Multicentury trends and the sustainability of coral reef fisheries in Hawai‘i and Florida

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Abstract
Global overfishing indicates a need to define fisheries sustainability thresholds and identify social factors promoting successful management, but rates of fishing and factors mediating sustainability over long timescales are largely unknown. Here, we reconstruct fisheries yield for the entire period of human habitation (five to seven centuries) for two coral reef ecosystems with substantially different fisheries histories (Florida Keys and the Hawaiian Islands) and evaluate the management strategies associated with periods of sustainable fishing. This involved a mixed methods approach, in which we estimated yield by fishery sector (commercial, subsistence, recreational and aquaculture) and characterized management strategies associated with periods of sustained high yields. We found differences between the two locations, with Hawai‘i sustaining yields of more than 12 mt km$^{-2}$ for four centuries prior to the arrival of Europeans. This period was characterized by adaptive management whose design and enforcement exhibited characteristics of common property resource governance systems, and which effectively protected reef habitat, vulnerable life-history stages for fish, and species with high susceptibilities to overfishing. Reefs in both Florida and Hawai‘i were exploited intensively after European contact, with sequential export-driven depletion evident in Florida over the past century. Today, both exhibit strikingly similar modern catch levels, with landings exceeding 10 mt km$^{-2}$ and evidence of overfishing. Our results demonstrate that management strategies and social institutions that support strict enforcement by a local rule-making authority have had substantial impacts on fisheries yields in the past and suggest that long-term sustainability of fisheries is possible, although rare today.

Keywords Catch reconstruction, common pool resources, historical ecology, institutions

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Introduction

As global limits on fisheries resources are approached (Pauly et al. 2002), it becomes essential to evaluate policies for increasing yields and supporting sustainable fisheries, including strategies that succeeded or failed in the past. In particular, the history of fishing on tropical islands provides a microcosm for evaluating limits to global fisheries, as these societies were often entirely dependent on local resources with few opportunities for geographic expansion, a complicating issue in analyses of sustainability of the global fisheries (e.g. Swartz et al. 2010). Today, a majority of coral reef fisheries are over-exploited, which has impacted the function of coral reef ecosystems and posed food security risk in tropical countries worldwide (Roberts 1995; Whitithingham et al. 2003). Coastal societies have fished reefs for millennia (Kirch 1982; Wing and Wing 2001), but past levels of fishing, sustainable exploitation rates, and the social factors that mediate the sustainability of fisheries in reef environments remain poorly understood (Cinner et al. 2009). Understanding factors supporting sustainability of fisheries requires investigation of fisheries yields, natural resource management strategies, and societal institutions, and how these interact over long timescales.

Resource sustainability can be defined in terms of maximum yield, optimum yield or minimum risk of extinction (Botsford et al. 1997; Reynolds et al. 2005). In multispecies coral reef fisheries, aggregation of landings is common and sustainable yield is frequently represented by a number of tons of fish and invertebrates that can be harvested annually per square kilometre of coral reef habitat (t km$^{-2}$) (Dalzell 1996). A wide range of sustainable fishing rates for coral reef fisheries have been proposed, from less than 1 t km$^{-2}$ to more than 25 t km$^{-2}$ (Dalzell 1996; Dalzell et al. 1996, Dalzell and Adams 1997; Newton et al. 2007). These have been developed from comparisons of landings data from modern fisheries data and ecosystem state (Newton et al. 2007) and surplus production models that use observations of annual fishing rates (Dalzell and Adams 1997). In all cases, however, sustainable fishing rates are based on short-term observations, and sustainability over time has not been quantified.

We seek to quantify sustainable fishing rates in coral reef ecosystems over century-long timescales and define sustainability at the ecosystem level as the ability to sustain extraction of fish and invertebrates at a constant level over time. Historical analyses are increasingly common in evaluations of fishing on coral reefs (Pandolfi et al. 2003; Saenz-Arroyo et al. 2005; Hardt 2009; McClanahan 2009a), as well as in other environments (Christensen et al. 2003; Ainley and Blight 2009), and have frequently revealed declines in groups of marine animals that occurred decades to centuries in the past (Pitcher 2001). Our objective was to quantify fishing in US reef ecosystems since the beginning of human settlement, identify periods in history when fisheries were sustainable, and characterize social and institutional factors associated with sustainable fisheries.

Catch reconstruction is one historical technique used to characterize past fisheries in the absence of robust landings data. This method relies on a diversity of data types, ranging from reported catch data to estimates of per-capita consumption (e.g. Zeller et al. 2007). Catch reconstructions have been useful for estimating rates of fishing in data-poor tropical regions where rates of unreported subsistence fishing are high and resources to collect landings data are limited (Polunin and Roberts...
1996). While imprecise, this method can provide a more accurate estimate of historical fisheries than one based on incomplete landings data, as a lack of data can erroneously imply zero catch. Reconstructions of coral reef catches have provided estimates of trends over time and characterized contributions of subsistence sectors to tropical fisheries economies that would be otherwise unknown (Zeller et al. 2006, 2007; Jacquet et al. 2010).

Here, we reconstruct historical yields for coral reef fisheries since human settlement for the Hawaiian archipelago and the Florida Keys and evaluate the social and institutional contexts associated with the historical trajectories of these fisheries. These locations contain the majority of coral reef ecosystems in the United States (Rohmann et al. 2005), have a long history of human settlement in coastal zones, and possess relatively robust historical data sets and catch statistics compared to other tropical regions. Further, they have histories of human settlement that differ substantially from each other, which provides an opportunity to evaluate the effects of different social histories on reef fisheries. Today, coral reef fisheries in both locations are over-exploited, and sustainable management is a priority (Ault et al. 1998; Friedlander and DeMartini 2002; Pandolfi et al. 2005; Williams et al. 2008). This comparative catch reconstruction was designed to estimate yields over long timescales and to identify key differences in the management of these systems that worked to sustain fisheries in the past and may help rebuild and sustain coral reef fisheries in the future.

