Conservation Biology

Contributed Paper

Comparison of Modern and Historical Fish Catches (AD 750–1400) to Inform Goals for Marine Protected Areas and Sustainable Fisheries

TIMOTHY R. McCLANAHAN* AND JOHNSTONE O. OMUKOTO

Wildlife Conservation Society, Marine Programs, Bronx, NY 10460, U.S.A.

Abstract: *We tested the unsustainable fishing hypothesis that species in assemblages of fish differ in relative abundance as a function of their size, growth rates, vagility, trophic level, and diet by comparing species composition in historical bone middens, modern fisheries, and areas closed to fishing. Historical data came from one of the earliest and most enduring Swahili coastal settlements (approximately AD 750–1400). Modern data came from fisheries near the archeological site and intensively harvested fishing grounds in southern Kenya. The areas we sampled that were closed to fishing (closures) were small (<28 km^2) and permanent. The midden data indicated changes in the fish assemblage that are consistent with a weak expansion of fishing intensity and the unsustainable fishing hypothesis. Fishes represented in the early midden assemblages from AD 750 to 950 had longer life spans, older age at maturity, and longer generation times than fish assemblages after AD 950, when the abundance of species with longer maximum body lengths increased. Changes in fish life histories during the historical period were, however, one-third smaller than differences between the historical and modern assemblages. Fishes in the modern assemblage had smaller mean body sizes, higher growth and mortality rates, a higher proportion of microinvertivores, omnivores, and herbivores, and higher rates of food consumption, whereas the historical assemblage had a greater proportion of piscivores and macroinvertivores. Differences in fish life histories between modern closures and modern fishing grounds were also small, but the life histories of fishes in modern closures were more similar to those in the midden before AD 950 because they had longer life spans, older age at maturity, and a higher proportion of piscivores and macroinvertivores than the modern fisheries. Modern closures and historical fish assemblages were considerably different, although both contained species with longer life spans.*

Keywords: Africa, fish bones, fisheries closures, historical ecology, Indian Ocean, no-take reserves, trophic cascades, zooarchaeology

Comparación de Capturas Modernas e Históricas (750-1400 AD) para Metas en Áreas Marinas Protegidas y Pesquerías Sustentables

Resumen: *Probamos la hipótesis de pesca no sustentable que plantea que las especies en ensambles de peces difieren en abundancia relativa como una función de su tamaño, tasas de crecimiento, vagilidad, nivel trófico y dieta mediante la comparación de restos óseos históricos, pesquerías modernas y áreas cerradas a la pesca. Los datos históricos provinieron de uno de los asentamientos costeros más perdurables de los Swahili (aproximadamente 750 – 1400 AD). Los datos modernos fueron obtenidos de pesquerías cerca del sitio arqueológico y de áreas de pesca intensiva en el sur de Kenia. Las áreas que muestreamos fueron cerradas a la pesca (cierres) eran pequeñas (<28 km^2) y permanentes. Los datos de los restos indicaron cambios en el ensamble de peces que son consistentes con una expansión leve de la intensidad de pesca y con la hipótesis de pesca no sustentable. Los peces representados en los ensambles de 750 – 950 AD tenían mayor longevidad,*

---

*Address for correspondence: Coral Reef Conservation Project, P.O. Box 99470, Mombasa, Kenya, email tmcclanahan@wcs.org

Paper submitted July 2, 2010; revised manuscript accepted February 23, 2011.

Conservation Biology, Volume 25, No. 5, 945–955

DOI: 10.1111/j.1523-1739.2011.01694.x

mayor edad de madurez y tiempos generacionales más largos que los ensambles de peces posteriores a 950 AD, cuando incrementó la abundancia de especies con mayores tallas corporales. Sin embargo, los cambios en las historias de vida de los peces durante el período histórico fueron una tercera parte menos que las diferencias entre los ensambles históricos y modernos. Los peces en el ensamble moderno tenían talla corporal menor, mayores tasas de crecimiento y mortalidad, una mayor proporción de microinvertívoros, omnívoros y herbívoros y mayores tasas de consumo de alimento, mientras que los ensambles históricos tuvieron una mayor proporción de piscívoros y macroinvertívoros. Las diferencias en las historias de vida entre cierres modernos y áreas de pesca modernas también fueron pequeñas, pero las historias de vida de peces en los cierres modernos fueron más similares a las de peces en los restos previos a 950 AD porque tenían mayor longevidad, mayor edad de madurez y una mayor proporción de piscívoros y macroinvertívoros que las pesquerías modernas. Los cierres modernos y los ensambles históricos de peces fueron considerablemente diferentes, aunque ambas contenían especies con mayor longevidad.

Palabras Clave: África, cascadas tróficas, ecología histórica, encierros para pesquerías, huesos de pez, Océano Índico, reservas sin captura, zooarqueología

Introduction

Rapid intensification and expansion of modern capture fisheries affects fishes and aquatic ecosystems (Jackson et al. 2001; Worm et al. 2009). Understanding the ecology of fish assemblages and ecosystems that are not fished helps to set goals for the management of marine resources and protected areas (Pitcher 2001; Sandin et al. 2008). Establishing these goals is challenging because most areas have been fished for over 20 million years (Lotze et al. 2006; Rick & Erlandson 2008). To understand and potentially recreate historical ecosystems, it is necessary to synthesize information on historical ecology, life history of species, and human use of resources.

Analyses of historical bone middens associated with fishing grounds have yielded insights into human colonization, resource use, and dependency on specific species and into the potential long-term effects of fishing (Rick & Erlandson 2008). There is considerable heterogeneity in exploitation patterns and intensity as a function of social, environmental, and ecological factors (Rose 2004). Some evaluations of bone middens show little detectable change in species composition over millennia (Dalzell 1998; Maschner et al. 2008), whereas other evaluations show major changes in species composition over a few centuries (Lotze & Milewski 2004; Rosenberg et al. 2005). Evaluations of middens associated with tropical fisheries and coral reefs, for example, show variable evidence of changes in fish assemblages (Wing & Wing 2001; Sabater & Carol 2009). Some investigators believe that midden data and written historical accounts have selectivity biases that make evaluating the state of historical ecosystems difficult (Baisre 2010).

