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Historical change in marine animal populations and coastal ecosystems in the
Caribbean and Florida Keys

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

in

Marine Biology

by

Loren Elizabeth McClenachan

Committee in charge:

Jeremy Jackson, Chair
Paul Dayton
Naomi Oreskes
Stuart Sandin
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Daniel Vickers

2009

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University of California, San Diego

2009

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monk seal. Proceedings of the Royal Society B-Biological Sciences 275:1351-1358.

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Fields of Study

- Coral reef ecology
- Historical ecology
- Human impacts on marine systems
- Marine fisheries management
- Extinction

ABSTRACT OF THE DISSERTATION

Historical change in marine animal populations and coastal ecosystems in the
Caribbean and Florida Keys

by

Loren Elizabeth McClenachan

Doctor of Philosophy in Marine Biology

University of California, San Diego, 2009

Professor Jeremy Jackson, Chair

Coral reefs are among the most degraded ecosystems worldwide, with declines in coral cover in excess of 80% and overfishing prevalent on the majority of reefs. Human activities have affected coral reef ecosystems for at least 1,000 years, and overfishing is typically the earliest human activity to impact coral reef environments. Thus, historical analyses of the effects of historical fishing are essential to assess changes that occurred before modern observations were made.

My thesis assesses long-term change in a variety of species and ecosystems in the Caribbean region. I compiled documents from historical archives and other repositories, extracted ecological data, and developed methods to analyze these data. Across the wider Caribbean region, I found declines of more than 99% in green

(*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtle populations and a severe reduction in nesting habitat. Next, I estimated historical population sizes for the Caribbean monk seal (*Monachus tropicalis*) to be 233,000 - 338,000 individuals, and determined that the prey biomass remaining in Caribbean reefs is insufficient to feed historical populations. I then focused on the sponge fishery in the northern Caribbean and determined that the population crash in several species of marine sponges (*Spongia* spp., *Hippospongia* spp.) in the first decades of the twentieth century was likely related to overfishing, and precipitated broader ecological and social changes.

In the Florida Keys, I quantified declines of large bodied fish using historical photographs, and determined that the largest fish are 50% shorter today than fifty years ago. I then analyzed historical fishing records for the goliath grouper (*Epinephelus itajara*) and determined that this species was depleted several decades earlier than previously thought. Next, I assessed change for a variety of coral reef organisms over the last several centuries and determined that declines occurred at relatively low human population densities, and did not follow a pattern of fishing down the food web as has occurred in temperate and oceanic environments. Finally, I assessed historical reasons for the continuation of recreational fishing despite the severe degradation that has occurred. These results have conservation implications both at the species and ecological level.

CHAPTER 1: Introduction

INTRODUCTION

Ocean ecosystems are in a state of crisis. Globally, three-quarters of fisheries are overexploited (Botsford et al. 1997), 35% of the world's mangrove forests have been destroyed (Valiela et al. 2001), and 80% of Caribbean coral reef coral cover has been lost in the last quarter century (Gardner et al. 2003). Most observed declines have occurred in the past half-century, but human activities have impacted watersheds, estuaries, and oceans for at least a thousand years (Jackson et al. 2001, Lotze et al. 2006, Roberts 2007, Dulvy et al. in press).

Scientists have systematically underestimated long-term changes for several reasons. Data are scarce from before scientific monitoring of fisheries and the advent of SCUBA-supported research (Dayton et al. 1998, Jackson et al. 2001); people typically consider changes that have occurred only in their own lifetimes (Pauly 1995); and researchers simply have not looked for the information necessary to assess population decline or extinction in the marine environment (Dulvy et al. 2003). Information that can be used to assess long-term ecological changes is often found in non-traditional data sources, such as fisheries logbooks, trade records, photographs, and historical descriptions. These data are often difficult to collect and in unfamiliar formats, but when they have been compiled and analyzed, researchers have discovered population declines frequently exceeding 90% (Myers and Worm 2003, Baum and Myers 2004, Ferretti et al. 2008, Rosenberg et al. 2006, Jackson 2008) and ecological

change across a wide variety of ocean ecosystems (Dayton et al. 1998, Jackson et al. 2001).

To date, most historical analyses of ecological change have addressed changes in temperate and pelagic ecosystems (Myers and Worm 2003, Lotze and Milewski 2004, Lotze 2005, Rosenberg et al. 2006). Analysis of long-term change in tropical coastal ecosystems has lagged for several reasons. First, archival materials in tropical regions are difficult to collect and are often in poor condition. The tropics have humid climates and periodic hurricane activity, neither of which is conducive to long-term preservation of written materials. Nations in the tropics frequently have long colonial histories and are often politically subdivided into small areas, so historical source materials are scattered in many locations and maintained by a diversity of national archives. For example, documents related to marine exploitation in the Caribbean exist in archives across Europe, North America, as well as the Caribbean, slowing data collection. Second, tropical coastal fisheries are usually multi-species and have a large subsistence component, so accurately discerning change for any one species is difficult. Thus, analysis of change requires an ecosystem approach and the inclusion of a variety of unusual information sources. Finally, historical ecology in tropical regions has been slow to develop because many scientists have undertaken research in their home countries, and the majority of historical marine ecologists to date have been from Europe, the United States, and Canada.

My thesis attempts to improve our knowledge of historical change in tropical marine environments by assessing long-term change in a variety of species and

ecosystems in the Caribbean region. I take two separate but complementary approaches to studying ecological change in tropical America. First, I analyze population change, range restriction, and ecological consequences of fishing on a species-level across large portions of the exploited species' range. This first, single species component of my thesis addresses two questions:

- How did populations of marine species respond to overexploitation?
- When these species are extant, how can conservation efforts better reflect historical patterns?

I conducted three separate analyses of species level change over large geographic areas, for the Caribbean green and hawksbill turtles (Chapter 2), the Caribbean monk seal (Chapter 3), and the Florida population of the goliath grouper (Chapter 6).

My second approach is to address multi-species change, and to incorporate historical analyses into my analyses of ecological change in coral reef and associated ecosystems. I focus on the Florida Keys for these analyses. Broadly, the questions I address are:

- What were the ecological consequences of multiple fisheries in tropical coastal ecosystems?
- How have social developments influenced fishing and environmental change?

Four of my thesis chapters address multi-species changes and social aspects of overfishing. I conducted an analysis of the sponge fishery in Florida in the late nineteenth and early twentieth centuries (Chapter 4), an analysis of shifts in the largest

fish caught in Key West from the 1950s to the present (Chapter 5), an overall synthesis of ecological change across all trophic levels in the Florida Keys region since the first reliable records were kept in the sixteenth century (Chapter 7), and a historical analysis of the reasons that sportfishing continues despite the loss of the largest reef fish (Chapter 8).

Together these seven analyses describe declines of more than 99% in several species of large marine vertebrates across much of the Caribbean region (Chapters 2 and 3); an early crash in populations of marine sponges that likely precipitated broader ecological and social changes in the early twentieth century (Chapter 4); shifts from large bodied to smaller bodied fish in the Florida Keys (Chapter 5); declines in populations of the goliath grouper several decades earlier than previously thought in south Florida (Chapter 6); declines across all of trophic levels of organisms over the last several centuries in Florida Keys's coral reef ecosystems (Chapter 7); and several historical reasons for the persistence of sportfishing despite this severe environmental decline in the Florida Keys (Chapter 8).

The conservation implications of these papers are two-fold. First, collecting nontraditional data and quantifying the population change that occurred before the onset of fisheries and ecological data provides tangible information that can be used in conservation assessments of endangered species, such as the green turtle and goliath grouper (Chapters 2 and 6). Each of these species was assessed without adequate long-term data, and it is my hope that revisions of their conservation status assessments will include the historical data presented here. Second, assessing ecological change over

long time scales provides evidence that entire ecosystems have been degraded, including species that provide prey and habitat structure for historically exploited marine predators (Chapters 3, 6, and 7). Thus, the recovery of historically exploited species requires broader ecosystem protection. Overall, I envision that these analyses will be used to increase and maintain protection of tropical marine ecosystems, and that the methods developed therein will be used to assess long-term ecological change in a variety of species and ecosystems around the world.



Figure 1. Conducting archival research in the United Kingdom Hydrographic office. Photo by Morgan Richie.

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CHAPTER 2: Conservation implications of historic sea turtle nesting beach loss

RESEARCH COMMUNICATIONS RESEARCH COMMUNICATIONS

Conservation implications of historic sea turtle nesting beach loss

Loren McClenahan^{1*}, Jeremy BC Jackson^{2,3}, and Marah JH Newman¹

LPopulations of endangered Caribbean sea turtles are far more depleted than realized because current conservation assessments do not reflect historic nesting data. We used historical sources to analyze changes in the numbers of nesting populations and population sizes for green and hawksbill turtles on all known nesting beaches in the Caribbean over the past millennium. We present the first maps of historic nesting populations, which provide the basis for an objective measure of changes in distribution and abundance. Our results indicate that 20% of historic nesting sites have been lost entirely and 50% of the remaining nesting sites have been reduced to dangerously low populations. Recent conservation efforts have resulted in large population increases at several nesting sites, but loss of widespread nesting throughout the Caribbean and reductions in the Caribbean-wide population since human hunting began indicate that Caribbean turtles are far from recovered. Focusing attention on a small number of nesting populations is a risk-prone strategy; conservation programs should instead broaden their scope to protect both large and small nesting populations throughout the Caribbean.

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By the beginning of the 20th century, green turtles (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) had been decimated by human hunting, making both species globally endangered (Meylan and Donnelly 1999; Seminoff 2002). These species filled unique ecological roles in seagrass and coral reef ecosystems, and their removal diminished the complexity and stability of the food web, as well as the intensity of biological disturbance on seagrass beds and coral reefs (Jackson 1997; Bjorndal and Jackson 2003). Population declines and the ensuing ecological changes occurred over many centuries; without historic data, the magnitude of change has been underestimated, a phenomenon known as the shifting baselines syndrome (Pauly 1995). Historic reductions in sea turtle populations have been recognized (Jackson 1997; Bjorndal and Jackson 2003), but pan-regional changes in numbers and distribution of nesting populations have not been systematically reviewed. To that end, we compiled a comprehensive list of historic nesting beaches for green and hawksbill turtles in the Caribbean and used the number of nesting sites to refine previous estimates of historic population size and the ecological consequences of loss.

Historical and archeological data provide a wealth of information that can be used to estimate early geographic ranges and population sizes of easily visible species such

as sea turtles that nest on land and whose high economic value stimulated exceptional records of their exploitation. For hundreds of years, green turtles provided nourishment for European colonists and African slaves on Caribbean sugar plantations. Hawksbill turtles were prized for their shells, which were fashioned into elaborate hair combs and other ornaments and distributed through carefully regulated trade networks (Roberts 1827; Dampier 1968). Both species of turtle were especially vulnerable to hunting during nesting (Roberts 1827; Dampier 1968; Rebel 1974; Jackson 1997). Early descriptions provide locations of nesting beaches, the magnitude of the population, sizes of adults found, and accounts of the hunt.

We compiled data on nesting beach location, density of turtles, and human exploitation summarized in trade records from 163 historic sources in four historic time periods for 20 regions of the Caribbean (WebTable 1). We mapped historic nesting beaches for green and hawksbill turtles, and used density descriptions and harvest data to categorize these sites as “major” and “minor” nesting sites (Figure 1; WebTable 2). Next, we calculated a range of Caribbean-wide population sizes for green and hawksbill turtles by estimating the number of adult turtles supported by one particularly well-documented major nesting site for each species and extrapolating across the region, using the total number of major and minor historic nesting beaches (WebTable 3). Two types of sources provided information about the size of populations: (1) observations from 20th century nesting beaches, and (2) historic harvest data. (Full materials and methods are available as Web-only material.) Finally, we refined calculations of historic turtle consumption in order to

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describe the ecological role of turtles in tropical marine ecosystems and the long-term effects of their removal.

■ Historic nesting beaches and population size

Historically, large nesting populations were found on beaches throughout the wider Caribbean. We found evidence for 59 historic green turtle nesting beaches, nine of which were considered to be major nesting populations based on density descriptions and harvest data (Figure 1a; WebTable 2). Green turtles in the Cayman Islands, for example, were found in "infinite numbers"; up to 50 nesting females could be taken in less than 3 hours (de Rochefort 1666). On the Mosquito Coast of Nicaragua there were "inexhaustible supplies of the finest green turtle" (Roberts 1827) and settlers "turned so many that [they] were obliged to desist" (Williams 1969). For hawksbill turtles, we located 55 historic nesting beaches, seven of which supported major historic populations (Figure 1b; WebTable 2). Major nesting beaches included the island of Roncador, off the Nicaraguan coast, which was "famous for the number of its turtles...the shore seemed black with turtles" (Squier 1865), and Chiriquí, Panama, which was considered to be the "most important nesting aggregation in the Caribbean" (Carr 1956).

We used these geographic nesting data to calculate a range of population sizes, based on quantitative modern nesting data and historic export data. For green turtles, observations from 20th century nesting in Tortuguero, Costa Rica (Troëng and Rankin 2005) indicate that this nesting site supported an average of 130 500 adults (WebTable 3). We first assumed that each of the nine historic major nesting sites supported populations as large as this recent Tortuguero population and that the remaining 50 minor nesting aggregations were each 10% of that value. These calculations yield an estimated historic population of 1.8 million adult green turtles (WebTable 3). Large as this number may seem compared with modern abundances of less than 300 000 (Seminooff 2002), historic hunting data indicate that the 17th century Cayman Island green turtle population alone was approximately 6.5 million adults (Jackson 1997; WebTable 3). Assuming that each of the nine major nesting beach populations was as large as the historic Cayman Island population and the 50 minor nesting aggregations were only 10% of this size yields a historic population for the Caribbean of around 91 million adult green turtles (WebTable 3).

For hawksbill turtles, observations of 20th century nesting at Chiriquí Beach, Panama (Meylan and Donnelly 1999), indicate that this nesting site supported 135 000 adults in the 1950s (WebTable 3). Assuming that the seven major nesting sites each had abundances comparable to that of Chiriquí, and that each of the remaining 48 minor nesting sites had populations of only 10% of this number, the total Caribbean population was 1.6 million adult hawksbill turtles (WebTable 3), compared to fewer than 30 000 today (Bjorndal and Jackson

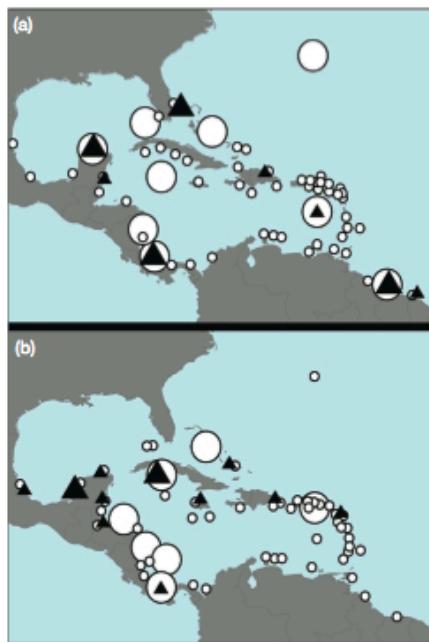


Figure 1. Nesting beach loss in Caribbean sea turtles. (a) Green turtles and (b) hawksbill turtles have lost most of their historic nesting sites (circles) and all major nesting sites (large circles) have been reduced or eliminated. Modern nesting beaches with >500 nesting females (large triangles) and 100–500 (small triangles) are mapped. All modern and historic nesting data are listed in WebTable 2.

2003). However, historic export data from the 19th century Bahamian fishery (Northcroft 1900) provide an estimate of 936 600 adults from just this region (WebTable 3). Extrapolating across the seven major and 48 minor nesting beaches gives a historic population estimate of 11 million hawksbill turtles in the Caribbean region (WebTable 3).

Our green turtle population estimate based on historic nesting data is more than two times greater than the 33–39 million green turtles estimated by Jackson (1997), and our hawksbill turtle calculation is 20 times greater than the extremely conservative estimate of 540 000 adult hawksbill turtles by Bjorndal and Jackson (2003). Our estimates may be high, as they assume that all major nesting sites were as large as the Bahamian and Cayman Island populations. Furthermore, some non-nesting turtles may have been mistaken for nesting females, potentially increasing the estimated number of nesting beaches. Because they are based on conservative and offi-

cially recorded estimates of catch, however, our estimates could also be too low. For example, Cayman hunting data do not reflect exploitation by Spanish, French, Dutch, and other English settlers and pirates in the Caribbean, who did not report their catch (eg Jackson 1924). While extrapolations from anecdotal historic evidence will never be precise, using true historic data provides an accurate assessment of the order of magnitude of change that cannot be determined from traditional ecological data, particularly for severely hunted populations.

■ Population declines and nesting beach loss

Our calculations based on historic export data show that modern populations of green and hawksbill turtles are 0.33% and 0.27% of their historic numbers, respectively. These calculations assume modern populations of 300 000 green and 30 000 hawksbill turtles. Such staggering declines in abundance have been compounded by the elimination of entire nesting populations that are extremely unlikely to become re-established (Seminoff 2002). The loss of even a single nesting site makes a permanent, irreversible dent in the sea turtle population, but loss of nesting beaches has not been quantified, nor used as a measure of population change across the Caribbean region. Our data indicate that historic hunting completely eliminated at least 17 green turtle and seven hawksbill nesting sites, including three major nesting beaches: Bermuda; Moskito Coast, Nicaragua; and Dry Tortugas, US (WebTable 2). Hunting also severely thinned turtles at the remaining sites, so that half of modern nesting populations have an uncertain future. So-called "nesting aggregations" are pitifully small, often consisting of females that nest singly. Such small sites include the once great Cayman Island green turtle rookery. Today, 55% of green turtle and 44% of hawksbill nesting beaches host fewer than 10 nesting females, or are described as having only rare nesting (Figure 2; WebTable 2). Historic data clearly show that each of these nesting sites supported large populations in the past.

■ Ecosystem consequences

The severe reduction of turtle numbers is of concern not only because of the turtles themselves, but also with regard to their previously important roles as ecosystem engineers in Caribbean ecosystems (Bjorndal and Jackson 2003). Green turtles feed primarily on turtle grass (*Thalassia testudinum*; Thayer *et al.* 1982) and hawksbill turtles have a unique dietary preference for marine sponges (Leon and Bjorndal 2002). Both turtle grass and sponges are important habitat-structuring species throughout the region. We estimated total food intake of historic populations of green and hawksbill turtles (WebTables 3 and 4). Ninety-one million green turtles consumed between 11 and 22 million metric tons dry mass (DM) of turtle grass, which amounts to 86% of the total area and up to 45% of the

annual productivity of seagrass beds (WebTables 3 and 4). Eleven million hawksbill turtles consumed between 0.9 million and 2.0 million metric tons DM of sponges annually, or 83% of the biomass and annual growth of sponges (WebTables 3 and 4). The geographic scale at which historic populations of turtles disturbed coral reef and seagrass communities is inconsistent with modern observations of seagrass beds that grow virtually unchecked by grazing and of coral reefs where few large predators remain. Our calculations indicate that today's green and hawksbill turtle populations consume just 0.1% of the area of Caribbean seagrass and reef sponges, respectively.

In the 1830s, the great naturalist, John J Audubon described the seagrass beds of the Dry Tortugas as "cut near the roots" by vast numbers of grazing green turtles (Audubon 1926), an ecological state also described by William Dampier in the 1680s (Dampier 1968). Our calculations agree with these descriptions (WebTable 4). Ninety-one million grazing green turtles left behind large patches of actively growing seagrass clipped down to the blade-sheath junction (Thayer *et al.* 1982). The ecological extinction of green turtles transformed an ecosystem with diverse species of seagrasses dominated by large herbivores into a detritus-based ecosystem dominated by overgrown monocultures of *T. testudinum*, with two important conservation implications.

First, the annual removal of 86% of mature seagrass blades would have greatly inhibited the spread of epiphytic organisms that characterize modern seagrass beds, and thus preempted the spread of seagrass wasting disease. The disease-causing parasitic protist, *Labyrinthula*, attaches preferentially to mature seagrass blades, from which it colonizes actively growing seagrass stems (Bowles and Bell 2004). Wasting disease is now widespread and is unlikely to disappear unless grazing is reintroduced on an appropriately large geographic scale, even if other factors such as excess nutrients also play a role in the spread of the disease (Pandolfi *et al.* 2005).

Second, in contrast to green turtles, grazing fishes and sea urchins lack the microbial symbionts that metabolize cellulose, which comprises most of the carbon in turtle grass blades. Their waste, as well as unconsumed turtle grass, is largely buried in sediments (Thayer *et al.* 1982), where it is no longer available to animals in the grazing food chain. The decline of green turtles has therefore resulted in a loss of productivity available to the animal food chain – including commercially exploited reef fishes – and therefore amounts to a reduction in protein-rich food available for Caribbean people.

Similarly, on reefs, historic consumption of sponges by hawksbill turtles was up to 800 times higher than that of modern populations (WebTable 4); this has implications for the sponge community composition and the relative abundances of sponges and reef corals (Bjorndal and Jackson 2003). Hawksbill turtles preferentially feed on non-toxic sponges when they are available, but can survive on a mix of toxic species (Leon and Bjorndal 2002).

Thus, as turtles declined in abundance, the relative quantities of toxic sponges that each hawksbill turtle consumed should also have decreased. Historical data support this hypothesis. Observations from the 17th through the 20th century indicate that toxicity of hawksbill turtle meat for human consumption has decreased over time (Table 1). This unanticipated result provides another independent measure of the extreme reduction in hawksbill turtle populations, as well as indirect evidence for changes in Caribbean benthic ecosystems.

The role of turtles as major agents of landscape-scale patterns of disturbance has been questioned, based on small-scale experimental studies that attempt to test the effects of turtle grazing in tiny plots (eg Bowles and Bell 2004). Such experiments cannot mimic the intensity of disturbance of tens of millions of turtles across the entire Caribbean any more than clipping a few small quadrats of prairie grass could possibly recreate the effects of 30 million American bison on the Great Plains (Isenberg 2000). Our historical data indicate that centuries ago, much of the mobile animal biomass in the Caribbean was concentrated in the bodies of large animals, an ecological possibility supported by modern surveys on isolated and protected reefs (Friedlander and DeMartini 2002). These data strongly suggest that the extirpation of large animals was the first step in dismantling Caribbean marine ecosystems, and circumstantial evidence – such as recent outbreaks of seagrass disease and coral overgrowth – supports the inference that breakdown in structural habitat magnified the loss of large animals. Clearly, successful conservation and management of turtles is an essential component in achieving ecosystem restoration.

■ Good news for sea turtles?

The protection of nesting beaches since the 1970s has resulted in extraordinary local population increases in short periods of time, particularly among green turtles (Hays 2004; Troëng and Rankin 2005). These encouraging results have led some to question whether green turtles are endangered within the Caribbean and greater Atlantic region (Broderick *et al.* 2006). Patterns in modern nesting data suggest that nesting beach conservation efforts have indeed been highly successful in reversing downward population

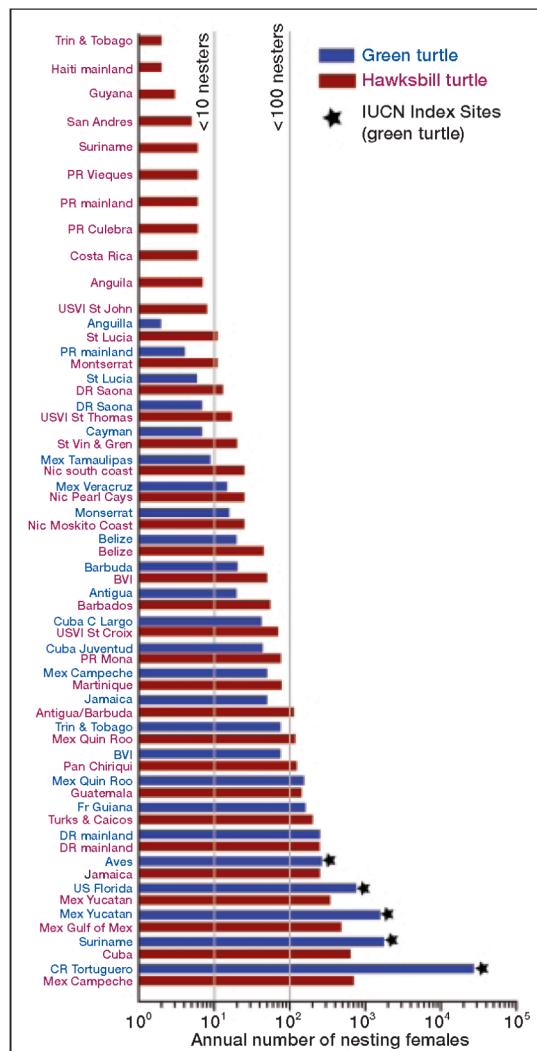


Figure 2. The number of females nesting annually on modern sites is very small and unevenly distributed, with 10% of sites hosting 90–95% of nesters. Large sites are the focus of conservation assessments such as the IUCN Red List Global Status Assessment for green turtles. The figure does not include 29 nesting sites for which reliable quantitative data do not exist; 24 of these sites are described as having rare, scattered, or infrequent nesting. All modern nesting data are listed in WebTable 2.

Table 1. Changes in hawksbill turtle toxicity

Date	Location	Observations of hawksbill turtle toxicity
1684	Panama	"Yet these Hawks-bills, in some places are unwholesome, causing them that eat them to purge and vomit excessively..." (Dampier 1684).
1760	French Caribbean	"...it is dangerous to eat of [the hawksbill's] flesh, which, though fat and delicious, is of so purgative a quality, that unless you take but a little, or are well assured that you have nothing to fear from its activity, you may expect to see yourself covered with pimples and blotches" (Jefferys 1760).
1770s	Nicaragua	"...this kind of Tortoise is not very agreeable to the taste, nor do we eat them" (Williams 1969).
1837	Florida	"The hawksbill ... is not highly valued for food" (Williams 1837).
1884	Caribbean	"The flesh of the hawksbill turtle is comparatively valueless; indeed, in the West Indies it is said that it possesses cathartic qualities in a high degree... I have seen it in Washington several times recently, both in the markets and before several restaurants in the city" (True 1884).
1900	Bahamas	"All three kinds [green, hawksbill, loggerhead] are eaten. It is an unfortunate policy which takes them recklessly each season – though they are pleasant enough to eat and most nourishing – and thereby causes turtle to become scarcer each year" (Northcroft 1900).
1945	Jamaica	"Formerly the chief value of the Hawksbill was for the shell, which sold at high prices. Now...the market is for meat, which finds a ready market locally" (Thompson 1945).
1974	Barbados and Panama	"Fishing is mainly for hawksbill for meat and shell.... The meat and eggs of the...hawksbill turtle are taken for local consumption" (Rebel 1974).

Hawksbill turtle meat was toxic until the mid to late 19th century when it began to be eaten without health consequences. These observations suggest that hawksbill turtles ate more desirable, less toxic sponge species as the turtles became less abundant and competition for food was reduced.

trends on a few well-studied beaches. Our analysis of trends among IUCN-assessed nesting beaches (Seminoff 2002) suggests that the situation has improved in the past decade; nesting data collected since 1994 show a population increase when compared to data collected between 1980 and 1994 (Figure 3; $P = 0.011$).

Despite recent conservation achievements, declaring success would be a mistake for two reasons. First, there is very little long-term data, despite the IUCN mandate to determine nesting beach trends over three generations.

Instead, short-term data are extrapolated over longer time periods, a dangerous method considering that population trends are known to be quickly reversible (Hays 2004; Troëng and Rankin 2005; Broderick *et al.* 2006). Time series that span more than one turtle generation exhibit significant declines; data extending over more than 40 years are highly likely to show long-term declines when compared with recent data (Figure 3; difference in results, $P = 0.029$). Because of this systematic difference in results, short-term data should not be used to infer long-term change. Using modern data to speculate about historic change is certain to dangerously underestimate long-term population change.

Second, despite some success at a few sites, most nesting beaches across the region have suffered enormous, unmeasured losses and are much smaller than those used in conservation assessments. The Caribbean component of the IUCN Red List Global Assessment (Seminoff 2002) was based on data from five nesting sites, four of which have increased over the past three decades. These increases demonstrate the efficacy of nesting beach protection, but should not be mistaken for a sign of effective conservation across the region, because these sites are anomalously large and well protected. The five IUCN sites are the largest sites in the Caribbean. Annual aggregations of nesting females range from about 300 at Aves Island in Venezuela to a few tens of thousands at Tortuguero, Costa Rica (Seminoff 2002; Figure 2; WebTable 2). Therefore, generalizations based solely on these few large beaches inevitably gives a false picture of the overall status of Caribbean green turtle populations. A more accurate assessment of regional change would consider trends on all known nesting beaches, despite lack of precision in numbers of nesting females on some smaller sites.

As Pauly (1995) emphasized in his landmark paper on "shifting baselines", most of the big changes to large marine vertebrate populations occurred many decades to centuries ago, prior to quantitative monitoring programs. Therefore, capturing the magnitude of these changes requires the use of historic data. Our imprecise but comprehensive historic nesting data describe changes over a

much broader geographic and temporal scale, providing a picture of regional depletion that has neither stabilized nor reversed. Of the 59 green turtle nesting beach sites documented in our study, 29% have been lost and 55% of the rest are so small that they will probably disappear if not protected. A strategy that focuses attention on a few exceptional nesting beaches runs the risk of allowing the destruction of smaller, historically important nesting beaches without realizing the losses that have occurred.

Determining conservation strategies for marine turtles over more than a few years inevitably involves a great deal of uncertainty. Important new tools, such as information gap theory, have been developed to explicitly include uncertainty when assessing possible management actions and determining the degree of risk that can be taken to achieve desired results (Ragen *et al.* 2005). The currently popular focus on nesting data from a few major nesting beaches (eg Broderick *et al.* 2006) ignores the uncertain future of nearly 90% of the remaining nesting beaches. This risk-prone strategy does not account for factors such as extreme storms, disease, or other catastrophic events.

Historically, green and hawksbill turtles were ubiquitous, abundant, and nested in high densities throughout the Caribbean. On an evolutionary timescale, widespread nesting was a risk-averse “evolutionary strategy” for the persistence of turtle species. Humans have reduced green and hawksbill turtles nesting beaches by one fifth and without proper protection, half of the remaining nesting beaches could soon be lost. Even very small nesting beaches do recover, however (Hays 2004), so that protection and scientific research funding should be extended across as many beaches as possible, especially those that were once important, but are now greatly reduced. Protecting more nesting beaches is not a politically or socially simple endeavor, but it is the only way to avoid the risk of putting all the remaining turtle eggs in a very few baskets.

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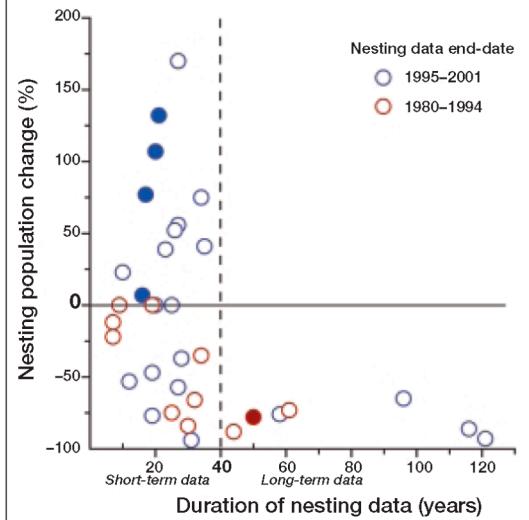


Figure 3. Shifting baselines in green turtle nesting trends and recent conservation success. Data used in the IUCN Red List Global Status Assessment for green turtles (Seminoff 2002) show very large declines in numbers of nesting females over the past century, but increases on particular nesting beaches in the last decade. Each circle represents a single Index Nesting Site used in the IUCN Assessment. All time series > 40 years (right of vertical dotted line) record population declines of 65–93%. Long-term data are significantly more likely to record population declines than shorter time series (two-tailed Fisher's exact test, $P = 0.029$). However, short-term time series ending after 1994 (blue circles) show increases when compared to similar time series ending in 1994 or before (red circles; two-tailed Fisher's exact test, $P = 0.011$). We calculated percent change using past and present nesting data (Seminoff 2002) and used the midpoint when a range of years was given. Solid circles indicate Caribbean index sites.

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CHAPTER 3: Extinction rate, historical population structure and ecological role of the Caribbean monk seal

Extinction rate, historical population structure and ecological role of the Caribbean monk seal

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The productivity and biomass of pristine coral reef ecosystems is poorly understood, particularly in the Caribbean where communities have been impacted by overfishing and multiple other stressors over centuries. Using historical data on the spatial distribution and abundance of the extinct Caribbean monk seal (*Monachus tropicalis*), this study reconstructs the population size, structure and ecological role of this once common predator within coral reef communities, and provides evidence that historical reefs supported biomasses of fishes and invertebrates up to six times greater than those found on typical modern Caribbean reefs. An estimated 233 000–338 000 monk seals were distributed among 13 colonies across the Caribbean. The biomass of reef fishes and invertebrates required to support historical seal populations was 732–1018 g m⁻² of reefs, which exceeds that found on any Caribbean reef today and is comparable with those measured in remote Pacific reefs. Quantitative estimates of historically dense monk seal colonies and their consumption rates on pristine reefs provide concrete data on the magnitude of decline in animal biomass on Caribbean coral reefs. Realistic reconstruction of these past ecosystems is critical to understanding the profound and long-lasting effect of human hunting on the functioning of coral reef ecosystems.

