO		Southern limit	OR-SD
			CHIASMODONTIDAE								
			<i>Chiasmodon niger</i> (Johnson 1864)	Black swallower	2			CICIMAR		Range extension South	CG
			URANOSCOPIDAE								
			<i>Kathetostoma averruncus</i> (Jordan & Bollman 1890)	Smooth stargazer	2	2		UF, LACM, SIO			SD-CH
			TRIPTERYGIIDAE								
			<i>Enneanectes carminalis</i> (Jordan & Gilbert 1882)	Carmine triplefin		1, 2		LACM	S	Northern limit	TEP
			<i>Enneanectes reticulatus</i> (Allen & Robertson 1991)	Flag triplefin		2		SIO		Northern limit	CZ

(continued)

TABLE 2 (Continued)

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ACTINOPTERI (continued)											
PERCIFORMES (continued)											
LABRISOMIDAE											
			<i>Alloclinus holderi</i> (Lauderbach 1907)	Island kelpfish	1, 2	1, 2	1	UABC, LACM, SIO	S		SD
			<i>Labrisomus multiporosus</i> (Hubbs 1953)	Porehead blenny	1, 2		1, 2	UABC	I	Northern limit	TEP
			<i>Labrisomus</i> sp.	Blenny		2		SIO			
			<i>Labrisomus xanti</i> (Gill 1860)	Largemouth blenny	1, 2		1	UABC, LACM	I	Northern limit	TEP
			<i>Paraclinus integripinnis</i> (Smith 1880)	Reef finspot	1, 2	1, 2	2	UABC, LACM, SIO	I		OR-SD
			<i>Starksia guadalupae</i> (Rosenblatt & Taylor 1971)	Guadalupe blenny		2		LACM			SD
			CLINIDAE								
			<i>Gibbonsia elegans</i> (Cooper 1864)	Spotted kelpfish	1, 2	1, 2	1, 2	UABC, LACM, SIO	I		OR-SD
			<i>Gibbonsia montereyensis</i> (Hubbs 1927)	Crevice kelpfish	1, 2	1, 2	1, 2	UABC, SIO	I	Range extension South	AL-SD
			<i>Heterostichus rostratus</i> (Girard 1854)	Giant kelpfish	1, 2	1, 2	1, 2	UABC, CAS, LACM, SIO	I, S		OR-SD
			CHAENOPSIDAE								
			<i>Neoclinus blanchardi</i> (Girard 1858)	Sarcastic fringehead	2, 3			LACM		Southern limit	OR-SD
			DACTYLOSCOPIIDAE								
			<i>Gillellus semicinctus</i> (Gilbert 1890)	Halfbanded stargazer	2			SIO		Northern limit	TEP
			BLENNIIDAE								
			<i>Hypsobleinnius gilberti</i> (Jordan 1882)	Rockpool blenny	1, 2		1, 2	UABC	I		SD
			<i>Hypsobleinnius jenkinsi</i> (Jordan & Evermann 1896)	Mussel blenny	1, 2	1, 2		UABC, SIO	I		SD-CZ
			<i>Hypsobleinnius gentilis</i>	Bay blenny	1		1		I		SD-CZ
			<i>Ophiobleinnius steindachneri</i> (Jordan & Evermann 1898)	Panamic fanged blenny	1, 2		1, 2	UABC	I, S		TEP
			<i>Plagiotremus azaleus</i> (Jordan & Bollman 1890)	Sabertooth blenny	1, 3				S		SD-PA- POI
			CALLIONYMIDAE								
			<i>Synchiropus atrilabiatus</i> (Garman 1899)	Blacklip dragonet	3						SD-CH- POI
			ELEOTRIDAE								
			<i>Eleotris picta</i> (Kner 1863)	Spotted sleeper	2			CICIMAR		Range extension North	TEP

(continued)

TABLE 2 (Continued)

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ACTINOPTERI (continued)											
PERCIFORMES (continued)											
GOBIIDAE											
			<i>Acanthogobius flavimanus</i> (Temminck & Schlegel 1845)	Yellowfin goby	3					Range extension South	NWP
			<i>Bathygobius ramosus</i> (Ginsburg 1947)	Panamic frillfin	1, 2		1	UABC	I	Range extension North	TEP
			<i>Lepidogobius lepidus</i> (Girard 1858)	Bay goby	3					Southern limit	EP
			<i>Lythrypnus dalli</i> (Gilbert 1890)	Bluebanded goby	1, 2	1, 2	1	CICIMAR, LACM, SIO	S		SD-PA-POI
			<i>Lythrypnus zebra</i> (Gilbert 1890)	Zebra goby	2	1, 2	2	LACM, SIO	S		SD-CZ
			<i>Rhinogobius nicholsii</i> (Bean 1882)	Blackeye goby	1, 2, 3	1	1	LACM	S	Southern limit	AL-SD
LUVARIDAE											
			<i>Luarus imperialis</i> (Rafinesque 1810)	Louvar	2			SIO			CG
SPHYRAENIDAE											
			<i>Sphyræna argentea</i> (Girard 1854)	Pacific barracuda	2		1	CICIMAR, SIO	S		NEP
			<i>Sphyræna lucasana</i> (Gill 1863)	Cortez barracuda	1, 2, 3			UABCS	S	Northern limit	CZ-MX
TRICHIURIDAE											
			<i>Lepidopus fitchi</i> (Rosenblatt & Wilson 1987)	Pacific scabbardfish	2			CICIMAR, LACM			OR-CH
SCOMBRIDAE											
			<i>Sarda chiliensis</i> (Cuvier 1832)	Pacific bonito	2		2	SIO			AL-PA
			<i>Scomber japonicus</i> (Houttuyn 1782)	Pacific chub mackerel	2			CICIMAR, SIO			TR
STROMATEIDAE											
			<i>Pepnilus simillimus</i> (Ayres 1860)	Pacific pompano	3						OR-CZ
COTTIFORMES											
HEXAGRAMMIDAE											
			<i>Ophiodon elongatus</i> (Girard 1854)	Lingcod			1		S	Range extension South	AL-SD
			<i>Zaniolepis frenata</i> (Eigenmann & Eigenmann 1889)	Shortspine combfish	2	2		LACM, SIO			OR-CZ
			<i>Zaniolepis latipinnis</i> (Girard 1858)	Longspine combfish	2			LACM, SIO			OR-SD

(continued)

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CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
COTTIFORMES (continued)											
COTTIDAE											
			<i>Chitonotus pugetensis</i> (Steindachner 1876)	Soughback sculpin	2	2		LACM			NEP
			<i>Clinocottus analis</i> (Girard 1858)	Woolly sculpin	1, 2	1, 2	1, 2	UABC, LACM, SIO	I		OR-SD
			<i>Icelinus cavifrons</i> (Gilbert 1890)	Pit-head sculpin	2			LACM		Southern limit	OR-SD
			<i>Icelinus fimbriatus</i> (Gilbert 1890)	Fringed sculpin	3					Range extension South	OR-SD
			<i>Icelinus quadriseriatus</i> (Lockington 1880)	Yellowchin sculpin	2, 3			CAS, LACM, SIO			OR-SD
			<i>Icelinus tenuis</i> (Gilbert 1890)	Spotfin sculpin		2, 3		LACM		Southern limit	NEP
			<i>Ruscarius creaseri</i>	Roughcheek sculpin	2			SIO		Southern limit	OR-SD
			<i>Scorpaenichthys marmoratus</i> (Ayres 1854)	Cabezon	1, 2	2	1	UABC, LACM, SIO	I, S		AL-SD
ANOPOLOMATIDAE											
			<i>Anoplopoma fimbria</i> (Pallas 1814)	Sablefish		2, 3		LACM		Southern limit	NEP
AGONIDAE											
			<i>Agonopsis sterletus</i> (Gilbert 1898)	Southern spearnose poacher	2			LACM, SIO		Southern limit	OR-CZ
			<i>Odontopyxis trispinosa</i> (Lockington 1880)	Pygmy poacher	2			LACM		Southern limit	NEP
			<i>Xeneretmus ritteri</i> (Gilbert 1915)	Stripefin poacher	3					Southern limit	SD
PLEURONECTIFORMES											
PARALICHTHYIDAE											
			<i>Citharichthys fragilis</i> (Gilbert 1890)	Gulf sanddab	2			CAS, SIO			SD-CZ
			<i>Citharichthys sordidus</i> (Girard 1854)	Pacific sanddab	2			CICIMAR, LACM, SIO			AL-CZ
			<i>Citharichthys</i> sp.		2			LACM			
			<i>Citharichthys stigmaeus</i> (Jordan & Gilbert 1882)	Speckled sanddab	2	2		CICIMAR, LACM, SIO			AL-CZ
			<i>Citharichthys xanthostigma</i> (Gilbert 1890)	Longfin sanddab	2	2		CICIMAR, SEMAR, CAS, LACM, SIO			SD-PA
			<i>Etropus crossotus</i> (Jordan & Gilbert 1882)	Fringed flounder	2			CICIMAR		Northern limit	AA
			<i>Hippoglossina stomata</i> (Eigenmann & Eigenmann 1890)	Bigmouth sole	2			CICIMAR, LACM			OR-CZ
			<i>Paralichthys californicus</i> (Ayres 1859)	California halibut	1, 2			IBUNAM, CICIMAR	S		OR-SD
			<i>Xystreureys liolepis</i> (Jordan & Gilbert 1880)	Fantail sole	2			LACM, SIO			OR-CZ

(continued)

TABLE 2 (Continued)

Systematic list of fishes of Cedros Archipelago, México, Northeastern Pacific. Classification according to Eschmeyer (2015).

*Common name sensu Page et al. (2013); 1 = Fiel record, 2 = Museum record, 3 = Literature; **Data from field surveys;

***BA = Biogeographic affinity: AL = Aleutian province, OR = Oregonian province, SD = San Diegan province,

CZ = Cortez province, MX = Mexican province, PA = Panamic province, PE = Peruvian province,

POI = Pacific Oceanic Islands province, CG = Circumglobal, CT = Circumtropical, NWP = Northwestern Pacific,

EP = Eastern Pacific, AA = Amphianmerican. sensu Love et al. (2005) and Robertson and Allen (2015).

CLASS	ORDER	FAMILY	Scientific name	Common name*	Cedros	San Benito	Natividad	Museum data	Habitat**	Notes	BA***
ACTINOPTERI (continued)											
PLEURONECTIFORMES (continued)											
BOTHIDAE											
			<i>Monolene asaedai</i> (Clark 1936)	Dark flounder	3					Range extension North	CZ-PA
PLEURONECTIDAE											
			<i>Glyptocephalus zachirus</i> (Lockington 1879)	Rex sole	3					Southern limit	NEP
			<i>Lyopsetta exilis</i> (Jordan & Gilbert 1880)	Slender sole	2	2		CICIMAR, SIO			AL-SD
			<i>Parophrys vetulus</i> (Girard 1854)	English sole	2			SIO		Southern limit	NEP
			<i>Pleuronichthys coenosus</i> (Girard 1854)	C-O sole			2	LACM		Southern limit	AL-SD
			<i>Pleuronichthys decurrens</i> (Jordan & Gilbert 1881)	Curlfin sole	2			CAS		Southern limit	AL-SD
			<i>Pleuronichthys ritteri</i> (Starks & Morris 1907)	Spotted turbot	2			LACM			OR-SD
			<i>Pleuronichthys verticalis</i> (Jordan & Gilbert 1880)	Hornyhead turbot	2		2	CICIMAR, LACM, SIO			OR-CZ
CYNOGLOSSIDAE											
			<i>Symphurus atricaudus</i> (Jordan & Gilbert 1880)	California tonguefish	2			CICIMAR, CAS, LACM, SIO			OR-PA
TETRAODONTIFORMES											
BALISTIDAE											
			<i>Sufflamen verres</i> (Gilbert & Starks 1904)	Orangeside triggerfish	1, 3				S	Northern limit	TEP
TETRAODONTIDAE											
			<i>Sphoeroides lobatus</i> (Steindachner 1870)	Longnose puffer			1		S		SD-CH
DIODONTIDAE											
			<i>Diodon holocanthus</i> (Linnaeus 1758)	Balloonfish	2			CICIMAR			CT

TABLE 3

Fish species that present range extension in their distribution in Cedros Archipelago. Reference corresponds to the most updated geographic distribution reference for these species. *Represents field records in this study.

Scientific Name	Reference	Extension to:	Northern End	Southern End
<i>Bathygobius ramosus</i> *	Robertson and Allen, 2015	North	24.55 N	06.11 S
<i>Eleotris picta</i>	Love et al. 2005	North	23.05 N	09.25 S
<i>Halichoeres notospilus</i> *	Robertson and Allen, 2015	North	26.13 N	06.93 S
<i>Hemiramphus saltator</i>	Love et al. 2005	North	26.01 N	09.25 S
<i>Lepophidium prorates</i>	Love et al. 2005	North	27.01 N	05.10 S
<i>Monolene asaedai</i>	Love et al. 2005	North	24.51 N	08.50 N
<i>Nannobranchium idostigma</i>	Love et al. 2005	North	27.20 N	35.75 S
<i>Platybelone argalus</i>	Love et al. 2005	North	26.10 N	35.75 S
<i>Prionotus ruscarius</i>	Love et al. 2005	North	26.00 N	35.75 S
<i>Acanthogobius flavimanus</i>	Love et al. 2005	South	52.10 N	32.68 N
<i>Chiasmodon niger</i>	Love et al. 2005	South	47.33 N	32.43 N
<i>Gibbonsia montereyensis</i> *	Love et al. 2005	South	53.75 N	29.05 N
<i>Icelinus fimbriatus</i>	Love et al. 2005	South	53.50 N	32.71 N
<i>Ophiodon elongatus</i> *	Love et al. 2005	South	55.00 N	29.61 N
<i>Phanerodon furcatus</i> *	Love et al. 2005	South	40.60 N	29.60 N
<i>Rhacochilus vacca</i> *	Love et al. 2005	South	53.75 N	29.03 N
<i>Sebastes flavidus</i>	Love et al. 2005	South	59.50 N	30.49 N
<i>Sebastes hopkinsi</i> *	Love et al. 2005	South	43.75 N	29.03 N
<i>Sebastes paucispinis</i>	Love et al. 2005	South	59.50 N	29.08 N

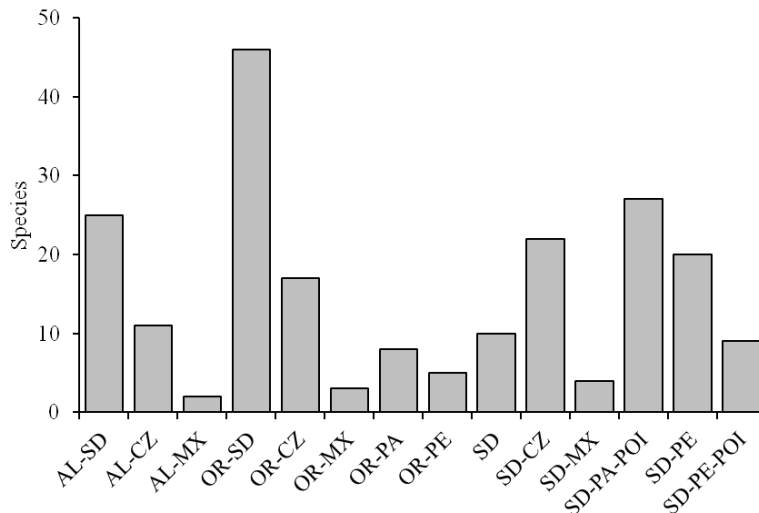


Figure 4. Distribution patterns of fish species of the Cedros Archipelago. (AL = Aleutian province, OR = Oregonian province, SD = San Diegan province, CZ = Cortez province, MX = Mexican province, PA = Panamic Province, PE = Peruvian province, POI = Pacific Oceanic Islands province)

rockpool blenny (*Hypsoblennius gilberti*), and the slender clingfish (*Rimicola eigenmanni*). Of these, the last four species were recorded in the field surveys at the CEA.

DISCUSSION

A comprehensive systematic checklist of the CEA, with a total of 269 species, is presented here. The biogeographic relationships of the fish assemblages from the CEA showed a separation from its counterparts in northern Baja California and California. Most of the fish community at the CEA (50%) has a temperate affinity (warm-temperate and cold-temperate) and the CEA

represents the distribution limit for 106 species (40% of the species reported). The distribution range extension for 19 species is documented.

Based on these results, the archipelago has high species richness, 50% of the known species for the entire San Diegan province (Miller and Lea 1976; Horn et al. 2006) and 15% of those in the Cortez province (Hastings et al. 2010; Palacios-Salgado et al. 2012), are reported in this small insular territory. The CEA might be richer than coastal lagoons and bays on the Baja California Peninsula (Danemann and De la Cruz-Agüero 1993; De la Cruz-Agüero et al. 1994, 1996; Rosales-Casián

1996; Galván-Magaña et al. 2000) and even comparable with larger islands in the Gulf of California (155–190 spp.: Del Moral et al. 2013) and with those islands in the Tropical Eastern Pacific (203–363 spp.: Robertson and Cramer 2009; Erisman et al. 2011).

The species richness found in the CEA is the result of a blend of species consisting of 3 large groups with patterns of geographical distribution: 1) temperate species (warm and cold temperate) with limited intrusion into subtropical waters (51% of the species), 2) tropical species with limited intrusion into warm-temperate waters, and 3) tropical species with extended incursion into temperate waters of the Eastern Pacific (eurythermal species).

Field records showed greater species richness in Cedros (78 species), followed by Natividad and San Benito Islands, with 56 and 54 species, respectively. Although sampling effort is an important factor in species record accumulation, the sampled area for Cedros, Natividad, and San Benito is equivalent in number of transects, but not for sampling sites. The proximity between islands could assume a similarity in the fish assemblage, however the area of the islands may be an important factor. The perimeter of the island is an indicator of habitat availability and therefore increasing potential to provide shelter for more species (Planes et al. 2012). This relationship could not be obvious on islands with similar perimeters, however, the perimeter of Cedros is 6-fold higher than Natividad and 8-fold higher than San Benito.

The resulting nMDS (based on subtidal field surveys from eleven North-Eastern Pacific islands) shows the qualitative differences in fish composition along the CEA and the Southern California Bight islands. This analysis does not show the similarity pattern between San Benito and some of the Channel Islands (California) found by Pondella et al. (2005). A group of 24 species have the largest dissimilarities contribution (78%) between sites; most of them have a tropical affinity (e.g., *Abudefduf troschelii*, *Apogon retrosella*, *Caulolatilus princeps*, *Halichoeres semicinctus*, and *Zapterix exasperata*). The overall differences in the species richness between our field records and previous studies in San Benito (i.e., Pondella et al. 2005) may be related to the inclusion of diverse habitats in the field surveys (i.e., tidepools, and soft bottom), but also by the new records of a these tropical affinity species to the assemblage. Furthermore, transitional regions may be strongly influenced by seasonality, where environmental conditions can be dominant for one of the two converging regions (Horn et al. 2006), therefore inducing a shift in the presence of fish assemblages.

Comparisons to other islands and coastal rocky ecosystems highlight the importance of the CEA in terms of connectivity between warm-temperate and tropical regions. Nevertheless, conservation and management

mechanisms such as Marine Protected Areas, Marine Reserves, or Marine Refuges have not yet been implemented in this region to date, excluding a small Marine Reserve at Natividad Island implemented by local fishermen 2006 (Micheli et al. 2012).

The fact that the CEA represents the distribution limit of 106 species (40% of the species reported) is evidence of the biogeographic transition zone. It has been extensively documented that the biogeographic boundaries work diffusely and that their boundaries are movable in response to climatic factors (Hubbs 1960).

This study represents the southernmost distribution extension for 10 species, and the northernmost distribution extension for 9 species. These findings may be explained by the scarcity of field studies in the region, but nevertheless, previous studies (Quast 1968; Mearns 1988; Lea and Rosenblatt 2000; Pondella et al. 2005; Palacios-Salgado and Ramirez-Valdez 2011) have noted a trend of tropical species being recorded farther north of their previously recognized distribution, especially crossing Bahía Magdalena, a geographic feature traditionally recognized as a biogeographical barrier. These extensions of distribution range may represent an indicator of the warming trend observed in this biogeographic province (Pondella et al. 2005).

In addition to the range extensions documented in this study, the record of tropical affinity species that have been reported in San Diego or even farther north are included. However, most of these records have been associated with El Niño events (Mearns 1988; Lea and Rosenblatt 2000). As some of the species were abundant and recurrent at the CEA, the record of these species in the CEA would represent their northernmost stable populations.

It is important to highlight the presence of some species in the archipelago that were absent in previous studies in the peninsula (Danemann and De la Cruz-Agüero 1993; Ruiz-Campos et al. 2010). This is the case for *Thalassoma lucasanum*, *Ophioblennius steindachneri*, *Chromis atrilobata*, and *Bodianus diplotaenia*, which were recorded farther north in Guadalupe Island (Reyes-Bonilla et al. 2010). The presence of fish species in islands and their absence on the mainland has been explained before by structural habitat differences rather than oceanographic differences (Ebeling et al. 1980), and this pattern can be important to consider when seeking to set priority among conservation areas. It also highlights the record in the Mexican coast for the Yellowfin goby (*Acanthogobius flavimanus*), a native species from the Northwestern Pacific that has been reported on the coast of California (Workman and Merz 2007).

To our knowledge, the presence of endemic species has not been recognized for the CEA. The record of *Gibbonsia norae* as an endemic species of Guadalupe Island

and San Benito (Hubbs 1960; Reyes-Bonilla et al. 2010) is now accepted as a semi-isolated population of *G. montereyensis* (Stepien and Rosenblatt 1991). Even though the proximity to the mainland may partly explain this absence of endemism, it is also known that limited endemism exists in the fish fauna of the west coast of the Baja California peninsula (Hubbs 1960).

This study demonstrates the importance of complementing recent underwater surveys with historical and museum records to prepare baseline information potentially useful for the conservation and management of fish communities. The CEA plays a key role on the connectivity in the biogeographic transition zone on the Pacific coast of the Baja California Peninsula.

SUMMARY

We documented the presence of 269 fish species in the Cedros Archipelago, and 105 species were recorded during field surveys. The observed species richness at the CEA may be the result of the confluence of three biogeographic provinces in the Pacific coast of Baja California peninsula, in addition to the proximity of the archipelago to the mainland coast and past terrestrial connection with the peninsula. Although habitat heterogeneity is an important factor in this ecosystem, our biogeographical analyses allowed us to identify the representation of 14 distribution patterns in the fish assemblage.

The biogeographic transition has a significant impact on the composition of fish communities in this region. That is evident when half of the species have temperate affinity and the rest is composed of species of tropical affinity and wide distribution. In addition, the implication as a biogeographic frontier is when the archipelago represents the distribution limit for 40% of registered species. Finally, the biogeographic analysis showed the low similarity between this island and its northern counterparts, marking the beginning of the transition to a subtropical region.

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CHAPTER 2:

Asymmetry across international borders: Scientific production, research, fishery and management trends, and economic value of the critically endangered giant sea bass (*Stereolepis gigas*)

ARTURO RAMÍREZ-VALDEZ

ABSTRACT

Binational cooperation in the management of shared fish stocks is often necessary to achieve sustainability and reduce uncertainty in future scenarios. The United States (U.S.) and Mexico have recognized, through management regulations and agreements, the need for binational cooperation in managing shared marine resources; this could include sharing data, equivalent management, equitable profits, and well-managed fishery stocks. However, unilateral

management decisions are often the rule, and these can generate asymmetric management, economic disparities, and compromise neighboring populations. Here we show that a broad asymmetry in the scientific knowledge, research, fishery and management trends, the spatial distribution of fishing, regulations, and economic value of the critically endangered giant sea bass (GSB; *Stereolepis gigas*) across the U.S.-Mexico border, creates a complex scenario for resource sustainability and undermines conservation efforts. Scientific knowledge, and research investment, are 5x and 10x higher in the U.S., respectively, despite the fact that the center of the GSB's geographic distribution occurs in Mexico. Fishery trends over the last century in the U.S. and Mexico revealed that the U.S. stock collapsed approximately 50 years before the GSB fishery moratorium in 1981, and the decline of the landings by the U.S. fleet in Mexican waters prior to 1980 was likely a result of the binational regulation of the commercial fishery and did not reflect a true population collapse in Mexican waters. Landings from the Mexican fleet have averaged 50 tonnes per year over the last 60 years. A higher proportion of catches in both countries was concentrated during the spawning season, and fish-market records show that the Mexican GSB fishery is significantly composed of immature individuals (48%). While contemporary catches extend throughout the geographic distribution range reported for the GSB, the main fishing grounds are concentrated south of the Baja California Peninsula. The consumption value in Mexico is 3.5 times higher than in the U.S., while the non-consumption value in the U.S. is 287 times higher. In the case of the GSB, asymmetries across the U.S.-Mexico are the main barriers to understanding the past and ensuring future sustainable fishing and population recovery of what is considered a critically endangered species.

INTRODUCTION

Political borders in the marine environment can cause asymmetry in scientific production, research, management outcomes, and economic revenues for transboundary ecosystems and fish populations (Maureaud et al., 2020; Munro, 2018; Palacios-Abrantes, Reygondeau, Wabnitz, & Cheung, 2020; Pinsky et al., 2018). For example, differences in research effort across political borders can trigger differences in scientific production, which in turn, may impact the perception of the status of marine resources on either side. Similarly, the asymmetric management of marine resources can threaten fish populations through overfishing, generate economic disparities, and compromise neighboring populations. Conversely, coordinated management of connected populations may allow for the replenishment of depleted stocks, improve population stability, and ultimately maintain genetic diversity (Paterson et al., 2015). Differences in the research and management of shared resources between nations are driven by a variety of factors, including perceptions of the importance of a resource, economic and social disparity, management priorities, and the number of resources available for research and management.

Cooperative management of shared fish stocks is often necessary to achieve sustainability and to reduce uncertainty in predictions of stock conditions (Cisneros-Montemayor, Ishimura, Munro, & Sumaila, 2020; Ishimura, Herrick, & Sumaila, 2013; Pinsky et al., 2018). Challenges to the effective management of transboundary fishery resources may be exacerbated by climate change and other environmental stressors that underscore the need to emphasize cooperative approaches for long-term sustainability (Free et al., 2020; Gaines et al., 2018; Miller, Munro, Sumaila, & Cheung, 2013). Despite the fact that as many as 693 demersal and 194 pelagic marine fish and invertebrate species worldwide are managed by more than one Exclusive Economic Zone

(EEZ), very few are cooperatively managed (Caddy, 1997; Palacios-Abrantes et al., 2020; Pinsky et al., 2018). The United Nations Convention on the Law of the Sea (UNCLOS) grants each country exclusive rights to set its own goals in the management and evaluation of resources within its EEZs, such goals are typically created without regard to neighboring states (Lane & Stephenson, 1995; Miller & Munro, 2004). However, such goals are typically created independently from neighboring states even though UNCLOS holds that nations must ensure that the fisheries within their EEZ are not overexploited and cooperate to establish adequate management measures for shared resources. A growing body of literature provides tools for navigating the complexities associated with the management of transboundary stocks in order to meet these goals (Miller & Munro, 2004; Molenaar & Caddell, 2019; Petersson, 2019; Pinsky et al., 2018). Asymmetry is thus not a steady-state issue but rather a dynamic one that is exacerbated as the distributions of fish stocks shift, the social and economic condition of nations change, and environmental stressors become more erratic.

Transboundary stock management can thus be complicated by environmental complexity but also by higher-level differences in capacity and social, economic and environmental policy, as highlighted in this study including the neighboring U.S. and Mexico. The marine environment off the coast of California (U.S.) and Baja California (Mexico) is part of the San Diegan province, which is considered a single marine biogeographic unit (Horn, Allen, & Lea, 2006; Ramirez-Valdez et al., 2015). Species in the region maintain genetic connectivity and utilize critical habitats on both sides of the border, which calls for increased management of shared fish stocks (Block et al., 2011; Chabot, Hawk, & Allen, 2015; Gaffney, Rupnow, & Domeier, 2007). In 2020, the U.S. and Mexico signed a trade agreement that includes provisions for preventing overfishing, reducing incidental catch, promoting the recovery of overfished stocks, and protecting marine habitat (U.S.-

Mexico-Canada Agreement Implementation Act: USMCA, 2020). Additionally, state-level regulations in both countries recognize the potential contribution of population sources by the other country, encourage regional approaches to marine management, and emphasize coordinated approaches to the management of shared fisheries (Baja California's Fishery Agency, 2018; Leet, Dewees, Klingbeil, & Larson, 2001). Despite clear environmental and economic justification for co-management, legal frameworks encouraging it, and a rich history of collaboration between scientists in Mexico and California, to date no co-managed species in this area.

An emblematic case of asymmetry in the research, fisheries, management, and economics of a shared marine resource between the U.S. and Mexico is the giant sea bass (*Stereolepis gigas*, hereafter GSB), a critically endangered marine fish species that ranges from Humboldt Bay in northern California to the tip of the Baja California Peninsula, including the entire Gulf of California (Cornish, 2004; Domeier, 2001). The GSB is the largest coastal bony fish in the Northeastern Pacific, growing up to 2.7 m in total length and weighing up to 255 kg (Allen, 2017; Allen & Andrews, 2012; Domeier, 2001). It is a top predator that preys on a wide range of fish and macro-invertebrate species and was once plentiful within the rocky reefs and kelp forests of Baja California and California through a genetically well-connected population (Chabot et al., 2015; Gaffney et al., 2007; Horn & Ferry-Graham, 2006; Tegner & Dayton, 2000; Vilalta-Navas et al., 2018). The GSB possesses several life history traits that make it vulnerable to overfishing and slow to recover when protected, including a slow growth rate, long lifespan (76 years), late onset of sexual maturity (11-13 years), and the propensity to form spawning aggregations at specific locations from July to November (Clark & Allen, 2018; Domeier, 2001; Hawk & Allen, 2014; House, Clark, & Allen, 2016; Sadovy et al., 2013).