Rebuilding fisheries and establishing management goals require combining knowledge of historical and current fishing effort and its effects on ecological communities with different management systems. These management systems include closures (areas closed to fishing) of different sizes, ages, connectedness, remoteness, and intensity and types of fishing in the area surrounding closures (Claudet et al. 2008; McClanahan et al. 2009). The extent to which small to moderate sized closures simulate extensive, historic, undisturbed ecosystems is unknown. Most of the world's marine protected areas (MPAs) are small, median size of 4.6 km^2, whereas the mean size of 544 km^2 is greatly influenced by 10 MPAs that constitute 58% of the total protected area (Wood et al. 2008). Considering the area requirements of some large and vagile marine species, most closures will not be of sufficient size to meet these area requirements in fished seascapes. Additionally, most no-take areas have been created since the 1990s (Wood et al. 2008), and it can take many decades for fish assemblages to recover fully from fishing (Russ 2004; McClanahan et al. 2007). Recovery does not necessarily represent a return to a pristine or undisturbed state; rather, recovery is a stabilization of the total abundance of fish and other affected species over a number of years (Babcock et al. 2010).

The current system of coastal management is expected to influence the composition of species in both exploited areas and areas closed to fishing (Claudet et al. 2010). For example, populations of large, slow-growing, highly vagile apex predators are more likely than populations of small, fast-growing, and site-attached species to decrease in abundance from intense fishing and their populations are unlikely to be maintained by small closures (Pauly et al. 1998; Pinnegar & Engelhard 2008; McClanahan & Hicks 2011). There may, however, be exceptions to the above responses of different populations to fishing that result from differences in the intensity and types of fishing, environment, and species composition (Claudet et al. 2010). We compared life histories of fish caught in intensive modern fisheries and small closures (<28 km^2) with excavated fish remains from one of the longest continuous Swahili coastal settlements (approximately AD 750–1400) in Shanga, Kenya (Mudida & Horton 1996). We aimed to identify changes in the historical time series that might be consistent with the unsustainable fishing hypothesis, which is that high levels of fishing lead to dominance of fast growing, short-lived species feeding at low trophic levels (Pauly et al. 1998; Pinnegar & Engelhard 2008). We asked whether the composition of fishes in the current permanent closures was more similar to those in the historical record or the modern fishery.

Methods

We combined 4 sources of species-level data: fish bones from a midden in Shanga (Mudida & Horton 1996), data from fish catches within 3 old (>25 years) Kenyan fisheries closures (Watson 1996; Kaunda-Arara & Rose 2004*a*, 2004*b*), hook and line and trap data collected from coral reefs in southern Kenya from 1998 to 2007 (McClanahan & Hicks 2011), and data on fish caught with all common gears collected from the 3 fisheries-landing sites nearest Shanga during 2 seasons in 2009 (J. Omukoto, unpublished data). To compare species composition and life history, we converted species-level catch data to life-history metrics weighted by the relative abundance of each species.

Study Sites and Species

Shanga is on the southern section of Pate Island within the Lamu archipelago of the northern coast of Kenya (Fig. 1). The midden was on a narrow, sandy peninsula, fringed by a tidal estuary and mangrove forest. Coral reefs and the open ocean are approximately 4 km seaward from the middens. Fish species identified in the midden are currently widespread throughout the western Indian Ocean and present in modern Kenyan catches (Mudida & Horton 1996). We examined data on the number of fishes collected from 3 closures (Kisite, Malindi, and Watamu Marine marine national parks), 6 modern southern Kenyan fishing grounds (Kenyatta, Chale, Mgwani, Mvuleni, Mwaepe, and Mwanyaza), and 3 modern Shanga-Pate fishing grounds (Ishakani, Rubu, and Pate Bay) (Table 1). The Kenyan marine national parks were closed to fishing in 1968 (Malindi and Watamu) and 1978 (Kisite). Fishing effort in Kenyan fishing grounds is high, with all reefs having >4 fishers/km^2/day (McClanahan et al. 2008). Both the closures and fisheries in southern Kenya were in shallow coral reefs (1–12 m at low tide). The benthic cover in fishing grounds and closures was dominated by hard-bottom coral reef and seagrass beds interspersed with sand and coral rubble. The studied reef fisheries were distributed along the entire Kenyan coast from Shanga in the north to Kisite in the south.

The environmental history of the Kenyan coast from AD 750 to present is not well known (Mann et al. 2009). The sea level has been stable since 2500 BP (Camoin et al. 2004), and seawater temperatures over the past 1400 years have fluctuated (Anderson et al. 2002). During the warm Medieval Climate Anomaly (AD 950–1250), mean seawater temperatures in the Indian Ocean probably were about 1 °C below present mean temperatures and possibly were driven by a negative climate feedback mechanism (Mann et al. 2009). During the Little Ice Age (AD 1400–1700) temperatures dropped further, but after AD 1700 the intensity of monsoons and upwelling off the coast of Somalia increased (Anderson et al. 2002). During the past approximately 80 years water temperatures and input of terrestrial-based sediments have increased, the El Niño Southern Oscillation has weakened, and the Indian Ocean Dipole has strengthened (Fleitmann et al. 2007; Nakamura et al. 2009). The abandonment of the historical settlement in Shanga coincided with the onset of the Little Ice Age after a series of strong El Niño years in the Pacific during the 14th century (Mann et al. 2009).

Collection of Field Data

We analyzed midden bone data from 12 phases (Horton 1996), each of which spanned approximately 50 years (Table 1). Mudida and Horton (1996) collected bones from a 5 × 5 m excavation pit (trench 2) at Shanga and sieved them through a 5-mm filter. They used cranial bones and vertebrae to identify species and compared bones from middens with bones from fish caught in the surrounding waters to confirm species identification. We used bones they collected from trench 2 because it contained the longest, most continuous, and greatest percentage of remains from marine fish. Additionally, the pit was well dated at a fine temporal resolution and bones were well preserved (Mudida & Horton 1996). We report numbers of bones per species per phase, which is expected to reflect the fish caught during that phase. There is physical evidence from the middens that fish were caught with hooks and indirect evidence that fish were caught with traps and spears but no physical evidence, such as bottom-line weights, that fish were caught with nets.

Catch-and-release fishing was allowed in the Kisite, Malindi, and Watamu marine national parks (closures) between 1995 and 2005. Local fishers caught fish with traditional traps and hand lines in Kisite from August to October 1995 (Watson 1996), Malindi in 2000, 2001, 2002 and 2005, and Watamu in 2000, 2002, and 2004 (Kaunda-Arara & Rose 2004*a*, 2004*b*). In the southern Kenyan fishing grounds, we measured catch (number of fish per person per day) by gear (hook and line and traditional traps) and species on haphazardly selected days between 1998 and 2007 to reduce seasonal or tidal biases that might be associated with a structured sampling design. We collected data at 3 landing sites on catches associated with all gears in use (beach seine, hook and line, shark net, set net, gillnet, cast net, and spear) in the current Shanga fisheries.

