Summer 2021

Recovery of the sea star Heliaster kubiniji from a mass mortality event, and additional dynamics of intertidal invertebrates within the Gulf of California

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Recovery of the sea star *Heliaster kubiniji* from a mass mortality event, and additional dynamics of intertidal invertebrates within the Gulf of California

By

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Accepted in Partial Completion
of the Requirements for the Degree
Master of Science

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Master’s Thesis

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May 8, 2021

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A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Carter Urnes
June 2021

Abstract

In 1978 populations of a charismatic and abundant intertidal sea star *Heliaster kubiniji* (Xantus) declined throughout the Gulf of California. Two years after this mass-mortality event, researchers found very low densities of *H. kubiniji* at many sites throughout the region and concluded that the species had not recovered. To my knowledge *H. kubiniji* densities in the Gulf of California have not been formally surveyed since the 1980 mass-mortality event. Although intertidal sampling has sporadically occurred within the region, many questions regarding invertebrate populations remain unanswered.

To better understand and predict the recovery of echinoderms from mass-mortality events, I returned to historically sampled sites in the Mexican states of Baja California and Baja California Sur to assess recovery almost 40 years after the mortality event. I conducted vertical transects on rocky intertidal beaches at 13 sites. Densities of *H. kubiniji* were found by dividing the total area surveyed by the number of *H. kubiniji* found. I also conducted interviews with community members collecting intertidal organisms to learn more about the local abundance, as well as whether these sea stars were being collected for sale as curios. The results of these surveys as they relate to the recovery of *H. kubiniji* are discussed in Chapter 1. During transect surveys to quantify the presence of *H. kubiniji*, as well as snorkel surveys at each site, I documented the presence and density of several other member of the Gulf intertidal community. I analyzed historical field notes for observations of the additional species at sites on the Baja California peninsula. I compared species presence and abundance in historical field notes to my own surveys and observations in 2017. Chapter 2 contains the results of this analysis of the broader Gulf intertidal community.

Surveys at several historically sampled sites suggest that *H. kubiniji* has recovered from the 1978 mass-mortality event at some sites on the Baja California peninsula. At other locations *H. kubiniji* has not recovered. Interviews suggest that the species is well known to locals and is rarely collected for sale commercially as a curio. Even infrequent collection events might slow the recovery of this species. Additionally, it might be more difficult for *H. kubiniji* populations to recover in some areas due to abiotic factors like exposure to cold temperatures during extreme winter low tides.

A comparison of historical field notes and 2017 surveys suggest that many species that were historically recorded at sites in the Northern and Central regions of the Gulf remain present. Although historical observations were sporadic and were not comprehensive, these data suggest that several species have declined at sites within the Gulf. The abundance of the Murcid gastropod *Hexaplex nigritus* might have decreased at sites in the Northern Gulf. For most species there was no evidence of change in the species distribution within the Gulf. However, several species of sea urchins were observed in 2017 outside their historical ranges. I present the 2017 presence and density of many Gulf intertidal species at sites for the first time. Hopefully this work will allow future researchers to accurately compare changes in the intertidal community of the Gulf.

Acknowledgements

I was supported in this research by a Graduate Fellowship in the Department of Biology at Western Washington University. Dr. Benjamin Miner provided formative critiques, suggestions, and ongoing encouragement. Dr. Alejandro Acevedo-Gutiérrez, Dr. Marion Brodhagen, and Dr. Deborah Donovan provided valuable feedback on the design of the research. Mike Dungan and Rick Brusca provided their personal field notes as well as their profound knowledge of the Gulf of California. Isaac Rysdahl graciously volunteered two months of his time as an exceptional field partner. Interviews with fishers would not have been possible without his Spanish language fluency or his compassionate and respectful demeanor. Cassidy Grattan found the first *H. kubiniji* of this research on a preliminary sampling expedition to Puertecitos. My life has been deeply enriched by their companionship. Muchísimas gracias a la gente de Baja California y Baja California Sur.

Table of Contents

Abstract iv

Acknowledgements v

List of Tables and Figures vii

Chapter 1 1

Chapter 2 23

Works Cited 46

Appendix A: Interview Questionnaire 52

Appendix B: Compilation of information for intertidal species 54

Appendix C: Compilation of field observations 78

List of Tables and Figures

Table 1: Site Names 17

Figure 1: Site Locations 18

Figure 2: Density of *H. kubiniji* at each site 19

Figure 3: Smoothed density plot showing the distribution of *H. kubiniji* sizes 20

Figure 4 : Size distribution of *H. kubiniji* at each site 21

Figure 5: Photo of *H. kubiniji* 22

Figure 6: Regions of the Gulf 42

Table 2: Site key 43

Table 3: 2017 Density measurements 44

Chapter 1: Recovery of the sea star *Heliaster kubiniji* from a 1978 mass-mortality event

Introduction

Disease-related, mass-mortality events have dramatic effects on marine populations and communities. Mass-mortality events are demographic catastrophes, which greatly decrease the size of the affected populations (1). Reduced population size of predators can increase prey population sizes and alter the dynamics of communities, and prey populations can remain large until predator populations recover (2). Researchers have observed community-wide changes after declines of keystone species, which modify their environment by consuming dominant competitors (3). For example, a widespread mass-mortality event of the grazing urchin *Diadema antillarium* was associated with a shift in many Caribbean coral reefs from coral- to algal-dominated ecosystems (4).

Disease-related mass-mortality events can be consequential to marine organisms. Marine mass-mortality events can be poorly monitored because they often take place in locations that are difficult to access. Marine diseases can also spread faster than terrestrial epidemics, and existing methods for managing terrestrial diseases have been largely ineffective in marine systems (5). Anthropogenic influences on marine systems are expected to accelerate the dispersal and intensity of pathogenic diseases, and the rate of marine diseases in fish and marine invertebrate populations is intensifying (6,7).

Since 2012, an unprecedented mass-mortality event has impacted populations of sea stars along the West Coast of North America. Known as sea star wasting disease (SSWD), it is the largest documented marine disease-related mortality event; hundreds of millions of sea stars are estimated to have died in populations from Alaska to the Pacific coast of Mexico (8,9). Individuals affected by SSWD characteristically display lesions, progressive tissue disintegration, and death (10). Long-term-monitoring data collected by the MARINe group documented declines in the density of the keystone species *Pisaster ochraceus* of more than 75% in 38 of 39 monitoring sites in Central and Southern California; some sites lost more than 99% of individuals (11). This event is especially notable because it has impacted more than 20 different species of sea stars, including some species which are distantly related, as well as species with dramatically different life histories (12).

Many questions remain regarding the causative agent and the potential recovery of populations from SSWD. Initially, researchers suggested that SSWD was associated with a marine densovirus in three highly impacted species (8). However, further research indicated that this densovirus was only associated with SSWD in the species *Pycnopodia helianthoides* (13). Elevated sea water temperatures are known to accelerate the progression of the disease, and might have exacerbated the effects of the disease, but are not believed to have caused the initial disease outbreak (10,11). Recovery has started to take place in some populations. In 2017, recovery had been documented in populations of *Pisaster ochraceus* in Washington's Salish Sea, and along the Oregon and Northern Californian coastline, although densities of sea stars at many locations remain below historical averages, and disease symptoms are still present at some locations (2,11).

In recent decades researchers have reported several other mass-mortality events in populations of asteroids on the West Coast of North America. A 1997 mortality event in the Channel Islands of California affected 10 species of sea stars, and was associated with a population decline of 75% in one species (14,15). Lesions consistent with SSWD were observed in two populations of the sea star *P. ochraceus* on the west coast of Vancouver Island in 2008, and increased temperature was associated with a higher intensity and more rapid progression of disease symptoms (16). Populations of the sea star *Leptasterias hexaxis* were extirpated from a 100km section of the North-Central California coast during a wasting event in 2011, and other sea stars exhibited elevated mortality (17). It is not known whether these disease events are all associated with the same agent, or whether a complex interaction of local biotic and abiotic factors is producing similar disease etiologies.

The sea star *Heliaster kubiniji* has also experienced a mass mortality event. In the summer of 1978, researchers in the Gulf of California (hereafter, the Gulf) observed progressive loss of limbs and tissue disintegration in the formerly ubiquitous intertidal sea star (18). Other echinoderms were also affected during this mass-mortality event, including the asteroids *Astrometius sertulifera* and *Echinaster tenuispina* (formerly *Othalia tenuispina*), and the holothuridian *Isostichopus fuscus*; however, data regarding mortality was apparently only collected for *H. kubiniji* (R. Brusca, pers. comm.). Mortality "approached 100 percent" at frequently monitored sites around Puerto Peñasco, Sonora (18).

H. kubiniji is an indiscriminate intertidal carnivore, and grazes predominantly on sessile mussels and barnacles (19). There is no evidence that it is routinely eaten by other marine organisms, although it is occasionally consumed by gulls (personal obs.) The dramatic mortality event in 1978 was thought to have been related to a persistent warm water event in the Gulf (18). In 1980, two years after this mortality event, Dungan and colleagues at the University of Arizona conducted surveys at sites throughout the Gulf and documented widespread declines in *H. kubiniji* (from >0.1 individuals/m^2 to less than 0.05 individual/m^2 (18)). Diversity surveys conducted during a 2004 cruise in the Gulf indicated that *H. kubiniji* densities remained below historical observations; however, this survey did not quantitatively measure the density of *H. kubiniji* (20). Surprisingly, there have been no quantitative studies specifically analyzing the recovery of this predatory sea star within the Gulf since 1980. Although the relationship between this mortality event and the ongoing West coast SSWD event is unclear, both events involve an abundant intertidal asteroid undergoing dramatic (>90%) mortality at many sites throughout its range.

The ability of a population of echinoderms to recover following a disease-related mass-mortality event is likely influenced by factors such as persistence of the disease, evolution of resistance, larval supply of new individuals, and existing community structure. SSWD on the west coast of North America appears to have persisted in some regions into 2018 and will likely inhibit recovery (MARINe Group). Genetic changes have been detected in populations since 2013 (21), but it is unknown whether these alleles improve resistance to future wasting events. In areas that experienced high levels of mortality, recovery must begin with the arrival of new larvae from a refuge of individuals that survived the wasting event. The dispersal of new larval recruits from other areas is likely to be highly species specific: after the West coast SSWD event *P. ochraceus* persisted to some degree at most sites after the mortality event and recruits appeared at some sites soon after, while the subtidal asteroid *Pycnopodia helianthoides* was "virtually extirpated" from regions of the Salish Sea and has declined in abundance by 80-100% across 3000 kilometers of Eastern Pacific Coastline (2,12,22). Finally, new recruits may find previously habitable areas drastically changed after a period of reduced abundance. Declines in Southern California Black Abalone populations associated with Abalone Wasting Syndrome resulted in previously bare surfaces becoming occupied by invertebrates and algae, and this new biological community severely limited the potential for abalone to re-occupy these spaces (23).

Contemporary populations of the sea star *H. kubiniji* provide a unique opportunity for studying the recovery of marine invertebrates from a mass-mortality event. *Heliaster kubiniji* was historically abundant in suitable intertidal habitat from Mexico to Panama (19). In 1940, ecologist Ed Ricketts described *H. kubiniji* as "the most common, obvious, and widely distributed shore starfish"(24). It is one of the only asteroid species known to have undergone a dramatic mortality event across a large part of its range (18). It has an important place in scientific literature, as Paine included *H. kubiniji* alongside *P. ochraceus* as a keystone species which modified its environment through grazing and prevented the monopolization of habitat by a spatial dominant; however, this was later called into question (3,25). These factors make the potential recovery of *H. kubiniji* relevant to intertidal communities within the Gulf as well as intertidal communities on the West Coast which have been impacted by the recent Sea Star Wasting Disease event.

The Gulf is a large and extremely productive marine ecosystem. Strong tidal mixing consistently moves deep, cold, nutrient rich water into the Gulf at depth and out to the Pacific Ocean at the surface (26). The Northern Gulf, from the mouth of the Colorado River to the Midriff Islands, is characterized by shallow waters (less than 100m) and predominantly alluvial substratum (Figure 1) (27). The central Gulf, from the Midriff Islands to the Guaymas Basin, contains a number of deeper basins separated by sills. This region experiences dramatic tidal mixing of deep, cold, nutrient rich water at the surface, contributing to its locally high productivity within the Gulf (26,28). The Southern Gulf is much deeper and is strongly influenced by the Pacific Ocean.

In order to document the recovery of *H. kubiniji* from a reported mass-mortality event in 1978 I visited intertidal sites in the Mexican states of Baja California and Baja California Sur. I sampled 13 sites along the coast of Baja California during the months of September and October 2017 (Figure 1, Table 1). In 1982 the density of *H. kubiniji* at 6 historical sites was less than 0.05 individuals/m^2 (18). Before the mass-mortality event, the density of *H. kubiniji* at each of these sties was greater than 0.1 individuals/m^2 (18). No historical density information existed for 7 additional sites. These sites were sampled in order to determine the presence of *H. kubiniji* in the Gulf of California more generally. The size of every individual *H. kubiniji* was recorded to generate a size distribution. I used field notes and personal communications to locate historical sites.

Methods

I surveyed 13 rocky intertidal sites along the Gulf of California in the Mexican states of Baja California and Baja California Sur (Figure 1). Sites were selected based on presence in the 1982 study which documented the mass mortality event, presence in historical field notes which were not part of the 1982 study, and based on suggestions from local fishers. The sites San Felipe, Coloraditos, Puertecitos, Bahía Concepción, Bahía de Los Ángeles, Punta Chivato, and Loreto were historical sites included in the 1982 study. The sites Punta Estrella, Punta Willard, and Puerto Escondido were included because they were referenced in historical field notes from Ricketts and Steinbeck, Brusca, or Dungan that were not part of the 1982 study. The sites El Sacrificio, Calamajué, and Las Ánimas were sampled based on suggestions from local fishers.

During surveys I placed transects perpendicularly to the shoreline to quantify the density of *H. kubiniji* at each site. Transects were located in areas of the beach with appropriate substrata for *H. kubiniji*, which are known to prefer "large, smooth, basalt-type rocks" (19). Transects were spaced at 10 m apart perpendicularly to the waterline. All surveys were initiated one hour before a low tide less than 0.0 m (mean lower low water). The top of each transect was established 7 meters from the water line. Each transect was extended to its maximum length as the tide dropped. Tidal elevation was recorded by noting the time at which the water level was at the bottom of the transect, as well as the time at which the tide inundated the top of the transect. I used headlamps and dive lights to survey sites at night. Transect surveys involved counting every *H. kubiniji* found within 1m of the transect. Organisms were counted if more than half of the central disk was within the transect. Every rock that could safely be manipulated by one individual was turned over and replaced in its original orientation. No rocks that were buried in the substrata were excavated. Densities of several other invertebrates were also recorded, and are presented in Chapter 2.

I was able to sample some sites in the Northern Gulf multiple times. Each time I sampled a site again I established additional transects in suitable substrate 10 meters from the previously sampled transect. The number of *H. kubiniji* and area of beach sampled were added to previous sampling events to calculate an average density for the site using a larger area of the beach. Because sampling of all sites within the Gulf was conducted over a short period of time (2 months) during which juveniles were not observed to be recruiting, I do not expect the density of *H. kubiniji* to have changed between site visits.

At three sites (Coloraditos, Bahía Concepción, and Puerto Escondido), I modified the transect methodology to account for unsuitable substrata. At Coloraditos a limited area of suitable substrate restricted the area which I was able to sample. I was able to conduct a survey using shorter transects (7m long) spaced more closely together (5m apart, instead of the usual 10m apart). At Bahía Concepción, much of the historically sampled site is a steep sand beach, and I similarly shortened the transects and placed them closer together. At Puerto Escondido a large marina has been constructed on the historical sampling location. I sampled a steep beach adjacent to the marina, which had suitable substate but only a few meters of intertidal habitat exposed at low tide. In order to establish the presence of *H. kubiniji* at this site (which was not surveyed by Dungan et al. after the wasting event but was historically visited by Ricketts and Steinbeck) I set out two 12m horizontal transects.

Diameter of each *H. kubiniji* was measured from ray tip to ray tip across the central disk using a flexible measuring tape. Because *H. kubiniji* has between 19 and 25 rays (19), diameter is an appropriate measurement for these roughly circular organisms. When organisms were found in contorted positions I measured diameter by gently removing the sea star from the substrata and placing the organism on a flat surface, which would cause the organism to spread along the surface and crawl away. Each *H. kubinji* counted in the survey was measured in order to generate a size distribution for *H. kubiniji* in the Gulf.

In order to establish if *H. kubiniji* was harvested by humans, I interviewed individuals at sites. I approached individuals who were actively harvesting marine invertebrates (digging for clams, collecting shells). After individuals gave consent to participate in a brief survey, I asked them a series of questions designed to understand harvest of marine invertebrates in the Gulf (Supplemental Figure 1). Several of these questions were designed to specifically understand the collection of *H. kubiniji*, as it is known to have been historically harvested for sale in curio shops (Brusca, personal communication). Interviews were completed in accordance with the Western Washington University Institutional Review Board under permit IRB# EX18-005.

The density of *H. kubiniji* was calculated at each site by dividing the total area surveyed by the number of *H. kubiniji* recorded. After the 1978 mortality event the density of *H. kubiniji* was less than 0.05 individuals/m^2 at six historically sampled site. Before the wasting event, *H. kubiniji* was present in suitable areas throughout the Gulf of California at densities of 0.1 to 1 individual/m^2. A density of *H. kubiniji* greater than > 0.05 individuals/m^2 is evidence of some recovery since the mortality event, and a density of > 0.1 individuals/m^2 is evidence of full recovery. Size distributions for *H. kubiniji* within the Gulf were visualized using the ggplot2 function in R (29).

Results

The densities of *H. kubiniji* at three historical sites (Bahía de Los Ángeles, Punta Chivato, and Loreto) were more than 5 times greater than the densities recorded after the 1978 wasting event (Figure 2), and similar to densities recorded in the Gulf before the mass mortality event. At three other historical sites (San Felipe, Coloraditos, and Bahía Concepción) I found no evidence of recovery. Densities at these sites were similar to what was recorded following the 1978 mass mortality event (0.0, 0.010, and 0.0 organisms/m^2, respectively)

Five sites without historical data (Punta Willard, El Sacrificio, Calamajué, Las Ánimas, and Puerto Escondido) exhibited densities of *H. kubiniji* similar to the historical (pre-mortality) density of >0.1 individual/ m^2 (0.585, 0.250, 1.842, 0.850, and 0.267 organisms m^2, respectively) (Figure 1; Table 2). At two additional sites without historical data (Punta Estrella and Puertecitos) I did not find evidence of recovery (densities of 0.034 and 0.042 organisms m^2, respectively).

The size distribution of *H. kubiniji* found at sampled sites showed a multimodal distribution with two obvious peaks at 25 and 100mm, respectively. Individuals ranged from 9mm to 182mm. The largest individual was found at Punta Estrella, a site with a low density of *H. kubiniji* and a relative lack of suitable substrata (size 182mm, density 0.034) (Figure 3).

In eleven interviews with individuals collecting marine invertebrates, no one reported knowledge of *H. kubiniji* harvest at that time. Two individuals reported that they had collected *H. kubniniji* for sale in unique events for specific buyers in the past, but that this was not a common practice. Every individual I spoke with was familiar with *H. kubiniji*, and some individuals reported observing *H. kubiniji* to be more common and visible in the winter than in the summer.

Discussion

Evidence for recovery

Thirty-nine years after *H. kubiniji* experienced a mass-mortality event in the Gulf three out of six historically sampled sites showed evidence of recovery, with densities of *H. kubiniji* greater than what was observed two years after the mass-mortality event and similar to what was observed before the mass-mortality event. Additionally, at five out of seven new sites for which there is no previous data, *H. kubiniji* was present in densities greater than what was observed at historically sampled sites before the mass-mortality event. Recovery at historically sampled sites and abundance at new sites each suggest that at some locations in the Northern and Central Gulf *H. kubiniji* populations have recovered from a historical mass-mortality event.

The size-distribution data reported in this study shows that *H. kubiniji* were present in the Northern and Central Gulf of California at sizes similar to historic observations. I found individuals ranging in size from 9mm to 182mm, which is within the expected range for the species. (18) . The smoothed density plot of the size distribution of each individual shows two peaks, which may represent a pulse of juvenile individuals that settled in the early in 2017 (Figure 3). The rate at which *H. kubiniji* develops within the Gulf is not known. The size distribution of individuals varied considerably among sites (Figure 4). This might be due to sporadic recruitment success at each site. While these data suggest that recovery has occurred at some sites within the Gulf, the life history characteristics of *H. kubiniji* remain poorly understood. Some of these characteristics, such as larval duration and population connectedness, are relevant to a complete understanding of how recovery occurred within the Gulf. Life history characteristics should be the subject of future research regarding *H. kubiniji*.

Site characteristics associated with recovery

In general, sites with physical characteristics that were amenable to *H. kubiniji* showed recovery from the 1978 mass-mortality event. One of these characteristics is strong tidal mixing of deep water to the surface. High densities of *H. kubiniji* were found at several sites near the Midriff Islands, which are in the most southern portion of the Northern Gulf. As incoming tides move water poleward from the deeper Southern Gulf, the Midriff Islands form an abrupt underwater barrier which forces deep, cool, nutrient-rich water to the surface. This dramatic tidal mixing is associated with moderated water temperatures and high primary productivity in the Central Gulf throughout the year (30). Moderated water temperatures might protect sea stars in this region from mortality caused by temperature extremes, which were associated with the 1978 mass-mortality event. Temperature extremes have also been associated with "winterkill" mortality events of intertidal fish in the northern Gulf (31). Additionally, high productivity in the Central Gulf might allow species that *H. kubiniji* consumes to grow more quickly and in higher densities, and this could allow sea stars in this region to feed without nutrient limitation.