Following the decline of the population in California, strong conservation regulations were incrementally imposed in the U.S. waters, while regulations in Mexico have remained nearly non-existent (Table 2.1) (Allen, 2017; Domeier, 2001; Pondella & Allen, 2008). In 1981, a ban on commercial and recreational GSB fishing was passed in the U.S.; however, after thirty-eight years into the fishing ban the U.S. population continues to be well below historical levels (Baldwin & Keiser, 2008; Dayton, Tegner, Edwards, & Riser, 1998; Ragen, 1990). GSB has not been issued a category of protection at the state or federal level in the U.S., and currently, there are no regulations in place for the Mexican commercial fishery, such a catch or size limits (DOF, 2006; Musick et al., 2011). GSB is an economically and culturally important resource both in the U.S. and Mexico. Recreational activities associated with the GSB represents a multi-million-dollar industry in California (Guerra, Madigan, Love, & Mccauley, 2017), while small-scale, commercial fishing communities in Mexico seem to have a strong linkage with this resource due to local traditions. Given the disparities in regulations and use of this shared and possibly recovering resource, future effective management will require an understanding of the synergistic effects of conservation in the U.S. and exploitation in Mexico on the population as a whole, which is not constrained by the international border.

In this study, we examined how the asymmetry in scientific production, and consequently management, may represent a challenge for the conservation and sustainability of this critically endangered species. More specifically, we aimed to analyze disparities between the U.S. and Mexico related to: (1) scientific production and research for GSB; (2) fishery and management trends; (3) spatial patterns of the contemporary fishery (2000-2016); and (4) the consumptive and non-consumptive economic value of GSB. This work represents the first study to incorporate historical and contemporary perspectives of the GSB fishery throughout its entire geographic

range. Our results indicate a clear need for cross-border collaboration in the management of this species and other exploited marine resources, particularly in the face of ever-increasing climate stressors (Cavole et al., 2016; Pinsky et al., 2018).

MATERIALS AND METHODS

The study encompasses the entire geographic distribution of the GSB in the Northeastern Pacific, ranging from Humboldt Bay, California (U.S.) to the Baja California peninsula and the Gulf of California (Mexico) (Fig. 2.1). However, adults are primarily found south of Point Conception and north of Bahía Magdalena (Love et al., 2005). Our data span more than 14 degrees of latitude (approximately 2,200 km) from Santa Cruz, California (37.6°N) to the southern range limit in the tip of the Baja California Peninsula (22.9°N), including the Gulf of California, Mexico.

Asymmetry in scientific production and research

We assessed the existing scientific production and research on the GSB by conducting systematic literature reviews on ISI Web of Science and Google Scholar that used the following search terms: “*Stereolepis gigas*”, “giant sea bass”, “black sea bass”, “mero gigante”, and “pescara” (Table 2.2); the latter two terms refer to the common names of GSB in Spanish (Page et al., 2013). In addition, we cross-checked the reference lists contained within all peer-reviewed articles focused on GSB. We downloaded and reviewed every article to filter those that mentioned GSB as part of the references or species lists. The main topic, year of publication, and the locations of the populations studied were extracted from each article. We then compiled this information to summarize what is known about the life history, ecology, genetics, fishery, and conservation of GSB (Supporting material 1). In addition, we incorporated data on GSB described in book chapters and grey

literature resources identified and cited within such articles. We also developed an accurate, updated GSB distribution map, using the information from the literature review, and incorporated data extracted from the Global Biodiversity Information Facility (gbif.org), California Department of Fish and Wildlife (CDFW), the California Recreational Fisheries Survey (CRFS) (<https://www.recfin.org/>), the Mexican government fisheries management agency (CONAPESCA), scientific collections in Mexico and the U.S., fishery-dependent data, and fishery-independent surveys.

We evaluated relative research efforts by compiling an exhaustive list of institutions and organizations from both countries that have been involved in GSB initiatives and requested information on project locations, total research funding, and project durations. Organizations included research groups within academic institutions, non-governmental organizations (NGOs), government agencies, aquariums, and independent specialists. As some respondents reported total research funding over the duration of multi-year projects, grant funds were divided by years of project durations to estimate annual spending. Mean annual values of research funds in the U.S. and Mexico were calculated by summing within years and dividing by the total number of years in which research funding was reported.

Fishery and management trends

Historical landings data for GSB from commercial and recreational fisheries in the U.S. (1913 to 1999) were extracted from graphs on reports of the CDFW using GraphClick v.3.0.3 (Arizona-Software, 2010) (Baldwin & Keiser, 2008; Domeier, 2001). Data from the commercial fishery were recorded in metric tonnes, whereas the data from the recreational fishery were reported based on the number of landed individuals. Historical landings data from the commercial fishery for GSB in Mexico (1957 to 1999) were obtained from the Sea Around Us Program

(<http://www.seaaroundus.org/>). These data are estimated using the baseline official landings reported for “meros y garropas” (seabasses and groupers) by CONAPESCA to FAO. The specific catch of GSB within that larger complex was calculated based on available peer-reviewed literature and independent reports of catch composition and estimates of unreported catch in Mexican fleets (Cisneros-Montemayor, et al. 2013). To assess possible causes for observed trends, we compared data to the timing of different management actions (Table 2.1).

Contemporary landings data for GSB (2000–2016) were obtained from CDFW for the U.S. and from a combination of the Mexico federal fisheries agency (CONAPESCA) and Baja California state fisheries agency (SEPESCA). All commercial and recreational landings data in the U.S. were recorded as incidental, as this species cannot be legally targeted, and commercial fishers can incidentally land no more than one GSB per trip. The CDFW database included catch location by 10×10 min blocks, date, total catch, and market price. Commercial fishery landings in Mexico were obtained as mandatory (but often uncertain) landings reports, which included the name of the fishing cooperative (or permit holder), catch site, date, total catch, and ex-vessel price.

We analyzed annual trends in the U.S. and Mexican commercial and recreational fisheries to explore whether contemporary fishing could pose a threat to the conservation of GSB. More specifically, we examined seasonal patterns of contemporary fishery landings (2000–2016) to determine if landings were elevated during certain seasons, such as those when GSB form spawning aggregations (Erisman et al., 2010). We used data from the U.S. commercial fishery (CDFW), and recreational fishery (CRFS) to analyze the number of fishing tickets and records by year and location to test for possible evidence of a population recovery. Assuming a relatively steady fishing effort, after a population rebound and subsequent expansion, the records coming from the fishery should increase in number and locations.

We additionally examined whether there were significant differences between total commercial fishery landings and official governmental reports through CONAPESCA, something that has been previously suggested (Cisneros-Montemayor et al., 2013). We tested for differences for four Mexican fishing cooperatives: SCCP Ensenada, Buzos y Pescadores de Natividad, Punta Abrejos, and Puerto Chale. First, to test for autocorrelation in fishery landings between years, we ran a linear regression between year and fishery data for each set of observations. We then tested for a 1-year lag by regressing the resulting residual values against the residual value of the prior year. After determining that there was no or minimal autocorrelation, we ran a paired two-tailed *t*-test between cooperative and CONAPESCA data.

To complement the historical (1900's) and contemporary (2000–2016) fisheries landing data, we set out to collect more recent information. In March 2017, we established a biological monitoring program focused on obtaining data and samples from the commercial fishery in Mexico, describing the catch composition of the GSB fishery, and the percentage of the total catch comprised of juvenile individuals. We obtained biological data and fish samples from fish markets, fishing cooperatives, recreational fishery tournaments, records shared over social media, and fishery-independent surveys. We measured the total length (TL) (to the nearest 0.1 cm), weight (to the nearest 0.1 kg) (Ramírez-Valdez et al., 2018), as well as catch site, date, type of record (e.g., fish market, recreational fishery, fishing cooperatives, etc.), and fishing gear. We systematically surveyed fish markets and collected fish samples on a monthly basis from March through December 2017 and then opportunistically thereafter. To calculate the percentage of the total catch comprised of juveniles, we assumed that GSB reached maturity at 11–13 years and approximately 800 mm TL (Hawk & Allen, 2014). To test for normality in length data, we used the Shapiro-Wilk test. We used the average tonnage of Mexican landings of GSB from 2000 to 2016 and the average

weight of the individuals sampled from the biological monitoring program to estimate the number of individuals harvested annually in the Mexican fishery. We used the median weight (1965–2006) of the U.S. fishery to estimate the number of individuals that were removed annually (Bellquist & Semmens, 2016).

Spatial patterns of the contemporary fishery

We used the average annual landings over the available data period (2000–2016) to identify the main fishing grounds for GSB. Landings data were associated with spatial data to the finest scale possible. In the U.S. we used a 10 × 10-minute grid of fishing blocks constructed by the CDFW, whereas for Mexico we used the coastal fishing concession area polygons of the fishing cooperatives as available from official data or provided by CONAPESCA (QGIS.org 2019). We assumed each record in the database represented a separate "fishing ticket," which we then used to evaluate the relative catch-per-unit-effort and areas of higher catch frequencies. We tested our assumption by evaluating the catch distribution recorded in the fishing tickets by polygon to see if the catches represent a likely similar trip length, as indicated by similar weights landed, or if they may include catch over several trips. To test for a correlation between the average yearly landings and the number of fishing tickets, we ran a linear regression by country. We use biogeographic provinces divisions rather than political ones because they make more biological sense as they follow the species distribution affinities. They may be more informative of population structure and therefore better suitable for fishery management.

Asymmetry in the economic value

We estimated the consumptive and non-consumptive ex-vessel value of the GSB in the U.S. and Mexico. The consumptive value was obtained using the commercial fishery landings and

ex-vessel price data obtained from government agencies CDFW (U.S.) and CONAPESCA (Mexico) from 2000 to 2016, converted to USD and adjusted for inflation.

The non-consumptive value for the U.S. was obtained from Guerra et al. (2017), who used a contingent valuation method to estimate the amount of money that SCUBA divers in southern California were willing to pay to encounter a GSB based on interviews of 265 scuba divers and the actual mean trip price currently paid by divers. To generate the same information for Mexico, we used the mean trip price per diver of the only two diving operations in Mexico that specifically offer dive encounters with GSB. In the fall of 2018 and 2019, three expeditions of 9 to 14 scuba divers were organized to dive and photograph GSB in three sites of the Baja California peninsula, Mexico. We interviewed the fishing cooperative and organizers of those expeditions to obtain the trip cost and number of divers.

RESULTS

Asymmetry in scientific production and research

Our literature review identified 52 unique peer-reviewed articles mentioning GSB. Only four mentioned GSB in the context of both countries, while 36 mentioned GSB in California's waters, and 12 did so for Mexican waters (Table 2.2; Fig. 2.2; Fig. 2.3). The number of published articles on GSB showed an upward trend since 2007, and 65% of the articles were published within the past 10 years. Of the 52 articles, only 19 articles focused on GSB beyond a simple mentioning. Only three of these 19 articles contained data and information from Mexico, and each of these also included data from the U.S. (Table 2.3).

We identified nine major topics associated with articles on GSB (Fig. 2.3). Research in the U.S. covers most topics fairly evenly, with a greater focus on ecology-related topics, while research in Mexico tends to be distribution and fisheries-related. Overall, most articles referred to

adult individuals or were non-specific with respect to life stage (Fig. 2.3). A summary of all the information compiled through the literature review is presented in Supporting material 1.

The GSB distribution map included 11,198 records of juvenile, adults, and larvae from Humbolt Bay, U.S. to Guaymas, Mexico, and the interior of the Gulf of California. We found no evidence of juvenile and adult individuals' records south of the Gulf, in the Mexican biogeographic province, and only one larva record off the coast of Oaxaca, Mexico. Since 2000, 50% of the records are concentrated in the biogeographic transition zone, between Punta Eugenia and Bahia Magdalena (Mexico), and 73% of the latitudinal distribution of the GSB is in Mexican waters (Supporting material 2).

Research and conservation groups in the U.S. and Mexico reported total spending of US \$754,697 in GSB research over the past 20 years (Fig. 2.4). Approximately 96% (US \$132,197 per year) of this amount was invested by groups from the U.S. and involved research in California. A total of US \$30,500 (US \$13,833 per year) has been invested in the GSB in Mexico, and research efforts began in 2017. Nine academic institutions and organizations have conducted research on GSB in California, while only one Mexican university and two NGOs have participated in research on GSB (Supporting material 3).

Fishery and management trends

Annual fishery landings of GSB in the U.S. and Mexico have been highly variable from the late 19th century to the present (Fig. 2.5). Commercial fishing of GSB in the U.S. began in the 1870s, while recreational fishing began in the mid-1890s. During this period, fish were targeted with set lines and hand lines. The history of the GSB fishery can be divided into five distinct periods: a) the development of the GSB fishery in the U.S.; b) the collapse of the fishery in the U.S. waters; c) the development of the GSB fishery in Mexican waters; d) the decline of the U.S.

landings from fish caught in Mexican waters and the rise of Mexican landings, and e) the contemporary fishery (2000–2016) in the U.S. and Mexico.

The first period (before 1923) represented the development of the commercial and recreational fisheries for GSB in California, where the U.S. fleet fished mostly in local waters but were supplemented by a small portion of landings coming from Mexican waters. In the second period (from 1923 to 1931), the U.S. fleet increased landings from central and southern California waters until a maximum of 111 tonnes of GSB were landed in 1929. During this time, U.S. commercial landings from fish captured in Mexican waters also increased rapidly until catches from Mexican waters eventually exceeded catches from within U.S. waters.

During the third period (from 1932 to 1945), the U.S. fishery dramatically shifted its fishing efforts to become entirely based on catches in Mexican waters. The local landings from the U.S. fleet collapsed completely and remained below 10 tonnes/yr for more than 20 years, while fleet landings in Mexican waters increased to 386 tonnes/yr and averaged 220 tonnes/yr during the third period. At the end of this period, a sharp decline in landings coming from Mexico was observed, apparently due to the U.S. entering World War II, an effect observed in most fisheries in California (CDFW, 2014). The absence of historical fishing statistics for that period of the Mexican fleet did not allow us to calculate the exact volume of catches, but the GSB fishery in Mexico was present to some degree such that in 1933 the California Fisheries Yearbook mentioned: “a considerable part of the [GSB] catch consists of fish caught in Mexican waters [...] most of this amount is taken by California fishers off the west coast of Lower California, but a few pounds are caught by Mexicans in the Gulf of California and shipped to Los Angeles by refrigerated trucks as a side issue to the totoaba fishery.” (Division of Fish and Game of California, 1935).

The fourth period (1946–1999) was marked by the decline of the U.S. commercial fishery in Mexican waters when catches fell from 152 tonnes in 1964 to 14 tonnes in 1972, which was concurrent with a binational agreement that restricted U.S. fleet operations in Mexican waters (Table 2.1, Fig. 2.5A). The commercial fishery for GSB in the U.S. closed in 1981, which by then was landing less than 2 tonnes/yr from fish caught in U.S. waters. In 1994, a ban for the use of gillnets was declared off the southern California coast (Fig. 2.5A). Thereafter, GSB landings in the U.S. waters were a result of legal, incidental catch. This period also coincided with the development of the Mexican fishery in the Baja California Peninsula in the late 1950s, when the first fishing cooperatives were founded. Before the 1980s, commercial landings by the Mexican fleet averaged 55 tonnes/yr and reached a maximum in 1983 with a reported 330 tonnes. These trends coincided with fishery landings for the Baja California Peninsula of the species clustered as “groupers and seabasses” in the 1980s, which included GSB and averaged 400 tonnes/yr (DOF, 2006).

The fifth period (2000–2016) was characterized by the stability of incidental landings of GSB by the U.S. fleet that averaged 2.6 tonnes/yr and landings from the Mexican fleet that averaged 50.5 tonnes/yr. Landings by the Mexican commercial fleet showed two peaks during this period, the first in 2010 at 78.8 tonnes, and the second in 2015 with 102 tonnes. However, commercial GSB catches in Mexico have never dropped below 33 tonnes/year since 2000. The development of the recreational fishery by the U.S. fleet began around the time the commercial fishery collapsed in California (Fig. 2.5B), peaked in 1963 (500 ind/yr), and then collapsed less than a decade later (< 50 ind/yr). The U.S. recreational fleet increased their fishing effort in Mexican waters during this same period, from 100 ind/yr in 1963 to 800 ind/yr in 1971, before declining in 1980.

We found a slight increase in the fishery landings trend of the Mexican commercial fishery during 2000–2016 ($R^2(17,16) = 0.131$, $p = 0.152$) and a positive correlation between landings and number of fishing tickets ($r(n = 1,312) = 0.775$, $p = 0.0002$), suggesting that the trend in catches is mainly the result of an increase in fishing tickets, which could be due to an increase in effort or an increase in catch reporting. The U.S. incidental catches showed a non-significant negative trend, which suggests that landings in the last 16 years have remained stable ($R^2(17,16) = 0.119$, $p = 0.174$). Stable U.S. landings and the number of fishing tickets were correlated ($r(n = 846) = 0.748$, $p = 0.0005$), suggesting that fishing records have not increased and that fishing tickets can provide a reliable estimate of the fishing effort. Additionally, we found an increase in the number of GSB records (individuals retained or released alive) in northern California ($R^2(14,13) = 0.450$, $p = 0.008$), reaching even San Francisco Bay (U.S.), which may be due to population increases or climate-driven shifts in distribution.

We found a statistically significant difference of the seasonal catches for the Mexican commercial fishery as determined by one-way ANOVA ($F(3,64) = 16.384$, $p < 0.05$, $n = 17$), with summer months recording the highest landings (Fig. 2.6). The U.S. incidental catches are also significantly different with higher landings in summer (one-way ANOVA ($F(3,64) = 13.276$, $p < 0.05$)). We found no significant difference (Two-sided paired t-test ($34,33) = 2.69$, $p = 0.135$) between the landings obtained from CONAPESCA and the landings coming from the fishing cooperatives, confirming the reliability of the official landings for this analysis (Supporting material 4). Fishery landings from the four fishing cooperatives showed the same trend with the official data on average.

Over 36 months (2017–2020) of monitoring, we sampled 209 GSB individuals from 28 locations across the Baja California Peninsula, the Gulf of California, and California: 112 from

fish market surveys, 53 from fishing cooperatives, 9 from fishing tournaments, and 35 from other sources (e.g., social media records, fish collections, fishery-independent surveys). Sampling records covered the geographic distribution range of GSB in Mexican waters with the highest number of samples obtained from regions with the highest commercial landings (Fig. 2.2). 74% of the records came from surveys in fish markets from Ensenada and Tijuana, the main commercial centers for all fisheries along the Baja California Peninsula. GSB sold in these markets were brought from numerous fishing grounds in the region. The records from fishing cooperatives and fishing tournaments represented a lower percentage (36%). However, they provided valuable information, as individuals were typically larger in size, and fishers reported precise geographic information on the site of capture. Our samples showed a normal distribution for total length and log-transformed body weight (Shapiro–Wilk $W > 0.8$; $p = > 0.05$). The body length of fish sampled ranged from 300 to 2300 mm TL (Figure 2.7A). Approximately 48.4% of the records were < 800 mm TL, indicating that the fishery is targeting a large number of presumed juveniles. The median weight of GSB individuals was 12.0 ± 3.2 kg MED \pm SE (Fig. 2.7B).

By using the median weight (wt ($n = 231$) = 51 kg) of the recreational fishery records from the U.S. fleet (1966–2008) reported by Bellquist & Semmens (2016), we estimated that the U.S. landings of 2.6 ± 0.2 (M \pm SE) tonnes/yr would represent a harvest of roughly 50 ± 2.61 individuals. Using the average Mexican landings (50.9 ± 4.1 M \pm SE tonnes/yr) and the median weight of individuals from our biological monitoring in Mexico (wt ($n = 182$) = 12 kg), we estimated that the number of individuals removed annually by the Mexican commercial fishery was approximately $4,244.9 \pm 345.07$ M \pm SEM ind/yr. The median better describes our weight data central location because they are skewed to the left; however, if we use the mean (32.1 kg), our

estimate is 1,721 individuals. Combined, the total catch from the U.S. and Mexico could represent up to $4,295.9 \pm 346.6 \text{ M} \pm \text{SEM}$ GSB individuals per year.

Spatial patterns of the contemporary fishery

Spatial patterns in fisheries landings matched the overall geographic distribution of GSB and were distributed from Monterey Bay, California, to the tip of the Baja California Peninsula, and inside the Gulf of California (Fig. 2.8). The highest landings were reported in Mexico in the region south of Sebastián Vizcaíno (28.5°N) and north of Bahía Magdalena (24.3°N), what is known as the transition zone of the temperate and subtropical systems (Figs. 2.8A, 2.8C). Isla de Cedros, Laguna de San Ignacio, San Juanico, and Bahía Magdalena were especially productive fishing grounds that collectively averaged more than 4 tonnes/yr. The highest annual average landings in the Gulf of California (Cortez province) occurred in the northern region, although Santa Rosalia, in the central region, has reported more total GSB catches (“fishing tickets”) over time. In the U.S., landings were concentrated in coastal waters off San Diego, Dana Point, San Pedro, and Santa Barbara, California, although the Channel Islands and the U.S.-Mexico border also showed a high number of landings (Fig. 2.8B).

Asymmetry in the economic value

The ex-vessel revenue of the GSB incidental catches by the U.S. fleet averaged US $\$15,133.9 \pm 1,211.5 \text{ (M} \pm \text{SE)}$ per year (Fig. 2.4). The average (2000–2016) official ex-vessel value after inflation was US $\$6.4 \pm 0.2 \text{ M} \pm \text{SE}$ per kg and has increased 40% since 2000. Ex-vessel revenues from the commercial fishing fleet in Mexico averaged US $\$54,051.8 \pm 4,533.4 \text{ M} \pm \text{SE}$ (Fig. 2.4). The average ex-vessel price was US $\$1.1 \pm 0.08 \text{ M} \pm \text{SE}$ per kg in Mexico and has decreased by 32% since 2000. Retail prices in Mexican fish markets were 559% higher (US $\$6.5$ per kg), indicating that most of the revenue made from catches is received by fish markets.

Guerra et al., (2017) reported the non-consumptive value of the GSB, considering divers' willingness-to-pay for a GSB sighting, was US \$2.3 million per year (Fig. 2.4), and the mean trip cost that SCUBA divers paid was US \$90.7 (median = US \$115). Through our interviews with dive expedition companies in Mexico, we estimated that the mean trip price that divers paid was US \$216.6 (median = US \$250) and the total economy associated to diving with GSB was US \$30,000 during the 2018–2019 period.

DISCUSSION

The results of this study revealed widespread asymmetry in the scientific production and research, fishery and management trends, spatial distribution of fishing, and economic value of GSB across the U.S.-Mexico border. Until recently, the GSB was rarely the focus of research; the vast majority of scientific studies and monetary investment took place within U.S. waters despite the fact that three quarters of the entire distribution and likely higher abundances of GSB can be found in Mexican waters. Historical patterns of fishery landings were easily described by five distinct periods of exploitation by the U.S. and Mexican fleets. After the apparent demise of the GSB fishery in Californian waters by the 1930s, the U.S. primarily fished in Mexican waters, leading to GSB landings that dwarfed even the highest values in California. By the 1980s, U.S. landings from Mexico ceased, concurrent with (and possibly a reflection of) a combination of a fishing ban on GSB in California, new binational treaties, and a proclamation of Exclusive Economic Zones (EEZ) between the U.S. and Mexico. The Mexican fishery landings have been relatively stable since the 1950s, but contemporary results indicate that a large proportion (48%) of the landings are comprised of juveniles. Although the GSB is not a target for the fishery in both countries for the most part, the largest proportion of landings are reported in summer, which coincides with the

spawning season. The spatial distribution of contemporary fishing ranges from sparse landings and effort from southern California in the form of incidental catch to high landings and possibly increasing effort concentrated off the southwestern half of Baja California, where some locations harvest more GSB than the total amount landed annually as incidental catch in U.S. waters. The non-consumptive value in the U.S. is 76 times higher than in Mexico, and still 33 times higher than the ex-vessel revenues of the two countries combined. Currently, the annual consumptive value of GSB is only 3.5 times higher in Mexico than in the U.S. despite nearly 20 times more annual landings in Mexico. Individual fisherman in Mexico receive a price of 13 times less than the price received at market, which may potentially fuel an increase in fishing effort in order to sustain the income of fishers. While GSB is considered a shared binational resource, the disparities in scientific production, research, fishery management, and economics of the species are striking, warranting future collaboration by researchers, fishers, and managers of both nations to understand the status of the population and develop joint management strategies to ensure that efforts for recovery and sustainable fishing are successful.

Asymmetry in scientific production and research

In this study, we found that strong asymmetry exists in the scientific production and research funding across the U.S.-Mexico border (Fig. 2.4). Despite the fact that the center of the GSB's geographic distribution occurs in Mexico, there are up to 5x more scientific articles published on the U.S. populations. Among the three articles that contained data on Mexican GSB populations, none addressed the past or ongoing fishery, a trends seen for many other coastal fisheries in the California Current region (Erisman et al., 2010; Johnson et al., 2017). Moreover, only 19 studies that focus exclusively on GSB exist in the literature, indicating that our understanding of the species life history, trophic ecology, physiology, population status, and

fisheries is limited in both countries. As most of the knowledge about the species has been generated in the last decade, a continuation and expansion of these efforts may be forthcoming and include insights on the potential vulnerability of GSB to climate change. Of all the financial investment in research directed at this species, less than 4% has been directed to populations in Mexico and very little prior to 2017. Given the productive fishery in Mexico and strong conservation efforts in the U.S., greater investment into research in both Mexico and the U.S. is needed in order to better understand and effectively manage this shared resource. In addition, research focusing on the connectivity of the GSB population and effects of conservation and active fisheries on stock structure and abundance throughout the broad species distribution will assist in developing transboundary science-based management (Chabot et al., 2015; Gaffney et al., 2007).

Incomplete and asymmetric scientific production and research may be impacting perceptions on the status of GSB populations for fishers and fishery managers and hinder their willingness to cooperate in shared resource management (Miller & Munro, 2002; Munro, 2018; Vosooghi, 2019). Although this asymmetry in scientific production may not be exclusive to the GSB fishery, it likely has affected fishery management on one side of the border and conservation efforts on the other side. Despite the fact that three-quarters of the species distribution is south of the U.S.-Mexico border, the Mexican government fisheries agencies and academic institutions have overlooked generating scientific knowledge of the GSB for the past 80 years since fishing cooperatives in the region were founded. The scientific community has highlighted the need for a transboundary perspective when developing research and management of natural resources (Aburto-Oropeza et al., 2018; Ramírez-Valdez et al., 2017), yet many political and administrative barriers to achieving this goal persist (e.g., permits, data standardization, data-sharing). Collaborative research programs between academic institutions, binational research grants, and

cooperation between state and federal governments could be the most achievable strategy to resolve some of the differences in scientific production that are impeding future management.

Fishery and management trends

Our analysis of GSB landings consisted of a holistic examination of varying trends over the last century in the U.S. and Mexico and revealed that the collapse of the GSB fishery and the population in U.S. waters occurred as early as 1932. Moreover, the subsequent decline of GSB landings by the U.S. fleet in Mexican waters prior to 1980 was likely a result of the binational regulation of the commercial fishery and did not reflect a true population collapse in Mexican waters. Historical fishing trends also show that as recently as 1970, the U.S. fleet was the main driver of GSB fishing effort and landings both in U.S. and Mexican waters before being replaced by the Mexican fleet. Decreases in U.S. landings in Mexico into the 1970s and 1980s were seemingly a consequence of the binational treaty on fisheries management signed in 1968 and a proclamation of EEZs in 1982, respectively, (Table 2.1) and not due to decreases in resource availability. We were able to reconstruct estimates of historic Mexican landings of GSB from reported landings of groupers and cabrillas (category where GSB is included) and data obtained from the Sea Around Us Program, which showed that periods of high landings by the Mexican fleet were not followed by collapses as had occurred in the U.S., with the exception of years following the 1981 peak of 333 tonnes. While it is difficult to assess changes in stock sizes exclusively from landings data (but see Pauly, Hilborn, & Branch, 2013), it is likely that the U.S. stock collapsed approximately 50 years before the implementation of the GSB fishery moratorium in 1981, much earlier than previously thought. Fluctuations in landings data from Mexican waters may track previous changes in abundance; however, landings from the Mexican fleet have averaged 50 tonnes per year over the last 60 years, indicating the possibility of a stable stock size

assuming static fishing effort. However, other factors such as catch rates remaining nearly constant even as abundance declines (hyperstability: Erisman et al., 2011) or fishers exploiting new locations for GSB are possibilities that were not assessed from historical data. Historical records of recreational GSB fishing in the U.S. occurred after the collapse of the commercial fishery, but it too appears to have ceased being common by the 1970s. Disparities between commercial and recreational landings in Mexico indicate that the large increase in GSB recreation fishing in the 1960s and 1970s was likely related to tourism or other socioeconomic factors and not necessarily the availability of GSB in fished habitats.