All gears have some level of selectivity for species and size, and this creates challenges when comparing fish catch over time and space when gear use is potentially

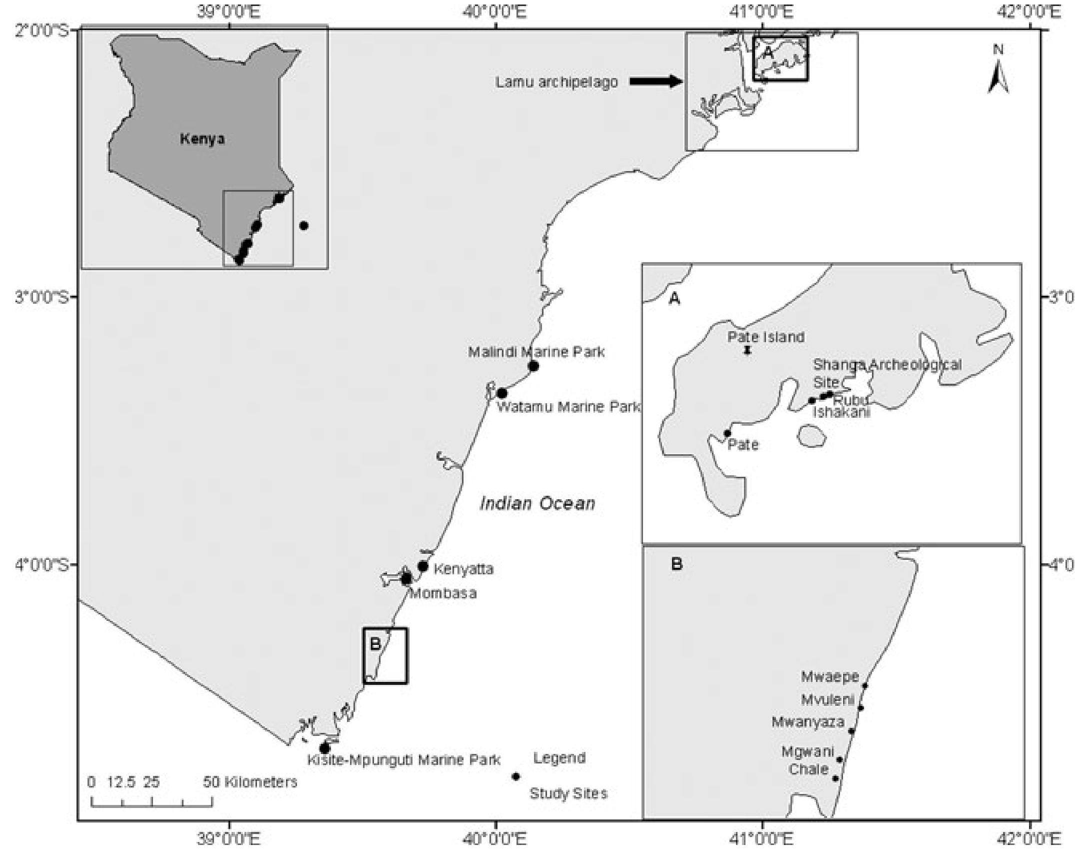

Figure 1. Kenyan coastline and study sites, with details of (a) northern sites and (b) southern sites. Sites include the midden in Shanga, fishing grounds near Shanga and southern Kenya, and marine parks, where experimental fishing was undertaken.

Table 1. Sample sizes and summary statistics per historical and modern catch periods (all species pooled) and estimated calendar years of the phases.*

Phase	*Sample size*	*Number of species*	*Mean number of individuals/species*	*SE of the mean*	*Years, data source*
1	63	16	3.9	0.5	~AD 750–800, midden bones
2	222	21	10.6	1.3	~AD 800–820, midden bones
3	161	18	8.9	1.1	~AD 820, midden bones
4	437	24	18.2	1.5	~AD 820–850, midden bones
5	449	19	23.6	1.8	~AD 850–900, midden bones
6	392	20	19.6	1.8	~AD 900–950, midden bones
7	846	22	38.5	2.4	~AD 950–1000, midden bones
8	1080	28	38.6	2.6	~AD 1000–1100, midden bones
9	666	26	25.6	2.2	~AD 1100–1150, midden bones
10	646	25	25.8	2.6	~AD 1150–1200, midden bones
11	436	27	16.2	1.9	~AD 1200–1300, midden bones
12	78	15	5.2	0.6	~AD 1320–1400, midden bones
13	3878	40	97.0	4.8	current (1995–2005), caught in closures (parks)
14	6076	39	155.8	5.1	current (1998–2006), caught in southern fishing grounds
15	547	27	20.3	1.0	current (2009), recorded at the 3 Shanga modern fish-landing sites

**Derived from Mudida and Horton (1996), Watson (1996), Kaunda-Arara and Rose (2004a, 2004b) and McClanahan et al. (2008).*

different or unknown (McClanahan & Mangi 2004; Supporting Information, Fig. S1). We expected restricting sampling to traps and hook and line to reduce the errors created by comparing gear with different selectivity. Nevertheless, we present catch data for all gears used for the modern fisheries. Results of previous research show that traps, seine, and gill nets catch similar species. Seine nets often displace or outcompete traps at high levels of fishing effort (McClanahan & Mangi 2004; McClanahan et al. 2008). However, when a gear type is no longer used, other types of gear can catch the amount and the species of fish that had been caught with the previously used gear (McClanahan & Hicks 2011).

Life History of Fishes

For each species of fish in the historical or modern data, we extracted values for 8 life-history traits from Fishbase (Froese & Pauly 2000) by using the country and species options: maximum body length in centimeters ($L_{\max}$); lifespan in years; generation time in years; age in years at first reproduction (maturity) (t_m); length in centimeters at maturity (L_m); mortality rate (M); growth rate coefficient (K/year), and length in centimeters at optimum yield (maximum biomass yield), (L_{opt}). We also classified each species by functional group (herbivores, omnivores, microinvertivores, macroinvertivores, piscivore-macroinvertivores, and piscivores), food consumption, and trophic level. Food consumption is the food consumed as a percentage of the individual body weight. Trophic level was calculated using the formula of Pauly et al. (2001) on the basis of weighted trophic levels of the species' diet. It is expected that there is variation within this trophic-level metric for each species but that this variation is considerably smaller than the variation between species, particularly in the tropics, where there are large differences in species life-history characteristics (Pauly 1998). To estimate species diversity or dominance for each phase, we calculated one minus Simpson's diversity index, $1-D$, where $D = \sum(n_i/N_t)^2$, n_i = total number of individuals of species i, and N_t = total number of individuals of all species in the sample. Zero indicates the lowest and 1 the highest diversity.