History of exploitation

In Hawai’i, subsistence fishing for reef species has been ongoing since Polynesian settlement around AD 1250 (Titcomb 1972; Kirch 1982; Wilmshurst et al. 2011). Human expansion throughout the archipelago is associated with high pre-contact human population densities and the development of large-scale aquaculture and agriculture to support these populations (Vitousek et al. 2004; Kirch 2007). After European contact in AD 1778, coral reef fishinsh became a minor part of the trading economies established between Native Hawaiian societies and foreign vessels. After 1819, more foreigners settled permanently in the islands and port cities quickly became focal points for ship provisioning and trade by foreigners engaged in various maritime industries in the Pacific. Commercial fisheries were initiated in the early 19th century and were supplied by Native Hawaiian fishers as early as the 1830s (Schug 2001), but outside of urban areas, subsistence reef exploitation continued relatively unchanged (Coulter 1931). By 1900, commercial fisheries had become a dominant feature in local island economies with fish markets established on each of the main Hawaiian Islands. In the 20th century, commercial fisheries shifted to pelagic species, but reefs continued to be targeted for subsistence fishing, which was fuelled by post-WWII population growth, increased coastal development and increased access to boats and fishing technologies (Glazier 2007).

The history of the Florida Keys is also characterized by a high reliance on coral reef fisheries, but several key differences exist between Floridian and Hawaiian fisheries history. While Hawai’i exhibited large pre-contact populations and extensive terrestrial resources, the Florida Keys supported a low population density for the majority of its human history, because of a lack of freshwater resources (Goode 1884; Goggin 1944). After European contact, fisheries developed in the Florida Keys because of their proximity to the mainland North American settlements and northern Caribbean islands. Reef-associated species, including turtles, groupers and sharks, were shipped from the keys to Cuba beginning in the late 1700s (Romans 1775; Collins 1885), and the economy of Key West developed in the 1800s around the export of reef sponges and marine turtles to Europe and North America (Goode 1884; Collins 1885). The Florida Keys were an accessible location for sport fishing beginning in the 1860s and the completion of a railroad linking north-eastern cities to Key West in 1912 facilitated access for tourists and recreational fishers (Wilder 1868; Hallock 1876; Giacobbe 1996; Mormino 2005). After World War II, both commercial and recreational fisheries expanded rapidly, with the number of registered vessels quadrupling between 1960 and 2000 (Ault et al. 1998).

Methods

We used catch reconstruction methods to estimate coral reef fisheries yields in Florida and Hawai’i since the beginning of human settlement (sensu Zeller et al. 2006). This method combines estimates of per-capita catch rates with reported fisheries yield data for the commercial, recreational, subsistence, and fish pond sectors, and uses archival and grey
literature sources to calibrate reconstructions when catch data are sparse or unavailable. We standardized catch by the total area of reef so that we could compare total yield between regions. Finally, we characterized the social factors in each location and identified elements of past management regimes that may have affected total yield.

**Reef area & fisheries species**

First, we estimated total reef area for each region. For Hawai‘i, estimates for the total area of coral reef in the main Hawaiian Islands from NOAA’s Biogeography Branch were used (1313 km$^2$) (Battista et al. 2007). These estimates are comprised of 15 different coral reef habitat types and were comparable with the estimates of potential coral reef area within the 10-fathom depth contour (1231 km$^2$) (Rohmann et al. 2005). Reef area estimates for the Florida Keys vary more widely depending on the types of habitat included and whether estimates are based on bathymetry or in-water surveys. On the basis of the depth profiles, Rohmann et al. (2005) estimated that 10 447 km$^2$ of potential coral ecosystem exists in the Florida Keys National Marine Sanctuary and the Dry Tortugas National Park; Spalding et al. (2001) suggested that 1250 of km$^2$ reef-building corals exist in south Florida; and Miller and Crosby (1998) used measured areas of coral-patch reef and coral platform margin reef to estimate that 325 km$^2$ of reef exists in this region. We used an estimated reef area of 501 km$^2$ which was derived using Rohmann et al.’s (2005) estimate of potential coral and quantified percentages of the following habitat types: aggregate reef, spur and groove, individual patch reef, pavement with sand channels, and aggregated patch reefs, reef rubble, and sand with scattered coral (S.O. Rohmann, unpublished data).

Because we chose to use a relatively restricted definition of reef habitat, we also restricted our species list to those that spend a significant portion of their history in reefs and were caught in reef environments. For Hawai‘i, species were included if they were reef-associated for a significant part of their life history or if the species were caught in shallow reef environments (<60 fathoms). This determination excluded deep-reef demersal species (bottomfish), but included species associated with estuarine/nearshore (e.g. *Mugil cephalus*, Mugilidae; *Chanos chanos* and Chanidae) and coastal pelagic environments (e.g. *Selar crumenophthalmus*, Carangidae; *Decapterus* spp. and Carangidae) that were commonly caught in reef environments using reef fisheries gears. Determinations were based on life-history characteristics described in Randall (2008); occasionally verifications were made with online databases (FAO 2010, Froese and Pauly 2010). Reef fish classifications for Florida were taken from Bohnsack et al. (1994), with occasional verifications made with FAO (2010), and Froese and Pauly (2010). Reef-associated species in Florida (e.g. *Scomberomorus cavalla*, Scombridae) were excluded if they were known to be caught primarily on non-reef environments, estuaries, or if found more than 10 fathoms.