Contemporary landings in the form of incidental catch in the U.S. and small-scale commercial fisheries in Mexico were variable since 2000 but comparatively stable when compared to the large fluctuations in landings observed during the last century. We detected a slight decreasing trend in landings in the U.S. and a slight increasing trend in landings and effort in Mexico, which should continue to be tracked in the future to help facilitate effective management whether it be for recovery or sustainable fishing. We estimated that the U.S. and Mexico land on average 50 and 4,244 individual GSB per year, respectively. Differences in the contemporary mean weight of GSB fished by the U.S. (51 kg) and Mexico fleets (12 kg) can be explained in part by the fishing methods used. Most catches from California come from gillnet fishing, while the highest proportion of Mexican commercial fishing is conducted with gillnets targeting white seabass and flatfish. Gear selectivity of the gillnets used in Mexico may result in the extraction of higher percentages of juveniles as observed in our biological monitoring program; however, abundances of juveniles across the U.S.-Mexican border have not been examined. While the U.S. landings remain consistently very low due the moratorium, the variability of annual catches from the Mexican commercial fishery may be due to changes in recruitment, as a response of the

climatic variability, and/or changes in fishing effort, as has been reported for other long-lived, aggregate spawning fish (Erisman et al., 2010; Roughgarden & Smith, 1996; Sadovy et al., 2013). The recruitment of this species may increase during strong El Nino events, which has been proposed for California (Schroeder & Love, 2002) and may also be true for Mexico, but there are no studies that examine population or recruitment variability in relation to climatic and environmental conditions. However, Pondella and Allen, (2008) found no correlation between the CPUE of the U.S. fleet and oceanographic variables (SST, PDO, and ENSO). GSB are not directly targeted by Mexican fisheries, but changes in the availability and market prices of other fished resources may cause shifts in target species in the future, further warranting increased research to understand the sustainability of current trends and future scenarios of GSB fishing effort in the region.

Our analysis combining fishery statistics and biological monitoring of the Mexican fleet allows us to estimate that the GSB population size could be larger than previously thought. Our estimate of GSB individuals removed per year for California is slightly lower than previously reported by Guerra et al. (2017), which could be explained by the different time frame studied. Chabot et al. (2015) estimated the effective population size of the species to be 500 females, including samples from California and Mexico, adding that this could be approximately 10% of the census population size. It is unlikely that the GSB census population size is 10% of the effective population size reported by Chabot et al., (2015) since the Mexican fishery would thus have been removing around 33% of the census population annually for at least the past 30 years. The ratio between the effective population size and the census population size could be lower for GSB, a fish species with long lifespans, long generation times, and lower fecundity. Low effective population sizes may be the result of small total population size, strongly fluctuating population

sizes, the existence of a bottleneck process in the population, unequal sex ratio, and variance in family size (Shrimpton & Heath, 2003). Several of them could be plausible scenarios for the GSB population. Therefore, it is necessary to incorporate more population parameters to obtain a better estimate of the population size for this species. At a minimum, our analysis shows that GSB may be more abundant than previously thought throughout its distribution.

A major warning signal of this fishery is the higher proportion of catches in both countries concentrated during the spawning season, the catch composition of the Mexican commercial fishery which includes a high proportion of immature individuals, and the potential hyperstability of the Mexican fishery landings. The largest proportion of landings is reported in summer, which coincides with the GSB spawning season (Clark & Allen, 2018; Domeier, 2001). By far, summer is the busiest season for the fishery in California, which increases the odds of incidental catches. In Mexico, this coincides with the finfish fishery season (i.e. white seabass, flatfish) which also coincides with the seasonal ban of the more profitable lobster, abalone, and sea cucumber fisheries (Baja California's Fishery Agency, 2018).

Spatial patterns of the contemporary fishery

Spatial analysis of the GSB fishery (2000–2016) revealed that catches in the U.S. waters were associated with major fishing zones while in Mexican waters landings were concentrated in traditionally productive fishing grounds across the temperate-tropical transition zone. Some of the most productive fishing grounds (i.e., Vizcaíno, Isla Cedros, Punta Abreojos, Bahía Tortugas, Ojo de Liebre) have average GSB catches of up to 5 tonnes per year, and the high productivity of these regions is also observed in other fisheries (i.e., lobster, abalone, barred sand bass, yellowtail) (Micheli, De Leo, Butner, Martone, & Shester, 2014; Paterson et al., 2015). In the 1970s, U.S. recreational fishing vessels visiting these same fishing grounds caught on average 70–100

individuals, sometimes up to 255 individuals on a three-day trip (Domeier, 2001). Contemporary catches extend throughout the geographic distribution range reported for the GSB, rejecting the hypothesis that parts of the population have been extirpated as a result of overfishing.

Since 2005, commercial fishery permits in the Baja California region have remained steady, as have the number of boats that each operates (Baja California's Fishery Agency, 2018). Our analysis shows that the fluctuation in the landings of the Mexican commercial fleet was highly correlated to the number of fishing tickets in the past 16 years, suggesting possible increases in effort. Although GSB is not a target fishery in most of the Baja California Peninsula fishing grounds, fishers with permits for a variety of species shift to finfish fishery (GSB among them) when other fisheries decline. In the current scenario of species (and fish stocks) on the move due to climate change (Pinsky et al., 2018), fishing pressure upon GSB populations may increase as a result of the decline of other fisheries or increases in the abundance of GSB in new regions.

Asymmetry in economic value

The economic value of the GSB differs greatly across the U.S.-Mexico border and is largely a result of different consumption and non-consumption values of GSB. The consumption value in Mexico is 3.5 times higher than in the U.S., while the non-consumption value in the U.S. is 76 times higher. The U.S. official ex-vessel price is six-fold the Mexican official price that is paid to fishers, although the non-official price observed in Mexican fish-markets is comparable with the U.S. ex-vessel price. The discrepancy between the low prices paid to fishers and the high prices paid by consumers at fish markets in Mexico causes fishers to increase fishing effort in order to reach an income that otherwise could be supported by increased ex-vessel prices. Leveling the profit field for fishers and fish markets holds the potential for less fishing effort, which may be

an effective strategy to minimize overfishing and develop sustainable fisheries management in Mexico.

One avenue of non-consumptive economic gain is through recreational SCUBA diving. Recreational SCUBA diving with GSB is expanding in Mexico, specifically in central Baja California where GSB's sightings are concentrated. However, this region has scarce tourist infrastructure as they are small fishing communities, and a GSB dive tourism industry only began to take shape in the last five years. Understanding the economic balances between management, resource value from fishers to market, and alternative sources of income, such as through tourism, should be considered as necessary steps to ensure the sustainability of the current fishery and conservation of GSB for other economic benefits.

CONCLUSIONS AND FUTURE DIRECTIONS

Examination of asymmetry across international boundaries should not serve to belittle certain nations, but rather to highlight how transboundary management of shared resources can be made more effective (Shackell, Frank, Nye, & Heyer, 2016). Shared fishery stocks are often more prone to overexploitation compared to solely-owned stocks as they often fall victim to “tragedy of the commons” scenarios between nations (McWhinnie, 2009; Ostrom, Burger, Field, Norgaard, & Policansky, 1999). Stocks should be understood and managed from a biological perspective (i.e., species distributions) rather than political one. Since 1970s, studies have pointed out the need for a transborder perspective in management, and since then numerous studies have added study cases and scenarios (Munro, 2018). Some success stories can provide a framework, such as the Pacific sardine, where multilateral agreements and research collaboration between the U.S., Canada, and Mexico (Cisneros-Montemayor et al., 2020) have been successful in maintaining sustainable populations. However, transboundary management has not occurred for GSB, nor for most other

fishery species between southern California and Baja California, including sharks, white seabass, and abalone (Holts, Julian, Sosa-Nishizaki, & Bartoo, 1998; Munguia-Vega et al., 2014; Romo-Curiel et al., 2016). Broad differences in scientific production and stock assessments generates a complex scenario that can hinder management and buy-in for conservation efforts. In the case of the GSB, asymmetries across the U.S.-Mexico are main barriers to understanding the past and ensuring future sustainable fishing and population recovery of what is considered a critically endangered species.

Our assessment of historical and contemporary landings data in the context of local and international policy revealed that changes in regulations have hidden historical collapses in the U.S. and created the false narrative that collapses in U.S. GSB populations occurred later than actually shown. While stocks in U.S. waters likely collapsed by the 1930s, U.S. landings from Mexico continued to remain high until binational agreements all but ended the U.S. fishery in Mexico. With this knowledge and the continuation of stable landings from domestic fisheries in Mexico, there is no concrete evidence that the GSB population ever collapsed in Mexico nor was reduced to levels observed in U.S. waters. Moreover, total catches of GSB have never been below 34 tonnes per year when adding the catches of both countries' commercial and recreational fisheries, with the exception of 2001 (Fig. 2.5C). This value represents 9% of this fishery's maximum peak in 1932 (414 tonnes), slightly lower than the criteria used to define the collapse of a fish stock (10%) (Pauly et al., 2013). There is enough scientific evidence to estimate that the GSB is composed of a single well-connected population throughout its entire distribution, with reproductive aggregations on both sides of the U.S.-Mexico border and movements of adult individuals that exceeds 56 km in 56 h (Burns, Clevenstine, Logan, & Lowe, 2020; Chabot et al., 2015; Clark & Allen, 2018; Gaffney et al., 2007). Even though currently the average landings of

both countries combined are below 15% of historic peak landings, this may represent a positive message about the GSB population and encouragement for the cooperative transboundary management of this species.

GSB is not registered as an endangered species in the U.S., a protected species in Mexico, or a regulated product by CITES which allows part of the fishing to be commercialized in the U.S. (Table 1). However, the IUCN Redlist classifies GSB as a critically endangered species due to the population being considered “severely fragmented, leading to a continuing decline of mature individuals”, but recognizes the lack of information on the Mexican fishery (Cornish, 2004). While U.S. populations of GSB still have very low abundances, the contemporary landings and spatial data suggest that the population size of this species across its entire distribution range is likely higher than previously thought, especially in Mexico where the fishery currently reports stable landings. Prior to effective management and future determinations of species status, we need a more thorough understanding of species distribution, abundances, population structure, and connectivity of GSB in different regions of its range, especially in Mexican waters where no fishery restrictions exist. With such an understanding, future collapses, as those experienced in the U.S. historically, may be prevented with better management and trade restrictions, yielding benefits to both recovery in the U.S. and sustainable fisheries in Mexico.

A combination of scientific inquiry and community-based involvement will be key in providing new information about GSB. While relatively low in volume, incidental catch from the U.S. fleet could be an excellent source of information. Since the inception of a ban on GSB catches in 1981 in California, there has not been any coordinated effort between government agencies and research institutions to gain knowledge from incidental catch. Given the possibility of a future increase in incidental catch as a result of population rebound, collaborations between U.S. fishers

and research institutions could greatly increase available sampling opportunities. In Mexico, the biological monitoring program that we developed as part of this study included the active participation of fishing cooperatives. Such programs should be expanded and continued, as many cooperatives self-manage fisheries through minimum size limits, quotas within fishing polygons, area or depth restrictions, and seasonal closures.

The balance of the consumption and nonconsumption values of GSB may provide conservation and economic benefits for the U.S. and Mexico. Prices paid to fishers prior to marketing in Mexico should be considered within management options for GSB and other species. A movement away from catching as much as possible to support their livelihoods to one where resources are appropriately valued and managed by quotas or other restrictions could yield equal or even larger earnings for fishers while reducing or maintaining landings. Additionally, building the infrastructure to benefit from non-consumptive activities, such as SCUBA diving or recreational catch and release, will diversify the economic opportunities available from the conservation of the species.

The information provided by this study may open the opportunity to discuss binational agreements in the management of this and other marine resources. The current vision in the fisheries management of shared stocks on allowing both parties to make responsible decisions within their EEZ has proven to be insufficient. Here, we have provided new information about GSB in the U.S. and Mexico and suggested possible solutions to increase knowledge, species conservation, and economic opportunities. Transfers of knowledge and collaboration by researchers, managers, and fishers are essential for developing shared resource management. The future fruition of conservation efforts coupled with possible shifts in species distributions in the face of climate change may result in a more equal proportion of the GSB population distributed in

the U.S. and Mexico. It is in the best interests of both parties to recover the population of the GSB, not only from an economic point of view but for its ecological role and cultural value.

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TABLES

Table 2.1. Management policies, conservation categorizations, and government regulations that impacted in the GSB management across the U.S. and Mexico territories

Year	Management regulation, policy, conservation evaluations	Source
1945	The U.S. Proclamation of exclusive jurisdiction of territorial sea	1
1966	Mexico - Proclamation of exclusive jurisdiction for fisheries purposes - 12 nautical miles	2
1968-1973	Mexico - United States Fisheries Agreement: Fishery [of GSB] will continue for five years beginning on January 1, 1968, up to a total volume that will not exceed the total catch taken by U.S. vessels in the five years immediately preceding that date. The U.S. fishing vessels will be permitted, during the same term of five years, to continue sport or re creational fishing in Mexican waters.	1, 2
1973	U.S. Federal Endangered Species Act of 1973; Not included	1
1981	California State Legislature banned the commercial and recreational fishing of GSB in California waters. A maximum of two incidentally caught GSB per trip in the commercial set gillnet and trammel net fisheries. Any fish so taken shall not be transferred to any other vessel. Vessels fishing in Mexican waters were allowed to land 450 kg of GSB per trip but only 1360 kg per year.	3
1982	The U.S. and Mexico proclamation of their Exclusive Economic Zones	4
1984	California Endangered Species Act of 1984; Not included	5
1988	California State Legislature amended GSB moratorium to allow only one incidental fish caught in Mexican waters to be landed in California.	6
1994	California State Legislature outlawed gill nets and trammel nets within 3 nautical miles of the mainland and 1 nautical mile of the islands)	7
1995	Mexican recreational fishery regulation NOM-017-PESC-1994; A maximum of one GSB per fisherman per day. Permits are required when fishing by vessels.	8
1996	IUCN Red List of Threatened Animals. First evaluation as a critically endangered species.	9
2000	American Fishery Society concept of Distinct Population Segments: Threatened, Vulnerable (U.S. Protection: None; CA: Protected)	10
2019	CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora; Not included	11
2020	USMCA - The U.S., Mexico, and Canada Agreement	12

1) The U.S. Government, 2) Mexican Government, 3) California State Legislature [FGC §8380, Title 14, CCR, §28.10], 4) UNCLOS (United Nations), 5) California State Legislature, 6) California State Legislature [FGC §8380], 7) California State Legislature Proposition 132, 8) DOF, 2013, 9) Cornish, 2004, 10) Musick et al., 2000, 11) CITES (2020), 12) United States-Mexico-Canada Agreement Implementation Act, (2020).

Table 2.2. Scientific knowledge on giant sea bass in peer-reviewed papers. WS= ISI Web of Science; GS= Google Scholar. GSB-listed= Papers that mention GSB. GSB-centric Paper= Papers that are focused on GSB. Giant sea bass, and black sea bass are common names in English used in the literature. Mero gigante, and pescara are common names in Spanish (census Page et al., 2013).

Keywords	Search Engine	Hits	GSB-listed
" <i>Stereolepis gigas</i> "	WS	14	14
	GS	420	47
giant sea bass	WS	14	14
	GS	386	22
black sea bass	WS	189	1
	GS	5230	0
"mero gigante"	WS	0	0
	GS	36	0
pescara	WS	278	0
	GS	58,500	0
Total unique peer-reviewed papers			52
Peer-reviewed papers - Information exclusively from U.S.			36
Peer-reviewed papers - Information exclusively from Mexico			12
Peer-reviewed papers - Information from both U.S. and Mexico			4
Total unique GSB-centric papers			19
GSB-centric papers - Data exclusively from U.S.			16
GSB-centric papers - Data exclusively from Mexico			0
GSB-centric papers - Data from both U.S. and Mexico			3

FIGURES

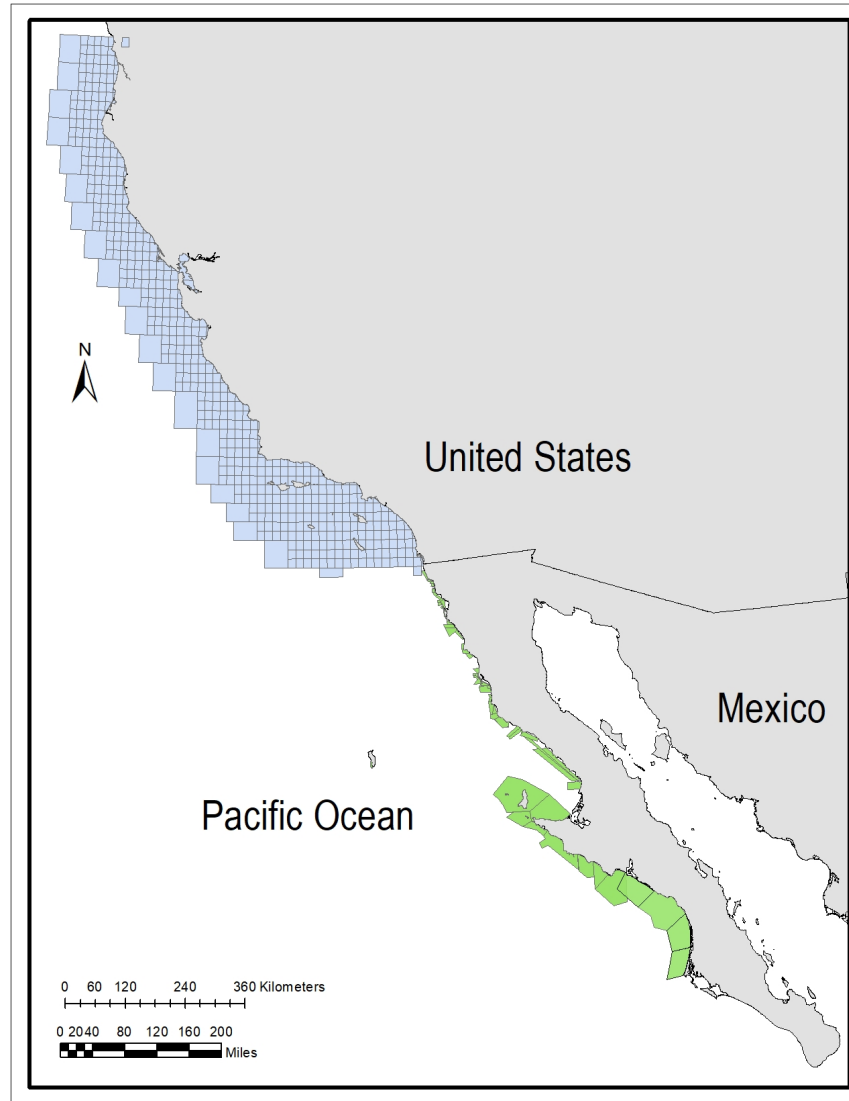


Figure 2.1. Study area and the spatial management of the fishery in both geographic regions; 10 × 10-minute grid blocks by California Department Fish and Wildlife (U.S.) and fishery concession areas by Mexican Fisheries Management Agency-CONAPESCA (Mexico).

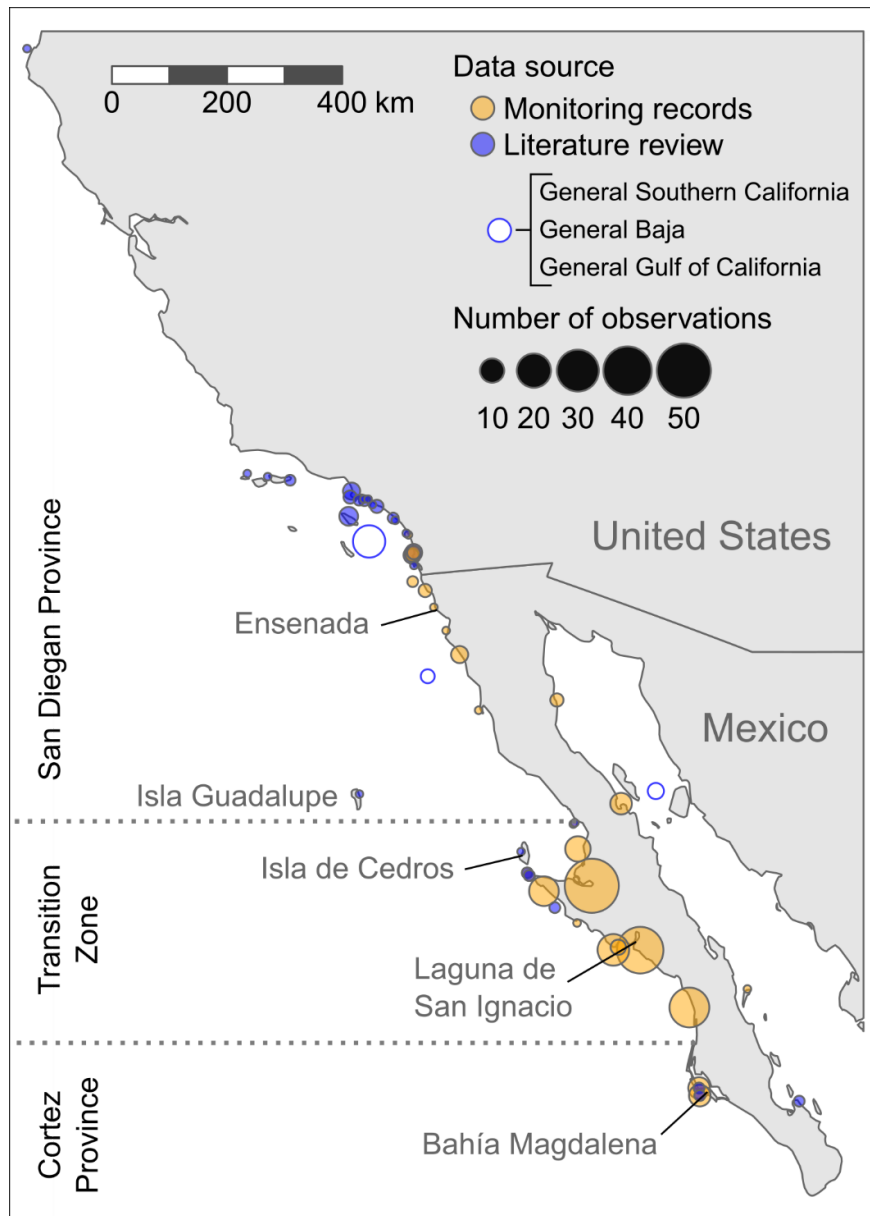


Figure 2.2. Spatial representation of the literature review (blue), and the biological monitoring program (orange). Peer-reviewed papers data not associated with a specific study site is included as General Southern California, General Baja or General Gulf of California. The literature review showed more sites included in more peer-reviewed papers (counts), north of the U.S.-Mexico border. Sites in Mexican waters mentioned GSB presence in species lists. Biological monitoring includes mostly data from the Mexican fishery.

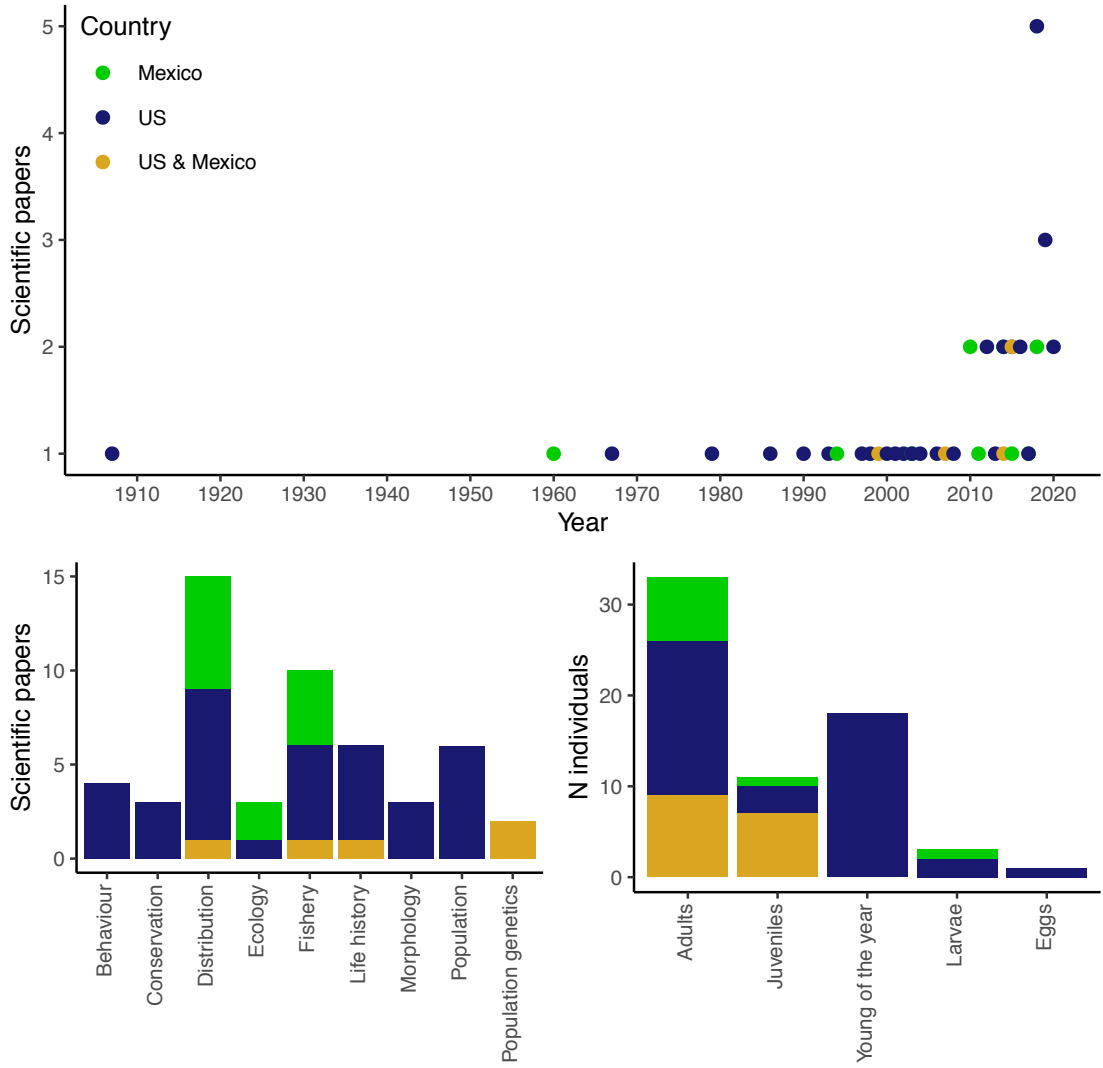


Figure 2.3. Synthesis of the literature review of the knowledge of the giant sea bass across its entire distribution. A) Giant sea bass research has recently increased, especially in Mexico. B) Most papers on giant sea bass are focused on the distribution and fishery of the species, with less emphasis on life history. C) The majority of papers focus on adult giant sea bass, though many papers also failed to mention specific life history stages.

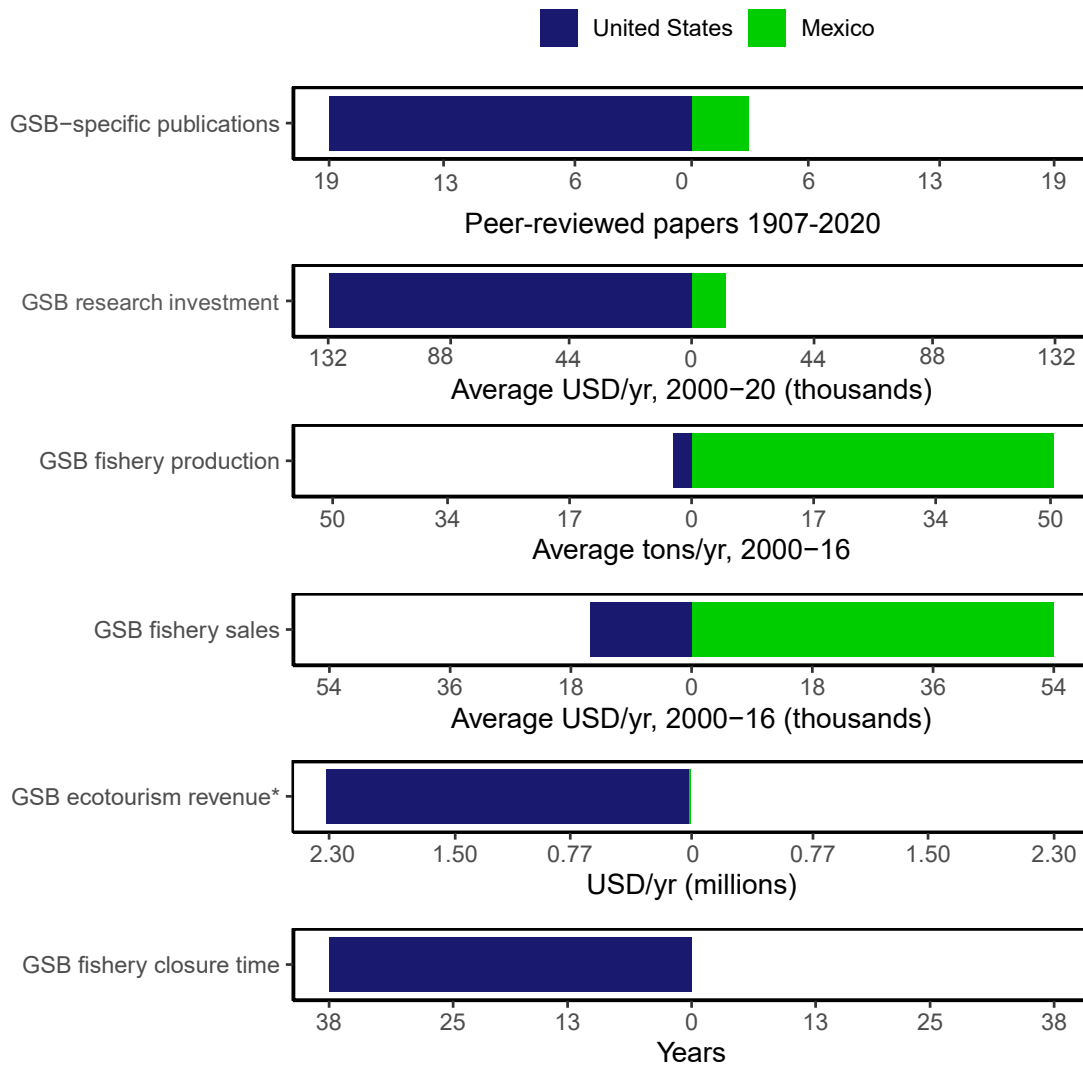


Figure 2.4. Management of the GSB across the U.S.-Mexico border is highly asymmetric. Despite little economic or scientific input Mexican fishery catches and revenue is high, a trend that is reversed in the United States. GSB ecotourism revenues after (Guerra et al., 2017).