Data Analyses

We examined the 12 phases in the midden as independent periods. We pooled data on fish abundance from the 3 closures into phase 13, from the 6 southern Kenyan fishing grounds into phase 14, and from the modern Shanga fishing grounds into phase 15. We based data on all the life-history, ecological, and trophic parameters for each phase on weighted mean values by individual or bone for each of the parameters for all 15 phases and 97 fish species. We used canonical correspondence analysis (CCA) to examine associations among life-history traits, functional groups, and other ecological metrics. Fish species in all the phases were dependent variables and the life-history traits and ecological metrics were independent variables (ter Braak & Šmilauer 2002). The CCAs included 34 species that occurred in over 3 phases. Associations between composition of fish species and the type of gear used in the Shanga fishing grounds were explored with detrended correspondence analysis (DCA). The main assumption of CCA is that the data are unimodal, which is commonly the case for weighted data on species abundance, but the tests are robust to significant deviations from this assumption (ter Braak & Šmilauer 2002). We conducted analyses with CANOCO for Windows 4.5 software (ter Braak & Šmilauer 2002).

Results

A total of 15,977 fish were sampled from middens, closures, and fisheries. There were 5476 samples of 97 species from the midden (Supporting Information). Multivariate evaluation of the life-history parameters indicated a strong split between the modern and historical catch assemblages with the first axis of the CCA, which explained 60% of the total life-history variance ($F = 6.83, p < 0.01$; Fig. 2). Fishes in the historical assemblage (phases 1–12) were older, had a greater length at maturity and at maximum and optimal yields, and longer life spans and generation times than modern assemblages, whereas the modern assemblage (phases 13–15) had faster growth and higher mortality rates (Table 2). The 3 phases of the modern catch contained more species associated with seagrass, such as marbled (*Leptoscarus vaigensis*) and stareye (*Calotomus carolinus*) parrotfishes, cigar wrasses (*Chelio inermis*), dories (*Lutjanus fulviflamma*), and humpback snappers (*Lutjanus gibbus*), than the historical phases, although these species were present in middens.

The second CCA axis explained 16% of the total life history variance. The 12 midden phases were separated by this axis, as were the 3 modern phases. The historical phases were separated by differences in age and body length. Older phases were dominated by fish species with longer life spans, and more recent phases were dominated by species with larger bodies. Despite the strong separation between historical and modern catches, body length of fishes in the modern Shanga fishing grounds was more similar to body length in late historical phases than in the modern southern Kenyan fisheries. The closures and the early historical phases had fishes with longer life spans. Rabbitfish (*Siganus sutor*), unicornfish (*Naso hexacanthus*), and the sky emperor (*Lethrinus mahsena*) were more abundant in modern closures than in modern fishing grounds.

The smallest number of fish bones (63) and species (16) were found in the first phase of the bone midden.

Table 2. **Summary (means and SD) of weighted life-history and ecological metrics for the fish assemblages among the 15 studied phases.**

Metric[b]	*Statistic*	*Phase of historical midden data*[a]												*Phase of modern catch data*		
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13 Kenyan closures*	*14 Kenya fish landings*	*15 Shanga fish landings*
Life history maximum length	mean	67.52	55.86	59.87	60.40	62.05	60.37	64.64	61.81	70.29	64.93	77.92	75.35	49.16	45.45	67.39
	SD	4.34	4.69	4.87	4.07	4.55	4.84	4.45	3.99	4.69	5.28	6.37	4.49	3.59	2.99	2.90
Length at maturity	mean	36.55	30.90	33.05	32.91	33.48	32.59	34.35	33.03	36.55	33.45	38.57	38.43	28.96	26.52	34.89
	SD	2.25	2.61	2.70	2.27	2.34	2.54	2.29	2.09	2.39	2.69	2.98	2.21	2.24	1.86	1.51
Length at maximum yield	mean	44.07	35.61	38.41	38.52	39.60	38.01	40.87	39.04	44.24	39.78	47.07	46.17	32.67	29.58	41.34
	SD	2.82	2.98	3.10	2.59	2.75	2.86	2.66	2.39	2.80	3.04	3.69	2.76	2.53	2.09	1.82
Age at first maturity (years)	mean	2.72	2.70	3.07	2.83	2.78	2.52	2.57	2.47	2.63	2.33	2.34	2.89	2.66	2.43	2.95
	SD	0.16	0.26	0.27	0.23	0.17	0.17	0.14	0.14	0.16	0.15	0.15	0.20	0.19	0.17	0.15
Life span (years)	mean	12.26	11.75	13.53	12.47	12.42	11.18	11.56	11.03	11.98	10.38	10.58	13.18	11.45	10.34	13.10
	SD	0.70	1.11	1.18	0.96	0.75	0.75	0.64	0.58	0.69	0.64	0.62	0.87	0.82	0.73	0.67
Generation time (years)	mean	3.73	3.52	4.11	3.77	3.83	3.39	3.56	3.38	3.71	3.14	3.21	3.99	2.66	2.43	2.95
	SD	0.22	0.34	0.36	0.30	0.24	0.23	0.21	0.19	0.23	0.19	0.20	0.27	0.19	0.17	0.15
Natural mortality (per year)	mean	0.56	0.58	0.53	0.57	0.63	0.66	0.65	0.69	0.66	0.71	0.66	0.57	0.70	0.78	0.63
	SD	0.06	0.06	0.06	0.05	0.08	0.09	0.08	0.07	0.08	0.10	0.08	0.05	0.07	0.06	0.04
growth constant (K/year)	mean	0.31	0.31	0.27	0.30	0.33	0.35	0.35	0.36	0.34	0.36	0.34	0.28	0.37	0.41	0.35
	SD	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.05	0.04	0.03	0.04	0.03	0.02
Ecological mean trophic level	mean	2.93	3.49	3.60	3.41	3.30	3.28	3.34	3.19	3.36	3.57	3.41	2.88	2.78	2.63	3.44
	SD	0.26	0.35	0.37	0.30	0.35	0.43	0.36	0.32	0.36	0.44	0.38	0.20	0.21	0.16	0.13
Food consumption (% body weight/day)	mean	10.63	10.36	8.96	9.79	10.24	9.12	9.96	11.04	10.23	10.07	9.49	9.32	11.54	14.18	9.69
	SD	1.09	0.85	0.68	0.69	0.94	0.82	0.91	1.03	1.08	1.13	1.04	1.06	1.14	1.10	0.62
Simpson's diversity index	mean	0.87	0.81	0.82	0.83	0.82	0.79	0.81	0.80	0.78	0.71	0.76	0.88	0.74	0.81	0.91
	SD	0.01	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.05	0.04	0.01	0.03	0.02	0.01