**Data availability**

Data availability varied across time and between the two locations, but primarily consisted of reported commercial and recreational landings data, estimates of per-capita consumption and population size, and observational data that inform trends in fishing rates over time. Species-specific commercial catch landings existed from the late nineteenth (Florida) and early 20th centuries (Hawai‘i), which is rare for tropical island fisheries. These catch data provided the basis for late-historical catch reconstruction and were supplemented with estimates of non-reported catch, population and effort data. For years in which catch, effort, population or observational data were missing, we linearly interpolated between estimated data points (*sensu* Zeller et al. 2006).

**Hawai‘i catch reconstruction**

For Hawai‘i, catch was reconstructed beginning in 1250, the estimated date for Polynesian settlement of the archipelago (Rieth et al. 2011; Wilmshurst et al. 2011). Commercial, recreational and subsistence fishing sectors are difficult to disentangle, as many fishers engage multiple fishing activities in a single trip (Glazier 2007). As such, catch reconstructions were grouped into commercial, fishpond aquaculture and non-commercial (subsistence/recreational/cultural) sectors, with the caveat that these categories are not mutually exclusive.

For the period prior to Western contact (AD 1250–1778), non-commercial (subsistence/recreational/cultural) fisheries yields were estimated based on per-capita consumption rates and estimates for human population size. Per-capita catch rates were anchored in AD 1250 to a conservative estimate of 182 kg person$^{-1}$ year$^{-1}$ proposed for pre-contact
Hawai‘i by Kirch (1982) and were adjusted downward by 20% to 145.6 kg person\(^{-1}\) year\(^{-1}\) during the late pre-historic period (AD 1400–1778) to account for increased proportions of agricultural and animal husbandry foods in diets and the imposition of consumption restrictions on some reef fauna (Table 1). This reduction is based on evidence of the development of large-scale agriculture complexes providing a larger agricultural subsistence base, evidence of increased animal husbandry during the late pre-historic period in ethnographic and archaeological records, and ethnographic and archaeological evidence of the imposition of chiefly controls on some reef resources limiting extraction and consumption (Vitousek et al. 2004; Titcomb 1972). The per-capita catch estimates used for the pre-historic period in Hawai‘i (AD 1250–1778) are analogous to contemporary estimates for fish consumption in rural, undeveloped Pacific islands (Gillett and Lightfoot 2001; Zeller et al. 2006), but should be viewed with caution owing to their uncertainty. Per-capita catch rates are degraded linearly to reported consumption estimates from the 1960s to 1980s, which range between 18.1 (1965) and 8.8 kg person\(^{-1}\) year\(^{-1}\) (1974) (Garrod and Chong 1978; Hudgins 1979; Shomura 1983) (Table 1). A demographic model developed by Dye and Komori (1992) (as reviewed by Kirch 2007) was used to estimate total human population in the pre-contact period (Figure S1). To keep the estimates conservative, pre-censal population estimates (<1831) at the low end of reported populations ranges were used (163,000 max population achieved) (Schmitt 1977; Dye and Komori 1992; Kirch 2007). Post-censal population data were derived from extant published statistics and the US Census Bureau (Schmitt 1977; US Census Bureau 2011).

Fishponds were also an important component of subsistence strategies in Hawai‘i, and hundreds were constructed and maintained in pre-historic times (Summers 1971; Kikuchi 1976). Native Hawaiians harvested juvenile reef species to stock fishponds and used fishponds in part as a means of risk management for food security (Kikuchi 1976; Costa-Pierce 1987). Fishponds were also symbols of chiefly power with restricted access and required significant labour investments to build and maintain (Kikuchi 1976). The production of fishpond aquaculture was calculated using reported yield data from the post-contact period, qualified estimates of production for the pre-historic period, and linear interpolation between estimates and yield data for periods where data were unavailable. The first fishponds were believed to have been constructed sometime after AD 1200 (Burney and Burney 2003), with the majority of fishponds constructed between AD 1300 and 1600 (Kikuchi 1976; Denham et al. 1999). Correspondingly, fishpond production was anchored at 0 at AD 1250 and linearly interpolated until Western contact at AD 1778. Fishponds were assumed to be at their maximum production capacity at the time of European contact, with estimates of production ranging from 902 to 1052 mt (1,988,922–2,320,405 lbs) for the entire archipelago (Kikuchi 1976; Costa-Pierce 1987). The first quantitative measurements of yield were reported in 1900 and 1902 by the US Fish Commission (Cobb 1902, 1905a, b). Historical estimates from the Cobb reports were used for the mid- to late 1800s and were corroborated with other archival information and reports that suggest fishpond production had decreased in the early 19th century (Stokes 1908; Coulter 1931; Summers 1971). In the 20th century, production estimates from archival sources and reports were used (DFG 1927–36, Hamamoto 1928; Konishi 1930a, 1933; Bell and Higgins 1939; Storm 1940; Haan and Tester 1949; Costa-

<table>
<thead>
<tr>
<th>Date (years, AD)</th>
<th>Per-capita catch rate (kg person(^{-1}) year(^{-1}))</th>
<th>Source and notes</th>
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<tr>
<td>Hawai‘i</td>
<td></td>
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<tr>
<td>1250–1400</td>
<td>182.5</td>
<td>Kirch 1982</td>
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<tr>
<td>1400–1778</td>
<td>146.5</td>
<td>20% reduction</td>
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<tr>
<td>1796–1960</td>
<td>139.3 → 24.5</td>
<td>Linear interpolation</td>
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<td>1960</td>
<td>18.1</td>
<td>Garrod and Chong 1978</td>
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<td>1970</td>
<td>10.2</td>
<td>Hudgins 1979</td>
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<td>1980</td>
<td>10.9</td>
<td>Shomura 1983</td>
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<tr>
<td>Florida</td>
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<tr>
<td>1840–1900</td>
<td>82.0</td>
<td>Average catch/population from Goode, Monroe County Statistical Abstract (1880)</td>
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<td>1900–1940</td>
<td>73.0</td>
<td>Average catch/population from Goode (1902, 1918, 1930)</td>
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<td>1940–2010</td>
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Pierce 1987) (Table S1). On the basis of the reported statistics, a percentage estimated as ranging from 38 to 63% of fish reported as ‘miscellaneous’ species were attributed to fishponds for the 1920s and 1930s (DFG 1927–36, Hamamoto 1928). When reported miscellaneous catch statistics were not disaggregated, a mean percentage of 53% of the total for fishpond production was used.