Substratum might have increased the rate of recruitment in some *H. kubiniji* populations. *H. kubiniji* prefers "large, basalt type rocks" (19). Substrata type is closely associated with survival in sea stars. Many sea stars have highly specific larval settlement cues, such as the Caribbean sea star *Oreaster reticulatus*, which preferentially settles on the undersides of pebbles encrusted with coralline algae (19,32). Small *Pisaster ochraceus* and *Evisterias troschelii* in Puget Sound have been found to be most abundant in areas with high structural complexity. By contrast, larger individuals of these species were found in open areas, possibly due to predation by gulls on smaller individuals (33).

Sites that are likely to retain larvae after spawning might also better support recovery. The sampling sites at Calamajué and Puerto Escondido are each located within semi-enclosed bays, which might retain larvae within them after spawning. These sites each exhibited a high density of *H. kubiniji* as well as many young sea stars less than 30mm in diameter. Sea stars less than 30mm in diameter were present at several other sites (Punta Willard, Puertecitos, Punta Chivato), but the highest densities of these "juvenile" individuals were documented at Calamajué and Puerto Escondido. Researchers have documented synchronous spawning and retention of larvae in enclosed bays after spawning in *P. ochraceus* and *P. helianthoides*; these characteristics likely contributed to a documented and dramatic recruitment event (34). Enclosed site locations might have maximized the probability that larvae were able to recruit to a juvenile size class, and this might have allowed *H. kubinijij* to recover more quickly at these sites.

Collection of curios might be slowing recovery

Sea stars are not harvested for human consumption; however, they have historically been collected and dried for sale to tourists as souvenirs (curios). None of the individuals I spoke with reported collecting or knowing of others collecting sea stars in the last two years. However, during interviews and informal conversations, I found evidence that *H. kubiniji* has been collected at Bahía de Los Ángeles and Las Ánimas. One local in Bahía de Los Ángeles reported that in 2011 a buyer was paying 6 pesos for sea stars of any species, to be dried and sold as curios. These curios apparently sold poorly, and the subject had not collected sea stars since that time. While sampling at Las Ánimas, a young person traveling with a group of men collecting aquarium fish gave us a dried *H. kubiniji* as a friendly gesture. Each of these incidents suggests that *H. kubiniji* was and is still collected. Calamajué, a site with notably high densities of *H. kubiniji*, is the site furthest from a paved road. The remote location of this site might have reduced commercial collection of *H. kubiniji* and allowed populations to recover to a greater degree than those at Las Ánimas and Bahía de Los Ángeles. I observed curio shops in towns with many tourists (like San Felipe, BC) selling dried individuals of the sea star *Phatiria unifascialis* as well as shells from Murex, *Olivella,* and *Conus.* I did not observe *H. kubiniji* for sale in curio shops; employees told me that *H. kubiniji* sold poorly compared to larger sea stars like *Phatiria unifascialis*. The curio trade clearly represents a threat to all intertidal marine life in the Gulf of California. While the interviews I conducted suggest that collection for curios is not preventing the recovery of *H. kubiniji* within the Northern and Central Gulf of California, even infrequent collecting events could be contributing to a spotty pattern of recovery.

Collection of adult *H. kubiniji* as curios should shift the size distribution of individuals at a site towards smaller individuals. Bahía de Los Ángeles is a site in which an individual reported collection of *H. kubiniji* for curios in 2011 but did not report curio collection since then. It is frequently visited by tourists and supports an extremely active intertidal fishery for octopus. These factors make it likely that Bahía de Los Ángeles would show the effects of curio harvest in contrast to an undeveloped site. Calamajué is an undeveloped site with similar densities of *H. kubiniji*. The size distribution of *H. kubiniji* at Calamajué is similar to the distribution at Bahía de Los Ángeles (apart from a dramatic pulse of juvenile recruits at Calamajué. This suggests that infrequent collection is not altering the size distribution of populations of *H. kubiniji* at Bahía de Los Ángeles.

<u>Slow recovery in the Northern Gulf</u>

I did not observe densities of *H. kubiniji* indicative of recovery at the four most northern sites in the Gulf. I found healthy individuals of adult size in low densities (< 0.05 individuals/m^2) at Punta Estrella and Coloraditos in the Northern Gulf. While this does not meet my criteria for recovery, it does suggest that *H. kubiniji* larvae occasionally disperse and survive in this region.

It is not clear why *H. kubiniji* populations have not recovered to their historic densities at four sites in the far Northern Gulf. One possibility is that there is a lack of a larval supply to this region. The presence of *H. kubiniji* in low densities at three of the four sites in the far Northern Gulf indicates that *H. kubiniji* larvae continue to be carried to this region from other parts of the Gulf where they are more abundant. *H. kubiniji* has been suggested to spawn in late winter (19) when an anticyclonic (clockwise) gyre is known to seasonally form in the northern Gulf (26,35); this pattern would carry larval *H. kubiniji* produced in the Central Gulf into sites in the far Northern Gulf. The larval duration of *H. kubiniji* is not known; however, a closely related species from the southern hemisphere (*Heliaster helianthus*) is believed to have 2-3 month larval duration, with a long dispersion potential (36).

Another factor impeding recovery in the far Northern Gulf might be the extreme tidal amplitudes in this region. Semidiurnal tides in the Gulf are amplified as they travel north from the Pacific Ocean, while a "virtual amphidromic region" in the central Gulf experiences low tidal variation all year: the spring tidal range is greater than 6m in the extreme Northern Gulf, while the spring tidal range is less than 1.5m in much of the Central Gulf (26). This large tidal range in the Northern Gulf leaves intertidal organisms exposed to stressful ambient temperatures for long periods of time during low tide events. During winter months, extreme low tide events expose intertidal organisms to cold temperatures, which can cause dramatic mortality events called winterkills. In a study of reef fish diversity, winterkill events have been found to be more limiting to diversity in the Northern Gulf than high summer temperatures (31). It is likely that exposure to ambient temperatures during extreme low tides at sites in the Northern Gulf is inhibiting the recovery of *H. kubiniji* at these sites.

The substrata in the far northern Gulf might be slowing recovery in this region. The Northern Gulf is dominated by sand and alluvial deposits from the Colorado River (19), and each site I sampled in the Northern Gulf was an isolated rocky outcrop surrounded by sandy beaches. *H. kubiniji* is largely restricted to rocky substrata. Brusca has suggested that this species prefers large, smooth, "basalt-type" rocks (19). There are comparatively more sites with rocky habitat in the Central Gulf than the Northern Gulf.

Finally, the four sites in the far Northern Gulf (San Felipe, Punta Estrella, Coloraditos and Puertecitos) are likely to be highly impacted by any harvesting of *H. kubiniji* for curios because these areas are more frequently visited by tourists than other, more remote locations on the Baja Peninsula. Each of these sites can be accessed from the border in under a day by traveling exclusively on paved roads. The town of San Felipe is a major hub for tourism in the Northern Gulf, and the number of hotel rooms and tourists has increased dramatically in the last several years (37). I observed several shops in downtown San Felipe selling curios. I observed a fisherman collecting snails (*Hexaplex sp.* and *Olivella sp.*) for sale at a historically sampled site in San Felipe; in conversation the fisherman reported that he was collecting them for sale as curios in town. I also observed a group of women collecting shells at Punta Estrella; they reported that they were selling the shells to a buyer in Ensenada. It is likely that *H. kubiniji* continue to be sporadically collected for sale as curios. While no individuals were observed or reported collecting *H. kubiniji* at any of these sites, it is likely that individuals would opportunistically harvest *H. kubiniji* if there was a market for their sale. The high rate of tourism in the far Northern Gulf is likely to increase the frequency of collection in this region, and this might intensify the harvest of *H. kubiniji* for curios in this region.

Overall, it is likely that *H. kubiniji* has been slowly recovering throughout the Gulf of California since the 1978 mass-mortality event, and that this recovery has been highly site specific. Interviews I conducted suggest that *H. kubiniji* has been present in the Northern and Central Gulf for decades. Many people in the Northern Gulf were familiar with *H. kubiniji* and colloquially referred to them as 'flores'. No individuals reported seeing dramatic changes in the abundance of *H. kubiniji*, so it is unlikely that this sea star has experienced additional mass mortality since 1978. Two individuals in the Central Gulf separately reported that *H. kubiniji* was more abundant from November to February, when they "cover the rocks". This is notable because most research trips to the Gulf are conducted during the summer months. This information suggests that after *H. kubiniji* abundance was dramatically reduced in the Gulf of California in the summer of 1978, populations have slowly recovered throughout the Northern and Central Gulf. Additional stressors like harvesting for curios and winterkill events might have impeded recovery in some locations, while isolated, protected sites with moderated conditions might have served as refugia for continued recovery. Previous studies of the population size structure of asteroids have used monthly sampling to generate a growth curve for populations (38,39). This sustained monitoring would enable a quantitative description of *H. kubiniji* ages and the rate at which these organisms are growing within the Gulf of California.

Implications for recovery on the West Coast

The recovery of sea stars on the West coast of North America from Sea Star Wasting Disease might have similarities to the recovery of *H. kubiniji* observed in this study. West Coast sea stars are likely to recruit sporadically from isolated source populations. Recovery might be faster in enclosed bays with high structural complexity where larval retention is high and rocky habitat is available, but recovery could be delayed in locations with dramatic temperature variations. Disturbance by humans is likely to slow rates of recovery, while remote, undisturbed populations might serve as 'source' populations in species with long larval dispersal potential.

A critical difference between these mass-mortality events is the causative agent, which may significantly impact the duration of the mass-mortality event. Populations of sea stars at some sites on the West coast continue to show wasting symptoms in 2021 and recovery at many sites has been extremely slow. In contrast the 1978 *H. kubiniji* mass-mortality event was associated in the 1982 publication with elevated sea water temperatures driven by El Nino oscillations that returned to long-term means in the winter of 1978 (18). While the abundance of *H. kubiniji* remained low for several years following the mass-mortality event in the Gulf, there is no evidence that wasting symptoms continued to occur in the Gulf. If West Coast Sea Star Wasting Disease continues to reduce sea star abundance on the West Coast, population densities could remain low for many years to come.

Table 1: Site names and locations in Baja California and Baja California Sur, with site codes, coordinates, total area surveyed at each site, and average density of *H. kubiniji*. Historical sites were sampled after the 1978 mass mortality event.

Site#	**Site Name**	**Latitude**	**Longitude**	**Area surveyed (m^2)**	**Density of *H. kubiniji***	**Historical?**
1	San Felipe	31.05355	-114.819	116	0	Yes
2	Punta Estrella	30.91491	-114.712	180	0.03	No
3	Coloraditos	30.58065	-114.668	208	0.01	Yes
4	Puertecitos	30.33987	-114.64	120	0.04	No
5	Punta Willard	29.84215	-114.407	198	0.59	No
6	El Sacrificio	29.75062	-114.344	60	0.25	No
7	Calamajué	29.693	-114.16	100	1.84	No
8	Bahía de Los Ángeles	29.03259	-113.554	304	0.40	Yes
9	Las Ánimas	28.80829	-113.355	40	0.85	No
10	Punta Chivato	27.0778	-111.947	30	0.47	Yes
11	Bahía Concepción	26.71346	-111.902	30	0	Yes
12	Loreto (El Bajo)	26.0906	-111.325	30	0.27	Yes
13	Puerto Escondido	25.81077	-111.307	24	1.92	No

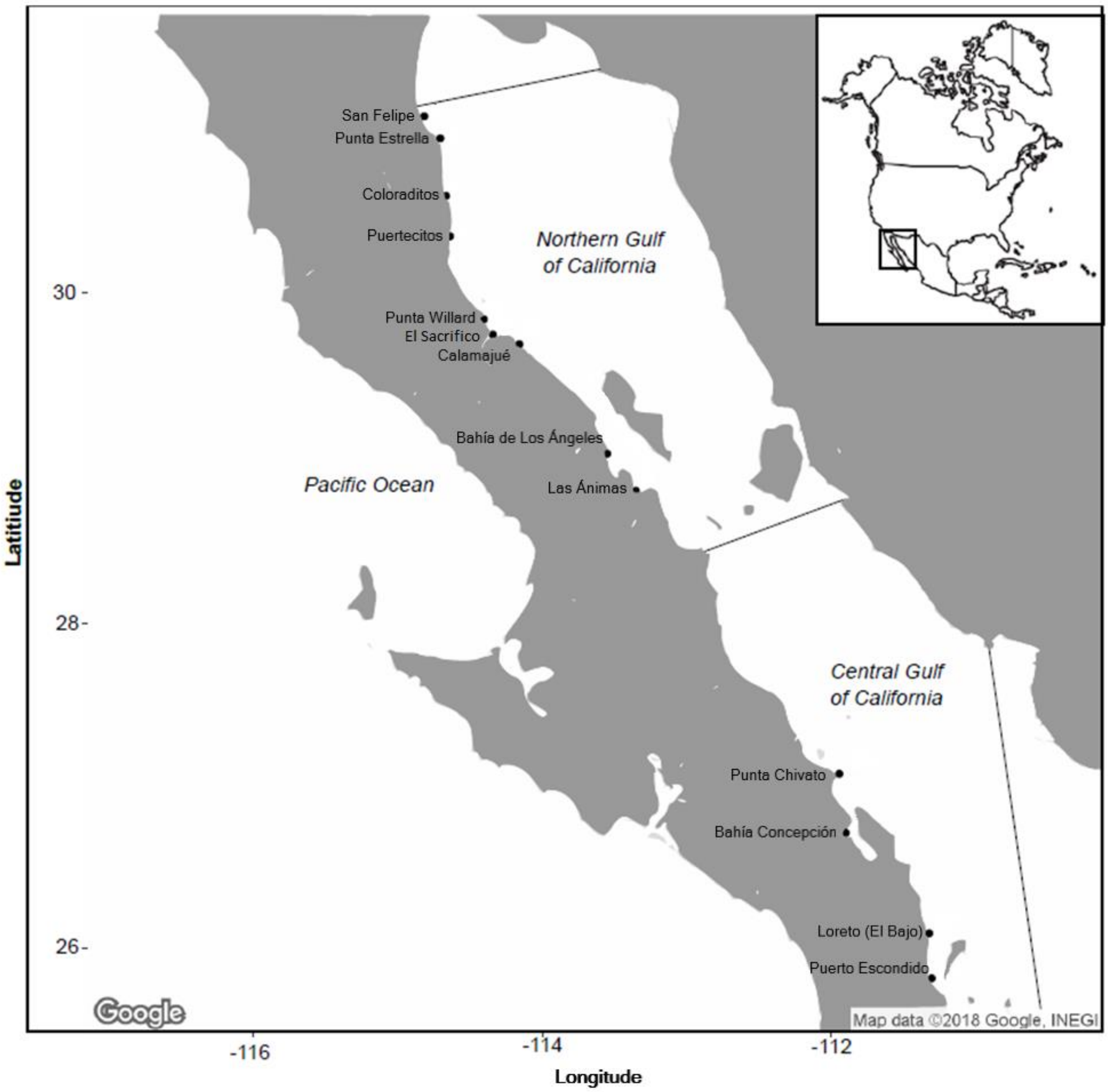

Figure 1: Site locations in Baja California and Baja California Sur where intertidal sampling was conducted.

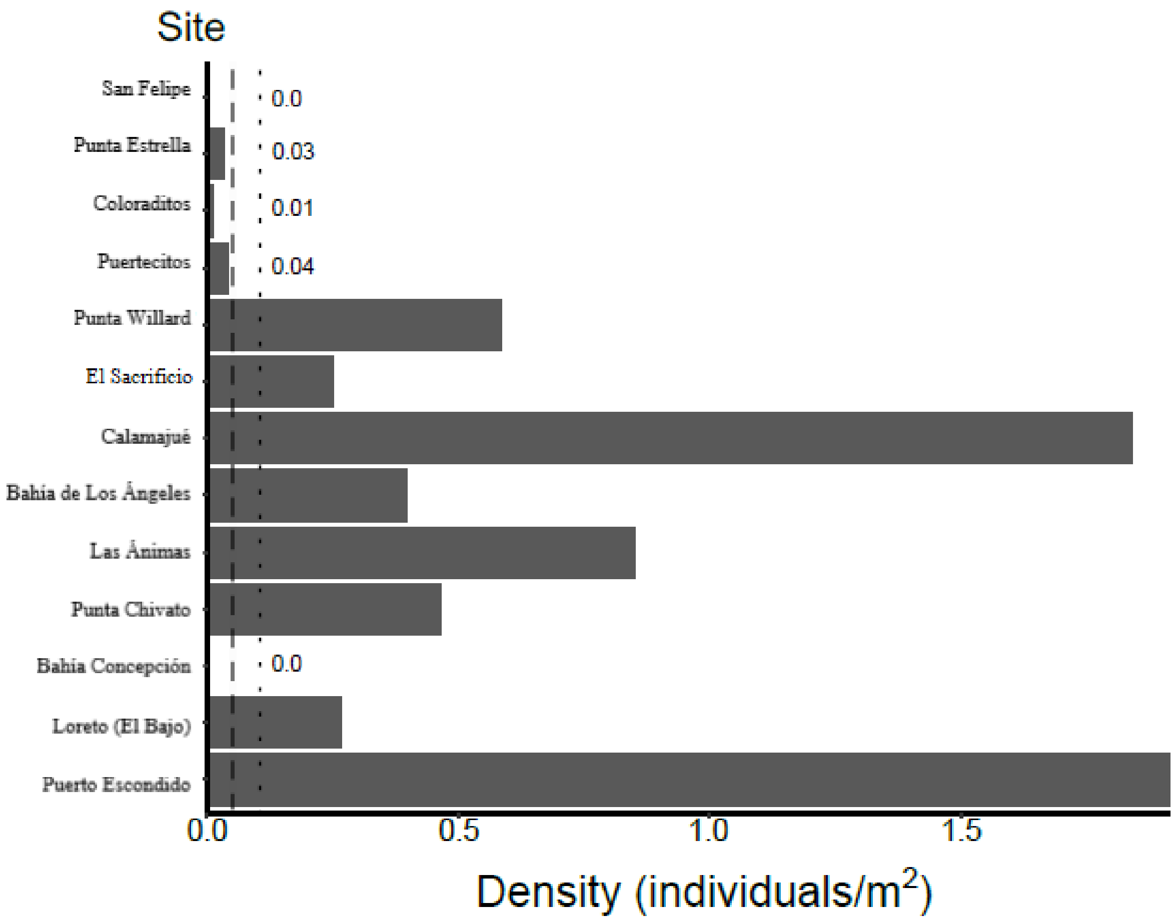

Figure 2: Density of *H. kubiniji* at each site. The dotted line shows .1 individuals/m^2 , which was believed to be the historical density of *H. kubiniji* at sites in these regions before the 1978 mass mortality event. The dashed line shows .05 individuals/m^2 , which was the density used by Dungan et al. to note a decline in the abundance of this species after the mass mortality event.

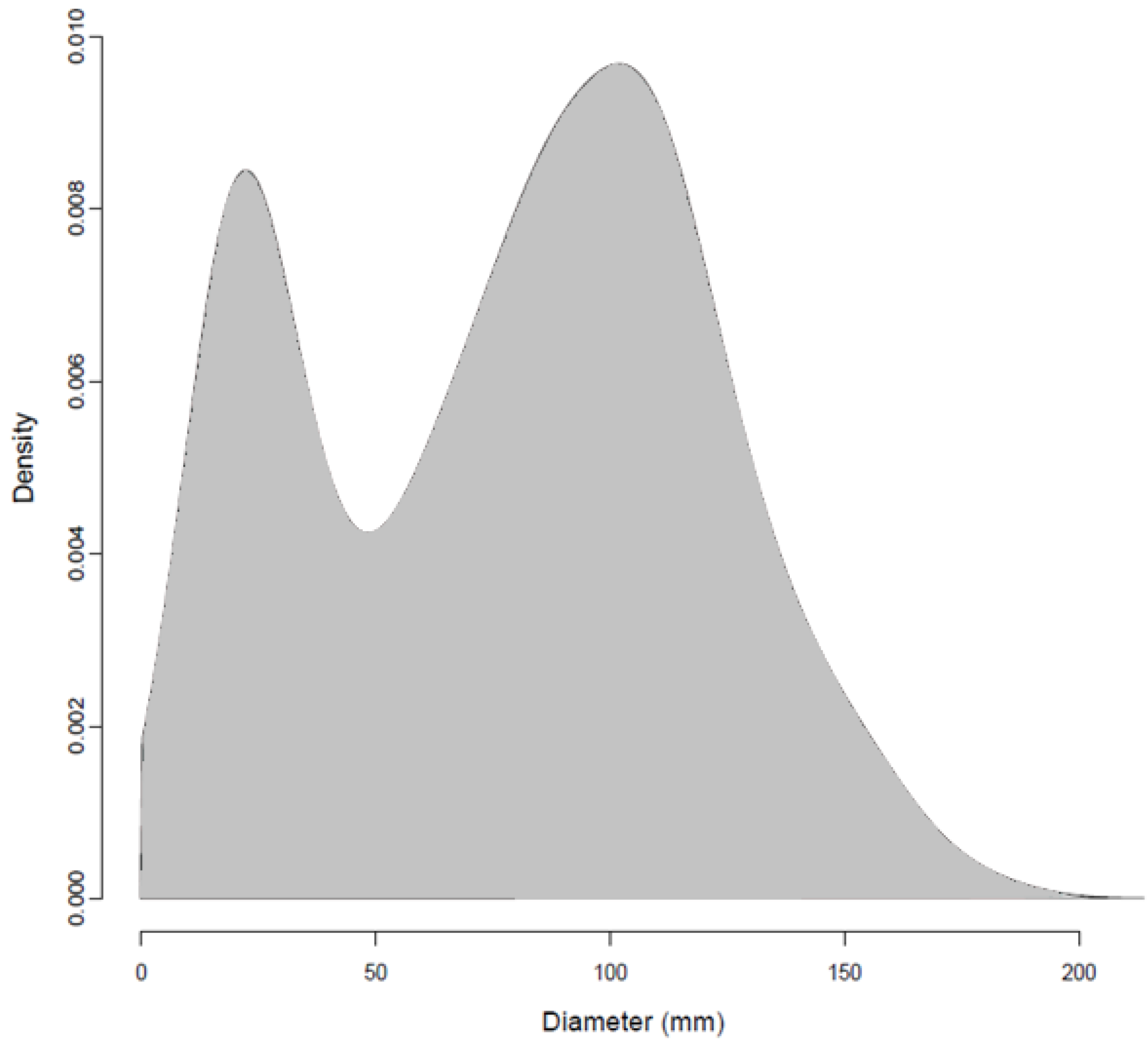

Figure 3: Smoothed density plot of the sizes of all *H. kubiniji* encountered in intertidal surveys (n=525). In this figure "density" refers to the probability density of individuals so that area under the curve sums to 1, and not density of individuals m^2.