[a] *Years of historical phases are given in Table 1.*

[b] *All length measurements are in centimeters.*

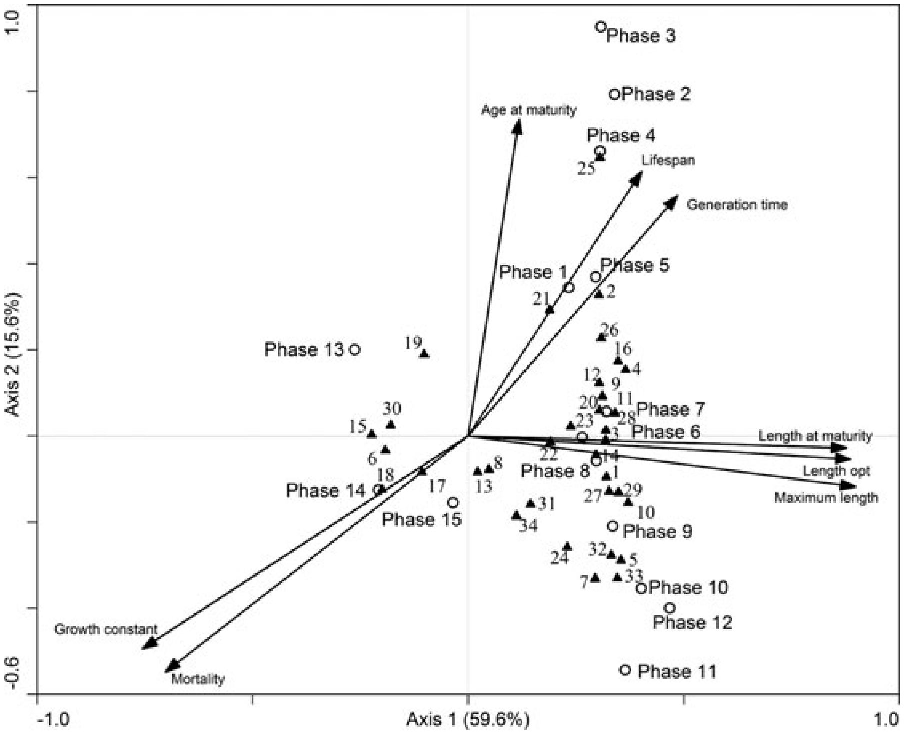

Figure 2. Results of canonical correspondence analysis with fish species composition as the dependent variable and life-history characteristics as independent variables: open circles, historical and modern catch periods (phases); closed triangles, species; arrow, life-history trait and direction of influence of the trait on the fish species (arrows point toward larger numbers); 1, Acanthopagrus berda (*Goldsilk seabream*)*; 2,* Acanthurus lineatus (*Lined surgeonfish*)*; 3,* Alectis indicus *(Indian mirrorfish or Indian threadfin); 4,* Arius spp. (*Broadsnouted catfish*)*; 5,* Carcharhinus limbatus wheeleri (*Blacktip and sharpnose blacktail shark*)*; 6,* Calotomus carolinus (*Stareye parrotfish*)*; 7,* Caranx sexfasciatus (*Bigeye trevally*)*; 8,* Cheilio inermis (*Cigar wrasse*)*; 9,* Epinephelus caeruleopunctatus (*Whitespotted grouper*)*; 10,* Gerres acinaces (*Pursemouth*)*; 11,* Gymnothorax favagineus (*Honeycomb moray*)*; 12,* Gymnothorax undulatus (*Leopard moray*)*; 13,* Leptoscarus vaigiensis (*marbled parrotfish*)*; 14,* Lethrinus lentjan (*Redspot emperor*)*; 15,* Lethrinus mahsena (*Sky emperor*)*; 16,* Lutjanus argentimaculatus (*River snapper*)*; 17,* Lutjanus fulviflamma (*Dory snapper*)*; 18,* Lutjanus gibbus (*Humpback snapper*)*; 19,* Naso hexacanthus (*Blacktongue unicornfish*)*; 20,* Papilloculiceps longiceps (*Madagascar flathead*)*; 21,* Plectorhinchus flavomaculatus (*Lemon sweetlip*)*; 22,* Plectorhinchus gaterinus (*Blackspotted rubberlips*)*; 23,* Plectorhincus schotaf (*Minstrel sweetlip*)*; 24,* Plectorhincus sordidus (*Black or redlip sweetlips*)*; 25,* Plectropomus punctatus (*Marbled leopardgrouper*)*; 26,* Plotosus limbatus (*Darkfin eel catfish*)*; 27,* Pomadasys multimaculatum (*Cock grunter*)*; 28,* Epinephelus lanceolatus (*Brindlebass*)*; 29,* Rhabdosargus sarba (*Gold sea bream*)*; 30,* Siganus sutor (*Whitespotted rabbitfish*)*; 31,* Sphyraena barracuda (*Great barracuda*)*; 32,* Stegostoma fasciatum (*Zebra shark*)*; 33,* Tripteredon orbis (*African spadefish*)*; 34,* Variola louti (*Lyretail grouper*). *(Codes and common names from Smith and Heemstra [1986].)*

Phases 1 and 5 had a shallow-water species of surgeonfish (*Acanthurus lineatus*) and the lemon sweetlips (*Plectorhinchus flavomaculatus*). The large-bodied (about 1 m) marbled leopard grouper (*Plectropomus punctatus*) occurred in phases 2, 3, and 4. Numbers of fish bones increased to a peak at phase 8 (AD 1000–1100) before declining. In phases 6–8 there were more maximum-length species and species with longer life spans than in earlier phases. Reef (*Carcharhinus* spp.) and zebra sharks (*Stegostoma fasciatum*); bigeye trevally (*Caranx sexfasciatus*); African spadefish (*Tripteredon orbis*); great barracuda (*Sphyraena barracuda*); and white-spotted (*Epinephelus caeruleopunctatus*), lyretail (*Variola louti*), and brindelbass (*Epinephelus lanceolatus*) groupers appeared in phases 6–8.