Keywords: historical ecology; coral reef; extinction; range restriction; monk seal; historical overfishing

1. INTRODUCTION

Historical analyses have revealed that coral reef communities are significantly altered due to human activity over the past 500 years and that historical data add a necessary dimension to the understanding of the structure and function of ecosystems without people (Jackson 1997; Jackson *et al.* 2001; Pandolfi *et al.* 2003; McClenachan *et al.* 2006). Quantitative data are often too incomplete to determine past ecosystem structure, so that historical reconstructions have been limited in either the temporal scale or the precision of the results. Historical and archaeological data for the Caribbean monk seal are unusually robust over the past 500 years, and they therefore provide an opportunity to reconstruct this component of Caribbean coral reef ecosystems.

Monk seals are large predators that feed on a variety of fishes and invertebrates, and their extinction undoubtedly contributed significantly to changes in Caribbean coral reef ecosystems. Such trophic-level omnivores are thought to have a disproportionate influence within tropical marine food webs, as their removal has consequences throughout the ecosystem (Bascompte *et al.* 2005). Thus, understanding how pristine coral reef ecosystems once functioned requires the inclusion of these formerly abundant predators. This study compiled historical and archaeological data on the extinct Caribbean monk seal and used these data to determine the location of breeding colonies, historical population size and the ecological consequences of removing this large animal from Caribbean coral reef communities.

The effects of the Caribbean monk seal's extinction in Caribbean coral reef ecosystems are clearly irreversible, but the precarious conservation status of the closely related Hawaiian and Mediterranean monk seals (*Monachus schauinslandi* and *Monachus monachus*) makes the understanding of the process and consequences of extinction important for current management regimes. Furthermore, quantifying the effects of this extinction contributes vital information necessary to understanding the various factors that have contributed to the historical degradation of Caribbean coral reef ecosystems.

(a) Historical background

The Caribbean monk seal is the only marine mammal to be driven extinct by humans in tropical seas. Hunting restricted the species' range and eliminated breeding colonies as early as the eighteenth century and the population was severely depleted at least 100 years prior to the extinction in 1952. Written accounts by Caribbean explorers and residents suggest that monk seal populations were historically widespread and abundant, so much so that particularly dense locations of seals were noted on nautical charts of the West Indies. Seals were a curiosity and source of food to early European explorers and castaways, including Christopher Columbus, who killed eight seals on the south coast of the Dominican Republic in 1494 (Colón 1959) and Juan Ponce de Leon, who killed 14 seals in the Dry Tortugas in 1512 (Herrera y Tordesillas 1725).

As settlers populated West Indian islands, they began to locate breeding colonies and hunt monk seals for oil, which was used to grease the machinery of sugar

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plantations. In the 1640s, Dutch settlers took regular sealing expeditions to Klein Curacao, a small island off the coast of Venezuela (van Grol 1934; Debrot 2000), and William Dampier, a well-known pirate and naturalist, noted in his travel diary in 1675 that both Spanish and British seal hunters frequented the Yucatan Peninsula (Dampier 1968). Jamaican plantation owners sent hunters north to the Bahamas, where they killed hundreds of seals nightly during the breeding season (Sloane 1707). Female seals were particularly vulnerable when they came onshore in winter to breed and nurse their pups (*Proceedings of the Government and Council of the Bahamas* 1722), but populations appeared to be robust. For example, after 50 years of intensive hunting, the seas of the Bahamas were said to abound with seals (Bruce 1970). By the mid-1800s, however, very few seals remained to sustain the industry (Gray 1850) and several breeding populations had been exterminated throughout the Caribbean (Allen 1880).

Naturalists and contemporary scientists began to describe the monk seal in the 1880s, so that the last six decades of the species' existence are remarkably well documented in scientific journals (e.g. Elliot 1884; Allen 1887; Townsend 1923). By this time, however, seals were found primarily on offshore atolls, so that the nineteenth-century scientists expended a large amount of effort looking for monk seals that were increasingly rare (figure 1). In fact, the species' range was severely restricted by 1900 (figure 2) and many subpopulations were probably already extinct. One naturalist observed that the few records of extant seal populations were accounts by fishermen and turtle hunters, and that the seals no longer existed in much of their former range (Allen 1880). Monk seal skeletons were valuable to natural history museums and other private collections, and, ironically, their collection by natural history enthusiasts—such as a 1911 expedition to Mexico that killed 200 seals and left few alive (Gaumer 1917)—drove the depleted population further towards extermination.

A small percentage of the total observations of seals were recorded by history, and reconstructing the historical population relies on these observations, as well as on limited archaeological data. These data are of varying usefulness. Many sources note the presence of monk seals, while a few describe breeding colonies and provide visual census data on the number of seals onshore. The geographical locations of seal observations and seal colonies through time give essential information on the rate of extinction in response to human hunting. Furthermore, existing quantitative data can be used to estimate historical population sizes within colonies and provide insights into the role played by these animals in coral reef ecosystems.

2. MATERIAL AND METHODS

(a) Estimating the number of breeding colonies

Historical data on the locations of monk seals in the Caribbean were compiled from archival and published sources, which included both historical narratives and archaeological records. In total, 140 observations were found, ranging in time from pre-European archaeological sites to the last recorded sighting in 1952. To determine which observations most probably represented breeding populations, observations were ranked according to the data

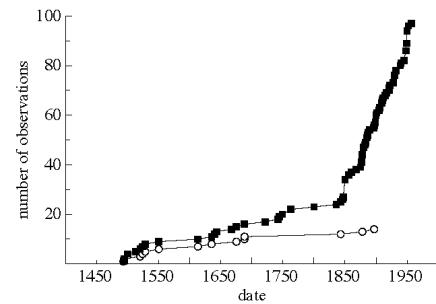


Figure 1. Monk seal discovery curve. Interest in the monk seal in the mid-nineteenth century led to increasing numbers of observations, but few new discoveries (this does not include archaeological or data taken from maps). Squares, independent observations; circles, new populations observed.

type. Eight data types were identified, in descending order of usefulness: (i) breeding colony observed, (ii) groups of seals observed on land during the breeding season, (iii) groups of seals observed on land, (iv) large abundance of seals observed, (v) presence observed, numbers unclear, (vi) seals observed in water or irregular presence noted, (vii) archaeological data, and (viii) place name or data from nautical chart.

It was assumed that only data of types 1–4 could be used to infer the existence of a breeding colony and that breeding colonies existed at a significant distance from each other. Therefore, information on maximum foraging distance and home range was used to estimate the number of independent breeding colonies from the highest quality data. While information on the Caribbean monk seal individuals' home range does not exist, data from closely related Hawaiian and Mediterranean monk seals provide insights into the probable behaviour of Caribbean seals. Hawaiian seals typically remain within 20 km of their home atolls (Stewart *et al.* 2006), but will travel to forage at distances ranging from 30 to 220 km (K. Abernathy 2006, personal communication). Estimates of the home range of Mediterranean monk seals are all less than 100 km (Berkes 1978; Guçu & Ok 2004). To estimate the number of observed breeding colonies, the locations for type 1–4 observations were mapped in a geographical information system database. Circles were used to represent the home range of a colony and first centred on each of the type 1 data locations. Additional circles were added until all type 1–4 observations were contained within a home range, with the goal being to minimize the number of circles. A radius of 150 km was used as the baseline case, but sensitivity analyses were performed using radii of 75–300 km. This implies a baseline minimum distance between groups of 300 km, with sensitivity analyses exploring distances ranging from 150 to 600 km.

The data that survived in the historical record are a small subset of the total number of actual observations throughout the five centuries of European occupation in the Caribbean. Likewise, archaeological evidence of monk seals has been uncovered in many locations, but data collection and species identification efforts have not been uniform across the Caribbean. Many colonies were probably unrecorded, and had disappeared entirely by the time organized scientific

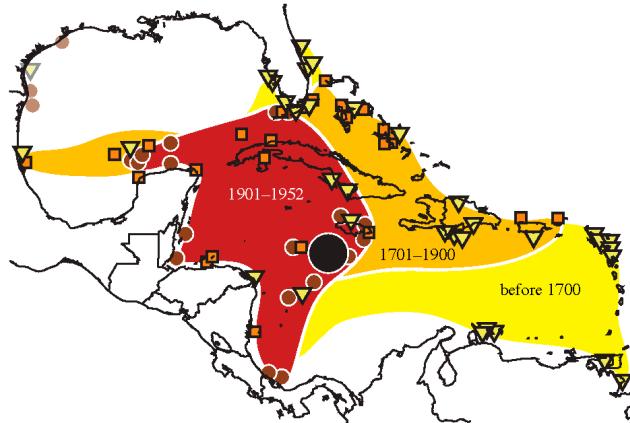


Figure 2. Total extent of the Caribbean monk seal range over time. Early observations (triangles, before the eighteenth century) were recorded as far east as the Lesser Antilles and Guyana. Observations from the eighteenth and nineteenth centuries (squares) were recorded in most of the Caribbean basin, but, by 1900, observations (small circles) were restricted to the western Caribbean and Gulf of Mexico. The most persistent population (large circle, last colony) was found on the Serrana Bank. Observations in the western Gulf of Mexico are unconfirmed.

efforts to document the population began in the late nineteenth century. Because such cryptic colonies certainly existed, observation frequency data were used to estimate the number of unseen colonies. This method follows those used for estimating total species richness from a small sample size. Non-parametric estimators were developed to estimate total species richness when observational effort data are unreliable, as they avoid making assumptions about discovery rates and instead rely on the frequency of observations of rare species (Hellmann & Fowler 1999; Chao *et al.* 2005). The number of undiscovered colonies of Caribbean monk seals was thus estimated from the frequency of observations of rare colonies, using the following equation:

$$C = D + (2n - 3)f_1/n - (n - 2)^2f_2/[n(n - 1)], \quad (2.1)$$

where C is the total number of colonies; D is the number of distinct colonies discovered in the sample; n is the sample size; and f_k is the number of colonies that are represented exactly k times in the sample.

(b) Estimating the colony-level extinction rate

The rate of extinction of colonies and the probability of survival based on colony location were determined using temporal and spatial data. For each colony, the following data were compiled: (i) the date of first observation, (ii) the dates for some number of repeated observations including the date of last observation, and (iii) the date when an observation was attempted but the colony no longer existed. As such, the dates that bound the true date of extinction exist, but the precise date of extinction was unknown. This type of data is often used in studies of nest survival for birds where observational data exist over time (Dinsmore *et al.* 2002; Rotella *et al.* 2004). The primary goal of a nest survival model is to estimate the probability that a nest will survive from one day to the next, from the time eggs are laid until the time the chicks fledge, and to determine whether variables are statistically related to that daily survival rate. Data used in

these models typically consist of the dates of first and repeated observations of the nest, with multiple days between observations. Nest survival models can be designed to specifically take account for the fact that researchers might not know the day on which the eggs were laid nor the exact day on which the nest failed (e.g. if it happens to fail between observations). For the monk seal analysis, we examine the probability that a monk seal colony will survive from one decade to the next, from the time it was first observed until the ultimate extinction of the species. This is analogous to a nest survival model where the time interval for survival is decades instead of days, colonies are only observed every few decades at best and all colonies happen to fail. The probability of survival was examined in relation to the colony's distance from the population's core area. Time was grouped into 10-year blocks and a set of *a priori* models were examined: (i) constant decadal survival rate across the entire time period, (ii) decadal survival rates constant within each century but different between centuries (sixteenth to twentieth centuries), (iii) decadal survival rates constant within each century except for the twentieth century when each decadal survival could differ, (iv) decadal survival being solely a function of distance, (v) decadal survival being a function of century and the colony's distance from the core, with the effect of distance constant across centuries and (vi) decadal survival being a function of century and distance, with the effect of distance varying by century. Models were fit using the nest survival function in the program MARK (v. 4.2, Colorado State University, Fort Collins, CO), and models were compared based on Akaike's information criterion (AICc) values.

(c) Estimating historical population size

Comprehensive, basin-wide survey data do not exist for the Caribbean monk seal, but limited quantitative data exist on population size and harvest rate for the northern Caribbean subpopulation. In 1688, hundreds of seals were killed per night (Sloane 1707); in the early eighteenth century, the seas

still abounded with seals (Proceedings of the Government and Council of the Bahamas 1722; Bruce 1970); in 1836, a visual census of 500 individuals was made (Nesbitt 1836); in 1850, very few seals remained to make seal hunting a viable business (Gray 1850); and in 1922, there were no seals left in the entire northern Caribbean (Neill 1957). These data were used with natural population parameters from extant monk seal species to estimate the population size in a nearly unhunted breeding colony in the seventeenth century. While hunting certainly occurred before 1688, this is a reasonable baseline because intensive hunting for monk seal oil was related to the development of the sugar industry, which began in the Caribbean islands in the mid-seventeenth century. The majority of northern Caribbean seals were brought to Jamaica, whose sugar industry developed slowly between the 1660s and 1680s (Sheridan 1994). Therefore, by 1688, intensive hunting for oil had occurred for only a few years.

A simple age-structured pooled-sex density-independent model was constructed including five age classes: 0, 1, 2, 3, and 4+. Survival for each age class was assumed to be 0.80, 0.85, 0.90, 0.90 and 0.95, respectively (Gilmartin *et al.* 1993). Only those individuals aged 4 and above were assumed to be reproductive and fecundity was assumed to range from 0.1 to 0.2 per individual (Rice 1973). The annual timeline of the model was set up as follows: (i) individuals are counted, (ii) natural mortality occurs, (iii) harvesting occurs and (iv) surviving individuals reproduce and then age. Therefore, the number of monk seals born in a given year equals fecundity times the number of individuals aged 4 and above who survive natural causes and are not killed during the hunt. Mathematically, this is written as

$$N(0, t) = (N(4+, t-1) \times S(4+) - H(4+, t-1)) \times R. \quad (2.2)$$

The number of individuals in the colony aged 1–3 equals the number of individuals of previous age in the previous year, who survive natural mortality and are not killed during the hunt. For ages 1–3,

$$N(i, t) = N(i-1, t-1) \times S(i-1) - H(i-1, t-1). \quad (2.3)$$

The number of individuals in the colony aged 4 and above equals the number of 3-year-olds in the previous year, who survive natural causes and are not killed during the hunt, plus the number of individuals aged 4 and above in the previous years, who survive natural causes and are not killed during the hunt. For ages 4 and above,

$$\begin{aligned} N(4+, t) = & N(3, t-1) \times S(3) - H(3, t-1) \\ & + N(4+, t-1) \times S(4+) - H(4+, t-1), \end{aligned} \quad (2.4)$$

where $N(i, t)$ is the number of individuals of age i at time t ; $S(i)$ is the survival rate from i to $i+1$; $H(i, t)$ is the number of individuals harvested at age i time t ; and R is the fecundity of the 4+ individuals. The age structure of the population in 1688 was assumed to equal the stable age distribution the population would achieve based on the assumed survivorship and fecundity estimates in the absence of harvest.

The total harvest across all ages in 1688 was assumed to equal 100 individuals per night for each night of the hunting season, which was assumed to range from 30 to 90 nights per year. We assumed this hunting duration because seals were probably hunted when the females were on land nursing their pups, as they would have been most vulnerable and visible to hunters during this time. In other species of monk seals,

nursing is known to occur for approximately 30–50 days, with some degree of overlap among individuals (Johanos *et al.* 1994). Thus, a range of 30–90 days probably covers the length of time at which peak hunting occurred for Caribbean monk seals.

It was assumed that the hunters were non-selective, so that total harvest was parsed out by age, based on the relative abundance at age for that year. The number of years in which hunting occurred at the rate of 100 individuals per night is unknown, and applying that assumption to many years leads to the extinction of the species far earlier than the historical data suggest. Therefore, the total harvest was assumed to change in proportion to the change in total population size, such that

$$\begin{aligned} \text{sum}[H(i, t)] &= \text{sum}[H(i, t-1)] \\ &\times \text{sum}[N(i, t)]/\text{sum}[N(i, t-1)]. \end{aligned} \quad (2.5)$$

For example, if the population decreased by 10% from one year to the next, the total numbers killed during the harvest would also decrease by 10%. The total population size in 1688 was then estimated, such that the total population size in 1836 equalled 500 individuals.

A Caribbean-wide population size was estimated by calculating the expected number of monk seals per area of reef in the northern Caribbean and applying that density to the reef area within the foraging distance of each colony. It was assumed that the number of seals depended on the reef area available for foraging, so that regions with vast expanses of reefs supported larger populations of monk seals. The number of monk seals for the northern Caribbean population was estimated using the model previously mentioned. Total reef area within 300 km of the northern Caribbean population, as well as each of the 12 other breeding colonies, was obtained (Spalding *et al.* 2001). The number of seals in each colony was calculated by multiplying the estimated density for the northern Caribbean population by the reef area for each colony.

(d) Determining historical reeffish biomass

A food web model was used to determine the implications of historical monk seal populations on Caribbean coral reef communities. Specifically, the model was structured to address the question of how much fish and invertebrate biomass would have been required to support historical monk seal populations. Monk seal population size estimates derived previously were converted to biomass per habitat area using an average biomass of 245 kg for adult and 50 kg for juvenile seals (Adam & Garcia 2003) and a total reef area in the northern Caribbean of 4400 square kilometres (Spalding *et al.* 2001). A food web model was constructed using Ecopath software and published biomass, productivity and consumption values (Polovina 1984). Fifteen functional groups were included: tiger sharks; monk seals; birds; reef sharks; turtles; small pelagic fishes; jacks; reef fishes; lobsters and crabs; bottom fishes; near-shore fishes; zooplankton; phytoplankton; heterotrophic benthos; and benthic algae. Ecopath is a predator-driven mass balance model, so that adjusting the biomass values of monk seals affects their prey groups (reef fishes and invertebrates), as well as the groups that serve as prey for these animals (zooplankton, other reef fishes and heterotrophic benthos). The range of historical monk seal biomass values calculated previously was

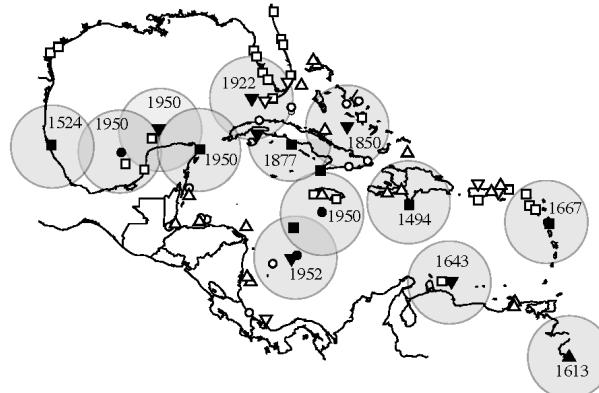


Figure 3. Locations of breeding colonies. Observations were coded and ranked into eight data types. Data types 1–4 were used to infer the presence of a breeding colony, assuming a minimum distance of 300 km between groups. Large circles represent the area encompassed by a 300 km home range and the date of last observation is listed for each colony. Data type: 1, observed breeding colony (filled circles); 2, groups of seals on land in the winter (filled down triangles); 3, groups of seals on land (filled squares); 4, large abundance (filled up triangles); 5, presence observed (open circles); 6, seals in water/irregular presence noted (open down triangles); 7, archaeological data (open squares); 8, place name or data from map (open up triangles).

Table 1. Historical monk seal colonies. (Thirteen colonies were estimated using data types 1–4 and the assumption that colonies existed at a distance of at least 300 km from each other.)

colony name	number of observations	highest ranked data type	latitude	longitude	date of last observation
Dry Tortugas	23	2	24.67	82.85	1922
A Triangulos	19	1	20.95	92.27	1950
Seal Cay, Ragged I	13	2	22.62	75.88	1850
Pedro	12	1	17.00	77.83	1950
A Alacran	9	2	22.50	89.70	1950
S Cuba	5	3	19.90	77.20	1877
Guadeloupe	4	3	16.25	61.58	1667
Curacao	4	2	12.00	68.65	1643
Anina	4	3	21.20	86.72	1950
Serrana	3	1	15.83	79.83	1952
Alta Vela	3	3	17.47	71.63	1494
Veracruz	2	3	21.45	97.22	1524
Guyana	1	4	7.00	60.00	1613
observations outside of colony	38				

incorporated into the model and prey biomass was then adjusted so that the model maintained equilibrium.

from 1 to 23 with a mean of eight observations per colony (table 1). The species richness estimator provides an estimate of 14 total breeding colonies, suggesting that one colony was overlooked in the historical record.

3. RESULTS

(a) Number of breeding colonies

Of the 140 total historical and archaeological observations of monk seals, 37 were ranked to be of data types 1–4. Four observations were of a breeding colony, 11 were of groups of seals on land in the winter, 10 were of groups of seals on land and 12 were of large abundances of seals. A mean distance of 300 km between colonies provides an estimate of 13 breeding colonies (figure 3) with a range from 8 to 16 breeding colonies.

The distribution of observations among 13 estimated colonies was used to predict the number of unseen colonies. The number of observations per colony ranged

(b) Colony-level extinction rate

The most robust model of colony-level extinction rate held the decadal extinction rate constant within each century but differed it by century and as a function of distance. Holding the effect of distance constant had an AICc weight of 0.53, and allowing the effect to differ between centuries had an AICc weight of 0.35. The third best model kept allowed the decadal extinction rate to differ by century but did not include distance as a covariate, and had an AICc weight of only 0.08.

The probability of colony extinction was zero for the sixteenth, seventeenth and nineteenth centuries and varied

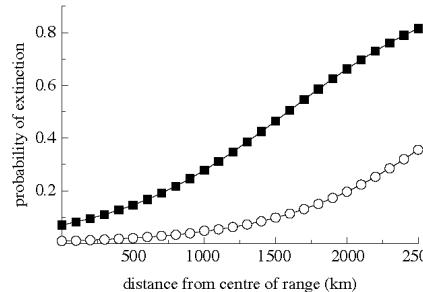


Figure 4. Probability of extinction. The extinction of Caribbean monk seal colonies occurred in two distinct phases. The probability of extinction in each phase is a function of the distance from the centre of the range, with colonies on the periphery having a higher probability of extinction in both the phases. Phase 1, eighteenth century (circles); phase 2, twentieth century (squares).

as a function of distance in the eighteenth and twentieth centuries. Thus, the extinction of monk seal colonies followed a predictable pattern in space and occurred in two distinct phases. The first wave of extinction in the eighteenth century eliminated colonies at the periphery of the species' range; colonies within 1500 km of the centre or the range had less than a 10% chance of going extinct while those at the maximum distance from the centre had a 35% chance of extinction (figure 4). In the second wave of extinction, those at the periphery still had a greater probability of extinction, but the probability for all colonies was increased.

(c) Historical population size

The total estimated number of seals in the northern Caribbean in the seventeenth-century population ranged from 48 156 to 227 648 individuals depending on the estimates of fecundity and number of nights of the harvest in 1688. Because the estimate of fecundity is considered low (Adam & Garcia 2003) and hunting at the highest rate of 100 seals per night probably occurred only during peak breeding season, the most conservative estimates of 48 156–69 810 seals in the northern Caribbean were selected. These estimates correspond to a hunting season of 30–45 days and a fecundity rate of 0.2. There are no variance estimates for the population sizes because the model was an algebraic one rather than a statistical one. It was flexible enough to always achieve the known population size of 500 in 1836.

The range of 48 156–69 810 seals on northern reefs is equivalent to 3.027–4.388 tons of monk seals per square kilometre of reef. The quantity of reef area available within 300 km of each colony ranged from 450 to 3150 km² so that the number of seals per colony ranged from 6800 to 70 000. The total Caribbean monk seal population for the entire Caribbean was estimated to be between 233 000 and 338 000 individuals.

(d) Historical reef fish biomass

Monk seals were ubiquitous predators on Caribbean coral reefs and would have required a large biomass of fishes and invertebrates to sustain their populations at unexploited

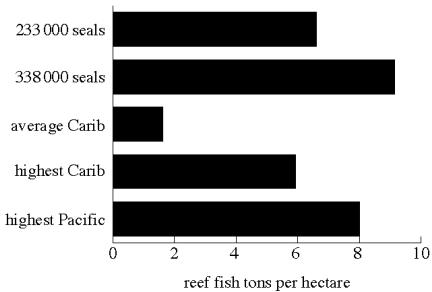


Figure 5. Historical reef fish biomass implied by monk seal population estimates. The biomass of reef fishes required to sustain the estimated population of historical monk seals (ranging from 233 000 to 338 000 seals in the entire Caribbean) is four to six times greater than the average Caribbean reef, which exceeds that found on the most pristine Caribbean coral reefs today (data from Newman *et al.* 2006) and is in the same range of the most pristine reefs worldwide (data from NOAA Fisheries, Pacific Islands Fisheries Science Center, Coral Reef Ecosystem).

levels. Results from the ECOPATH model suggest that the range of 3.027–4.388 g m⁻² of monk seals would have consumed 660–915 g m⁻² of reef fishes and from 71.5 to 103 g m⁻² of lobsters and crabs (figure 5). These historical abundances are approximately three to five times more than those found on typical Caribbean coral reefs, more than twice that measured on the most pristine Caribbean reef and similar to those measured on the most remote coral reef atolls in the Pacific (figure 5).

4. DISCUSSION

Before intensive human hunting, monk seals were found in dense colonies throughout the Caribbean, both on mainland coasts and offshore islands and atolls. Historical data describe 13 breeding colonies, but patterns in the data suggest that at least one colony escaped mention in the historical record. Three locations emerge as candidates for this unrecorded colony: the Little Bahama Bank; eastern Honduras; and eastern Venezuela. Large numbers of descriptions of seals in the water in the Little Bahama Bank and several distinct place names in eastern Honduras suggest the presence of colonies, and the distance between the colonies in Klein Curacao and Guyana make it probable that an intermediate colony existed in eastern Venezuela.

The most persistent monk seal populations were found on offshore atolls, far from human disturbance and in the centre of the range in the central-western Caribbean. The extinction of colonies followed a predictable pattern in time and space, with colonies far from the species' population centre having a significantly higher probability of extinction earlier in time (figure 4). This pattern can be explained by two factors. First, these colonies were on the edge of the species' range and therefore less likely to be repopulated if reduced by hunting. Second, the reef area in the eastern Caribbean is less than that in Central America and the western Caribbean islands, so colonies in the Lesser Antilles probably supported fewer individuals. Although colonies on the edge of the range were eliminated quickly, the persistence of those in the centre

and on offshore atolls indicates that monk seals are resistant to moderate to intense levels of human disturbance, which suggests that proper protection has the potential to save the remaining Hawaiian and Mediterranean monk seal colonies from extinction.

The widespread presence of dense monk seal colonies and their prominent role in pristine reefs provide evidence that the entire reef community has suffered major declines in overall animal biomass. In the Caribbean, colonies were found on mainland coasts, islands and atolls close to productive coral reef communities, where high densities of fishes are known to have existed based on the historical data (e.g. Wallace 1955). Estimates of the historical fish biomass suggest that historical reefs were several times more productive than those in the Caribbean today. These results support hypotheses of total ecosystem effects of historical overfishing (Jackson *et al.* 2001; Pandolfi *et al.* 2003), and suggest that fishing and hunting has reduced animal biomass so that a once abundant predator such as the monk seals could not survive on the fish resources that remain in depleted Caribbean reefs. Values derived from Ecopath must be interpreted cautiously as the model does not respond dynamically and therefore cannot account for changes such as prey switching, which is a characteristic of omnivorous monk seals. Nevertheless, these results provide yet further evidence on the magnitude of decline that has occurred in fish populations. Observations of emaciation in the Hawaiian monk seal have caused speculation that intensive fishing has reduced the prey base for this species as well (Craig & Ragen 1999). Hawaiian monk seal recovery may be limited by food availability, even at severely depleted population levels, which suggests that intensive overfishing has lowered the carrying capacity for large predators across coral reef ecosystems. Thus, successful recovery plans must include efforts to reduce pressure on overexploited fish stocks used by these marine predators.

The reef fish and invertebrate biomass required to support Caribbean monk seal populations exceeds that observed in the most pristine and protected reef ecosystems in the Caribbean, and the average Caribbean reef has less than 25% of the fishes found on historical reefs (figure 5; Newman *et al.* 2006). Estimates of historical fish densities are more similar to those observed in the most remote Pacific coral reef atolls, a result which indicates that reefs in the Caribbean were as productive as pristine Pacific reefs today. The close agreement between historical analyses and modern empirical data from remote reefs (Friedlander & DeMartini 2002, Sandin *et al.* 2008, NOAA Fisheries, Pacific Islands Fisheries Science Center, Coral Reef Ecosystem 2002, 2004, unpublished data) suggests that pristine reef systems contain similar biomasses of reef fishes across ocean basins. The loss of productivity and dramatic change in overall biomass in Caribbean reef ecosystems underscores the continued need to rebuild fish populations, even in areas with the most protected and effective management regimes.

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**CHAPTER 4: Social conflict, overfishing and disease in the
Florida sponge fishery, 1849-1939**

Social Conflict, Over-Fishing and Disease in the Florida Sponge Fishery, 1849–1939

Loren McClenachan

During the late 19th century, poor coastal fishermen in Florida prospered from the sale of millions of pounds of bath sponges to the North American metropolises of New York, Chicago and St Louis. ‘Sponger money’ was said to ‘ever flow’ (Sweeting, undated) and fishing for marine sponges formed the basis of entire local economies along the coast. Money flowed into the pockets of small-scale fishermen who transformed living sponges into Florida’s most valuable marine commodity. Until 1905, the banks of marine sponges in the reefs and hard-bottom environments of the Florida Keys were partially protected from over-fishing by the awkwardness of the fishing gear. Key West spongers used long-handled rakes to grope for sponges in the shallows, leaving deep-water sponges to grow and reproduce.

However, this rosy picture of prosperity faded for these ‘traditional’ boat-based fishermen during the early years of the 20th century. The declining health of marine sponge populations – together with an unexpected combination of technological innovation, war and discovery – initiated a dramatic and permanent change in the industry. Mediterranean sponge fishermen revolutionized the Florida fishery by introducing diving technology and shifting the centre of the fishery north to the Gulf Coast. Commercial divers from Greece could take sponges from water depths unimaginable to the Key West spongers, and their ability to access pristine sponge banks and more efficient sponge curing techniques helped them to outcompete traditional fishermen. In 1905, Greek divers began to arrive in Florida in gold rush proportions, and by 1910 they outnumbered the Key West fishermen (Moore, 1910). Social conflict, intensified by an increasingly over-fished resource, characterized the Florida sponge fishery during the early 20th century.

This chapter explores the conflict between Greek fishermen in Tarpon Springs and the Key West fishermen who were largely of Bahamian descent. It argues

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that the last three decades of the fishery were characterized by market-driven resource competition between two ethnically different groups of fishermen. This social conflict was heightened by overstressed sponge resources that eventually disappeared entirely due to a synergistic relationship between over-fishing and disease in the marine environment. Two themes central to historical marine ecology emerge from the story of sponge fishing in Florida. First, changes in technology can revolutionize a fishery and temporarily breathe life into a dying industry, but ultimately push a resource to commercial and ecological extinction. Second, the interaction between over-fishing and disease in the marine environment is not an exclusively modern phenomenon. Understanding synergistic stresses on structural elements of the marine community is central to environmental conservation, particularly in coral reef ecosystems that have been plagued by various unknown diseases.

At its peak, the fishery in the northern Caribbean removed 47 million pounds (lb) of live sponge annually, and over-fishing was evident in both quantitative and qualitative descriptions of the fishery in Florida. A resource manager during the early 20th century observed that there were so many boats and so few sponges left on the reefs that the spongers could ‘hardly wield their poles without collision’ (Moore, 1910, p440). Despite efforts on the part of the Key West fishermen to limit the activity of divers, high levels of fishing continued. Disease drastically reduced the remaining commercial sponge populations in 1939, leaving the fishermen in a ‘pitifully destitute condition’ (Barbour, 1945, p113). The era of sponge fishing lasted less than a century, but was critical to early economic development and has left its mark both on the culture of south Florida and the ecology of the reefs. Those reefs have yet to recover from the annihilation of commercial sponge species.

MARINE SPONGE BIOLOGY AND USES

Alive on a coral reef, marine sponges superficially resemble the coral itself: large living masses shaped like barrels, long asymmetrical fingers or compact spheres. Fish and lobsters congregate around them. Hawksbill turtles sit on the seafloor and tear through their thick skin and hard skeleton to feed on the living matter inside. Biologically, they are nothing like corals or any other animal. The most basic of multicellular organisms, sponges are simple in their structural design – essentially, a series of tiny canals that direct water from the surrounding environment to deep within the sponge body where nutrients are extracted; but they host a complicated assortment of biological symbioses and chemical compounds. Bacteria and other micro-organisms that can resist digestion often inhabit the sponge so that more than half of the living tissue in a sponge can be comprised of a cocktail of chemically defended micro-organisms (Lee et al, 2001).

As living water filters, marine sponges do their job better than any other animal in the ocean. Oysters and other bivalves use small hairs to grab relatively large

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pieces of suspended organic matter from the water; but sponges assimilate particles ranging over an order of magnitude in size and can subsist entirely on the smallest bacteria (Stuart and Klumpp, 1984). The nutritional value of these tiny bacteria is low so that sponges need to be remarkably efficient both at extracting cells from the water and pumping seawater through their canals. They have perfected the art of water filtration; tropical sponges can remove over 90 per cent of the bacteria present in the water and can cycle through up to 20,000 times their own volume in a 24-hour period (Reiswig, 1971, 1974). In the Caribbean, where sponges abound, they effectively clean the bacteria in the water surrounding the reef several times per day (Reiswig, 1974).