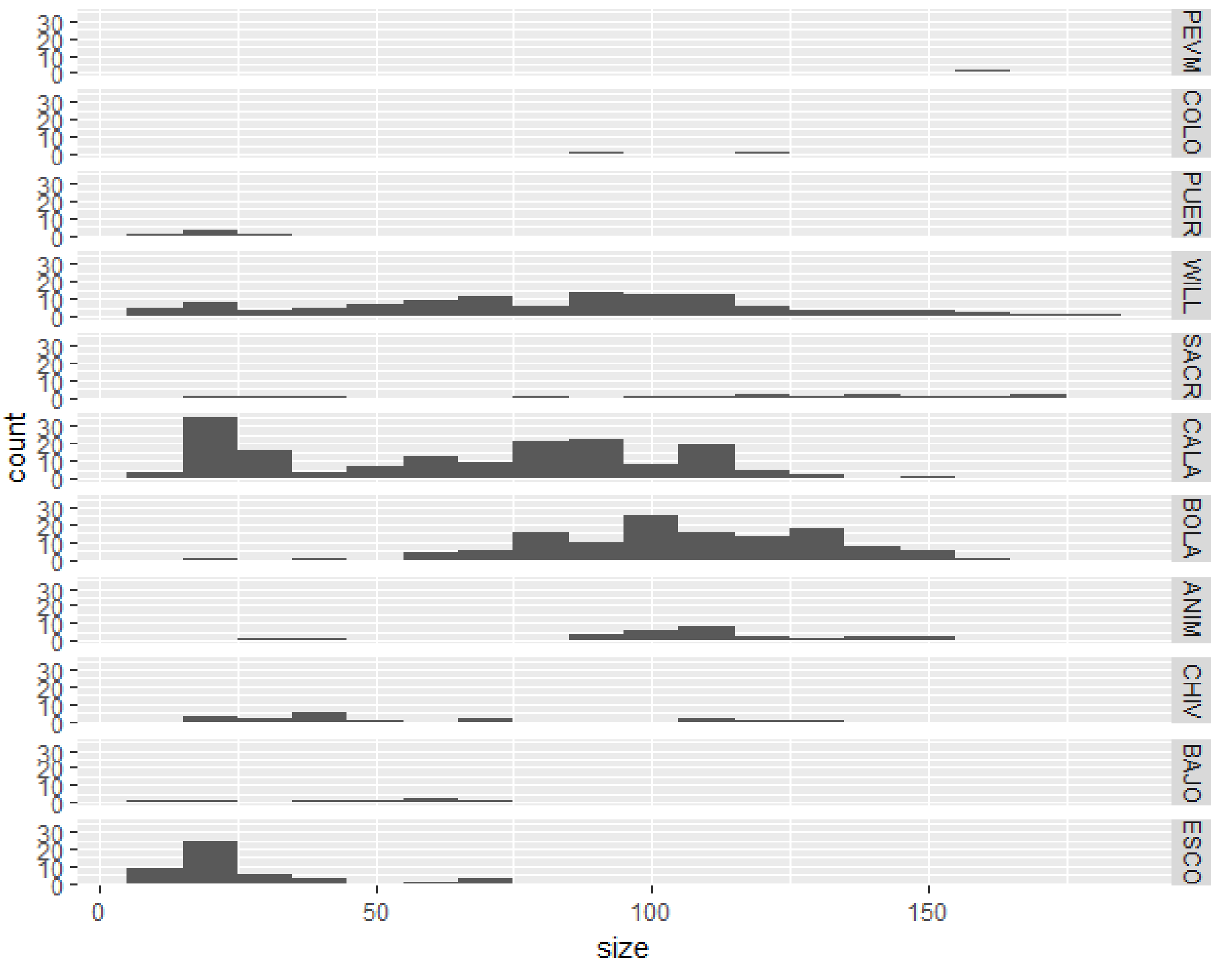

Figure 4: Size distribution of *H. kubiniji* at sites where the species was observed.

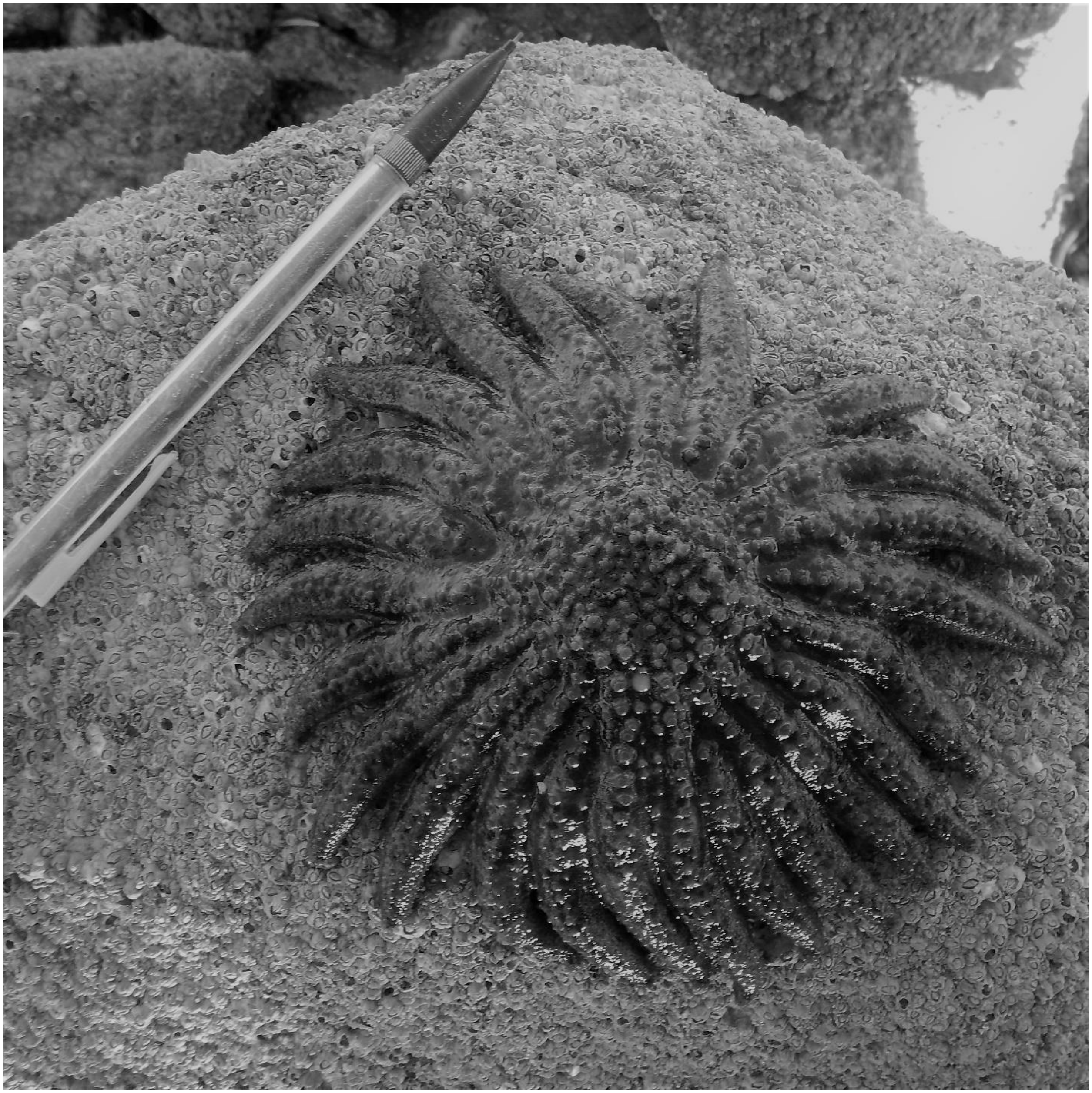

Figure 5: *Heliaster kubiniji*, the Gulf Sun Star. Photo by the author.

Chapter 2: Evaluating current and past abundances of intertidal marine invertebrates within the Gulf of California using historical field notes

Introduction

The Gulf of California ("the Gulf") is a highly diverse region. The Gulf contains a high number of endemic species including the critically endangered vaquita porpoise (*Phocoena sinus*), more than 80 species of endemic fish, and more than 750 species of endemic invertebrates (40,41). The region contains many species from the more temperate Californian bioregion to the north as well as species from the tropical Panamanian bioregion to the south (42). At least 5,969 species of marine organisms have been identified within the Gulf, and it has been suggested that an equal number of invertebrate species in the region might remain undescribed (41).

The geologic formation of the Gulf occurred in several stages from about 12.5 million years ago, as oblique rifting pulled apart a series of basins along the margin of the Pacific Plate and the North American Plate (43). The proto-gulf began to flood from south to north, beginning with the Southern Gulf from 10-7 million years ago and concluding with the flooding of the northern Gulf 6.3 million years ago (44). This process created a series of deep basins connected by underwater sills (Figure 6).

The physical characteristics of the Gulf contribute to high regional biodiversity. Strong tidal mixing consistently moves cold, nutrient rich water into the Gulf from deep below the Gulf entrance and out to the Pacific Ocean at the surface (26). The Northern Gulf, from the mouth of the Colorado River to the Midriff Islands, is characterized by shallow waters (less than 100m) and predominantly alluvial substratum(27). The Central Gulf, from the Midriff Islands to the Guaymas Basin, contains several deeper basins separated by sills. Tidal mixing across these sills transports deep, cold, nutrient rich water to the surface, contributing to high productivity (26,28). The Southern Gulf is much deeper and is strongly influenced by the Pacific Ocean. Because the mouth of the Gulf is not separated from the Pacific Ocean at depth by a sill it is highly influenced by oceanographic signals from the Pacific Ocean (26).

Impacts on intertidal communities within the Gulf

It is likely that several human activities have had negative impacts on the abundance of intertidal invertebrates within the Gulf. Anthropogenic climate change, harvest for the curio trade, and commercial harvest of edible species have each impacted the intertidal populations of the Gulf ecosystem. Additionally, mass-mortality events have historically impacted species of Gulf invertebrates. A lack of long-term monitoring research has prevented accurate documentation of the impacts of these events on populations of intertidal organisms within the Gulf.

a. Anthropogenic Climate Change

The impacts of anthropogenic climate change on the intertidal organisms of the Gulf are likely to alter species distributions and might cause extirpation of some species from the Gulf. The impacts of atmospheric warming are difficult to predict in the highly dynamic environment of the Gulf. Global climate models suggest that greenhouse warming in the tropical Pacific is likely to increase the frequency of strong El Niño events (45). Seasonal climate dynamics within the Gulf are strongly influenced by the ENSO circulation pattern. Strong El Niño events are associated with increased winds towards the equator, which is associated with upwelling in the Eastern Gulf (26). If atmospheric warming leads to direct sea surface temperature warming within the Gulf, then it is likely that range expansions of Southern Gulf species would occur, as these organisms would be able to disperse and recruit in the more temperate Central and Northern regions. However, the consequences of global climate forcing within the Gulf remain uncertain. It is possible that strong tidal mixing within the Gulf might sustain temperate conditions despite some atmospheric warming.

b. Human collection of intertidal organisms

The commercial curio trade is a global trade system in which organisms are collected and preserved for sale as decorative pieces. The marine curio trade often includes echinoderms, mollusks, and fish, which are collected and distributed worldwide. Species of marine invertebrates, which are colorful and relatively large, are likely to be targeted by commercial curio collectors.

Echinoderms are a large component of the global curio trade. A 2004 survey of the echinoderm curio trade in México estimated that 880,000 sea stars and 48,000 sea urchins are collected in México each year, including the sea stars *Pisaster ochraceus* and *Oreaster reticulatus* and the urchin *Echinometra vanbrunti* (46). While many individuals purchasing curios are tourists visiting México from other countries, a substantial domestic market also exists; individuals selling echinoderm curios in México reported that domestic buyers purchased about as many or more than foreign buyers (46). In addition to echinoderms, shells from marine mollusks are often targeted as curios due to their attractive appearance. Unfortunately, very little literature exists on the harvest of marine mollusks for curios in México.

Increasingly, live invertebrates are being collected worldwide to support a booming ornamental aquarium trade. A study of harvest data from Florida documents a 10-fold increase in invertebrate collections for the curio and ornamental aquaria trade from 1994 to 2007; 9 million individuals, including grazing snails, hermit crabs, and echinoderms, were collected in 2007 alone (47). Fishers collecting invertebrates and reef fish for export in the aquaria trade have recently been observed at sites in the Northern and Central Gulf (personal obs.).

c. Large-scale fisheries for export

Several benthic intertidal invertebrates in the Gulf face pressure from commercial fishing conducted for export. The sea cucumber *Isostichopus fuscus* has been reduced in abundance throughout the Gulf due to a commercial fishery conducted primarily for export. *I. fuscus* is the most heavily exploited sea cucumber in the Gulf, and has been extirpated at sites throughout the Gulf due to overfishing (48). Harvest of *I. fuscus* within the Gulf begin in 1988, peaked in 1991, and by 1994 the fishery was closed, and the species was listed in Mexico as an endangered species. The fishery was reopened with increased regulation in 2007 (49). This species has a high market value in Asia, and populations of this species continue to decline despite federal protections throughout the Gulf (50).

Harvest of *I. fuscus* on the Baja California peninsula is centered around Bahía de Los Ángeles, where the density of *I. fuscus* decreased by almost 50% between 2007 and 2013, where much of the harvest was likely conducted without regulation as poaching (49). The lucrative international market for *I. fuscus* has made it difficult to prevent harvest of the species within the Gulf.

Slow growing species and species in which large individuals contribute disproportionately to reproduction are especially vulnerable to commercial harvest. The muricid gastropods *Hexaplex eurythrostomus* (Pink Murex) and *Hexaplex nigritus* (Black Murex) were both formerly abundant members of the Gulf intertidal community. The abundance of these large gastropods has declined dramatically throughout the Gulf. In 1940 Ricketts and Steinbeck noted large numbers of Murex at every rocky intertidal site, while in 2004 Sagarin et al. did not find either species at any of 12 rocky intertidal sites (20). Each species is highly vulnerable to reductions in population due to commercial harvest. Commercial harvest of each species has targeted breeding aggregations, which might comprise as many as 12,000 individuals. Fidelity to breeding locations might increase the impact of this harvest on population structure (51). Individuals of each species do not reproduce until they are between two and three years old, with *H. nigritus* growing slower than *H. erythrostomus*. Unless commercial harvest is limited these populations are likely to continue to decline.

d. Mass-mortality events

Mass-mortality events are sudden, widespread mortalities, and can affect one or more species. Mass-mortality events of a single species can have dramatic effects on marine communities, which might persist for many years. A mass-mortality event of the Caribbean urchin *Diadema antillarium* in 1983 effectively extirpated the urchin from many Caribbean coral reef communities. The loss of *D. antillarium* reduced grazing on benthic algae and has been associated with a shift from a coral dominated benthic community to an algal dominated benthic community at sites throughout the species range. Thirty years after this mass-mortality event, *D. antillarium* populations and large-coral communities have not recovered at many sites in the region (4).

Historically, some mass-mortality events of marine invertebrates have impacted many species concurrently. In 1997 surveys in the Channel Islands of California documented lesions and a "wasting" phenotype in 10 species of sea stars, three species of urchins, two species of brittle star, and one species of sea cucumber (52). This mass-mortality event occurred during a dramatic El Niño event, and might have been associated with warm water temperatures. Recently, an ongoing mass-mortality event of sea stars on the West Coast (Sea Star Wasting Syndrome) has been linked to several abiotic and biotic factors (13) (11).

A 1978 mass-mortality event extirpated the Gulf sun star *Heliaster kubiniji* from many sites within the Gulf (18). Additionally, the Asteroids *Astrometis sertulifera* and *Echinaster tenuispina* and the Holothurian *Isostichopus fuscus* are known to have been impacted during this 'wasting' event (40).

Predictions for the future

Based on existing information, it is likely that the combined threats of overfishing and climate change will extirpate some intertidal species from the Gulf. Concurrently, more complex changes in the abiotic conditions of the Gulf due to anthropogenic climate change are likely to occur. The frequency of strong ENSO events is likely to increase, which might impact upwelling and primary productivity in the Eastern Gulf. Other consequences of anthropogenic forcing might include anomalous weather events, which intertidal organisms might be especially vulnerable to if they are exposed to extreme heat or cold during low tide (31).

Commercially harvested species, especially those which are sold on global markets, might be extirpated from accessible sites if harvest continues. This is likely to include the sea cucumber *I. fuscus*, the murcid gastropods *H. erythrostomus* and *H. nigritus,* and might also include commercially harvested species in the genus *Octopus*. Systems of marine protected areas have been established in many areas globally in order to protect species which are at risk of extirpation due to commercial harvest. These areas may be an appropriate tool for the protection of these threatened species within the Gulf (49).

Evaluating changes in abundance

All available information suggests that the abundance and diversity of intertidal marine invertebrates within the Gulf has declined dramatically over the last 80 years. In 1940, the intertidal ecologist Ed Ricketts and the author John Steinbeck surveyed the biodiversity of the Gulf comprehensively; they established 24 collection sites throughout the Gulf and documented more than 567 species (53). In 2004 a group of scientists and journalists chartered a similar boat and retraced the path of this historical collection in order to assess changes relative to the observations of Steinbeck and Ricketts. These scientists documented reductions in the abundance of many organisms and the diversity of many sites throughout the Central and Southern Gulf (20). Dramatic declines were found in the abundance of large gastropods (including *Hexaplex* snails), asteroids (fewer species at 11 of 12 sites) and holothuroids. Few species seemed to be positively impacted, including vermetid gastropods and jumbo squid, which were not documented in the 1940 expedition. These publications represent the most robust historical data analysis for sites on the west side of the Gulf.

My predictions were that many species, which had been historically documented at other sites would be present in densities lower than historical densities. My work was partially designed to expand upon the 2004 sampling expedition carried out by Sagarin et al. (2008). I used similar monitoring techniques at additional sites which have been infrequently visited. These sites were documented as historical sampling locations in field notes by Ricketts and Steinbeck or by other Gulf researchers. Instead of sampling the entire diversity of a site, I focused sampling on a subset of charismatic intertidal species. In general, this research was intended to provide the groundwork for future long-term monitoring.

Methods

To expand the available data regarding historical abundances of marine invertebrates in the Gulf of California, I revisited sites where ecologists had historically studied marine intertidal communities.

While conducting intertidal transect surveys to quantify the density of the sea star *H. kubiniji* (Chapter 1), I documented the occurrence of other invertebrates that I could quickly and accurately identify from the clades of Echinoderms (Asteroidea, Echinoidea, Holothuroidea) and Mollusca (Gastropoda and Bivalvia). I recorded the density of these species at each site with intertidal transects. Additional snorkel surveys conducted at each site were intended to document the presence of more uncommon or cryptic marine invertebrates. To determine whether these species have changed in distribution or abundance, I compiled data about their historical occurrence from previously unpublished field journals. I compared these observations with published assessments of range and abundance as well as iNaturalist observations.

A. Historical Data Compilation

I compiled a list of historical species observations from previously unanalyzed field notes. I received field notes from Dr. Mike Dungan pertaining to work he conducted in the Gulf in 1980 and 1984. These notes record exploratory trips he conducted while preparing research on the decline of the sea star *Heliaster kubiniji* (18), as well as notes taken while leading class trips as a graduate student at the University of Arizona. I also received field notes from Dr. Richard Brusca, who has uploaded many of his field notes to his personal website. I analyzed field notes recorded by Brusca from 1975, 1976, 1979, 1980, 1981 and 1984. I also included species observed in 1940 by Steinbeck and Ricketts (53). I only included site surveys conducted by Steinbeck and Ricketts at sites which were also sampled by Brusca or Dungan.