The CCA with the independent ecological variables diet, trophic level, and rate of food consumption produced distinctions among assemblages similar to the analysis that included life-history variables, where historical and modern assemblages were separated strongly by the first axis ($F = 8.09$, $p < 0.01$; Fig. 3). Simpson's diversity index did not differ strongly among the assemblages. The historical assemblages included a higher percentage of species at higher trophic levels and of

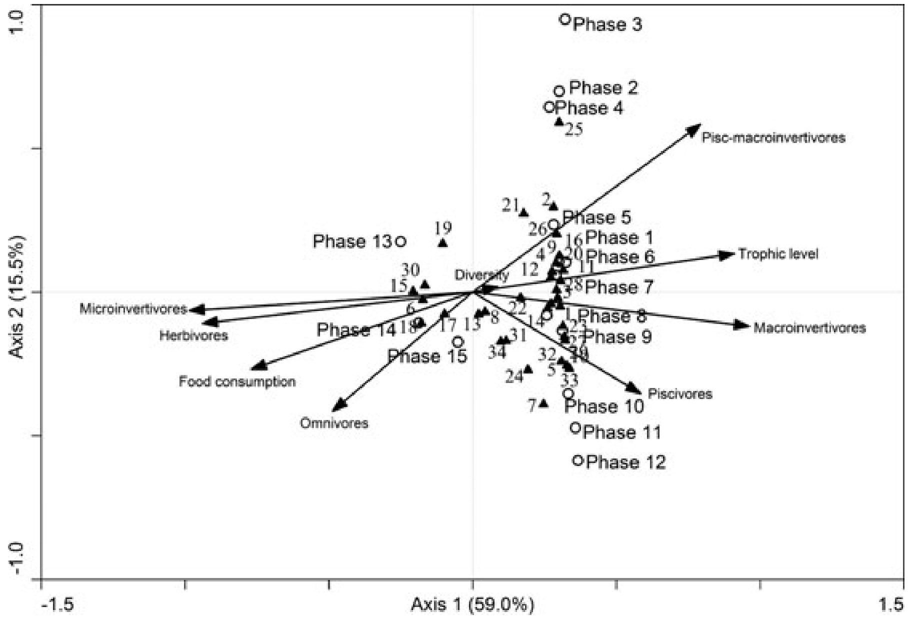

Figure 3. Results of canonical correspondence analysis with species composition as the dependent variable and functional groups, trophic level, and feeding consumption as independent variables (open circles, historical and modern catch periods [phases]; closed triangles, species; arrow, ecological characteristics, trophic functional groups, and direction of influence on the fish species; species codes are as in Fig. 2).

piscivore-macroinvertivores, macroinvertivores, and piscivores, whereas the modern assemblage had more herbivores, omnivores, microinvertivores, and species with higher food-consumption rates. The modern closures had a greater percentage of microinvertivores and piscivore-macroinvertivores than the modern fishing grounds.

Discussion

Historical and modern assemblages were notably different, and life history, diet, and trophic level of species' assemblages explained nearly 60% of this variance. These differences are consistent with an unsustainable fishing hypothesis in which an increase in fishing effort and time is predicted to reduce abundance of slow-growing apex predators and mean trophic level and to increase abundance of opportunistic species (those with broad diets, high feeding rates, and high growth and mortality rates) (Pauly et al. 1998). Heavy fishing allows a few species that feed low in the food web and have high growth and mortality rates to persist, which can maintain high-fisheries production (McClanahan et al. 2008). Heavy fishing eliminates or greatly reduces abundance of species with long generation times, large body size, slow growth rates, and species that compete with humans for food (Pauly et al. 1998; Pinnegar & Engelhard 2008). The historical patterns we observed have also been observed along gradients of fishing effort in Kenya's modern fishery (McClanahan et al. 2008; McClanahan & Hicks 2011).

The 650 years of historical data indicated small changes that might be associated with the early stages of fishing expansion from nearshore to offshore locations, possibly associated with improved fishing vessels and gear during the later 400 years. Many of the species in the early stages of the midden are associated with seagrass and reefs that are a few meters deep, whereas the later phases included more species typically found at depths of 5–20 m (Smith & Heemstra 1986). In these later phases, fishes with large body sizes but shorter life spans increased in abundance.

As the numbers of fish bones increased in the middens, so did the numbers of domesticated animals (Table S1). Mudida and Horton (1996) concluded that the earliest human inhabitants of the study region could have survived on nearshore shellfish and possibly the blood of domestic animals. By approximately AD 1000, however, sheep and goats began to dominate the human diet. The abundance of molluscs used for food and ornaments declined at the same time, and by about AD 1375 bones of domestic animals outnumbered fish bones in the midden. Mudida and Horton (1996) found evidence that the abandonment of the settlement was associated with looting. These observations suggest that access to resources, culture, and dietary choices rather than simply hunting of the largest predators dictated human diet.

The midden contained bones of the same fish species that are commonly caught today, but also contained bones of a number of large apex predators that are uncommon today. The greatest change over the 650 years was a reduction in the life spans of the fish. There was no evidence of increased abundance of fast-growing herbivores and microinvertivores. A core group of species was present in all phases, including the 2 seagrass-feeding parrotfishes, the dory snapper, and the cigar wrasse. In the modern assemblages, these core species and species that feed on microinvertebrates were more abundant, whereas apex predators and species that feed on macroinvertebrates were less abundant.

Despite some differences in gear use, there were relatively minor variations in composition of the catch assemblage between the fished grounds of southern Kenya and Shanga. Fishing in the modern Shanga was less intensive than in the south and may reflect fewer people in the north. Nevertheless, life-history attributes of all modern assemblages were consistent with those expected from heavy fishing; greater abundance of seagrass-associated species and lower abundance of apex predators and herbivorous and carnivorous species associated with coral reefs (McClanahan et al. 2008).

Fishes in modern government closures did not strongly resemble the historical assemblage; rather, they were a variation of the modern fisheries. Closures had greater abundance of piscivore-macroinvertivorous and microinvertivorous species with longer life spans and lower abundance of herbivorous species than heavily fished reefs (McClanahan et al. 2010). These closures are among the oldest and best managed in the western Indian Ocean and have a high biomass of fish (McClanahan et al. 2009). There is evidence, however, that even up to 38 years after closure, some species and trophic groups had not yet recovered, notably triggerfish (macroinvertivore) and rabbitfish (herbivores), but piscivores were not well sampled in the modern assemblage (McClanahan et al. 2007).