Well over 1000 genera of marine sponges exist; but only two have commercial value. Species of *Hippospongia* and *Spongia*, which are found on reefs, hard-bottom communities and sandy bottoms at depths between 2m and 60m, have been fished for centuries because their naturally soft and absorbent dried skeletons had endless uses before the invention of modern plastics. Early Europeans made sponges into padding for their helmets, lightweight and transportable drinking devices and even early municipal drinking water filters (Anonymous, 1939; Hall and Dietrich, 2000). Unlike most sponges, the skeletons of commercial sponges are not made of chalk-like calcium carbonate or glass-like silica spicules. Instead, once the living tissue is removed, all that remains of *Hippospongia* and *Spongia* is an ornate matrix of spongin: a soft, elastic protein-based fibre.

In the century before synthetic sponges, personal hygiene, house and car cleaning, medical surgery and the fine arts all required natural sponges. Art historians can date pieces of pottery by the type of sponge used to apply the glaze, while natural sponges played a role in women's reproductive freedom. Doused with 'antiseptic', they were commonly marketed as underground contraceptives during the late 19th century when planning parenthood was highly controversial (Brodie, 1994). Commercial grades of sponge correspond to different species (see Table 3.1). The most valuable sponges – the wool and velvet sponges – were prized for their soft texture. Species of *Spongia* supplied lower-grade sponges, including the wire and hardhead sponges, whose names imply that they were more frequently used for house cleaning than the more delicate tasks of applying pottery glaze or preventing pregnancy.

MANNING THE KEY WEST SPONGE FISHERY FROM BAHAMIAN WATERS, 1839–1890

Although politically part of the United States' newly acquired state of Florida, 19th-century Key West was in reality a tiny Caribbean island outpost with fewer than 1000 residents, accessible only by boat and isolated from the rest of the nation. Its modest economy was local and marine based, with few products for export, the despatch of live fish to Havana occupying more than one third of Key West's boat

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Table 1 Species targeted in the Florida sponge fishery

Trade Name	Value	Species
Wool	Very high	<i>Hippoppongia lachne</i>
Velvet	Very high	<i>H. gossypina</i>
Yellow	High	<i>Spongia barbara</i>
Grass/Vase	Varies	<i>S. graminea</i>
Wire	Low	<i>S. sterea</i>
Glove	Very low	<i>S. cheiris</i>
Reef	Very low	<i>S. obliqua</i>
Hardhead	Very low	<i>S. agaracina</i>

Source: data derived from Moore (1910)

traffic during the 1830s (KWCHR, 1837–1840). The discovery of sponges that could be dried and shipped to northern cities was therefore a boon to the local economy and a resource that poor men could easily turn into money. In the first years of the fishery, spongers simply waded into ‘shoal waters in the immediate vicinity of Key West’ where sponges were pulled by hand (Moore, 1910, p435). Fishermen tore sponges from the ocean floor, brought them to the surface, squeezed them hard so that the ‘gurry’ – the living tissue, associated bacteria and organic material – oozed out of the animal. The dead skeleton was then left to soak, before being dried and cut into geometric shapes for sale.

As the industry developed, small boats became necessary to access sponges in deeper water (see Figure 3.1), and men who were familiar with such sponge fishing vessels began to arrive in the Florida Keys from the nearby Bahamas. The Bahamian sponge fishery was the first in the Caribbean and had existed for a decade before the first Florida sponge was exported in 1849. Experienced Bahamian spongers were drawn to the economic opportunities in Florida and driven from the Bahamas by poor conditions that existed there for black labourers. In the Bahamas, sponge fishermen, like workers on the colony’s pineapple plantations or sisal farms, were typically ex-slaves who owned limited personal property and had little chance of improving their income and their families’ welfare. Despite the seemingly endless boatloads of marine sponges pulled from the reef and exported during the mid 19th century, workers remained poor. White men in Nassau controlled the business and spongers were remunerated by shares, which were sometimes paid in kind – usually supplies – rather than in cash (Johnson, 1988). The decline of the practice of salvaging shipwrecks – an industry that had employed nearly half of the Bahamas’ able-bodied men during the 1850s (Albury, 1975) – and the collapse of the pineapple and sisal agriculture in the 1870s left large numbers of Bahamian workers reliant on a sponge industry that provided little financial reward (Johnson, 1988).

The sponge industry in Florida offered employment that experienced Bahamian boatmen badly needed and for which they were well qualified (see Figure 3.2). The

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Figure 1 Schooners at Key West Sponge Docks, 1902

Source: image from the Monroe County Public Library photograph collection

first Bahamian settlers in Key West during the 1840s were financially independent fishermen and wreckers; but as industry developed in Key West, opportunities for labourers increased. By 1885, six schooners were engaged exclusively in transporting Bahamians from Nassau to Key West (Blake, 1885). As word spread that there were 'places in the world where not only a high rate of wage is paid, but the people get paid in cash' (Powles, 1888, p88), Bahamians came to Key West in droves, contributing to the doubling of the island's population between 1880 and 1890. These migrants frequently brought their entire families or, in one case, 'a whole collection of families', which expressed their 'disgust with the Colony' and left 'their substantial houses' in Rock Sound for south Florida. Like most of their compatriots, these 40 or so Bahamians did not return (Haynes-Smith, 1896). Accordingly, by 1890, Bahamians comprised over one quarter of the 20,000 residents of Key West – and a majority of its 2000 spongers (Brice, 1897).

Bahamian boatmen were attracted to Key West by the improved economic opportunities afforded by the sponge industry, and black fishermen further found opportunity for advancement in the burgeoning city. The racial dynamics of

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Figure 2 Sponge workers trimming sponges, Nassau, the Bahamas, circa 1932

Source: C. M. Yonge (photo credit), Natural History Museum, London, UK

Florida's sponge industry were complex, but black men – particularly those with families – encountered a degree of acceptance within the south Florida fishing community (Goode and Collins, 1887). Race relations in south Florida during the mid 19th century were influenced as much by Cuban society as that of the American south or the Bahamas. Cubans considered south Florida to be 'so much a part of their own country' and fishermen and labourers came and went through the porous national border (James, 1998, pp237). Cuba, the Bahamas and south Florida all had slightly different racial etiquettes, and many black men found a respectable place in this international maritime frontier. During the 1890s, black fishermen were central to the sponge industry and a high degree of racial mixing occurred aboard sponge boats. Some 65 per cent of Key West spongers were black and most boats contained crews of both black and white spongers (Cobb, 1902). As time passed, black spongers were among those who successfully sought sanctions from the legislature to curb the activities of immigrant Greek divers.

PROSPERITY AND UNINTENTIONAL CONSERVATION, 1890–1905

Evidence of sponging was everywhere in late 19th-century Key West, where backyards and boat-yards were piled high with drying sponges (see Figure 3.3). By the turn of the century, total annual export was in the range of several hundred

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thousand pounds of dried sponges, the equivalent to over 1 million pounds of living animals. These sponges supplied more than half of the total American market. The optimism for the future of the industry was reflected in popular culture; the song 'Sponger Money Never Done' was sung both in the Bahamas and Key West during the 19th century (Rolle, 1940; Dean, 1981; Sweeting, undated):

... Look in my trunk and see what's there, sponger money,
One hundred dollars was my share, sponger money,
I'm gonna take away your woes, sponger money,
I'm gonna buy you fine new clothes, sponger money,
Then when we go out on the street, sponger money,
You'll be lookin' nice and neat, sponger money,
Then all the boys will envy me, sponger money,
Then all the girls will fall for me, sponger money,
Money don't make me you know, sponger money,
Sponger money ever flow, sponger money,
Tell ev'rybody in town, sponger money,
Me and my gal gon' dance 'em down, sponger money,
Sponger money never done, sponger money.



Figure 3 Sponges drying on a platform at the rear of sponge house, Key West, December 1921

Source: R. E. Coker (photo credit), NARA, College Park

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The days of wading into shallow water and collecting sponges from the reefs were gone, however, and it became necessary to travel to ‘deeper and deeper water year after year’ to find marketable sponges (Brice, 1897, p267). When sponges in the shallows disappeared, spongers adopted the makeshift technology of long-handled rakes with hooks on the ends and oil from nurse shark livers, which they poured on the water’s surface on choppy days to smooth the surface ripples. Spongers looked through the clear water of the Keys, located banks of living sponges on the sea floor, and pulled them with their rakes. In 1888, marking the further depletion of shallow-water sponges, a new kind of hook was developed to better access the sponges in water deeper than 30 feet (9m) (Brice, 1897). By the 1890s, shallow-water sponges were nearly ‘fished out’ (Brice, 1897, p267) and spongers had been forced out to sea, ‘until the maximum depth in which sponging is possible’ had been reached (Smith, 1898, p232).

The Key West fleet was comprised of 100 to 200 small sailing vessels worked by crews of five men or less. These vessels typically embarked on week- to month-long fishing trips, during which two-man dinghies were despatched over reefs (see Figure 3.1). The limited technological advances in the industry served primarily to extend the area accessible to sponge boats into deeper water; but without diving gear, expansion was limited. Before 1905, the biggest technological innovation was the ‘water telescope’, essentially a glass-bottom bucket that replaced shark liver oil and improved the sponger’s ability to see the bottom. Because access to sponges was ultimately limited by depth, sponging became a profession in which individual skill made a great difference. In deep water – depths of over 40 feet (12m) – just one third of the spongers had ‘sufficient strength, keenness of sight and skill with the pole to work successfully’ (Moore, 1910, p439). Prosperity was thus linked to specific talents, and as the fishery became more developed, competition fiercer and the sponges more depleted, many spongers found the industry to be less welcoming than it had been when they arrived from the Bahamas.

Just as the shallow banks within wading distance of Key West had been depleted, the sponges at depths of 30 to 40 feet (9m to 12m) were proving finite. Declines in size and quality of sponges were noticed by the 1890s, and the large sponges that had frequently occurred in the past were ‘rarely, if ever, seen’ by the end of the century (Brice, 1897, p268). Spongers themselves noted declines in yields. A typical trip in the 1880s brought in 1000 to 1500 bunches of sponges; by the late 1890s, 500 bunches were considered a good cargo (Brice, 1897). Sponge grounds were simply ‘much less productive than formerly’, a predicament acknowledged by ‘practically everyone who is in a position to express an intelligent opinion’ (Smith, 1898, p232). Inshore grounds were abandoned and smaller catches per vessel were noted, while yields primarily comprised the smallest sponges (Smith, 1898).

Intensive fishing in shallow water drove such decline; but protection of stocks was granted by the clumsy nature of the fishing gear and the inaccessibility of sponges in deeper water. The most valuable sheepwool sponges were commercially extinct in near-shore areas by the turn of the century, but they were markedly

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more abundant in waters deeper than 40 feet (12m), illustrated by the fact that experienced captains were 'in the habit of running offshore from time to time to take a sight' of the bottom with their water glasses. If conditions were favourable and the water was clear, they could easily 'take more sponges in a day than they could in a week on the overworked inshore grounds' (Moore, 1910, p439). Sponges had been spotted far deeper: one was brought up from 100 feet (30m) on a fishing line and several men reported banks as deep as 120 feet (37m) – but these were impossibly deep (Moore, 1910). As long as abundant deep-water sponges remained untouched, they acted as a *de facto* reserve population that helped to reseed the shallow-water sponge banks.

TECHNOLOGICAL REVOLUTION AND COMPETITION IN THE MARKETPLACE, 1905–1910

During the early 1870s, a second sponge ground had been discovered in the Gulf of Mexico, on Florida's west coast, and a small number of boats worked on these banks for nearly three decades (see Figure 3.4). The distance back to Key West made large-scale sponging in the gulf impractical, and catches of the few boats that worked there were sold to three dealers in Tarpon Springs. In 1895, just 5 per cent of Florida's sponges were sold in Tarpon Springs (Schroeder, 1924; see Figure 3.5). However, fear of Spanish vessels during the Spanish American War drove Key West fishermen to land their catch in Tarpon Springs, and soon this small settlement became a real rival to Key West (Cobb, 1902). By 1902, sponge fishermen brought nearly 20 per cent of the total catch to sell in Tarpon Springs (Schroeder, 1924). Growth of the sponge market attracted settlers, and among the shore-side workers in Tarpon Springs were Greek men from the Mediterranean sponge-diving industry (see Figure 3.6). Like many divers, they considered fishing sponges with rakes – as was done throughout the Caribbean – to be primitive since this ripped the sponges and resulted in an imperfect product. An investigation of the deep-water sponges in the eastern Gulf of Mexico found enough to warrant establishing a diving company, and the first successful diving season was completed in 1905 (Moore, 1910).

Diving increased the depth at which sponges could be collected from 40 to 180 feet (12m to 55m), making accessible thousands of new sponge banks. The addition of deep-water sponging grounds on the Gulf Coast increased the area open to spongers from 4000 to 10,000 square miles (10,300 to 25,900 square kilometres), stretching from the Keys in the south to Apalachicola, high up on the peninsula (see Figure 3.4). The new diving boats were extremely successful at finding and exploiting rich banks that yielded significant quantities of large, valuable sponges, the like of which had not been landed for half a century. One diving boat was memorialized for collecting 500 bunches of high-quality sponges in five days 'without moving much over a mile' (Moore, 1910, p443). In the first

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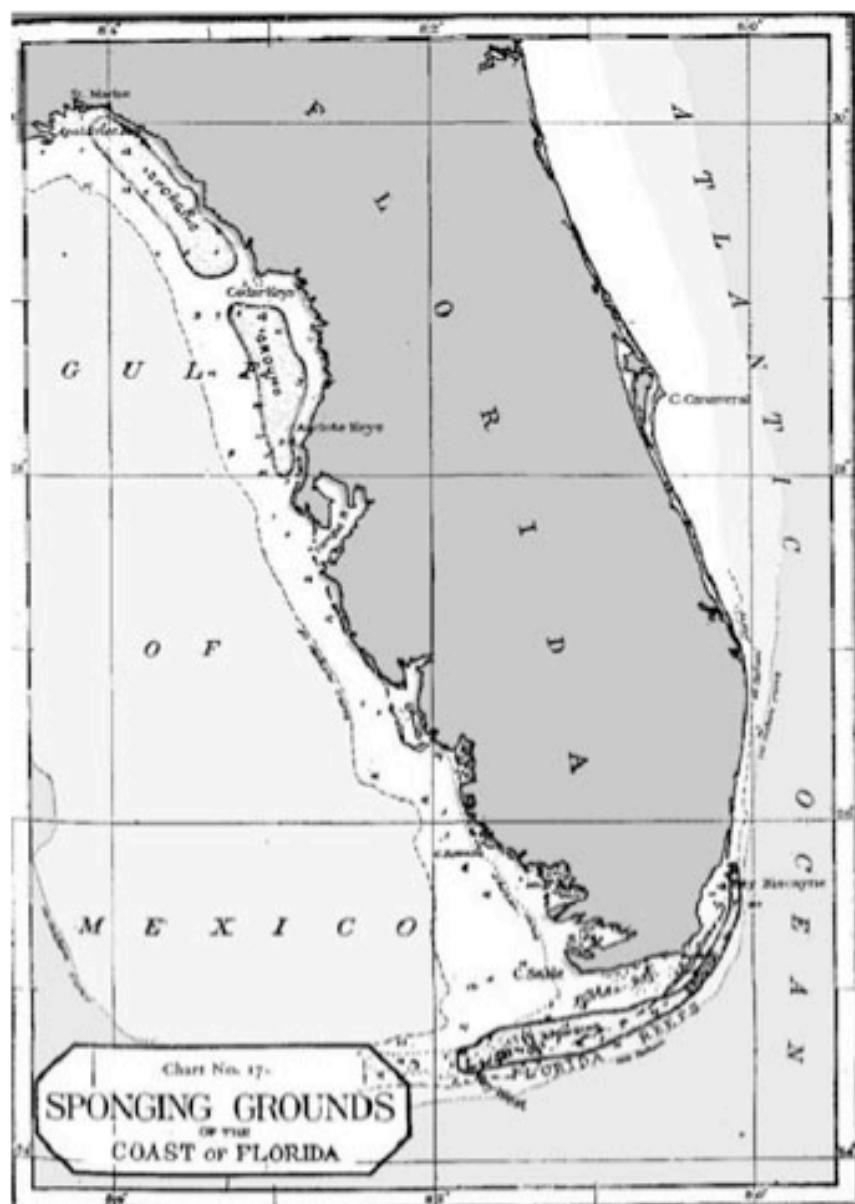


Figure 4 *Florida sponging grounds*

Source: adapted from Goode (1887); view colour version at www.hull.ac.uk/oceanspast

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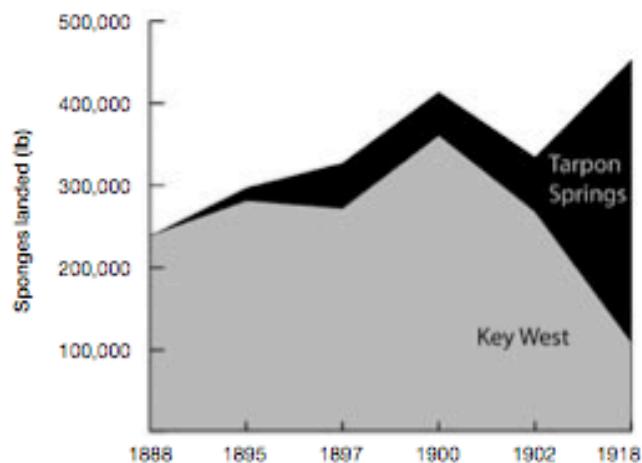


Figure 5 Sponge catches, Key West and Tarpon Springs, 1888–1918 (lb)

Source: Schroeder (1924)

six weeks of diving in 1906, over US\$60,000 worth of sponges were landed, more than 75 per cent of the total annual gulf catch by traditional methods (Cobb, 1902; Moore, 1910). By mid May 1906, there were 50 diving boats employed and 55 more rigged and waiting for crews, 'which could not be supplied despite a great influx of Greek divers and boatmen' (Moore, 1910, pp442–443). The desperate need for divers and the tremendous profit to be made was advertised in New York City and Greece, and hundreds of divers came to harvest the rich crop of sponges in the gulf. Within a year, the population of Tarpon Springs had grown from 700 to 800, with more arriving 'on every train' (Moore, 1910, p443).

The first months of sponge diving in Florida were both successful and profitable, but prices crashed as the supply of sponges from the gulf expanded rapidly. Sponges that were worth \$8 to \$10 in the opening weeks of 1906 were selling for \$3 by May (Moore, 1910). Without market controls, intensive fishing lowered prices; without controls on the fishery, lowered prices increased competition and stimulated more intensive fishing. Divers continued to make profits; but their efficient methods and access to deep-water sponges severely disadvantaged the boat-based spongers. Greek diving boats operated in pristine deep-water sponge beds, where large numbers of high-quality sponges were found. Additionally, they could work on days when the water was choppy, generally stayed out on the grounds longer and cured the sponge catch on board rather than sailing at the end of each week to crawl: shallow-water pens used by spongers and turtle fishermen. Key West boats, in contrast, could only make trips when the water was clear and were confined to the same tired sponge banks that had been worked for decades (Moore, 1910). These practices translated

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into a measurable economic advantage for the Greek spongers. In 1909, *Filmore*, a Greek schooner with a crew of ten spongers, made US\$2180 on a 60-day fishing voyage, whereas a comparable Key West schooner employing 13 spongers made US\$1180 on a 42-day trip. These figures suggest that Greek sponging boats earned nearly 70 per cent more per day on the water than the Key West fishing boats working with traditional methods (Moore, 1910).

The Key West spongers initially complained only about the drop in wholesale sponge prices and considered the 'trouble with the Greeks' to be a temporary annoyance rather than a career-ending event. Massive quantities of cheap sponges continued to be available in Tarpon Springs, however, and sponge buyers overlooked Key West markets. This 'cut-throat competition', together with a declining yield from the overworked sponge banks, quickly forced many boat-based spongers out of the industry. Between 1900 and 1908, the number of men in the raking fishery declined by more than 50 per cent (Moore, 1910).

COMPETITION AND VIOLENCE ON THE WATER, 1910–1939

Economic competition characterized the early stages of the diving industry; but as more boats crowded onto the waterfront, competition over access to grounds was not far behind. At first, recognizing that they were newcomers intruding on the Florida sponging grounds, the Greek divers treated the traditional spongers respectfully and confined work to sites far offshore (see Figure 3.6). The deep-water sponges were more valuable; but additional dangers incurred with deep diving made inshore diving desirable. As it became more apparent that the 'loud threats' of some of the Key West spongers were largely idle, divers became more confident and moved shoreward into the shallow sponge beds (Moore, 1910, p444).

Fierce competition led to changes in the method of fishing as the boat-based spongers attempted to increase their efficiency and stay in business. The Key West men were desperate to find sponges and gathered around productive patches, so that it was common to see them packed so tightly together that the small boats collided (Moore, 1910). In order to make sponging in over-fished areas worthwhile, the spongers changed their method from blindly wielding their poles over known sponge beds to systematically surveying larger grounds and dropping anchors on discovered sponge banks. This method increased productivity in regions where the sponges had become 'too few and scattered for the usual methods to yield results' (Moore, 1910, p440). Finally, in the most depleted areas, vessels began to anchor close to the sponging grounds at night so that they could be first on the grounds in the morning, when the winds were light and the conditions best for work (Moore, 1910).

Greek divers could work as deep as 180 feet (55m); but they preferred to dive on shallow, more heavily fished sponge beds, an irony that revealed the relative inefficiency of the traditional spongers. Despite decades of fishing and declines in

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Figure 6 Greek sponge divers, Tarpon Springs, circa 1931

Source: W. L. Schmitt (photo credit), Smithsonian Institution Archives

yield, sponges still remained in shallow water, hidden in crevices or under ledges. In fact, the largest complaint of the Key West spongers was that Greek divers thoroughly denuded the bottom of all sizes of sponges, leaving fewer to reseed the beds (*KWC*, 8 June 1938). In particular, where divers worked on already depleted grounds, it was clear that the diving industry exhausted sponge populations. Opposition from the boat-based spongers crystallized, and bills were introduced into the state legislature to restrict the use of diving equipment. Among the most convincing arguments for restrictions was that the beds were 'already worked to or beyond their limits of productiveness' and that diving increased 'the draft upon them [and] must be injurious' (Anonymous, 1939, p111). Eventually, three types of bills passed: the diving fishery was closed from May to September, shallow-water and near-shore diving was prohibited, and the minimum size of sponges was increased from 4 to 5 inches (10cm to 13cm) in diameter (Moore, 1910; *KWC*, 30 June 1938).

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By the 1920s, the sponge grounds were neatly parcelled and the season divided; but frequent incursions were made. In 1931, 40 miles' (64km) worth of buoys were sought to 'mark the line between diver and hooker territory on the Taylor County battle front' (*FOR*, October 1931, p13). In the same year, 76 divers were fined for violating the shallow-water ban. In the Keys, law enforcement was most vigilant as local authorities tried to catch divers from the gulf violating the law. Raids on non-local boats were frequent, but convictions were rare. In one case in 1930, a boat was raided in the Marquesas, uninhabited islands just west of Key West, and seven men were charged with taking undersized sponges. The conviction was particularly satisfying for local spongers as several of the guilty men were former Key West spongers who had defected to Tarpon Springs to work for a diving operation (*KWC*, 26 June 1930).

Law enforcement officers attempted to keep divers out of shallow water; but angry spongers often took matters into their own hands. Violent confrontations on the waterfront escalated in the Florida Keys and along the Gulf Coast, with angry spongers even resorting to arson. In 1918, Key West spongers set fire to a Greek sponging vessel, the first of four craft to 'be mysteriously destroyed' in the Keys. A schooner 'burned to the water's edge' in 1923 and Greek spongers were warned in the local newspaper to leave the Keys completely (*KWC*, 27 April 1933). A national fisheries trade journal considered such acts of violence to be 'one chapter in a decade or more of warfare' between the sponge divers and boat-based spongers (*FOR*, October 1931, p13).

CONSERVATION ETHICS IN A TIME OF SCARCITY

By 1927, there were just 60 boats and 500 men in the Key West sponge fishery – compared with over 2000 men during the 1880s; but the number of spongers was set to drop even further. In 1938, 40 men in Monroe County called themselves spongers, but there were only five who worked regularly: 'Ben Felton, Nelson Spencer, William Spencer, James Thompson and John Spencer' (*KWC*, 8 June 1938). The Key grounds had been considered exhausted at the turn of the century, and under continued pressure, its sponge banks were almost commercially extinct by the 1930s. Along with over-fishing, blockages in freshwater outflow from the Everglades due to the Key West railroad extension contributed to sponge mortality throughout the Keys (Moore, 1910). As the numbers of spongers and the available sponge supply shrank, Key West fishermen fought to maintain a presence in the fishery by means that were at least moderately conservationist. Many of their economic interests became aligned with a conservation ethic as they pressed for legislation to protect the deep-water sponge banks and their own inefficient techniques.

Limiting technology certainly helped to maintain sponge populations, particularly in deep water, and Key West spongers were fiercely protective of their

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local rights and suspicious of any type of technological progress that threatened to constrain their rights. They were said to hold antagonistic attitudes towards any kind of innovation, whether it was diving equipment or sponge culture, even though the latter may have aided the recuperation of the beds. Correctly perceiving the privatization of the ocean bottom as a threat to their immediate livelihoods, Key West spongers rejected attempts to experiment with aquaculture. A lack of proactive government mediation caused sponge fishermen to be pitted against businessmen and scientists interested in aquaculture. In one case involving experimental seeding of sponges, more than 100 men protested a court order to not disturb sponges in the shallow bay of Sugarloaf Sound (*KWC*, 13 October 1930). Spongers in the Florida Keys thus clung to a way of life that had been prosperous a generation earlier, but was on the brink of collapse by the 1930s.

Key West spongers who did not leave the business during the 20th century fought to stay relevant, while the Tarpon Springs fishery appeared optimistic and ascendant. Three times more sponges were landed in Tarpon Springs than in Key West in 1918 (Schroeder, 1924; see Figure 3.5) and the sponges were worth up to 90 per cent more per pound than those from shallower water (*KWC*, 14 April 1930). Confident in their huge profits, gulf divers attempted to expand the area fished and the number of divers in the industry. In 1934, they sought a special permit from the US Immigration Department to enable 40 Greek divers to enter the country (*FOR*, April 1934, p12). Divers complained that large numbers of deep-water sponges existed in the Keys that were lost to the industry and tried on several occasions to establish a base in the Florida Keys (*FOR*, May 1938, p10). Intending to circumvent the hostility of Key West spongers, they petitioned for permission to establish themselves in Miami (*KWC*, 10 April 1930).

Optimism in the diving industry fuelled high levels of investment, which ultimately caused the Tarpon Springs fishery to grow beyond the capacity of the sponge resource. The continued influx of divers was unsustainable, particularly as a pathological disregard for conservation laws eroded the strength of the diving industry. The lack of a conservation ethic among divers – particularly with respect to taking undersized sponges – led boat-based spongers to believe that divers would stop at nothing until all the sponges were gathered from Florida. Boat-based spongers in the Keys and Taylor County resented depletion of their sponge beds by divers and confrontations over taking small sponges fuelled turf battles and cries for further diving restrictions (*FOR*, May 1938, p10). In 1935, the federal government sent an officer to enforce size limits in the gulf. Three years later, a state conservation vessel was despatched to Monroe County to enforce the ban on shallow-water diving (*KWC*, 22 September 1938). Despite the presence of a conservation official, every diving boat was said to have 5in sponges among its catch, leading a former president of the Tarpon Springs sponge exchange to urge Washington to take a more aggressive stance on the protection of abused sponge beds in the gulf (*KWC*, 17 November 1938).

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Despite a common desire to turn marine sponges into a cash income, the Greek divers and the boat-based spongers differed in their perspective on conservation and on limiting exploitation. To some degree, Key West fishermen were more ecologically benign, simply because of their inability to reach sponges in deeper water. Had they been able to do so, they certainly would have taken more sponges. Unlike Greek divers, however, the Key West fishermen were not reputed to take small sponges habitually, and they appeared to have a better sense of the limits of the sponge resource, at least in the later years of the fishery. Many Greek divers came as single men to Tarpon Springs, either directly from the over-fished Mediterranean sponge banks or from New York City, and therefore had a relatively high degree of mobility. Diving required substantial capital investment and division of labour so that the businessmen running the industry were farther removed from the environment itself (Brice, 1897). In contrast, the Key West sponge industry comprised a collection of small-scale entrepreneurs who knew no waters other than the Caribbean, had very little capital invested and few alternatives if the industry failed. Thus, these fishermen had a stronger connection to the future ecological state of the marine environment. Key West spongers sought to limit the excesses of the divers both to protect themselves and to protect the sponge resource, upon whose profits the city of Key West was built.

DISEASE, OVER-FISHING AND THE UNRAVELLING OF FLORIDA'S CORAL REEF ECOSYSTEMS

In December 1938, spongers on the other side of the Gulf Stream in the Bahamas began to have an odd and disconcerting experience, one which old-timers who had been in the business since boyhood had never witnessed. Instead of pulling up intact sponges, sponge hooks came to the surface with only slivers and strings; the rest of the sponge skeleton had disintegrated (Anonymous, 1939). When sponges were cut open 'rotten and evil smelling tissue' was exposed (Walton-Smith, 1941, p419). The 'mysterious blight' that struck sponge beds in the Bahamas 'quickly reached epidemic proportions', leaving the ocean floor covered with thousands of bleached and rotted sponges (*FTU*, 6 April 1939). By February, 'there remained no sponge-bearing bank unaffected' in the Bahamas (Galtsoff et al, 1939, p807), and Key West fishermen watched their sponge banks with dread anticipation. In March, signs of disease appeared and by May the Key West sponges showed considerable damage from blight. By the end of 1939, the yellow and vase sponges had suffered nearly 100 per cent mortality, while 70 per cent of the valuable sheepwool sponges had been eliminated from the Keys (Galtsoff, 1939). Although overflowing fresh water and local pollution were both blamed, the culprit appeared to be a fungus-like filament, which started in a small area of the sponge and expanded until the entire sponge was consumed (Galtsoff et al, 1939).

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Initial fears that the blight would also affect the sponge beds in the gulf went unfulfilled during the year. In May 1939, Tarpon Springs sponge sales were at their highest in five years (*FOR*, May 1939, p9). By early 1940, however, the disease had made its way up the coast and Greek divers observed extensive sponge mortality as deep as 70 feet (12m) (*FTU*, 6 April 1939). By the end of 1940, the remaining sponge fishermen in Florida were out of work. The disease devastated the industry, leaving fishermen 'destitute' (Barbour, 1945, p113). Flooding the market with sponges in 1906 had caused local prices to drop by two-thirds, but wiping out the northern Caribbean sponge banks caused global prices to increase from US\$2 to US\$30 per lb between 1939 and 1945 (Tierney, 1949).

While the immediate cause of sponge mortality was disease, the fishermen were far from blameless in the disappearance of the stock. Evidence of over-fishing throughout Florida is prevalent, both in descriptive accounts and in fisheries statistics. In 1930, gulf divers complained that there were so few sponges left in the gulf that could be legally taken by diving (*KWC*, 10 April 1930) that they were obliged to travel long distances to find their prey, as far as five times the distance their predecessors had travelled in the first decade of the 20th century. In the early years of the fishery, large vessels in bay grounds had fished 30km to 50km from the shore, and many divers worked in the shallow waters, taking the scraps left behind by the boat-based spongers (Moore, 1910). By 1938, divers had moved far offshore, some going up to 240km from the coast to find sponges. During the 1930s, the best sponges were found only at depths of up to 120 feet (37m) (*FOR*, May 1938, p3). The size of individuals had also declined consistently, 'owing to the intense fishery' that allowed sponges 'no opportunity to grow' (Moore, 1910, p429).

The disease that exterminated Florida's sponge community during the 1930s was intimately linked to over-fishing, both in the long and short term. Most obviously, the very act of sponge fishing spread the disease more quickly and effectively than the water current could have alone. A common belief existed that 'sponges contain seeds' and squeezing the sponge 'gurry' into the water released these seeds, starting new growths (Moore, 1910; Anonymous, 1939, p74). This idea was entirely erroneous, but probably contributed to the distribution of virulent microbes among sponge populations. Therefore, the spongers themselves were probably vectors of dispersal, spreading the disease from one isolated bed to another.

Over a longer time-scale, over-fishing very likely increased the concentrations of bacteria and other particles of organic matter – including algal and fungal cells – in the seawater over the sponge beds. The sponges' remarkably efficient filters can remove over 90 per cent of the bacteria from seawater (Reiswig, 1971). Sponges are the only animals on coral reefs that fill this ecological role. The 4 million lb of live sponges taken from the Florida Keys in a typical year would have assimilated more than 70 metric tonnes of organic material annually and taken over 5 tonnes of bacteria from the water – more than 5 million trillion individual bacterial cells (calculations based on data in Reiswig, 1971, 1974). Over the course of the fishery,

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traditional spongers and divers took more than 1.5 billion lb of living sponges from the northern Caribbean (see Figure 3.7), so that the water during the 1930s was certainly richer in bacteria, fungi, algae and other tiny particles than it had been a century earlier. The community dynamics of microbes in the sea and within sponges are complex; but evidence exists to indicate that at high concentrations, bacteria that are typically benign can become virulent (Miller and Bassler, 2001), and in waters with high levels of organic matter, diseases are more prevalent (Hodges et al, 2005; Kline et al, 2006; Smith et al, 2006). Far from passive free-floating cells, pelagic bacteria are known to attack organic matter and transform biogeochemical cycles (Azam, 1998). It is likely that over-fishing of sponges – the only effective filter feeder in the coral reef ecosystems of the northern Caribbean – fundamentally altered the microbial community in a manner ultimately fatal to their existence (Hobbie et al, 1977; Azam et al, 1983; Moriarty et al, 1985).