Notes in field journals were searched for relevant comments regarding the occurrence and abundance of intertidal organisms. I compiled records of all echinoderms and of the mollusks *Aplysia californica*, *Hexaplex eurythrostomus*, *Hexaplex nigritus, Octopus bimaculatus,* and *Octopus fitchi*. I chose to include these mollusks because their charismatic size would make them likely to be noted in general site surveys and might make these species vulnerable to harvest. This resulted in an analysis of 43 species of the Gulf intertidal community (species are compiled in Appendix B). This analysis lumps together multiple historical observations of a species at a site; for example observations of *Heliaster* *kubiniji* at Bahía de Los Ángeles by Ricketts in 1940, Dungan in 1980, and Brusca in 1980 are compiled into one observation that *H. kubiniji* has been historically present at this site.

B. 2017 Density Data

In the fall of 2017, I conducted field work in the Northern and Central regions of the Gulf. My primary objective was to document the abundance of the Gulf Sun Star (*Heliaster kubiniji*) using intertidal transect surveys and interviews with local fishers (Chapter 1). A secondary objective of this field work was to document the presence and abundance of other intertidal invertebrates. In transect surveys, I limited my data collection to 10 echinoderms and large gastropod species, which were common throughout the northern and central Gulf. I did not include species that were small and cryptic, or species that would require taking voucher specimens to confidently identify. This excluded ophiuroids from transect surveys.

I recorded the presence and density of each organism when identified in intertidal transect surveys conducted at 13 sites. In locations that were historically visited, field notes were used to establish transects as close to historical sampling locations as possible. If definitive sampling locations in field notes did not exist, transects were located in areas of the site with large, cobble-type rocky substratum, which is preferred by *H. kubiniji* (19). Three transects were spaced at 10 m apart across the beach, perpendicularly to the waterline. All surveys were conducted during a low tide of less than 0.0 m (mean lower low water). One hour before low tide the top of each transect was established 7 meters from the water line. Each transect was extended to its maximum length as the tide dropped. I used lights to survey sites during low tides that occurred at night.

Transect surveys involved counting all echinoderms and large gastropods found within 1m of the transect. Organisms were counted if more than half of the organism was within the transect. Every rock that could safely be manipulated by one individual was turned over and replaced in its original orientation. No rocks that were buried in the substrata were excavated.

Small intertidal *Octopus* sp. of the northern gulf were classified as *Octopus fitchi* during field work. However, identification of the small octopods of the Gulf is complicated due to several cryptic species, and the taxonomy of *O. fitchi* is currently under revision (54). For this study, *O. fitchi* were identified non-lethally, as they appeared in transects. Because we did not measure physical attributes of these individuals, it is possible some of these organisms were *O. alecto*. Taxonomic relationships between the benthic shallow water octopuses of the Gulf are in flux (55,56)

C. Shifts in species distribution

Using species descriptions from Brusca (1973), Bertsch and Aguilar Rosas (2016), and the Gulf of California Invertebrate Database (40), I summarized the historical range of the 43 intertidal echinoderms and gastropods. I compared these historical ranges with more recent observations using the citizen science platform iNaturalist. This information is compiled in Appendix B.

D. Recovery from 1978 mass-mortality event

I used data collected from historical and personal species observations to assess the current population state of species in the Gulf known to have been impacted by a 1978 mass-mortality event at sites in the Northern and Central regions of the Gulf. I considered the Asteroids *Heliaster kubiniji*, *Astrometis sertulifera* and *Echinaster tenuispina* and the Holothurian *Isostichopus fuscus*.

Results

A. Historical Data Compilation

Historical field notes were a valuable source of information about the presence of intertidal species at some sites within the Gulf. Previously unanalyzed field notes recorded by Dungan, Brusca, Ricketts and Steinbeck included observations of 43 different species at 9 sites in the Northern and Central Gulf; in total these historical field notes produced 88 observations of species at particular sites. Since many species were observed at multiple sites in in the historical record the total number of these species/site observations is greater than the number of species. These observations were compared with 90 observations of species at sites recorded in 2017, in order to identify if species had persisted at sites, expanded into new sites, or were regionally less common. All species observations from historical field notes are compiled along with 2017 species observations in Appendix C.

Surveys conducted in 2017 found that in 41 of 88 instances species continued to be present at sites where they were historically observed. In an additional 19 cases when I failed to document a historically observed species at the particular the site where the species was historically observed I documented the species in the same region (Northern or Southern Gulf) where they had been historically observed. Sixty-eight percent of species (60/88) were consistently found in the region of the Gulf where the species was historically observed. Thirty-two percent (28/88) of species observations at sites were not found in surveys in the region where they were historically present. Of these absences, 13 species observations (14.7 percent of total historical site observations) were species observations collected more recently by Brusca or Dungan, and 15 observations (17%) were observations collected by Rickets and Steinbeck in 1940.

Thirty-six species observed at sites in 2017 did not correspond to any observations of the same species from the same region of the Gulf in the analyzed historical field notes. However, reference materials on species ranges within the Gulf suggest that nearly all these 2017 observations do not correspond to species introductions or range expansions. Instead, this survey of field notes captures a limited slice of the observations of naturalists in the region. Only two of these species observations occurred at sites outside of expected historical ranges: the southern Gulf urchins *Toxopneustes roseus* and *Tripneustes depressus* were observed outside of expected historical ranges in at sites in the Central Gulf (discussed below).

Historical field notes occasionally recorded the density of intertidal organisms. Four species were recorded in field notes along with estimations of density at a site: the large and commercially harvested gastropod *H. nigritus*, the smaller and infrequently harvested gastropod *Turbo fluctuosa*, and the urchins

Echinometra vanbrunti and *Eucidaris thouarsii*, which are not known to be harvested. Brusca observed the gastropod *Hexaplex nigritus* as “abundant” at San Felipe in the Northern Gulf in 1975. Similarly, Dungan recorded *H. nigritus* at San Felipe in 1984 as “common”. During field work conducted in the fall of 2017, *H. nigritus* was present at the historically sampled site near San Felipe at a density of 0.275 individuals /m^2, and at a nearby site at Punto Estrella at a density of 0.133 individuals /m^2. In 2017 local fishers were observed collecting *H. nigritus* for personal consumption. Dungan recorded the urchin *Echinometra vanbrunti* as “common” at Punta Willard in 1984, and observed 5 individuals in 1980 at a nearby site (Punta Chivato). In 2017, *E. vanbrunti* was observed during a subtidal snorkel survey at Punta Willard, and was present intertidally at sites further south in the Gulf (recorded at densities of 0.082 ind./m^2 at Bahía de Los Ángeles, 0.133 ind./m^2 at Punta Chivato, and 0.45 ind/m^2 at Puerto Escondido).

Dungan recorded the urchin *Eucidaris thouarsii* as “common” at Punta Willard in 1984. In 2017, *E. thouarsii* was present intertidally at a density of 0.061 ind./m^2, and was observed during a subtidal snorkel survey. Dungan recorded the gastropod *Turbo fluctuosa* as “abundant” at Bahía de Los Ángeles in 1980. During intertidal surveys in 2017 *T. fluctuosa* was observed in densities of 1.595 ind./m^2, and was observed during a subtidal snorkel survey at the site.

B. 2017 Density Data

I documented the density of 10 intertidal species as they occurred in intertidal transects at 13 locations performed in the Northern and Central regions of the Gulf. The species documented were the asteroids *Heliaster kubiniji*, *Pharia pyramidata*, and *Phatiria unifascialis*, the echinoids *Echinometra vanbrunti* and *Eucidaris thouarsii*, the holothuroid *Holothuria lubrica*, and the gastropods *Hexaplex eurythrostomus*, *Hexaplex nigritus*, *Turbo fluctulosa*, and the cephalopod *Octopus fitchi*. These data are presented in Table 3.

The sea star *H. kubiniji* was commonly observed at sites in both the Northern and Central regions of the Gulf. The location of sampling transects was based on habitat that would be appropriate for this species (Chapter 1). This sea star was especially abundant at remote sites near the Midriff Islands: it was present at a density of 1.84 individuals/m^2 at Calamajué. It was present at lower densities at developed sites in both the Northern and Central regions of the Gulf.

The sea cucumber *H. lubrica* was the most common organism recorded within our transect surveys. This species was recorded at every sampling site. At some sites this species occurred at high densities, up to 15.47 individuals/m^2 at Punta Willard.

A small species of intertidal octopus, which we identify as *O. fitchi*, was consistently present at sites in the Northern Gulf at relatively high densities. *O. fitchi* was observed from San Felipe south to El Sacrificio in densities between 0.36 and 0.02 individuals/m^2 . The taxonomy of the intertidal octopus species within the Gulf is unresolved and we did not collect voucher specimens of this (or any) species. It is possible that these observations represent more than one species.

C. Possible Range Shifts

I found two southern-Gulf echinoids (*Toxopneustes roseus* and *Tripneustes depressus*) in the Central Gulf, outside of their expected range. Each of these species has been repeatedly documented in the Central Gulf by observers on iNaturalist. *T. roseus* has been observed at least twice in near the Midriff Islands of the Central Gulf, and *T. depressus* has been observed at least 5 times.

Forty-one additional species I studied remained present within the expected historical range of the species; for these species there is no evidence that a range shift has occurred. Observations in 2017 during sampling in the Gulf matched general range distributions compiled from field guides and the Gulf of California Invertebrates Online Database.

D. Recovery from 1978 mass-mortality event

Astrometis sertulifera: This species was historically observed by Steinbeck and Ricketts in 1940 at six collection sites in the Central Gulf, suggesting that it was historically widespread in the region. It was noted by Brusca in 1976 at Coloraditos and Punta Chivato in the Northern and Central Gulf, respectively. Since the 1978 mass-mortality event, I observed the species in 2017 at Puerto Escondido, and two iNaturalist observations have recorded the species in the vicinity of the Midriff Islands. This suggest that the species is present in the Central Gulf, and that species abundance likely remains low following the 1978 mass-mortality event.

Echinaster tenuispina: This species was historically observed by Steinbeck and Ricketts in 1940 at two collection sites in the Northern Gulf (including Bahía de Los Ángeles), and they noted that the species was more common the further north they traveled in the Gulf. It was noted by Brusca in 1976 at Coloraditos. Since the 1978 mass-mortality event, the species has been observed by Dungan in 1980 at Coloraditos, and I observed the species during subtidal snorkel surveys in 2017 at three sites in the Northern Gulf (Puertecitos, Punta Willard, and Bahía de Los Ángeles). It has been recorded by iNaturalist observers (as *E. tenuispinus*) on 21 occasions in the Gulf, from the Midriff Islands in the Central Gulf to Isla San Jose in the Sothern Gulf. Observations suggest this species has recovered to some degree from the 1978 mass-mortality event, and is currently present at sites in the Northern and Central Gulf. Recovery of this species from the 1978 mass-mortality event is difficult to assess due to ongoing collection of the species as a curio. The species exhibits a photopositive response, climbing onto the surface of rocks during the day where it is easily collected by tourists.

Heliaster kubiniji: This species was historically observed by Steinbeck and Ricketts in 1940 at 19 collection sites in the Northern, Central, and Southern regions of the Gulf; they noted that the species was "the most common, obvious, and widely distributed shore starfish" in the Gulf. It was also observed in 1976 by Brusca at Coloraditos. Since the 1978 mass-mortality event, the species has been documented by Brusca in 1980 at Bahía de Los Ángeles, and by Dungan in 1980 at Bahía de Los Ángeles and Bahía Concepción, and in 1984 at El Bajo and Puerto Escondido. The 1978 mass-mortality event was the specific focus of a 1982 publication. I observed the species at 8 out of 11 sites in the Northern and Central Gulf, with low densities which do not suggest recovery at sites in the far Northern Gulf and at higher densities suggesting recovery at sites throughout the southern portion of the Northern Gulf and the Central Gulf. (see Chapter 1). The species has been documented on iNaturalist within the Gulf on at least

137 occasions, spanning the entire extent of the Gulf. This suggest that *H. kubiniji* has recovered at many sites throughout the Gulf.

Isostichopus fuscus: This species was historically observed by Steinbeck and Ricketts in 1940 in three collection events at two sites in the Southern and Central Gulf (Brusca annotates this as "surprising", as the species has been quite common in more recent decades). Field notes record that it was observed at Punta Chivato by Dungan in 1980 and by Brusca in 1984. I observed the species in 2017 at three sites (Punta Willard, Punta Chivato, and Puerto Escondido), and iNaturalist observations have recorded the species on 48 occasions from the Midriff Islands to Cabo Pulmo reef. Evaluation of the recovery of this species is hindered by widespread and aggressive commercial harvest. It is likely the species was either not strongly impacted by the mass-mortality event, or recovered quite quickly, since commercial harvest of the species commenced in 1988 and continued until 1994, when the fishery was closed (49).

Discussion

Historical surveys of the Gulf indicate a high abundance of intertidal invertebrates at many locations. Subjective observations suggest that over the last 80 years these populations have diminished, largely due to human harvest. Future impacts of anthropogenic climate change might accelerate the rate at which populations decline. A lack of annual intertidal monitoring at sites in the Central and Northern regions of the Gulf has impeded quantitative assessment of the magnitude of these declines. In this work, I present data from historical field notes which indicate that abundances of the murcid gastropod *Hexaplex nigritus* might have decreased at sites in the Northern Gulf. In order to facilitate future monitoring in this region, I present the results of intertidal transect monitoring, which evaluated the density of many common intertidal community members at sites throughout the Northern and Central Gulf for the first time. During these surveys, I documented two Southern Gulf echinoids in the Central region of the Gulf; species ranges are likely to continue to shift due to accelerating anthropogenic climate change. Finally, I documented the recovery of three species impacted by a 1978 mass-mortality event, which primarily impacted the sea star *Heliaster kubiniji*. These organisms have likely recovered to some degree, but abundance might remain below long-term historical levels due to human harvest.

Species absences at sites in the Southern Gulf

At several sites in the Central Gulf I failed to observe species where they were historically observed, likely due to development at these sites. Nineteen of species absences occurred at sites in the Central Gulf, especially at the sites Bahía Concepción (8) and Puerto Escondido (8). Eleven of the 16 species absences at these two sites were only documented by the 1940 survey conducted by Ricketts and Steinbeck. It is likely that the 1940 survey of these sites was far more detailed than my survey, which was focused on intertidal asteroids. While the 1940 expedition spent several days at the site and used intensive collecting techniques, such as dredging, I conducted one subtidal snorkel survey and one intensive intertidal transect. It is, however, likely that species at these sites have been disturbed by human activity in the intervening years. The sampling site in Puerto Escondido has had a large commercial marina constructed on top of it, sampling was carried out in a pocket beach adjacent to a large dock. Bahía Concepción has been developed as a vacation destination, and we found evidence that shells (specifically *Turbo* snails) were frequently collected from the beach. Thus, although differences in sampling intensity make it impossible to confidently say these species are absent from southern Gulf sites, obvious impacts of development are likely to have affected the respective intertidal communities.

Species changes at Bahía de Los Ángeles

A comparison of historical field notes and my 2017 surveys suggest that community changes have occurred at Bahía de Los Ángeles, and these changes are likely due to human activity. Six of the 9 species absences recorded at sites where they were previously documented in the Northern Gulf occurred in Bahía de Los Ángeles. This site is comparatively more developed than much of the Northern Gulf, and the town's economy is largely supported by tourism, fishing for commercial sale, and fishing for personal subsistence. *Octopus* was historically documented by Ricketts and Steinbeck at this site but was not noted by other observers. Bahía de Los Ángeles is the site of an intensive *Octopus* fishery, and we did not observe the species intertidally during shallow snorkel surveys. We did observe fishers collecting *Octopus* in deeper water by skin diving. Additionally, most of the intertidal space surrounding the survey location has been impacted by development for tourism. It is likely that some reductions in species at this site have occurred.

Murcid gastropod declines throughout the Gulf

Two commercially harvested mollusk species, *Hexaplex nigritus* and *H. eurythrostomus*, appear to have declined in density due to collection at some sites. *H. erythrostomus* was absent at Bahía Concepción and Puerto Escondido, and *H. nigritus* was absent at Bahía Concepción. Due to the development that has occurred at these highly accessible sites, it is likely that this commercially harvested species has been extirpated from these locations. At San Felipe in the Northern Gulf, both Brusca and Dungan had noted *H. nigritus* as “abundant” and “common”, respectively, while my surveys in 2017 recorded the small individuals in relatively low densities (0.275 individuals /m^2), and observed fishers collecting the species at low tide. These species are likely to have been impacted by human collection throughout the Gulf.

Possible range shifts

Only two species of the 43 surveyed showed evidence of a range shift. I found two southern-Gulf echinoids (*Toxopneustes roseus* and *Tripneustes depressus*) in the Central Gulf, outside of their expected range. Each of these species has been repeatedly documented in the Central Gulf by observers on iNaturalist. This might indicate a northern range shift due to changing physical conditions in the Gulf. I am unable to directly link the presence of these species to climate forcing, which will likely affect the complex circulation patterns of the Gulf in subtle ways. If these observations do represent a northern range expansion, it alternatively possible that changes in the biotic community of the Gulf, like overfishing, are allowing this species to disperse into areas where they might have been historically limited by predation. These species should be more closely monitored to document possible future changes to the species range.

No evidence exists to support possible range shifts in the 41 additional Gulf invertebrate species that this study examined. Species range distributions within the Gulf are poorly studied, and it is likely that many intertidal organisms within the Gulf exhibit complex distributional patterns (58). A lack of long-term monitoring data might be preventing stakeholders from identifying range shifts in intertidal Gulf species. iNaturalist might help stakeholders to monitor changes in the distribution of marine invertebrates in the Gulf.

Recovery from mass-mortality events

The four species of Gulf invertebrates known to have been impacted by a 1978 mass-mortality event (*Astrometis sertulifera*, *Echinaster tenuispina*, *Heliaster kubiniji*, and *Isostichopus fuscus)* each remain present at some sites in the Central and Northern Gulf, although they are present at densities lower than what was historically observed. The proximal cause of the 1978 mass-mortality event is not definitively known; it might have been associated with a warm water event and strong winter winds (18). Due to infrequent monitoring of intertidal populations in the Central and Northern Gulf, intertidal invertebrates in these regions might have undergone other mass-mortality events between the 1978 event and this study in 2017.

Baseline data for future monitoring

My study provided baseline densities for 10 common intertidal species in the Northern and Central regions of the Gulf. This will enable researchers to more accurately document future changes in species density at each of these sites. These 10 organisms represent key members of the intertidal community in the Northern and Central Gulf, and changes to their distribution or density could have consequences for their communities. This will enable individuals to more accurately document future changes in species density at each of these sites. The full impacts of anthropogenic climate change in the Gulf are likely to be complex and difficult to predict. Robust networks of intertidal monitoring must be established within the Gulf on order to quantity the magnitude of these changes as they occur. The MARINe network on the West Coast provides an excellent template for this type of monitoring (59).

One limitation of these data at all sites is a failure to intensively survey ophiuroids. Ten of the 28 species absences occurred in brittle stars, which were intensively surveyed by Ricketts. Surveys in 2017 were focused on Asteroids and intertidal transects did not document ophiuroids due to difficulties in identification and high numbers of individuals present at some sites. While these organisms were captured opportunistically in underwater snorkel surveys, the 2017 is a poor representation of the presence of ophiuroids at all sites.

The future of the Gulf remains unwritten. Physical attributes such as dramatic tidal mixing could protect some sites in this region from the impacts of climate forcing and provide refugia for impacted species to disperse to other sites. Yet human harvest continues to target these especially diverse sites. A robust intertidal monitoring program is the best method by which ecologists and stakeholders can evaluate and respond to the progressive changes in this regions intertidal communities.