Commercial coral reef fishery catch was reconstructed by combining reported catch data with estimates of non-reported catch derived from anecdotal and historical descriptive sources and linearly interpolating for years in which catch data were missing. Commercial catch data were extracted from several sources, including a major quantitative survey of fisheries conducted in 1900 and 1903 by the US Fish Commission (Cobb 1902, 1905a,b), statistics collected by the Division of Fish and Game of the Territory of Hawai‘i in the 1920s and 1930s (DFG 1927–36), and statistics from the Division of Aquatic Resources, Department of Land and Natural Resources, State of Hawai‘i from 1948 to 2009 (DAR 2009). These records were supplemented by unpublished reports from the University of Hawai‘i, the US Bureau of Fisheries, and other archival sources (Hamamoto 1928; Konishi 1930a,b, 1933; Bell and Higgins 1939; Storm 1940) (Table S2). Commercial fisheries were anchored at 0 at 1820, when the first commercial fisheries markets were established in the major port cities (Schug 2001), and linear interpolation was used to estimate catch between 1820 and 1900 and during other data-less periods (1901–02, 1904–24, 1939–47). To calculate unreported commercial catch, conservative estimates were derived from quantitative estimates and qualitative descriptions in archival sources and published reports. For example, reported catch from 1925 to 1936 includes only data from the Honolulu and Hilo markets where fisheries products were sold through licensed fishing companies who were required to report catch to the Division of Fish and Game. On other islands, fishers engaged in the sale of fish to middlemen, fish merchant stall owners, or directly to consumers, rather than through an established fishing company that reported their statistics to the state (Bell and Higgins 1939; Cobb 1902, 1905a,b; Storm 1940). When quantitative estimates of non-reported catch were reported, they were used verbatim to calculate non-reported catch. For example, non-reported catch was estimated to be 34% in 1927 and 1925 (Hamamoto 1928; Konishi 1930a). For the years 1929–38, a conservative estimate of 25% additional catch was added to the reported catch to account for unreported commercial catch outside of the main markets (Table S2).

**Florida catch reconstruction**

For Florida, populations prior to European contact are highly uncertain, so catch was reconstructed beginning in 1513, the first European contact (Worth 2006). For the period 1513–1840, catch rates were estimated for subsistence fishing only, based on population data and per-capita catch rates. Owing to the large informal sector in the commercial fisheries sector in the Florida Keys (Goode 1884; Collins 1885), unreported commercial catch was considered to be a part of the subsistence catch between 1840 and WWII. Human population for the Florida Keys was estimated at approximately 1000 individuals before European arrival, with a reduction to 100 individuals by 1760 (Worth 2006). Beginning in 1840, decadal census data are available for Monroe County (White 1991). Before European contact, reef fish contributed up to 83% of the Caribbean diets, being highest on islands with few terrestrial resources like the Florida Keys (Wing and Wing 2001). Because of the similar reliance on reef fish between Caribbean and Pacific islands, the estimate of per-capita catch from Pacific fish–based economies of 182 kg person\(^{-1}\) year\(^{-1}\) (Kirch 1982) was used to estimate total fish consumption before European settlement. There was no agriculture in the Keys, and European fisheries were significant (Fontaneda 1575; Romans 1775; Goggin 1944), and there is no evidence to suggest that the per-capita catch rate declined before the early 19th century. For the period of initial American settlement (1840–1900), agriculture and other industry had become minimally established. For this time period, per-capita catch rates were estimated as 82 kg person\(^{-1}\) year\(^{-1}\) based on reported average landings of 910,000 kg of fish per year in 1880 (Goode 1884) and reported population of 10,940 (White 1991). Per-capita catch rates for the first portion of the twentieth century (1900–40) were estimated as 73 kg person\(^{-1}\) year\(^{-1}\) based on average estimated catch rates from 1902 (34.4 kg person\(^{-1}\) year\(^{-1}\)), 1918 (31.7 kg person\(^{-1}\) year\(^{-1}\)), and 1930 (139.2 kg person\(^{-1}\) year\(^{-1}\)). In the last portion of the twentieth century, per-capita catch rates were not used, as subsistence fishing was assumed to be replaced by commercial and recreational fishing after WWII (Table 1).
Commercial fisheries for the Florida Keys included both fish for local sale and export. Directly reported non-export commercial catch data were available for select years beginning in 1880 (USFC 1881–1938). These data are segmented by species, and non-reef-associated species were excluded from total landings. Export catch was significant in the Keys, particularly for shipment to Cuba (Collins 1885; Brice 1897). From 1840 to 1930, unreported commercial export catch rates were estimated based on the semi-quantitative reports of export extracted from archival documents. For example, in the 1840 and 1850s, approximately 100 shipments of reef fish were made annually to Cuba (Anonymous 1858). This export ceased during the Spanish American war but began again during the 1910s; by 1923, daily shipments of fish were sent to Cuba in boxes that held 410 kg of fish (Schroeder 1924). No evidence was found for export to Cuba after 1930. On the basis of this information, export rates were estimated to be 40 mt year$^{-1}$ (100 shipments $\times$ 410 kg) between 1840 and 1898, and 100 mt year$^{-1}$ (245 days $\times$ 410 kg) between 1910 and 1930. Modern commercial landings data become available in 1977 (Bohnscak et al. 1994; FFWCC 1993–2008). These data are similarly segmented by species, and non-reef-associated species were excluded.