Whatever the ultimate cause of the sponge epidemic, the near complete elimination of two genera of marine sponges from the northern Caribbean within one year was not an isolated disaster, but rather linked to a general decline in the integrity of coral reef communities. A measurable trend towards decreased plant and animal biomass and increased bacterial concentrations is a major concern in modern coral reef ecosystems, including those in the Florida Keys (Pandolfi et al, 2005). In pristine reef ecosystems, abundant long-lived corals build habitat for

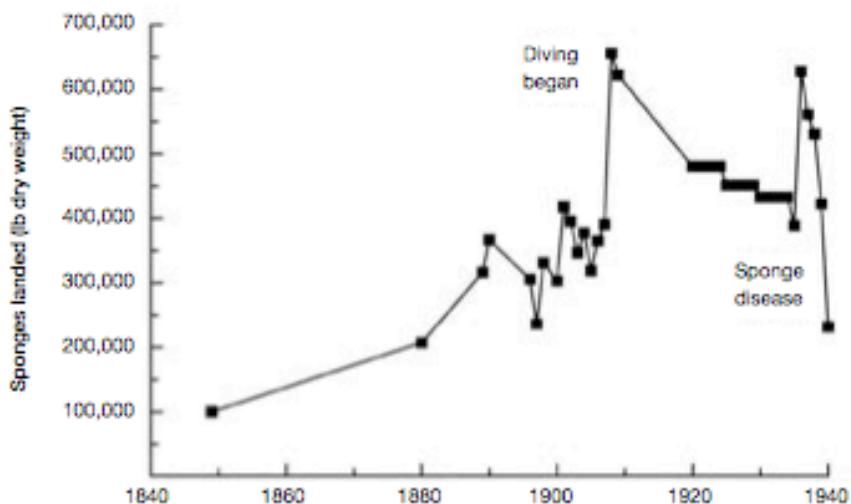


Figure 7 Florida sponge catches, 1839–1940 (lb dry weight)

Source: data derived from Moore (1910) and Stuart (1948)

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large animals, fishes and invertebrates. In contrast, reefs degraded by humans ‘are little more than rubble, seaweed and slime’ (Pandolfi et al, 2005, p1725). High levels of microbial activity in degraded systems are averse to maintaining biomass in large animals. In ecosystems with dominant microbial communities, fisheries production has even been diminished as a higher proportion of organic matter is locked into the microbial loop (Azam, 1998). It is difficult to demonstrate a link between disease and decreased animal biomass historically; but modern trends of increased disease, diminished water quality and reduced animal biomass certainly suggest that such a connection exists.

In the Florida Keys, the disappearance of commercial sponges was an important component of the unravelling of the coral reef ecosystems, and one with unexpected ecological and social consequences. Along with decreased water quality, the ecological extinction of sponges reduced benthic habitat structure so that in the decade following the 1939 sponge disease, lobsters that are known to live in close association with sponges began to appear in smaller numbers (KWC, 1949). Loss of productivity in the lobster fishery is a striking example of how degraded ocean ecosystems become much less valuable to people. Just as the decline of sponges altered the microbial community in a manner ultimately detrimental to sponge health, over-fishing fundamentally altered the reef community in the Florida Keys so that it no longer supports commercially viable fisheries for sponges or lobsters.

Over-exploitation and marine ecological degradation are related to the insatiable demands placed on a resource by external markets – such as those for bath sponges throughout North America during the early 20th century – and to advancements in fishing technology that drive an already stressed resource to commercial and ecological extinction. In south Florida, primitive fishing technology protected sponges far more effectively than either government regulation or the limited conservation ethic of the fishermen could have done; rapid technological advance obliterated these deep-water refuges. Similar scenarios have occurred under the sea and have been particularly harmful to communities of benthic invertebrates. Animals attached to the ocean floor, such as sponges and oysters, are vulnerable in their immobility and irreplaceable in their ecological role. In temperate bays and along tropical coasts, comparatively clumsy, labour-intensive fishing gear protected oysters – filter-feeding animals that provide essential habitat to fish and invertebrates. Fishermen working in sailing vessels along the Atlantic Coast of North America used oyster tongs to grab oysters from their reefs, and free-divers in the Caribbean and tropical Pacific gathered pearl oysters for over three centuries. In both ocean basins, deep-water refuges existed for oysters. During the late 19th and early 20th centuries, however, large-scale dredging and mechanized diving eliminated these refuges and, like sponges, oysters can now be taken wherever they grow. As a consequence, over-fished modern oyster reef ecosystems have been characterized by disease, decreased water quality and loss of architectural structure, as well as the loss of commercial productivity to fishermen.

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Particularly in tropical environments with high biological diversity, ecological interactions are complicated and nearly impossible to reconstruct precisely with sparse historic data. By reconstructing the history of the sponge fishermen and sponge community, this chapter has attempted to tell a story of change in both the human and ecological communities. This synthetic approach to historical ecology highlights elements of complex interactions among members of the marine community and between humans and the environments that sustain them. This story of sponge fishing in Florida provides a poignant example of how long-term environmental stress caused by over-fishing lowers biological and commercial productivity, increases the likelihood of punctuated disease events, and takes a harsh toll on people who make their living on the seas.

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**CHAPTER 5: Documenting loss of large trophy fish from
the Florida Keys with historical photographs**

Contributed Paper

Documenting Loss of Large Trophy Fish from the Florida Keys with Historical Photographs

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Abstract: *A loss of large vertebrates has occurred in aquatic and terrestrial ecosystems, but data to measure long-term population changes are sparse. Historical photographs provide visual and quantitative evidence of changes in mean individual size and species composition for groups of marine fish that have been targeted by sport fishing. I measured such trends for 13 groups of recreationally caught "trophy" reef fish with photographs taken in Key West, Florida, from 1956 to 2007. The mean fish size declined from an estimated 19.9 kg (SE 1.5) to 2.3 kg (SE 0.3), and there was a major shift in species composition. Landings from 1956 to 1960 were dominated by large groupers (*Epinephelus spp.*), and other large predatory fish were commonly caught, including sharks with an average length of just <2 m. In contrast, landings in 2007 were composed of small snappers (*Lutjanus spp.* and *Ocyurus chrysurus*) with an average length of 34.4 cm (SE 0.62), and the average length of sharks declined by more than 50% over 50 years. Major declines in the size of fish caught were not reflected in the price of fishing trips, so customers paid the same amount for a less-valuable product. Historical photographs provide a window into a more pristine coral reef ecosystem that existed a half a century ago and lend support to current observations that unfished reef communities are able to support large numbers of large-bodied fish.*

Keywords: coral reefs, historical ecology, overfishing, reef fish, shifting baselines

Documentación de la Pérdida de Peces de Trofeo en los Cayos de Florida con Fotografías Históricas

Resumen: *Una pérdida de vertebrados mayores ha ocurrido en ecosistemas acuáticos y terrestres, pero los datos para medir los cambios poblacionales a largo plazo son escasos. Las fotografías históricas proporcionan evidencia visual y cuantitativa de cambios en el tamaño individual promedio y de la composición de especies en grupos de peces marinos que han sido blanco de la pesca deportiva. Medié esas tendencias en 13 grupos de peces de arrecife capturados recreativamente como "trofeos" mediante fotografías tomadas en Key West, Florida, desde 1956 a 2007. El peso promedio de los peces declinó de unos 19.9 kg (ES 1.5) a 2.3 kg (ES 0.3), y hubo un cambio mayor en la composición de especies. Las capturas entre 1956 y 1960 estuvieron dominadas por meros (*Epinephelus spp.*) grandes, y otros peces depredadores eran capturados comúnmente, incluyendo tiburones con una longitud promedio de poco menos de 2m. En contraste, las capturas en 2007 fueron compuestas de pargos (*Lutjanus spp.* y *Ocyurus chrysurus*) pequeños con una longitud promedio de 34.4 cm (ES 0.62), y la longitud promedio de los tiburones declinó más de 50% en 50 años. La gran declinación en el tamaño de los peces capturados no se reflejó en los precios de los viajes de pesca, así que los clientes pagaron la misma cantidad por un producto menos valioso. Las fotografías históricas proporcionan una visión de un ecosistema arrecifal coralino prístino que existió hace medio siglo y proporcionan soporte a los comentarios actuales de que las comunidades arrecifales no explotadas son capaces de soportar numerosos peces de talla grande.*

Palabras Clave: arrecifes de coral, ecología histórica, directrices cambiantes, peces de arrecife, sobrepesca

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Introduction

A gradual loss of large vertebrates, ranging from bison to monkeys to sharks, has occurred in aquatic and terrestrial ecosystems (Hill et al. 1997; Isenberg 2001; Baum et al. 2003) so that the density at which populations of megafauna existed in pristine ecosystems is often unknown (Jackson et al. 2001). Comparative ecological studies in degraded and protected areas provide evidence of the size and abundance of the largest vertebrates in less disturbed environments (e.g., Hill et al. 1997; Peres 2000; Dulvy et al. 2004), and records of hunting and fishing suggest historical population sizes (e.g., Jackson 1997; Myers & Worm 2003; McClenachan & Cooper 2008). Nevertheless, data related to exploitation are not always available over long enough timescales to measure change accurately, and too few regions exist with pristine megafauna populations. Thus, long-term declines in populations of the largest animals often go undocumented or are supported by anecdotes alone. Where they have been preserved, historical photographs taken by trophy hunters or fishers provide striking visual evidence of the size of the largest animals in the past, which can be quantified and used to help determine changes over long timescales. In this case study, I used historical photographs of trophy fish caught from waters around coral reefs surrounding Key West, Florida to determine the decrease in size of the largest predators from this marine environment.

In the ocean long-term population declines owing to fishing and hunting have been shown for species targeted by or caught as bycatch in commercial fisheries. Such studies have been limited by a lack of data, but as a general rule, data sets compiled over longer periods detect greater degrees of loss for large marine vertebrates, regardless of species. For example, Baum et al. (2003) showed declines of 75% in populations of several species of large pelagic and coastal sharks over just 15 years. Myers and Worm (2003) found that large predatory fish biomass has been reduced by 90% over the last 50 years, and Rosenberg et al. (2006) determined that biomass of today's Atlantic cod (*Gadus morhua*) populations on Canada's Scotian Shelf is just 4% of values in the 1850s. For green turtles (*Chelonia mydas*), length of observation of population size is strongly correlated with degree of loss assessed; nesting populations observed for at least 40 years were always assessed by the IUCN (Seminoff 2002) to be <40% of historical abundances, whereas the status of those populations observed for fewer years varied greatly with respect to historical abundance (McClanahan et al. 2006). Thus, for large marine vertebrates that have been hunted and fished over long timescales, historical data sets are needed to assess long-term population change.

Coral reef fish populations have been heavily exploited over long timescales (Pandolfi et al. 2003), and the level of fishing intensity influences community composition

(Koslow et al. 1988; Russ & Alcala 1989). Comparative ecological studies in degraded and protected areas show that the abundance of the largest-bodied animals, which are frequently top predators, varies greatly under different fishing regimes. For example, the biomass density of apex predators in coral reef environments in the northwestern Hawaiian Islands is more than 60 times greater than in the more heavily fished main Hawaiian Islands (Friedlander & DeMartini 2002). In the Pacific Line Islands the biomass of top predators ranges from 85% of total coral reef fish biomass in well-protected and remote reefs to 19% in more heavily fished reefs in the same archipelago (Sandin et al. 2008). Larger-bodied animals are exploited preferentially and take longer to recover (Jennings et al. 2001; Reynolds et al. 2005), so large fish are depleted before smaller individuals (Pauly et al. 1998). Thus, the size structure of fish communities provides an indirect measurement of fishing intensity and degree of overexploitation at the species level (Beverton & Holt 1956; Ricker 1975; Gulland & Rosenberg 1992) and the community level (Pope & Knights 1982; Gislason & Rice 1998). Multi-species analyses of size structure are particularly applicable to high-diversity fish communities in tropical regions (Gislason & Rice 1998; Dulvy et al. 2004; Graham et al. 2005), although their efficacy is inconsistent (Rochet & Trenkel 2003; Stobberup et al. 2005).

The Florida Keys contains a coral reef ecosystem in which fish communities have been subject to commercial, recreational, and subsistence fishing for hundreds of years (e.g., Romans 1775; Davidson 1889) and a sharp increase in the amount of recreational fishing pressure over the last 4 decades (Ault et al. 1998). A previous retrospective analysis (1979–1996) of the Florida Keys' reef fish communities showed that the largest and most desirable species of fish have been depleted and remain in an overfished state (Ault et al. 1998, 2005). Results also suggest that many fishery declines occurred prior to the 1980s because several fish stocks remained at constant low levels throughout the study period. Such patterns make sense because fishing effort was intense before 1979.

Traditional ecological and fisheries data do not exist to measure declines that occurred in Florida Keys reef fish communities before 1979, but photographs of trophy fish caught around Key West have been preserved since the mid-1950s. These photographs contain information on the species composition and size structure of landings from a time before ecological and fisheries-dependant data existed. Photographs were taken of fish caught on headboats (i.e., large charter boats that carry up to 75 passengers on day trips) by a single photographer from 1956 to 1985 and were preserved in historical archives. I took similar photographs of modern trophy fish caught on Key West headboats in 2007 and compared the historical photographs with these modern pictures to assess

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changes in the largest fish present on the reef. Secondarily, I assessed species composition of the catch to determine whether changes in the average size of the largest fish were due to shifting taxonomic composition of the catch or reduction in size within groups. Analyses based on these nontraditional data sources offer a baseline size structure for a time period for which there are no quantitative fisheries catch data.

Methods

I quantified changes in size structure of reef fish communities over the past 5 decades (1956–2007) with photographic data from the recreational fishing industry in the Florida Keys. Historical photographs represented 865 individual trophy fish caught between 1956 and 1985 aboard headboats in Key West, Florida (Fig. 1). These fish were caught by passengers on 2 companies' boats and landed at the Key West docks. The same 2 charter boat companies continue to operate in much the same fashion in Key West, and in January and August of 2007, I took a second set of photographs representing 410 individual trophy fish landed at the Key West docks and displayed in a similar manner (Fig. 1). In both modern and historical photographs, I considered for analysis all individuals hung on the display boards that were visible from head to tail.

To transform historical photographs into quantifiable data, I ensured that the photographs were comparable across time periods. First, I determined that the photographs were taken in a consistent manner and for the same purpose. The archival photographs were taken by a professional photographer, Charles Anderson, and represent the largest individuals caught on any particular day on 1 of 2 fishing boats. After each fishing trip, the largest trophy fish were displayed on hanging boards, and customarily a voluntary, nominal monetary pool was awarded to the passenger who caught the largest fish. Hanging the fish for display represented the process of determining the largest individual, provided an opportunity for passengers to pose with their trophies, and allowed captains to advertise for future trips. Piles of smaller fish below the display board were present in many photographs, further distinguishing the trophies from the average fish caught. Thus, the fish hung on the display boards in each photograph represented a set of the largest individuals caught daily.

All trophy fish were caught on boats fishing on and around coral reefs, so the photographs represent individuals caught in an area of similar habitat in the vicinity of Key West. The fishing sites remained relatively constant over time because distance traveled to the fishing grounds was limited by speed of the vessel, hours available to fish, and reef location. These headboats took day and half-day trips, typically within an hour's travel time of



Figure 1. Trophy fish caught on Key West charter boats: (a) 1957, (b) early 1980s, and (c) 2007.

the dock (Gulfstream III Fishing Inc. 2007). Furthermore, the captain, rather than the passengers, determined the fishing sites. Although different captains may have favored different reef areas, it was typical for captains to have a regular circuit of known reef sites. These sites were more consistent than those fished by smaller charter boats that take longer trips tailored to the desires of the passengers. Use of data from the past did not allow for a randomized sampling design, but these data provided a consistent measure of the relative size of the largest fish

caught from a limited area sampled by the same fishing boats over the last half century.

Next, I determined the dates the photographs were taken. Photographs from 1956 to 1960 had dates printed on their reverse sides, and I recorded the dates of the photos I took in 2007. Those taken between 1965 and 1985 did not have discreet dates, so I used information in the photographs to establish approximate dates. All photos from this time period were taken of fish caught aboard the vessels of a single charter boat company, Gulfstream Fishing, Inc., but 2 different boats were used between 1965 and 1985: the *Gulfstream II* (1965–1979) and the *Gulfstream III* (1980–1985) (T. Hambright, personal communication). All photographs included the name of the boat on which the fish were caught, so it was possible to subdivide photos into 2 categories: 1965–1979 and 1980–1985. Thus, I delineated 4 discreet time periods: 1956–1960 (period A), 1965–1979 (period B), 1980–1985 (period C), and 2007 (period D).

I identified each fish displayed to species or lowest taxonomic classification possible. Individuals I could not identify because of the condition of the photograph or condition of the fish were not included in the analysis. I determined the total length (TL) of each fish by measuring the fish relative to the height of the display board. I measured the heights of the actual display boards in August 2007 and determined the size had not changed over time (T. Hambright, personal communication). I printed each photograph and measured the fish and the hanging board. If the photograph was taken at an angle, I made several measurements across the hanging board to account for apparent size differences due to visual perspective. I converted the calculated fish lengths to biomass with standard length-weight relationships typical for each species but not specific to the Florida Keys (Froese & Pauly 2007). I identified and measured 1275 fish from these photographs.

The issues to be addressed were whether the size of the largest reef fish caught and displayed decreased over time, and the extent and timing of any measured change. Thus, I pooled the data from all fish and analyzed the combined data in terms of the mean size of trophy fish caught in each time period and the size spectrum of these fish. In size-spectra analyses, the $\log_{10}(x+1)$ number of individuals per size class is regressed on the \log_{10} midpoint of each length class (sensu Graham et al. 2005) and the slopes of these linear regressions are compared. In more heavily fished communities, slopes are expected to be more steeply negative owing to reduced numbers of individuals in the larger size classes (Dulvy et al. 2004; Graham et al. 2005). I grouped trophy fish from the photographs into 10-cm size classes (20 cm through 340 cm) for each time period and performed a one-way analysis of covariance (ANCOVA) on size classes with data across time periods to determine differences among slopes.

I assessed changes in the composition of landings to determine whether changes in mean size of trophy fish were due to shifting taxonomic composition of the catch or to reductions in size within groups. I divided data into 13 taxonomic groups for comparison and determined the composition of the landings as a percentage of individuals and a percentage of biomass for each time period. Sample sizes were not large enough to determine species-specific changes over time.

Because the modern photographs were taken over 2 months, January and August, it was important to know whether this restricted temporal sampling would bias the results, so I analyzed data for seasonal differences in mean size. To determine seasonal trends I used early photographic data from this study and data for the *Gulfstream* headboat collected by the National Oceanographic and Atmospheric Administration (NOAA) headboat sampling program from 1981 to 2006.

Finally, I compared modern data from the photographs of trophy fish from Key West with NOAA landings data from all headboats in the Florida Keys and Dry Tortugas for the year 2006 to determine the extent to which these data were representative of total landings in the headboat industry. I also compared my data with data for the *Gulfstream* collected by the NOAA headboat sampling program from 1981 to 2006 to determine whether the mean size of fish in the photographs was different from the mean size of fish measured by NOAA. I expected that the fish in the NOAA database would be larger than the average fish in the photographs due to the selective subsampling of only trophy fish in my study.

Results

The average length of individual trophy fish declined from 91.7 cm (SE 2.4) to 42.4 cm (SE 1.1), and the average weight declined from 19.9 kg (SE 1.5) to 2.3 kg (SE 0.3) between 1956 and 2007 (Fig. 2; Table 1). Significant differences in mean size were detected among all time periods (one-way analysis of variance [ANOVA], $p < 0.01$), except between the periods of 1956–1960 and 1965–1979. Even when species with current fishing restrictions—such as Nassau grouper (*Epinephelus striatus*), goliath grouper (*E. itajara*), and sawfish (*Pristis* spp.)—were excluded from the analyses, significant ($p < 0.01$) declines in individual size were detected (Fig. 2). Analysis of size spectrum differences among time periods showed that the proportion of small individuals among the trophy fish increased over time. Significant differences in slopes existed among all time periods (one-way ANCOVA $p < 0.01$); post hoc comparisons of slopes revealed significant differences among all pairs of time periods except for A and B, with the strongest differences ($p < 0.001$) between periods A and D.

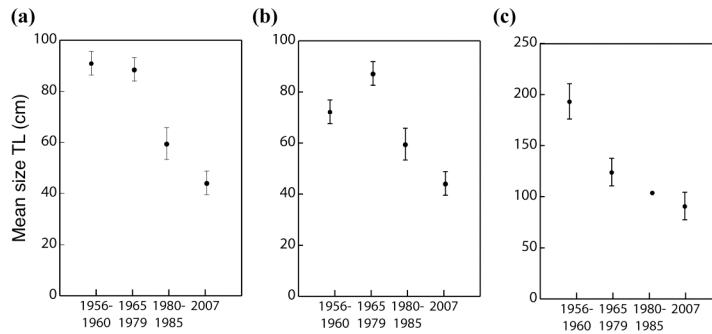


Figure 2. Mean size and standard error of (a) trophy fish in 1956–1960, 1965–1979, 1980–1985, and 2007, (b) trophy fish excluding species whose capture is currently prohibited, and (c) sharks in 1956–1960, 1965–1979, 1980–1985, and 2007 (TL, total length).

Within groups, no significant declines in length were detected except for sharks and *Epinephelus* groupers. The length of sharks, the most diverse taxonomic group and largest type of reef fish targeted, dropped from 195.2 cm (SE 16.4) in 1956–1960 to 90.9 cm (SE 5.5) in 2007 (Fig. 2; Table 1). Significant differences in the mean size of sharks were found among all time periods (one-way ANOVA $p < 0.01$) except between the periods of 1965–1979 and 2007. Sample sizes were small, but these results suggest a loss of large predatory sharks from south Florida waters prior to 1965, particularly when the species caught are considered. Of the 16 individual sharks caught and photographed between 1956 and 1960, 4 individuals were hammerhead (*Sphyrna mokarran* and *S. lewini*) and 3 were great white (*Carcharodon carcharias*) sharks. Between 1965 and 1979, only 1 hammerhead and 1 great white shark were photographed, despite equivalent numbers of total sharks in the sample. The most commonly caught species in this second time period were reef (*Carcharhinus perezi*) and silky (*C. falciformis*) sharks. In 2007 the only species of sharks caught and photographed were immature sharpnose (*Rhizoprionodon terraenovae*), reef (*Carcharhinus spp.*), and bonnethead (*S. tiburo*).

Declines in the size of *Epinephelus* groupers caught and displayed were detected in 2007 owing to restrictions on harvest of 2 of the largest species targeted, goliath (*E. itajara*) and Nassau (*E. striatus*) groupers. A moratorium on these species was enacted in 1990 and 1997, respectively (Reef Fishery Management Plan 2008 [Gulf of Mexico Fishery Management Council 2008]). Therefore, declines detected in *Epinephelus* groupers did not represent actual declines in the size of fish.

Thus, with the exception of sharks, declines in size of trophy fish caught in the recreational fishery were due to shifts in composition of landings rather than declines in mean size of individuals within groups. A closer examination of the taxonomic breakdown of the landings showed a shift of dominance from large-bodied to smaller-bodied groups over time (Fig. 3). Large *Epinephelus* grouper, whose average size was 135.3 cm (SE 3.2) in this sample, were 25% of the landings by individuals and 66% of the landings by biomass between 1956 and 1960.

Table 1. Sample size (n), mean length (L, cm), and standard error (SE) for each group of fish species and time period examined in a study of trophy fish landed in Key West Florida.

Species group	1956–1960		1965–1979		1980–1985		2007	
	n	L (SE)	n	L (SE)	n	L (SE)	n	L (SE)
Sharks	16	195.2 (16.4)	15	120.2 (15.1)	1	102.4 (na)	12	90.9 (5.5)
<i>Epinephelus</i> spp.	110	135.3 (3.2)	44	136.2 (6.6)	0	na	6	37.4 (6.9)
<i>Rachycentron canadum</i>	56	89.1 (1.8)	42	122.0 (3.3)	0	na	17	109.1 (2.5)
<i>Sphyraena barracuda</i>	28	92.0 (3.8)	13	110.0 (5.3)	0	na	2	108.5 (6.5)
<i>Scomberomorus</i> spp.	26	91.7 (3.7)	17	93.7 (2.7)	1	68.8 (na)	14	72.4 (9.0)
<i>Seriola</i> spp., <i>Caranx</i> spp.	14	88.1 (23.6)	38	99.0 (3.6)	0	na	2	51.5 (2.5)
<i>Mycteroperca</i> spp.	54	57.0 (1.6)	19	75.6 (3.9)	6	62.5 (3.2)	16	62.0 (2.1)
<i>Trachinotus</i> spp.	8	82.9 (4.1)	65	87.2 (2.5)	7	75.5 (5.8)	0	na
<i>Lutjanus</i> spp.	53	51.0 (1.4)	49	55.2 (1.2)	7	51.3 (9.8)	186	33.1 (0.9)
<i>Lachnolamus maximus</i>	18	46.9 (1.7)	27	55.4 (1.7)	3	49.9 (3.7)	3	41.7 (1.2)
<i>Ocyurus chrysurus</i>	17	40.0 (2.2)	16	50.2 (2.1)	2	47.1 (1.6)	100	38.0 (0.7)
<i>Haemulon</i> spp.	19	51.3 (2.2)	36	69.7 (1.5)	11	54.0 (1.5)	11	47.4 (5.0)
<i>Calamus</i> spp.	1	60.7 (na)	0	na	0	na	38	30.9 (8.1)
Other	4		19		3		3	
Total	424	91.7 (2.4)	400	90.0 (2.0)	41	59.5 (2.6)	410	42.4 (1.1)

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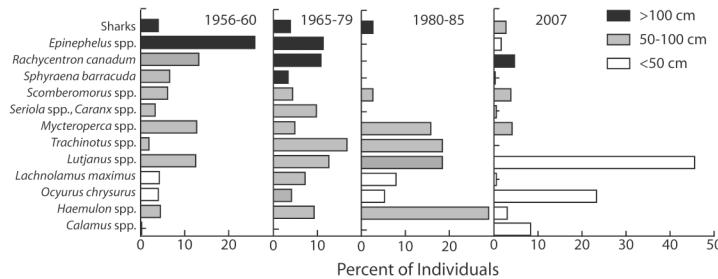


Figure 3. Species composition of displayed trophy fish in 1956–1960, 1965–1979, 1980–1985, and 2007 arranged in order of size from largest (sharks) to smallest (Calamus spp.). The mean size of each group within time period is indicated with shading.

By the second time period (1965–1979), this group had dropped to 12% of total landings by individuals and 33% by biomass, although no decrease in the average size of individuals occurred. Between 1965 and 1979, trophy fish landings were dominated by reef-associated pelagic fish, such as permit (*Trachinotus* spp.) and jacks (*Seriola* spp.). Together, these groups comprised 26% of the fish photographed and their average length was 87.3 cm (SE 2.5) and 98.5 (SE 3.6), respectively. In 2007, 72% of the trophy fish were snappers (*Lutjanus* spp. and *Ocyurus chrysurus*) with an average length of 32.8 cm (SE 0.83) and 37.7 cm (SE 0.83), respectively (Fig. 3).

Data from NOAA headboat landings confirmed the high abundance of small reef fish caught in modern recreational fisheries and demonstrated that the individuals in the photographs were indeed trophy fish. The mean length of fish measured by the NOAA headboat sampling program from the *Gulfstream* was 33.1 cm (SE 0.9) compared with 42.4 cm (SE 1.1) from the photographs. Differences existed in the species composition between the trophy fish and NOAA landings data for all of the Florida Keys and Dry Tortugas. In particular, the abundance of Lutjanid snappers was 24% greater among the trophy fish than in the total landings, and grunts were 33% more abundant in the landings data (Supporting Information).

No significant difference was detected in mean size of fish caught and photographed in January and August 2007, but some seasonal differences were detected in historical photographs (1956–1960) (Supporting Information). There was no significant difference in mean size of trophy fish caught in January and the rest of the year (86.8 cm [SE 7.1] vs. 92.1 cm [SE 2.5]), but fish caught in August were significantly smaller than those caught the rest of the year (59.1 cm [SE 3.1] vs. 98.8 cm [SE 2.5], $p < 0.0001$). The NOAA headboat sampling program maintains a large database of all types of fish landed, not just the largest individuals with which this study was concerned. Analysis of fish caught on the *Gulfstream* charter boat (1981–2006) showed that significant differences existed between January and August and the rest of the year. Fish caught in January were significantly larger (34.6 cm [SE 5.0] vs. 33.0 cm [SE 0.9], $p < 0.001$), whereas those caught in August were significantly smaller (31.8

[SE 2.3] vs. 34.6 cm [SE 0.9], $p < 0.0001$). These results suggest there may be some seasonal bias in the modern photographic data, particularly for fish caught in August. The sample size for modern photographic data from the month of August ($n = 45$) was lower than from January ($n = 365$), however, so any seasonal bias for smaller fish in the pooled data is likely small.

Discussion

A decrease in the size of trophy fish caught by Key West fishing boats has occurred over the last 50 years, reflecting a loss in the largest fish from the coral reef environment. The results of my analysis of historical photographs support results from prior analyses, which show that major declines have occurred in populations of large fish in Florida Keys' ecosystems and that chronic overfishing was occurring by the 1970s (Ault 1998, 2005). My results further suggest that loss of large sharks occurred before the mid-1960s. Observed historical declines in Florida Keys reef fish populations cannot be attributed to the recreational fishery alone. Both commercial and recreational fishing have contributed to declines, and before the 1970s the number of commercial fishing vessels targeting Florida Keys reef fish exceeded those in the recreational fishery (Ault et al. 1998).

These results provide evidence of major changes over the last half-century and a window into an earlier, less disturbed reef fish community, but communities of coral reef fish of the Florida Keys in the 1950s were themselves not undisturbed. Commercial fishing for reef sharks in the 1930s and 1940s reduced shark populations before the 1950s, and large groupers have been commercially fished since at least the 1880s. Thus, pristine coral reef ecosystems supported far more large fish than are implied by these historical photographs. More early data, such as records from the shark fishing industry in the 1930s and 1940s and information from the accounts of individual fishers from the early 20th century, could help contextualize this measured change in reef fish populations of the Florida Keys.

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My results add a temporal component to differences measured in comparative ecological surveys in coral reefs, which show unfished reef communities contain more large predators and more fish biomass per unit area than heavily fished coral reef communities (Friedlander & DeMartini 2002; Newman et al. 2006; Sandin, et al. 2008). Although the photographs I used did not provide a direct measure of overall biomass per unit area in the reef environment, they demonstrated that large fish were more abundant in the past. Furthermore, early photographs show piles of small fish below the hanging racks displaying the large trophy fish. Because they were not displayed as trophy fish, I did not consider them in this analysis, but their presence suggests historical reefs around Key West included large numbers of reef fish, large and small. The increase in small individuals displayed as trophy fish therefore may represent an overall reduction of fish biomass per unit area in the reef surrounding Key West, as would be expected on the basis of results from comparative ecological studies in modern reef communities.

The relationship between increased fishing pressure and declines in fish size is well developed, but the relationship between ecological degradation and marine-based tourism, a multibillion-dollar industry in the Florida Keys (Johns et al. 2001), is ripe for investigation. Conventional economic thought holds that decreased ecological health should lead to decreases in marine-based tourism revenues because customers' willingness to pay for services decreases with declining environmental health (Brown et al. 2001). In the case of fishing-based tourism, changes in the availability or size of fish would be expected to affect the overall value of the sport-fishing industry because the value of smaller fish in degraded reef habitats to anglers is less than that of large fish in a healthy reef environment (Gabelhouse 1984).

In Key West the order of magnitude reduction in size of fish caught by sport fishers over the last 5 decades would be expected to affect the price paid per trip or the number of people participating in the fishery, but neither has occurred. Despite a decline of 88% in fish weight, no significant trend in the cost of fishing trips, as shown in the price advertised in the photographs, was detected over the last 50 years. When adjusted for inflation (U.S. Department of Labor 2007), the trip cost ranged from \$40 to \$48 (in 2007 U.S. dollars) per person per day between 1956 and 2007. Furthermore, the number of people participating in the fishery did not decline. The data from NOAA headboat surveys from 1982 to 2006 showed no significant change in either the number of headboats trips leaving from Key West or the mean number of passengers per trip between 1982 and 2006.

Although these observations require further analyses, the continued viability of sport fishing based on increasingly small individuals in a degraded reef environment indicates a decoupling of the health of the marine en-

vironment from the value of the marine-based tourism industry. This shifted baseline (Pauly 1995) within the recreational fishing community suggests that reduced demand for recreational fishing trips may not occur in response to fish becoming smaller and more difficult to catch, and people will continue to fish while marine ecosystems undergo extreme changes in community structure.