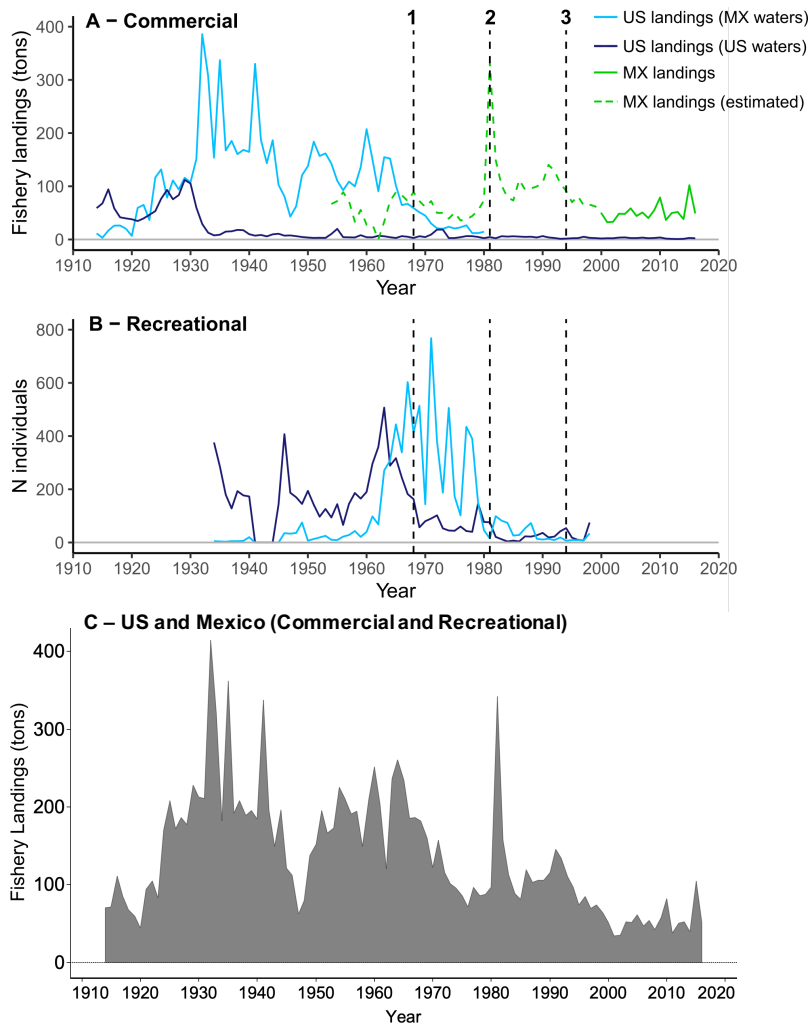


Figure 2.5. Historic and contemporary fishery landings of Giant sea bass in the U.S. and Mexico show strong variability over time. A) Commercial fishery by the U.S. and Mexico fleet, B) Recreational fishery by the U.S. fleet, C) U.S. and Mexico GSB commercial and recreational fishery landings merged. Important historical milestones are indicated by dashed red lines. Events that impacted GSB fishery management: 1 – Mexico-U.S. fisheries agreement; 2 – U.S. ban on commercial GSB harvesting; 3 – U.S. ban on gill nets and trammel nets within certain distances of the coastline, for more information on these events see Table 1. Historical data on commercial catches shows that population collapse in the U.S. waters occurred in the 1930s, much earlier than previously thought. Additionally, contemporary catches in Mexico have remained remarkably consistent, averaging 50.9 ton/yr. Despite the perceived collapse of Mexican GSB populations in 1972 by the U.S. fleet landings, Mexican fleet landings indicate that political legislation (rather than population collapse) was truly limiting catches in the 1970s. Data source: U.S.: CDFW (2001) and CDFW dataset (2000-2017). Mexico: CONAPESCA dataset (2000-2017), SeaAroundUs (1955-1999).

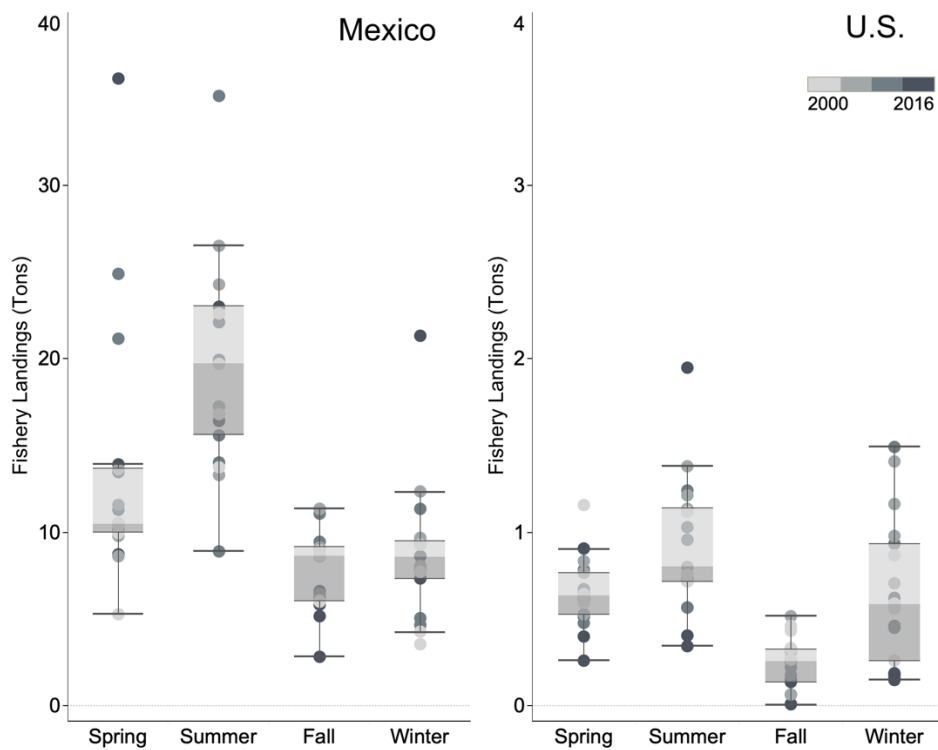


Figure 2.6. Giant sea bass contemporary catches (2000-2016) are highest in the summer, in both the U.S. and Mexico. In Mexico, this corresponds in part to the closure of the lobster fishery from April to September. Data source: Mexico = CONAPESCA-SEPESCA official landings; U.S.= CDFW fishery Landings.

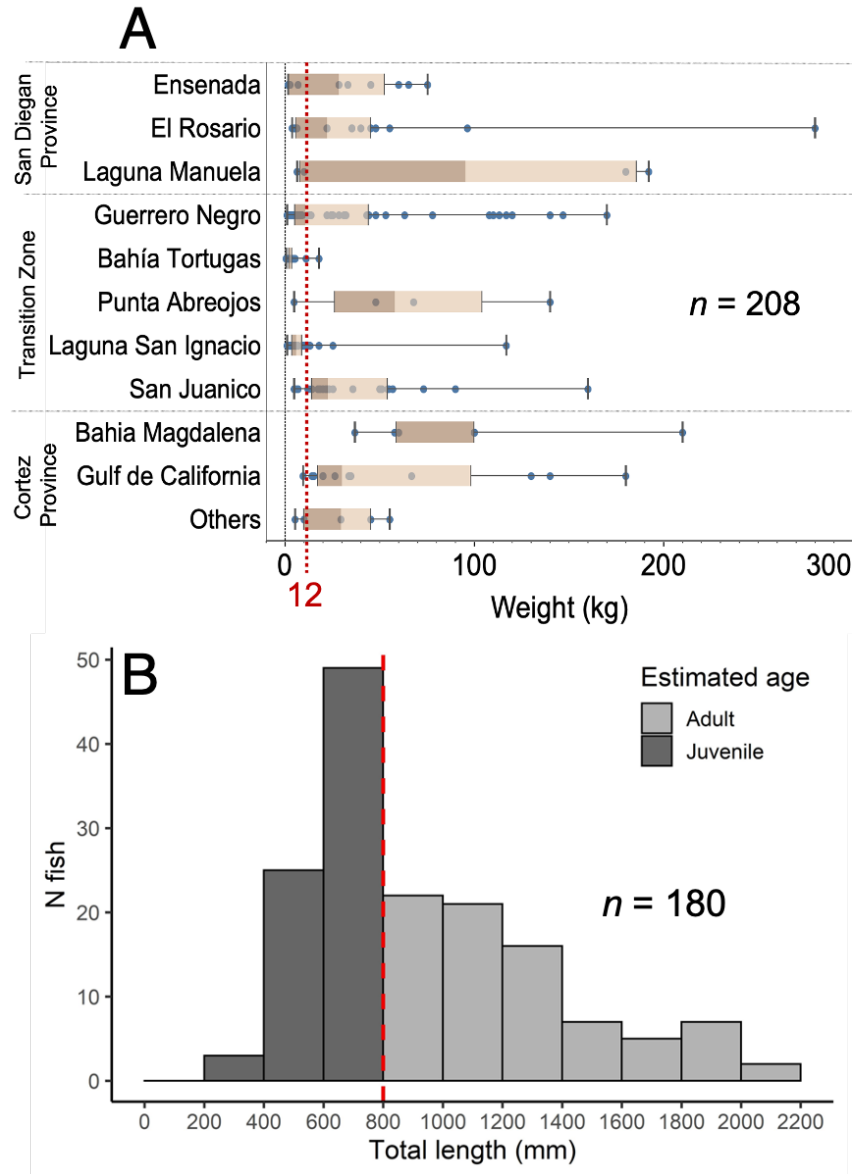


Figure 2.7. A) Box plot indicating the GSB body weight (kg) sampled through the Mexican fishery monitoring program. Median weight of 210 samples (12 kg) in red dotted line. Locations have been divided into one of three biogeographic regions: San Diegan province, Cortez province, and a transitional zone. All regions show a wide range of total weight. B) Total length of 180 samples of giant sea bass sampled through the fishery monitoring program. 48.4% of samples were shorter than 800 mm TL, indicating that many individuals may be juveniles (after Hawk & Allen, 2014).

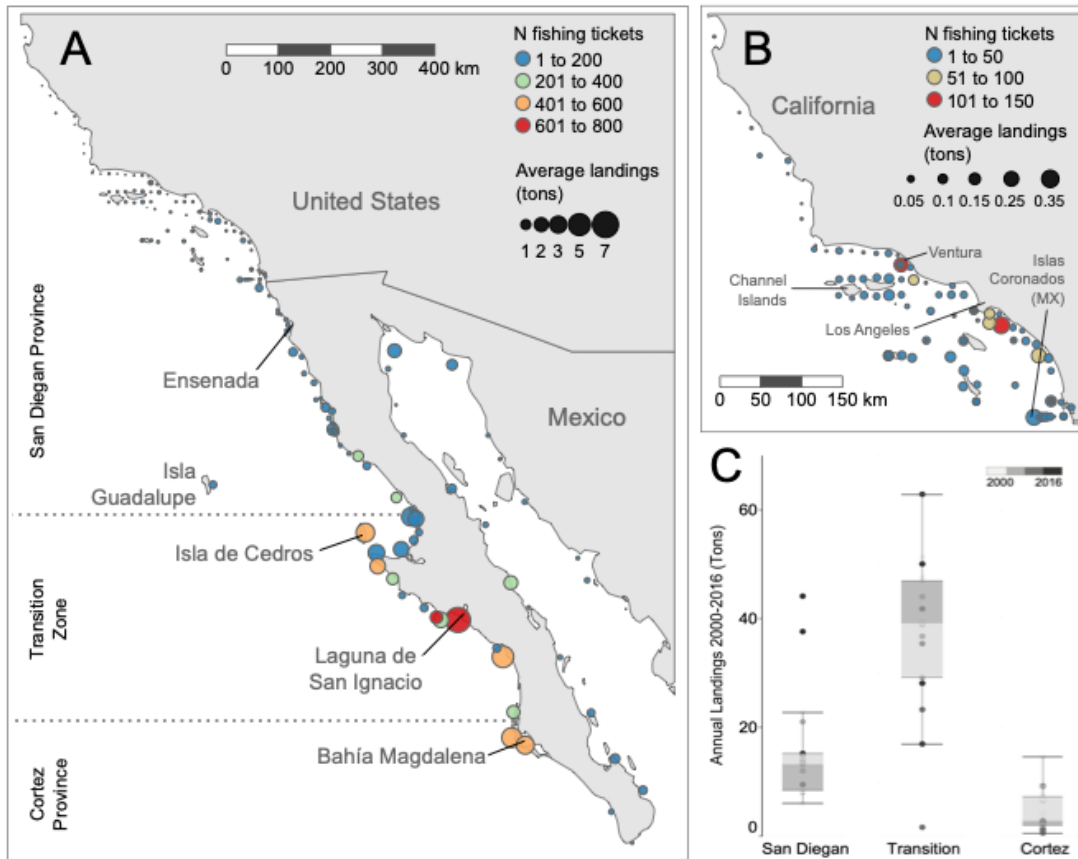


Figure 2.8. Spatial representation of the contemporary 2000-2016 annual average fishery landings of giant sea bass from the U.S. and Mexico commercial fleets shows much higher landings in Mexico. When divided into biogeographic regions, the transitional zone between the San Diegan and Cortez provinces has the highest proportion of total landings. The number of events (tickets) corresponds to the number of GSB caught. A) Entire GSB range; B) California subset; C) average annual landings from 2000-2016. Data source: Mexico = CONAPESCA-SEPESCA official landings; U.S.= CDFW fishery Landings.

SUPPORTING MATERIAL

Supporting material 1. Synthesis of scientific knowledge from the giant sea bass result of the literature review.

Characteristic	Value	Reference
Taxonomy		
Synonyms	<i>Stereolepis californicus</i> Gill 1863; <i>Megaperca ischinagi</i> Hilgendorf 1878	(Fricke, Eschmeyer, & Van der Laan, 2020)
Life history		
Clutch size (eggs)	60 million	(Domeier, 2001) (Benseman & Allen, 2018; Shane, Watson, & Moser, 1997)
Egg size (mm)	1.6 (1.5-1.6)	(Shane et al., 1997)
Larvae	Lecithotrophic	(Shane et al., 1997)
PLD (days)	26.8 ± 2.4	(Benseman & Allen, 2018)
Size at settlement TL (mm)	14.4 ± 3.0	(Benseman & Allen, 2018)
Age at first breeding (yr)	11-13 (18-24 kg)	(Domeier, 2001; Fitch & Lavenberg, 1971)
Life span- Otolith thin-sections (yrs)	76 (2003 mm SL)	(Hawk & Allen, 2014)
Life span - Radiocarbon (yrs)	51 (2200 mm TL)	(Allen & Andrews, 2012)
Reproductive mode	Oviparous, gonochoric, dioecious (sexual dimorphism*)	(Clark & Allen, 2018; Domeier, 2001; Fitch & Lavenberg, 1971)
Reproductive mode	Pelagic spawners	(Benseman & Allen, 2018; Clark & Allen, 2018)
Reproductive season	July-November (September)	(Benseman & Allen, 2018; Clark & Allen, 2018)
Reproductive strategy	Pelagic spawners; aggregations (> active at 1700-2000 hrs)	(Clark & Allen 2018; Domeier 2001) (Clark & Allen, 2018; House, Clark, & Allen, 2016)
Max. obs. agg. (ind)	20-24	(Gaffney, Rupnow, & Domeier, 2007)
Sex ratio	1:1 (inferred)	(Gaffney, Rupnow, & Domeier, 2007)

Characteristic	Value	Reference
TL max (mm)	2700 (2500)	(Allen, 2017; Domeier, 2001; IGFA, 2020)
SL max (mm)	2003	(Hawk & Allen, 2014)
Wt mx (kg)	253 (255)	(Allen & Andrews, 2012; Domeier 2001)
HL max (mm)	57	(Allen & Andrews, 2012)
YOY TL (mm)	145	(Allen & Andrews, 2012)
YOY growth rate (mm/day)	1.23	(Benseman & Allen, 2018)
Weight - Age relationship	$y=0.029x-0.085$; $R^2=0.9013$; $p<0.001$	(Hawk & Allen, 2014)
Length (SL) - Length (TL) relationship	$a=1450$; $b=-10.87$; $R^2=1.21$	(Williams et al., 2013)
Length (SL) - Weight relationship	$a=1.07E-04$; $b=-2.8$; $R^2=0.99$	(Williams et al., 2013)
Length (SL) -Age relationship	$K=0.044$; $t_0=-0.345$; $L_\infty =2026.2$; $R^2=0.911$; $p<0.001$	(Hawk & Allen, 2014)
Growth Model - von Bertalanffy	$L_\infty 2026.2$; $K 0.044$; $t_0 -0.345$	(Hawk & Allen, 2014)
YOY Length (TL) - Age relationship	$y=1.23x-18.49$; $R^2=0.908$; $p<0.0001$	(Benseman & Allen, 2018)
YOY black phase TL (mm)	10 - 21	(Benseman & Allen, 2018)
YOY brown phase TL (mm)	23 - 33	(Benseman & Allen, 2018)
YOY orange phase TL (mm)	41 - 185	(Benseman & Allen, 2018)
Natural mortality rate	6%	(Schroeder & Love, 2002)

Ecology

Distribution	Humboldt bay, California ¹ , to the tip of the Baja California peninsula and Gulf of California ²	(¹ Boydston, 1967; ² present study)
Foraging mode	Macro-carnivore	(Fitch & Lavenberg, 1971; Love, Brooks, Busatto, Stephens, & Gregory, 1996)
Trophic level	3.74	(Vilalta-Navas et al., 2018)
Prey items	rays, skates, lobster, crabs, flatfish, small sharks, squid, blacksmith, ocean whitefish, red crab, sargo, sheephead, anchovies, mantis shrimp	(Domeier, 2001; Fitch & Lavenberg, 1971; Love et al., 1996)

Characteristic	Value	Reference
Generation time (yrs)	7 - 10	(Domeier, 2001;
Ecol. density YOY	0.4/100 m ² ± 1 SD	Benseman & Allen, 2018)
Mean biomass density adults	40 kg /1000m ²	(House et al., 2016)
Population size	Pre-exploitation biomass SoCal 1,300 tons (1,179 tonnes)	(Ragen, 1990)
Home range (km)	56 (Travel > 400 km / 140 days)	(Burns, Clevestine, Logan, & Lowe, 2020)
Habitat affinity	Marine neritic	(Cornish, 2004)
YOY habitat	canyons 2-18 depth; mudflats and coastal lagoons	(Benseman & Allen, 2018; Couffer et al., 2015; Love, 2011)
Juvenile habitat	soft muddy bottom; flat sandy bottom (12-21 m depth)	(Love, 2011)
Adults Habitat	edges of nearshore rocky reefs and kelp forest (10-46 m depth)	(Love, Mecklenburg, Mecklenburg, & Thorsteinson, 2005; Miller & Lea, 1972)
Northernmost distribution record	Humboldt Bay, California, U.S.	(Boulenger, 1907)
Southernmost distribution record	Southern tip of Baja California Peninsula (larvae records from Oaxaca, Mex)	This study
Symbiosis behavior	Cleaned by four species	(Dewet-Oleson & Love, 2001)
Resilience	Low; minimum population doubling time > 14 years (t _m =11; t _{max} =75)	(Musick et al., 2000)
Population genetics		
Mean Nucleotid diversity	0.09	(Gaffney et al., 2007)
Mean Nucleotid diversity	0.001 ± 0.001	(Chabot, Hawk, & Allen, 2015)
Haplotype diversity	13 (h= 0.88)	(Gaffney et al., 2007)
Haplotype diversity	4 (0.162 ± 0.064)	(Chabot et al., 2015)
Effective population size Ne	502.84 x 10 ⁻³ ; Ne Est ² 152.8; NeEst ² 95% CI 84–539.2	(Chabot et al., 2015)
Avg. observed heterozygosity	0.654-0.706	(Chabot et al., 2015)
Observed number of alleles	112 (59-81)	(Chabot et al., 2015)
Avg. allelic richness	8.87 (4.54-4.81)	(Chabot et al., 2015)

Characteristic	Value	Reference
	df 121; sum of sq 517.492; variance	
Fst values	4.289; 1 % var	(Chabot et al., 2015)
Fixation index (FST)	0.01 (p=0.034)	(Chabot et al., 2015)
Fishery		
Commercial catch vs SST correlation	r= -0.338 (p=0.340)	(Pondella & Allen, 2008)
Commercial catch vs PDO correlation	r= -0.284 (p=0.426)	(Pondella & Allen, 2008)
Commercial catch vs ENSO correlation	r= -0.166 (p=0.646)	(Pondella & Allen, 2008)
Median Size Recreational Fishery in the U.S. (1966-2008) (kg)	50	(Bellquist & Semmens, 2016)

Supporting material 2. Giant sea bass geographic distribution map based on 11,198 records from 509 sites across the Northeastern Pacific extracted from the Global Biodiversity Information Facility (gbif.org), California Department of Fish and Wildlife (CDFW), the California Recreational Fisheries Survey (CRFS) (<https://www.recfin.org/>), the Mexican government fisheries management agency (CONAPESCA), scientific collections⁽¹⁾ in Mexico and the U.S., fishery-independent surveys⁽²⁾, and data from Proyecto Mero Gigante. Seventy-three percent of the GSB distribution is found in Mexican water based on all records shown on the map, except for the larval record in Oaxaca, Mexico. The Oaxaca record represents an isolated record from the next southernmost record for more than 1500 km with no confirmed adult records in between.



(1) Scientific collections

- Scripps Institution of Oceanography (SIO)
- Universidad Michoacana de San Nicolás de Hidalgo (UMSNH)
- Universidad Autónoma de Baja California (UABC)
- Centro de Investigaciones Costeras at Universidad de Guadalajara (U de G)
- Centro Interdisciplinario de Ciencias Marinas del IPN (CICIMAR)
- Centro de Investigaciones Biológicas del Noroeste (CIBNOR)

National Fish Collection at Universidad Nacional Autónoma de México (UNAM)
Fish collection at ICMYL Mazatlán (UNAM)
Universidad Autónoma de Sinaloa at Mazatlán (UAS)
Centro de Investigación en Alimentación y Desarrollo at Sonora (CIAD Sonora)
Fish Collection at Universidad Autónoma de Nuevo León (UANL)
Fish Collection at Universidad Autónoma de Guerrero (UAGro)
The López-Perez Lab at the Universidad Autónoma Metropolitana (UAM)
Fish Collection at Universidad Autónoma de Nayarit (UAN)
Universidad del Mar at Puerto Ángel, Oaxaca (UMAR)

(2) Fishery independent surveys

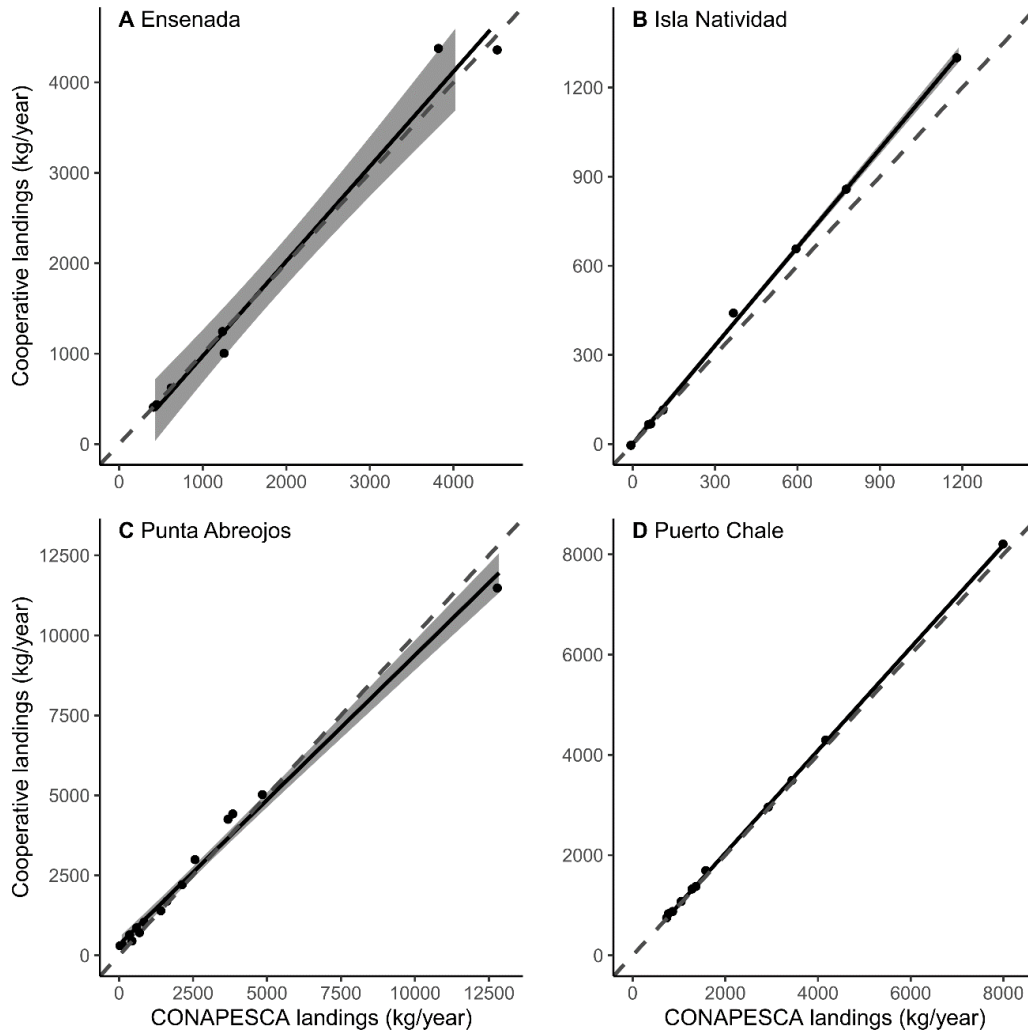
Fish surveys from Proyecto Mero Gigante
Fish surveys from the ONG Comunidad y Biodiversidad, A.C. (COBI)
Fish surveys Reyes-Bonilla Lab at the Universidad Autónoma de Baja California Sur
Fish surveys from the ONG Ecosistemas y Conservación: Proazul Terrestre A.C.
Fish surveys from Centro para la Biodiversidad Marina y Conservación, A.C.

Supporting material 3. Economic investment on giant sea bass research and husbandry.