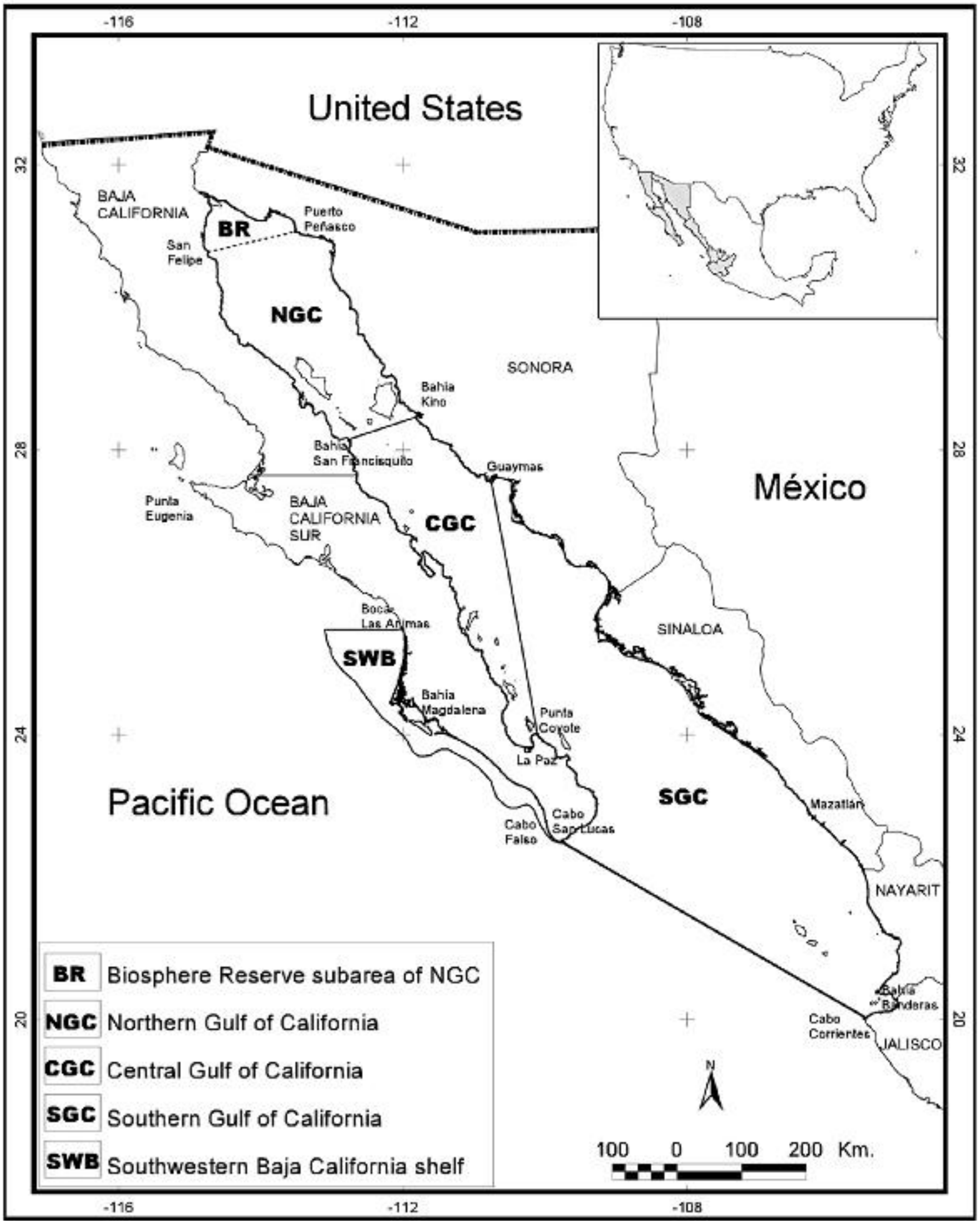

Figure 6: Regions of the Gulf from Gulf of California Marine Invertebrate Database (40)

Table 2: Site Key, containing site number, site names, and GPS coordinates for sites visited during 2017 surveys in the Gulf

Site #	Site Name	Latitude	Longitude
1	San Felipe	31.054	-114.819
2	Punta Estrella	30.915	-114.712
3	Coloraditos	30.581	-114.668
4	Puertecitos	30.340	-114.640
5	Punta Willard	29.842	-114.407
6	El Sacrificio	29.751	-114.344
7	Calamajué	29.693	-114.160
8	Bahía de Los Ángeles	29.033	-113.554
9	Las Ánimas	28.808	-113.355
10	Punta Chivato	27.078	-111.947
11	Bahía Concepción	26.713	-111.902
12	Loreto (El Bajo)	26.091	-111.325
13	Puerto Escondido	25.811	-111.307

Table 3: Densities of selected intertidal organisms as measured in the Fall of 2017 during intertidal transects surveys at sites in the Northern and Central Gulf

Species	**Clade**	**Site**	**Latitude**	**Longitude**	**sitemark**	**Density (ind./m^2)**
Heliaster kubiniji	Asteroidea	San Felipe	31.054	-114.819	1	0.000
Heliaster kubiniji	Asteroidea	Punta Estrella	30.915	-114.712	2	0.034
Heliaster kubiniji	Asteroidea	Coloraditos	30.581	-114.668	3	0.010
Heliaster kubiniji	Asteroidea	Puertecitos	30.340	-114.640	4	0.042
Heliaster kubiniji	Asteroidea	Punta Willard	29.842	-114.407	5	0.585
Heliaster kubiniji	Asteroidea	El Sacrificio	29.751	-114.344	6	0.250
Heliaster kubiniji	Asteroidea	Calamajué	29.693	-114.160	7	1.842
Heliaster kubiniji	Asteroidea	Bahía de los Ángeles	29.033	-113.554	8	0.399
Heliaster kubiniji	Asteroidea	Las Animas	28.808	-113.355	9	0.850
Heliaster kubiniji	Asteroidea	Punta Chivato	27.078	-111.947	10	0.467
Heliaster kubiniji	Asteroidea	Bahía Concepción	26.713	-111.902	11	0.000
Heliaster kubiniji	Asteroidea	Loreto (El Bajo)	26.091	-111.325	12	0.267
Heliaster kubiniji	Asteroidea	Puerto Escondito	25.811	-111.307	13	1.917
Pharia pyrimidata	Asteroidea	Punta Willard	29.842	-114.407	5	0.005
Pharia pyrimidata	Asteroidea	El Sacrificio	29.751	-114.344	6	0.050
Pharia pyrimidata	Asteroidea	Bahía de los Ángeles	29.033	-113.554	8	0.003
Pharia pyrimidata	Asteroidea	Punta Chivato	27.078	-111.947	10	0.100
Pharia pyrimidata	Asteroidea	Puerto Escondito	25.811	-111.307	13	0.042
Phatiria unifascialis	Asteroidea	Coloraditos	30.581	-114.668	3	0.048
Phatiria unifascialis	Asteroidea	Punta Willard	29.842	-114.407	5	0.066
Phatiria unifascialis	Asteroidea	El Sacrificio	29.751	-114.344	6	0.183
Phatiria unifascialis	Asteroidea	Punta Chivato	27.078	-111.947	10	0.133
Echinometra vanbrunti	Echinoidea	Bahía de los Ángeles	29.033	-113.554	8	0.082
Echinometra vanbrunti	Echinoidea	Las Animas	28.808	-113.355	9	0.025
Echinometra vanbrunti	Echinoidea	Punta Chivato	27.078	-111.947	10	0.133
Echinometra vanbrunti	Echinoidea	Puerto Escondito	25.811	-111.307	13	0.458
Eucidaris thouarsii	Echinoidea	Punta Willard	29.842	-114.407	5	0.061
Eucidaris thouarsii	Echinoidea	El Sacrificio	29.751	-114.344	6	0.150
Eucidaris thouarsii	Echinoidea	Bahía de los Ángeles	29.033	-113.554	8	0.026
Eucidaris thouarsii	Echinoidea	Punta Chivato	27.078	-111.947	10	0.433
Eucidaris thouarsii	Echinoidea	Puerto Escondito	25.811	-111.307	13	0.083
Holothuria lubrica	Holothuroidea	San Felipe	31.054	-114.819	1	0.009

Holothuria lubrica	Holothuroidea	Punta Estrella	30.915	-114.712	2	0.011
Holothuria lubrica	Holothuroidea	Coloraditos	30.581	-114.668	3	0.087
Holothuria lubrica	Holothuroidea	Puertecitos	30.340	-114.640	4	1.492
Holothuria lubrica	Holothuroidea	Punta Willard	29.842	-114.407	5	15.465
Holothuria lubrica	Holothuroidea	El Sacrificio	29.751	-114.344	6	2.117
Holothuria lubrica	Holothuroidea	Calamajué	29.693	-114.160	7	11.320
Holothuria lubrica	Holothuroidea	Bahía de los Ángeles	29.033	-113.554	8	11.612
Holothuria lubrica	Holothuroidea	Las Animas	28.808	-113.355	9	12.525
Holothuria lubrica	Holothuroidea	Punta Chivato	27.078	-111.947	10	6.400
Holothuria lubrica	Holothuroidea	Bahía Concepción	26.713	-111.902	11	2.700
Holothuria lubrica	Holothuroidea	Loreto (El Bajo)	26.091	-111.325	12	10.667
Holothuria lubrica	Holothuroidea	Puerto Escondito	25.811	-111.307	13	1.250
Hexaplex eurythrostomus	Mollusca	San Felipe	31.054	-114.819	1	0.009
Hexaplex eurythrostomus	Mollusca	Coloraditos	30.581	-114.668	3	0.072
Hexaplex nigritus	Mollusca	San Felipe	31.054	-114.819	1	0.276
Hexaplex nigritus	Mollusca	Punta Estrella	30.915	-114.712	2	0.133
Hexaplex nigritus	Mollusca	Coloraditos	30.581	-114.668	3	0.029
Octopus fitchi	Mollusca	San Felipe	31.054	-114.819	1	0.121
Octopus fitchi	Mollusca	Punta Estrella	30.915	-114.712	2	0.356
Octopus fitchi	Mollusca	Coloraditos	30.581	-114.668	3	0.250
Octopus fitchi	Mollusca	Puertecitos	30.340	-114.640	4	0.125
Octopus fitchi	Mollusca	Punta Willard	29.842	-114.407	5	0.258
Octopus fitchi	Mollusca	El Sacrificio	29.751	-114.344	6	0.017
Turbo fluctulosa	Mollusca	San Felipe	31.054	-114.819	1	0.017
Turbo fluctulosa	Mollusca	Punta Estrella	30.915	-114.712	2	1.022
Turbo fluctulosa	Mollusca	Coloraditos	30.581	-114.668	3	0.428
Turbo fluctulosa	Mollusca	Puertecitos	30.340	-114.640	4	0.058
Turbo fluctulosa	Mollusca	Punta Willard	29.842	-114.407	5	1.611
Turbo fluctulosa	Mollusca	El Sacrificio	29.751	-114.344	6	1.783
Turbo fluctulosa	Mollusca	Calamajué	29.693	-114.160	7	0.010
Turbo fluctulosa	Mollusca	Bahía de los Ángeles	29.033	-113.554	8	1.595
Turbo fluctulosa	Mollusca	Bahía Concepción	26.713	-111.902	11	0.067

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Appendix A: Interview form for local fishers. IRB# EX18-005

Interview Number

Location

Date and Time

”Are you at least 18 years old?” YES

1. Do you live here? How many years have you lived here?

____

2. What do you do for work here?

____

3. Do people ever harvest any of these organisms near this town? Has it happened Only once or twice, a few times a year, about once a month, or about every week, or about every day? Others?

Pepino del Mar	Never, Rarely, Yearly, Monthly, Weekly, Daily
Murex Negro/Rosado	Never, Rarely, Yearly, Monthly, Weekly, Daily
Pulpo	Never ,Rarely, Yearly, Monthly, Weekly, Daily
Cangrejo Nadador	Never, Rarely, Yearly, Monthly, Weekly, Daily
Cucharacha del Mar	Never, Rarely, Yearly, Monthly, Weekly, Daily
Camaron	Never, Rarely, Yearly, Monthly, Weekly, Daily
Hatcha Larga	Never, Rarely, Yearly, Monthly, Weekly, Daily
Others?	

4. Do people ever harvest sea stars to sell? Yes/ No

a. How often? Rarely, Yearly, Monthly, Weekly, Daily

b. Where?

5. Have you noticed any new marine organisms in this area that you did not see in the past?

Type: When:

6. Have you ever seen many sea creatures dead on the shoreline? Which organisms? When?

7. Did people used to catch fewer, about the same, or more marine organisms here?

8. Over your life, in what ways have you seen the marine life in this town change?

Appendix B: Compilation of available information by species

This Appendix compiles information from several collecting trips to the Gulf including Steinbeck and Ricketts in 1940 (53), Dungan in 1980 and 1984, and Brusca in 1975, 1976, 1979, 1980, 1981 and 1984, the *Handbook to the Common Intertidal Invertebrates of the Gulf of California* by Brusca (19), *Invertebrados Marinos del Noroeste de México* by Bertsch and Aguilar-Rosas (57), the Gulf of California Invertebrate Database (https://www.desertmuseum.org/center/seaofcortez/database.php) (40), and iNaturalist observations (https://www.inaturalist.org) (Updated on 3/28/2021).

Using this information, I assess the abundance of the species relative to a theoretical pre-1940 baseline. I characterize each species as Possibly Reduced, Possibly More Abundant or No Evidence of Change. All emphasis is my own.

Site Abbreviations used in Appendix D:

SANF- San Felipe

COLO- Coloraditos

PUER- Puertecitos

WILL- Punta Willard

BOLA- Bahía de Los Ángeles

CHIV- Punta Chivato

BAJO- El Bajo (N. of Loreto)

CONC- Bahía Concepción

ESCO- Puerto Escondido

Asteroids

Acanthaster ellisii **(**syn w. A. planci?)

Observed at ESCO by Ricketts 1940

S&R: Puerto Escondido (Col. No. 11)

Other Obs. : none
Brusca: "largely subtidal, **occasionally brought up by the shrimp trawlers**, but also occurs in the low intertidal. . . I have recorded A. ellisii at Isla San Jose, Isla Espiritu Santo, all along the southeast Gulf coast and in the Tres Marias Islands."
Bertsch: " Centra Gulf to Isla Clarion, Might occur in Galapagos, northern Peru; throughout the Indo-Pacific. . . Although it **feeds on Corals** it **is curiously rare on the Gulfs only true coral reef at Cabo Pulmo**
GoC: Not uncommon in the southern Gulf, nor in the central Gulf during warm periods (e.g. summers), but rare in the northern Gulf (seen during exceptionally warm periods, such as El Niño years). Some studies (including one molecular study) have suggested that A. ellisii is a synonym of the Indo-West Pacific species Acanthaster planci (Linnaeus, 1758). However, they are morphologically distinct. **The E Pacific species feeds mostly on non-coral prey** (e.g. algae, gorgonians), but it also grazes on coral.
Northernmost record MEX, BCS, I. Rasa
Southernmost record MEX, BCS, Cabo Pulmo
World Distribution PET;ILTM;IREV;IGAL
Shallowest depth 0m Greatest depth 40m
iNaturalist:52 observations in GoC, including 5 in 2018 in the Midriff Islands near northern range limit

No evidence of change

Amphiaster insignis

S&R: not Obs.
Other Obs.: ESCO by Dungan 1984
Brusca: "An **attractive and distinctive** sea star. . . Occurs in the Central and lower Gulf at least as far south as Panama"
Bertsch: "Has been **trawled** by commercial fishermen and scientific expeditions"
GoC: **Often picked up (and killed) by shrimp trawlers. Once common in the N Gulf, but now increasingly rare.**
Northernmost record MEX, BCS, B. Magdalena; MEX, BC, Rocas Consag
Southernmost record PAN, I. Medidor
World Distribution PET;IREV
Shallowest depth 0m Greatest depth 125m
iNaturalist: 1 observation from near BOLA

Possibly reduced by trawling and collecting

Asteropsis carinifera

S&R: not Obs.
Other Obs. Urnes 2017 at CHIV and ESCO
Brusca: not included
Bertsch: Central GoC to Panama, throughtout the Indo-Pacific (where it is) **one of the most common and widely distributed sea stars**
GoC: The arms of this **distinctive** sea star are distinctly triangular in cross-section, giving their aboral side a keeled appearance.
Northernmost record MEX, BC, B. San Luis Gonzaga
Southernmost record PAN
World Distribution PET;IREV:IGAL;IMAL;PW;OI;CT
Shallowest depth 0m Greatest depth 36m
iNaturalist: 6 observations in the Gulf, from La Paz north to BOLA

No evidence of change

Astrometis sertulifera

S&R: Isla Espíritu Santo (Col. No. 4), Marcial Reef (Col. No. 10), Isla San Marcos (Col. No. 15), Bahia San Carlos/ Punta Trinidad (Col. No. 16), Bahía de San Francisquito (Col. No. 17), Isla Ángel de la Guarda (Col. No. 19)

Other Obs. Brusca in 1976 at CHIV and COLO, at ESCO by Urnes 2017
Brusca: Range Oregon and Washington (quest. Vancouver) to Mazatlan and Galapagos, smaller intertidal individuals can be confused for *Echinaster tenuispina*
Bertsch: **Reportedly also affected by 1978 wasting event**
GoC: Its numbers were reduced in the echinoderm wasting disease epidemic that struck the Gulf in the late 1970s. . . Astrometis californica Verrill, 1914 might be a variant
Northernmost record CAN, BC, Vancouver Island
Southernmost record PER, I. Lobos de Afuera
World Distribution PET;PNET;PSET;IGAL
Shallowest depth 0m Greatest depth 156m
iNaturalist:1 observation in GoC near Bahia Kino

Possibly reduced, observed widely by S&R but infrequently in the Gulf today, possibly slowly recovering from 1978 wasting event

Echinaster tenuispina

Bruscas describes this species as "essentially a GOC endemic species", and a "variant form" found in Bahia Magdellena

S&R: Isla Espíritu Santo (Col. No. 4), Marcial Reef (Col. No. 10) (noted to be **more common the farther north they traveled**), Bahía de Los Ángeles (West) (Col. No. 18), Isla Ángel de la Guarda (Col. No. 19)

Other Obs. Urnes 2017 at Puertecitos , Willard and BOLA, Dungan 1980 at COLO, Brusca 1976 at COLO (Syn with Othilia tenuispina)

Brusca: "**Photopositive**, usually being found on the tops of rocks during the day, rather than hiding beneath them. . . Very common from El Golfo de Santa Clara to Bahia Kino, but occurs only sporadically south of the midriff region." "**once very common, now less so due to uncontrolled beach tourism**"- in S&R obs list
Bertsch: This species suffered a **drastic population decline in 1978** from a widespread infection
GoC: "**Formerly one of the most common seastars of the N Gulf littoral; now rare, at least in part due to collecting by tourists and locals (for the curio shops)**. Once abundant intertidally, now most frequently found subtidally and on offshore islands. This spcecies **suffered in the wasting disease event of the late 70s** (which mainly struck Heliaster), which no doubt contributed to its reduced numbers ever since"
Northernmost record MEX, SON, El Golfo de Santa Clara
Southernmost record PAN
World Distribution PET;PNET
Shallowest depth 0m Greatest depth 73m
iNaturalist: 4 observations, 2 in the Central Gulf and 2 in the Southern Gulf. The species *E. tenuispinus*, which might be identical, has 21 observations in the GoC, from the Northern Gulf to La Paz

Possibly reduced, first by the 1978 wasting event, subsequently by intensive collecting due to its photopositive response

Heliaster kubiniji

Documented today throughout the Central Gulf, historically by Ricketts at BOLA, Concepcion, Escondido. Urnes found one individual 18cm in diameter at near San Felipe

Bertsch: Bahia Magdelena to Nicaragua

Brusca: **Common in the gulf**, less common at Guaymas and Mazatlan, "one of the first littoral invertebrates to begin reproducing after the cold winter draws to a close early in the year"

S&R: Cabo San Lucas (Col. No. 2), Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4), La Paz sand flats (Col. No. 5) (Heliaster sp. as well as H. kubiniji), Bahia La Paz (Col. No. 7), Islote Cayo (Col. No. 8), Marcial Reef (Col. No. 10), Puerto Escondido (Col. No. 11), Puerto Escondido inner bay (Col. No. 12), Loreto (Col. No. 13), Bahía Concepción east (Col. No. 14), Isla San Marcos (Col. No. 15), Bahia San Carlos/ Punta Trinidad (Col. No. 16), Bahía de San Francisquito (Col. No. 17), Bahía de Los Ángeles (West), (Col. No. 18), Isla Ángel de la Guarda (Col. No. 19), Isla Tuburon (Col. No. 20), Guaymas (Col. No. 21), Isla Espiritu Santo (Col. No. 24),

Other Obs. Brusca 1976 Coloraditos, Brusca 1980 BoLA, Dungan 1980 BoLA, Dungan 1980 Concepcion, Dungan 1984 El Bajo, Dungan 1984 Escondido, Urnes 2017
Brusca: "**I have collected it in abundance throughout the northern Gulf**, and in fewer numbers at Guaymas and Mazatlan, the occurance of this speciese north of Mexico is unlikely. One of the first Northern Gulf littoral invertebrates to begin reproducing after the cold winter draws to a close early in the year"
Bertsch: "Scattered occasional records exist from (Pacific) Baja California and southern California, probably El Nino related. This species was once the most abundant sea star in the GoC, in 1978 populations were almost completely wiped out by a widespread infection. That decline was exacerbated by the collection of numerous specimens for sale in curio shops. The species now seems to be increasing in numbers"

GoC: “The largest individuals reach ~23 cm in diameter, but I've not seen one this size since the 1970s. **Formerly common throughout the Gulf (less so in the southern Gulf).** However, the 1978 El Niño event that spawned the echinoderm wasting disease epidemic in the Gulf killed most Heliaster in the Gulf (and several other echinoderms), and **recovery has been very slow**. Although young H. kubiniji began to be common in the 90s, by 2017 even these were scarce again. **Adult H. kubiniji have been found only since the late 1990s**, and they are restricted almost entirely to offshore islands and the Baja peninsula.”
Northernmost record USA, CA, Cabo Mendocino (outlier)
Southernmost record NIC, Macuoba
World Distribution PET;PNET
Shallowest depth 0m Greatest depth 40m
iNaturalist: 137 observations throughout the GoC from Penasco to Cabo Pulmo.