This case study reflects local changes in reef fish communities around Key West, Florida, but anecdotal evidence suggests that similar declines in populations of large fish have occurred throughout the southeast region and along both coasts of the United States. Similar sets of historical data exist for marine and freshwater fish and potentially for terrestrial species hunted for sport as well. These data can be used on a case-by-case basis to provide information on which historical baselines can be established. Such analyses help describe the structure of ecosystems that existed in the recent past and can be used to establish goals for restoration of large predators on land and in the water.

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Supporting Information

Comparison of data from photographs with NOAA landings data for headboats operating in the Florida Keys and Dry Tortugas (Appendix S1) and seasonal differences in the size of fish caught and photographed on Key West headboats, 1956–1960 and 2007 (Appendix S2), are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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CHAPTER 6: Historical declines of goliath grouper populations in South Florida, USA

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*Contribution to the Theme Section Range-wide status and conservation of the goliath grouper**



Historical declines of goliath grouper populations in South Florida, USA

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ABSTRACT: Historical data are important in fisheries management and conservation, particularly for species which suffered significant population declines prior to the collection of ecological data. The globally endangered goliath grouper *Epinephelus itajara* was fished intensively long before data on population size were first collected. Historical population estimates have significant management implications, as the estimated time to full recovery depends on the size of the baseline population before depletion. Evidence used previously suggests that goliath grouper populations in Florida were reduced by as much as 95 % relative to estimated baseline levels at the time of protection in 1990 and have since recovered to more than 30 % of these values. However, actual historic abundances are not well known because few early data exist. I present 2 new data sets: (1) historical photographs of 'trophy fish' and (2) newspaper articles from the Florida Keys. I analyzed goliath grouper in photos taken of fish caught on Key West charter boats from 1956 to 1985 to assess changes in abundance before the fishery was closed in 1990. The average number of individuals displayed per trip decreased before 1960 and was reduced by 86 % before 1979. Further evidence of declines is found in newspaper accounts of landings (1923 to 1977), which show decreases in the maximum individual fish size caught and the proportion of large grouper caught from land vs. offshore before 1950. These results demonstrate population declines over longer time scales than are currently considered and suggest that recent increases do not represent significant recovery compared to population abundances before depletion.

KEY WORDS: Historical ecology · Shifting baselines · Historical overfishing · Goliath grouper · *Epinephelus itajara*

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INTRODUCTION

The degradation of marine ecosystems by overfishing over several human generations has resulted in lowered expectations for the natural abundances of marine animals and the value that marine ecosystems can provide to people (Pauly 1995, Jackson 1997, Dayton et al. 1998). Populations of marine fishes, turtles, and other large vertebrates that appear robust today are often small fractions of those observed by early explorers, naturalists, and fishermen (Jackson et al. 2001). When placed in a historical context, even populations that are considered depleted by modern standards are more severely reduced. Such shifting ecological baselines are difficult to quantify because historical data are sparse, typically qualitative, and not easily compared with modern fisheries and ecological data. Within the field of

historical marine ecology, methods have been developed to integrate historical data into traditional ecological analyses in order to understand long-term trajectories of ecosystem change and the cumulative impacts that human activity has had on marine systems (e.g. Jackson et al. 2001, Baum et al. 2003, Myers & Worm 2003, Pandolfi et al. 2003, Lotze & Milewski 2004, Saenz-Arroyo et al. 2005, Lotze et al. 2006, McClenahan et al. 2006, Rosenberg et al. 2005, Ferretti et al. 2008, McClenahan & Cooper 2008, Jackson 2008). Such analyses have become useful in assessing recovery and conservation status for marine animals around the world and are particularly relevant for the goliath grouper *Epinephelus itajara* in south Florida, USA.

Epinephelus itajara has been severely overfished throughout its range in both the tropical eastern Pacific and tropical western and eastern Atlantic, and is con-

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sidered to be Critically Endangered by the International Union for Conservation of Nature (IUCN 2007). In Florida, populations reached their lowest levels in the late 1980s, and a fishing moratorium was enacted in 1990 (NMFS 2006). Since protection, the population has begun to rebuild (NMFS 2006), but assessing population status is difficult without standard time-series data. Commercial and recreational catch statistics, which are typically used in stock assessments, are considered to be unreliable for the goliath grouper in USA waters (NMFS 2006, Porch et al. 2006). Instead, indices of abundance considered in the most recent status assessment (NMFS 2006) were developed using a set of logbook records of a single diver in south Florida (1982 to 2002) (Porch & Eklund 2004), surveys conducted by volunteer divers organized by the Reef Education and Environmental Foundation (1993 to 2002) (Porch & Eklund 2004), catch and effort data collected in the Everglades National Park creel fishery for juvenile goliath grouper (1973 to 1999) (Cass-Calay & Schmidt 2003), and anecdotal estimates of population change observed by 9 individual divers and anglers who were present in the Florida Keys before the early 1960s (Porch et al. 2006). Models based on these data sets suggest that the goliath grouper spawning stock biomass was reduced to 5 to 10% of virgin levels before the harvest ban in 1990 (Porch et al. 2006).

The goliath grouper population in South Florida has increased since protection in 1990 and is thought to have reached 31 to 36% of its pristine population biomass (NMFS 2006). Based on these recent trends, *Epinephelus itajara* has been reclassified to be no longer a species of concern in US waters (NMFS 2006). However, the reference points for recovery that were used to support reclassification were developed using data beginning in the 1970s and 1980s along with questionable assumptions, namely that (1) the population was in a pristine state in 1950, and (2) the most severe declines occurred in the 1980s (NMFS 2006, Porch et al. 2006). While it is clear that the *E. itajara* population was severely depleted by the late 1980s, few data exist to support assumptions about earlier changes. Therefore, historical data are needed to more accurately determine reference points for modern status assessments. In the present study, 2 new sets of historical data were analyzed: (1) photographic data from Key West charter boats (1956 to 1985) and (2) newspaper articles from the 'Key West Citizen' (1923 to 1977).

MATERIALS AND METHODS

Historical photographs. A series of photographs of large 'trophy' fish landed at the Key West, Florida docks between 1956 and 1985 was preserved in the

Monroe County Library's historical archives. These photographs contained information on the species composition and size structure of the landings of the largest reef fish before ecological and fisheries-dependent data began to be collected. Photographs were taken of fish caught on 2 headboats (large charter boats that carry up to 75 passengers on day trips) operating out of Key West by a single professional photographer, Charles Anderson. In each photograph, large trophy fish were displayed on hanging boards (Fig. 1). Hanging the fish for display represented the process of determining the largest fish caught on each trip, for which a voluntary monetary pool was typically awarded, and provided an opportunity for passengers to pose with their trophies and for captains to advertise for future trips (pers. obs., D. Gallagher pers. comm.). The photographs were both sold to the passengers, many of whom were from out of town, and sent to their local newspapers across the United States in hopes of attracting attention to Keys' fishing (D. Gallagher pers. comm.). Piles of smaller fish below the display board were present in many photographs, further distinguishing the trophies from the average fish caught. Therefore, the trophy fish hanging on display boards in the photographs represented the largest fish caught on any particular day.

Goliath grouper were frequently larger than the passengers themselves and were second in size only to sharks among the fish caught and displayed on these trips. While catching goliath grouper may have been a common occurrence for local Key West fishermen (E. Little pers. comm.), these large fish were likely a novelty to out-of-town anglers who went fishing on headboats and for whom the photographs were taken. Thus, it is likely that goliath grouper were targeted by the headboats throughout all time periods and displayed and photographed when they were caught. The assumption that frequency of display can be used as an indicator of relative availability underlies all analyses of photographic data.

All fish were caught on boats that target coral reef-associated fishes in close proximity to Key West. The distance traveled to the fishing grounds is limited by the speed of the vessel, the hours available for fishing, and the location of the reef. These charter boats take one-day and half-day trips, typically within an hour's travel time of the dock (Gulfstream Fishing Inc. 2007). Thus, the fish displayed in the photographs represented the largest fish taken in a limited area within 1 h of Key West sampled by the same fishing boats over time using similar gear and methods (Fig. 2).

Photos taken between 1956 and 1960 include dates, so the exact day and year the fish were caught were known. Those taken between 1965 and 1985 did not



Fig. 1. Examples of photographs from historical archives. Fish caught on the 'Gulf Stream' charter boat on (A) 14 April 1957, (B) 9 March 1958, and (C, D) between 1965 and 1979

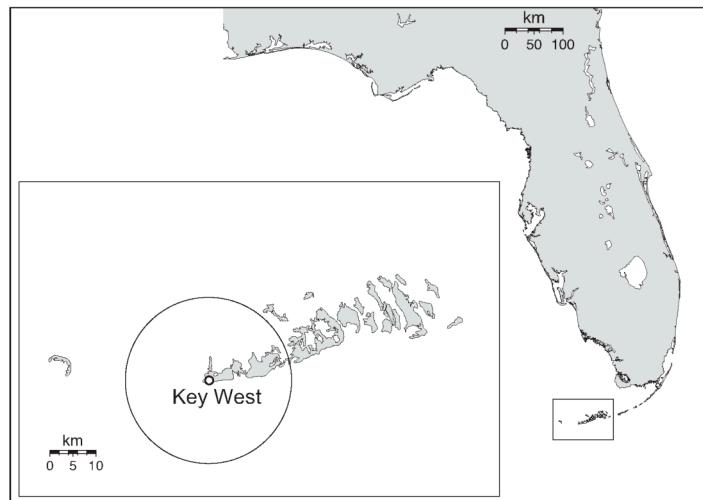


Fig. 2. Study area around Key West, Florida, where headboats operated

have associated dates so it was necessary to use visual information to date the photos. The most consistent and reliable information to determine the year the photograph was taken is the name of the boat, which was displayed in each photo (Fig. 1). The name of the charter vessel changed in 1980 (T. Hambright pers. comm.), so this dataset was segmented between 1965 to 1979 and 1980 to 1985. No photos were preserved for 1961 to 1964.

In order to generate quantitative data from these photographs, it was necessary to standardize photographs across time periods. All displayed fish that could be seen from head to tail and identified were included in the analysis. The total length (TL) of each fish was calculated relative to the height of the hanging board in the photograph (Fig. 3), which was measured in August 2007 and determined not to have changed over time (T. Hambright pers. comm.). If the perspective of the photograph was at an angle, several measurements of height were taken across the display board and averaged. The calculated fish lengths were converted to biomass using length/weight regression parameters (Froese & Pauly 2007).

A total of 852 fish and 136 ind. of *Epinephelus itajara* were identified and measured. The data were analyzed in terms of (1) species composition, as both a percent of individuals (number of goliath grouper / number of all individuals $\times 100$) and a percent of biomass for each time period (biomass of goliath grouper / bio-

mass of all individuals $\times 100$), (2) size frequency distribution of *E. itajara* within time periods, analyzed using a Kolmogorov-Smirnov test, (3) number of *E. itajara* caught, landed and displayed on each day of fishing, analyzed using a Student's *t*-test for combined data (1956 to 1960, 1965 to 1979) and a 1-way ANOVA for annual data for years in which photos from multiple trips survived (1957, 1958, 1959, 1960, 1965 to 1979), and (4) biomass of *E. itajara* caught, landed and displayed on each day of fishing, analyzed using Student's *t*-test for combined data (1956 to 1960, 1965 to 1979).

Historical newspaper articles. Early newspaper articles in the Florida Keys frequently reported large fish that were caught locally, both from docks and bridges, and those landed by boats in the Lower Keys. All relevant articles published in the 'Key West Citizen' between 1923 and 1977 were reviewed and information on the size of the fish and the location the fish was caught was recorded. Data was available for 26 yr during this time period. The weight of the largest fish reported for each year of data was recorded and the relationship between maximum size and year was estimated using ordinary least-squares for pooled data as well as data separated by fish caught from land and offshore. Finally, the percent of these largest fish caught from land vs. offshore was determined for 1923 to 1950 and 1951 to 1977.

RESULTS

Photographic data

Goliath grouper were among the largest fish commonly caught and displayed as 'trophy fish' in historical photographs. In the period between 1956 and 1960, 102 individual goliath grouper appeared in photographs, or 65% of the biomass and 24% of the individuals displayed (Fig. 4). Between 1965 and 1979, only 34 individual goliath grouper appeared in photographs, or 32% of the biomass and 9% of the individuals displayed (Fig. 4). No goliath grouper appeared in photographs between 1980 and 1985 (Table 1).

Displayed *Epinephelus itajara* ranged from 75 to 220 cm, and the size frequency distribution varied slightly between the 2 time periods (Fig. 5). The median, first, and third quartile lengths of fish photographed in 1956 to 1960 were 141, 116, and 160 cm, respectively, while those of 1965 to 1979 were 142, 126, and 179 cm, respectively. No

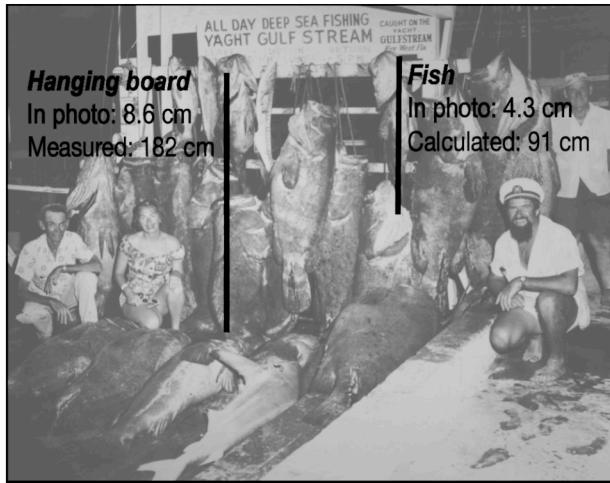


Fig. 3. Method of measuring fish from the Key West charter boats. The wooden structure on which the fish are hung (the hanging board) was measured on site in Key West. The height of the hanging board from the ground to the point at which it attaches to the sign was 182 cm. Fish lengths were then calculated relative to the height of the hanging board in the photo

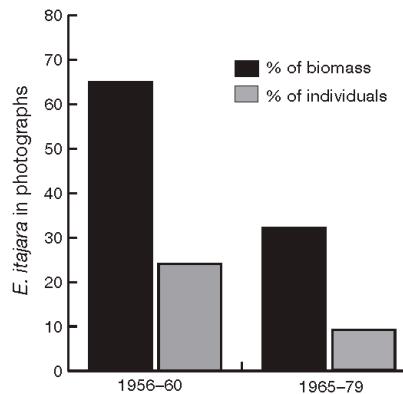


Fig. 4. *Epinephelus itajara*. Percent of individuals (gray) and percent of biomass (black) of goliath grouper in photographs, 1956–1960 and 1965–1979

Table 1. *Epinephelus itajara*. Average number of goliath grouper caught per trip, 1956–1979. Data from 1965–1979 and 1980–1985 were grouped because annual data were not available during this time period

Year	Number of trips	Number landed	Per trip landings (SE)
1956	1	7	7.0
1957	5	35	7.0 (2.6)
1958	9	24	2.9 (1.2)
1959	8	11	2.0 (0.7)
1960	13	16	1.4 (0.5)
1965–79	35	34	1.0 (0.2)
1980–85	2	0	0

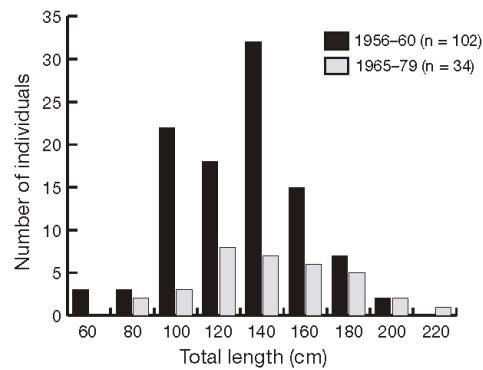


Fig. 5. *Epinephelus itajara*. Size distribution of goliath grouper 1956–1960 (black) and 1965–1979 (gray)

significant difference in the cumulative distribution was detected between the 2 time periods (Kolmogorov-Smirnov test, $D = 0.22$, $p = 0.16$).

A closer examination of the number of goliath grouper photographed per trip shows a steady decline over time in the numbers of individuals and corresponding per trip biomass. The maximum number of observed individuals photographed on 1 boat was 16, with an estimated combined biomass of 890 kg. The average annual number of individuals photographed per trip declined significantly for both pooled data for 1956 to 1960 (2.8 ± 0.6 , mean \pm SE) and 1965 to 1979 (Table 1; $t(69) = 2.89$, $p < 0.01$) and for annual data for years in which photos from multiple trips survived (Table 1; 1-way ANOVA $F_{4,65} = 7.51$, $p < 0.0001$). Average biomass of *Epinephelus itajara* caught and photographed per trip declined significantly ($t(69) = 2.2$, $p < 0.05$) from 153 ± 34 kg during 1956 to 1960 to 69 ± 15 kg during 1965 to 1979.

Newspaper data

Results from the analysis of the largest goliath grouper reported in the 'Key West Citizen' indicate that the largest goliath grouper were less frequently caught from shore after 1950. In the first half of the time period (1923 to 1950), 69% of the largest individual goliath grouper were caught from shore, whereas only 8% of the largest fish were caught from shore between 1951 and 1977 (Fig. 6). These data also demonstrate a significant declining trend in the maximum size of goliath grouper caught in the Lower Keys between 1923 and 1977 ($R^2 = 0.23$, $p < 0.01$; Fig. 6). Declines in the size of the largest fish were significant for fish caught from land ($R^2 = 0.32$, $p < 0.01$), but the trend was non-significant for fish caught offshore ($R^2 = 0.17$, $p = 0.13$).

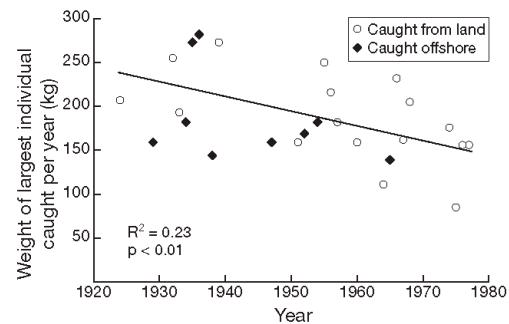


Fig. 6. *Epinephelus itajara*. Change in maximum weight of goliath grouper 1923 to 1977 reported in the 'Key West Citizen'

DISCUSSION

Photographic data show that in the 1950s, boats often returned with large numbers of goliath grouper, the combined biomass of which likely outweighed that of the passengers on board on many days. The decline in absolute and relative abundance of goliath grouper in photographs of Key West trophy fish suggests that local population declines occurred between 1956 to 1960 and 1965 to 1979. These could be due to changes in fishing practices, rather than changes in abundance. However, it is unlikely that goliath grouper were targeted or photographed less frequently after 1960, since goliath grouper remained an important sport fish until the closure of the fishery in 1990. This was as true for boat-based fishery as for spear fishermen. Moreover, goliath grouper continue to be caught and released by anglers (Cass-Calay & Schmidt in press, this Theme Section). Goliath grouper are among the largest reef fish, so it is very likely that they were photographed as trophy fish at least as frequently as other species, and likely were photographed whenever they were landed by the headboats. Thus, declines in the abundance of goliath grouper in photographs relative to other species, as well as the decrease in per-trip landings between 1956 and 1979 suggests early and significant population declines of goliath grouper in the vicinity of Key West. No goliath grouper appeared in photographs between 1980 and 1985, which could be due either to this localized depletion or to the small number of trips for which photographic data survived from this time period (Table 1).

No significant change in the size distribution of goliath grouper occurred between 1956 to 1960 and 1965 to 1979. This result is surprising, given the fact that the number of goliath grouper caught declined and is likely due in part to the small sample sizes. Size frequency analyses are typically conducted with >100 individual fish collected on time scales of 1 yr or shorter (Gulland & Rosenberg 1992), so that samples of 102 ind. over 5 yr and 34 ind. over 15 yr are not sufficient to represent the size structure of the population. More historical data for both time periods would help to better determine the relationship between size and number of fish caught.

In contrast to ambiguous results from the analysis of size frequency, results from the newspaper analyses suggest that the size of the largest fish declined significantly between 1923 and 1977, and that the largest goliath grouper were less abundant close to shore after 1950. While reductions in the size of the largest fish should not be interpreted as a direct metric of population decline, larger-bodied animals are exploited preferentially (Pauly et al. 1998), so that the size of the largest fish can be an indirect indicator of overall avail-

ability (Gulland & Rosenberg 1992). Declines in size and shifts to catching the largest fish offshore suggest that nearshore depletion of the largest goliath grouper was occurring by 1950.

Recent genetic research has produced more resolved data showing a strong signal of geographic isolation among individuals (Craig et al. in press). This work suggests that the status of the goliath grouper should be evaluated more conservatively. Similarly, the historical data presented here suggest that the status of the goliath grouper in the United States should be evaluated more conservatively, given the long history of exploitation relative to the short period of protection. Goliath grouper recovery to date (Cass-Calay & Schmidt in press) is promising, but these results suggest that this population recovery is less significant than implied by current assessments, which indicate that populations have recovered to 31 to 36 % of 'virgin' biomass since protection (NMFS 2006). Biological reference points used in the assessment were derived from recently collected data and based on assumptions that major declines occurred in the 1980s and that the population was in a pristine state in 1950 (NMFS 2006). Given the 7-fold decrease in the number of goliath grouper photographed per trip between 1956 and 1965 to 1979, and declines in the number of goliath grouper relative to other smaller trophy fish species, the photographic data suggest that the catch of goliath grouper was declining well before the 1980s. Newspaper data suggest nearshore declines before 1950. Each historical dataset represents a different indicator of abundance, but all suggest decline over long time scales. Taken together, they provide evidence that populations were not pristine in 1950 and were declining well before 1980. Therefore, the assumptions used in models of goliath grouper population status should be reexamined, so that historical baselines are set on a more appropriate time scale, and management should proceed cautiously and continue to protect this valuable and vulnerable species. Particularly because so few time-series data exist for the goliath grouper, both in the past and present, it is essential to include all reliable sources of data in assessing population status and trends. Without historical baselines, restoration targets for many species of historically exploited marine animals are far too low and management decisions are made without a proper ecological context.

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CHAPTER 7: How to disassemble a coral reef: Historical declines in Florida Keys' reef ecosystems

ABSTRACT

Few pristine tropical marine ecosystems remain around the world. In the Florida Keys, coral reef, mangrove, and seagrass communities have been degraded by multiple human impacts over centuries, so that the original structure of these ecosystems is unknown. The objectives of this research were to create baselines for marine organisms in the Florida Keys beginning in the sixteenth and seventeenth and centuries, when Europeans first began to occupy the region, and to analyze the sequence and causes of subsequent decline. We found that populations of large bodied animals, such as marine turtles and monk seals, were depleted first, regardless of trophic level, and there was little evidence that the sequence of exploitation followed trophic level as it has in temperate and oceanic ecosystems. The removal of structural elements, such as marine sponges, corals, and mangroves, reduced the overall area of habitat and three-dimensional complexity, and overfishing by subsistence, commercial, and recreational fishers caused further declines. Human population growth was a strong driver of depletion even before export markets were established, suggesting that tropical marine ecosystems can be depleted even at low population levels. However, the development of export markets and infrastructure to support commercial fisheries strongly intensified the depletion of marine animals, and the sequence of decline followed market forces. Synergistic effects among multiple human impacts intensified declines, which have altered the dynamics of coral reef food webs.

INTRODUCTION

Long-term ecological changes have been demonstrated in a variety of marine ecosystems (Dayton et al. 1998, Jackson et al. 2001). Declines in the relative abundance of organisms have frequently exceeded 90% (Myers and Worm 2003, Baum and Myers 2004, Lotze and Milewski 2004, Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2005b, McClenachan et al. 2006a, Rosenberg et al. 2006, Ferretti et al. 2008, Jackson 2008, McClenachan and Cooper 2008). Coral reefs are among the most degraded ecosystems worldwide, with declines in coral cover in excess of 80% and overfishing prevalent on the majority of reefs (Gardner et al. 2003, Newton et al. 2007). Changes to coral reef ecosystems have occurred over centuries and have involved declines in the abundance of organisms at all trophic levels (Pandolfi et al. 2003, Pandolfi et al. 2005, Hardt 2008). However, unlike temperate ecosystems, where changes have been well-described over long times scales (Lotze and Milewski 2004, Lotze 2005), few in-depth historical ecology studies of long-term change have been conducted in tropical environments. Thus, the relative abundances of exploited organisms are known only in the most basic terms. Even in the Florida Keys, which is a well-studied and economically important area in the richest nation in the world, little understanding exists of the degree and sequence of decline of marine resources.

In the Florida Keys, as in most coral reef ecosystems, pollution, climate change, and fishing are known to act synergistically to cause and perpetuate declines in ecosystem health, as measured by decreased coral cover, increased algal abundance,

and declines in the abundance of large bodied vertebrates (Pandolfi et al. 2005, Kline et al. 2006, Knowlton and Jackson 2008). While it is clear that pollution, disease, and climate change have had immense negative impacts on coral communities in the second half of the twentieth century, historical ecological analyses in a variety of coastal ecosystems have demonstrated that fishing is the earliest cause of decline in marine ecosystems, often occurring centuries before other stressors (Jackson et al. 2001). Therefore, this research focuses on documenting, describing and analyzing the effects of exploitation on the marine communities in the Florida Keys in order to estimate the major changes that occurred prior to the late twentieth century.

We take an ecosystem approach to measuring decline (*sensu* Lotze and Milewski 2004), focusing on coral reef and associated mangrove and seagrass ecosystems in the Florida Keys. Although it is well known that tropical marine ecosystems have experienced major declines over century long time scales (Jackson 1997, Pandolfi et al. 2003, Pandolfi and Jackson 2006), very little historical work has been done to estimate changes in abundance on a species by species basis. We address this by synthesizing quantitative and qualitative data for the last 500 years on the abundance, distribution, and exploitation of six major groups of organisms that comprise coral reef, mangrove, and seagrass ecosystems. The major questions addressed by this research are: (1) How have population abundances of prominent species in coral reef, mangrove, and seagrass ecosystems changed in the last 500 years in the Florida Keys? And (2) How have these ecosystems changed qualitatively as a result of changes in population abundances of key species?

METHODS

Study region

The Florida Keys extend westward from the tip of the Florida peninsula, from Key Biscayne to the Dry Tortugas (Figure 1). The Keys themselves have a total land area of approximately 266 km² (NOAA n.d.), and a diversity of nearshore habitats, including some of the northernmost coral reefs in the Atlantic, as well as associated seagrass and mangrove habitat. The diversity of habitats in the Florida Keys region corresponds with a spectrum of physical conditions, ranging from the shallow (2m average depth) and calm Florida Bay northwest of the island change, to the fore reef which drops off sharply to a pelagic system characterized by deepwater currents.

A combination of factors, including the warm Gulf Stream, broad continental shelf, and absence of major rivers provide conditions ideal for the development of an extensive reef tract, and nearly continuous reef structure exists from Biscayne Bay to the Tortugas Bank (Rohmann et al. 2005). Between 1,150 km² and 1,400 km² of hard bottom, patch reef and bank reef exist, dominated by *Montastraea annularis*, *Siderastrea siderea*, *Colpophyllia natans*, and *Acropora palmata* (Andrews et al. 2005). Florida's reefs provide habitat for approximately 260 species of reef fish. However, a majority of targetted species is overexploited (Ault et al. 1998).

In the shallow Florida Bay, seagrasses are the dominant biological feature. Seagrass beds cover more than 16,000 km² in the southeastern Gulf of Mexico between the Florida Keys and Cape Romano, forming the most extensive seagrass

beds in the world (Fourqurean et al. 2003). Beds of turtle grass (*Thalassia testudinum*) are common in shallow areas (<2m) of stable salinity that characterize the Florida Bay, and give way to manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*) in deeper and more dynamic regions (Fourqurean et al. 2003). An additional 1,000 km² of seagrass beds exist on the Atlantic Ocean side of the Florida Keys, intermingled with reef habitat (Iverson and Bittaker 1986, Zeiman et al. 1989). Seagrass beds provide food and shelter for a many species of economically important fish and invertebrates (Thayer et al. 1999), as well as a number of wading birds, manatees (*Trichechus manatus*) and green turtles (*Chelonia mydas*) (USFWS 1998).

Mangroves comprise the third important component of Florida Keys' marine environment. Red (*Rhizophora mangle*), black (*Avicennia germinans*), and white (*Languncularia racemosa*) mangrove trees fringe the islands of the Florida Keys, dot the Florida Bay, and line estuaries along the southern end of the Florida peninsula and Gulf Coast. As of 1981, mangrove communities covered approximately 1,570 km² in Monroe, Dade and Collier counties (Odum et al. 1985). The Florida mangrove system stabilizes sediments, and produces underwater habitat for attached organisms such as oysters, sponges, and algae, as well as for juvenile fishes and invertebrates (Ley and McIvor 2003). Almost all of the important commercially and recreationally caught fish species in south Florida depend on mangroves for a portion of their development, and they serve as rookeries for coastal and wading birds, including the endangered the brown pelican (*Oelicanus occidentalis*), the roseate spoonbill (*Ajaja ajaja*), and brown noddy (*Anous stolidus*) (Odum et al. 1985).

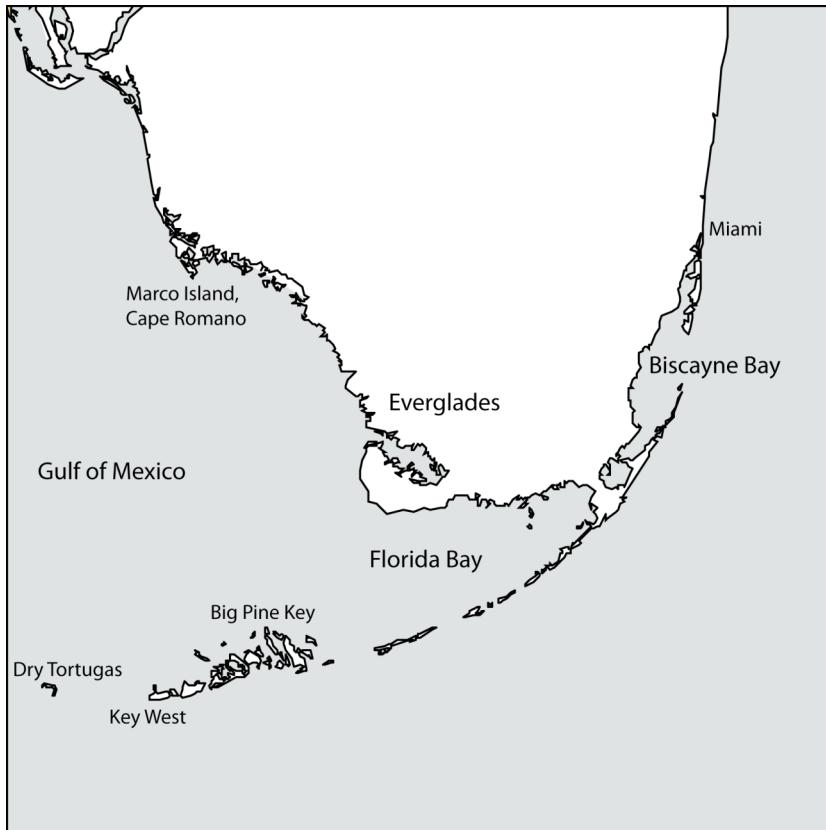


Figure 1. Map of study area with locations described in analysis

Organisms and general approach

In order to reconstruct the history of ecological change in the Florida Keys ecosystem, we assessed change in population abundances for species within six major groups of organisms that compose coral reef and seagrass ecosystems. Within each organism type, we determined species and species groups that (a) are ecologically significant and represent a range of feeding strategies, trophic levels, and ecological

function and (b) have extant historical records. We then assembled these historical records and assessed change in abundance over time. The species and species groups for which we were able to describe or assess long term change are: Marine mammals (monk seals, manatees, and whales); Sea birds (terns, noddies, gulls, and boobies); Marine reptiles (green turtles, hawksbill turtles, loggerhead turtles, leatherback turtles, and crocodiles); Marine fish (sharks, sawfish, groupers, and mixed reef fish); Mobile invertebrates (spiny lobsters, conch, and urchins); and Structural organisms (coral, mangrove, seagrass, and sponges).

Species groups span a range of categories for ecological, historical, and taxonomic reasons. Large tetrapods such as monk seals, green turtles, and manatees, are highly visible, well understood taxonomically, and historical fisheries data are available at the species level. Large tetrapods also have clear and individually disproportionately large effects on their environment, so that their ecological extinction alters the functioning of the entire ecosystem (Thayer et al. 1984). Good historical data are also available at the species level for commercially valuable invertebrates such as spiny lobster and conch. For other groups, such as reef fish, sharks, and most invertebrates, fisheries data do not distinguish among species. For these groups, we assessed change on a family or genus rather than a species level, which is appropriate because of the functional and ecological redundancy of species within these groups.

Sources and data types

A great variety of archives contain information that can be used to reconstruct baselines for marine organisms and their subsequent decline. We first determined the most meaningful types of historical sources and their principal repositories. South Florida was part of the Spanish and British Empires before it became a territory of the United States, and was populated by immigrants from Cuba, the Bahamas, and Europe. Thus, sources of information about historical exploitation and ecological state are located in archives in Great Britain, Spain, the Bahamas, and throughout the United States. In total, we visited 23 historical archives and other repositories of historical documents, where we collected and digitized source materials. We digitized 537 sources, which included 150 manuscripts and photo collections, 127 books, 124 journal articles, 45 sets of newspaper articles, 36 maps, 35 reports, 18 magazine articles, 2 sets of artwork, and 2 unpublished theses. A complete list of references used to determine occurrence, abundance, and change of species over time can be found in McClenachan and Jackson (2007). From these digitized source materials, we extracted information on natural history, abundance, distribution, and fishing effort for each species or species group.