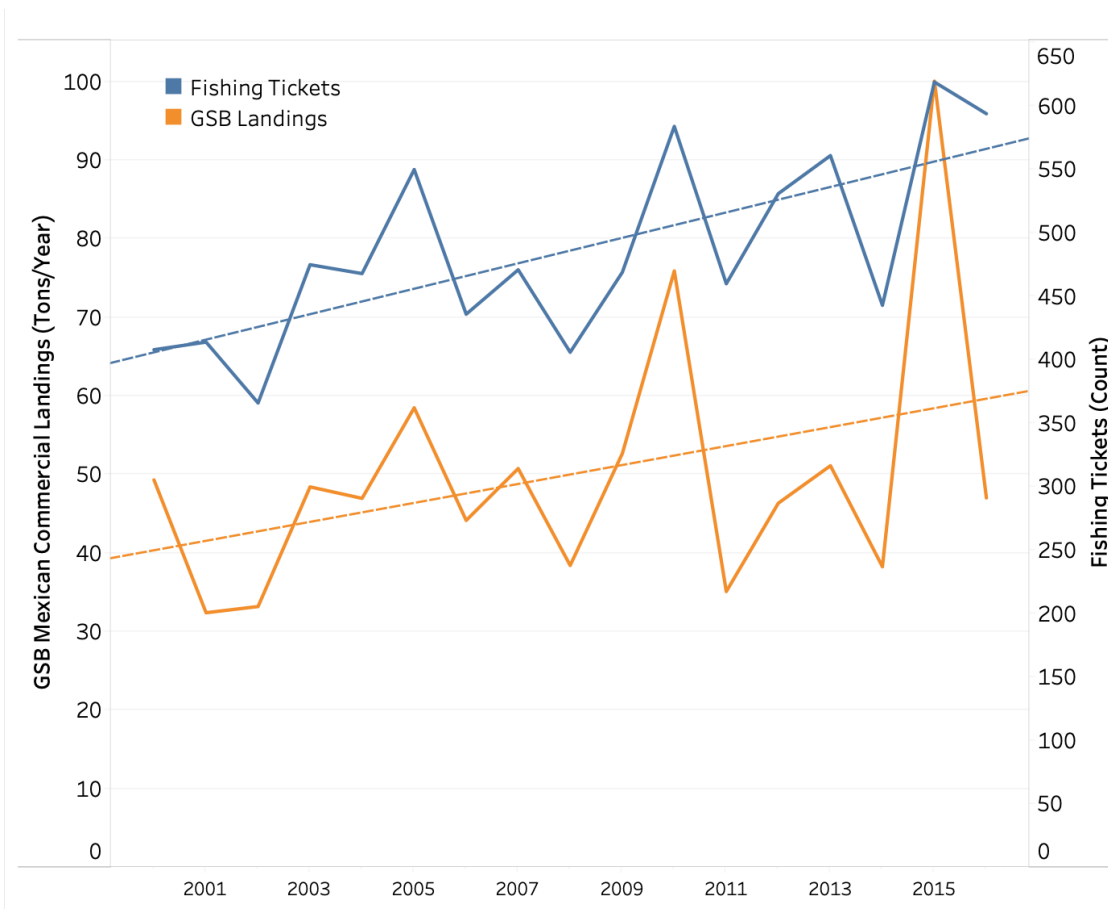
Country	Reference	GSB Project Topics	Period	Years	Funds allocated (US\$)	Funds allocated/Year (US\$)
U.S.	1	GSB Conservation	2016-2019	3	\$35,000	\$11,667
	2	YOY GSB growth & release	2018-2019	1	\$37,000	\$37,000
	3	Adults movements patters, Habitat preferences	2016-2020	5	\$40,000	\$8,000
	4	Age-Growth, Population genetics, Distribution, Courtship behavior, YOY distribution, Sound production	2010-2020	9	\$30,500	\$3,389
	5	Nursery habitat and Distribution of YOY	2015-2020	4	\$27,697	\$6,924
	6	Adults movements patters, Habitat preferences, Reproductive biology, Population genetics, Fishery	2000-2009	8	\$400,000	\$50,000
	7	Adults movements patters, Habitat preferences, Fishery	2002-2006	4	\$70,000	\$17,500
	8	Adults movements. Trophic ecology. GSB conservation	2012-2020	7	\$42,000	\$6,000
	9	Population size. Economic Value. Spotting GSB website	2014-2020	5	\$42,000	\$8,400
U.S. Total			2000-2020	19	\$724,197	\$148,880
Mexico	10	Age-Growth, Population size, Aggregation site, Fishery, Populations genetics	2017-2020	3	\$25,000	\$8,333
	11	Population size, Aggregation site, Fishery, Populations genetics	2018-2020	1	\$5,000	\$5,000
	12	Populations genetics, Age-Growth	2018-2019	1	\$500	\$500
Mexico Total			2017-2020	3	\$30,500	\$13,833
U.S. and Mexico Total					\$754,697	

1-Aquarium of the Pacific, 2-Cabrillo Aquarium, 3-CSU LB, 4-CSU Northridge, 5-M. Couffer, 6-M. Domeier, 7-Pfleger I.E.S., 8-SIO, 9-UCSB, 10-SIO-Proyecto Mero Gigante, 11-Comunidad y Biodiversidad, A.C. (COBI), 12-Proyecto Mero Gigante-UABC.

Supporting material 4. Giant sea bass Landings data from CONAPESCA do not statistically differ from data gathered directly from four fishing cooperatives. The four fishing cooperatives have an important share in catches, averaging 2-4 tons per year.



Supporting material 5. Commercial fishery landings of giant sea bass from the Mexican fleet (tonnes/yr) and fishing tickets (count).



Supporting material 6. Linear regressions of the giant sea bass fishery trends in the U.S. and Mexico.

Dependent variable	Independent variable	P	Slope	Adj. R ²
US commercial landings (US waters)	Year	< 0.001	-0.56	0.43
US commercial landings (MX waters)	Year	0.159	-0.74	0.015
US recreational landings (US waters)	Year	< 0.001	-2.96	0.23
US recreational landings (MX waters)	Year	0.227	1.40	0.008
MX total landings (after 2000)	Year	0.116	1.34	0.10

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CHAPTER 3:

The economic value of the kelp forest ecosystem services across political borders:
an approach with commercial fishery ex-vessel value

ARTURO RAMÍREZ-VALDEZ

ABSTRACT

Kelp forests are ecosystems prevalent in temperate shallow rocky reefs that provide ecosystem services to humans. On the Pacific coast of North America, iconic giant kelp forests are a shared ecosystem distributed across Mexico and the United States (U.S.) border and which connects species' populations and sustains diverse marine communities. However, current trends show that coastal towns and cities will continue to grow in the region, increasing the anthropogenic pressures on kelp forests. Furthermore, there is no robust estimation of the economic impact nor the habitat loss and subsequent loss of biological diversity caused by the increasing anthropogenic impacts. By using remote sensor technology with Landsat satellite images, we obtained the kelp forest cover and analyzed its temporal trends within Fishing Management Areas (FMA) that we associated with information on the fishery landings of species that rely on this ecosystem. Giant kelp cover showed a decrease in El Niño events and an increase during La Niña. The cover decrease related to warm waters is more prolonged and severe at the southern limit of its distribution. We found a positive correlation between kelp cover and fisheries landing for species such as lobster, sea urchin, and abalone. We also found a non-significant positive relationship for giant sea bass and California sheephead fisheries. The economic value of the kelp forest ecosystem by area coverage was up to 20 times higher in Mexico (US\$6 million km²/yr) than in California (US\$250,000 yr⁻¹), based on the total fisheries value. The abalone fishery has the highest economic value (US\$5.3 million per yr), while the red sea urchin fishery has a better economic value per kelp coverage ratio (US\$290,000 km²/yr). This represents the first effort to assess the economic

value of the kelp forest ecosystem throughout its distribution in the Northeastern Pacific and proposes a binational perspective on the understanding and management of the marine resources.

INTRODUCTION

Marine ecosystem services are seriously undervalued, resulting in a general underinvestment in conservation and many lost opportunities for economic growth and poverty reduction (Costanza et al., 1997; Lange and Jiddawi, 2009). Economic valuation provides a powerful tool for sustainable development by showing how dependent economy really is on an ecosystem, and by illustrating what could be the social impact if the ecosystem service it provides is not protected (Beaumont et al., 2008). Paradoxically, direct users and policy-makers, who appreciate consumptive uses the most, have historically undervalued these ecosystems. Although consumptive uses represent only a small proportion of an ecosystems' total value, economic data generated by these uses are the most frequent type of data available to valuate ecosystem services.

The kelp forests provides a wide range of services for human populations including: food and natural products, recreational and commercial fisheries, ecotourism opportunities, cultural value, nutrient cycling, and the resilience of other marine and coastal ecosystems (Pendleton and Rooke, 2010; Tegner and Dayton, 2000b; Wilmers et al., 2012). Although poorly valuated to date, these services nevertheless are vital to human welfare. Among these ecosystem services, those of direct use such as commercial fisheries, represent an important economic and social component. General estimations highlight that compared with other ecosystems, kelp forest ecosystem services rank among the highest in economic value (Costanza et al., 1997). Among these ecosystem services, those of direct use such as commercial fisheries, represent an important economic and social component.

On the Northeastern Pacific coast, the forests formed by giant kelp (*Macrocystis pyrifera*) are the most biodiverse and productive marine ecosystems that provide food, create habitat, and sustain trophic webs (Dayton, 1985; Schiel and Foster, 2015). Species part of these kelp forests' trophic webs are among those that represent an important fishing value and support the economy of many coastal towns and cities across two nations, the United States (U.S.) and Mexico. The kelp forest ecosystems in this region have experienced two very different histories in their fisheries management; along the coast of California (U.S.), a long history of fishing pressure and later collapse of economically important fisheries (Tegner and Dayton 2000), early efforts of spatial fishery management, and more recently the implementation of marine reserves networks (Marine Life Protection Act). Contrastingly, the kelp forests off the coast of the Baja California Peninsula (Mexico), have experienced more recent fishing pressure and efforts to improve fishery management, yet are still without marine protected areas. In general, fishing is an important economic activity through the distribution of the kelp forest across the U.S.-Mexico border. For instance, the California commercial and recreational fishery generated approximately US\$24.9 billion in sales and more than 142,000 direct and indirect jobs in 2016 (NOAA, 2016). Ex-vessel revenues for the commercial fishery in the Baja California Peninsula region (Baja California and Baja California Sur), generated approximately US\$228 million and more than 8,000 direct jobs in 2016 (CONAPESCA 2018, SEPESCA 2016). These economic benefits support an important social structure in the region beyond sales and direct jobs; this economy impacts tourism, food industry, and has roots in the local communities of both countries.

There are several important commercial and recreational fisheries of invertebrates throughout this region that support social well-being and are part of the ecosystem services that giant kelp forests provide, such as abalone (*Haliotis* spp.), California spiny lobster (*Panulirus*

interruptus) and sea urchins (*Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus*), as well as fish such as giant sea bass (*Stereolepis gigas*) and California sheephead (*Semicossiphus pulcher*; Love et al., 1998; Schroeder and Love, 2002). The California spiny lobster, red sea urchin, and purple sea urchin represent a good example of the asymmetry in management and economics associated with their fishery across the US-Mexico border (Figs. 3.1–3.2). These shared stocks are being fished with comparable techniques; however, the associated catch and the economy are considerably different.

Despite the ecological and economic importance of the giant kelp forest ecosystem, there has only been a limited focus of conservation efforts across its distribution in both the U.S. and Mexico. Although there is information on some of the ecosystem services that kelp forests provide to humans in the region, as far as we know, there is no published information that integrates these ecosystem services and relates them to kelp forest cover. An effort to study this ecosystem from a binational perspective is also absent, which would make ecological and economic sense, as it encompasses its entire distribution and both countries share the majority of economically important species. In ecosystems shared between nations, such as kelp forest, the actions taken by one nation invariably affect the other.

Ecosystem services valuation represents a powerful tool for decision-making based on the economic value of marine resources, allowing identification of opportunities to improve marine management and sustainable development. Here we estimate the economic value of the giant kelp forest ecosystems across the entire geographic distribution in the Northeastern Pacific, based on some of the most important fisheries in the region. To test the hypothesis that the kelp cover has a direct bearing on the production of commercially important fisheries, we evaluated the giant kelp cover inside Fishery Management Areas (FMA) that span all the geographic distribution of the

giant kelp and compared it with the fisheries production within those FMA. Overall, an economic valuation will contribute to better-informed decision-making to protect these ecosystems.

MATERIAL AND METHODS

Study area

Giant kelp (*Macrocystis pyrifera*) distributional range in the Northeastern Pacific extends from Sitka, Alaska (US) to south of Punta Eugenia, Baja California Sur (Mexico), however, well-defined submerged forests can only be found south of Santa Cruz, California (Cavanaugh et al., 2019; Macaya and Zuccarello, 2010; Schiel and Foster, 2015). This study spans the distribution of submerged giant kelp forests, which encompass more than 10 degrees of latitude (approximately 1600 km), from Seal Rock, Santa Cruz (U.S.; 36.5° N) to the southern range limit near Bahía Asunción, Baja California Sur (Mexico; 27.1° N) (Fig. 3.3). Giant kelp in the west coast of North America occurs primarily on shallow rocky reefs (5–25 meters) that are distributed in patches.

The main oceanographic driver in this region is the California Current System (CCS), which is one of the five most productive marine ecosystems on the planet (Checkley and Barth, 2009; McClatchie, 2014). The high productivity of the CCS is mainly attributed to Equator-ward transport of temperate waters, as well as favorable winds for coastal upwelling, which together generate an offshore transport of surface waters and advection of relatively cold and nutrient-rich waters to the surface (Checkley and Barth, 2009).

Spatial approach

We used 182 Fishery Management Areas (FMA) along the study area (Fig. 3.3; Table 3.2). The FMA are polygons representing ocean habitat used by the U.S. and Mexico fishery government agencies to spatially manage marine fisheries. The Mexico's FMA are 81

“commercial fishing concessions polygons” granted to fishermen cooperatives by CONAPESCA (The National Commission for Fisheries and Aquaculture). The Mexican FMA essentially function as Territorial Use Rights for Fisheries (TURFs) for fishers from coastal communities. In the case of the US, the FMAs are 10-minute latitude \times 10-minute longitude grid blocks established back in the 1930s by the California Department Fish and Wildlife (CDFW). These grid blocks extend throughout California coast within the Economic Exclusive Zone of the U.S. and are used for spatial management of all fisheries. We integrated all FMA in a Geographic Information System (GIS) using ArcGIS v10.8 to facilitate spatial analysis. In the case of Mexico, 74 fishing concessions granted to species that rely on the giant kelp forests were used. For the U.S., we filtered 101 out of 554 10 \times 10-minute grid blocks that were within a 30-meter-deep bathymetry layer along the coast from the US-Mexico border to Santa Cruz, California and the Channel Islands (Fig. 3.3).

Kelp cover

Giant kelp (*Macrocystis pyrifera*) forest cover (km²) within all 182 FMA was estimated using high-resolution satellite imagery. We used images of the Landsat 5 Thematic Mapper sensor with 30 m spatial resolution nearly continuously from 2000 to 2017. The satellite image processing followed the same methodology used for the terrestrial vegetation as the spectral signature of a giant-kelp canopy is similar to that of photosynthetically active terrestrial vegetation (Fig. 3.4) (Cavanaugh et al., 2010; Jensen et al., 1980). Landsat 5 Thematic Mapper obtains data in 7 spectral bands: blue (450 to 520 nm), green (520 to 600 nm), red (630 to 690 nm), near-infrared (760 to 900 nm), short-wave infrared (1500 to 1750 and 2080 to 2350 nm), and longwave (thermal) infrared (10400 to 12500 nm; Cavanaugh et al., 2011). The kelp near-infrared (Band 4) radiance signal, while elevated compared to that of water, spans only the lowest ~40 brightness values

detectable by Landsat 5 Thematic Mapper. Each of the Landsat scenes covers an area 170×180 km, so multiple scenes were used to cover the entire study region (Fig. 1). During preprocessing, Landsat images were geometrically corrected using ground control points and a digital elevation model to achieve a scene-to-scene registration accuracy <7.3 m (Lee et al. 2004). We were able to discriminate zero values due to the absence of kelp from zero due to satellite image reading errors (*i.e.* clouds, wind). We developed an automated classification and quantification process in order to consistently and efficiently transform the Landsat 5 Thematic Mapper images into maps of kelp canopy cover. A detailed method of procedure and image calibration is described in Cavanaugh, Siegel, Reed, & Dennison, (2011) and Bell, Cavanaugh, Reed, & Siegel (2015).

We obtained annual average kelp cover values for each FMA from seasonal values. FMA with values of zero in the entire data series were eliminated, assuming the non-existence of the specific giant kelp habitat.

Fishery landings and revenues

Commercial fishery landings datasets from 2008 to 2017 were obtained from fishery government agencies for three commercially important invertebrate species that rely on the kelp forest ecosystem; California spiny lobster (*Panulirus interruptus*), red sea urchin (*Mesocentrotus franciscanus*), and purple sea urchin (*Strongylocentrotus purpuratus*) (Table 3.1). In addition, two fish species, California sheephead (*Semicossyphus pulcher*), and giant sea bass (*Stereolepis gigas*), and the abalone's species-complex were included in the analysis, all of which are important in the maintenance of the kelp forest ecosystem trophic web and with asymmetric fisheries management across the U.S.-Mexico border (Table 3.1). Mexican commercial fishery landings were obtained from the Mexican federal fishery agency CONAPESCA. The U.S. commercial fishery landings were obtained from the California Department of Fish and Wildlife (CDFW). In both cases, the

U.S. and Mexico fishery landings were obtained from fishing tickets, which include species, catch site FMA-associated, and date.

Fishery landings were analyzed independently by species, and annual Fishery Production was obtained by dividing annual fishery landings (kilograms) by the area within the FMA (km²):

$$\text{Fishery Production} = \frac{\text{Fishery landings [kg]}}{\text{FMA [km}^2\text{]}}$$

We obtained the economic revenues for each fishery using the official price for each species reported by government agencies. For the U.S., the revenues for each fishery were calculated with the average annual market price per pound (converted to kg) reported by the CDFW and were corrected for inflation to 2018 by using the Consumer Price Index (World Bank). In the case of Mexico, we used the same market price reported by CDFW for California spiny lobster, and Red and purple sea urchins. These three species are exported to Asia, and the market for both, the U.S. and Mexico, are comparable. In the case of abalone, California sheephead, and Giant sea bass we used the official market price by CONAPESCA (CONAPESCA, 2018). We also corrected for inflation to 2018 by using the Consumer Price Index (World Bank) for these species. By using the same price for some of these fisheries, we not only facilitate the analysis but also focused on the differences in production more than in price.

Kelp cover size versus fishery production

We selected 10 years (2008-2017) where the kelp cover and commercial fishery landings overlap was greatest. We performed the analysis using the percentage of kelp cover within the FMA, due to the variability of the FMAs area and therefore the area of kelp coverage inside (Fig. 5). The giant kelp coverage within each FMA was transformed into a percentage of coverage from the total area:

$$\%FMA \text{ Kelp cover} = \frac{\text{Kelp coverage [km}^2\text{]}}{\text{FMA [km}^2\text{]}}$$

The %FMA kelp cover was classified in three categories based on the data distribution: Low coverage (<0.1% of kelp cover within the FMA), Medium (between 0.1 – 1.0% of FMA kelp cover) and High (> 1.0% of FMA kelp cover). The number of FMA in each of the kelp cover categories was variable by year and by species. In the case of the US, the FMA is the same for all the species analyzed. In the case of Mexico, for most cases, the FMA is the same, but there are a few exclusive FMAs for lobster and sea urchin fishery. The summary of FMA in each kelp cover category is presented in Table 2.

Statistical analysis

We tested differences in FMA size between countries and within countries (*t*-test). In addition, we tested differences in FMA kelp coverage by latitude, using the geographic location of each FMA with respect to the polygon centroid. We also tested differences in FMA kelp coverage between countries and within countries. We use linear regressions to test the relationship between kelp coverage and production for each fishery. The significance of the fishery production between the kelp cover size within the FMA was tested using one-way analysis of similarities (ANOSIM). While the significance of the fishery production between the kelp cover size within the FMA and between countries was tested using 2-way ANOVA

RESULTS

Spatial approach

The area and shape of the 182 FMA varied between and within the U.S. and Mexico. The average area of the FMA was 252 km² (± 582.05 SD), with a minimum value of 0.9 km² and a maximum value of 5,379 km² (Table 2). The size of the FMA within countries was even more

variable, the mean size for the US FMA was 191 km² (\pm 94.05 SD), while the mean size of the FMA in Mexico was 327 km² (\pm 860.72 SD). There are major differences between the FMA of both countries, the shape, the location with respect to the coast, and the management of the fisheries within them are just some of these differences. The *t*-test ($t = 0.679$; $P < 0.01$) shows significant differences in area between FMAs in the U.S. and Mexico.

With the exception of the fishing concessions on the islands, the Mexican FMAs are distributed along the coast according to the availability of the habitat, and their extension varies according to the depth at which the species included in the fishing concession are distributed. On the other hand, the U.S. FMAs extend to greater depths than the kelp distribution.

Kelp cover within FMAs

On average, the US FMAs have higher kelp cover compared to those located south of the U.S.-Mexico border. The two-way ANOVA analysis showed significant differences between the kelp coverage within the FMA with respect to latitude and year. The year 2013 had the highest kelp coverage, while 2016 was the year with the lowest kelp coverage. The kelp coverage within the FMAs was variable over time and also across the geographical range of distribution. Neither the latitudinal gradient ($R^2 = 0.0256$, $P = 0.119$) nor another geographic pattern was detected. The size distribution of kelp cover within the FMAs showed most of them had less than 1% kelp coverage within them, with a mean of 0.45%.

Kelp cover size versus fishery production

The fishery production increases when the kelp cover area within the FMAs is higher in the case of spiny lobster, purple sea urchin, red sea urchin, and abalone (one-way ANOVA, $P < 0.05$; Figs. 3.6–3.7). Although the relationship between fishery production and kelp cover was not significant for all fisheries evaluated (Table 3.3), the difference between the kelp cover categories;

high, medium and low, was significant. The greater the kelp cover inside the FMAs, the greater the production of the analyzed fisheries. This difference was not significant in the two fish species, where even when the same pattern of greater fishing production with greater kelp cover, however, the differences between the categories were not significant.

Kelp cover size versus fishery production by country

The fisheries production of California spiny lobster, red sea urchin, and purple sea urchin split by country showed the same relationship, higher production to higher kelp cover (Figs. 3.8–3.10). California spiny lobster production was significantly higher in FMAs with the highest kelp cover, and it was up to three times higher on average than medium kelp cover in Mexico, and more than double for the U.S. (Fig. 3.8). The California spiny lobster production was still higher on FMA with medium kelp cover compared with low kelp cover, however, these differences were not significant in the case of Mexico. Red sea urchin production was up to 16th times higher on average in FMAs with higher kelp cover compared with medium kelp cover in Mexico, and more than double for the U.S. (Fig. 3.9). We did not find differences in the red sea urchin production between FMAs with medium and low kelp cover in the U.S. and Mexico. Purple sea urchin fishery production was significantly higher in FMAs with the highest kelp cover for both, Mexico and the U.S., however, the production in Mexico is four digits higher than the U.S. (Fig. 3.10). The average fishery production of purple sea urchin in FMAs with higher kelp cover was up to 54-fold the average of medium kelp cover in Mexico.

Kelp forest cover and commercial fisheries value

A positive relationship exists between the proportion of kelp coverage within the FMAs and the mean economic value (2008-2017) of the fisheries (Fig. 3.11). Our analysis shows that: a) the higher the proportion of kelp cover within the FMA, the greater the value of the fishery, and b) the

ratio of the kelp cover within the FMA and the economic inputs as a result of the fishery production is higher for species that depend more on kelp, such as abalone and sea urchins. The abalone fishery in Mexico is by far the one with the highest economic yield and between the major showing the greatest relationship with kelp coverage within FMAs (US\$ 51,000 per 1.03% of kelp cover) together with red sea urchin and purple sea urchin fisheries in Mexico. The finfish fisheries, giant sea bass, and California sheephead, showed a lower ratio of economic value and kelp cover. The lobster fishery in Mexico stands out with the lowest kelp coverage ratio of all, it is the second most economically profitable fishery. The economic value of the kelp forest increases in fisheries that rely on kelp as part of their food sources and decreases in fisheries for species that are not directly dependent on kelp, such as the carnivorous giant sea bass and California sheephead.

DISCUSSION

Our results show that the value of the ecosystem services provided by the kelp forests may be higher than US\$9 million per year, considering only the extractive services of the commercial fishery, which represent a small fraction of all the benefits we obtain from this ecosystem. This study provides relevant information for managers and decision-makers with implications for public policies in the regulation and conservation of the coastal resources of both countries, the U.S. and Mexico. Giant kelp forests are not only the most productive marine ecosystem in the region, but also support economically important species (Tegner and Dayton 2000). Considering only the abalone fishery in Mexico, for example, the economic value of production can be up to US\$8 million in a fishing season. Unlike other services that ecosystems provide to humans, in this case, the loss of the giant kelp forest would also represent the total loss of some of these fisheries as they are highly dependent on the existence of giant kelp for their subsistence.

The contrast of the fishery production of the same species (*i.e.*, lobster, red sea urchin, and purple sea urchin) in the U.S. and Mexico is an excellent example of how management beyond biological factors or the market is decisive in the benefits we get from the fisheries. When comparing the geographical distribution of these three species and their ecological densities, the differences across the U.S.-Mexico border are not significant (Edwards and Estes 2006, Torres-Moye et al. 2014). The pressure that economic markets exert on these resources applies equally to the products from both sides of the border since both Mexico and the U.S. export their products to Asia (CDFW 2016, SEPESCA 2018). Even when both countries have management by quotas and size limits, probably the most significant difference is that Mexico's fisheries management is by territorial-use rights (TURF). In contrast, in the U.S., fisheries are managed through individual licenses.

The asymmetry in the fisheries management across the U.S.-Mexico border explains, for the most part, the differences in production. Management differences include the designation of fishing grounds, recreational fishing permits for important commercial species, and individual fishing permits versus territorial concessions. Fishing concessions in Mexico are assigned to organized groups of fishermen called cooperatives, who fish or harvest one or more resources inside the same FMA. In the U.S., permits are granted to individual fishers, and these permits are not linked to a specific fishing ground or FMA. Although it may seem that in both cases the fishing effort is stable over time, in the case of Mexico, no more fishing concessions have been granted and the fisher members are constant, while in California the number of active fishers has been relatively stable since 2003 (CDFW 2016), the major difference can occur in terms of the pressure to specific fishing grounds, the number of traps used, and the possibility of transferring individual permits.

The greater fishing production in Mexico of benthic species (*i.e.*, spiny lobster, sea urchin) is the result of the combination of greater fishing landings and FMAs specifically directed to the habitat of these resources. While lobster landings are higher in Mexico, this is not the case for the two species of sea urchin. Unlike the FMAs in California, the FMAs in Mexico are mostly smaller areas and specially designated to areas where the species is present at a density to support a fishery. The design of the FMAs in the U.S. represents a standardized management for all the fishing resources, independently of their ecological density inside the polygon, even if the species density is low to support a fishery. The FMAs in Mexico were designed to set polygons in areas where the presence of the species can support a fishery.

Our analysis successfully shows a positive relationship between the giant kelp forests cover and the fishery production of the analyzed fisheries. The higher the percentage of giant kelp cover within the FMAs, the greater the production of the fisheries. This relationship is even more significant in those species that depend directly on giant kelp, such as abalone and sea urchin species (Leighton 2000, Tegner and Dayton 1981). Even though lobster does not feed on giant kelp, their most common preys do, which is why other studies have found the same relationship between giant kelp density and spiny lobster harvest (Guenther et al. 2012).

The relationship between the percentage of giant kelp cover within the FMAs and the fishery production was positive but not significant for the two fish species. Both species of fish are common residents of the kelp forests, and studies have analyzed their close relationship with this ecosystem (Tegner and Dayton, 2000a). While California sheephead is probably the most important predator of adult sea urchins and they can become the largest component of their diet, Giant sea bass feed on a wide variety of invertebrates associated with giant kelp (Domeier, 2001;

Hamilton and Caselle, 2015). However, these species are also commonly found on rocky reefs on the edge of kelp forests, areas that are frequently visited by fishers.

Contrary to what previous studies reported, our results do not show an effect of a trophic cascade in the kelp forests as a result of fishing for predators of this system (Guenther et al., 2012; Lafferty, 2004; Tegner and Dayton, 1981). Fishing can trigger a trophic cascade effect on ecosystems by selectively changing the abundance of specific species and thus altering the composition and structure of communities (Tegner and Dayton, 1981). In this case, the extraction of lobsters by the fishery could increase the abundance of sea urchins which, due to the grazing effect, would decrease the giant kelp cover. Guenther et al. (2012) found no evidence that the lobster fishery indirectly impacted giant kelp biomass through increased urchin abundance, however, they reported a decrease in urchin abundance due to the top-down effect. In contrast, our results indicate that both, lobster and sea urchin show greater fishery landings in the presence of greater giant kelp cover.

Our results show that the positive relationship of giant kelp cover and sea urchin-lobster fishery production is maintained throughout the entire study region and across a political border, even in the face of wide differences in the fisheries management scheme. The giant kelp forests in the Northeastern Pacific are fairly equally present in coastal extent in both the U.S. and Mexico, and our results coincide with previous studies in pointing out that the density of giant kelp does not show a latitudinal gradient across this geographic region (Edwards, 2004; Edwards and Estes, 2006). On the other hand, both countries exert fishing pressure on both the spiny lobster and sea urchin, and, in most cases, these fisheries occur within the same FMAs. Asymmetries in the spatial management of fisheries, including the number of species being fished, fishing quotas, and fishing pressure per habitat, can be a limiting factor for this relationship to be maintained. Although

previous studies have shown the positive relationship between giant kelp cover and California spiny lobster production, and giant kelp cover and sea urchin production, what makes an even more persuasive argument is this study successfully shows this relationship across different geographic areas and different management schemes (Guenther et al., 2012; Tegner and Dayton, 1981).

This study successfully shows that the economic value of kelp forests ecosystem is significantly higher than previously thought, considering only the value of the commercial fishery. Previous work has directed efforts to economically value algal beds and kelp forests, considering different ecosystem services (Costanza et al. 1997, Vasquez et al. 2014). Costanza et al. (1997) assigned a value of US\$19,004 ha/yr to algal beds from a global perspective, while Vasquez et al. (2014) valued the kelp forests in northern Chile in US\$540 million per year. Our results indicate that the value of giant kelp forests can reach a value of US\$8.5 million per year, considering only five fisheries.

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TABLES

Table 3.1. Economically important species of invertebrate and fish closely associated with the Giant Kelp forest ecosystem.

Taxonomic group	Common name	Scientific name
Invertebrate	abalone	<i>Haliotis</i> spp.
Invertebrate	purple sea urchin	<i>Strongylocentrotus purpuratus</i>
Invertebrate	red sea urchin	<i>Mesocentrotus franciscanus</i>
Invertebrate	California spiny lobster	<i>Panulirus interruptus</i>
Fish	California sheephead	<i>Semicossyphus pulcher</i>
Fish	giant sea bass	<i>Stereolepis gigas</i>

Table 3.2. Fishery Management Areas (FMA) for commercial fisheries in both geographic regions; 10 × 10-minute grid blocks by California Department Fish and Wildlife (U.S.) and fishery concession areas by Mexican Fisheries Management Agency-CONAPESCA (Mexico).