Possibly reduced, initially by 1978 wasting event, subsequently by collecting

Leiaster teres

S&R: Puerto Escondido (Col. No. 11) Puerto Escondido inner bay (Col. No. 12)
Other Obs.
Brusca: not in field guide
Bertsch:”Central gulf to Islas Galapagos. . . has a characteristic coloration (brilliant purple) and glossy appearance
GoC: “The validity, and relationahips, of L. teres and L. glaber Peters, 1852 (Mozambique) are unclear (see Jangoux 1980).”
Northernmost record MEX, BC, I. San Pedro Mártir
Southernmost record PAN, Golfo de Chiriqui
World Distribution PET;PC;IMAL;IGAL
Shallowest depth 0m Greatest depth 57m
iNaturalist:7 observations in the GoC, mostly in the Southern Gulf

No evidence of change

Linckia columbiae

S&R: El Mogote (Col. No. 6) (Brusca has “Linckia (?)”), Bahia San Carlos/ Punta Trinidad (Col. No. 16), Bahía de Los Ángeles (West), (Col. No. 18), Isla Ángel de la Guarda (Col. No. 19), Isla Tuburon (Col. No. 20)

Other Obs.
Brusca: “from the intertidal and subtidal at Puertecitos, Puerto Libertad , and throughout the southeast coast of the gulf.”
Bertsch: range from Southern CA, throughout the Gulf, to Peru and Galapagos
GoC: “**Formerly common in the rocky intertidal; now largely restricted to the subtidal due to collecting by tourists and locals**.”
Northernmost record USA, CA, San Pedro
Southernmost record PER
World Distribution PET;IREV;ICOC;IGAL

Shallowest depth 0m Greatest depth 100m
iNaturalist: No observations in the GoC, but recently reported from Southern California

Possibly reduced due to collecting. Widely documented by S&R

Luidia phragma

S&R: Bahía Concepción east (Col. No. 14) (**Brusca annotates "a very common subtidal species** taken by S&R only at this location, 7 fathoms, in "crab nets")
Other Obs.
Brusca: "An **attractive and common** sea star , , , Ranges from the northern Gulf to chile. It is commonly picked up in the nets of the shrimp trawlers"
N Bertsch:"range Bahia Magdelena, and from the northern GoC to Chile
GoC: **Frequently captured (and killed) by shrimp trawlers**. Predatory. Dioecious, oviporous, broadcast spawners, planktonic larvae.
Northernmost record MEX, BC, B. San Quintín
Southernmost record PER, Paita
World Distribution PET;PSET;IREV
Shallowest depth 0m Greatest depth 385m
iNaturalist: 9 observations in the Gulf

Possibly reduced, although it was only documented at one location by S&R

Mithrodia bradleyi

Consistent records from the central gulf: Ricketts at BOLA and ESCO, Brusca at CHIV, Urnes at BAJO and ESCO

Bertsch: Pt Eugenia, Cfrom Central Gulf south to Peru

Brusca: "Not reported north of Guaymas in the Gulf. Range Panama and Galapagos to the Gulf".

S&R: Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) Marcial Reef (Col. No. 10) Puerto Escondido (Col. No. 11) (15 inches in diameter) Loreto (Col. No. 13) Bahía de Los Ángeles (West), (Col. No. 18) Isla Ángel de la Guarda (Col. No. 19)

Other Obs. Brusca at Punta Chivato in 1984 and Urnes 2017 at Puerto Escondido and El Bajo
Brusca: "**I have encountered this species in most rocky, shallow subtidal regions from Guaymas south, including all of the southern Gulf islands**. It has previously been reported from rocky shores at a low tide zone to 13 fathoms in the panamic region. Its range is listed by other authors as panama and the Galapagos to the GoC and also in Hawaii. It has not been reported north of Guaymas in the Gulf"
Bertsch: "from Punta Eugenia, BCS, and from the central GoC south to Peru"
GoC: According to Pope & Rowe (1977), Mithrodia clavigera (Lamarck, 1816) is the senior synonym of M. bradleyi, but not all workers accept this synonymy. The long arms and distinctive orange-pink body color are diagnostic. A single Southwest Baja record needs verification.
Northernmost record MEX, BC, I. Ángel de la Guarda, Puerto Refugio

Southernmost record Peru
World Distribution PET;CT;IREV;ILTM;IMAL;IGAL;ICLI
Shallowest depth 0m Greatest depth 50m
iNaturalist: 35 observations in the Central and Southern Gulf

No evidence of change, widely observed historically and currently

Nidorellia armata

S&R: Cabo Pulmo (Col. No. 3) El Mogote (Col. No. 6) (with a "?" by Brusca) Puerto Escondido (Col. No. 11) (Brusca annotates "a very common shallow-water sea star in the Gulf, but collected by S&R only at Pulmo Reef and Puerto Escondido")

Other Obs. Urnes 2017 at Puerto Escondido
Brusca: "Upper GoC to Peru and the Galapagos Islands, and is most often encountered when diving"
Bertsch: Throughout the Gulf of California to northern Peru and the Islas Galapagos
GoC: **Once common intertidally, for most "mainland" sites it is now rare**.
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record PER, Trujillo Sur
World Distribution PET;PSET;ILTM;IMAL;IGAL
Shallowest depth 0m Greatest depth 73m
iNaturalist:52 observations throughout the Central and Southern Gulf

No evidence of change

Pentaceraster cumingi

S&R: Cabo San Lucas (Col. No. 2) Cabo Pulmo (Col. No. 3), Isla Espíritu Santo (Col. No. 4), Bahia La Paz (Col. No. 7), Puerto Escondido (Col. No. 11) (annotation: as *Oreaster occidentalis*, a junior synonym; a widespread tropical east Pacific species)

Other Obs. Urnes 2017 at Escondido and Chivato
Brusca: (as *Oreaster occidentalis*) "Ranges from the norther FoC to Peru and the Galapagos and is restricted to the lowest low tide zone and the subtidal, being most frequently encountered when one dives over rocks in 2-10m of water"
Bertsch: "Throughout the Gulf of California to northern Peru and the Galapagos islands also in the southwestern Caribbean and Hawaii. Large aggregation are reported in mid summer months in the central GoC, particularly on the Baja California coastline."
GoC: Still commonly seen under the name Oreaster occidentalis. Reyes-Bonilla et al. (2016) document a mass migration of this species in the southern Gulf
Northernmost record MEX, SON, I. Tiburón
Southernmost record PER, I. Lobos de Afuera
World Distribution PET;PSET;PC;IREV;ILTM;ICOC;IGAL
Shallowest depth 0m Greatest depth 200m
iNaturalist: 109 observations, almost all in the Central and Southern Gulf

No evidence of change

Pharia pyramidata

Limited historical obs. (Ricketts ESCO, Brusca CHIV, Dungan COLO), widespread today (Urnes obs. at COLO, PUER, WILL, BOLA, CHIV, ESCO)

S&R: Cabo Pulmo, Isla Espíritu Santo, Bahía La Paz. Islote Cayo, Bahía San Marcial, Puerto Escondido, Isla Tiburón

Bertsch: throughout the gulf, to N. Peru and Galapagos

Brusca: N. Gulf to Peru and Galapagos, "in greatest abundance on the low intertidal and subtidal rocks of Bahia San Carlos and Puerto Lobos, north of Guaymas"

S&R: Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) Bahia La Paz (Col. No. 7) Islote Cayo (Col. No. 8) Marcial Reef (Col. No. 10) Puerto Escondido (Col. No. 11) Isla Tuburon (Col. No. 20)

Other Obs. Dungan 1984 at Coloraditos, Brusca 1976 at Punta Chivato, Urnes throughout Gulf (Coloraditos, Puertecitos, Willard, Bahía de Los Ángeles, Punta Chivato and Puerto Escondido)
Brusca:"undoubtably one of the most beautiful sea strs of the eastern Pacific, ranging from the northern Gulf to Peru and the Galapagos. I have found it in greatest abundance on the low intidal and subtidal rocks of Bahia San Carlos and Puerto Lobos, north of Guaymas
Bertsch: Throughout the GoC to northern Peru and the Galapagos, also on some of the west Baja California islands
GoC: Along with Phataria unifascialis, this is one of the predominant sea stars in the Central and Southern Gulf.
Northernmost record USA, CA, Santa Catalina I.
Southernmost record PER, Zorritos
World Distribution PET;PNET;ILTM;IREV;IGAL
Shallowest depth 0m Greatest depth 140m
iNaturalist: 72 observations in the GoC, mostly in the southern Gulf with a scattering in Central and Northern

No evidence of change

Phataria unifascialis

S&R: Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) La Paz sand flats (Col. No. 5) Bahia La Paz (Col. No. 7) Islote Cayo (Col. No. 8) Marcial Reef (Col. No. 10) Puerto Escondido (Col. No. 11) Loreto (Col. No. 13) Bahía Concepción east (Col. No. 14) Isla San Marcos (Col. No. 15) Bahía de San Francisquito (Col. No. 17) Bahía de Los Ángeles (West), (Col. No. 18) Isla Ángel de la Guarda (Col. No. 19) Isla Tuburon (Col. No. 20) Guaymas (Col. No. 21) Isla Espiritu Santo (Col. No. 24)
Other Obs. Urnes 2017 in the Northern Gulf (Coloraditos, Willard, BoLA, Chivato, Bajo) Dungan 1980 at Chivato, Dungan 1984 at El Bajo
Brusca: "very common starfish of the mid and lower gulf, only occasionally turning up north of the midriff region" range from Lower Gulf to Peru including Galapagos
Bertsch: Throughout the Gulf, to northern Peru and Galapagos, "the most abundant shallow water sea star in rocky habitats in the Goc"

GoC: Along with Pharia pyramidata, this is one of the predominant sea stars in the Central and Southern Gulf. . . This family of sea stars is probably entirely dioecious, broadcast spawners
iNaturalist: 90 obs in the GoC from the Central and Southern Gulf. Many around loreto

No evidence of change

Holothurians

Euapta godeffroyi

Only observed at ESCO, by Ricketts and Urnes

Bertsch: southern GC to Costa Rica and Panama, common Indo-Pacific species

Brusca: Indian ocean to Hawaii and Panamic region, "I have found it with irregularity throughout the southern Gulf"

S&R: Puerto Escondido (Col. No. 11) Puerto Escondido inner bay (Col. No. 12) Isla Espiritu Santo (Col. No. 24) (a large, conspicuous synaptid cucumber; surprisingly taken at only 2 localities)

Other Obs. Urnes 2017 at Puerto Escondido
Brusca: "one of the most unusual holothurian in the Gulf. . . a widespread Indo-Pacific form, known from throughout the Indian Ocean and east to Hawaii and the Panamic region. I have found it with irregularity throughout the southern Gulf."
Bertsch: "Southern GoC to Costa rica and Panama. . . Comes out to feed at night"
GoC: One of the most distinctive cucumbers in the Eastern Pacific. A tropical trans-Pacific species.
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record CHI, Iquique
World Distribution PET;PSET;PW;PC;OI
Shallowest depth 0m Greatest depth 79m
iNaturalist: 11 obs in the GoC

No evidence of change

Holothuria arenicola

S&R: Isla Espíritu Santo (Col. No. 4), Puerto Escondido (Col. No. 11), Loreto (Col. No. 13), Isla Ángel de la Guarda (Col. No. 19), Isla Tuburon (Col. No. 20)(unclear, might have been either *H. arenicola* or *H. impatiens*)
Other Obs. Urnes 2017 at Puertecitos, Bahía Concepción and Punta Willard, Brusca 1976 at Punta Chivato
Brusca: (as *Brandtothuria Arenicola*) from the upper GoC to Ecuador and the Galapagos
Bertsch: (not included, possibly considers synonymous with *H. impatiens*)
GoC: Type locality is Philippines. A cosmotropical species known from all the world's tropical seas
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record ECU, B. Santa Elena
World Distribution CT;IREV;IGAL;ICOC
Shallowest depth 0m Greatest depth 121m

iNaturalist: 5 observations in the GoC from Cabo Pulmo to Puerto Penasco

No evidence of change

Holothuria impatiens

S&R: Isla Espíritu Santo (Col. No. 4), La Paz sand flats (Col. No. 5), El Mogote (Col. No. 6), Puerto Escondido (Col. No. 11), Isla Ángel de la Guarda (Col. No. 19), Isla Tuburon (Col. No. 20)(unclear, might have been either H. arenicola or H. impatiens). Annotation "a circumtropical species; S&R describe this as the second most common sea cucumber from their expedition"

Other Obs. Urnes 2017 at Willard
Brusca: (as *Brandtothuria impatiens*) "Ranges from the upper GoC to Columbia and the Galapagos Islands and is nearly circumtropical"
Bertsch: Bahia Rosario (pacific side), throughout the GoC, to Ecuador and the Galapagos, circumtropical. "The abundance of this species is not related to food but to microhabitat availability"
GoC: A circumtropical species known from all the world's warm seas. Quite common in the Gulf.
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record ECU, B. Santa Elena
World Distribution CT;PET;PNET;OI;AE;AW;PW;PC;IGAL;ICOC;ILTM;IREV
Shallowest depth 0m Greatest depth 67m
iNaturalist: 5 observations in GoC

No evidence of change

Holothuria lubrica

S&R: Cabo San Lucas (Col. No. 2), Isla Espíritu Santo (Col. No. 4), Puerto Escondido (Col. No. 11), Loreto (Col. No. 13), Isla San Marcos (Col. No. 15), Bahia San Carlos/ Punta Trinidad (Col. No. 16), Bahía de San Francisquito (Col. No. 17), Bahía de Los Ángeles (West), (Col. No. 18) Isla Ángel de la Guarda (Col. No. 19), Guaymas (Col. No. 21), Isla Espiritu Santo (Col. No. 24). Annotates "= Slenkothuria lubrica; the sulfur cucumber; **the most common sea cucumber taken during the expedition and the most common littoral cucumber in the Sea of Cortez today")**

Other Obs. **Observed by Urnes in 2017 at every site**, in average densities up to 15 ind/m, also widespread obs. by Dungan and Brusca
Brusca: (as *Selenkothuria lubrica*) "One of the most common cucumbers in the GoC. . . Ranges from the upper GoC to Ecuador and the Galapagos"
Bertsch: "From Punta Eugenia, BCS, south to Ecuador and the Islas Galapagos, and throughout the GoC. This abundant GoC species congregates in areas where there are currents, feeding more or less continuously night and day"
GoC: The most common and abundant sea cucumber in the Gulf; under intertidal & subtidal rocks and boulders. A tropical trans-Pacific species.
Northernmost record MEX, BCS, B. Magdalena;MEX, SON, Puerto Peñasco
Southernmost record ECU, B. Santa Elena
World Distribution PET;PNET;IGAL;ILTM;IREV
Shallowest depth 0m Greatest depth 55m
iNaturalist: 57 obs. throughout the Gulf, 5 obs. on the Pacific Coast

No evidence of change

Holothuria rigida

Only observation Ricketts at ESCO

Brusca describes from Upper GC to West Coast of BC to Galapagos

Described in Brusca as *Fossothuria rigida*

Not described in Bertsch

S&R: (Bruscas summary misspells as *Holothura rigida*) El Mogote (Col. No. 6) Puerto Escondido (Col. No. 11)
Other Obs.
Brusca: (as *Fossothuria rigida*) "Ranges from the upper GoC and the west coast of Baja California to the Galapagos Islands ans is also found in Africa and the Red Sea"
Bertsch: (not included)
GoC: A circumtropical species that is fairly common the Gulf of California.
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record PAN, Is. Secas
World Distribution PET;IGAL;PC;OI;AW;CT
Shallowest depth 0m Greatest depth 22m
iNaturalist: No observations globally

No evidence of change

Isostichopus fuscus

Historical from central gulf (Ricketts ESCO, Dungan and Brusca at CHIV) Urnes WILL CHIV, ESCO

Bertsch: B. Vizcaino south to Ecuador ang Galapagos, throughout the Gulf. Scarce due to over-exploitation by divers

Brusca:"

GCD:

Distribution in Gulf GCN;GCC;GCS;RB

Northernmost record MEX, SON, Puerto Peñasco; MEX, BCS, B. Vizcaíno

Southernmost record CHI, Patagonia

S&R: Isla Espíritu Santo (Col. No. 4), Marcial Reef (Col. No. 10), Puerto Escondido inner bay (Col. No. 12). (Annotates "as Stichopus fuscus; it is surprising that **this very common Gulf sea cucumber was found only at two localities by the expedition**")

Other Obs. Dungan 1980 at Chivato, Brusca 1984 at Chivato, Urnes 2017 at Punta Willard, Punta Chivato, Puerto Escondido

Brusca: “Sheltered areas where wave shock is not too great… occurs in greatest numbers where abundant detritus exists, such as near the mouths of estuaries or broad algal covered reefs. . . Ranges from the upper GoC to Ecuador and the Galapagos Islands”
Bertsch: Range “Bahia Vizcaino, south to Ecuador and the Islas Galapagos; throughout the Gulf of California. . . **Regrettably this species is scarce because of over-exploitation by divers, most were sold for foreign consumption. The Mexican federal government issued strict closure of its capture but despite being listed by CITES, it is still exploited. Even a little might be too much given the precarious existence of this species**.”
GoC: **Once very common in the Gulf, this species was over-exploited in the 1990s so much that large individuals are now uncommon** (2017). Listed as an endangered species in 1994 (Norma Oficial Mexicana 1994), it is gradually recovering, but most individuals might be reaching sexual maturity (at around age 5) for the first time now (2001). Occasionally found in tidal lagoons, but more commonly found on subtidal rocky bottoms. Become reproductively active in the summer months. Pañola-Madrigal et al. (2017) recently discussed its life history. Deposit feeder.
Northernmost record MEX, SON, Puerto Peñasco; MEX, BCS, B. Vizcaíno
Southernmost record CHI, Patagonia
World Distribution PET;PNET;PSET;IREV;ILTM;ICOC;IGAL
Shallowest depth 0m Greatest depth 39m
iNaturalist: 48 obs. in the GoC from midriff south to Cabo Pulmo, 3 obs on the Pacific Coast of Baja

Possibly reduced by widespread and aggressive harvest

Neothyone gibbosa

S&R: La Paz sand flats (Col. No. 5) Puerto Escondido (Col. No. 11) Bahía de Los Ángeles (West), (Col. No. 18)

Other Obs. Brusca 1984 at Chivato, Observed on Hancock expedition 1932 (?)
Brusca: “throughout the gulf, and has been reported from Peru. . . Found in great numbers at Guaymas, Bahia Kino and Bahia Pulmo”
Bertsch:
GoC: Not to be confused with N. gibber (Selenka, 1867).
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record PER, I. Lobos de Afuera
World Distribution PET;PSET;IGAL
Shallowest depth 0m Greatest depth 50m
iNaturalist: No observations

No evidence of change

Mollusk

Aplysia californica

Observed sporadically (Ricketts ESCO, Brusca BOLA and COLO, Urnes ESCO)

Bertsch: throughout the Gulf

Brusca: N. California to N. GC

S&R: El Mogote (Col. No. 6) Islote Cayo (Col. No. 8) (“"sea rabbits" (probably *Aplysia* sp.)”) Puerto Escondido inner bay (Col. No. 12) ("giant sea hares") Isla Ángel de la Guarda (Col. No. 19) Isla Espiritu Santo (Col. No. 24)

Other Obs. Brusca 1979 at BoLA and “Aplysia sp.” at Coloraditos, Urnes 2017 at Puerto Escondido
Brusca: “Northern California to the Northern GoC”
Bertsch:”Throughout the GoC, along the Pacific coast of Baja California to northern California, also reported from el Salvador and Japan. . . Eaten by sea turtles”
GoC:
Northernmost record USA, CA, Humboldt Bay
Southernmost record MEX, SIN, Mazatlán
World Distribution PET;PNET
Shallowest depth 0m Greatest depth 30m
iNaturalist: 70 obs. throughout the GoC, 3 observations on the Pacific Coast of Baja

No evidence of change

Hexaplex eurythrostomus

S&R: Cabo Pulmo (Col. No. 3) (annotates Ricketts note “probably Phyllonotus regius” with “presumably Chicoreus erythrostomus”) La Paz sand flats (Col. No. 5) Puerto Escondido (Col. No. 11) Bahía Concepción east (Col. No. 14) (shells only) Guaymas (Col. No. 21)

Brusca annotates “the pink-mouth murex. S&R found this to be the most common large snail of their expedition and, although they list it from only a few locals it was likely present at all rocky shore sites they visited. Indeed, it was once the most common littoral and shallow subtidal large snail throughout the Gulf; but no longer, due to intense over-collecting. Large specimens are now exceedingly rare intertidally.”