The types of available sources differ among species groups and across time, and yield a variety of data types (Table 1). The earliest observers of the marine environment were Spanish and British explorers, who wrote about marine organisms that would provide fellow sailors with sustenance or imperil their ships. Sailors described in great detail the location of the reef tract, whose undetected presence

frequently caused shipwrecks, and provided advice for procuring food from the sea, such as the best locations to harvest green turtles and spiny lobsters. Eighteenth century natural historians described new and exotic species, often commenting on their distribution and abundances, and astute travelers described the numbers and nationality of fishers in the Keys as a way of assessing the political economy of the region. The nineteenth century marked the beginning of modern scientific data collection, whose sophistication increased through time. By the turn of the twentieth century, detailed information on the local flora and fauna and intensity of fishing effort was recorded for many species groups.

Each data source yields a different type of information that can contribute to historical reconstructions of abundance and fishing effort (Table 1). Early writings by naturalists, investors, settlers, and fishers include a large amount of natural history data, albeit in anecdotal form. Surveyors, oceanographers, and government fisheries officials recorded numerical data on the abundance and distribution of marine species, as well as fishing catch and effort. The combination of source materials varies across groups, but the overlap of data types provides a more complete picture than any one data source alone.

Table 1. Data sources and information type by time period

Dates	Dominant Political Group	Most Important Data Sources	Types of Information
Pre 1559	Native American	Explorers, shipwrecked sailors, archaeological data	Narrative descriptions, lists of species harvested
1559-1763	Spanish	Explorers and buccaneers	Narrative descriptions
1763-1783	British	British naturalists and surveyors	Admiralty charts, natural history descriptions, descriptions of fisheries
1783-1821	Spanish	Very limited	Absence of data
1821-1845	US (Territory)	American naturalists, surveyors, settlers, investors	Sailing charts, natural history descriptions, descriptions of fisheries
1845-present	US (State)	American naturalists, fisheries scientists, fishers, ecologists	Newspaper articles, sportfishing records, commercial fishing statistics, export records, photographs, early and modern scientific data

Data analysis

The goal of this analysis was to determine order of magnitude changes in the abundance of marine organisms that would be undetectable by analyses of traditional ecological and fisheries data, whose collection post-dated ecological changes by decades to centuries. For this reason, we considered and incorporated all credible source material that we found, across all levels of precision present in each individual data source. In this way, we have maximized generality and realism at the expense of precision (Levins 1968). Our approach of focusing on order of magnitude changes over decade to century long time scales, rather than precisely measured fluctuations of the recent past, is appropriate for analysis of change in ecosystems whose degradation began long before scientific data began to be collected (Jackson and Alexander in press). For example, several species of marine fish that were commonly caught in the Florida Keys in the 1880s were rare by the 1950s (McClenachan et al. 2006b), so that assessing change in the last few decades would yield an extremely shifted baseline. Further, at least two species of large marine tetrapods were rare in Florida before the first fisheries data were collected in the 1880s (this study), underscoring the fact that accurate assessments of long term declines cannot be measured by a few decades of precisely measured population assessments or commercial fisheries data.

In this context, we analyzed the historical data to determine changes in absolute abundance, relative abundance, loss of species range, declines in size, and changes in catch composition for each species or species group. Data varied among groups, but for each that was the object of a directed commercial or recreational fishery, we

synthesized the available data to determine the timing and intensity of the fishery and an estimate of the number of individuals taken at the peak or over the course of fishery. For species that were not part of a major directed fishery but whose populations have changed due to other events, we documented the historical change using quantitative and qualitative historical observations on abundance over time.

HISTORY OF EXPLOITATION

Changes in coral reef ecosystems have been shown to occur prior to European colonization in the Caribbean. For example, in Jamaica, analysis of archaeological remains shows unambiguous degradation of nearshore marine resources before European arrival, with a decline of 75% in the average fish size and a reduction in the mean trophic level of fish consumed between 850 and 1430 A.D. (Hardt 2008). In the Turks and Caicos, green turtles were locally extinguished by native hunters before European arrival (Carlson 1999) and in St. Augustine Florida, geographically close to the study site in this investigation, archaeological evidence demonstrates early changes in the diversity and trophic levels of exploited sharks, rays, and bony fishes (Reitz 2004).

Two Native American groups, the Tequesta and Calusa Indians, utilized the Keys for marine resources, and at least two Calusa villages existed in the Florida Keys (Fontaneda 1575), most likely on Matacumbe Key and Key West (Goggin 1950, Swanson 2002, Worth 2006). The pre-contact population size of the Calusa in all of

southwest Florida is estimated as approximately 21,000 people, with 90-95% of the population located along the coast, and approximately 1,000 people in the Keys (Worth 2006). A sixteenth century shipwrecked sailor wrote that the Calusa subsisted on fish, turtles, seals, whales, and lobsters (Fontaneda 1575), and archaeological investigations in the Upper Keys uncovered the remains of large numbers of birds, fish, and shellfish, including queen conch (*Strombus gigas*) and several smaller gastropods (Goggin 1944). At a site on nearby Marco Island, an estimated three million m³ of shellfish remains were uncovered (Widmer 1988), suggesting that marine resources were heavily exploited. Unlike native populations in much of the Caribbean that were rapidly destroyed by European colonists, the Calusa effectively resisted for more than a century, and populations persisted in south Florida until the first decade of the eighteenth century, when more than 10,000 people were captured by English-allied slave raiders. The remaining population of fewer than 100 people fled to the Keys where they lived until they were finally removed to Cuba in 1760 (Worth 2006). The Calusa very likely maintained a dependence on marine resources marine in the Keys until late eighteenth century, but little quantitative analysis of faunal remains in archaeological materials has been conducted (K. Walker, personal communication). Therefore, for most species, we analyzed the history of exploitation based on written documentation by European explorers and settlers.

Along with fishing and hunting native populations, commercial fishing by Cuban and Bahamian settlers has occurred in the Keys since the beginning of the sixteenth century. The channel between Florida and the Bahamas was part of a major

Spanish sailing route, and British pirates set up camps in the Florida Keys, where they relied heavily on marine resources for food. Cuban fishers frequented the Keys, particularly Key West and Bahia Honda, to catch turtles, sharks, and finfish such as red drum, black drum, and pompano, which they sold in the Havana fish market. In the late eighteenth century, fishers were so numerous that contemporary observers described the coast of Florida as “covered with fishermens’s huts” (Romans 1775).

Britain controlled Florida from 1763 to 1783, when surveyors worked to map the coastline and chart the bottom type from the Dry Tortugas to Key Biscayne. Surveyors described abundant marine resources, writing that there was enough fish in the Keys to supply entire Caribbean region (Gauld 1796). The chief British surveyor went so far as to request that the sailors on his ships be reduced to two thirds of the standard food rations because they could easily feed themselves on the turtles, lobsters and fish that were found throughout the Keys (Gauld 1796).

The Treaty of Versailles returned Florida to Spain in 1783, and Spain maintained control of Florida until 1821, when Florida became a United States’ territory. In the 1820s, a slow influx of immigrants began to make permanent settlements in the Keys. Skilled Bahamian seafarers immigrated to the Keys and established a local fishing economy based on extraction of conch, sponges, and finfish. Though politically part of the United States, Key West during the early nineteenth century was in reality a tiny Caribbean island outpost with fewer than 1,000 residents, accessible only by boat and isolated from the rest of the nation, but strongly integrated into the northern Caribbean economy. Its economy was local and marine-based with

few types of products for export, so that the relative importance of fish was high. In the 1830s, exporting live fish to Havana occupied more than one third of Key West's boat traffic (U.S. 1837-1888). By the 1840s, more than 100 boatloads of fish were brought each year to Havana, where the fish market had become known for its variety and quantity of fresh fish (U.S. 1837-1888, Turnbill 1840).

By the time Florida was granted statehood in 1845, Key West had grown to be the most populous city in Florida, with approximately 3,000 residents. In the 1850s,

more than half of the people of Key West were Bahamian immigrants whose chief

businesses were "fishing, sponging, turtling and wrecking" (Anonymous 1853).

Commercial fishing connected the Florida Keys with the Caribbean, as well as the rest

of the Atlantic. Men who fished in the summer season on New England's George's

Bank traveled to Florida in the winter to fish between Key West and Tampa for mullet

and other fish intended for the Havana market. Once in Florida, these fishers made

monthly fishing trips that yielded 300,000 to 500,000 pounds of fish (Anonymous

1858).

In the second half of the nineteenth century, two new export fisheries, green

turtles and sponges, grew to dominate Florida Keys fishing effort. The first Key West

green turtle cannery opened in 1849, and sponges were exported for the first time in

the same year. By 1890, turtles and sponges were the two major marine exports sent to

northern markets. As the local population expanded, fishing for reef fish increased,

and by the time that the first Federal fisheries assessments were conducted in the

1880s, fishing provided employment for over 2,400 Florida residents. The twenty-one

schooner rigged vessels that fished for large groupers and red snapper for the Havana market fished in the area north of Key West and along the western edge of the Tortugas reef bank. Forty sloop-rigged vessels, whose average length was twenty-four feet, fished for smaller fish to be sold in the local market. These boats worked near and around Key West, typically within four miles of the town. All fishing boats had live wells, as fish were sold primarily directly from the boats. Annual landings in the 1880s averaged two million pounds (Goode 1887a).

Despite the intensive fishing and hunting in Key West and the Dry Tortugas, the Keys remained disconnected from the rest of the continental United States until the completion of the Florida East Coast Railway in 1896 and the Key West Extension in 1912. The railroad connected Key West to the eastern seaboard, which increased the number of settlers and visitors to the Keys, and prompted the growth of the recreational fishery, which previously had been restricted to a small number of adventurous boat-based fishers. The first ice plant was built in 1920, allowing fish to be preserved and shipped longer distances. Improved employment prospects in Key West stimulated a further influx of Bahamian settlers, with an estimated 10,000 to 12,000 Bahamians immigrants settling in south Florida in the first two decades of the twentieth century (Albury 1975).

In the twentieth century, both commercial and recreational fisheries developed in Florida. Several Florida commercial fisheries reached their peak in landings in the 1970s and 1980s, including spiny lobster with 5,179 metric tons landed in 1972 for the entire state, grouper with 6,324 metric tons in 1982, and snapper with 232 metric tons

in 1987 (NMFS 2009a). Recreational fishing expanded after 1960, with the number of recreational fishing vessels more than quadrupling between 1964 and 2000, compared with commercial fishing vessels which have increased by less than a factor of two in the same time period (Ault et al. 2001). Though the catch of individual recreational fishing vessels is much less than that of commercial boats, the cumulative effect of recreational fishing on fish stocks has exceeded that of commercial fishing in several Gulf states (Coleman et al. 2004).

Other human factors including deforestation, drainage projects, climate change, and introduced species have contributed to the transformation of the Florida Keys marine ecosystems in the last century. In particular, redirection of fresh water on the Florida mainland and the construction of the Overseas Railroad caused major changes in the hydrology of the Florida Bay and Keys prior to WWII (Brewster-Wingard and Ishman 1999, Fourqurean and Robblee 1999). Recent population expansion and failure to treat human waste, along with high levels of land clearing for construction, contributed to increased levels of suspended sediments and nutrients in reef and seagrass environments (Andrews et al. 2005). Coral disease and climate have led to further reef degradation in the last few decades (Andrews et al. 2005). While we discuss the synergistic effects of a variety of human pressures, the primary purpose of this study was to evaluate early changes in marine ecosystems due to hunting and fishing. Thus, the focus of the analysis is on the long-term effects of extractive activities.

RESULTS

Changes in organisms over time

We describe changes in abundance, distribution, and responses to exploitation for organisms in the Florida Keys marine ecosystem in descending taxonomic order, starting with marine mammals and finishing with structural organisms. Exploitation did not occur simultaneously among groups, with larger vertebrates typically being exploited first. For example, green turtles were heavily exploited before fishing for some species of reef fish began in earnest. Therefore, the timescales for our analysis vary. In each case, we provide the historical evidence of abundance and exploitation, describe the nature and the extent of the fishery, and when possible, estimate historical population size or relative abundance over time. Where appropriate, we provide analysis of linkages among organisms and describe cascading effects of decline in order to describe broader ecological change.

Marine mammals

Monk seal remains have been found in archeological remains in the lower Florida Keys (Swanson 2000, Adam and Garcia 2003), as well as mainland Florida (Ray 1961, Fradkin 1976, Cumbaa 1980, Wing and Loucks 1984, Wing 1992). Seals were present in the Keys upon European arrival; the first Spanish sailors arrived in 1513 and killed fourteen seals in the Dry Tortugas. A Spanish sailor who was shipwrecked in the Florida Keys in 1545 and lived in various villages with Calusa Indians for seventeen years wrote that seal meat was reserved for high-ranking people

(Fontaneda 1575), suggesting that they may have already been rare. In the mid eighteenth century, however, British explorers observed that the Florida Keys “abounded with great plenty of seal” (Roberts 1763) and a nineteenth century map of the Dry Tortugas labels “Seal Island” (de Brahm 1770s). Monk seals in Florida were killed commercially for their oil, which was used by the Spanish for treating the bottoms of their boats (Roberts 1763). In 1742, a British warship was wrecked at the Dry Tortugas and her crew of 287 men was marooned for sixty-three days. The ship’s log records almost daily capture of seals for men to eat (Swanson 2000). In twenty days of record keeping, at least thirty-four seals were killed, with up to six seals taken in one day (Viele 2000). “Small seals,” which were likely pups, were also killed, suggesting the persistence of a robust breeding colony. By the 1870s, the Dry Tortugas colony had been eradicated and monk seals were only occasional visitors to Florida; rare individuals that were observed were presumed to be strays from the Bahamas (Allen 1880). The last known seal in Florida waters was killed in 1922 near Key West and the Caribbean monk seal was globally extinct by 1952 (Neill 1957).

Monk seals were historically ubiquitous throughout the Caribbean, with pre-exploitation populations estimated as more than 200,000 individuals (McClenachan and Cooper 2008). Based on analysis of monk seal historical data for the Caribbean, it is likely that at least one breeding colony existed in the Florida Keys region, which was almost certainly in the Dry Tortugas. The densities at which monk seals existed in the rest of the Caribbean were estimated as twelve to eighteen adult seals per km² of reef (McClenachan and Cooper 2008). If the reef area of the Keys is assumed to be

between 1,150 and 1,400 km², the total pre-exploitation population would have been between 13,800 and 25,200 individuals. However, this estimate is likely too high, as observations do not support population abundances of this size, and Florida was at the northernmost extent of the monk seal's range, at least at the time of European contact. It is possible that the northern limit of the monk seal range in the sixteenth century was an artifact of long term history of hunting by native people on the mainland. Seal remains have been found as far north as Cumberland Island, Georgia in a nomadic aboriginal site from 1,300 to 2,600 years ago (Milanich 1971), as well as at sites ranging from 500 to 4,000 years old in Miami and along both coasts of the Florida Peninsula (Ray 1961, Fradkin 1976, Cumbaa 1980, Wing and Loucks 1984, Wing 1992, Adam and Garcia 2003). Most monk seal bones are found in food remains of nomadic peoples, so are not necessarily representative of the location the animal was killed, but the wide-ranging nature of the remains prior to European contact suggests an already restricted distribution.

Manatees have been considered to be naturally low in abundance in the Florida Keys due to limited freshwater resources. However, a large quantity of ideal habitat existed in the Everglades, similar to that in Central America, where manatees were historically abundant (Dampier 1729, Mckillop 1985). It is possible that that native people in Florida hunted manatees extensively, as occurred in Belize and other locations around the Caribbean, reducing their population abundances. Few post-contact references exist in the Florida Keys, even though manatees were preferred food for both Spanish and British colonists wherever they were encountered in the

Caribbean (Hardt 2008), suggesting that low population abundances existed at the time of European contact. While there is no evidence for historically high population in the Keys, abundant manatee populations were described on the Florida peninsula. European settlers hunted them with seines, harpoons, and rifles for food, sport, and for the ivory derived from their rib bones (Williams 1837). By the 1920s, manatees had “become quite rare” (Henshall 1921) and were considered to be “almost exterminated in Florida” (Anonymous 1929). Current populations for the state of Florida are approximately 4,000 individuals.

Whales were seasonally abundant in south Florida, and were killed by Native Americans along the east coast of Florida and in the Keys (Fontaneda 1575, San Miguel late 1500s). One Spanish priest reported “a great number of the spine bones of the whales which the Indians kill” along the coast (San Miguel late 1500s), and a letter written to the Spanish crown mentions hunting whales to the southeast of Florida (Anonymous 1519-1648). New England whaling vessels worked in Florida and the Bahamas in the eighteenth century (Schoepf 1788), but by the nineteenth century whales were observed to be “much rarer than the manatee” (Davidson 1889). Likewise, dolphins were abundant along the Florida coast, and were hunted for food by Native Americans (Widmer 1988). In the nineteenth century, there was speculation about the profitability of hunting dolphins for their valuable oil, (Williams 1837), but this fishery was never established.

Sea birds

Colonial sea bird populations have been reduced by humans since at least the 1770s, when Cuban colonists frequented the Keys and Dry Tortugas to collect the eggs. Hunters primarily took tern eggs, favoring eggs from the sooty tern (*Sterna fuliginosa*), which was known as the “egg bird.” In the 1830s, John J. Audubon described the “persons called Eggers” who arrived each spring in the Dry Tortugas at the same time as the “clouds of sea-fowl” to collect seabird eggs (Audubon 1832). By 1890, several species, including herring gulls (*Larus argentatus*), laughing gulls (*Larus atricilla*), royal terns (*Sterna maxima*), least terns (*Sterna antillarum*), sooty terns (*Sterna fuliginosa*), and brown noddies (*Anous stolidus*), were considered to be severely diminished by egg collecting, while the red-footed booby (*Sula sula*) was reduced by direct hunting (Scott 1890).

Robertson (1964) estimated populations of sooty terns in the 1830s as 40,000 in the Dry Tortugas after heavy exploitation. This species’ population rebounded in the twentieth century, and likely reached pre-exploitation abundances of more than 100,000 individuals by 1940 (Robertson 1964, Scherbaum 1997). The population size subsequently varied greatly throughout the twentieth century, ranging from 25,000 to 40,000 in recent years (Florida Fish and Wildlife Conservation Commission 2003). Despite its relatively high numbers, the bird’s restricted range on Bush Key in the Dry Tortugas qualifies it as a Species of Special Concern by the Florida Committee on Rare and Endangered Plants and Animals (Kale 1978). Sooty terns appear to have had a restricted range historically, as they nested on East Key and Bird Key in the Dry

Tortugas, but were not observed elsewhere (Scott 1887, 1888, 1890, Bowdish 1909, Pangburn 1919).

Roseate terns (*Sterna dougalli*) have been severely reduced from historical numbers, and only 350 pairs nest in three colonies today. In the early nineteenth century this species nested throughout the Keys, but was restricted to the Dry Tortugas by the early twentieth century (Robertson 1964). The Tortugas colony has disappeared, and nesting shifted back to the lower Keys. Other species of terns have been completely eradicated. Royal and sandwich terns were historically very abundant in the Dry Tortugas and present in great numbers throughout the Keys, but no breeding colony exists for either species in South Florida today, although both species nest in northern Florida.

Brown noddies had estimated populations of 40,000 in 1830, and populations remained steady until the early twentieth century. In 1919 this colony was estimated at 35,000 nests (Robertson 1964). The introduction of rats reduced the population to 400 pairs by 1938, and current population abundances are between 2,500 and 3,000 pairs (Robertson and Woolfenden 1992), with breeding occurring only on Bush Key in the Dry Tortugas (Kale 1978). This implies a reduction of 65 to 80% since the 1830s, after diminishment by egg collection had already occurred (Table 4).

Marine reptiles

Green turtles were historically a preferred food source for Caribbean islanders (McClanahan et al. 2006a), and likewise were hunted by native people in the Florida

Keys (Fontaneda 1575). Green turtle remains have been excavated in sites throughout south Florida (Wing and Reitz 1982), and were present in great numbers when Spanish explorers arrived. Sixteenth century Spanish explorers named the Dry Tortugas for the large number of green turtles present, killing more than 160 and observing that they “might have taken more had they wished them” (Herrera y Tordesillas 1730). By the eighteenth century, settlers from the Bahamas and Cuba were visiting the Keys “constantly” to catch turtles (de Brahm 1770s), and sailors relied on populations of turtles for food when they traveled through the Keys. In particular, Key West and Bahia Honda were noted nesting spots that could be counted upon to provide turtles during the nesting season (Gauld 1796). The eggs of nesting turtles collected from beaches were also a coveted food source. In the early nineteenth century, egg collectors from Cuba and the Keys visited the Dry Tortugas (Audubon 1832), and Key West residents collected eggs along the beach, so that it was rare to find a nest that had not been evacuated by local egg collectors (Hackley 1830-1857). By the 1830s, turtle hunting had become such an important part of Keys’ culture and cuisine that a turtle crawl, or holding pen, was considered to be as essential to Florida settlers as “a barn is to a northern farmer” (Williams 1837). A good turtler could catch ten to twenty turtles per day, and turtle meat was found commonly in local fish markets (Williams 1837).

In the early nineteenth century, turtle populations were heavily exploited, but still robust. In the 1830s, Audubon and others described the turtles in the Keys as abundant enough to keep the seagrass constantly cropped by their grazing, confirming

observations made 150 years earlier by William Dampier (Dampier 1729, Audubon 1832, McCall 1868). Hunting intensified in the next few decades, as turtle canning for shipment to northern restaurants began. The demand for turtle meat quickly outstripped the supply of local turtles, and turtles were commercially extinct in the Keys by the 1890s, when fishers began to travel to Central America to hunt turtles for the cannery.

Commercial hunting records exist beginning in the 1880s, but the locations where the turtles were caught were unfortunately not recorded. Thus, these records cannot provide a reliable estimate of turtles caught in the Keys. However, it is possible to make basic estimations of local consumption before the turtle cannery opened. In 1840, there were 688 residents in Key West. If we assume that each person consumed one pound of turtle meat per week, which is conservative based on contemporary descriptions of turtle consumption (Hackley 1830-1857) and that the average turtle contained 40 to 100 lbs of edible meat (Goode 1884), this suggests that 358 to 894 individual turtles were caught annually for local consumption. In contrast, between the years 2000 and 2006, an average of 44 nests were laid annually in Monroe County, which corresponds to approximately 55 adult turtles, assuming that the average interval between nesting is 2.5 years and each female lays four nests per year (McClenachan et al. 2006a). In the all of Florida, fewer than 5,600 nests have been laid annually in recent years, which corresponds to a population of approximately 7,000 adult turtles (NMFS 2007a). Thus, the number of green turtles killed annually for local consumption in Key West in the early 19th century exceeds the current

breeding population of Monroe County by at least six times, and represents 5-12% of the population of the entire state today.

Other large-bodied marine reptiles, including the hawksbill turtle (*Eretmochelys imbricata*), leatherback turtle (*Dermochelys coriacea*), loggerhead turtle (*Caretta caretta*), and crocodile (*Crocodylus acutus*) are endangered throughout their range, and historical evidence exists for larger populations of each species in the Florida Keys. In the 1830s, John Audubon described four species of turtle (green, hawksbill, leatherback, and loggerhead) as nesting so abundantly in the Keys that “on certain parts of the shore hundreds of turtles are known to deposit their eggs within the space of a mile” (Audubon 1832). Hawksbill turtles nested on the outer keys only (Audubon 1832), and were considered to be rare relative to the green turtle in the 1830s (Williams 1837). However, hawksbill turtles were abundant enough to sustain commercial hunting through the early twentieth century, when the average price for turtle shell in the Keys was three to four dollars per pound (Blatchley 1932). Regionally, enormous hawksbill populations existed in areas with remote beaches, such as the Bahamas and the Caribbean coast of Central America (McClenachan et al. 2006a). Despite low historical abundances relative to other species in the Keys, hawksbill turtles were certainly more abundant in the past than they are today, as numbers of nesting females in Florida are estimated at one to two individuals for the entire state (Meylan 1999).

Leatherback turtles also nested with some frequency in the Florida Keys in the nineteenth century (Audubon 1832), but today a total of ten to twelve individual

leatherback turtles nest in Florida each year (Scott 2003). Perhaps because they were not hunted as vigorously and have a more pelagic distribution than green and hawksbill turtles, the loggerhead is the most abundant turtle in Florida today with more than 15,000 females nesting in south Florida and continued nesting on the Dry Tortugas (NMFS 2007b).

Historically, the crocodile nested in the upper Florida Keys and individuals were found as far south as Key West. Hunting for hides and land clearing for development eliminated nesting sites before the 1970s, and today crocodiles nest only in southern Biscayne Bay and northeastern Florida Bay (Kushlan and Mazzotti 1989, Mazzotti 1999). The total number of crocodiles in south Florida at the turn of the twentieth century is thought to have been between 1,000 and 2,000 individuals (Ogden 1978), implying a reduction of 50 to 90% to current populations of 200 to 500 individuals (King et al. 1982). However, crocodiles were already considered to be rare in by 1900 (West 1900, Barbour 1945), implying reductions on the higher end of the estimated range (Table 4).

Marine fish

The first anecdotal observation of decline in fish populations occurred in the 1830s, when settlers complained that fishing was “drastically reduced” because of Native American fishing (Knetsch 2001). This observation is highly unlikely to be reflective of actual decline, as the Native population in the Keys had been removed, and was instead likely related to the ongoing Seminole Wars in Florida. Data exist to

reliably quantify changes in marine fish populations over the last 130 years. Evidence of decline includes (i) absence or rarity of historically common species, (ii) declines in the size of the largest fish, (iii) increased distance traveled to catch fish (iv) declines in catch per fisherman, and (v) declines in the abundance of species groups including sharks, sawfish, and groupers.

In the 1880s, the United States Commission on Fish and Fisheries published an analysis of the history, contemporary state, and potential for fisheries development, as well as the natural history and habits of commercial fishes. This series, “The Fisheries and Fisheries Industries of the United States,” provides the first comprehensive historic information on Florida Keys’ coral reef fish populations. Most significantly, this document lists the most commonly caught reef fish in Key West the 1880s (Goode 1887a). These were compared with observations of abundance from the mid twentieth century and early 21st century (McClanahan et al. 2006b). One fifth of historically common species were rare by the middle of the twentieth century and one half are rare today (Table 2). Four of the species commonly caught in the 1880s (*Epinephelus nigeritus*, *E. drummondhayi*, *E. striatus*, and *Pagrus pagrus*) are globally Critically Endangered or Endangered (IUCN 2009).

While declines have occurred in the number of abundant species since the 1880s, fishing in the last fifty years has most affected long-lived species, top predators and large bodied fish. Approximately 10% of long-lived fishes (species with population doubling time >4.5 years) were rare by the middle of the twentieth century, but that number increased to 56% in 2005. Seventeen percent of top predators (fish

with a trophic level of 4.5 or higher) were rare by the mid twentieth century and 67% of these fish are rare today (McClenachan et al. 2006b). The mean size “trophy” reef fish that appeared in photographs taken by recreational fishers in Key West, Florida from 1956 to 2007 declined from an estimated 19.9 kg (SE 1.5) to 2.3 kg (SE 0.3), and there was a major shift in species composition from large groupers (*Epinephelus* spp.), and other large predatory fishes to small snappers (*Lutjanus* spp. and *Ocyurus chrysurus*) (McClenachan 2009a).

Table 2. Most commonly caught fish in 1880 in Key West. Originally published in McClenachan et al. 2006b.

Most commonly caught (1880s)	Rare 1940s-1950s	Rare 2005
<i>Epinephelus striatus</i>	No	Yes, Endangered (IUCN)
<i>Pagrus pagrus</i>	No data	Yes, Endangered (IUCN)
<i>Epinephelus drummondhayi</i>	No data	Critically Endangered (IUCN)
<i>Epinephelus nigritus</i>	No data	Critically Endangered (IUCN)
<i>Caranx hippos</i>	Yes	Yes
<i>Cephalopholis fulva</i>	Yes	Yes
<i>Holacanthus tricolor</i>	Yes	Yes
<i>Mycteroperca interstitialis</i>	Yes	Yes
<i>Kyphosus sectator</i>	No	Yes
<i>Lutjanus synagris</i>	No	Yes
<i>Mycteroperca bonaci</i>	No	Yes
<i>Scomberomorus maculatus</i>	No	Yes
<i>Scomberomorus regalis</i>	No	Yes
<i>Lutjanus campechanus</i>	No data	Yes

Table 2, continued.

Most commonly caught (1880s)	Rare 1940s-1950s	Rare 2005
<i>Holacanthus ciliaris</i>	Yes	No
<i>Epinephelus morio</i>	No	No
<i>Haemulon flavolineatum</i>	No	No
<i>Lutjanus apodus</i>	No	No
<i>Chaetodon ocellatus</i>	No	No
<i>Lutjanus griseus</i>	No	No
<i>Ocyurus chrysurus</i>	No	No
<i>Sphyraena barracuda</i>	No	No
<i>Decapterus punctatus</i>	No	No data
<i>Caranx cryos</i>	No	No data
<i>Scomberomorus caballa</i>	No	No data

Concurrent with declines in large desirable species were increases in the distance that fishers traveled to catch large fish. In the nineteenth century, commercial fishing grounds were limited to areas no more than ten miles from Key West, and most fishing occurred from shore or small boats that stayed within four miles of Key West (Goode 1887a). In the early twentieth century, common fishing gear included cast nets and gill nets, which were deployed from small boats operating close to shore, and more fish were caught using shore lines than with any other method in 1902 (U.S.F.C 1895-1940). Similarly, recreational fishers have been forced farther from shore in last century. Before 1950, a majority (69%) of the largest goliath grouper was caught from shore. After 1950, the proportion dropped to only 8%, suggesting that

these large fish were no longer abundant close to land (McClenachan 2009b).

Decreases in the average catch per fisherman have occurred in the last century, after initial increases due to increased efficiency of gear and decreases in the number of small-scale fishers (Table 3). Catch per unit effort (CPUE) is a common measure of changes in abundance of targeted fish. In Monroe County, the number of pounds of fish caught annually by each licensed commercial fisherman reached its peak in the 1930s at more than 10,000 lbs per fishers. The current CPUE is less than one third of these peak values. Further, a shift from finfish and turtles to invertebrates has occurred. Today's landings are overwhelmingly dominated by spiny lobster, with more than one third of the catch comprised of this one species, and two of the five most commonly caught species are invertebrates (Figure 2). In contrast, the most commonly caught species by weight historically were large bodied species such as green turtle, Spanish mackerel, and king mackerel (Figure 2).

Table 3. Catch per unit effort (CPUE) over time in Monroe County

Year	Number of fishers	Total catch (lbs)	lbs per fisherman
1895	1,641	3,208,070	1,955
1902	2,265	2,179,640	962
1918	458	3,252,295	7,101
1928	484	3,501,976	7,235
1929	619	4,501,532	7,272
1930	515	5,323,003	10,336
1931	468	2,374,867	5,075
1934	435	4,646,600	10,682
1936	235	1,506,000	6,409
1937	297	1,882,300	6,338
1938	332	1,683,900	5,072
2007	3,082	9,578,308	3,108

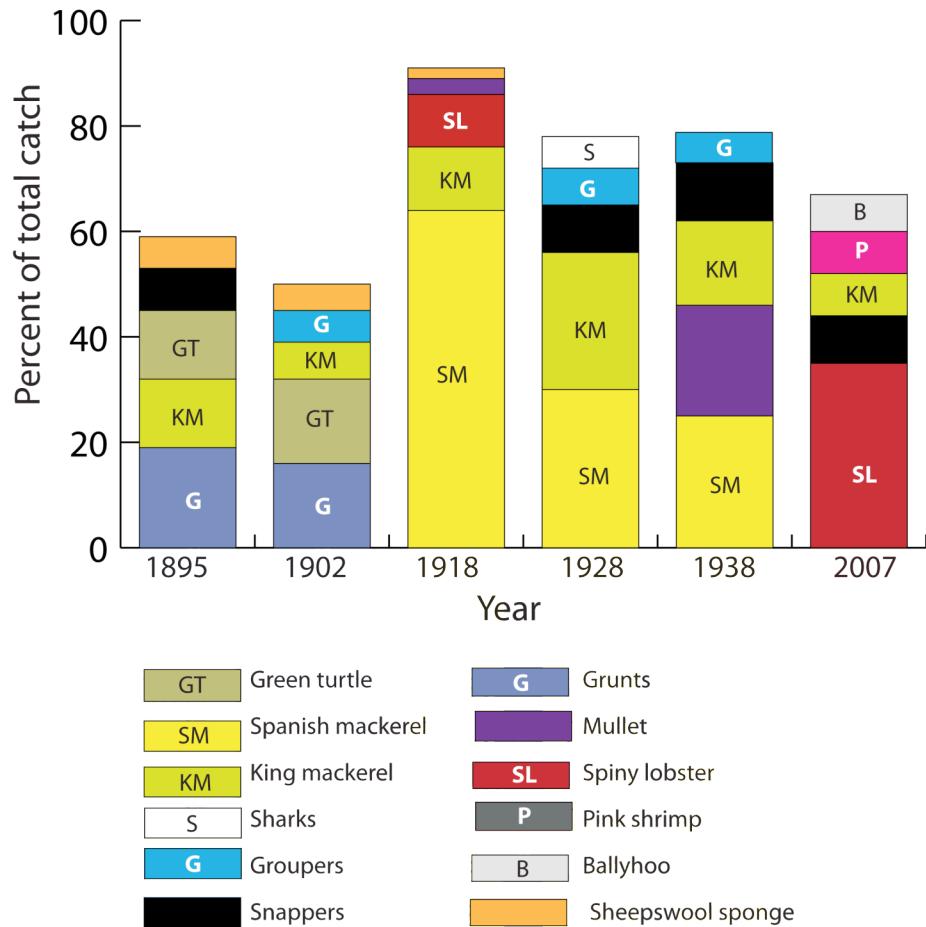


Figure 2. Catch composition through time in Monroe County. The top five most commonly caught groups in select years, 1895-2007.