Country	FMA (count)	Mean (km ²)	Max (km ²)	Min (km ²)	SD	Var
Mexico	78	338.95	5379.00	1.10	±875.38	766283.27
US	101	191.10	289.23	0.87	±94.06	8847.05
Total	179	255.89	5379.00	0.87	±586.27	343715.30
T-Test		0.1250*				

Table 3.3. Summary of regression analyses on 10-year mean fishery production (kg/km²) and percentage of Giant Kelp cover within the Fishery Management Areas (FMA).

Fishery	N	R ²	P	L.R. Equation
CA spiny lobster	105	0.1116	0.334	$y = 42.537x + 27.098$
Purple sea urchin	118	0.829	0.911	$y = 735.95x + 74.331$
Red sea urchin	119	0.806	0.898	$y = 1768.8x - 172.07$
Abalone	62	0.8345	0.913	$y = 2339.5x + 344.02$
Giant sea bass	107	0.0054	0.073	$y = 0.1354x + 0.6768$
CA sheephead	36	0.0006	0.249	$y = 0.6979x + 22.661$

FIGURES

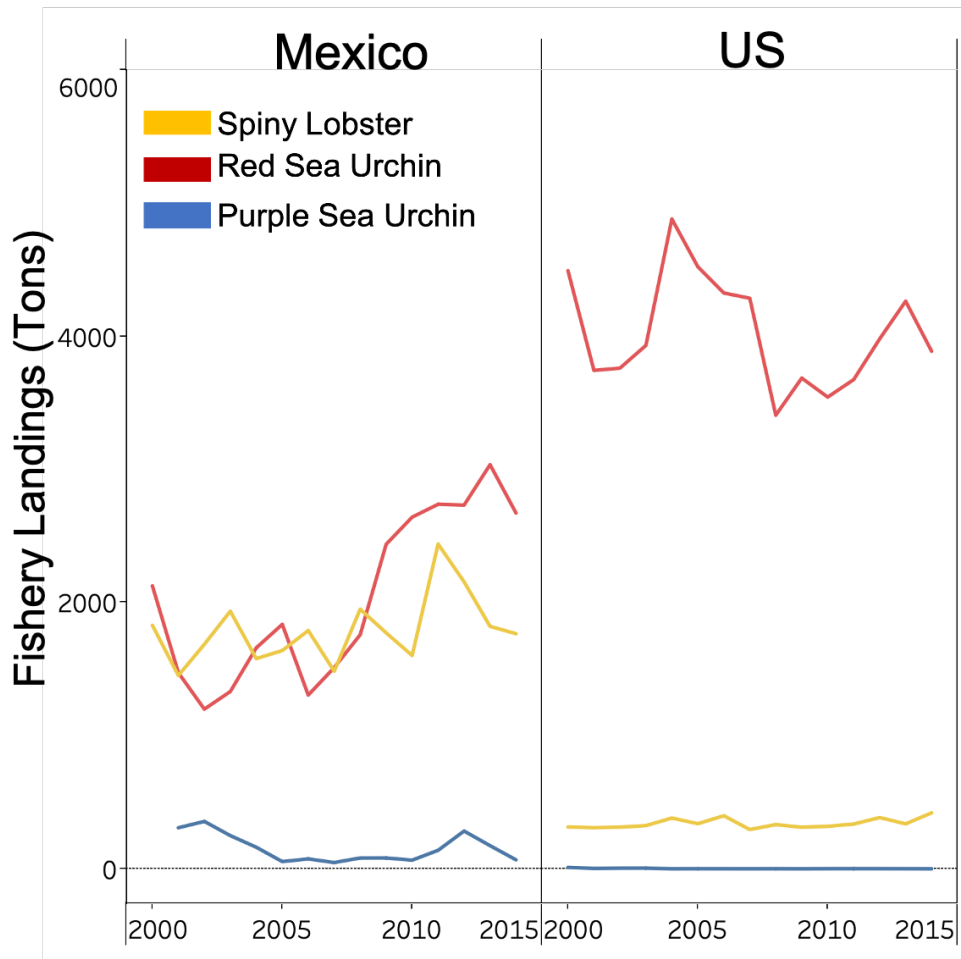


Figure 3.1. 2000-2015 Fishery landings (Tons/yr⁻¹) of three of giant kelp forest-associated species California spiny lobster (*Panulirus interruptus*), red sea urchin (*Mesocentrotus franciscanus*), purple sea urchin (*Strongylocentrotus purpuratus*) by country, Mexico and the U.S. Data source: CDFW (U.S.) and CONAPESCA (Mexico).

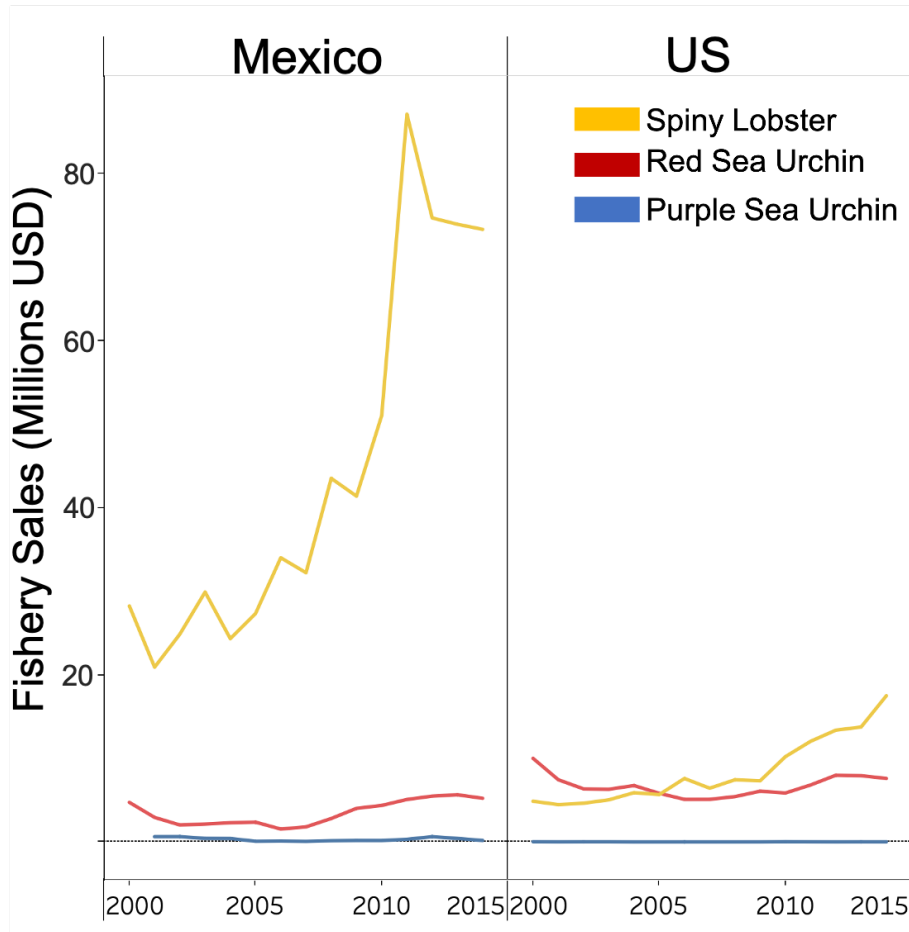


Figure 3.2. 2000-2015 Fishery Sales (USD/yr⁻¹) of three of giant kelp forest-associated species California spiny lobster (*Panulirus interruptus*), red sea urchin (*Mesocentrotus franciscanus*), purple sea urchin (*Strongylocentrotus purpuratus*) by country, Mexico and the U.S. Data source: CDFW (U.S.) and CONAPESCA (Mexico).

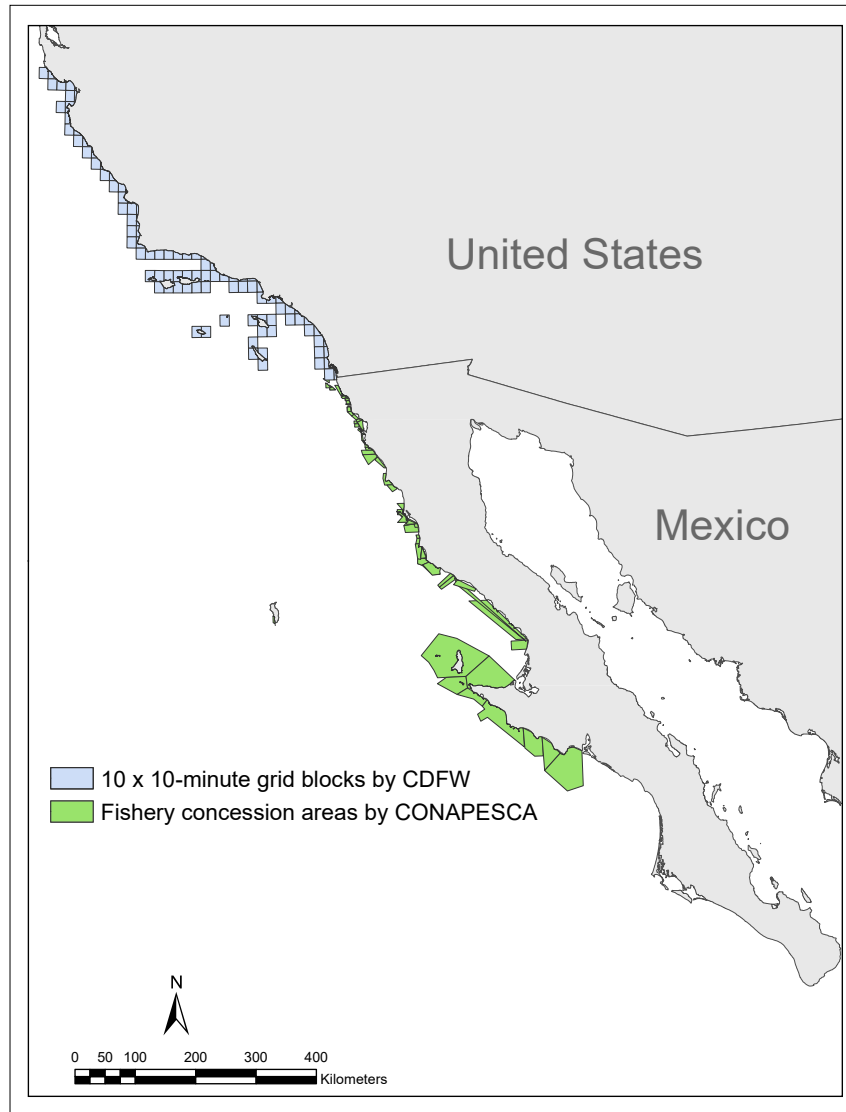


Figure 3.3. Fishery Management Areas (FMA) for commercial fisheries in both geographic regions; 10x10-minute grid blocks by California Department Fish and Wildlife (U.S.) and fishery concession areas by Mexican Fisheries Management Agency-CONAPESCA (Mexico).



Figure 3.4. Landsat 5 Thematic Mapper image displaying the kelp cover in a small section of the study area; south of Bahia Todos Santos, Ensenada, Mexico, (Fall 2008).

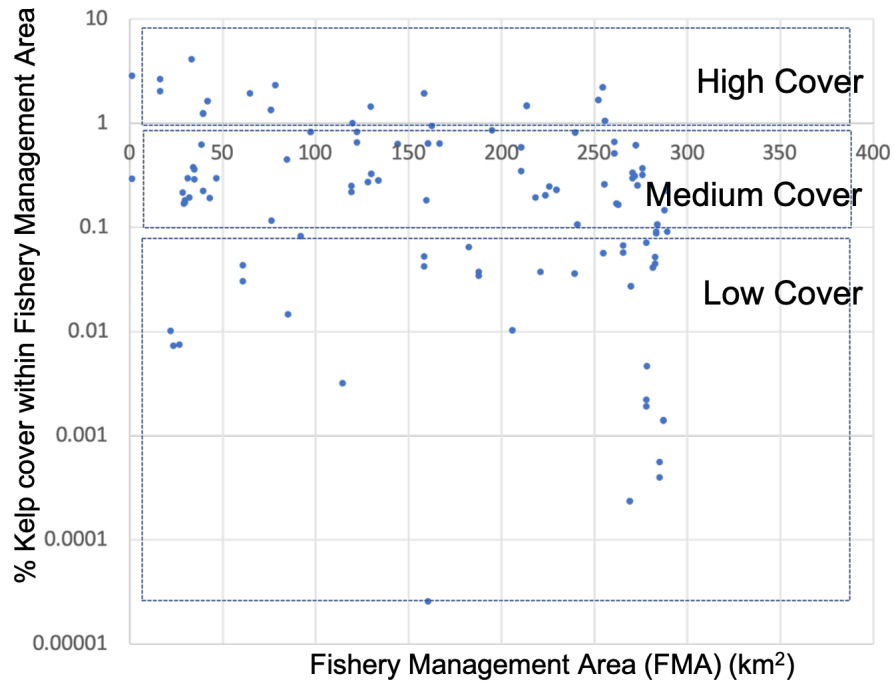


Figure 3.5. Percentage of kelp cover categories within the Fishery Management Areas (FMA); Low (< 0.1%), Medium (0.1 – 1.0), High (> 1.0%).

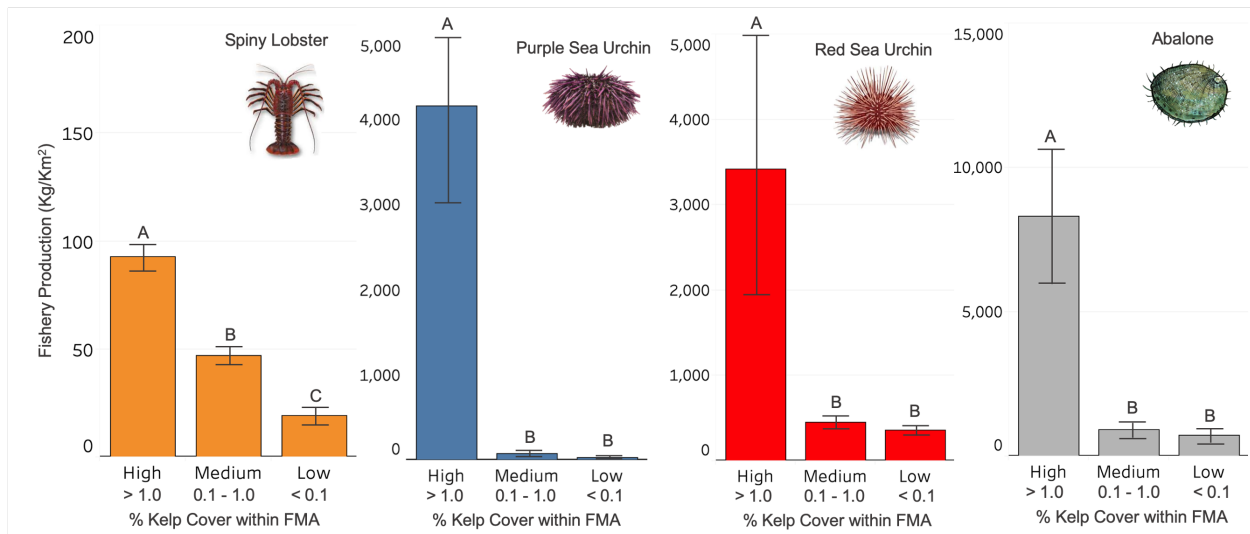


Figure 3.6. 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA; California spiny lobster (*Panulirus interruptus*), purple sea urchin (*Strongylocentrotus purpuratus*), red sea urchin (*Mesocentrotus franciscanus*), and abalone (*Haliotis* spp.). Data are presented as mean \pm S.E.M. where bars sharing a letter are not significantly different from one another (ANOVA post hoc $P < 0.05$).

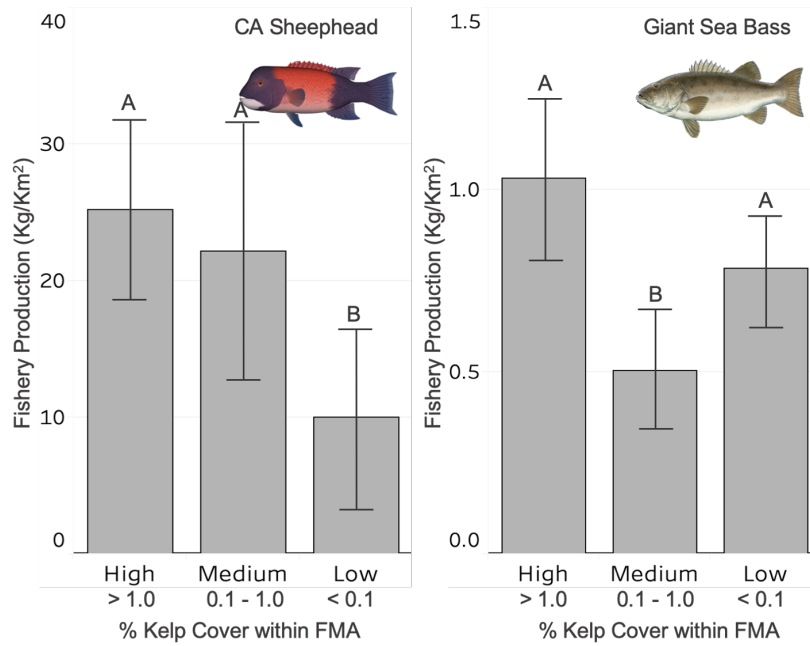


Figure 3.7. 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA; California sheephead (*Semicossiphus pulcher*), Giant sea bass (*Stereolepis gigas*). Data are presented as mean \pm S.E.M. where bars sharing a letter are not significantly different from one another (ANOVA post hoc $P < 0.05$).

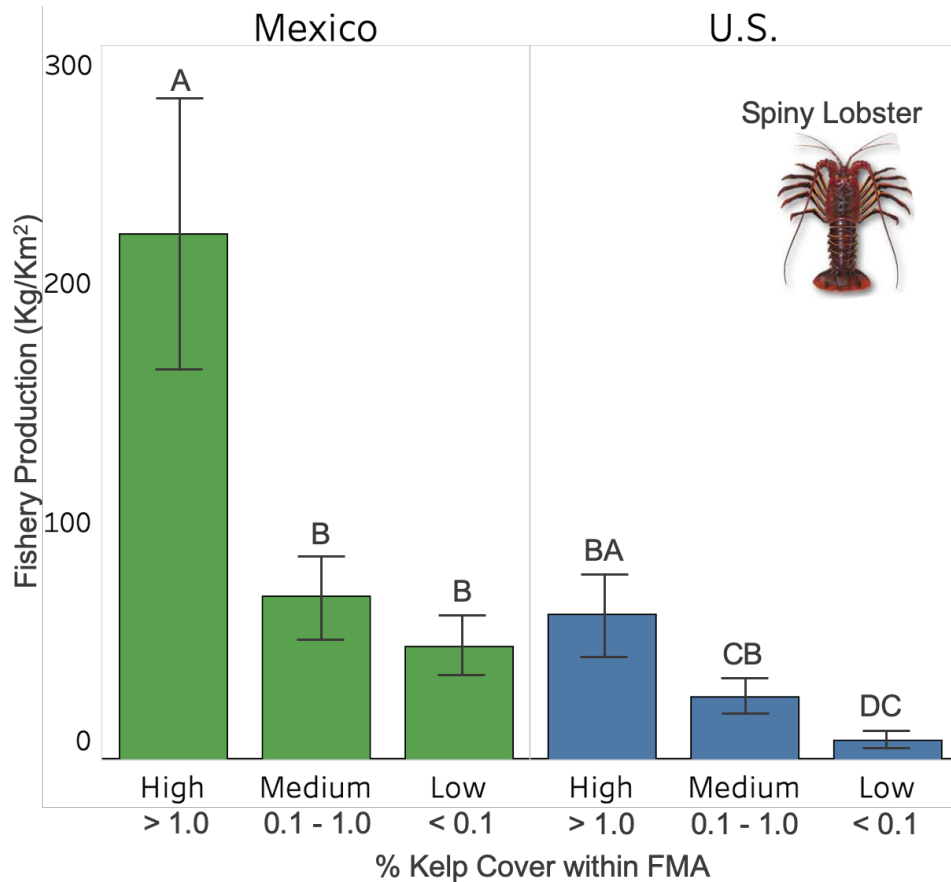


Figure 3.8. California spiny lobster (*Panulirus interruptus*) 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA by country, the U.S. and Mexico. Data are presented as mean \pm S.E.M. where bars sharing letter are not significantly different from one another; first letter= within country, second letter= between countries (Two-way ANOVA, $P < 0.05$)

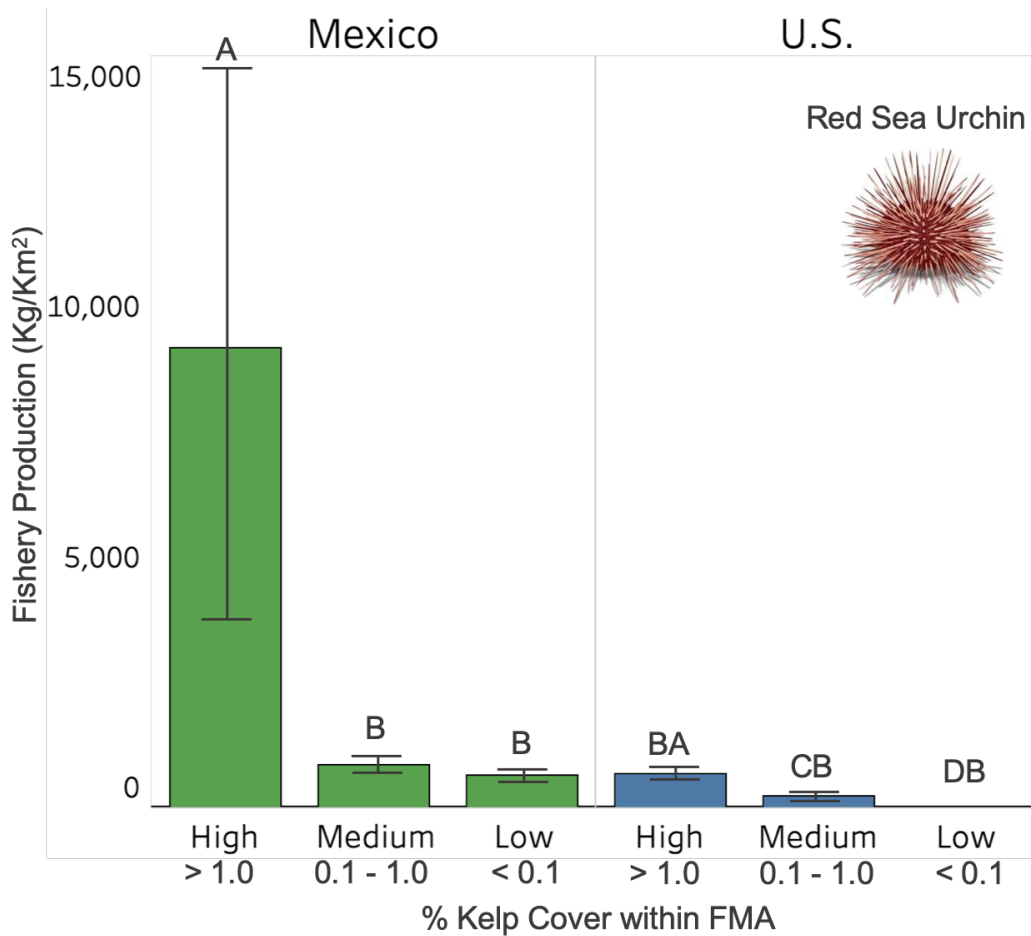


Figure 3.9. Red sea urchin (*Mesocentrotus franciscanus*) 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA by country, the U.S. and Mexico. Data are presented as mean \pm S.E.M. where bars sharing letter are not significantly different from one another; first letter= within country, second letter= between countries (Two-way ANOVA, P< 0.05).

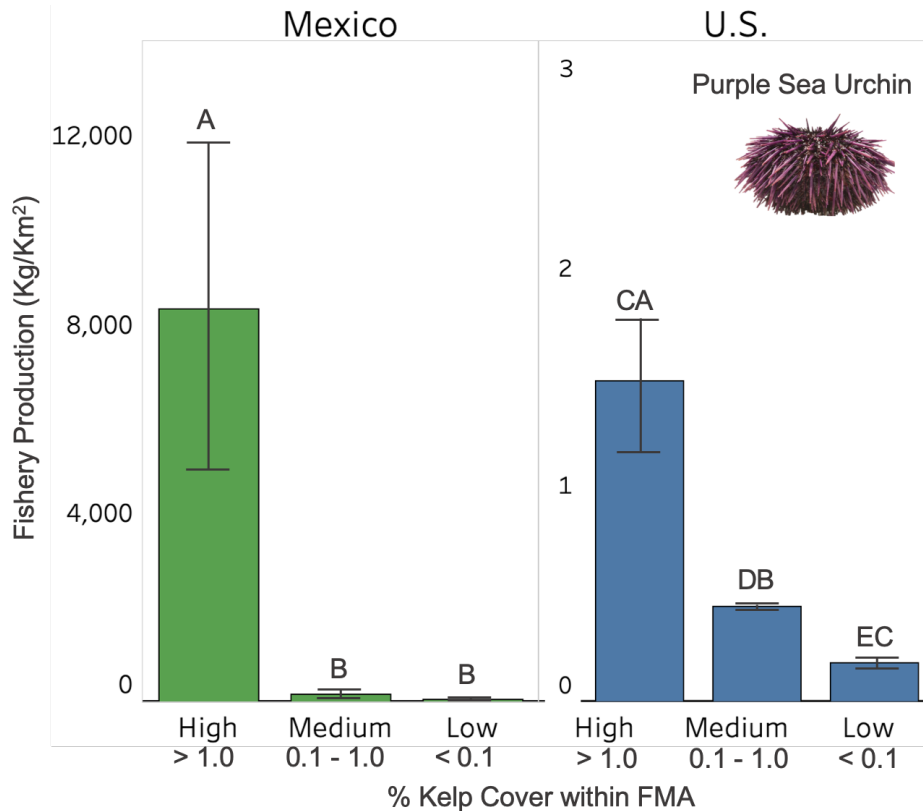


Figure 3.10. purple sea urchin (*Strongylocentrotus purpuratus*) 10-year (2008-2017) average fishing production (kg/km²) according to the kelp cover size within the FMA by country, the U.S. and Mexico. Data are presented as mean \pm S.E.M. where bars sharing letter are not significantly different from one another; first letter= within country, second letter= between countries (Two-way ANOVA, $P < 0.05$).

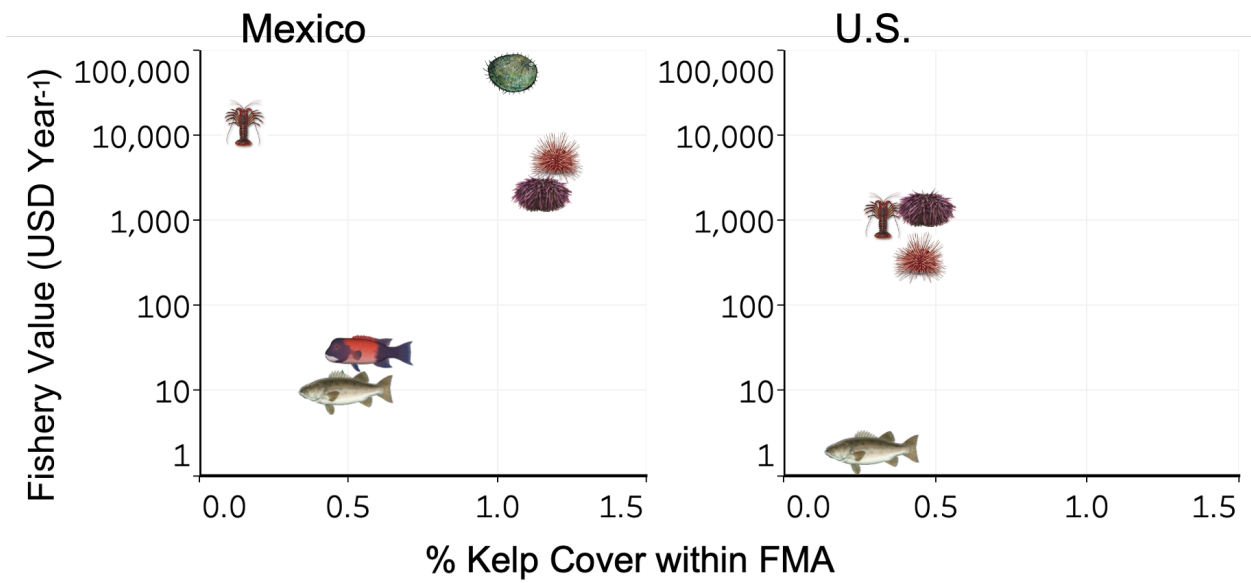


Figure 3.11. Relationship between economic value (USD/yr⁻¹) of 10-year average fishery production (2008-2017) considering fishery sales alone and the percentage of giant kelp cover within the FMA by country, the U.S. and Mexico.

CHAPTER 4:

Mexico-California binational initiative of kelp forest ecosystems and fisheries

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Mexico-California Bi-National Initiative of Kelp Forest Ecosystems and Fisheries

White Paper for the Environmental Working Group of the UC-Mexico Initiative

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Table of Contents

I.	Abstract.....	2
II.	Impacts of Kelp Forests on Human Welfare	5
III.	Kelp forests in a Binational Context	7
IV.	Theoretical Framework	9
V.	Policy Responses and Challenges	12
VI.	Human Impacts on Kelp Forests: What Do We Know?.....	13
VII.	Unanswered Questions	15
VIII.	Thinking Ahead: Priorities for Future Bi-national Research and Training Initiatives	17
IX.	Acknowledgements	19
X.	Endnotes	20
XI.	References	21

Abstract

The coastal forests formed by the giant kelp *Macrocystis pyrifera* are iconic and primary habitats distributed discontinuously from central Baja California (Mexico) to central California (USA). The giant kelp creates a biogenic habitat that supports high levels of species diversity and productivity in the region, acting as a refuge, nursery and food provider for many species.