(variously noted as *Phyllonotus erythrostomus*, *Phyllonotus bicolor* (a junior synonym), and *Chicoreus erythrostomus*)
Other Obs. Dungan 1980 at Coloraditos and Bahía Concepción, Urnes 2017 in the Northern Gulf (San Felipe, Coloraditos, Bahía de Los Ángeles)
Brusca: (as H. erythrostomus) “Distribution: throughout the GoC, South to Peru. . . Large numbers are dredged up by shrimp fishermen and sold to tourists; common”
Bertsch: (as P. erythrostomus) “throughout the Gulf to as least Costa Rica. . . This is the most common murex in the GoC. . . During breeding season they might congregate in large numbers, sometimes a hundred or more”
GoC: “Once so common intertidally that you almost stepped on one with each step you took, but now largely restricted to the subtidal (due to over-collecting). Often found in N. Gulf shell middens. Frequently captured (and killed) in shrimp trawls. Steinbeck and Ricketts (1940) commented that "murex

snails" are the most abundant large gastropods in the Gulf; their numbers have plummeted since that time. BML”
Northernmost record MEX, SON, Punta Pelícano
Southernmost record MEX, NAY, I. Isabel
World Distribution ENGC
Shallowest depth 0m Greatest depth 100m
iNaturalist: (as H. erythrostomus) 60 observations in the GoC from Puerto Penasco to Cabo Pulmo

Likely reduced by widespread and aggressive harvest

Hexaplex nigritus

S&R: no obs.
Other Obs. Brusca 1975 at San Felipe, Dungan 1984 at San Felipe and Puertecitos Dungan 1980 at Coloraditos and Bahía Concepción, Urnes 2017 at San Felipe and Coloraditos)
Historical observations indicate high densities (“abundant”-Brusca 1975, “Common”- Dungan 1984), but Urnes recorded low densities in transect surveys (.27/m at SANF, .03/m at COLO)
Brusca: (as *Muricanthus nigritus*) Endemic to the Gulf of California; common in the north
Bertsch: “Distribution: Bahia Magdalena BCS throughout the GoC to Manzanillo, Colima. Often occurs in huge breeding aggregations (up to 5000 individuals) which act like temporary reefs providing refucge and habitate for juvenile fishes crustaceans and mollusks. Preys especially on bivalves. . . This species was eaten by the Seris after being roasted under a brush fire”
GoC: Once so common intertidally that you could hardly take a step without walking on them, now they are largely restricted to the subtidal zone due to over-collecting. Common in No. Gulf shell middens. Heavily over-harvested commercially since the early 1990s, largely for the Asian market. As of ~2005, fishers have begun targeting the subtidal summer breeding aggregations. Studies by R. Cudney-Bueno and colleagues have shown this snail to reach reproductive maturity between 2 and 3 years, and to live for at least 8 years, allowing for multiple reproductions. In the N Gujlf, offshore breeding aggregations (April to September) can reach several metric tons in biomass.
Northernmost record USA, CA, La Jolla
Southernmost record MEX, OAX, Golfo de Tehuantepec
World Distribution PET;PNET
Shallowest depth 0m Greatest depth 60m
iNaturalist: 33 obs in the GoC, with a cluster around Bahia Kino, two more reported from pacific BCS

Likely reduced by widespread and aggressive harvest

Octopus bimaculatus

S&R: La Paz (sand flats) Isla San Marcos, Bahía San Carlos, Bahía de Los Ángeles, Isla Ángel de la Guarda,

S&R: “Octopus” or “Octopus sp.” : Cabo Pulmo, Isla Espíritu Santo, El Mogote, Bahía de Los Ángeles, Tidal flats N. of Bahía de Los Ángeles

Brusca: “Rocky intertidal from Puerto Penasco and San Felipe to La paz, and from Point Concepcion to Punta Santa Eugena BC

Bertsch: Throughout the GoC to Panama, and From Southern California to Cabo San Lucas "Commercial divers collect this large species throughout the Gulf, Seriously impacting its population levels
GoC: Heavily harvested for the local seafood market. Hooka divers use traps and gaffs, and they walk/work the low tide rocky shores with gaffs also. The Mexican government has declared the fishery to be at its maximum sustainable yield. Females reach maximum gonadal development beginning in Might. Recent research suggests the Gulf species "O. bimaculatus" could actually be an undescribed species. In the Gulf, this octopus will squirt ink up to 2 ft. in a straight stream at a predator, even a human standing in a tidepool reaching into it to handle the animal. Very similar, and often confused with, O. bimaculoides (though slightly larger and with longer arms). One of three Octopus species harvested commercially in the Gulf (O. bimaculatus, O. bimaculoides, O. hubbsorum).
Northernmost record USA, CA, Point Conception
Southernmost record MEX, JAL
World Distribution PET;PNET
Shallowest depth 0m Greatest depth 55m
iNaturalist: 4 observations in the GoC near Puerto Penasco (11 obs. in GoC of *O. bimaculoides*, 13 obs. in GoC of *O. hubbsorum*)

Likely reduced by widespread and aggressive harvest

Octopus fitchi

S&R:
Other Obs. Urnes 2017 observed this species at consistent densities at sites in the northern Gulf (San Felipe (0.12 ind. /m^2), Coloraditos (0.25 ind. /m^2) Puertecitos (0.125 ind. /m^2) and Punta Willard (0.257 ind. /m^2)
Brusca: "Endemic to the upper gulf. It is the most commonly encountered octopus in the rocky intertidal, especially at San Falipe and Puerto Penasco. Berry also reports it from the Salton Sea (!!)"
Bertsch: "throughout the GoC. . . This uncommon species can cause painful bites"
GoC: One of the most commonly encountered octopuses in the Northern Gulf of California. Recent research suggests this species might belong to a different genus, but a new assignment has not yet been made (Feb. 2012). Although small, this species is quick to bite and some people react to an apparent toxin in the salivary fluids. Especially common on tidal flats in the upper Gulf.
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record MEX, SON, Guaymas
World Distribution ENGC
Shallowest depth 0m Greatest depth Unknown
iNaturalist: 4 observations in the GoC, at Penasco, Kino, and La Paz

No evidence of change

Megapitaria squalida or *Megapitaria aurantiaca* (Chocolate Clam)

S&R: El Mogote, Isla San Marcos, Bahía de Los Ángeles (West), Estero Agiabampo

S&R: El Mogote (Col. No. 6) Puerto Escondido inner bay (Col. No. 12) Isla San Marcos (Col. No. 15) Bahía de Los Ángeles (West), (Col. No. 18) Estero Agiabampo (Col. No. 23)

Other Obs. Urnes interviewed a marina-worker in Puerto Escondido who reported a “predatory” fisherman who did not respect community harvesting limits and regulations and who had severely depleated chocolate clam abundances in that region.
Brusca:
Bertsch: throuout the GoC, to Peru (M. squalida) or Ecuador (M. aruantiaca). “Clam widely used as food since pre-Hispanic times and is in high demand in the national market today”
GoC: (M. squalida) Harvested commercially. Gárate-Lizárraga et al. (2004) describe paralytic shellfish toxins in this clam from Bahía de La Paz (2001-2002). This species, and also M. aurantiaca, are both called almeja chocolata and are consumed locally in growing numbers. The commercial fishery for M. squalida in Sonora and Sinaloa is growing
Northernmost record MEX, BCS, Laguna Ojo de Liebre;MEX, BC, San Felipe
Southernmost record PER, Sechura
World Distribution PET;PNET;PSET;IGAL
Shallowest depth 0m Greatest depth 180m
(M. aruantiaca)
This species, and also (especially) M. squalida, are both called almeja chocolata and are consumed locally in growing numbers. This is probably what Steinbeck & Ricketts (1941) called "Macrocallista aurantiaca."
Northernmost record MEX, BC, B. de Los Ángeles
Southernmost record PER, Sechura
World Distribution PET;PSET;IGAL
Shallowest depth 0m Greatest depth 30m
iNaturalist: (M. squalida) 48 obs. throughout the GoC (M. aurantiaca) 25 obs. throughout the GoC

Likely reduced due to widespread and aggressive harvest

Pinna rugosa (Common ‘hatcha’)

S&R: Isla Espíritu Santo (Col. No. 4) Puerto Escondido (Col. No. 11), Bahía Concepción east (Col. No. 14)

Other Obs.
Brusca: “Known locally as “hatcha larga”. . . Southern BC and throughout the Gulf, south to Peru”
Bertsch: Laguna Manuela, Pacific BC, throughout the GoC to Peru. “A major food item in the restaurants and coner sea food stands of BCS and Sonora
GoC: Harvested commercially and sold as scallops (callo de hacha); the meat is sweet and delicious. Almost certainly over-harvested and threatened, although few data are available.
Northernmost record MEX, BC, San Felipe
Southernmost record PAN
World Distribution PET;IGAL;ICLI
Shallowest depth 0m Greatest depth 12m
iNaturalist: 17 obs. in the GoC

Likely reduced due to widespread and aggressive harvest

Atrina tuberculosa (less common ‘hatcha’ (S&R did not differentiate))

S&R: La Paz sand flats (Col. No. 5), Bahía Concepción east (Col. No. 14)(questionable, see Brusca)

Other Obs.
Brusca: "throughout the gulf, south to Panama. . . An important food source in certain localities, often referred to as "hatcha china""
Bertsch: Not included
GoC: Similar to Pinna rugosa, but larger and more "ham-shaped" (rather than elongate and fan-shaped), and preferring muddier and somewhat shallower habitats. Harvested commercially, the adductor muscle is sold as "scallops" or "hacha." Greatly over-harvested and disappearing from most areas in the Gulf
Northernmost record MEX, BC, Rocas Consag
Southernmost record PER, Punta Negra
World Distribution PET;IGAL
Shallowest depth 0m Greatest depth 23m
iNaturalist:18 obs. in the GoC, all north of Bahia Kino, where there is a cluster of obs.

Likely reduced due to widespread and aggressive harvest

Ophiuroids

Ophiactis simplex

S&R: Cabo Pulmo (Col. No. 3) Loreto (Col. No. 13) Isla Tuburon (Col. No. 20)
Other Obs. Brusca 1976 at Punta Chivato
Brusca:"I have found this species to be common throughout the gulf and have collected it in great abundance from the pores of large sponges (*Geodia*, *Leucosolenia*, and *Leucetta*) and living in the thick mats of algae on rocks. This species ranges from southern California and the upper Gulf to Peru"
Bertsch: Not noted
GoC: Lives commensally with sponges, mussels, and other bivalves. Species in this genus reproduce both sexually and asexually (by binary fission).
Northernmost record USA, CA, northern Channel Islands
Southernmost record PER, B. Independencia
World Distribution PET;PNET;PSET;ICOC;IGAL;IMAL;ILTM;IREV
Shallowest depth 0m Greatest depth 302m
iNaturalist: No obs.

No evidence of change

Ophiocoma aethiops

Observed three times in the central gulf, (Ricketts BOLA, Brusca CHIV, Urnes BAJO)

Bertsch: B. Vizcano, throughout GC, south to Peru. "common"

Brusca: Upper gulf to panama and the Galapagos

S&R: Cabo San Lucas (Col. No. 2) Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) La Paz sand flats (Col. No. 5) Bahia La Paz (Col. No. 7) Loreto (Col. No. 13) Bahía de Los Ángeles (West), (Col. No. 18) Bahía de Los Ángeles (Ballenas Canal) (Col. No. 18) Isla Tuburon (Col. No. 20) Isla Espiritu Santo (Col. No. 24)

Other Obs. Brusca 1976 at Punta Chivato, Urnes 2017 at Punta Willard
Brusca:"This species is common on rocky shores, under rocks in sand or muddy sand of the lower mid intertidal zone, from the upper Gulf to Panama and the Galapagos Islands
Bertsch: "From Bahia Vizcaino, BC, to Northern Peru and throughout the GoC. . . This common brittle star is very active and thought to be a scavenger and opportunistic feeder
GoC: Formerly one of the most common large intertidal invertebrates found throughout the Gulf; **now rare due to over-collecting**; today most frequently found on offshore islands.
Northernmost record MEX, SON, Puerto Peñasco
Southernmost record PER, I. Lobos de Afuera
World Distribution PET;PSET;IREV;ILTM;ICOC;IGAL;IMAL
Shallowest depth 0m Greatest depth 30m
iNaturalist: 41 obs. throughout the GoC

Possibly reduced, but remains widespread

Ophiocoma alexandri

S&R: Isla Espíritu Santo (Col. No. 4) La Paz sand flats (Col. No. 5) Bahia La Paz (Col. No. 7) Marcial Reef (Col. No. 10) Loreto (Col. No. 13) Isla Ángel de la Guarda (Col. No. 19) Isla Espiritu Santo (Col. No. 24)

Other Obs. Brusca 1976 at Coloraditos, Urnes 2017 at Punta Willard
Brusca: "Another large brittle star, common in the rocky low mid intertidal from the upper Gulf to Panama and the Galapagos Islands and also possibly occurring in the Caribbean region
Bertsch: Througohut the GoC to Columbia and the Galapagos. . . This abundant species can attain sizes comparable to *O. aethiops* but is normally smaller. It is more common than *O. aethiops* in the GoC. These two species overlap in distribution as well as in habitat
GoC: This species, and O. aethiops, are the largest brittle stars in the Sea of Cortez. O. aethiops has a larger disk, but O. alexandri has longer arms. **Both species were very common in the Gulf's intertidal zone until ~1980, when they began to decrease in abundance**. Today they are found only in relatively inaccessible habitats. Probably a suspension feeder.
Northernmost record USA, CA, Santa Catalina I.
Southernmost record ECU, I. Cupica
World Distribution PET;PNET;IREV;ILTM;ICOC;IGAL;IMAL
Shallowest depth 0m Greatest depth 70m
iNaturalist: 23 obs. throughout the GoC

Possibly reduced but remains widespread

Ophioderma panamense

S&R: Isla Espíritu Santo (Col. No. 4) (for some reason this is the only locality at which the expedition collected this very common littoral species, which occurs throughout the Gulf) Isla Espiritu Santo (Col. No. 24)

Other Obs. Brusca 1975 at San Felipe, Brusca 1976 at Coloraditos and Punta Chivato, Urnes 2017 at San Felipe, Punta Chivato, El Bajo, and Puerto Escondido
Brusca: "Ranges from southern California and the upper Gulf to Peru and the Galapagos Islands"
Bertsch: "From southern California to northern Peru and the Islas Galapagos; throughout the Gulf of Califonia. Also reported from Hawaii. . . This brittle star is particularly abundant in the intertidal zone. There are three color phases of this species, each associated with a particular habitat"
GoC: Formerly one of the most common large intertidal invertebrates; **now rare due to over-collecting, primarily by tourists**. A predatory carnivore.
Northernmost record USA, CA, San Pedro
Southernmost record PER, Paita
World Distribution PET;PNET;ICOC;IGAL;IGUA;ILTM;IREV
Shallowest depth 0m Greatest depth 20m
iNaturalist: (as *o. panamensis*) 24 obs in the GoC

Possibly reduced, but remains widespread

Ophioderma teres

S&R: Isla Espíritu Santo (Col. No. 4) La Paz sand flats (Col. No. 5) Bahia La Paz (Col. No. 7) Puerto Escondido (Col. No. 11) Loreto (Col. No. 13) Bahía Concepción east (Col. No. 14) Bahia San Carlos/ Punta Trinidad (Col. No. 16) Bahía de San Francisquito (Col. No. 17) Bahía de Los Ángeles (West), (Col. No. 18) Isla Ángel de la Guarda (Col. No. 19) Guaymas (Col. No. 21) Isla Espiritu Santo (Col. No. 24)

Other Obs. Dungan 1980 obs at Bahía de Los Ángeles, Urnes 2017 obs. at Bahía de Los Ángeles
Brusca: "Ranges from the upper Gulf to Panama, reappearing again in the Galapagos Islands
Bertsch: Not included
GoC: Formerly **common in the intertidal region throughout the Gulf; now rare due to over-collecting, primarily by tourists.** A classic Tropical East Pacific species, the S California records being outliers. Predatory carnivores.
Northernmost record USA, CA , Newport Bay
Southernmost record ECU, I. La Plata
World Distribution PET;PNET;ILTM;IGAL
Shallowest depth 0m Greatest depth 54m
iNaturalist: 1 obs at Puerto Penasco

Possibly reduced due to collecting by tourists

Ophionereis annulata

S&R: Isla Espíritu Santo (Col. No. 4) La Paz sand flats (Col. No. 5) Bahía Concepción east (Col. No. 14) Bahia San Carlos/ Punta Trinidad (Col. No. 16) Bahía de Los Ángeles (West), (Col. No. 18) Bahía de Los

Ángeles (Ballenas Canal) (Col. No. 18) Isla Ángel de la Guarda (Col. No. 19) Isla Espiritu Santo (Col. No. 24)
Other Obs. Brusca 1975 at San Felipe, Dungan 1980 at Coloraditos, Bahía de Los Ángeles, Brusca 1976 at Punta Chivato, Urnes 2017 at Puertecitos
Brusca: “Ranges from southern california and the upper Gulf to Ecuador and the Galapagos”
Bertsch: “the most common intertidal brittle star in the Gulf” From Pt Concepction to Ecuador and the Galapagos, throughout the GoC
GoC: One of the most common and abundant brittle stars in the Gulf of California (and in certain places in Southern California). Most often found under rocks and in large sponges. Arm span 50-100 mm. Larvae are lecitotrophic and planktonic.
Northernmost record USA, CA, San Pedro
Southernmost record ECU, B. Santa Elena
World Distribution PET;PNET;ICOC;IGAL;IREV;ILTM;IGUA
Shallowest depth 0m Greatest depth 229m
iNaturalist: 33 obs. from throughout the Gulf

No evidence of change

Ophiothrix spiculata

S&R: Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) El Mogote (Col. No. 6) Puerto Escondido (Col. No. 11) Bahía Concepción east (Col. No. 14) Isla San Marcos (Col. No. 15) Isla Ángel de la Guarda (Col. No. 19) Isla Tuburon (Col. No. 20)

Other Obs. Brusca 1976 at Coloraditos and Chivato, Dungan 1980 at Bahía de Los Ángeles,
Brusca: “often abundant among the roots of the red mangrove trees, especially in association with estuarine sponges. It ranges from Monterey California, and the upper Gulf to Peru and the Galapagos Islands, and is abundant throughout its range.
Bertsch: “Range from Moss Beach, Central California to Bahia de Sechura, Peru, and the Galapagos Islands; throughout the GoC
GoC: Commonly, though not always, found commensally with sponges. Might occur in huge numbers offshore and in deeper water. . . Ophiothrix species are dioecious broadcast spawners with planktotrophic larvae.
Northernmost record USA, CA, Monterey Bay
Southernmost record PER, I. Lobos de Afuera
World Distribution PET;PNET;PSET;IREV;ILTM;ICOC;IGAL;ART
Shallowest depth 0m Greatest depth 2059m
iNaturalist: 18 obs. throughout the GoC

No evidence of change

Echinoidea

Arbacia stellata *A. incisa*

S&R: Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) Bahia San Carlos/ Punta Trinidad (Col. No. 16) Bahía de Los Ángeles (West), (Col. No. 18) Isla Ángel de la Guarda (Col. No. 19) Isla Espiritu Santo (Col. No. 24)

(these are the urchins S&R noted at Pulmo Reef, “penetrated all but the heaviest part of the soles of our rubber boots”)

Other Obs. Dungan 1980 obs at Bahía de Los Ángeles, Punta Chivato, brusca 1976 obs. at Punta Chivato, Urnes 2017 at BoLA,Chivato, Puerto Escondido
Brusca: (as *A. incisa*) “**One of the more common urchins** of the Gulf. . . prefers surf-protected rocky shores and is found in the mid and low intertidal from southern California and the upper GoC to Peru and the Galapagos
Bertsch: “Throughout the GoC, from Bahia Magdalena, BCS to Peru and the Islas Galapagos, Rarely reported from Newport Bay, Southern California. . . **very common in the Gulf**
GoC: The correct name of this species is in dispute (D.L Pawson, pers. comm.). A motile, grazing, herbivore. Dioecious, broadcast spawner with planktotrophic, calcareous-based larvae.
Northernmost record USA, CA, Newport Beach
Southernmost record PER, Is. Chinchas
World Distribution PET;PNET;PSET;IGAL
Shallowest depth 0m Greatest depth 90m
iNaturalist: 1 obs. in the GoC near La Paz, 1 near BOLA, 2 in Pacific BC

No evidence of change

Diadema mexicanum

S&R: Isla Espíritu Santo (Col. No. 4) Marcial Reef (Col. No. 10)

“**curiously, S&R collected this common, toxic-spined species only twice**, at Punta Lobos and at Marcial Point”
Other Obs. Brusca 1984 at Punta Chivato, Dungan 1984 at El Bajo, Urnes 2017 at Punta Chivato and Puerto Escondido
Brusca: “Occurs from the mid-GoC (BoLA and Bahia Kino) and lower west coast of Baja to Columbia and the Galapagos. . . In the gulf **it probably occurs in greatest numbers between Loreto and Cabo san Lucas**
Bertsch: “Lower west coast of BCS, throughout the GoC to the Islas Galapagos. . . Various studies have documented changing density patterns of this species, which change its bioerosive effects on corals”
GoC: The spines are coated with a mildly toxic slime. Opportunistic predators. The Puget Sound record is an outlier; the core distribution of this tropical species ends in Southern California. A nocturnal, omnivorous grazer and scavenger, and occasional opportunistic predator. Dioecious broadcast spawner.
Northernmost record USA, WA, Puget Sound
Southernmost record COL, Punta Utría
World Distribution PET;PNET;IGAL;ICOC;IMAL;ILTM;IREV
Shallowest depth 0m Greatest depth 113m
iNaturalist: 19 obs in GoC, mostly in the southern Gulf

No evidence of change

Echinometra vanbrunti

S&R: Cabo San Lucas (Col. No. 2) Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) Marcial Reef (Col. No. 10)