Recreational fisheries began in the Florida Keys in the 1860s (Wilder 1868; Hallock 1876), intensified after 1896 (Mormino 2005), and grew rapidly after World War II (Giacobbe 1996). From the period 1860–95, recreational landings were estimated to be 10% of the subsistence fisheries. From WWII to 1980 and 1993–2008, recreational landings were estimated from the calculated ratio of recreational to commercial landings reported in Bohnscak et al. (1994) for the period 1980–92. This ratio is consistent with ratios for the Gulf of Mexico and the South-east Atlantic region determined by Coleman et al. (2004) for the years 1986–2002. From 1896-WWII, recreational landings were estimated as 50% of the post-WWII ratio.

Results

Population history

Long-term human population trends in both Hawai’i and Florida exhibited low densities before the 20th century, relative to modern population densities in tropical island nations, which can exceed 3000 people per km$^2$ of reef (Newton et al. 2007). In the period prior to Western contact, Hawaiian populations were estimated at 200 people per km$^2$ of reef during the late pre-historic period (~AD 1450–1778) and now exceed 1000 people per km$^2$ of reef (Fig. 1). The resident population of the Florida Keys was substantially lower than that of Hawai’i, reaching a maximum of 160 people per km$^2$ of reef. In both locations, population values reflect only permanent residents and do not include the extensive tourist traffic, estimated to exceed four and six million people annually in the Florida Keys and Hawai’i, respectively (FDEP 2010, HTA 2010).

Fisheries by sector

The relative contribution of different fisheries sectors changed over time and varied between the two locations (Fig. 2). Pre-European fisheries in both the Florida Keys and Hawai’i were subsistence only, and commercial fisheries became important in both regions in the early nineteenth century. However, early commercial fisheries in Florida had a substantial export component, while commercially caught reef species were primarily consumed locally in Hawai’i, with the exception of a few short-lived commercial ventures for reef species (e.g. bêche-de-mer and shark fins) (Kittinger et al. 2011). Fishpond aquaculture is unique to Hawai’i, comprising up to 9% of the total yield during the late pre-historic period (~AD 1400–1778). Both locations experi-

Figure 1  Population per km$^2$ of reef over time in Hawai’i (red line) (AD 1250–2010) and Florida (blue line) (AD 1513–2010). Fifty-year increments are used for the pre-historic period (<1778), census units are used for the historic period (1778–1910), and censal and inter-censal estimates are used for the modern period (1910–2010).
enced rapid development in the commercial fisheries sector in the second half of the 20th century, and recreational fisheries developed concurrently, contributing substantially to the total catch over the past half century.

**Historical fishing rates**

Trends in annual coral reef fisheries yields differ markedly between the Florida Keys and Hawai’i (Fig. 3). In Hawai’i, the total yield for wild-caught coral reef fisheries (excluding fishpond aquaculture) was greatest in the three centuries prior to European contact (AD 1450–1778). Reef fisheries yield exceeded 5 t km$^{-2}$ by AD 1400, achieved a maximum at AD 1450 of >17 t km$^{-2}$ and ranged from 12–17 t km$^{-2}$ until European contact in AD 1778, a period during which rates of fishing appeared to be sustainable. After contact, catch decreased steadily and reached a post-contact nadir in 1878 of 3.6 t km$^{-2}$, which is primarily attributed to the rapid depopulation of the archipelago owing to the introduction of epidemic diseases to which Native Hawaiians had little to no immunity. Subsequently, yield increased in the late 1800s to 10.4 t km$^{-2}$. A temporary reduction occurred in the middle of the 20th century owing to a closure of nearshore fisheries zones during WWII. In Florida by contrast, total catch remained below 5 t km$^{-2}$ until 1930. Before European settlement, catch was well below 1 t km$^{-2}$ and slowly increased until the second half of the 20th century, when rates increased rapidly, exceeding 20 t km$^{-2}$ for much of the 1980s and 1990s. Reductions in overall landings occurred since the mid-1990s, with a decline of 50% between 1996 and 2008. Despite markedly different exploitation histories, the level of modern extraction in Florida and Hawaiian coral reefs is similar. Over the

**Figure 2** Total reef fisheries yield by sector for Hawai’i (a) and Florida (b).
last decade, an average of \(12\text{ to } 13 \text{ t km}^{-2}\) has been extracted from Florida’s reefs and \(10\text{ to } 12 \text{ t km}^{-2}\) from Hawaiian reefs (Fig. 3).

Evidence for early species-level overfishing

Overall trends in coral reef fisheries provide a means to compare fisheries catch rates over long timescales, but these can mask changes in populations of individual species. Comparisons between landings data from the late nineteenth and early twentieth centuries and modern data for the same species suggest species-level over-exploitation for select species before the onset of modern fisheries. In both locations, commercially favoured species, ranging from groupers (Serranidae) to green turtles (Chelonia mydas, Cheloniidae), reached their maximum catch rates in the late nineteenth and early 20th centuries. Current catch rates for several species are small fractions of historical catch rates, and many of these species are now endangered (Table 2). The peak catch year for many species may have been earlier, as the earliest quantitative survey of commercial reef catch was conducted in 1885 in Florida and 1900 in Hawai‘i.