Finally, historical declines in abundance occurred for several large bodied fish, including sharks, sawfish, and groupers. Sharks were historically abundant throughout the Keys, and in the 1880s, it was common for sharks to “swarm about the wharves, feeding on refuse fishes” (Jordan 1884). Commonly observed species included the great white shark (*Carcharodon carcharias*), nurse shark (*Ginglymostoma cirratum*), smooth hammerhead (*Sphyrna zygaena*), bonnethead (*Sphyrna tiburo*), bull shark (*Carcharhinus leucas*), and Atlantic sharpnose shark (*Rhizoprionodon terraenovae*)

(Jordan 1884, Henshall 1889). Fishers complained that sharks “are exceedingly troublesome” as they “nearly always follow a boat trolling, and will usually take the whole or a part of some of the fishes” off the hook. The number of sharks swarming around a small fishing boat commonly reached fifteen to twenty individuals, each several hundred pounds in weight (Gregg 1902). It was “no unusual thing in the Florida Keys for sharks to cause a fisherman who uses hand lines to abandon his anchorage for the day, so vicious and persistent is their attack on the fishes which he and his men are pulling in” (Ehrenreich 1920).

A shark fishery began in the 1920s in the Keys for leather, oil, and fins, which focused primarily on nurse, sandbar, and tiger sharks, with incidental catch of sawfish and hammerhead sharks (K.W.C. 1923-1996). Independent scientific investigations to determine “the destructiveness of sharks to commercial fisheries” in the 1920s revealed that the nurse, tiger, and dusky were the most commonly caught. In one day of shark fishing, twenty-four tiger sharks, nine dusky sharks and three hammerhead sharks were taken on Big Pine Key, 70% of which measured more than two meters in length (Higgins 1924). Landings of 100 individuals per day in the fishery were reported from Big Pine Key (K.W.C. 1923-1996) and Monroe County landings peaked at three million lbs in 1934 (U.S.F.C 1895-1940), which is the equivalent of 12,000 250 lb sharks, the average size for this time period (K.W.C. 1923-1996). In contrast, commercial landings from Monroe County in 2007 totaled only 265,000 lbs, less than 10% of the catch in the 1930s. The primary use of sharks in the 1940s was for Vitamin D, from shark liver oil, so that when synthetic vitamins were developed in the late

1940s, this fishery was eliminated. Sharks were targeted by recreational fishers in the latter half of the twentieth century, and photographic data indicate a decline in the largest sharks after 1960 (McClenachan 2009a).

While it is not possible to quantify declines in the population sizes of individual shark species due to the non-specific nature of historical landings records, it is possible to infer changes from historical catch records. The average number of sharks caught per day using hook and lines and gillnets from small boats in the 1930s was more than twenty individuals (based on data taken from *Key West Citizen*).

Assuming that the average amount of time spent fishing was between six and eight hours means that the average number of individual sharks caught per hour was 2.5 to 3.3 individuals. Between 1982 and 1992, recreational fishers in Florida caught on average 1 shark per hour, with the assistance of modern fishing technologies (Brown 1999), implying a strong reduction in abundance. Furthermore, the average length of sharks photographed by recreational fishers declined by more than 50% over in the second half of the twentieth century with a shift from large hammerheads (*Sphyrna* spp.) to juvenile bonnethead (*Sphyrna tiburo*) and reef sharks (*Carcharhinus* spp.) (McClenachan 2009a). Together this evidence suggests that the large schools of large-bodied sharks that would follow behind fishing boats in the early twentieth century no longer exist in the Florida Keys.

Smalltooth sawfish (*Pristis pectinata*) were historically abundant in south Florida and the Keys, observed by sailors in schools (Henn 1893). They are found in great abundance in archeological sites on Marco Island, suggesting heavy exploitation

before European contact (I. Quitmyer, personal communication). In the late nineteenth and early twentieth century, sawfish were frequently entangled in turtle and gill nets, and for this reason were “detested by fishers” (Ehrenreich 1920). Thus, they were killed both as bycatch and eradicated to avoid net damage (Goode 1884). One early twentieth century fisherman reported that sawfish were common, and “one need not have any compunctions of conscience at killing a sawfish, and need not turn it loose again after capturing it, for the sawfish belongs to the shark tribe, and the shark is persona non grata to the fisherman” (Winter 1918). As a target species, sawfish were regularly caught by recreational fishers for their large size and saw, which was a prized trophy, and by commercial fishers for their skins, which were turned into leather (Ehrenreich 1920). Photographs of fishing boats from the early twentieth century show up to twenty-five individuals caught daily (Figure 3a), and contemporary accounts describe two sawfish caught in less than two hours and one sawfish caught, along with five sharks and one ray, in a morning of fishing (Endicott 1925).

The small-tooth sawfish has suffered extreme reductions in distribution, from the entire eastern seaboard of the United States to remote regions in south Florida (NMFS 2009b). The Florida Keys and Everglades region has historically been the center of sawfish abundance, and the Everglades serve as a stronghold for the species today (Poulakis and Seitz 2004). Sawfish were described as “exceedingly abundant” in the Everglades in the late nineteenth century (Goode 1884), and a continuous record of their presence exists since that time. No quantitative catch records exist from the

Florida Keys or Everglades, but in the Indian River, an area from which sawfish have been completely eradicated, a nineteenth century fisherman reported catching more than 300 sawfish in one season (Evermann and Bean 1898). It is likely that similar numbers could have been caught in the Keys region.

Regional declines in sawfish populations seem to have occurred most strongly before 1965 (NMFS 2009b). Occurrences north of the Florida Keys and Everglades have been noteworthy since the early twentieth century, and bycatch data from shrimp trawlers suggests a rapid decline in the species during the period 1950-1964. During a 1973-1976 fish survey in the Florida Bay, only three juvenile and adult specimens were captured along the northern Florida Bay shoreline, and an extensive multi-year study in the 1970s of the Indian River Lagoon, an area of great historical sawfish abundance, did not encounter any individuals. Based on range contraction and qualitative data on abundance, the sawfish recovery team estimated the population has declined at least 95% since European settlement (NMFS 2009b) (Table 4).

Groupers were historically important food fish and were so abundant that “Grupper Banks,” was labeled on early charts of the Florida Keys (de Brahm 1770s), denoting locations where these fish could be caught, and likely where spawning aggregations occurred. The goliath grouper in particular suffered massive declines before the 1990s, when the species was protected due to severe depletion. While the absolute change in abundance of this species cannot be calculated, historical data suggest that declines have been occurring since the first half of the twentieth century, if not earlier. The average number of individuals caught per recreational fishing trip in

Key West (Figure 3) decreased before 1960 and was reduced by 86% before 1979.

Further evidence of declines is found in newspaper accounts of landings (1923-1977),

which show significant decreases in the maximum size of goliath grouper caught and

the proportion of large grouper caught from land vs. offshore before 1950

(McClenachan 2009b). Other species of grouper have been severely reduced as well.

Warsaw grouper (*Epinephelus nigritus*) speckled hind (*Epinephelus drummondhayi*),

and Nassau grouper (*Epinephelus striatus*) were all commonly caught species in the

nineteenth century and they are all now listed as Endangered or Critically Endangered

by the IUCN (Table 2, Table 6).



Figure 3. Scenes of abundant marine animals in the past. (A) Sawfish caught in 1930s (MCPL), (B) Sponges drying Key West, December 1921 (R. E. Coker, NARA, College Park) (C) Goliath grouper and other large fish caught (April 14, 1957) 1956 (MCPL), (D) Sign warning of sharks around fishing wharf in Key West (MCPL).

Mobile Invertebrates

Spiny lobsters (*Panulirus argus*) historically were found in great abundance in the Florida Keys. The British surveyor George Gauld wrote in 1763, “There are such quantities of the largest [lobster], that a boat may be loaded with them in a few hours,” and his contemporary William de Brahm confirmed that lobster “to the weight of five pounds apiece” live “in great numbers in the holes of the coral rocks, on the mangrove islands” (de Brahm 1772, Gauld 1796). In the 1880s, lobster was the preferred bait for

finfish fisheries, and in its natural environment, provided food for a vast variety of reef and pelagic fish. A nineteenth century fisheries biologist wrote, “These reefs... are exceedingly well populated with ... invertebrate animals ...and therefore, we find about them an abundance of fishes, attracted by the vast stores of food” (Goode 1887b). When Smithsonian scientists visited the Keys in 1906, they wrote that they were able to catch “a big lot” of lobsters in a half hour from the edge of the mangrove, several of which were 5lbs each, and reported that “they could have gotten a boatload.” In a separate expedition, they caught seventy-five lobsters in a short time on Molasses Key (Bean 1903-1908).

By the 1920s, however, lobster were said to be “rapidly disappearing” (Munroe and Gilpin 1930) and in 1935 the local newspaper reported that “trapping has so depleted the supply that families and individuals are finding it increasingly difficult to find an adequate supply of this food” (K.W.C. 1923-1996). In 1931, a lobster hatchery released twenty million juvenile lobsters around Key West to increase the local supply (K.W.C. 1923-1996). Landings for this time period ranged from a high of 283,915 lbs in 1918 to 53,200 lbs in 1938 in Monroe County, with a consistent decline over this twenty-year period (U.S.F.C 1895-1940). In the 1940s, the price of lobsters tripled and fishers agreed that the population was experiencing a crash (Walton Smith 1958). Intensive fishing throughout the second half of the twentieth century further reduced populations. Lobsters that are inter-tidal or easily visible from the surface, as described by eighteenth and nineteenth century fishers are virtually nonexistent today.

Quantitative data are available beginning in the 1880s from the trap fishery, and it is possible to compare these data with modern abundances to arrive at an estimate of relative abundances over the last century. Modern commercial fisheries are primarily trap fisheries, but when lobsters were abundant, it was more efficient to catch them with nets and spears. Lobster netting typically yielded 50 to 100 lobsters per night in 1923, with a range of 36 to 1,000 lobsters per night (Schroeder 1924). Between 1902 and 1918, the number of lobsters caught in traps ranged from 3% to 23% of the total catch (U.S.F.C 1895-1940). If we assume conservatively that before 1950, only 10% of lobsters were caught in traps, it is possible to arrive at an estimate of catch per trap (Figure 4). These data suggest a 90% reduction in catch per trap between 1880 and the modern fishery.

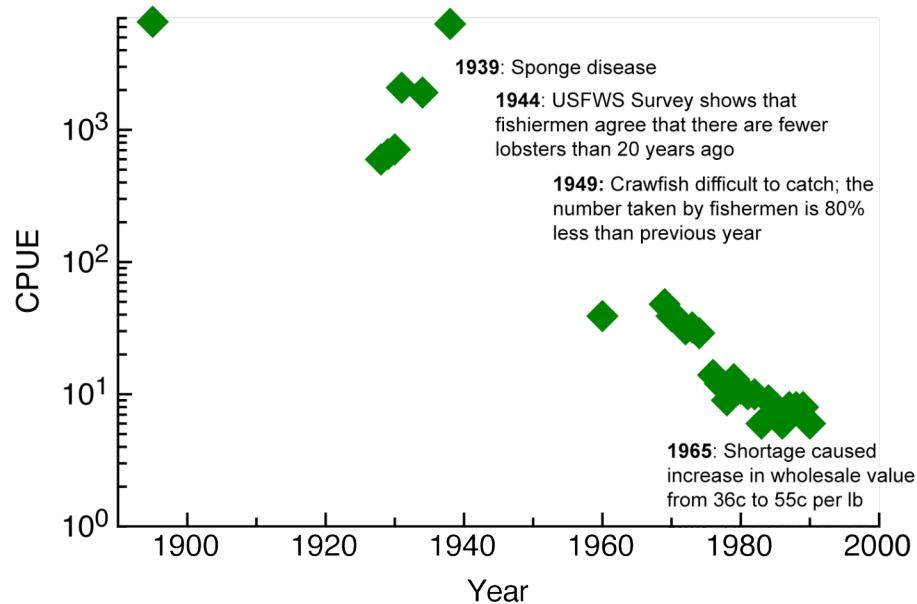


Figure 4. Declines in CPUE (lbs per trap per year) in the lobster fishery

Separate scientific investigations of trap efficiencies in the 1920s and 1980s further support these estimations. In 1923, the average catch per trap in the Keys' commercial fishery was four per day, and exceptional catches of six to fourteen individuals per day were not uncommon (Schroeder 1924). Similar numbers were reported if the traps were left in for a week, as in-trap mortality occurred over time. Thus, an average catch per week of six individuals would be conservative. In 1988, catch efficiencies were estimated for different bait types, and the mean catch per week for soak times of six to fourteen days ranged from 0.8 individuals to 2.39 individuals (Heatwole et al. 1988). For traps baited with fish, as was common in the 1920s, the average number of lobsters caught was 0.6 per week. Assuming an average weekly catch of 6 individuals in the 1920s suggests a decline of 90% between 1923 and 1988 (Table 4).

Finally, evidence exists that the average size of spiny lobsters has declined. In the 1920s, the average market size was 1 lb and 99% of the lobsters sold were between 0.5 and 6 lbs (Schroeder 1924). Between 1967 and 2003, 99% of lobsters collected had carapace lengths from 50 to 119 mm (Ehrhardt 2008), which corresponds to weights of 0.25 to 2.5 lbs (Simpson 1976).

Queen conch (*Strombus gigas*) was one of the most commonly caught food items for Native Americans in the Keys (Goggin 1944), and was historically taken for subsistence and bait by European settlers, as well as for local sale. For many poor residents in Key West, conch meat was one of the “main articles of food” and people

gathered conch shells to be shipped abroad for use in making buttons (Anonymous 1929). The primary market was for shell, and few modern large shell middens remain as they do as in other areas of the Caribbean (Stoner and Ray 1996, Torres and Sullivan-Sealey 2002, Schapira et al. 2009). However, if the site on nearby Marco Island, where an estimated three million m³ of conch were uncovered (Goggin 1944), can be taken as a representative example, billions of individual conch were harvested from the Keys before European contact. At a similar site in the Dominican Republic, the number of individual queen conch per m³ of midden ranged from 860-1391 (Torres and Sullivan-Sealey 2002), suggesting that the Marco Island site contained somewhere in the range of 2.6 to 4.2 billion individual conch.

Landings records suggest continuously low levels of conch harvest in the early twentieth century. Officially reported landings varied from 2,000 to 20,000 lbs of meat between 1902 and 1938 in Monroe County (U.S.F.C 1895-1940), but that amount were almost certainly incomplete, as many poor residents harvested conchs for subsistence, and did not report these landings. In the early 1920s, when landings averaged 2,000 lbs, a fisheries scientist observed that “conchs are plentiful enough to supply the present demand, but the supply could easily be depleted by overfishing” (Schroeder 1924). Such overfishing may have occurred, as harvest levels reached ten times that value before 1940. In the mid-1940s, a disease hit the conch population in the Keys, leaving “innumerable dead and empty shells” and forcing Florida to import conch from the Bahamas (K.W.C. 1923-1996). Populations recovered by the mid-1950s, but in the following two decades, fishing and another disease event reduced

populations to levels that could no longer sustain harvest. Commercial harvest of queen conch in the Florida Keys was banned in 1975, and a ban on recreational harvest of the species was enacted in 1986. By the 1990s, conchs had “all but vanished from local waters” (K.W.C. 1923-1996). Reflecting region-wide decline, the species was listed in Appendix II by the Convention on the International Trade in Threatened and Endangered Species (CITES) in 1994. Despite protection from harvest, the queen conch has not recovered, and it is likely suffering from diminished recruitment due to small spawning aggregations (Stoner and Ray-Culp 2000, Gascoigne and Lipcius 2004).

The long-spined black sea urchin (*Diadema antillarum*) was historically abundant in the Keys, described by Agassiz (1880) as common among coral heads. Mid twentieth century writers warned swimmers to take care “not to step on any of the great spiny sea urchins which abound” (Barbour 1945). Densities were approximately five individuals per m², prior to the pan-Caribbean mass mortality event in 1983 (Lessios et al. 1984), which was followed by a second mortality event in 1991 in the Florida Keys (Chiappone et al. 2002). Current population densities are no greater than 0.05 individuals per m², two orders of magnitude less than historical densities (Chiappone et al. 2002).

Structural organisms

For most of their history recent history, coral reefs in the Florida Keys have been covered by extensive stands of *Acropora* and other stony corals. Sailing charts

from the eighteenth and nineteenth centuries show coral banks stretching the length of the Florida reef tract, and one particularly detailed nineteenth century chart of the Key West harbor represents the vertical extent of coral reefs (Bache 1851). Few early quantitative data on coral abundance exist, but nineteenth century natural histories of the Florida Keys describe lush and abundant corals in the Keys. Agassiz (1880) wrote “the reef, for a stretch of several miles, nearly reaches the surface and forms a long level ledge entirely covered with living corals.” *Acropora palmata* was the dominant species in shallow waters, with growth “so close that there are hardly any intervals to be filled by dead corals” (Agassiz 1880). *Diploria*, and *Millepora* inhabited slightly deeper waters, and “massive heads” of *Porites* and *Sidastrea* built the foundation of the reefs.¹

Coral harvesting has occurred since at least the 1850s. In the construction of Fort Jefferson, 22,000 cubic yards of coral was taken and turned into concrete, including all of the coral from Bush Key. In the early twentieth century, coral was harvested for decorative purposes, sent throughout the United States. A coral excavator wrote, “There were few places left to find really first-rate coral... One fine stand of staghorn coral remained on a finger off Looe Key... At Looe Key, we dropped anchor over a forest of staghorn coral. Below the trees looked upward from the reef in clumps, each tree a full 5 feet across. It was a job of brute strength to steady

¹ Historical names have changed. I used: Madrepora=Acropora; Orbicella = Montastraea; Astrea = Siderastrea. Maeandrids = Diplorias (F. Nunez, personal communication)

each tree and chip it free at the base with a chisel-pointed crowbar" (Meylach and Whited 1971).

Despite harvesting, live coral cover remained abundant throughout the Keys through the 1960s, and it was not until the 1970s that concerns about coral health in the Florida Keys began to emerge. Ecologists observed declines in recruitment rates and increases in the numbers of diseased corals, which they linked to declines in water quality over the preceding two decades (Dustan 1977, Dustan and Halas 1987). A combination of physical disturbance, sedimentation and disease caused significant loss of reef building coral cover in the 1970s (Dustan and Halas 1987), which continued into the next decade. (Porter and Meier 1992) measured declines in coral cover ranging from 7 to 44% between 1984 and 1991 at sites from Key West to Miami, with no recruitment observed over this time period for massive frame building corals. Disease increased in the 1990s, affecting *Acropora palmata*, and *A. cervicornis* particularly; declines of 93% and 98% respectively were measured from 1983-2000 in some areas (Miller et al. 2002) (Table 4). Disease and bleaching continue to cause declines in other reef building corals in the Keys. Eighty-five percent of species are currently affected, with high incidence found in framework builders such as *Acropora* and *Montastrea* (Porter et al. 2001). Overall, current coral cover in the Florida Keys National Marine Sanctuary is well below 10% (Andrews et al. 2005) compared with close to 50% on more pristine reefs (Sandin et al. 2008).

Marine sponges (*Spongia* spp. & *Hippospongia* spp.) were harvested in great quantities from Florida Keys' reefs, beginning in the 1840s. By 1900, the total annual

export was in the range of several hundred thousand pounds of dried sponges, the equivalent of over one million pounds of living animals. The depletion of coastal sponge banks can be tracked by changes in the distance from shore sponge fishers traveled and the depth at which they harvested sponges. In the 1840s and 1850s, fishers were able to wade into the shallow water in the immediate vicinity of Key West and pulled sponges by hand (Moore 1910). As the industry developed, small boats became necessary to access sponges in deeper water, and spongers began to use long-handled rakes with hooks on the ends to pull the sponges to the surface. In 1888, marking the depletion of sponges in less than 30 feet of water, a new kind of hook was developed to better access deeper-water sponges (Brice 1897). Declines in the size and quality of sponges harvested from depths of 30 to 40 feet were noticed by the 1890s, and the large sponges that had frequently occurred in the past were “rarely, if ever, seen” by the end of the century (Brice 1897). By the end of the 1890s, shallow-water sponges were nearly “fished out” (Brice 1897), the most valuable sheepwool sponges (*Hippospongia lachne*) were commercially extinct in near-shore areas, and all sponges were “much less productive than formerly” (Smith 1898). Inshore grounds were abandoned and spongers had been forced out to sea, “until the maximum depth in which sponging is possible” had been reached (Smith 1898). By the 1890s, smaller catches per vessel were noted, and yields primarily comprised the smallest sponges (Smith 1898). A typical trip in the 1880s brought in 1000 to 1500 bunches of sponges; by the late 1890s, 500 bunches were considered a good cargo (Brice 1897).

Overfishing destroyed shallow water sponges, and a disease event in the 1930s

further reduced sponge populations at all depth ranges. By the end of 1939, the yellow and vase sponges (*Spongia barbara*, *S. graminea*) had suffered nearly 100% mortality (Table 4), while 70% of the valuable sheepswool sponges (*H. lachne*) had been eliminated from the Keys (Galtsoff 1939). Although overflowing fresh water and local pollution were both blamed, the culprit appeared to be a fungus-like filament, which started in a small area of the sponge and expanded until the entire sponge was consumed (Galtsoff et al. 1939). Along with over-fishing, blockages in freshwater outflow from the Everglades due to the Key West railroad extension contributed to sponge mortality throughout the Keys (Moore 1910).

Mangroves were a dominant and ubiquitous feature of the Florida Keys, and were described by the first Europeans to arrive. Early explorers described the Florida Keys as containing “an infinite number of mangrove islands” (de Brahm 1772), so thick that “nothing except a canoe can pass through over the shoals” (Gauld 1796). The first navigational charts show images of these mangroves (Gauld 1775, Gauld 1820, DeMayne 1821), which have certainly been reduced over time. In the late eighteenth century, the island of Key West, which is virtually devoid of mangroves today, was described as having very thick trees, and the highly developed islands to the east, or what is now Stock Island and Boca Chica were described as a series of small mangrove islands (Gauld 1796). The total extent of change since European arrival is not possible to quantify, but aerial photos from the mid twentieth century show that 15% of the 8,306 ha of mangrove forest present in aerial photos from 1945-1959 have been cleared in the Upper Keys, and the mean size of mangrove plots

decreased from 67.5 ha to 28.1 ha. (Strong and Bancroft 1994). The Lower Keys were more heavily populated earlier than Upper Keys so that early mangrove clearing was likely higher in this region. Further, extensive clearing occurred in the Upper Keys region prior to 1945, particularly in the development of Miami Beach in the 1910s (Carson 1955), suggesting that the estimates of decline are extremely low.

Seagrass beds have always been an important feature of Florida Keys ecosystems, appearing on eighteenth century sailing charts of the Florida Bay (Gauld 1775). However, a combination of freshwater diversion and overexploitation of herbivores led to large-scale declines in seagrass beds the late twentieth century, which had cascading effects throughout the ecosystem. In 1987, extensive areas of turtle grass (*Thalassia testudinum*) began dying rapidly in the Florida Bay. By 1991, 4,000 ha had disappeared completely and an additional 24,000 ha were affected (Robblee et al. 1991).

Seagrass mortality was blamed on elevated water temperatures, hypersalinity, and excessive seagrass biomass leading to hypoxia and sulfide toxicity, and disease (Dirako et al. 2003). The most commonly cited long-term cause of the seagrass die-off in the early 1990s is hypersalinity due to diversion of freshwater on Florida's mainland, which is well supported by multiple long-term records. Analyses of coral growth rates and coral fluorescence patterns (Smith et al. 1989), as well as $\delta^{18}\text{O}$ records, $\delta^{13}\text{C}$ records from corals (Swart et al. 1996, Swart et al. 1999) and mollusks (Halley and Roulier 1999) and the community composition of foraminiferal and mollusc assemblages (Brewster-Wingard and Ishman 1999) indicate that circulation

patterns and water chemistry in the Florida Bay have changed since the freshwater diversions began on the Florida Peninsula in the 1880s. The construction of the Overseas Railway between 1906-1912 further restricted interchange between the Florida Bay and pelagic water. Circulation within the Bay decreased between 1910 and 1940 (Halley and Roulier 1999), and coral growth rates decreased between 1906 and 1914 (Hudson et al. 1989). Freshwater runoff into Florida Bay decreased between 1912 and 1931, and has declined by as much as 59% since diversions began in 1881 (Smith et al. 1989). In response, the average salinity in Florida Bay increased from 1880 to the present, with higher salinity fluctuations after 1940 (Swart et al. 1996, Brewster-Wingard and Ishman 1999). Salinity in the 1989-90 season was the highest recorded since 1824 (Swart et al. 1999), due in part to a period of drought between 1987 and 1991, which led to localized salinity levels close to 70 ppt (Fourqurean and Robblee 1999).

Along with decreases in water circulation and increases in salinity, Florida Bay has suffered the near complete elimination of a once abundant mega-herbivore, the green turtle. Historical populations of abundant green turtles clipped seagrass blades at their roots, and in that way maintained beds of seagrasses devoid of long blades on which disease agents could grow (Bjorndal and Jackson 2003). This was true in the Florida Keys through at least the mid-1830s. A traveler in the late 1820s wrote, “The green turtle feeds principally on marine plants, but more especially the plant here called ‘turtle-grass’ which is found on the outside of the Keys. As it grows in tolerable deep water, the turtles dive after it, and cutting it off at the roots close to the sand, eat

the tender parts only: the remainder comes to the surface; and where the animals are numerous, large fields of this herbage are formed. Indications of this had not escaped the sagacious observation of the fishers, and hence their wish to be upon the spot before the turtle came to feeds" (McCall 1868). This observation was confirmed by John Audubon in the 1830s, when he visited the Keys and wrote, "The food of the green turtle consist chiefly of marine plants...which they cut near the roots, to procure the most tender and succulent parts. Their feeding-grounds, as I have elsewhere said, are easily discovered by floating masses of these plants on the flats or along the shores to which they resort" (Audubon 1832). While changes in salinity have certainly affected the fluid environment of the Florida Bay, the loss of herbivory on any significant scale, and the associated increase in decomposing seagrass blades (Thayer et al. 1982) facilitated the rise of seagrass disease.

DISCUSSION

Several types of evidence exist for the degradation of coral reefs in the Florida Keys over long time scales in the Florida Keys. The most compelling include declines in catch per unit effort (CPUE), as was shown for spiny lobsters and goliath grouper, as well as overall catch of reef fish; geographic declines, such as the increased distance from shore fishers needed to travel to collect sponges and catch reef fish and loss of breeding populations of birds and spawning aggregations of groupers; declines in the size of the largest fish; and the absence of once common organisms, such as

green turtles, and several species of now endangered but historically common reef fish. Together, the evidence that emerges from disparate historical sources describes long-term decline across all trophic levels in Florida Keys coral reef ecosystems. These reductions occurred in stages corresponding with different levels of human population size and integration into regional, national, and global economies. The stages and causes of declines in the Florida Keys are not unique to this region and time, but rather have important links to coral reef ecosystems and lessons for management worldwide.

By way of conclusion, we discuss several lessons learned about the causes and consequences of declines in coral reef ecosystems in the Florida Keys, and link these to other regions facing similar threats. First, the historical ecological analysis of the Florida Keys demonstrated that depletion due to subsistence fishing can occur at low population densities, without links to outside markets. Second, when export markets are developed, rapid declines occur in the population abundances of exploited species. The collapse of one target species due to fishing for export often led to the development of a fishery for another species. In the highly diverse ecosystems of the Florida Keys with multiple desirable species, the sequence of exploitation was linked to the development of new markets rather than descending trophic level, which is the typical sequence of exploitation in marine ecosystems. Third, synergistic interactions among multiple human impacts have occurred through time, and evidence exists for synergies between overfishing and disease as early as the 1930s. Finally, human

hunting and fishing has altered the relative abundances of species groups, and benefited from disruptions to the food web, at least in the short term.

Depletion due to subsistence fishing at low population densities

The Florida Keys were sparsely inhabited before European contact, and remained so throughout the first four centuries of European exploration. Spanish, British, Cuban, and Bahamian visitors came to the Keys to fish and hunt, but until 1880, fewer than 10,000 residents lived in all of Monroe County. Even so, evidence exists for declines in the abundance of harvested species at low human population densities, even in the absence of extensive export markets. Monk seal (*Monachus tropicalis*) populations were reduced to low abundances before European settlement, and lobster (*Panulirus argus*) populations were quickly reduced due almost entirely to fishing for local markets and bait in the first few decades of the twentieth century.

Such historical data can help to ascertain the human population densities that coral reef fisheries can sustain, and contribute to analyses based on twentieth century observations of the carrying capacity for humans dependent on coral reef fisheries. Population densities on tropical islands today range from ten people per km² of reef in the Marshall Islands to more than 10,000 in Sri Lanka, and most islands with more than 1,000 people per km² of coral reef were evaluated to have overexploited fisheries (Newton et al. 2007). However, overexploitation can occur at much lower population densities, even without fishing for export markets. For example, in San Blas, Panama, local subsistence fishing and construction activities severely reduced populations of

reef fish and coral cover before extensive export markets were developed in the 1970s (Jackson 1997, Guzman et al. 2003). This depletion occurred at human population densities of less than 40 people per km² of reef². Similarly, in Kirimati Island in the central Pacific, 6,000 residents have caused declines in fish populations with less than 300 people per km² of reef (Walsh in prep).³ The Florida Keys supported fewer than twenty people per km² of reef before 1950,⁴ which would rank it among the lowest in world. Yet, depletion of several guilds had already occurred by the early twentieth century. Human population was centered on and around Key West, so the population density was higher in this region, but even if the population density was an order of magnitude greater, or 200 people per km² of reef, minimal impacts would be expected. These case studies of high impact at low population density show that population densities in most areas exceed those required to overexploit coral reef fisheries.

Research that considers management regimes for coral reef fisheries demonstrates that the number of people that can be supported by a given reef may be related to the absolute size of the community, rather than the population density. This is due to the fact that resource conservation measures can be enforced through social pressure in small communities (Cinner 2005). In Southeast Asia, for example, Cinner (2005) found that communities of fewer than 6,000 people can effectively manage reef fisheries, but above that population size, management structures are ineffective. If this holds true across regions, the Florida Keys exceeded this threshold in the 1870s; the

² Calculations are based on 24,000 people & 638 km² of reef (Guzman et al. 2003, Andrefouet and Guzman 2005)

³ Calculations are based on 22 km² of reef (100 m x 70km x 20 km x 2).

⁴ Calculations are based on 29,957 people & 1150-1400 km² of reef

population of Key West climbed from just over 5,000 people in 1870 to just under 10,000 people in 1880. Further, immigrants with diverse backgrounds arrived in the Keys, complicating management and causing social conflict related to resource conservation (McClenachan 2008). Thus, in the case of the Florida Keys, the human population density may have been less important than the ability to effectively enforce regulations, which may have been related to the size of Key West and the backgrounds of its inhabitants. More broadly, reef-dependant communities with members that have heterogeneous cultural backgrounds may have a more difficult time agreeing on management and therefore sustaining a small population without overexploiting their resources.

Rapid and sequential depletion due to development of export markets

While local populations can alter coral reef ecosystems and cause the decline of species that are killed for local consumption, the carrying capacity of coral reefs is rapidly exceeded when products from the marine environment are taken for export markets. This is particularly true for sessile and non-migratory species, such as benthic invertebrates, but can also affect the abundance of populations of large migratory vertebrates. In the Florida Keys, rapid decline following the development of export markets occurred for both green turtles (*Chelonia mydas*) and sponges (*Hippospongia* spp., *Spongia* spp.) between 1850 and 1890. Market driven exploitation of bird's eggs caused declines in populations of herring gulls (*Larus argentatus*), laughing gulls (*Larus atricilla*), royal terns (*Sterna maxima*), least terns (*Sterna antillarum*), sooty

terns (*Sterna fuliginosa*), and brown noddies (*Anous stolidus*) before 1890, and the red-footed booby (*Sula sula*) was reduced by direct hunting before 1850. In the case of marine fish, the development of ice-packing technologies and the construction of the Overseas Railroad facilitated large-scale extraction in the first two decades of the twentieth century. Fish were packed and shipped from Florida throughout the eastern seaboard.

In the Florida Keys, the commercial extinction of one fishery often caused the rapid development of a fishery for a new target species or species group. Before WWII, the economy of the Keys was limited, with few industries and products providing employment to a large percentage of the population. Thus, the crash of one fishery led to the development of a need for a new substitute income source. The first two export fisheries, sponges and turtles, became economically intractable in the first decades of the twentieth century, resulting in a large number of underemployed fishers. The shark fishery was developed in the 1920s and 1930s to turn marine resources into much needed cash. While large animals such as birds, turtles, and sharks were exploited before smaller reef fish, this serial depletion was linked to markets rather than caloric content or trophic level of the target species. In this way, fisheries followed a pattern of sequential depletion, whose sequence corresponded to the development of new markets rather than to trophic level. Thus, “fishing down the food web” as described by Pauly et al. (1998) did not occur in the Keys in the same way that it has in temperate and pelagic ecosystems.