Other Obs. Dungan 1980 (density 5 ind/m) Dungan 1984 at Willard, El Bajo and Puerto Escondido, Brusca 1984 at Punta Chivato, **Urnes 2017 took densities of this species (ind/m^2) at BoLA (0.08) Punta Chivato (0.133) Puerto Escondido (0.458)**
Brusca: "this is **one of the most common sea urchins of the Gulf**. . . from the upper Gulf to Peru and the Galapagos Islands. .. At Bajia Kino I have regularly observed handfuls of these urchins congregated on the sand under a single rock, and at Cabo San Lucas I've seen them so thick on the rocks as to obscure the substrate entirely"
Bertsch:"Bahia Magdalena, BCS, to Peru and the Islas Galapagos; throughout the GoC. . . **This is the most common sea urchin in the Gulf and throughout the Panamic region**
GoC: Southern California records need verification.
Northernmost record Southwest Baja California
Southernmost record PER, I. Lobos de Afuera
World Distribution PET;PNET;PSET;IGAL;ICOC;IREV;ILTM
Shallowest depth 0m Greatest depth 106m
iNaturalist: 97 obs. throughout the GoC, 6 from the Pacific Coast of BCS

No evidence of change

Eucidaris thouarsii

S&R: Cabo San Lucas (Col. No. 2) Cabo Pulmo (Col. No. 3) Isla Espíritu Santo (Col. No. 4) La Paz sand flats (Col. No. 5) Bahia La Paz (Col. No. 7) Islote Cayo (Col. No. 8) Marcial Reef (Col. No. 10) Puerto Escondido (Col. No. 11) Loreto (Col. No. 13) Bahía Concepción east (Col. No. 14) Isla San Marcos (Col. No. 15) Bahia San Carlos/ Punta Trinidad (Col. No. 16) Bahía de San Francisquito (Col. No. 17) Bahía de Los Ángeles (West), (Col. No. 18) Isla Ángel de la Guarda (Col. No. 19) Isla Tuburon (Col. No. 20) Isla Espiritu Santo (Col. No. 24)

(**one of the most common urchins in the Gulf; collected "at practically every suitable collecting place")**
Other Obs. **Urnes 2017 measured density at Willard (0.06) BoLA (0.02) Punta Chivato (0.43) and Puerto Escondido (0.08),** and observed it additionally at Puertecitos. Dungan 1984 at Willard, El Bajo, and Puerto Escondido. Brusca 1984 at Punta Chivato.
Brusca: "**One of the most common echinoids of the Gulf** and the Panamic region in general. . . The most characteristic urchin of tropical and subtropical west America, ranging from the upper GoC to Ecuador and the Galapagos. . . During unusually warm years I have noted its occurance along the western shores of Baja
Bertsch:"Southern California to Ecuador and the Islas Galapagos; throughout the GoC. . . This species is **common throughout the Gulf**, But rare north of central west Baja California (occurances might be restricted to El Nino phenomena)
GoC: **Common subtidally; now rare intertidally due to over-collecting**. In the Galapagos Islands, this species is an important corallivore. An omnivorous grazer and scavenger. Dioecious broadcast spawners; planktotrophic larvae.
Northernmost record USA, CA, Santa Catalina Island
Southernmost record ECU, B. Santa Elena
World Distribution PET;PNET;IREV;ILTM;IGUA;ICOC;IMAL;IGAL

Shallowest depth 0m Greatest depth 150m
iNaturalist: 51 obs in the GoC, in all regions, mostly near Loreto and La Paz

Possibly reduced, although remains widespread

Toxopneustes roseus

S&R: **Not observed**
Other Obs. Urnes 2017 at Punta Chivato and Puerto Escondido
Brusca: "A beautiful and robust sea urchin fairly **common in the extreme southern Gulf**, especially around Cabo Sand Lucas, La Paz and the coral reefs of Bahia Pulmo. . . distributed from the southern Gulf to Ecuador, including most offshore islands"
Bertsch: "Bahia Tortugas, BCS, south to Ecuador and the Galapagos; throughout the GoC. . . The large, rose colored pedicellariae are venomous"
GoC: Once fairly common in the low intertidal of the central and southern gulf, this species has largely disappeared on "mainland" shores due to over-collecting; it is still fairly common subtidally and on the islands.
Northernmost record MEX, SON, Guaymas
Southernmost record ECU, I. La Plata
World Distribution PET;PNET;IREV;ILTM;IGAL
Shallowest depth 0m Greatest depth 55m
iNaturalist: 35 obs. in the GoC, including two near Isla Tiburon (range expansion?)

Possibly expanding range north. S&R did not observe, recent observations by Urnes and on iNaturalist observed as far north as the Midriff Islands

Tripneustes depressus

S&R: Isla Espíritu Santo (Col. No. 4) "a trans-Pacific species; collected only at this locality"

Other Obs. Urnes 2017 at Punta Chivato and El Bajo
Brusca: "it has been reported from the lower west coast of Baja and the southern Gulf, as well as the offshore islands of Socorro, Clarion, and the Galapagos. I have recorded it from Cabo San Lucas, Isla San Jose, and the Pulmo Reef Area"
Bertsch: "Lower outer coast of the Baja California Peninsula; common in the southern Gulf of California, and south along the Mexican coast and offshore islands to the Islas Galapagos. . . During a multi year survey it comprised over 40% of the urchin fauna on Isla San Jose in the southern GoC"
GoC: (as *T. gratilla*) A trans-Pacific and a trans-Atlantic species). Lessios et al. (2003; Evolution 57, pp. 2026-2036) synonymized the E. Pacific species Tripneustes depressus with the Central/Indo-West Pacific species Tripneustes gratilla, on the basis of morphology and molecular data. These leaves only 2 species in this genus.
Northernmost record MEX, BC, I. Ángel de la Guarda
Southernmost record PAN, Golfo de Panamá
World Distribution CT;PET;IREV;IGAL;IMAL
Shallowest depth 0m Greatest depth 73m

iNaturalist: 80 observations within the Gulf. 4 obs. near BoLA and 1 observation near Isla Tiburon. 1 observation of *T. gratilla*, south of La Paz

Might be more frequently found in central gulf than previously thought

Appendix C: Compilation of field observations This table contains each observation of echinoderms and selected mollusk species in field notes from Steinbeck and Ricketts (listed as Ricketts), Field notes provided by Mike Dungan and Richard Brusca, and Field observations by Urnes

Site	Species	Group	Observer	Year	Density	Comments
ESCO	*Acanthaster planci*	asteroid	Ricketts	1940		
ESCO	*Amphiaster insignis*	asteroid	Dungan	1984		
CHIV	*Asteropsis carinifera*	asteroid	Urnes	2017		
ESCO	*Asteropsis carinifera*	asteroid	Urnes	2017		
COLO	*Astrometis sertulifera*	asteroid	Brusca	1976		
CHIV	*Astrometis sertulifera*	asteroid	Brusca	1976		
ESCO	*Astrometis sertulifera*	asteroid	Urnes	2017		
BOLA	*Astropecten armatus*	asteroid	Ricketts	1940		
BOLA	*Echinaster tenuispina*	asteroid	Ricketts	1940		
COLO	*Echinaster tenuispina*	asteroid	Brusca	1976		recorded as *Othilia tenuispina*
COLO	*Echinaster tenuispina*	asteroid	Dungan	1980		recorded as *Othilia tenuispina*
PUER	*Echinaster tenuispina*	asteroid	Urnes	2017		
WILL	*Echinaster tenuispina*	asteroid	Urnes	2017		
BOLA	*Echinaster tenuispina*	asteroid	Urnes	2017		
BOLA	*Heliaster kubiniji*	asteroid	Ricketts	1940		
CONC	*Heliaster kubiniji*	asteroid	Ricketts	1940		
ESCO	*Heliaster kubiniji*	asteroid	Ricketts	1940		
COLO	*Heliaster kubiniji*	asteroid	Brusca	1976		
BOLA	*Heliaster kubiniji*	asteroid	Brusca	1980		many young
BOLA	*Heliaster kubiniji*	asteroid	Dungan	1980		under rocks
CONC	*Heliaster kubiniji*	asteroid	Dungan	1980		
BAJO	*Heliaster kubiniji*	asteroid	Dungan	1984		
ESCO	*Heliaster kubiniji*	asteroid	Dungan	1984		
COLO	*Heliaster kubiniji*	asteroid	Urnes	2017	0.01	
PUER	*Heliaster kubiniji*	asteroid	Urnes	2017	0.04	
WILL	*Heliaster kubiniji*	asteroid	Urnes	2017	0.59	
BOLA	*Heliaster kubiniji*	asteroid	Urnes	2017	0.40	
CHIV	*Heliaster kubiniji*	asteroid	Urnes	2017	0.47	
BAJO	*Heliaster kubiniji*	asteroid	Urnes	2017	0.27	
ESCO	*Heliaster kubiniji*	asteroid	Urnes	2017	1.92	
ESCO	*Leiaster teres*	asteroid	Ricketts	1944		
BOLA	*Linckia columbiae*	asteroid	Ricketts	1940		
CONC	*Luidia phragma*	asteroid	Ricketts	1940		
BOLA	*Mithrodia bradleyi*	asteroid	Ricketts	1940		
ESCO	*Mithrodia bradleyi*	asteroid	Ricketts	1940		
CHIV	*Mithrodia bradleyi*	asteroid	Brusca	1984		
BAJO	*Mithrodia bradleyi*	asteroid	Urnes	2017		
ESCO	*Mithrodia bradleyi*	asteroid	Urnes	2017		
ESCO	*Nidorellia armata*	asteroid	Ricketts	1940		

ESCO	*Nidorellia armata*	asteroid	Urnes	2017		
ESCO	*Pentaceraster cumingi*	asteroid	Ricketts	1940		
CHIV	*Pentaceraster cumingi*	asteroid	Urnes	2017		
ESCO	*Pentaceraster cumingi*	asteroid	Urnes	2017		
ESCO	*Pharia pyramidata*	asteroid	Ricketts	1940		
CHIV	*Pharia pyramidata*	asteroid	Brusca	1976		
COLO	*Pharia pyramidata*	asteroid	Dungan	1984		while snorkeling
COLO	*Pharia pyramidata*	asteroid	Urnes	2017		
PUER	*Pharia pyramidata*	asteroid	Urnes	2017		
WILL	*Pharia pyramidata*	asteroid	Urnes	2017	0.01	
BOLA	*Pharia pyramidata*	asteroid	Urnes	2017	0.003	
CHIV	*Pharia pyramidata*	asteroid	Urnes	2017	0.10	
ESCO	*Pharia pyramidata*	asteroid	Urnes	2017	0.04	
BOLA	*Phataria unifascialis*	asteroid	Ricketts	1940		
CONC	*Phataria unifascialis*	asteroid	Ricketts	1940		
ESCO	*Phataria unifascialis*	asteroid	Ricketts	1940		
CHIV	*Phataria unifascialis*	asteroid	Dungan	1980		
BAJO	*Phataria unifascialis*	asteroid	Dungan	1984		
COLO	*Phataria unifascialis*	asteroid	Urnes	2017	0.05	
WILL	*Phataria unifascialis*	asteroid	Urnes	2017	0.07	
BOLA	*Phataria unifascialis*	asteroid	Urnes	2017		
CHIV	*Phataria unifascialis*	asteroid	Urnes	2017	0.13	
BAJO	*Phataria unifascialis*	asteroid	Urnes	2017		
ESCO	*Euapta godeffroyi*	holoth	Ricketts	1940		
ESCO	*Euapta godeffroyi*	holoth	Urnes	2017		
ESCO	*Holothuria arenicola*	holoth	Ricketts	1940		
CHIV	*Holothuria arenicola*	holoth	Brusca	1976		
PUER	*Holothuria arenicola*	holoth	Urnes	2017		
CONC	*Holothuria arenicola*	holoth	Urnes	2017		
ESCO	*Holothuria impatiens*	holoth	Ricketts	1940		
WILL	*Holothuria impatiens*	holoth	Urnes	2017		
BOLA	*Holothuria lubrica*	holoth	Ricketts	1940		
ESCO	*Holothuria lubrica*	holoth	Ricketts	1940		
CHIV	*Holothuria lubrica*	holoth	Brusca	1976		
SANF	*Holothuria lubrica*	holoth	Dungan	1980		
BOLA	*Holothuria lubrica*	holoth	Dungan	1980		
BOLA	*Holothuria lubrica*	holoth	Brusca	1981		
WILL	*Holothuria lubrica*	holoth	Dungan	1984		
CHIV	*Holothuria lubrica*	holoth	Brusca	1984		
SANF	*Holothuria lubrica*	holoth	Urnes	2017	0.01	
COLO	*Holothuria lubrica*	holoth	Urnes	2017	0.09	
PUER	*Holothuria lubrica*	holoth	Urnes	2017	1.49	
WILL	*Holothuria lubrica*	holoth	Urnes	2017	15.46	
BOLA	*Holothuria lubrica*	holoth	Urnes	2017		
BOLA	*Holothuria lubrica*	holoth	Urnes	2017	11.61	

CHIV	*Holothuria lubrica*	holoth	Urnes	2017	6.4	
CONC	*Holothuria lubrica*	holoth	Urnes	2017	2.7	
BAJO	*Holothuria lubrica*	holoth	Urnes	2017	10.67	
ESCO	*Holothuria lubrica*	holoth	Urnes	2017	1.25	
ESCO	*Holothuria rigida*	holoth	Ricketts	1940		
ESCO	*Isostichopus fuscus*	holoth	Ricketts	1940		
CHIV	*Isostichopus fuscus*	holoth	Dungan	1980		
CHIV	*Isostichopus fuscus*	holoth	Brusca	1984		
WILL	*Isostichopus fuscus*	holoth	Urnes	2017		
CHIV	*Isostichopus fuscus*	holoth	Urnes	2017		
ESCO	*Isostichopus fuscus*	holoth	Urnes	2017		
CHIV	*Neothyone gibbosa*	holoth	Brusca	1984		subtidal
ESCO	*Aplysia californica*	mollusk	Ricketts	1940		
BOLA	*Aplysia californica*	mollusk	Brusca	1979		many young
ESCO	*Aplysia californica*	mollusk	Urnes	2017		
COLO	*Aplysia sp.*	mollusk	Brusca	1979		breeding and depositing egg masses
CONC	*Hexaplex eurythrostomus*	mollusk	Ricketts	1940		
ESCO	*Hexaplex eurythrostomus*	mollusk	Ricketts	1940		
COLO	*Hexaplex eurythrostomus*	mollusk	Dungan	1980		
CONC	*Hexaplex eurythrostomus*	mollusk	Dungan	1980		
SANF	*Hexaplex eurythrostomus*	mollusk	Urnes	2017	0.01	
COLO	*Hexaplex eurythrostomus*	mollusk	Urnes	2017	0.07	
BOLA	*Hexaplex eurythrostomus*	mollusk	Urnes	2017		
SANF	*Hexaplex nigritus*	mollusk	Brusca	1975		Abundant
COLO	*Hexaplex nigritus*	mollusk	Dungan	1980		
CONC	*Hexaplex nigritus*	mollusk	Dungan	1980		
SANF	*Hexaplex nigritus*	mollusk	Dungan	1984		common, mostly young <75mm
PUER	*Hexaplex nigritus*	mollusk	Dungan	1984	0.05	
SANF	*Hexaplex nigritus*	mollusk	Urnes	2017	0.28	
COLO	*Hexaplex nigritus*	mollusk	Urnes	2017	0.03	
BOLA	*Octopus bimaculatus*	mollusk	Ricketts	1940		
WILL	*Octopus bimaculatus*	mollusk	Urnes	2017		
SANF	*Octopus fitchi*	mollusk	Urnes	2017	0.12	
COLO	*Octopus fitchi*	mollusk	Urnes	2017	0.25	
PUER	*Octopus fitchi*	mollusk	Urnes	2017	0.13	
WILL	*Octopus fitchi*	mollusk	Urnes	2017	0.26	
BOLA	*Octopus sp.*	mollusk	Ricketts	1940		
CONC	*Turbo fluctulosa*	mollusk	Dungan	1980		
WILL	*Turbo fluctulosa*	mollusk	Dungan	1984		
SANF	*Turbo fluctulosa*	mollusk	Urnes	2017	0.02	
COLO	*Turbo fluctulosa*	mollusk	Urnes	2017	0.43	
PUER	*Turbo fluctulosa*	mollusk	Urnes	2017	0.06	

WILL	*Turbo fluctulosa*	mollusk	Urnes	2017	1.61	
BOLA	*Turbo fluctulosa*	mollusk	Urnes	2017	1.60	
BOLA	*Turbo fluctuosa*	mollusk	Dungan	1980		abundant
BOLA	*Turbo fluctuosa*	mollusk	Urnes	2017		
CHIV	*Ophiactis simplex*	ophio	Brusca	1976		
BOLA	*Ophiocoma aethiops*	ophio	Ricketts	1940		
CHIV	*Ophiocoma aethiops*	ophio	Brusca	1976		
BAJO	*Ophiocoma aethiops*	ophio	Urnes	2017		
COLO	*Ophiocoma alexandri*	ophio	Brusca	1976		
WILL	*Ophiocoma alexandri*	ophio	Urnes	2017		
SANF	*Ophioderma panamense*	ophio	Brusca	1975		
COLO	*Ophioderma panamense*	ophio	Brusca	1976		
CHIV	*Ophioderma panamense*	ophio	Brusca	1976		
SANF	*Ophioderma panamense*	ophio	Urnes	2017		
CHIV	*Ophioderma panamense*	ophio	Urnes	2017		
BAJO	*Ophioderma panamense*	ophio	Urnes	2017		
ESCO	*Ophioderma panamense*	ophio	Urnes	2017		
BOLA	*Ophioderma teres*	ophio	Ricketts	1940		
CONC	*Ophioderma teres*	ophio	Ricketts	1940		
ESCO	*Ophioderma teres*	ophio	Ricketts	1940		
BOLA	*Ophioderma teres*	ophio	Dungan	1980		
BOLA	*Ophioderma teres*	ophio	Urnes	2017		
BOLA	*Ophionereis annulata*	ophio	Ricketts	1940		
CONC	*Ophionereis annulata*	ophio	Ricketts	1940		
SANF	*Ophionereis annulata*	ophio	Brusca	1975		
CHIV	*Ophionereis annulata*	ophio	Brusca	1976		
COLO	*Ophionereis annulata*	ophio	Dungan	1980		
BOLA	*Ophionereis annulata*	ophio	Dungan	1980		
PUER	*Ophionereis annulata*	ophio	Urnes	2017		
CONC	*Ophiothrix spiculata*	ophio	Ricketts	1940		
ESCO	*Ophiothrix spiculata*	ophio	Ricketts	1946		
COLO	*Ophiothrix spiculata*	ophio	Brusca	1976		
CHIV	*Ophiothrix spiculata*	ophio	Brusca	1976		
BOLA	*Ophiothrix spiculata*	ophio	Dungan	1980		
BOLA	*Arbacia stellata*	urchin	Ricketts	1940		
CHIV	*Arbacia stellata*	urchin	Brusca	1976		
BOLA	*Arbacia stellata*	urchin	Dungan	1980		
CHIV	*Arbacia stellata*	urchin	Dungan	1980	5	
BOLA	*Arbacia stellata*	urchin	Urnes	2017		
CHIV	*Arbacia stellata*	urchin	Urnes	2017		
ESCO	*Arbacia stellata*	urchin	Urnes	2017		
CHIV	*Diadema mexicanum*	urchin	Brusca	1984		
BAJO	*Diadema mexicanum*	urchin	Dungan	1984		
CHIV	*Diadema mexicanum*	urchin	Urnes	2017		
ESCO	*Diadema mexicanum*	urchin	Urnes	2017		

CHIV	*Echinometra vanbrunti*	urchin	Dungan	1980	5	
WILL	*Echinometra vanbrunti*	urchin	Dungan	1984		Common
CHIV	*Echinometra vanbrunti*	urchin	Brusca	1984		
BAJO	*Echinometra vanbrunti*	urchin	Dungan	1984		
ESCO	*Echinometra vanbrunti*	urchin	Dungan	1984		
WILL	*Echinometra vanbrunti*	urchin	Urnes	2017		
BOLA	*Echinometra vanbrunti*	urchin	Urnes	2017	0.08	
CHIV	*Echinometra vanbrunti*	urchin	Urnes	2017	0.13	
BAJO	*Echinometra vanbrunti*	urchin	Urnes	2017		
ESCO	*Echinometra vanbrunti*	urchin	Urnes	2017	0.46	
BOLA	*Eucidaris thouarsii*	urchin	Ricketts	1940		many young
CONC	*Eucidaris thouarsii*	urchin	Ricketts	1940		
ESCO	*Eucidaris thouarsii*	urchin	Ricketts	1940		
WILL	*Eucidaris thouarsii*	urchin	Dungan	1984		Common
CHIV	*Eucidaris thouarsii*	urchin	Brusca	1984		
BAJO	*Eucidaris thouarsii*	urchin	Dungan	1984		
ESCO	*Eucidaris thouarsii*	urchin	Dungan	1984		
PUER	*Eucidaris thouarsii*	urchin	Urnes	2017		
WILL	*Eucidaris thouarsii*	urchin	Urnes	2017	0.06	
BOLA	*Eucidaris thouarsii*	urchin	Urnes	2017	0.03	
CHIV	*Eucidaris thouarsii*	urchin	Urnes	2017	0.43	
ESCO	*Eucidaris thouarsii*	urchin	Urnes	2017	0.08	
CHIV	*Toxopneustes roseus*	urchin	Urnes	2017		
ESCO	*Toxopneustes roseus*	urchin	Urnes	2017		
CHIV	*Tripneustes depressus*	urchin	Urnes	2017		
BAJO	*Tripneustes depressus*	urchin	Urnes	2017		