Effects of management systems on fishery sustainability

Coral reef fisheries in the Florida Keys and Hawai‘i exhibit very different social and management histories. Florida is characterized by high connectivity to regional markets, a lack of historical or traditional management systems, and intensive commercial fishing for targeted species that led to sequential commercial depletion. Fishing for export markets drove fisheries development as early as the 1760s, and signs that depletion of local target populations was causing sequential exploitation were evident by 1890. Major commercial export fisheries developed for green turtles and reef sponges in the middle of the 19th century, and...
both fisheries reached a peak in the 1880s (McClanachan 2008, 2009b). Evidence for severe depletion of sponge populations was evident by the 1890s, with catches declining by 70% in one decade (Collins 1885; Brice 1897; Smith 1898). Turtles, which were the most commonly consumed food item in the Keys in the early 1800s, were commercially extinct by the 1890s (Williams 1837; Brice 1897). A fishery for reef sharks developed in the 1920s in response to a shortage of employment opportunities for local fishers, reaching a peak catch of 1.5 million kg in 1934 (USFC 1881–1938). Following the collapse of the shark fishery, several non-reef species were intensively targeted (McClanachan 2009a,b), and in the 1990s, the spiny lobster fishery became a primary commercial target, reaching a peak of over 3 million kg in 1996. In 1994, the use of entangling nets was banned in the state of Florida, and landings dropped over the next decade (Adams et al. 2009) (Fig. 2c).

By contrast, a period of sustained high fisheries yield in Hawai’i occurred in the pre-contact period between AD 1400 and 1778. These fisheries were multispecies and intensively managed to maintain high yields for a dense human population that was geographically isolated. Specific management practices likely contributed to the maintenance of such high rates of fish extraction, including protection of reef habitat, vulnerable life-history stages for fish, and species with a high susceptibility to overfishing (Poepoe et al. 2003). The Native Hawaiian management system also exhibited indirect controls on effort through chiefly restrictions on access to material goods for gears, specific species, and through development of fishpond aquaculture, which may have potentially offset pressure on wild stocks. For example, offshore fishing practices were primarily carried out by a limited-entry professional fishing class who were familiar with their local environment, and materials for the gears and canoes required for these activities were restricted by chiefs. For some highly vulnerable species (e.g. turtles and sharks), stringent restrictions were placed on consumption, reducing pressure on these stocks. Regulations were also species- and area specific and subject to enforcement by a locally based manager that had the flexibility and capacity to be highly adaptive and quick to respond to any perceived declines in species abundances (Table 3).

### Table 2: Peak catch years and landings for favoured coral reef fisheries species. Modern landings (mean for the last 10 years of catch data) are calculated as a percentage of peak catch.

<table>
<thead>
<tr>
<th>Species</th>
<th>Peak year</th>
<th>Peak landings (kg)</th>
<th>Modern landings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawai’i</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bonefish (Albula glossodonta, Albulidae)</td>
<td>1900</td>
<td>145 927</td>
<td>1.92%</td>
</tr>
<tr>
<td>Limpets (Cellana spp., Naccellidae)</td>
<td>1900</td>
<td>66 800</td>
<td>7.53%</td>
</tr>
<tr>
<td>Mullet (Mugil cephalus, Mugilidae)</td>
<td>1900</td>
<td>337 096</td>
<td>1.14%</td>
</tr>
<tr>
<td>Spiny lobster (Panulirus marginatus, Palinuridae)</td>
<td>1900 (1989)</td>
<td>39 878</td>
<td>4.71%</td>
</tr>
<tr>
<td>Pacific threadfin (Polydactylus sexfilis, Polynemidae)</td>
<td>1903</td>
<td>49 782</td>
<td>0.50%</td>
</tr>
<tr>
<td>Milkfish (Chanos chanos, Chanidae)</td>
<td>1903</td>
<td>158 270</td>
<td>0.56%</td>
</tr>
<tr>
<td>Big-eye scad (Decapterus spp., Carangidae)</td>
<td>1903</td>
<td>644 868</td>
<td>50.13%</td>
</tr>
<tr>
<td>Hawaiian grouper (Hyporthodus guentius Serranidae)</td>
<td>1931</td>
<td>37 740</td>
<td>53.05%</td>
</tr>
<tr>
<td>Amberjack (Seriola dumerii, Carangidae)</td>
<td>1934</td>
<td>39 794</td>
<td>13.91%</td>
</tr>
<tr>
<td>Florida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green turtle (Chelonia mydas, Cheloniidae)</td>
<td>1895</td>
<td>186 428</td>
<td>n/a; Endangered Species</td>
</tr>
<tr>
<td>Hawksbill turtle, (Eretmochelys imbricata, Cheloniidae)</td>
<td>1895</td>
<td>18 309</td>
<td>n/a; Endangered Species</td>
</tr>
<tr>
<td>Grunts (Haemulon spp., Haemulidae)</td>
<td>1895</td>
<td>281 355</td>
<td>8%</td>
</tr>
<tr>
<td>Spanish mackerel (Scomberomorus maculatus, Scombridae)</td>
<td>1918</td>
<td>938 762</td>
<td>16%</td>
</tr>
<tr>
<td>Sawfish (Pristis spp., Pristidae)</td>
<td>1928</td>
<td>20 455</td>
<td>n/a; Endangered Species</td>
</tr>
<tr>
<td>Conch (Strombus spp., Strombidae)</td>
<td>1928</td>
<td>7091</td>
<td>n/a; Catch prohibited</td>
</tr>
<tr>
<td>Goliath grouper (Epinephelus itajara, Serranidae)</td>
<td>1929</td>
<td>15 864</td>
<td>n/a; Catch prohibited</td>
</tr>
<tr>
<td>Sharks (Carcharhinidae, Girgylomostomatidae, Sphyridae)</td>
<td>1934</td>
<td>1 363 636</td>
<td>15%</td>
</tr>
</tbody>
</table>