Kelp forests provides ecosystem services to humans worth billions of dollars globally. These services include food and natural products, chemical products, recreational and commercial fisheries, ecotourism opportunities, cultural value, and nutrient cycling. Coastal human populations rely on many of these ecosystem services.

Beyond its economic benefits, giant kelp, together with the species that inhabit the kelp forests, play a significant role in climate control by regulating carbon flows, acting as a reserve and sink for carbon dioxide on living tissue, and facilitating the burial of carbon in sea bed sediments. Giant kelp and the biological communities that it supports will likely react to climatic and non-climatic changes in complex and unexpected ways.

In California and Baja California, giant kelp forests can be expected to contract in their southern extent due to warming waters, reductions in nutrient availability, increasing wave disturbance and grazing by warm-water herbivores. In ecosystems shared between nations, such as kelp forest, the actions taken by one nation invariably affect the other. Effective management of such systems therefore requires strong cooperation.

What is the problem? What are the critical issues?

The United States of America (USA) and Mexico together account for more than 2,600 km of coastline in the temperate sea of the Northeastern Pacific, which hosts a huge diversity of species ranging from locally resident populations important for sustaining food webs, to large predators and other mobile organisms that cross the national borders regularly. At least 220 species of macroalgae (Murray and Littler 1981), 3,000 species of marine macroinvertebrates (Cadien and Lovell 2015), 519 species of fish (Horn et al. 2006), 29 species of marine mammals (Daugherty 1985) and five species of marine reptiles (Beltz 2006) are distributed throughout the temperate region of Northeastern Pacific. This region is delimited by the northern border of Washington (USA) and the southern end of the Baja California Peninsula (Mexico). Conservation of marine biological diversity along this broad geographical region is important not only for maintaining the demographic and genetic flow among populations on both sides of the border, but also to maintain critical ecosystems services for coastal human populations.

The marine territory off the coast of California and Baja California is part of the California Current System (CCS), which is one of the five most productive marine ecosystems on the planet (Fig. 1). The CCS has a high productivity as a result of temperate water movement towards the equator as well as favorable winds for coastal

upwellings, which together generate an offshore transport of surface waters and advection of cold and nutrient-rich waters to the surface (Checkley and Barth 2009). Throughout the CCS, there is a diversity of oceanographic features that lead to a variety of habitat types within the system (Spalding et al. 2007; Greene et al. 2013; Morgan et al. 2015) (Fig. 1). Among them, coastal forests formed by the giant kelp *Macrocystis pyrifera* are primary habitats that support the high diversity and productivity of the region, acting both as nursery and food providers for many species.

Giant kelp forests can be considered the submerged counterparts of rain forests. They are among the most species-rich communities in temperate seas and among the most productive ecosystems on Earth (Schiel and Foster 2015; Reed and Brzezinski 2009). Kelp forests are a complex three-dimensional habitat structured by a second layer of understory macroalgae attached to the sea bottom (Dawson et al. 1960). They create biogenic habitats that provide refuge for numerous species, including many of economic importance for fisheries (Foster and Schiel 1985; Hernández-Carmona et al. 1989; Parnell et al. 2010a; Torres-Moye et al. 2013).

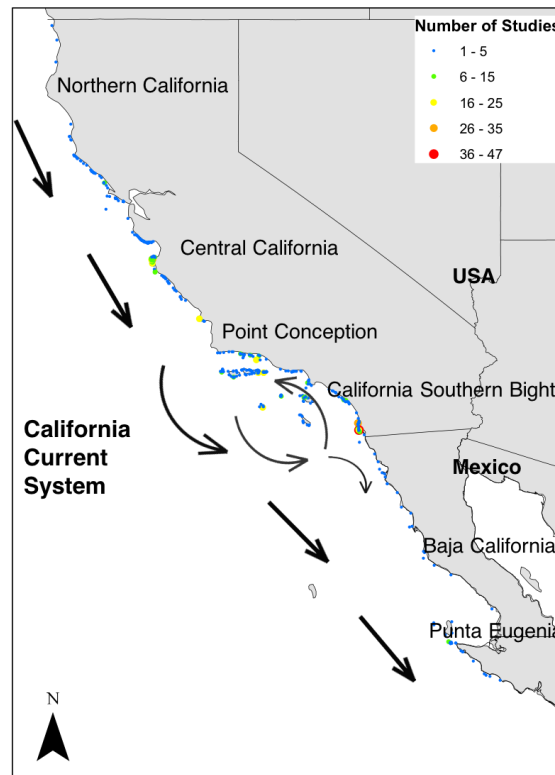


Figure 1. Geographic localization and main oceanographic features in the California Current System, including study sites and study effort in number of peer-review papers of the kelp forest ecosystem across the California (USA) and Baja California (Mexico) coast.

Historically, the latitudinal range of giant kelp on the west coast was thought to extend from Sitka, Alaska, at 57°N to Bahía Magdalena, Mexico, at 24°N, as its southernmost limit (Setchell and Gardner 1925; Dawson et al. 1960; Macaya and Zuccarello 2010; Schiel and Foster 2015) (Fig. 1). Several variables acting at different

scales and different life history stages of the giant kelp control those distribution limits. Temperature and its relationship with nutrient availability, together with the availability of hard substrate, are among the most important (Jackson 1977; Hernandez-Carmona et al. 2001; Edwards and Hernández-Carmona 2005; Edwards and Estes 2006).

Giant kelp is an “ecosystem engineer” (sensu Jones et al. 1994) and generally the dominant species of the community, accounting for a disproportionately large share of the biomass in the system (Dayton 1985; Dayton et al. 1992; Steneck et al. 2002; Rassweiler et al. 2008; Reed et al. 2008; Schiel and Foster 2015). Giant kelp can grow up to 60 m in length at a maximum rate of 60 cm per day, with densities sometimes exceeding 1.5 adult plants/m² with more than 10 stipes/m², which explains its high contribution of biomass relative to other species in the community (Carr 1994; Edwards 2004; Reed et al. 2009). The abundance of biomass of giant kelp is very dynamic in space and time as a result of its seasonal variations, grazing, storms, episodic oceanographic events and long-term climate changes (Dayton and Tegner 1984; Hernández-Carmona et al. 1989, 2001; Reed et al. 2011; Schiel and Foster 2015).

Global climate plays a vital role in determining the distribution, structure, function, and biodiversity of giant kelp forests. As a result of rapid atmospheric climate change, coastal water temperature, nutrient availability, pH, wave disturbance, and sea level are all changing or forecast to change in coming decades (IPCC 2013, 2014). Overlaid on these large-scale stressors are other local stressors on giant kelp forests resulting from coastal development and urbanization, such as runoff of sediments and nutrients, overfishing, and invasive species. Giant kelp and the biological communities that it supports will likely react to climatic and non-climatic changes in complex and unexpected ways (Crain et al. 2008; Johnson et al. 2011). In California (USA) and Baja California (Mexico), giant kelp forests may be expected to contract in their southern extent due to warming waters, reductions in nutrient availability, and increases wave disturbance and grazing by warm-water herbivores (Ridgway and Hill 2012). Changes in sea level are harder to predict but could lead to increases or decreases in available habitat depending on nearshore bathymetry and coastal management (e.g., shoreline armoring). We should also expect direct and indirect effects of climate change on kelp forest organisms. Members of kelp forest communities, especially calcifying organisms or those existing near their thermal limits, may change in abundance and distribution in response to warming and ocean acidification (OA). Changes in the abundance and distribution of giant kelp will have indirect effects on fishes and invertebrates that depend on giant kelp for shelter or food, as well as competing species of algae that thrive in the absence of giant kelp. Ecological surprises such as complex, cascading interactions, the immigration of novel species, or unexpected local adaptation to climate stressors are very likely and challenge our ability to accurately predict the future of giant kelp forests in a changing climate.

In ecosystems shared between nations, such as kelp forest, the actions taken by one nation invariably affect the other. Effective management of such systems therefore most commonly one that involves strong cooperation. The research benefits realized from international initiatives are as essential to scientific progress as they are to environmental preservation. Understanding how climate change will impact nearshore ecosystems, such

as the large kelp forests along the California and Baja California coasts, will require geographically extensive assessments of these effects and solid understanding of the ecology and oceanography of this region.

Impacts of Kelp Forests on Human Welfare

Early in the last century (1910) the population of California was 2.4 million, while Baja California had only 9,760 inhabitants. By the end of 2015, the population of California increased more than 11-fold to 39.14 Million and the population of Baja California more than 300-fold to 3.15 million (US Census Bureau; Mexico National Institute of Statistics and Geography-INEGI). This population growth significantly exceeded the growth rate of total population in the respective countries, due to a mixture of migration, economic expansion, and political developments (Rubin-Kurtzman et al. 1996). Population growth increased pressure on local ecosystem services, and signs of over-exploitation have been documented in the region (Clough-Riquelme and Bringas-Rábago 2006; Shaw et al. 2011). Resources that sustain quality of life have shown signs of deterioration, including air and fresh water (Cramer 1998; Mumme 1999). For example, overfishing has led to major declines in some fisheries in this region (Tegner and Dayton 2000; Schroeder and Love 2002; Erisman et al. 2011).

Kelp forests provide ecosystem services to humans worth billions of dollars globally (Costanza et al. 1997, 1998; Carr and Reed 2016). These valuable services include food and natural products (Leachman 1921; Mead 1976), chemical products (Neushul 1987), recreational and commercial fisheries (Dayton et al. 1998; Tegner and Dayton 2000), ecotourism opportunities (Pendleton and Rooke 2006), cultural value (Leachman 1921), wave and current attenuation (Gaylord et al. 2007; Garden and Smith 2015), and nutrient cycling (Jackson 1977; Wilmers et al. 2012). As ecosystem engineers, kelps transform marine habitats by controlling sediment dynamics, reducing the turbulent mixing beneath the canopy and controlling the water flow. Altogether, this causes fairly uniform vertical currents within the kelp forest with less shear than outside, which results in shoreline protection (Jackson 1983; Eckman et al. 1989; Rosman et al. 2007; Stewart et al. 2009; Garden and Smith 2015).

Since the early 1900s the harvest of giant kelp has been an important source of food, chemicals, fertilizers, and alginates, and more recently kelp has been used as animal feed (Schiel and Foster 2015). Harvest occurred along the coast of California and Baja California, although the major effort was concentrated from Santa Barbara to San Diego and in the northern Baja California region, from Playas de Tijuana to El Rosario (Robledo 1998; Bedford 2001; Casas-Valdez et al. 2003). Kelp harvest became the largest industry ever created from the processing of marine plants in the United States (Neushul 1987). Global demand for alginate has continued in recent decades and the industry has an estimated value of \$ 318 million, but the large-scale harvest of giant kelp in California and Baja California ended in 2006 due to increased production costs and the opening of foreign markets (Bixler and Porse 2010; Schiel and Foster 2015). Following

the closure of the industrial harvest of giant kelp, an artisanal harvest has remained on both sides of the border to produce feed for abalone farms (Schiel and Foster 2015).

Aesthetic characteristics and the ecological significance of kelp forests attract a large number of visitors who participate year-round in a variety of recreational activities such as diving, snorkeling, kayaking, and boating. Tourism and recreation are one of the main economic sectors for both California and Baja California, contributing 22% of the gross state product of California (Kildow and Colgan 2005) and up to 12% for Baja California (SECTURE 2000). Activities related to the sea in California are estimated to involve up to 12.2 million people annually (Pendleton and Rooke 2006), of which kelp forest-related activities are a significant part (Schiel and Foster 2015). Snorkeling and diving are two important marine recreational activities in California, in 2000 alone, there were an estimated 1.38 million dives and 3.82 million snorkeler-days (Leeworthy and Wiley 2001). In 2000, estimates put the annual value of scuba diving in California at \$20-69 million and the annual value of snorkeling activities at \$19-114 million in 2000 (Pendleton and Rooke 2006). Other marine recreational activities potentially related to the use of kelp forest ecosystems, such as kayaking, wildlife viewing, boating, and bird watching, account for another \$72.7 million per year (Pendleton and Rooke 2006).

Reliable estimates of revenues from recreational activities related to kelp forests in Baja California are not available. The small number of service providers, low human populations and limited promotion of these activities suggest that revenues are lower in Baja California than in California. Nevertheless, the economic potential for marine recreational activities in Baja California is well understood and potentially large (GEBC 2015a). The gross value of tourism for Baja California in 2001 was \$2.59 billion (GEBC 2015b) and recreational activities generated \$3.79 million.

Fisheries associated to kelp forest provide economic and social support for the region. Throughout the CCS, several species of invertebrates such as abalone (*Haliotis* spp.), lobster (*Panulirus interruptus*), and sea urchins (*Strongylocentrotus* spp.), in addition to species of fish including giant sea bass (*Stereolepis gigas*), white sea bass (*Atractoscion nobilis*), yellowtail (*Seriola lalandi*), rockfishes (*Sebastes* spp.), kelp bass (*Paralabrax clathratus*), and California sheephead (*Semicossyphus pulcher*), are caught both recreationally and commercially, from shore or at sea (Love et al. 2002). It is impossible to isolate the effects of kelp forests versus other habitats on these fisheries because most species are not exclusive to one habitat type. California commercial fishing generated around \$113 billion in sales in 2008, while the recreational fishery generated \$106 billion in sales, including \$55 million for the issue of fishing licenses (CDFG 2009). Commercial fishing generated 1.5 million jobs, and the recreational sector accounted for another 534,000 (NOAA 2008). Commercial fishery revenues in Baja California currently are much lower. Approximately \$27 million and 30,628 direct jobs (SEPESCA 2015) were generated by these activities and about \$127,000 were collected from sales of sport fishing permits in 2008 (Sosa-Nishizaki et al. 2013).

Beyond its economic benefits, giant kelp, together with the species that inhabit the kelp forests, may play a significant role in climate control by regulating carbon flows, acting as a reserve or sink for carbon dioxide on living tissue, and facilitating the burial of carbon in sea bed sediments. By increasing kelp biomass, atmospheric carbon dioxide

could potentially be reduced and sequestered in a reservoir where it could remain for long periods of time by exporting drifting algae to the deep sea (Wilmers et al. 2012). However, Reed and Brzezinski (2009) argue that, unlike other coastal ecosystems, kelp forests contribute little to carbon sequestration because the vast majority of kelp carbon is rapidly degraded and re-mineralized, and the main storage of kelp carbon is in the standing biomass.

Kelp forests in a Binational Context

The equator-ward flow of the California current in the CCS and its coastal countercurrents promote the transport of larvae and early-stage individuals throughout the region and influence the distribution of the adult stages of many species (Horn et al. 2006). Several studies have documented the relationship between species populations on the two sides of the USA-Mexico border in terms of distribution (Horn et al. 2006), larval dispersal (Cowen 1985; Funes-Rodriguez et al. 2015), migration (Aalbers and Sepulveda 2015) and genetic connectivity (Iacchei et al. 2013; Munguía-Vega et al. 2015; Johannson et al. 2015). The white sea bass (*Atractoscion nobilis*) is a good example of a trans-boundary resource with documented population connectivity across the border that supports both recreational and commercial fisheries (Vojkovich and Reed 1983; Aalbers and Sepulveda 2015; Romo-Curiel et al. 2016). Historically, the USA fishing fleet has been larger than the Mexican fleet, in terms of both vessels and landings within Mexican waters. Reports show that in some years up to 80% of the total landings by the commercial fleet of California were from in Mexican waters (Vojkovich and Reed 1983). After a decline in commercial catches in the 1960s, restoration strategies were adopted in California with little success. Research interest on both sides of the border has fostered a new effort to determine the population dynamics of the species across its entire distribution (Aalbers and Sepulveda 2015; Romo-Curiel et al. 2016).

Recent studies of the spiny lobster (*Panulirus interruptus*), one of the most important commercial fisheries in the region, showed high connectivity among populations along its distribution in the Pacific (Miller 2014). Genetic differentiations that have been found between some populations can be explained by coastal upwelling (Iacchei et al. 2013; Funes-Rodriguez et al. 2015). A similar pattern has also been observed in populations of barred sand bass (*Paralabrax nebulifer*) throughout the Pacific USA-Mexico region. Despite the decline of populations due to commercial fishing pressure in California and Baja California, there is a high degree of genetic diversity and genetic mixing (Erisman et al. 2011). These results suggest the existence of a single large population of barred sand bass in the Northeastern Pacific, reiterating the trans-national nature of marine species in the region (Paterson et al. 2015).

The following are some examples of studies that examine population connectivity and demographic connectivity across the California and Baja California borders for different taxa of kelp, invertebrates and fish.

1) **Kelp.** Several surface canopy-forming kelp species have distributions that encompass both California and Baja California. These are the giant kelp (*Macrocystis pyrifera*), elk kelp (*Pelagophycus porra*), and feather boa kelp (*Egregia menziesii*). Out of these three species, giant kelp is the most thoroughly studied. Empirical and theoretical studies of giant kelp dispersal (Gaylord et al. 2006; Hernández-Carmona et al. 2006; Reed et al. 2006), spatial analysis population analyses (Cavanaugh et al. 2014; Castorani et al. 2015), and molecular tools (Alberto et al. 2011) have improved our understanding of the propagule dispersal, patch and metapopulation dynamics, population genetics, and molecular ecology of this species. These studies suggest that spore transport by oceanographic currents is an important determinant of population and demographic connectivity among giant kelp patches (Alberto et al. 2011; Castorani et al. 2015; Johannson et al. 2015). While population connectivity depends primarily on the absolute number of dispersers between populations, demographic connectivity depends on the relative contribution to the growth rates of the population of dispersers and local recruitment (Lowe and Allendorf 2010). The spore dispersal between patches of kelp forests is not limited enough to prevent demographic connectivity, yet not broad enough to result in homogenous, panmictic populations (Gaylord et al. 2006; Reed et al. 2006; Alberto et al. 2011). Demographic connectivity can strongly determine the population dynamics of giant kelp, increasing the probability of colonization and persistence through time (Castorani et al. 2015).

2) **Invertebrates.** Kellet's whelk (*Kelletia kelletii*) is an abundant predator in the kelp forest ecosystem and an emerging fishery in California since 1979 (Hubbard 2008). Zacherl et al. (2003), using microchemistry in larval protoconchs and statoliths of Kellet's whelk, found that populations north and south of California's Point Conception showed a different chemical composition that might reflect differences in the population source providing recruits. Similarly, Torres-Moye (2012) examined the genetic diversity between island and coastal populations of the limpet *Megathura crenulata* and sea star *Patiria miniata* using the mitochondrial DNA control region. He suggests that the short larval duration of the *M. crenulata*, combined with intense harvest pressure, may limit the dispersal capabilities of this species, compared with the sea star *P. miniata*.

Studies of the sea star *Pisaster ochraceus* along the CCS (Vancouver Island to Punta San Carlos, Baja California) using mitochondrial DNA suggest that genetic homogeneity exists among populations, due to the transport of larvae along the CCS that coincides with the reproductive peak of this species (March to June), when the current has a strong southward flow (Fontana-Urbe 2005). Studies of the pink abalone (*Haliotis corrugata*) found a low to moderate genetic diversity at five locations of the northeastern Pacific of Mexico and the USA (Díaz-Viloria et al. 2009).

3) **Fish.** Many fish species have restricted movement when adults; however, for species with pelagic larvae ocean currents may disperse them over large distances—up to hundreds of kilometers (Kinlan and Gaines 2003; Freiwald 2012). California sheephead (*Semicossyphus pulcher*), kelp bass (*Paralabrax clathratus*), and kelp rockfish (*Sebastes atrovirens*) are some of the most abundant species throughout the trans-boundary region and are subject to commercial and recreational fisheries; however, their management and conservation are performed independently in each country.

The connectivity of California sheephead populations has been examined by recruitment, genetic analysis and ocean circulation patterns. Cowen (1985) use a combination of field counts and age-structure data to suggests that larval supply to populations in the Southern California bight is variable and relies on anomalous recruitment related with El Niño or La Niña events, with warm northward flow carrying the larvae of these and other species into the waters of California (Cowen 1985; Methot et al. 2004). Selkoe et al. (2007) used three different datasets including time series of larval abundance and microsatellite markers analysis to investigate whether California sheephead and kelp bass populations depend on Mexican populations. They found very localized population connectivity and very little exchange between California and Baja California populations. Bernardi et al. (2003), using DNA analysis, found the presence of population structure between northern and southern Baja California populations in some kelp-associated fish species like opaleye (*Girella nigricans*) and sargo (*Anisotremus davidsoni*), but no structure in others (*Halichoeres semicinctus* and *Semicossyphus pulcher*).

In sum, several approaches have been used to study connectivity along the California Current System, such as recruitment and ocean circulation patterns (Cowen 1985; Cowen et al. 2006; White et al. 2010), microchemistry (Simmonds et al. 2014; Zacherl 2005; Warner et al. 2005), and genetics (Palumbi 1995; Fontana-Uribe 2005; White et al. 2010; Torres-Moye 2012). Whilst some of the outcomes from these population connectivity studies show the importance of local fisheries management schemes, the majority suggest that regional management is the most appropriate strategy for future interventions.

Theoretical Framework

The study of kelp forests along the California Current System (CCS) have had two very different histories. On the one hand, along the coast of California, a long history of fishing pressure (Tegner and Dayton 2000), continuous long-term scientific monitoring programs (Tegner and Dayton 1987; Foster et al. 2013; Kenner et al. 2013; Kushner et al. 2013), and more recently, networks of marine protected areas (Botsford et al. 2014), all highlight the large quantity of coastal human impacts, both positive and negative, on the ecosystem. The investment of research effort along this coast makes giant kelp forests without question the most studied kelp system of the Northeastern Pacific, and may be globally (Schiel and Foster 2015). In contrast, the kelp forests off the coast of Baja California have received much less attention, both from large-scale fishery pressure, research monitoring initiatives and spatial protection schemes. For example, there is no equivalent marine protected area network along the Baja California coastline.

We conducted a systematic literature review of peer-reviewed papers to assess the state of scientific knowledge on the kelp forest ecosystem along the California and Baja California coastline. The review finds differences in study effort on the two sides of the border and identifies temporal and spatial trends between studies. We found more than 40 times more peer-reviewed papers on kelp forest ecosystem topics in California than in

Baja California. Research focusing on kelp forest ecosystems in California dates back to the 1940s (Andrew 1945), while for Baja California the pioneering studies began three decades later. The first publication on kelp forests in Baja California published by Mexican researchers appeared early in the 1970s (Guzmán del Prío et al. 1971). Out of a total of 236 articles in the review, only 9 peer-reviewed papers include sites on both sides of the border, highlighting the lack of studies taking a binational approach. Study sites in the region of Baja California and northern California stand out as the most recently documented. The best-documented kelp forests of the region, based on number of publications, are located in Southern California near Point Loma and La Jolla (Fig. 1).

Ecological comparisons between kelp forest communities in California and Baja California has been challenging, as the majority of data collected from different monitoring programs are not standardized. However, seminal work by Edwards (2004) shows responses and impacts of the El Niño 1997-1998 from central California to its southernmost limit in Baja California. Existing monitoring programs range in taxonomic complexity from exhaustive lists including both conspicuous and cryptic fish, macroinvertebrates, and macroalgae (Vantuna Research Group, UABC), to programs that capture the majority of non-cryptic biodiversity (SDSU, Partnership for the Interdisciplinary Study of Coastal Oceans: PISCO, COBI-Stanford) and programs that focus on key species of economic or ecological importance (Reef Check CA, Channel Islands National Park Service: CINPS). Sampling effort (sites and years) also varies among programs.

Daily sea surface temperatures have been recorded at several locations along the California coast as part of the Shore Station Program, with temperature records going back nearly a century at the Scripps Institution of Oceanography Pier in southern California and Pacific Grove in central California. Paleo-climate records, mainly in the form of sediment cores from anoxic basins within the wide southern California shelf, extend our knowledge of climatic fluctuations within the CCS much further back in time (Schimmelmann and Lange 1996). Together, these records provide evidence that temperatures and productivity within the CCS have fluctuated greatly in the past, and that the ecology of pelagic ecosystems responds strongly to these fluctuations (McGowan et al. 2003; Di Lorenzo et al. 2013).

In contrast, the paleo-record for inner shelf benthos communities, such as kelp forests, is sparse or non-existent (Braje et al. 2009). However, cartographic and aerial photographic records extend our knowledge of kelp canopy coverage back to the beginning of the 20th century in some areas, with annual resolution in southern California available from the 1960s onward. Further, for benthic algae that do not produce a floating canopy at the surface, populations have been studied for the past several decades using *in situ* diver surveys such as those associated with the CINPS kelp forest monitoring program, San Diego State University, USGS kelp forest monitoring program at San Nicolas Island, the coordinated PISCO, California Reef Check, Santa Barbara Coastal Long Term Ecological Research program, and numerous independent academic research groups. Together, these activities have shown that benthic macroalgae and kelp canopy cover are highly sensitive to seasonal, inter-annual and decadal-scale fluctuations in oceanographic conditions within the CCS (Jackson 1977; Dayton et al. 1984, 1999;

Edwards 2004; Edwards and Estes 2006; Parnell et al. 2010b; Kenner et al. 2013; Bell et al. 2015). With this information, we can divide our framework of the bi-national kelp forest ecosystem into two periods:

(a) The system before and during the 1970's. The dynamic forcing of the CCS is closely related to large-scale decadal North Pacific climate modes such as the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008). These modes have been related to corresponding patterns in several biological time series, such as the alternating anchovy/sardine cycle within the CCS. Inter-annual and seasonal patterns of variability are superimposed onto these decadal climate modes (Sugihara et al. 2012). Positive El Niño Southern Oscillation years (ENSO) are associated with a deepened thermocline, warmer waters, and lower nutrients. Positive decadal climate modes magnify these effects of El Niño. For instance, there was a large positive shift in the PDO during the late 1970s that has been recognized as a North Pacific-wide regime shift, with profound declines in productivity and fish stocks within the CCS (McGowan et al. 2003; Holbrook et al. 1997; Chavez et al. 2003; Koslow et al. 2013).

Cool, dense waters beneath the thermocline are replete in inorganic nitrogen, the main limiting nutrient in the CCS for algal growth, while warmer waters above the thermocline are more depleted in nitrogen (Jackson 1977). Seasonal upwelling, forced by equatorward winds during spring and summer along the CCS, pumps sub-thermocline, cool nutrient-rich water up onto the shelf (Huyer 1983; Checkley and Barth 2009). However, the upwelled water is also low in oxygen and pH, thereby increasing the risks of hypoxia and acidification to coastal ecosystems (Nam et al. 2011). Since the coastal thermocline is depressed during positive phases of the PDO, seasonal upwelling provides only a limited nutrient subsidy during these periods and a concomitant El Niño tends to further limit subsidies.

The structure of the CCS changed during the regime shift of the late 1970s (Miller et al. 1994). For instance, zooplankton volumes decreased in a step manner across this shift (McGowan et al. 2003) and the CCS has freshened and warmed since that time (Bograd et al. 2003; Di Lorenzo et al. 2005). Concomitant increases in the stratification of coastal waters, which decrease mixing of nutrient rich sub-thermocline waters with nutrient-depleted surface waters (Bograd et al. 2003), and subsequent decreases in oxygen content within the surface waters were also observed during this shift (Bograd et al. 2008).

(b) The system after the 1970's. Major secular trends have been observed since the regime shift of the 1970s. These include further warming and freshening of the CCS, decreasing oxygen and pH, a thickening and shoaling of the oxygen minimum zone (a zone of low oxygen between 300 and 500 m deep off California), and rising sea levels. These trends are superimposed onto cyclical decadal ocean climate modes, and thus represent potential thresholds for potent regime shifts in the future.

Adding to this uncertainty is the likelihood that upwelling winds will increase with global warming, perhaps buffering the nutrient risk to coastal ecosystems such as kelp forests while further exacerbating hypoxia and OA (Bakun 1990; Rykaczewski and Dunne 2010). The degree to which humans have contributed to these secular trends has

been the subject of much debate, but it is clear that warming and sea level rise will continue on a global scale (Stocker 2014). Storms, a major source of disturbance for kelp forests (Bell et al. 2015), may also continue to intensify as they appear to have done in the North Pacific in the latter half of the 20th century (Seymour et al. 1989; Graham and Diaz 2001).

Sea level will rise ~1 m by the end of this century, though recent evidence of ice instability and the risk of ice collapse in the West Antarctic Peninsula and the Greenland Ice Shelf suggest that global sea level could rise much faster (Dutton et al. 2015). On a local scale, sea level rise may cause giant kelp to migrate shoreward in order to track changes in light availability (Kinlan et al. 2005; Graham et al. 2007). In areas with insular kelp forests or where shorelines are reinforced to prevent coastal erosion, sea level rise may constrict the effective habitat area for giant kelp growth (Graham et al. 2007). In contrast, the impact of sea level rise on giant kelp distributions will probably be minimal on linear, unmodified coastlines (Graham et al. 2007).