Small closure areas, short closure times, low levels of connectedness, and heavy fishing around the borders of closures are likely to influence assemblages of fish and other species in closures and produce assemblages that do not represent historical ecosystems (Claudet et al. 2008). Extensive modification of marine ecosystems may be largely irreversible given current spatial and temporal extents of management.

The species we found in the midden are currently present in the country and the region. Nevertheless, the probability that their abundances will increase to historical levels is small given the area and connectivity needed for them to remain viable and given current human resource use and climate-change effects. The proposal to rebuild ecosystems rather than to achieve sustainable use of resources (Pitcher 2001) is likely to decrease fishing yields considerably and could take centuries to accomplish given current fishing effort. Projections of rapid recovery of fishes in closures and fisheries have not accounted for the recovery at the species level or considered the many life histories that are common to undisturbed coastal ecosystems (Jones & Schmitz 2009). Consequently, in tropical countries with high dependence on natural resources, a combination of closure networks, more-extensive restrictions on the take of apex predators, and provision of alternative sources of protein and livelihoods to reduce fishing effort may be the most feasible social-ecological management system in the near term.

We assume that the fish assemblages at our study sites were well reconstructed by our methods and less influenced by climate and oceanographic change than by fishing. There are problems with use of catch data to reflect assemblaghes of fish in situ and with the use of midden bones to reflect catch (Erlandson & Rick 2008; Branch et al. 2010). Catch, for example, does not sample the full assemblage of fish because gears are selective and under-sample small fish that are the most abundant species (McClanahan et al. 2010). Nevertheless, the gear effect was not large and was considerably smaller than the phase or time and space effect. For example, species composition in 2 modern phases (14 and 15), one with and one without restrictions on gear, was more similar to each other than species composition in any other phases. This high level of similarity probably occurred because the gears (traps, beach seines, and gill nets) have similar selectivity (McClanahan & Mangi 2004).

The midden data are temporally extensive but have limited spatial extent and possibly reflect nonrandom discard and different decay rates of small and large bones (Erlandson & Rick 2008). The high diversity of bones in the middens and the similarity of Simpson's diversity index over time do not, however, suggest different rates of decay. Additionally, over time, composition of the core group of species was augmented by apex and mesopredators, which generally have large cranial bones and vertebrae. We expected the small size of the mesh used to sample the midden and the use of the larger cranial bones and vertebrae for identification to reduce error. Moreover, there was no monotonic trend in bone size, and large-bodied fish species were found throughout the phases.

Restricted spatial extent and replication in the midden data was the greatest challenge to comparisons over the long periods we considered. Accordingly, we sampled over large spatial and temporal extents in the modern assemblage and compared fishing near Shanga with fishing at sites distributed throughout Kenya. Sample sizes from middens are often small and bones offer low taxonomic resolution. We were able to identify bones to the species level on the basis of specimens from the modern catch, and sample size was considerable for both the historical and modern sample.

Abiotic environmental change over time must also influence and contribute to the total observed variation. Data on nearshore environmental variables from this region are sparse and data on their relation to historical fish communities are not available. Seawater temperatures may have been somewhat lower and waters cleaner historically than today, but the effects of these differences on historical or comtemporary fish fauna are unknown. We suspect that the environmental differences between historical and modern periods were not large, had minor effects on the fish communities, and were not in a direction that would confound a test of the unsustainable fishing hypothesis.

Our comparison of catches in permanent fisheries closures and open-access fisheries show that small differences in fish catch can often reflect larger differences in the in situ fish assemblages (McClanahan et al. 2010). We documented relative declines in piscivores and macroinvertivores and increases in herbivores and microinvertivores over the past 1250 years. Relative changes are not absolute changes and, therefore, it is likely that the absolute abundances of herbivores and microinvertivores, but not piscivores and macroinvertevores, were greater in the past. Reductions in piscivores and macroinvertivores are likely to increase abundances of their prey and thus have possible cascading effects on reef ecology (O'Leary & McClanahan 2010). Consequently, the differences between historical and modern catch assemblages we documented are likely to reflect ecosystem-level changes, which will be challenging to document through scientific means and to reconstruct through management.

Acknowledgments

The Wildlife Conservation Society supported this research through financial assistance from the WIOMSA-MASMA (Western Indian Ocean Marine Science Assocation--Marine Science for Management) program and the Tiffany Foundation. We greatly appreciate the assistance of C. Abunge, C. Hicks, B. Kaunda-Arara, S. Kitema, S. Mangi, P. Mutisya, and M. Watson in the collection of the field data and the comments of C. Hicks, T. Branch, W. Cheung, and J. Cinner on the manuscript. Fisheries leaders and Kenya's Fisheries Department assisted with data collection at fish-landing sites. Kenya Wildlife Service (N.A. Muthiga) allowed experimental fishing in the parks. Kenya's Ministry of Science and Technology provided research clearance.

Supporting Information

Information on other types of bones excavated together with the fish bones in the historical trench (Appendix S1), DCA results of species composition and gear types for the Shanga modern fisheries (Appendix S2), and a list of species found in the study phases (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Anderson, D. M., J. T. Overpeck, and A. K. Gupta. 2002. Increase in the Asian Southwest Monsoon during the past four centuries. Science **297:**596–599.

Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. D. Lafferty, T. R. McClanahan, and G. R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academic Sciences **107:**18256–18261.

Baisre, J. 2010. Setting a baseline for Caribbean fisheries. Journal of Island and Coastal Archaeology **5:**120–147.

Branch, T. A., R. Watson, E. A. Fulton, S. Jenning, C. R. McGilliard, G. T. Pablico, D. Ricard, and S. R. Tracey. 2010. The trophic fingerprint of marine fisheries. Nature **468:**431–435.

Camoin, G. F., L. F. Montaggioni, and C. J. R. Braithwaite. 2004. Late glacial to post glacial sea levels in the Western Indian Ocean. Marine Geology **206:**119–146.

Claudet, J., et al. 2008. Marine reserves: size and age do matter. Ecology Letters **11:**481–489.

Claudet, J., et al. 2010. Marine reserves: fish life history and ecological traits matter. Ecological Applications **20:**830–839.

Dalzell, P. 1998. The role of archaeological and cultural-historical records in long-range coastal fisheries resources management strategies and policies in the Pacific Island. Ocean and Coastal Management **40:**237–252.

Erlandson, J. M., and T. C. Rick. 2008. Archaeology, marine ecology, and human impacts on marine environmens. Pages 1–19 in T. C. Rick, and J. M. Erlandson, editors. Human impacts on ancient marine ecosystems. University of California Press, Berkeley.