1First year for which catch data are available. Peak catch for spiny lobster in Hawai’i was in 1989, but the vast majority of this catch was from the north-western Hawaiian Islands.
The results of our historical reconstruction of catch of coral reef fisheries in Hawai‘i and Florida suggest that even at high population sizes in conditions of limited resources, societies can develop and maintain a sustainable level of resource extraction. In pre-contact Hawai‘i, the human population approached 200 people per km$^2$ of reef, densities that compare with those on moderately populated tropical islands today, including Fiji, the Solomon Islands and American Samoa in the Pacific, and the Bahamas, Bermuda, and Antigua in the Caribbean (Newton et al. 2007). Unlike modern island societies, Hawaiians depended entirely on local production and were able to sustain annual catches from reef environments exceeding 12 mt km$^{-2}$ of reef for more than 400 years. Modern extraction from global reefs is highly variable, ranging from less than 1 mt km$^{-2}$ to more than 40 mt km$^{-2}$ annually; however, median yield for island nations is just 3 mt km$^{-2}$, and most reefs that support annual catches >5 mt km$^{-2}$ also exhibit signs of over-exploitation (Newton et al. 2007). Thus, while catch levels in pre-contact Hawai‘i were within the range of reported estimates of catch from modern reefs (e.g. Jennings and Polunin 1995; Maypa et al. 2002; Dulzell and Adams 1997), the fact that these high yields were apparently sustainable over centuries represents a fundamental difference from modern observations of sustainability thresholds in reef fisheries.

Our analysis suggests that high historical yields in pre-contact Hawai‘i were sustained with a diverse suite of effectively enforced management measures that ensured resource persistence in a risk-prone environment. Reef fisheries were multispecies and managed with adaptive strategies, many of which have modern analogues, including time/area closures, community-based management, regulation of

<table>
<thead>
<tr>
<th>Modern management practice</th>
<th>Traditional management practice</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1. Time/area closures</strong></td>
<td>Makahiki festival: reef areas closed for part of the annual festival and tribute collection, which lasted 1–3 months</td>
</tr>
<tr>
<td></td>
<td>Akū/Ōpelu kapu (taboo): a rotating 6 month closure on skipjack tuna and mackerel scad marked by ceremonies in January and July; closures coincide with species’ spawning cycles</td>
</tr>
<tr>
<td></td>
<td>Spawning aggregation restrictions: select reef species restricted from harvest during lunar spawning cycles using moon calendars</td>
</tr>
<tr>
<td></td>
<td>Monthly closures: Reefs were closed four times each month for 3 days for religious ceremonies</td>
</tr>
<tr>
<td></td>
<td>Discretionary closures: chiefs or their agents could close reef areas based on their assessment of resource or ecological conditions or for other social reasons</td>
</tr>
<tr>
<td><strong>2. Community-based management</strong></td>
<td>Access: Reef areas were accessible only by residents within a single land-to-sea division, or ahupua’a, which was managed by the chief and his agents and restricted access to the local community</td>
</tr>
<tr>
<td><strong>3. Regulation of gear and effort</strong></td>
<td>Professional fishing class: chiefs sponsored a professional fishing class that focused on deeper reef areas and limited gear availability and effort beyond shallow reef zones</td>
</tr>
<tr>
<td></td>
<td>Boat building: chiefs controlled the forested uplands and the access to large trees required for canoe building</td>
</tr>
<tr>
<td></td>
<td>Gears: chiefs often regulated materials for fishing gears through tribute systems, which concentrated access to gears and materials for gears with the chiefs and their agents</td>
</tr>
<tr>
<td><strong>4. Aquaculture</strong></td>
<td>Fishponds: reef species were harvested as juveniles to stock fishponds, and fishponds served as insurance against famines</td>
</tr>
<tr>
<td><strong>5. Restrictions on consumption of vulnerable species</strong></td>
<td>Gender restrictions: turtles and reef fish, including predatory jacks, sharks, rays and goatfish, could not be consumed by women</td>
</tr>
<tr>
<td></td>
<td>Class restrictions: turtles were reserved for high priests and chief; large piscivores and some herbivorous fish were reserved for chiefly classes; episodic or stochastic fish aggregations were subject to chiefly sanction</td>
</tr>
<tr>
<td><strong>6. Fostering a conservation ethos</strong></td>
<td>Social norms discouraged overharvest and wasting; for example, all fish caught should be consumed</td>
</tr>
</tbody>
</table>

Discussion

The results of our historical reconstruction of catch of coral reef fisheries in Hawai‘i and Florida suggest that even at high population sizes in conditions of limited resources, societies can develop and maintain a sustainable level of resource extraction. In pre-contact Hawai‘i, the human population approached 200 people per km$^2$ of reef, densities that compare with those on moderately populated tropical islands today, including Fiji, the Solomon Islands and American Samoa in the Pacific, and the Bahamas, Bermuda, and Antigua in the Caribbean (Newton et al. 2007). Unlike modern island societies, Hawaiians depended entirely on local production and were able to sustain annual catches from reef environments exceeding 12 mt km$^{-2}$ of reef for more than 400 years. Modern extraction from global reefs is highly variable, ranging from less than 1 mt km$^{-2}$ to more than 40 mt km$^{-2}$ annually; however, median yield for island nations is just 3 mt km$^{-2}$, and most reefs that support annual catches >5 mt km$^{-2}$ also exhibit signs of over-exploitation (Newton et al. 2007). Thus, while catch levels in pre-contact Hawai‘i were within the range of reported estimates of catch from modern reefs (e.g. Jennings and Polunin 1995; Maypa et al. 2002; Dulzell and Adams 1997), the fact that these high yields were apparently sustainable over centuries represents a fundamental difference from modern observations of sustainability thresholds in reef fisheries.