Climate change will also cause indirect, habitat-mediated effects on kelp forest communities if warming does impact the abundance and distribution of giant kelp. It is likely that the nature and functioning of kelp forests will change, especially south of Point Conception (Parnell et al. 2010b). The distribution of giant kelp may even exhibit long-term contraction similar to short-term contractions observed during previous ENSOs (Ladah et al. 1999; Edwards and Hernández-Carmona 2005). While short-term patterns provide much needed insight into how the range limits of kelp forests are impacted by ENSO conditions, it is unclear how continued warming of eastern Pacific coastal waters will impact future range shifts in these forests that may result from ENSO events.

Policy Responses and Challenges

Cooperative activities between the USA and Mexico take place under a number of treaties and agreements. Although there have been successful bi-national agreements regarding the use of common terrestrial resources between both countries, there are few examples of bi-national agreements regarding the management of marine resources.

The connectivity among many marine populations on the two sides of the USA-Mexico border highlights the importance of binational coordination and collaboration in the management of marine resources. Government instruments for resource management in California (e.g. Marine Life Management Act) and Baja California (e.g. State Fishery Inventory) recognize the potential contributions of population sources located in the territorial waters of the respective neighboring state. Joint research is needed to improve our understanding of these contributions and promote binational management.

Differential fishing pressure for some species and the consequent status of the population is another factor that needs careful binational consideration. For example, populations of lucrative pink abalone (*Haliotis corrugata*) in the central region of the Baja California Peninsula show a high allelic diversity, a larger effective population size, and lack of a recent genetic bottleneck. This is contrary to what has been reported for the populations in California, which is consistent with the collapse of the fishery in 1990s (Munguía-

Vega et al. 2015).

Marine protected areas (MPAs) are spatial management tools used to protect and restore marine ecosystems (Lubchenco et al. 2003), with the aim to maintain or enhance the ecosystem services that the oceans provide. Traditionally, MPAs were established independently through community-based government effort (Gleason et al. 2010). However, recently there have been examples of regional-scale planning processes to design MPA networks, which are ecologically connected and managed as a larger system (Airame et al. 2003; Fernandes et al. 2005; Saarman et al. 2013; Botsford et al. 2014). The scheme, design, and implementation of MPAs are significantly different between the USA and Mexico. For example, the Marine Life Protection Act (MLPA) initiative successfully redesigned California's existing MPAs through a legal mandate, but in Baja California (BC) there is a lack of similar MPA networks or initiatives (Morgan et al. 2005; Arafeh-Dalmau 2016).

Between 2004 and 2011, with a scientific advisory team involving stakeholders directly in its design, the MLPA initiative public-private partnership planned MPAs networks in four separate regions of California's coast (Kirlin et al. 2013; Botsford et al. 2014). This effort resulted in 124 marine protected areas, including 9.4% of state waters placed in no-take marine reserves.

In Mexico, MPAs are indistinctly called Natural Protected Areas, and in the Pacific coast of Baja California there is a lack of decreed no-take MPAs. In December of 2016, the Mexican government declared all the islands on the Pacific coast of Baja California Peninsula as a biosphere reserve, extending the protection to the marine territory that surrounds the islands, including their kelp forest ecosystems (DOF 2016). This decree restricts some fishing activities around the islands, yet they can not be considered no-take MPAs. There is, however, one example of successful establishment of a MPA through community-based processes led by local fisherman. In 2006, 8% of the fishing grounds around Isla Natividad were voluntarily established by the fisherman as no-take areas (Micheli et al. 2012). Collaborative efforts between local fisherman and NGOs might be a starting point for a community-based process to design and establish MPAs in Baja California (Arafeh-Dalmau 2016).

Human Impacts on Kelp Forests: What Do We Know?

Human activities have become ecological drivers of kelp forest communities, through pollution from storm water and wastewater, land use practices that affect coastal sedimentation, and disposal of dredged sediments (Dayton et al. 1998). The introduction of exotic species and serial overfishing of key predators and herbivores can affect non-targeted species via interactive cascades among interdependent species (e.g., Byrnes et al. 2006). All of these effects have been well documented and are known with relative certainty. It is clear that changes in ocean temperature and acidity may interact with one another and/or have differing impacts on these forests, further complicating the issue (Brown et al. 2014; Gaitán-Espitia et al. 2014).

One of the most studied processes in kelp forests is the dynamic relationship between kelp grazers and their predators, which can be greatly impacted by humans who harvest both (Mann 1982; Dayton 1985). Sea urchins are the most important kelp grazers, and their fecundity and grazing activity are so great that they can quickly overgraze entire kelp forests (Estes and Palmisano 1974; Ebeling et al. 1985). These areas, termed ‘urchin barrens’, are typically less productive and diverse than forested areas, and they can persist for decades (Graham 2004). Classical “top-down” control of kelp forests by sea otters (*Enhydra lutris*), voracious predators of sea urchins, has been suggested for central California kelp forests (Tinker et al. 2008; Carr and Reed 2016). Sea urchin outbreaks and overgrazing have been attributed to the removal of sea urchin predators such as large spiny lobsters and California sheephead (*Semicossyphus pulcher*) in southern California forests (Hamilton and Caselle 2015). There is also evidence that protecting areas from harvest in MPAs reduces sea urchin overgrazing, thereby enhancing production, diversity, and resilience to disturbances such as storms (Nichols et al. 2015).

Living in highly-variable nearshore environments, giant kelp has developed acclimation mechanisms to cope with temperature variability (Koch et al. 2016). However, extreme temperatures may play a role in determining latitudinal range limits in giant kelp, which has evolved to grow along a 30-degree latitudinal range in the Northeast Pacific Ocean spanning a temperature gradient from less than 2°C to over 20°C (Graham et al. 2007; Macaya and Zuccarello 2010). Warming could expand giant kelp forests at high latitudes, but polar distributions are also constrained by low light and herbivory (Gaines and Lubchenco 1982; Van den Hoek 1982; Jackson 1987). At low latitudes, giant kelp distributions are thought to be limited by warm temperatures, low nutrients, and competition with other species of macroalgae (Steneck et al. 2002; Schiel and Foster 2015).

Two recent events provide excellent case studies on the ecological effects of warming on giant kelp forests and provide hints at potential future scenarios. In central California, a thermal outfall from the Diablo Canyon nuclear power plant heated a small cove by an average of +3.5 °C for a decade (1985–1995). In a rigorous 18-year study carried out before and after warming, Schiel et al. (2004) found that elevated temperatures created ecological ‘winners’ that were mainly southern species that can colonize and compete for resources, and ‘losers’, that were northern affinity species which distribution may be contracted north or adapt to new conditions, algae and invertebrates among them, with 38% increasing, 49% decreasing, and 13% showing no change relative to control areas.

Another recent study found equally surprising results. From late 2013 to 2016, anomalously warm water in the northeastern Pacific Ocean (dubbed “the Blob”) followed by very strong El Niño conditions caused rapid warming of coastal waters along the coast of California and Baja California (Cavole et al. 2016; Di Lorenzo & Mantua 2016). Despite anomalously high temperatures for 31 of 34 months (up to 5 °C above the 1982–2014 average) and low nutrients (< 1 µmol nitrate L⁻¹) for 19 of 34 months, the abundance and composition of giant kelp, understory macroalgae, sessile invertebrates, and reef fishes did not change substantially in this particular region of southern California (Reed et al. *in review*). Sea urchins and sea stars, however, declined dramatically due to

diseases that can be magnified by warming (Reed et al. *in review*). The combined effects of the warm Blob and El Niño during 2015–2016 devastated giant kelp and red sea urchin populations in southern Baja California (G. Torres-Moye *personal observation*). Changes associated with the Blob event, but also reported for El Niño seasons, have included geographical shifts of species such as pelagic red crabs and tuna; the decline or closure of commercially important fisheries, including market squid and Dungeness crab; and the stranding of marine mammals and seabirds (Lea and Rosenblatt 2000; Chavez et al. 2002; Cavole et al. 2016).

In addition to more variable physical conditions and extreme events, the CCS is subject to a suite of chemical changes associated with climate change, including OA and hypoxia (Feely *et al.* 2008; Chan *et al.* 2008; Doney et al. 2009). In particular, severe hypoxic conditions have been observed off the coast of Oregon, USA, since 2002 and subsequently at other locations within the California Current (Chan *et al.* 2008; Micheli *et al.* 2012; Booth *et al.* 2014). Both et al. (2014) examine data of water quality monitoring program and found that dissolved oxygen (DO) had declined up to four times faster than offshore waters over the last 15 years, such low dissolved oxygen levels have no precedent over the past 50 years (Chan *et al.* 2008; Booth *et al.* 2014; Chu et al. 2015). Seasonal events of OA, are already appearing along the continental shelf of CCS, with the upwelling of corrosive seawater, approximately 40 years earlier than predicted by models (Feely et al. 2008; Doney et al. 2009). Concurrently, over the past 50 years, oceanographic measurements have revealed negative trends of DO concentrations in waters overlaying the Oxygen Minimum Zone (OMZ), naturally oxygen-depleted deep waters found between 600-1200 m depths (Stramma et al. 2008). The OMZ has shoaled by 90 m off southern California (Bograd *et al.* 2008), and circulation models predict that the oxygen content of the global ocean will decrease by 1-7% over the next century (Keeling *et al.* 2010). Documentation of climate-driven hypoxia on continental shelves and coastal areas (Chan et al. 2008; Booth et al. 2014) and the observed acidification trends (Feely et al. 2008; Doney et al. 2009) suggest that hypoxia and acidification will have important influences on the structure, function and flow of services of coastal marine ecosystems.

Unanswered Questions

Kelp forests provide a wide range of ecosystem services above and beyond those discussed previously, including nutrient cycling, biodiversity, wave attenuation, cultural heritage and the resilience of marine and coastal ecosystems. Although poorly evaluated to date, these services nevertheless are vital to human welfare. The biogenic structure that kelp creates may help prevent coastal damage caused by erosion, floods, and storm events (Smale et al. 2013). Giant kelp can reduce currents and dampen higher frequency internal waves (Rosman et al. 2007). The effect of attenuation is correlated with the extent, density, and morphology of canopy-forming kelps and understory macroalgae assemblages (Eckman et al., 1989; Gaylord et al. 2007; Rosman et al. 2007).

The species diversity in kelp forests, while supporting some of the aforementioned ecosystem services, may also enhance the productivity and ecological

resilience of the ecosystem, increasing also its ability to implement internal mechanism that ameliorate the impact of a disturbance (Léveque 2003; Hughes and Stachowicz 2004). Numerically abundant species in kelp forest systems are unlikely to go extinct as a result of human pressures, but habitat fragmentation and population decline are expected to reduce the genetic diversity within populations (Hughes and Stachowicz 2004). How to estimate the economic value of biodiversity is not well understood. Diversity could affect a wide variety of services that humans receive from ecosystems, underscoring the need for resource management to consider the important role of maintaining biodiversity (Beaumont et al. 2008). Biodiversity is maintained by genetic, species and functional diversity within an ecosystem. The loss of the former can often result in the loss of the latter two. Biodiversity associated with kelp forests (Graham et al. 2007) may represent a reservoir of genetic diversity and resources for future use (Vasquez et al. 2013).

Atmospheric climate change may be altering nutrient delivery to giant kelp forests by changing the frequency and intensity of upwelling in the eastern North Pacific Ocean. When nutrient limitation causes widespread extinction, such as during very strong El Niño events, demographic connectivity with remnant populations (Castorani et al. 2015) or deep-water populations (Ladah and Zertuche-González 2004), or local survival of latent developmental stages (Carney et al. 2013), may be important for recovery. For shorter, seasonal episodes of limited upwelling, other sources of nitrogen may sustain giant kelp growth and persistence, including terrestrial runoff or ammonium excreted by reef animals or effluxed from sediment (Hepburn and Hurd 2005; Fram et al. 2008; Brzezinski et al. 2013). However, relatively little is known about the role of ammonium in supporting giant kelp through low-nitrate periods, nor whether ammonium dynamics will shift under climate change (Brzezinski et al. 2013; Schiel and Foster 2015).

Although nutrient availability can limit persistence, giant kelp has the potential to adapt to local conditions. In laboratory experiments and field transplantations, giant kelp from warm-water populations has greater survival and growth under warm, low-nutrient conditions than giant kelp from colder-water populations (North 1971; Kopczak et al. 1991). With climate-driven changes to nutrients and temperatures anticipated in the coming century, more work is needed to assess the scales and consequences of local adaptation in giant kelp (Johansson et al. 2015; Schiel and Foster 2015).

Since the 1950s, wave energy has increased globally, including in the eastern North Pacific Ocean (Bromirski et al. 2003; Gulev and Grigorieva 2004; Menéndez et al. 2008; Ruggiero et al. 2010; Seymour 2011; Young et al. 2011). Under most emissions scenarios, climate models predict increasing wave magnitudes in temperate regions, including western North America, due in part to increasing frequencies of large cyclones in the South Pacific and storm intensification in the North Pacific (Easterling et al. 2000; Wang and Swail 2006a, 2006b, Leslie et al. 2007; Meehl et al. 2007; Semedo et al. 2013). Ongoing and future intensification of waves may have important repercussions for the distributions and dynamics of giant kelp forests, potentially leading to persistent local extinctions of giant kelp and shifts in the benthic community towards understory algae that are more resistant to large swells (Dayton et al. 1992, 1999; Byrnes et al. 2011).

Unfortunately, there is limited and sometimes-conflicting information about the direct effects of OA on kelp forest organisms (e.g., Dillon 2014; Fernandez-Subiabre 2015). Most studies suggest that non-calcifying algal species, such as giant kelp, will experience few negative effects and may possibly benefit from OA, for example, by increasing photosynthesis (Harley et al. 2012, Koch et al. 2013, Schiel and Foster 2015). The potential for marine species to adapt to OA is not well known and community effects may vary. Harley et al. (2012) hypothesized that, in contrast to the negative direct and indirect effects of warming, giant kelp from the southern range limits may respond positively to direct and indirect OA effects. The combination of species-specific OA impacts has the potential to reshape kelp forest community structure, shifting competitive interactions between fleshy and turf algae species and/or increasing grazing activity of abundant herbivores that feed on kelp (Hepburn et al. 2011; Dillon 2014).

We can safely assume that population connectivity of animals associated with kelp forest in California and Baja California is mainly regulated by oceanographic processes. Nevertheless, a lack of accurate, quantitative descriptions of ocean circulation at different scales, as well as the increase on frequency and intensity of oceanographic variability generated by climate change, limit our understanding of connectivity processes. Few studies have examined the connectivity of kelp forest species across different spatial scales along their distributional range. The conservation and management of species that inhabit kelp forests will benefit from the combined knowledge of connectivity among populations across the California and Baja California border, and from understanding its seasonal and annual variability (DiBacco et al. 2006; Le Corre et al. 2012).

Thinking Ahead: Priorities for Future Bi-national Research and Training Initiatives

Cooperative activities between the US and Mexican governments take place under a number of arrangements and treaties. There are, however, few examples of binational agreements regarding the management of marine resources, possibly because of a lack of appreciation of the advantages for each nation of binational efforts. Even though binational collaboration can be challenging due to language barriers, differential development of scientific structure and human resources, and disproportional funding, pursuing binational research, increasing cooperation, and building infrastructure undoubtedly generates shared benefits, such as better fisheries management, marine conservation strategies, and collaboration in scientific research and monitoring. An excellent example of the advantages and benefits of closer collaboration, especially in the research perspectives was provided by the Joint Working on Ocean Sciences between the Mexican National Sciences Academy (Academia Mexicana de Ciencias) and the US National Research Council (NRC), that produced a template for increased cooperation between ocean scientists and policymakers from Mexico and the United States, to the benefit of the citizens of both nations (AMC-NRC 1999). Mexican and US agencies should cooperate in establishing a coordinated observing system that improves marine monitoring efforts. Government agencies and foundations should fund coordinated marine research that addresses challenges from a transboundary perspective. The

coordination between the two countries would improve if there were a continuous communication channel to address opportunities and challenges that are of binational interest. Capacity building is needed to move forward on all of these issues, and agencies should provide support for cross-border programs designed to provide training, field and laboratory experience to graduate students of both countries, as well as promote mechanisms for scholarly exchanges. The Mexican government should also investigate the need to establish a government entity responsible for marine affairs, including oceanic science and technology.

Monitoring change, anticipating possible ecological responses, and supporting social and ecological adaptation are key current and future priorities for maintaining the coastal ecosystems and economies along the **California Current System**. Bi-national coordination and new initiatives in support of coastal ecosystems and economies are most urgently needed in at least three areas: (1) coastal biophysical monitoring; (2) coordination of research on social-ecological coastal systems; and (3) capacity building, exchange of perspectives, and transfer of skills and technologies.

Coastal biophysical monitoring. Tracking physical variability and ecological responses requires continued monitoring, particularly in highly variable and heterogeneous ecosystems such as the upwelling ecosystems of the CCS. Several nearshore ecological monitoring programs exist in California and Baja California, particularly for kelp forest ecosystems, but most have been concentrated in specific locations, have never been integrated regionally, and face an uncertain future because of declining resources allocated to monitoring. Expanding, coordinating and integrating physical and ecological nearshore monitoring is critical in order to determine how regional climate and oceanographic events translate into physical variability along the coastline and across the CCS, the patterns and drivers of this variability, the influences on ecosystem function and flow of services; and the locations, species, and functions that are most vulnerable or resilient to climate change.

Social-ecological coastal systems. Understanding how ecosystems and human communities respond to, and are affected by, regional change requires that these two dimensions of coastal systems be investigated simultaneously. Social-ecological systems (SES) frameworks have been applied to investigating the resilience of coastal fisheries to climate variability and fishing intensity in central California (Aguilera et al. 2015), the role of exclusive access privileges and co-management in underlying the high performance of some fisheries in central Baja California (McCay et al. 2014), and trade-offs in achieving ecological and social sustainability across different regions of the Baja California Peninsula (e.g., Leslie et al. 2015). Bi-national, collaborative application of this framework, spanning the great ecological, social, and institutional diversity of the CCS, would produce crucial insights on the behaviors and feedbacks of coastal SES, and would provide critical information and networks for designing and implementing adaptive strategies.

Capacity building, exchanges, and technologies. A third critical need is to promote a greater flow and exchange of knowledge, competences, and technologies across the region, as well as between researchers and policy makers. The CCS contains a

large number of academic institutions, NGOs, agencies, and voluntary citizen groups with enormous potential for tackling the grand challenges of the 21st century. However this potential is not fully realized because of the fragmentation, inefficiency, and isolation of research and education, caused mainly by political barriers. Expanding current mechanisms for facilitating exchange of skills and technologies, and for building capacity in the future generation of researchers, educators and decision-makers, is a key priority.

Citizens' involvement and participation are critical elements spanning these three future priorities. New programs need to involve fishers, divers, educators and a suite of other stakeholders in data collection and use. Evidence suggests that kelp forests in Baja California are contributing to the replenishment of California kelp forests, their biodiversity, genetic structure, and linked fisheries (Alheit & Bakun 2009; White et al. 2010). These southern kelp forests are likely to suffer the consequences of overfishing and climate change before California forests do because the southern limit kelp forests live at the edge of their physiological tolerance, where an increase in the mean sea temperature would likely jeopardize nutrient supply. In addition, Baja California kelp forests have not benefited from recent conservation and management actions in the US such as the Marine Life Protection Act's network of MPAs. This scarcity of conservation strategies and management actions stresses the importance of calling the attention of government agencies, not only addressing this opportunity, but even more, to tackle this issues from a bi-national perspective. Thus, to improve the adaptive capacity of this ecosystem and support effective management actions, we must look at the Baja California-California system as a whole. Bi-national collective action, through citizens' participation and the transparent generation and use of information, is our best hope in the face of a changing climate and escalating pressures on coastal ecosystems and human communities.

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Endnotes

Allelic diversity.- the actual number of alleles present at a locus, the specific location or position of a gene's DNA sequence, on a chromosome.

Aragonite.- a mineral consisting of calcium carbonate, typically occurring in white seashells

Conspicuous fish.- fish species that are clearly visible and attract the attention for size and/or color.

Cryptic fish.- classification of fish species that for its size, color (camouflage) or behavior are difficult to notice.

Ecosystem engineer.- is any organism that creates, significantly modifies, maintains or destroys a habitat. These organisms can have a large impact on the species richness and landscape-level heterogeneity of an area.

Genetic bottleneck.- is a sharp reduction in the size of a population due to environmental events (such as earthquakes, floods, fires, disease, or droughts)

Hypoxia.- oxygen deficiency in a biotic environment.

Ocean acidification.- Ocean acidification is the decline in surface seawater pH caused by the sustained absorption of anthropogenically-derived atmospheric CO₂ (Caldeira and Wickett 2003).

Oxygen Minimum Zone.- sometimes referred to as the shadow zone, is the zone in which oxygen saturation in seawater in the ocean is at its lowest. This zone occurs at depths of about 200 to 1,000 meters, depending on local circumstances.

Pelagic ecosystems.- marine organism that live in the water column of coastal and ocean but not on or near the bottom of the sea. They can be contrasted with demersal fish, which live on or near the bottom, and reef fish, which are associated with coral reefs.

Resilience.- was defined as the amount of disturbance that an ecosystem could withstand without changing self-organized processes and structures (defined as alternative stable states).

Sessile invertebrates.- Organisms that usually live on a substrate without the ability to move

Top-down control.- refers to when a top predator controls the structure or population dynamics of the ecosystem. The classic example is of kelp forest ecosystems. In such ecosystems, sea otters are a keystone predator. They prey on urchins which in turn eat kelp.

Upwelling.- is a process in which deep, cold water rises toward the surface.

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Chapter 4, in full, is a preprint of the material as it appears in UC Office of the President: UC-Mexico Initiative 2017. **Ramírez-Valdez A.**, O. Aburto-Oropeza, N. Arafah Dalmau, R. Beas-Luna, J.E. Caselle, M.C.N. Castorani, K. Cavanaugh, M. Edwards, G. Hernández-Carmona, A.F. Johnson, H.M. Leslie, G. Montaña-Moctezuma, F. Micheli, J. Palleiro Nayar, P.E. Parnell, D.C. Reed, O. Sosa-Nishizaki, J. Torre, G. Torres Moye, J.A. Zertuche-González, P. Raimondi. 2017. Mexico-California Bi-national initiative of kelp forest ecosystems and fisheries. White paper prepared for UC-Mexico Initiative. 48p. The dissertation author was the primary investigator and author of this material.

CONCLUSIONS

ARTURO RAMÍREZ-VALDEZ

This work has analyzed a selection of marine resource management and conservation case studies from across the United States (U.S.)-Mexico political border. The analysis included the evaluation of asymmetry in scientific knowledge, resource management strategies, and ecosystem services. This final section presents the main conclusions of the analysis of fish distribution in the biogeographic transition between the warm-temperate and subtropical systems, the analysis of asymmetry in the management of the giant sea bass and kelp forest, and the review of the existing knowledge of the kelp forests throughout California (U.S.) and Baja California (Mexico) and how climate change will likely impact them.

The first chapter reviewed the distribution of fish species to the south of the U.S.-Mexico border region. This analysis show that the Cedros archipelago fish community is a species-rich assemblage, with a fairly even blend of temperate and tropic-subtropical affinity species. The marked break between the San Diegan and the Cortez biogeographic provinces includes five continental islands and is located in the east-central region of the Baja California Peninsula. To the north of the Cedros archipelago, temperate species associated with rocky reefs and kelp forests begin to be dominant until Point Conception, California. To the south of the Cedros archipelago, species associated with the tropical Cortez and Mexican provinces begin to appear, mainly associated with mangrove ecosystems in estuaries and bays located in Bahia Magdalena. Species

of affinity to cold-temperate waters and tropical-subtropical species are proportionally represented in this region.

In addition, 38% of the registered species have their distribution limit within this small geographic region. Of the nineteen species that presented new occurrences in the Cedros archipelago, ten were extensions south of previous distribution limits, two which were San Diego. The limited sampling effort south of the U.S.-Mexico border may be the most likely reason for the changes in known distribution. This work represents the first exhaustive fish checklist in the northern region of the Baja California Peninsula, different from that of Guadalupe Island. This study has shown the need for better scientific knowledge of this taxonomic group in the region and how this lack of knowledge can contribute to inadequate perceptions in the distribution of species.

The asymmetry in the management of shared resources between nations generates complex scenarios that hinder optimal use, creates disadvantages for one or both actors, and stifles conservation efforts. Two such scenarios on the U.S.-Mexico border are addressed with two chapters; (a) the critically endangered giant sea bass (*Stereolepis gigas*), and (b) the ecosystem services of the giant kelp forest ecosystem. The conclusions of these case studies are presented below:

The conclusions of the critically endangered giant sea bass (GSB) have been revealed as marked asymmetry in the scientific knowledge and management of the species across the U.S.-Mexico border, creating a complex scenario for fishery management and hampering conservation efforts. California introduced a ban in 1982 after the collapse of GSB stocks due to overfishing, yet it is still an open fishery in Mexico today. This has led to a difference in the regulation of the fishery of the species, implications for the different managements of the fisheries, and knowledge of the species and its populations. The work in these chapters have collectively found that

extremely strong asymmetry exists in scientific knowledge, economic input, and conservation methods across the U.S.-Mexico border, political regulations have both hidden and created illusions of false historical population collapses, and the total population size of GSB is likely higher than previously estimated.

The analyses of the historical landings of the GSB reveal that the collapse of its populations occurred much earlier than previously thought and that landings decline from the U.S. fleet in Mexican waters may be the result of regulation of the commercial fisheries between the U.S. and Mexico. The fishery landings analysis highlights three major findings: (a) high annual variability in catches, (b) location of main fishing grounds in southern Baja California, and (c) the population size of this species is likely higher than previously thought. The analysis from biological monitoring in the Mexican fleet leads to estimations that the GSB population size could be larger than we previously thought. The catches from the U.S. and Mexican waters combined, totaling more than 53 tons per year, could represent up to 2,120 giant sea bass individuals per year. Considering that up to 48.4% of the GSB landed by the Mexican commercial fishery are juvenile individuals, the adult individuals removed annually could be up to 1,026. A possible future scenario could see both countries with an equal proportion of the GSB population. However, sustainable stocks in this scenario will not be likely without setting the foundations for binational management. It is in the best interests of both parties to recover the population of the giant sea bass from the perspective of fishing, its ecological role, and its cultural value.

In the giant kelp *Macrocystis pyrifera* forests ecosystem services, when considering only the extractive services of the commercial fishery, which represents a small fraction of all the benefits we obtain from it, the results show the value provided may be upwards of US\$9 million per year. Giant kelp forests are iconic ecosystems providing a wide range of services including

direct use examples such as commercial and recreational fisheries, which represent an important economic and social component. The economic value estimates of the giant kelp forests ecosystem across the entire geographic distribution in the Northeastern Pacific are based on the most representative goods and services that this ecosystem provides to humans. Considering just the abalone fishery in Mexico, the economic value of production can be up to US\$8 million in a fishing season. Unlike services that other ecosystems provide to humans, the loss of the giant kelp forest would also represent the total loss of some of these fisheries as they are highly dependent on the existence of giant kelp. The greater fishing production in Mexico of benthic species (i.e., spiny lobster, sea urchin) is the result of the combination of greater fishing landings and fishery management areas specifically directed to the habitat of these resources. This study successfully shows that the economic value of kelp forests ecosystem is significantly higher than previously thought considering fisheries alone. The results indicated the value reaching US\$8.5 million per year when considering only five fisheries.

The coastal forests formed by the giant kelp *Macrocystis pyrifera* are primary habitats. In California and Baja California, they support high levels of species diversity and productivity in the region, acting as a refuge, nursery, and food provider for many species. The kelp forests and the populations of species that inhabit this ecosystem across the U.S.-Mexico border are connected through migration, dispersal, and genetic connectivity. Despite forming the same large marine ecosystem, the forests of California and Baja California have two very different histories. California's kelp forests have a long history of kelp harvesting, fishing pressure, pressure from recreational activities, continuous long-term monitoring programs, and a network of marine protected areas. While the fishing pressure on the kelp forest in Baja California is more recent, few research monitoring initiatives exist, and a lack of spatial protection schemes is notable. There are

more than 40 times more peer-reviewed papers on kelp forest ecosystem topics in California than in Baja California, furthering the asymmetric knowledge and management in the region. The lack of studies taking a binational approach is glaring when out of a total of 236 articles in the review, only nine peer-reviewed papers include sites on both sides of the border. As a result, the best strategy in the long run is transboundary cooperation through sharing cross-border marine resources and acknowledging the actions taken by one of the invariably parties affects the other.

In addition to its ecological importance, giant kelp forests and the ecosystem services they provide to humans are worth millions of dollars to the U.S. and Mexican economies, which may be lost or decreased due to climatic and non-climatic change stressors. Coastal human populations rely on many ecosystem services that kelp forest provide such as food and natural products, chemical products, recreational and commercial fisheries, ecotourism opportunities, cultural value, and nutrient cycling. The physical environment that supports kelp forests includes hard bottoms in waters shallow enough for light-limited germination and growth, exposure to cool nutrient-rich waters, surge, and low risks of sedimentation and turbidity. Human activities have become ecological drivers of kelp forest communities and the impacts of pollution, land use practices, disposal of dredged sediment, introduction of exotic species and overfishing of key predators and herbivores have been well documented and are relatively known. Although the same level of certainty is not available for the consequences, it is clear that changes in ocean temperature and acidity may interact with one another and have different impacts on these forests and that the kelp forests in the California and Baja California region are currently under stress due to overfishing, overgrazing, heat waves, and climate change. The literature review showed that the giant kelp and the biological communities it supports will likely react to climatic and non-climatic changes in

complex ways, likely by contracting their southern extent due to warming waters, reductions in nutrient availability, increasing wave disturbance, and grazing by warm-water herbivores.