Fleitmann, D., R. B. Dunbar, M. McCulloch, M. Mudelsee, M. Vuille, T. R. McClanahan, J. E. Cole, and S. Eggins. 2007. East Africa soil erosion recorded in a 300 year old coral colony from Kenya. Geophysical Research Letters **34** DOI:04410.01029/02006GLO028525.

Froese, R., and D. Pauly, editors. 2000. Fish Bases 2000: concepts, design and data source. ICLARM, Makati, Philippines. Available from www.Fishbase.org (accessed March 2008).

Horton, M. 1996. The chronology and development of Shanga. Pages 394–406. Shanga: the Archaeology of a Muslim Trading Community on the Coast of East Africa. The British Institute in Eastern Africa, London.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293:**629–638.

Jones, H. P., and O. J. Schmitz. 2009. Rapid recovery of damaged ecosystems. Public Library of Science ONE **4**(5): e5653. DOI:10.1371/journal.pone.0005653

Kaunda-Arara, B., and G. A. Rose. 2004a. Effects of marine reef National Parks on fishery CPUE in coastal Kenya. Biological Conservation **118:**1–13.

Kaunda-Arara, B., and G. A. Rose. 2004b. Out-migration of tagged fishes from marine reef National Parks to fisheries in coastal Kenya. Environmental Biology of Fishes **70:**363–372.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletions, degradation, and recovery potential of estuaries and coastal seas. Science **312:**1806–1809.

Lotze, H. K., and I. Milewski. 2004. Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecological Applications **14:**1428–1447.

Mann, M. E., Z. Zhang, S. Rutherford, R. S. Bradley, M. K. Hughes, D. Shindell, C. Ammann, G. Faluvegi, and F. Ni. 2009. Global signatures and dynamical origins of the Little Ice Age and Medieval climate anomaly. Science **326:**1256–1260.

Maschner, H. D. G., M. W. Betts, K. L. Reedy-Maschner, and A. W. Trites. 2008. A 4500-year time series of Pacific cod (*Gadus macrocephals*) size and abundance: archaeology, oceanic regime shifts, and sustainable fisheries. Fishery Bulletin **104:**386–394.

McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications **17:**1055–1067.

McClanahan, T. R., N. A. J. Graham, S. K. Wilson, Y. Letourneur, and R. Fisher. 2009. Effects of fisheries closure size, age, and history of compliance on coral reef fish communities in the western Indian Ocean. Marine Ecology Progress Series **396:**99–109.

McClanahan, T. R., and C. C. Hicks. 2011. Changes in life history and ecological characteristics of coral reef fish catch composition with increasing fishery management. Fisheries Management and Ecology **18:**50–60.

McClanahan, T. R., C. C. Hicks, and E. S. Darling. 2008. Malthusian overfishing and efforts to overcome it on Kenyan coral reefs. Ecological Applications **18:**1516–1529.

McClanahan, T. R., B. Kaunda-Arara, and J. O. Omukoto. 2010. Composition and diversity of fish and fish catches in closures and open-access fisheries of Kenya. Fisheries Management and Ecology **17:**63–76.

McClanahan, T. R., and S. C. Mangi. 2004. Gear-based management of a tropical artisanal fishery based on species selectivity and capture size. Fisheries Management and Ecology **11:**51–60.

Mudida, N., and M. Horton. 1996. Subsistence at Shanga: the faunal record. Pages 378–393. Shanga: The Archaeology of a Muslim Trading Community on the Coast of East Africa. The British Institute in Eastern Africa, London.

Nakamura, N., H. Kayanne, H. Iijima, T. R. McClanahan, S. K. Behera, and T. Yamagata. 2009. Mode shift in the Indian Ocean climate under global warming stress. Geophysical Research Letters **36:**DOI:10.1029/2009GL040590.

O'Leary, J. K., and T. R. McClanahan. 2010. Trophic cascades result in large-scale coralline algae loss through differential grazer effects. Ecology **91:**3584–3597.

Pauly, D. 1998. Tropical fishes: patterns and propensities. Journal of Fish Biology **53 (Supplement A):**1–17.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. Fishing down marine food webs. Science **279:**861–863.

Pauly, D., M. L. Palomares, R. Froese, P. Sa-a, M. Vakily, D. Preikshot, and S. Wallace. 2001. Fishing down Canadian aquatic food webs. Canadian Journal of Fish and Aquatic Science **58:**1–12.

Pinnegar, J. K., and G. H. Engelhard. 2008. The 'shifted baseline' phenomenon: a global perspective. Reviews in Fish Biology and Fisheries **18:**1–16.

Pitcher, T. J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. Ecological Applications **11:**601–617.

Rick, T. C., and J. M. Erlandson 2008. Human impacts on ancient marine ecosystems: a global perspective. University of California Press, Berkeley.

Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. Canadian Journal of Fish and Aquatic Science **61:**1553–1557.

Rosenberg, A. A., W. J. Bolster, K. E. Alexander, W. B. Leavenworth, A. B. Cooper, and M. G. McKenzie. 2005. The history of ocean resources: modeling cod biomass using historical records. Frontiers in Ecology and the Environment **3:**84–90.

Russ, G. R. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. Oecologia **138:**622–627.

Sabater, M. G., and B. P. Carroll. 2009. Trends in reef fish population and associated fishery after three millennia of resource utilization and a century of socio-economic changes in American Samoa. Reviews in Fisheries Science **17:**318–335.

Sandin, S. A., et al. 2008. Baselines and degradation of coral reefs in the Northern Line Islands. Public Library of Science ONE **3**(2): e1548.

Smith, M. M., and P. C. Heemstra. 1986. Smiths' sea fishes. Springer-Verlag, Berlin.

ter Braak, C. J. F., and P. Šmilauer. 2002. CANOCO Reference manual and CanoDraw for Windows user's guide: software for canonical community ordination. Version 4.5. Microcomputer Power, Ithaca, New York.

Watson, M. 1996. The role of protected areas in the management of Kenyan reef fish stocks. Environmental Economics. University of York, York, United Kingdom.

Wing, S. R., and E. S. Wing. 2001. Prehistoric fisheries in the Caribbean. Coral Reefs **20:**1–8.

Wood, L., L. Fish, J. Laughren, and D. Pauly. 2008. Assessing progress towards global marine protection targets: shortfalls in information and action. Oryx **42:**340–351.

Worm, B., et al. 2009. Rebuilding global fisheries. Science **325:**578–585.