Despite the extirpation of a sequence of targeted species, the coral reefs of the Keys were able to support increasing levels of exploitation until the middle of the twentieth century. Newton et al. (2007) estimated that coral reef ecosystems can sustain extraction on the order of five metric tons per km² per year. Prior to the 1940s, commercial fishing removed less than 2.5 metric tons per km² per year from Florida Keys' reefs. Thus, despite collapses of individual fisheries and populations of large marine animals, overall, the fisheries of the Florida Keys were still developing. However, commercial fisheries landings exceeded eight metric tons per km² of reef in the 1980s, and in the last two decades, landings have fallen to less than four metric tons per km² of reef per year. This decline in total landings suggests that the commercially exploited fisheries of the Keys have completely collapsed, and with no new fisheries to exploit, the sequence of decline has come to an end.

Synergies among human impacts

Combinations of factors and cascading negative consequences have contributed to declines in Florida's coral reefs over long time scales. In the Florida Keys, disease events have caused a widespread collapse of formerly abundant species including sponges, conch, turtles, and sea urchins (Table 6). While these data are limited, the frequency of disease episodes appears to be increasing in the twentieth century. Most significantly, this analysis demonstrates that synergies between disease and overfishing are not exclusively a phenomenon of the last few decades. Both the

example of sponge disease in the 1930s and seagrass die-off in the 1990s demonstrate the interactions between disease events and the declines of larger marine animals.

The first major disease event recorded in the Florida Keys, the rapid die-off marine sponges in the 1930s, was intricately related to overfishing, both over the long and short terms. Over the short term, spongers likely contributed to the spread of the disease from one isolated bed to another. A common belief existed among spongers that “sponges contain seeds” and squeezing the sponge “gurry” into the water released these seeds, starting new growths (Moore 1910, Anonymous 1939). This idea was erroneous, and probably contributed to the distribution of virulent microbes among sponge populations. Over a longer time-scale, over-fishing of sponges very likely increased the concentrations of bacteria and other particles of organic matter – including algal and fungal cells – in the seawater over the sponge beds because of the loss of the filtration provided by sponges. The sponges’ remarkably efficient filters can remove over 90% of the bacteria from seawater, and sponges are the only animals on coral reefs that fill this ecological role (Reiswig 1971). The four million pounds of live sponges taken from the Florida Keys in a typical year would have assimilated more than 70 metric tons of organic material annually and taken over five tons of bacteria from the water (calculations based on data in Reiswig 1971, 1973). Over the course of the fishery, traditional spongers and divers took more than 1.5 billion lbs of living sponges from the northern Caribbean, so that the water during the 1930s was certainly richer in bacteria, fungi, algae and other tiny particles than it had been a century earlier. The community dynamics of microbes in the sea and within sponges

are complex, but evidence exists to indicate that at high concentrations, bacteria that are typically benign can become virulent (Miller and Bassler 2001), and in waters with high levels of organic matter, diseases are more prevalent (Hodges et al. 2005, Kline et al. 2006, Smith et al. 2006). Far from being passive free-floating cells, pelagic bacteria are known to attack organic matter and transform biogeochemical cycles (Azam 1998). It is likely that over-fishing of sponges – the only effective filter feeder in the coral reef ecosystems of the northern Caribbean – fundamentally altered the microbial community in a manner ultimately fatal to their existence (Hobbie et al. 1977, Azam et al. 1983, Moriarty et al. 1985).

More recently, a combination of changes in upland water flow and overfishing of green turtles facilitated the growth of epiphytic fungus on seagrass blades, contributing to declines of seagrass beds and culminating with a disease event in the 1990s. This rapid decline in seagrass beds had negative consequences for the recruitment of commercial and recreationally caught fish. Decomposition and resuspension of sediments following the loss of extensive beds of *Thalassia testudinum* led to widespread increases in turbidity and phytoplankton abundance, which began to affect other benthic animals, including sponges. Several species of sponges experienced mortality close to 100% in some areas between 1991 and 1993. Declines in sponge abundance were hypothesized to trigger reductions in the abundance of spiny lobster, which depend on sponges for nursery habitat (Butler et al. 1995). Further, declines in the landings of commercial shrimp, which depend on Florida Bay seagrass as nursery habitat, occurred concurrent with seagrass mortality.

Within the fish community, shifts in species composition occurred, in particular, increases in the abundance of pelagic planktivorous species occurred following the seagrass decline (Thayer et al. 1999).

While these disease events are linked to overfishing, declines in water quality are certainly a major factor in the increased frequency of disease events. Sponge disease occurred when fewer than 15,000 people inhabited the Keys, so pollution is unlikely as the cause. However, more recent disease events are related to increased levels of pollution. For example, white pox disease on stony corals has been linked to human fecal bacteria (Patterson et al. 2002) and the increased incidence of fibropapilloma tumors in green turtles, which were not present in historical photographs is also linked to pollution (Herbst and Klein 1995).

Food webs

Finally, declines of formerly abundant species have had significant impacts on the dynamics of coral reef ecosystems, and have altered the energy flow through food webs. In the 1770s, when British surveyors first described the Keys, large populations of top predators consumed abundant reef fish and invertebrates (Figure 6). By the 1880s, monk seals and green turtles had declined in abundance, but there were still plenty of sharks, fish, lobsters and conch. Nineteenth century biologists described the amazing productivity of Florida's reefs, which attracted and concentrated large marine animals (Goode 1887b). By 1950, monk seals had disappeared entirely, and populations of most reef organisms had been reduced. The last fifty years has seen the

severe reduction in all targeted marine animals, except those that attained early protection, such as marine birds and turtles. The animal biomass present in Florida Keys' coral reefs has been extracted over the last 300 years, and maintained at low levels; virtually none of the largest animals that historically inhabited reefs are present in ecologically significant numbers.

The consumption rates of these large animals rival that of human fishing. For example, monk seals in the Caribbean were estimated to consume more than 600 metric tons of fish per km² annually (McClenachan and Cooper 2008). While this estimate is likely too high by at least order of magnitude, as coral reefs typically can only sustain fishing at the rate of approximately 5 metric tons per km² per year (Newton et al. 2007), it is true that species that were once enormously abundant are now ecologically extinct, and that these animals consumed the same types of reef fish and invertebrates that are targeted by humans (Table 5). The small reef fish, lobsters, and conchs that once attracted large sharks and pelagic fish to Florida reefs are now fished by people, and release from predation has likely augmented biomass available to fishers. The five most commonly caught commercial species in the Florida Keys are spiny lobster, snappers, king mackerel, pink shrimp and ballyhoo (Figure 2). With the exception of king mackerel, these would have been prey items for the now extinct monk seal, as well as groupers and sharks, whose populations have been drastically reduced of (Table 4, Table 5). The fact that sustained fishing of spiny lobster at levels nearly ten times that of the 1920s—when they were first considered depleted—suggests that this fishing is facilitated by the removal of large fish and monk seals.

In conclusion, the Florida Keys reefs of today are highly altered from their original state, with the reduction of most species groups, and limited prospects for recovery. The early protection given to birds and turtles, as well as more recent protection of several species of fish, has had mixed results. While populations of some birds and the fish species have responded to protection by increasing their numbers, others have not. Populations of the Nassau grouper and queen conch have both failed to rebound, likely due to Allee effects related to reproduction. Green turtle numbers have increased in mainland Florida and other areas that have been protected, but in the Keys, the breeding population is still very small, likely due to reduction in beach area sufficiently secluded for nesting. Populations of goliath grouper, as well as those of the black and red grouper, have responded quickly to complete protection from fishing and the institution of closed areas, but the degradation of the whole ecosystem, and increased human fishing for smaller snappers and lobsters will certainly restrict the potential for recovery of these marine predators to anywhere near their historical population sizes. Thus, the restoration of the coral reef ecosystem of the Florida Keys to its full historical ecological function is unlikely, but the recovery of populations of particular species is possible with proper protection. It may be feasible to imagine and attempt to restore pieces of the reefs of the past, but the bounty of reef ecosystems as described by the first British sailors and American settlers has long been spent.

Table 4. Decline across species groups trophic levels (TL) in the Florida Keys. The timing and estimate of percent decline is given for each species

Species Group	Species	TL	Fisheries	First		Percent Decline
			Start	Evidence	Crash	
Marine mammal	Monk seal (<i>Monachus tropicalus</i>)	4.5	Pre-contact	1880	1922	100%
Marine reptile	American crocodile (<i>Crocodylus acutus</i>)	4	No data	1900	Before 1970	50-90% since 1900
Marine bird	Brown noddies (<i>Anous stolidus</i>)	3.5	1770s	1830s	1930	65-80% since 1830
Marine fish	Smalltooth sawfish (<i>Pristis pectinata</i>)	3	Pre-contact	1900	before 1965	At least 95% since 1900
Mobile invert.	Spiny lobster	2	Pre-contact	1910	1975	90%
Structural element	<i>Acropora palmata</i> & <i>A. cervicornis</i>	1.5	1850	1970s	1980	93% & 98% from 1983-2000
Structural element	<i>Hippospongia</i> spp. & <i>Spongia</i> spp.	2	1840	1895	1939	70-99%

Table 5. Species that have disappeared or become endangered

Species	Status	Historical Description	Major Diet Items
Monk seal (<i>Monachus tropicalis</i>)	Globally extinct	Keys "abounded with great plenty of seal" (1760s)	Reef fish and invertebrates
<i>Goliath grouper</i> (<i>Epinephelus itajara</i>)	Critically Endangered (IUCN)	16 caught by 1 boat (1957)	Crustaceans and reef fish
<i>Small toothed sawfish</i> (<i>Pristis pectinata</i>)	Critically Endangered (IUCN)	> 300 caught by 1 fisherman in 1 season (1890s)	Sm. schooling fish (e.g., mullet, herring)
<i>Warsaw grouper</i> (<i>E. nigritus</i>), <i>Speckled hind</i> (<i>E. drummondhayi</i>)	Critically Endangered (IUCN)	Among most commonly caught species (1880s)	Crustaceans, fish
<i>Elkhorn coral</i> (<i>Acropora palmata</i>)	Critically Endangered (IUCN)	Thick growth to the surface (1880)	
<i>Green turtle</i> (<i>Chelonia mydas</i>)	Endangered (IUCN)	Dry Tortugas named for great number nesting (1514)	Turtle grass
<i>Nassau grouper</i> (<i>E. striatus</i>), <i>common seabream</i> (<i>Pagrus pagrus</i>)	Endangered (IUCN)	Among most commonly caught species (1880s)	Reef fish, invertebrates
<i>Royal & sandwich terns</i> (<i>Sterna maxima</i> , <i>S. sandvicensis</i>)	Colonies extirpated from Keys	Present in great numbers prior to 1900	Sm. fish <20 cm (e.g., sardines, ballyhoo)
<i>Queen conch</i> (<i>Strombus gigas</i>)	CITES Appendix II	Common food, used for bait	Algae, seagrass

Table 5 continued.

Reef fish = parrotfish, wrasses, damselfish, squirrelfish, snapper and grunts;
Invertebrates= crustaceans, squid, octopus (monk seal), crustaceans, amphipods, echinoderms, mollusks (sea bream); **Crustaceans**=spiny lobster, crabs, shrimp

Table 6. Marine organisms that have been affected by disease epidemics

Group Affected	Dates	Comment
Sponges	1939, 1990s	All species of <i>Spongia</i> and <i>Hippoplospongia</i> eliminated
Conch	mid-1940s	No live conchs from Key West to the Marquesas
Turtles	1920s on	Fibropapilloma tumors not found in historical photos
Seagrass	mid-1940s, 1990s	Die off linked to declines in other marine organisms
Diadema	1983	Part of Caribbean-wide epidemic
Coral--Elkhorn	1996	Complete die off; various other coral diseases have occurred

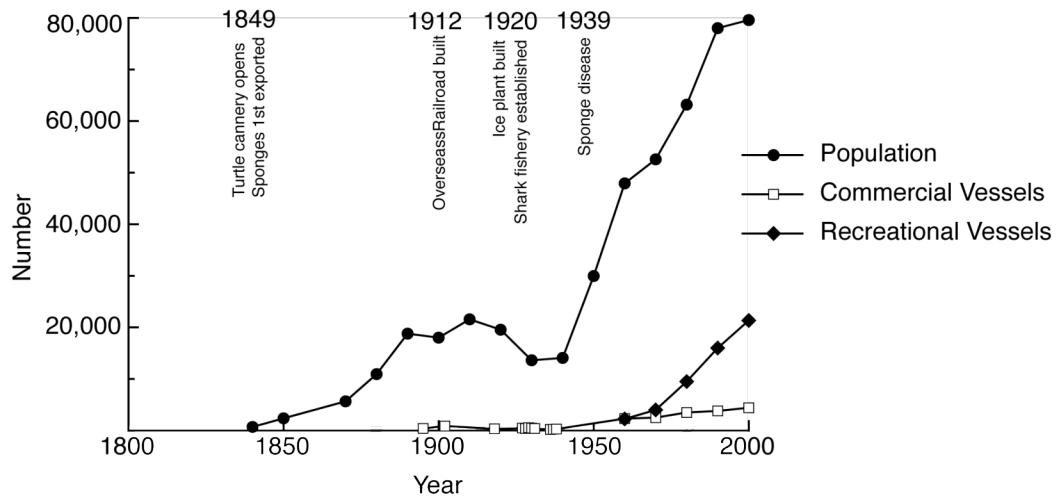


Figure 5. Drivers of decline in marine resources, including population growth, expansion of commercial and recreational fishing fleet, and links to external markets.

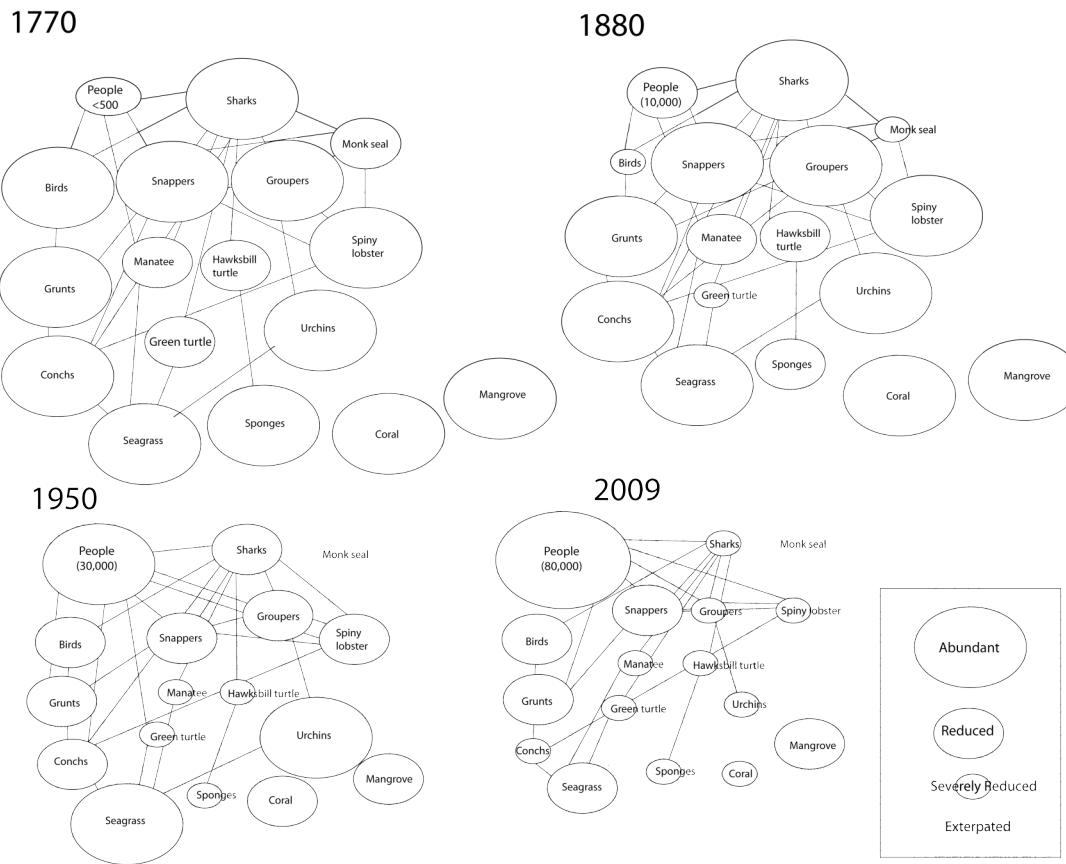


Figure 6. Food webs showing the relative abundance of major species groups in 1770, 1880, 1950 and 2009.

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CHAPTER 8: Images of a fisherman's paradise: How the Florida Keys lost all its fish

ABSTRACT

The image of the Florida Keys as surrounded by pristine seas is in stark contrast to the environmental reality of overfishing and habitat destruction below the water's surface. That a place could be simultaneously severely environmentally degraded and maintain an image of untouched wilderness is a testament to the lasting effects of early and sustained image building about the region. This final chapter investigates the image that developed of the Florida Keys through the writings of anglers and tourism interests in the late 19th and early 20th century and argues that this image superseded the reality observed by masses of fishermen visiting to and retiring to south Florida in the mid 20th century. Nineteenth-century sportfishing was an activity for elite anglers who could afford the long distance travel from northern cities and had the constitution to enjoy rugged, hot, and unpredictable fishing conditions. These fishermen envisioned themselves as connected to nature through their fishing lines and were concerned with environmental conservation, albeit with self-interested motivations. In south Florida, the writings of these anglers, including Ernest Hemingway, between 1890 and 1930 captured the imagination of an American public that began to arrive in Florida with ideas of the wilderness and adventure that awaited them. The transformation of sportfishing from an activity for "gentleman anglers" into one accessible to all hard working Americans democratized the recreational fishing industry but simultaneously distanced anglers from the natural environment. Instead of observing the decline of fish populations through their own eyes, anglers instead

envisioned themselves living out adventures described by earlier generations, so that environmental degradation was largely overlooked by the sportfishing community. The Florida Keys provide a case study for this phenomenon but similar events occurred in southern California, northern Maine, and several inland fisheries.

INTRODUCTION

The Florida Keys today draw “visitors from around the world” who come to experience the “priceless natural resources” advertised by the Tourism Board and numerous hotels and resorts. Among the most enticing natural features is the “extraordinary reef ecosystem” which draws more than a million tourists annually and is said to offer the “best saltwater sportfishing in all of North America” (Florida Development Council n.d., Sportfishing n.d.). For fishermen along the East Coast of the United States, the Florida Keys are an exotic destination achievable by car. Large migratory billfish brought in by the Gulf Stream and brightly colored snappers and groupers lend an air of glamour to Florida fishing. The Keys are described as a rare wilderness close to home, and anglers dream of settling into retirement where fishing is “a way of life” (Florida Development Council, n.d.).

However, this picture of pristine seas full of fish is in stark contrast to the reality below the water’s surface. Florida’s reefs are in serious trouble. Massive overfishing has removed the largest fish, and 90% of Florida’s two most common reef

building corals died suddenly in the 1990s, leaving behind dead skeletons covered with algae that fish cannot eat (Pandolfi et al. 2005). Catching “The Big One” has become nearly impossible, since the largest fish are small sharks that could be caught by children, and the average fish is smaller than a dinner plate (McClenachan 2009). The contrast between the perception of the Keys as a pristine wilderness and the reality of dead reefs is greater still when we look back in time to see the enormous changes that have occurred.

The human effects of fishing on coral reefs in south Florida have been profound. In my dissertation research I found that marine turtles were reduced to a fraction of their pre-Columbian population before 1890, monk seals were locally extinct by 1920, and sponges were decimated by 1940 (this document, Chapter 7). Fish have declined in size by 90%, and several species of large game fish are in danger of extinction. Yet fishermen continue to travel to the Keys and businesses dedicated to charter fishing still thrive (McClenachan 2009).

As I was looking for the evidence of quantitative ecological changes that I reported in the first chapters of my dissertation, a different sort of question began to emerge for me. I began to wonder, How did this discrepancy arise? How do recreational fishermen accept such massive changes and still consider the Keys an “angler’s paradise”? This final chapter will summarize the declines in large fish that have occurred over the last half-century, and conclude with several possible historical roots for the difference between the image and reality of fishing in the Florida Keys.

BACKGROUND: DECLINES IN LARGE FISH

Historical marine ecology aims to characterize and measure long term ecological changes with historical sources. Recent studies have shown declines as much as 99%, in the abundance of marine animals, including sharks, turtles, seals, and fish (Baum and Myers 2004, Jackson et al. 2001, Lotze and Milewski 2004, Myers and Worm 2003). In the archives in Key West, Florida, I found a set of several hundred photos taken of trophy fish, and I used them to measure changes in fish communities. These photos showed fish caught primarily by novice fishermen on large, bottom-fishing charter boats, termed “party” or head boats. In the 1950s, several party boat companies existed in the Keys. These boats were described as “a good bet for the casual fisherman;” passengers were given tackle, sold beer, and promised a good time (Francis 1958). Boat captains took groups of up to seventy fishermen on day trips to local reefs to fish for species including groupers, snappers, jacks, and sharks. At the end of each day, the boat’s crew hung the largest fish, and tourists posed for a souvenir photograph. All of the photographs that I discovered were taken by Charlie Anderson, a local photographer who had a business selling photos to tourists. The photos were also mailed to newspapers throughout the United States to advertise to future tourists.

The same boats operate today, and I took similar photos myself in 2007. The photos show the largest fish caught on one day of fishing, and contain information on the fish present on the reefs close to Key West over the last half century. I identified

the fish and measured them relative to the height of the display board. In total, I measured 1,285 fish, which I separated into thirteen groups. I found that the largest fish that were commonly caught in the 1950s are no longer present. In the 1950s, sharks and groupers larger than the fishermen themselves were commonly caught. Early landings were dominated by large groupers with an average size of nearly one and half meters. In the 1970s, the most commonly caught fish, permits and jacks, were slightly smaller on average. And in 2007, the trophy fish were small snappers, barely twelve inches in length.

All together, I found that the average size of the largest fish declined by 90%. These photos are striking, and quantifying declines demonstrated the magnitude of change. However, a nagging question remained, particularly in light of the fact that I also discovered that there was no concurrent change in the price per trip over time. In other words, fishermen today are paying the same amount, relative to income, to catch a 12-inch fish as they did in the 1950s to catch fish that were 5 and 6 feet long. I began to wonder, Why do people pay hundreds of dollars to catch a fish that is worth less than \$10? Do fishermen realize that they are receiving a severely degraded product? I want to suggest three possible reasons that fishermen continue to dedicate time and money to catch small fish.

The first reason may be incredibly obvious. One appeal of recreational fishing that should not be underestimated is summarized by the cliché displayed on T-shirts & bumper stickers across America, “A bad day fishing beats a good day working.” The avid angler and writer, Zane Gray himself described the fish he caught as “incidental.”

Instead, he wrote, the reward is “the incalculable and intangible knowledge [that] emanate from the swelling and infinite sea.” (Gray 1919: 108). Thus, the fact that the fish are small and no longer bountiful maybe insignificant if the purpose of the trip is simply to relax, observe the ocean, or drink beer, with the thrill at the possibility of also catching a fish.

However, I believe that the relative appeal of being out of doors does not provide the whole explanation for continued fishing despite the near disappearance of fish. I want to argue that there is something unique about the Keys that causes the current-day reality to be obscured by nostalgia for a type of fishing that existed a century ago. The myth of the Keys as a tropical paradise for salt-water anglers began in the 1870s and was spread widely in the first half of the 20th century. Anglers responded by flocking to the Keys, particularly in times of prosperity: the 1920s, and after WWII. The myth that the Keys are a haven for fishermen is maintained today, and works towards the detriment of the fish populations.

THE EVOLUTION OF RECREATIONAL FISHING, 1870-1960

Florida was the least densely populated southern state when it joined the Union in 1845, and the chain of islands stretching westward from its southernmost point were distant tropical islands. After the Civil War, articles and books began to appear extolling the virtues of Florida for sportsmen and settlers. The Florida Keys were featured in articles appearing in *Atlantic Monthly*, *Century Magazine*, and *Outing: An*

Illustrated Magazine of Recreation. Among other things, writers described them as “a paradise of the fishermen” (Holder 1891). Typical of the genre was a 1870s book called “Camp Life in Florida,” which listed the numerous fish that could be caught in the Keys, and the fun that could be had doing so. Wrote C. Hallock: “The shallow water was literally alive with sheepshead, weakfish, red-fish, pompano, cavalli, grouper, etc. In the deeper water there roamed dozens of voracious sharks. Frank amused himself for over an hour, hunting sharks with a shot gun” (Hallock 1876: 281). The Keys were accessible only by boat, and sportfishing was an activity for elite anglers who could afford long distance travel from northern cities and had the constitution to enjoy rugged, hot, and unpredictable fishing conditions. Their ability to put up with swarms of mosquitoes, sharks, crocodiles, and the pervasive humidity added to the intrigue of their stories. For most readers, however, the articles and books acted not as travel guides, but rather descriptions of inaccessible and far-off islands to be imagined rather than visited.

Vacation in the nineteenth century was a privilege of the upper class, and this was particularly true for visitors to Florida, for which the trip required hiring guides and carrying the fixtures of a camp. Though sometimes arduous, camping vacations were gaining in popularity in the late nineteenth century, fueled by romantic writings on the value of wilderness. Such outdoor tourism was a mark of upper class status, and helped urban dwellers feel connected to the natural world (Sjovold 1999). Nineteenth century anglers envisioned themselves as connected to nature through their fishing lines, and thought of themselves as sensitive observers of the environment, as well as

its guardians against growing industrial pressures (Parenteau 2004). Beginning in the 1870s, sport-fishing interests played a central role in sponsoring fishing laws, albeit in ways that made them the principal beneficiaries of new regulations.

Throughout the late nineteenth century, the Florida Keys were featured in book and articles, but it wasn't until infrastructure was built that they became accessible to average Americans. Tourism closely tracked the geographic expansion of the railroad system, as new lines provided easy and comfortable transit, and railroad companies advertised for resorts along their routes (Aron 1999). When the Flagler Railroad's East Coast Extension reached Key West in 1912, eager visitors began to arrive, and many took advantage of the Long Key Fishing camp, built in 1906, as a base for fishing expeditions.

By the nineteen-teens, many working class Americans had begun to take vacations. The increased ease of travel made more destinations accessible, and the two-week vacation had become a common workplace benefit (Aron 1999). Economic prosperity in the 1920s, and the brief, but intense, land boom stimulated Florida's tourism, prompting more people to visit the Keys in one decade than in the past fifty years. The writings of Zane Gray, Ernest Hemingway and others echoed the voices of earlier writers, and captured the imagination of an American public that for the first time had the ability travel to Florida, witness its wilderness, and experience the adventure of catching large exotic fish. The transformation of sportfishing from an activity for "gentleman anglers" and rugged frontiersmen into one accessible to all hard working Americans democratized recreational fishing, but simultaneously

distanced anglers from the natural environment (Sjovold 1999). The adventures were smaller and the wilderness harder to find as throngs of fishermen began to arrive with ideas of the pristine seas that awaited them.

Zane Gray, the most prolific and widely-read author on the subject of sport fishing, described the effect that increased numbers of fishermen were beginning to have on populations of fish. “The waste has been enormous,” he wrote. “Tons of fish are brought in only to be thrown to the sharks.” As a founding member of the Long Key Fish Camp and President in the year that his popular book, “Tales of Fishes” was published, he was intensely concerned with preserving local fish. He promoted sportsmanship as conservation, suggesting that the best fishermen were those who allowed the fish a sporting chance. In particular, he championed the use of lighter fishing tackle. In 1919 he wrote, “If fishermen will only study the use of light tackle they will soon appreciate a finer sport, more fun and gratification, and a saving of fish. I mention this here to give [the wastage] a wide publicity. It is criminal in these days and ought to be stopped” (Gray 1919).

The 1930s brought the effects of the Great Depression, the destruction of the railroad in the most intense hurricane ever to hit the North American continent, and declines in the two major commercial industries in the Keys: cigar making and sponge fishing. In many cases, short-term economic slumps reduce human pressure on the natural environment, and in the Keys, the downturn resulted in a drop in the numbers of anglers and tourists. It wasn’t until after WWII that large numbers of anglers returned to the Keys, and this time the fish had no champion such as Gray, and no

reprieve at the hands of economic depression or natural catastrophe. Like in the 1920s, the prosperity following WWII ushered masses of visitors to Florida. The creation of the automobile culture had made out of the way places accessible and the addition of rural electricity, public potable water, and the use of DDT to control mosquitoes jump-started growth (Aron 1999). The population of Key West and the number of registered business both doubled between 1940 and 1950 (Monroe County 1991).

Florida Keys fishing was now available to anyone who had a car and a week or two of vacation. Books were written catering to “the local workingman who does his fishing on weekend, and the tourist who saves up all year for his fishing trip to Florida” (Francis 1958). Articles appeared in magazines such as *Sports Illustrated*, *Field and Stream*, and *Hunting and Fishing*, one of which likened arriving for the first time to Florida to being “turned loose in a candy factory; [a fisherman] hardly knows where to start” (Francis 1958). Together with population growth and infrastructure development, the expansion of the headboat industry allowed people who had never held a fishing pole to spend a day trying their luck. Fish-finding technologies made fishing less about deeply understanding the habits of fish and natural conditions than interacting with these new machines. This transition to modern tourism was the death knell for reef fish populations in the Keys.

NOSTALGIA FOR BIG FISH

As fishing became more accessible and less adventurous, advertisers increasingly relied on links to the past, enticing anglers with nostalgia and descriptions of mythical large fish that had been caught by “European royalty” and “business tycoons” as well as the locally beloved Ernest Hemingway and Zane Gray (Florida Development Council n.d., Sportfishing n.d.). The Florida Keys’ Tourism board liberally mixed history into descriptions of the modern fishing experience to help the potential tourist feel like a frontiersman, and to obscure the fact that fish in the Keys were disappearing.

The history of nostalgia in tourism is closely tied with environmental destruction, both because of the desperate need for generating industry in places historically dependent on natural resources, and because of the desire of urban tourists to escape to a simpler place and time. In late nineteenth century Nantucket for example, affluent tourists nostalgic for the glory days of whaling and yearning for pre-Industrial simplicity began to arrive on the island, finding the run-down shacks a whimsical reprieve from urbanizing Boston. Not coincidentally, the decrepit buildings from the prosperous whaling days of the recent past were signs of isolation and economic failure (Brown 1995).

In the Florida Keys, this nostalgia extended beyond large fish. The “Turtle Kraals” restaurant based on the long-defunct turtling industry, the annual Ernest Hemingway look-alike contest, and ubiquitous references to pirates all signify some

desire to escape the present and live out a fantasy from the past. The myth of the Florida Keys as a place to catch big fish contains elements of the same yearning for a time when the ocean was bountiful and the constraints of modern life fewer. The picture that developed of the Florida Keys through early writings superseded the reality observed by of 20th century fishermen. In this way, individual fishermen's perception of their experience was pre-molded and fishermen envisioned themselves living out adventures described by earlier generations.

I want to finish by suggesting a final reason that recreational fishing continues despite a lack of fish, and argue that far greater regulation of game fishing is needed. Recreational fishing differs from commercial fishing in one essential way: anglers do not need to make a profit to justify their time on the water. Anglers are not reactive to economic pressures as are commercial fishermen, and therefore are less reactive to changes in the environment that affect their catch.

Big distant fish, such as those that could once be caught in the Florida Keys, have value even if they are mythical because the value resides not the actual fish, but rather, the experience of catching the fish, and in some cases, the idea of the experience of catching the fish. In short, anglers will continue to go fishing after the last fish is gone because there are no actual consequences of returning from a fishing trip defeated. For this reason, economic forces will not prevent overfishing. Neither will reliance on anglers to self-regulate. Zane Gray described the particular brand of individualism that made promoting conservation difficult among recreational fishermen. "The difficulties of introducing a sportsman-like ideal have been

manifold," he wrote. "A good rule of angling philosophy is not to interfere with any fisherman's ways of being happy, unless you want to be hated. It is not easy to influence a majority of men in the interests of conservation" (Gray 1919). Gray's words have become more true in the last eighty years, as the number of recreational fishermen has grown. Thousands of anglers want to preserve the right to fish, and are deftly represented by groups such as the Coastal Conservation Association, which lobbies to maintain free access and minimize restrictions. Changes in ethics, as advocated by Zane Gray, are apparent in growing numbers of catch and release fishermen, but increases in individual ethics have not kept pace with the growth in fishing effort.

Citizens concerned with the marine environment should then ask, Why do we let fishermen continue to extract the last fish from the sea? I believe that a partial explanation can be offered by the history of recreational fishing as one characterized by greater access for more people over time, and in the Florida Keys, reliance on nostalgia that obscures actual declines. The myth that large fish exist and that everyone deserves to catch them must be de-bunked if any remnant of the fish of the past are to be preserved.

In conclusion, the Florida Keys have suffered the effects of both intensive fishing and intense image building over several generations. That a place could be simultaneously severely environmentally degraded and maintain an image of untouched wilderness is a testament to the lasting effects of early and sustained image building. Unraveling this story is one step in acknowledging the extreme changes that

have occurred, and in developing political will to better regulate overexploited fish populations.

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