Our analysis suggests that high historical yields in pre-contact Hawai‘i were sustained with a diverse suite of effectively enforced management measures that ensured resource persistence in a risk-prone environment. Reef fisheries were multispecies and managed with adaptive strategies, many of which have modern analogues, including time/area closures, community-based management, regulation of
gear and effort, aquaculture, restrictions on vulnerable species, and reduction in waste in harvest (Table 3). In pre-contact Hawai’i, however, rules were accompanied by robust socio-cultural institutions that exhibited a high degree of compliance owing to draconian punishments for rule breakers and incentives for adherence among community members. Social institutions for reef fisheries management in pre-contact Hawai’i exhibited characteristics associated with successful common pool resource governance systems, including well-defined boundaries, local rule-making authority, effective monitoring and enforcement, access to conflict resolution mechanisms and community self-determination (Malo 1951; Titcomb 1972; T’i 1993; Kittinger et al. 2011). These design principles are associated with many successful institutions for common pool resource management systems in modern contexts, ranging from water resources to forestry and fisheries systems (Ostrom 1990; Agrawal 2001; Pagdee et al. 2006; Basurto and Ostrom 2009). While modern coral reef management frequently employs analogous management strategies to those used in Hawai’i (Cinner et al. 2009), overharvesting is still common in systems characterized by a lack of reciprocity, communication, or trust among resource users and ineffective enforcement of mutually agreed upon rules (Basurto and Ostrom 2009; Berkes 2010; Wamukota et al. 2012). Further, differences exist in the goals of management strategies employed by both historical and modern societies, such as aquaculture. Fishponds did not contribute substantially to total fish production in pre-contact Hawai’i (Fig. 2), but likely provided insurance for food security in the case of disturbances such as droughts, floods or storms. Further, Hawaiians stocked fishponds with juvenile herbivorous species that fed on algae that sequestered nutrients from upland agricultural systems, potentially reducing nutrient run-off to reefs. The majority of modern aquaculture, by contrast, does not currently help address sustainable yields, as wild-captured fish are diverted to support farmed fish, much of which is intended for luxury food products for wealthy nations (Naylor et al. 2000).

While common pool resource governance systems and management strategies aimed at maintaining food security were effective at maintaining high reef fisheries yields in pre-contact Hawai’i, the commodification of reef resources in colonial times in both locations led to declines in favoured species and the elimination of some populations altogether. Peaks in landings occurred in the nineteenth and early twentieth centuries in response to targeted fishing for preferred species, many of which are now endangered (Table 2). In Florida, rapid expansion of single-species fisheries followed a pattern of serial commercial exploitation with crashes in populations of targeted species such as sponges and turtles leading to the development of new commercial fisheries for export markets. The Florida Keys were connected to a wider economic network in the Caribbean and mainland United States, making residents less dependent on the sustainability of local resources than were societies on more remote islands. These differences demonstrate that social histories have a strong influence on the historical trajectory of the fishery and that modern fisheries that appear similar in yield can be the result of very different environmental histories. Likewise, this historical comparison provides a word of caution against defining a single sustainable yield for reef fisheries. Catches of more than 12 mt km⁻² were apparently sustainable over several centuries in pre-contact Hawai’i, but Florida’s rapid expansion of single-species fisheries in the early 19th century resulted in population crashes in less than one century, demonstrating that differences in social history and fisheries strategies affect total yield.

Florida and Hawai’i are unique in that they have species-specific fisheries data spanning more than a century, as well as information on social history that can be used to contextualize these historical fisheries and their management. To some extent, differences in social and ecological parameters between the two regions may inform understanding of historical trajectories of fisheries in regions that do not exhibit the same richness of historical data sets. Biological and social parameters that influence historical fisheries include the degree of economic and ecological connectivity, functional redundancy among targeted species, habitat type and heterogeneity, the types of fish extracted and harvesting methods, the degree to which fisheries are multi- vs. single-species focused, and the governance systems and human institutions for fishery management. Florida, for example, is representative of the greater Caribbean in that most islands were characterized by high economic and ecological connectivity and a lack of customary resource management systems. In fisheries with similar characteristics, high sustained yields over centuries should not be expected.
However, in regions of the Caribbean where plantation culture dominated or freshwater resources were greater than in Florida, human population densities were higher and reef fisheries were exploited more intensively (e.g. Hardt 2009), demonstrating strong local differences in fisheries histories. In Hawai‘i and the Pacific, many island systems were isolated and vulnerable to disturbances that threatened human lives in pre-contact times. Socio-cultural institutions and other adaptations such as fishponds probably arose as an adaptive response to social and environmental drivers, including ensuring a stable supply of resources in a stochastic environment (Kittinger et al. 2011). Customary institutions for fishery resource management exist in many locales globally (Johannes 2002, Cinner et al. 2009), and more research is needed to understand the historical development of these systems, their impact on linked social and environmental sustainability, and their application and integration into contemporary governance systems.

Rebuilding reef fisheries that are critical to food security and ecological health requires understanding the full productive capacity of these ecosystems, as well as histories of past use and management. Likewise, successfully managing natural resources requires understanding the complex interplay of social, institutional and ecological factors that influence resource sustainability and social and environmental outcomes (Cinner et al. 2009; Ostrom 2009; Basurto and Coleman 2010; Persha et al. 2011). If contemporary management strategies in intensively used reef fisheries are to be successful, they will require robust social institutions and consideration of variability in social capacity and ecosystem dynamics that exist in the tropics. Although no panaceas to the sustainability of fisheries exist, governance systems that incorporate the elements of successful common pool resource institutions into place-based management strategies are more likely to result in social and ecological successes (Ostrom 2007; Basurto and Ostrom 2009). The methods for achieving sustainable fisheries governance are likely to vary based on the place-specific contextual factors, including the historical trajectory of the fishery and its associated management systems. The evidence we present from historical reconstructions shows that reef fishery sustainability has been achieved in the past, which can guide actions for a more sustainable future for reefs and the communities that depend on them.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** A demographic model for pre-contact Hawai‘i developed by Dye and Komori (1992) (as reviewed by Kirch 2007), used for estimating total human population.

**Table S1.** Hard point data from historical and archival sources and total estimated production yields for fishpond aquaculture in the Hawaiian archipelago.

**Table S2.** Hard data points for reported catch for commercial fisheries in the Hawaiian archipelago and the Florida Keys from 1895 to 2008. *Included in Cobb’s estimates. **Data are reported annually by species.

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