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Coral Reefs

Reefs since Columbus

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Abstract. History shows that Caribbean coastal ecosystems were severely degraded long before ecologists began to study them. Large vertebrates such as the green turtle, hawksbill turtle, manatee and extinct Caribbean monk seal were decimated by about 1800 in the central and northern Caribbean, and by 1990 elsewhere. Subsistence over-fishing subsequently decimated reef fish populations. Local fisheries accounted for a small fraction of the fish consumed on Caribbean islands by about the mid nineteenth century when human populations were less than one fifth their numbers today. Herbivores and predators were reduced to very small fishes and sea urchins by the 1950s when intensive scientific investigations began. These small consumers, most notably *Diadema antillarum*, were apparently always very abundant; contrary to speculation that their abundance had increased many-fold due to overfishing. Studying grazing and predation on reefs today is like trying to understand the ecology of the Serengeti by studying the termites and the locusts while ignoring the elephants and the wildebeeste. Green turtles, hawksbill turtles and manatees were almost certainly comparably important keystone species on reefs and seagrass beds. Small fishes and invertebrates feed very differently from turtles and manatees and could and can not compensate for their loss, despite their great abundance long before overfishing began. Loss of megavertebrates dramatically reduced and qualitatively changed grazing and excavation of seagrasses, predation on sponges, loss of production to adjacent ecosystems, and the structure of food chains. Megavertebrates are critical for reef conservation and, unlike land, there are no coral reef livestock to take their place.

Introduction

The status and trends of the world's coral reefs are highly controversial and, until very recently, have attracted far less attention than has been lavished on the decline of tropical forests. This is partly a function of our greater ignorance about coral reefs and their briefer period of study. But it is also true that coral reef ecologists have been so devoted to dissecting small-scale processes that they have not seen the reefs for the corals.

Ecology is a young science, with little reliable descriptive information from before the 1920s (Elton 1927; Hutchinson 1978) and virtually no time series population data extending of back for more than a century. The situation is even worse for marine communities like coral reefs because of the difficulty of making observations underwater. Thus reef ecologists have been forced to try to explain patterns of distribution and abundance exclusively in terms of the events of the past few years using "real time" observations and experiments. Their success is manifest in our rapidly growing understanding of how environmental variation and biological interactions can shape reef communities (Connell 1978; Hughes 1989; Knowlton et al. 1990), although the importance of events rare on the scale of human lifetimes is only beginning to be understood (Woodley et al. 1981; Jackson 1991; Knowlton 1992; Hughes 1994).

In the process of these endeavors, however, reef ecologists have turned their backs on history and assumed that what they were studying was "normal," despite the lack of rigorous baseline data for the condition of coral reefs preceding the industrial revolution and the onset of worldwide, exponential human population growth. As a result, many reef ecologists have concluded that coral reefs are healthy in the face of overwhelmingly increasing evidence to the contrary. Indeed, the idea for this study arose from my feeling like Cassandra in the face of such denial during the 1993 Miami Colloquium on *Global Aspects of Coral Reefs*: *Health, Hazards and History*. Most felt at the beginning of the colloquium that the condition of coral reefs was on the whole rather good, despite Wilkinson's (1992) plenary paper at the 7th International Coral Reef Symposium about widespread devastation worldwide. However, by the end of the Colloquium, there was a beginning acceptance that the situation was perhaps bad in the Caribbean, but only recently, and probably not in the pacific.

The problem is that everyone, scientists included, believes that the way things were when they first saw them is natural. However, modern reef ecology only began in the Caribbean, for example, in the late 1950s (Goreau 1959; Randall et al. 1961; Randall 1965) when, enormous changes in coral reef ecosystems had already occurred. The same problem now extends on an even greater scale to the SCUBA diving public, with a whole new generation of sport divers who have never seen a "healthy"reef, even by the standards of the 1960s. Thus there is no public perception of the magnitude of our loss.

Another insidious consequence of this "shifting baseline syndrome" (Pauly 1995; Sheppard 1995) is a growing eco-management culture that accepts the *status quo*, and fiddles with it under the mantle of experimental design and statistical rigor, without any clear frame of reference of what it is they are trying to manage or conserve. These are the coral reef equivalents of European "hedgerow ecologists" arguing about the maintenance of diversity in the remnant tangle between fields where once there was only forest.

Let me say from the start that I am not going to make some romantic appeal to set back the clock, nor propose draconian scenarios that ignore the realities of inexorable human population growth and underdevelopment. Instead, my goal is to set the stark realities we face in a deeper historical perspective than the last few decades in order to (1) silence absurd notions of multiuse sustainability and (2) help to define better the limited alternatives available. I will limit my discussion to the Caribbean, and principally to Jamaica, because I know the Caribbean best and Jamaica is arguably the worst case today in that region. Jamaica also offers the best historical record, which extends back nearly 350 years, and provides startlingly good but unexploited information for ecological assessment.

I will first work backward from the present to re-examine aspects of the classic story relating overfishing, the mass mortality of the long-spined sea urchin *Diadema antillarum*, and the collapse of Caribbean coral reefs in Jamaica and elsewhere (Lessios et al. 1984; Hay 1984; Hughes 1994). This is not to deny the important consequences of overfishing, but to show that we have been at least partly wrong about the historical role of the sea urchin. I will then work forward from 1492 to examine the extraordinarily rapid depletion of large consumers on coral reefs and their environs, which were once the equivalents of the wildebeeste and elephants of the Serengeti plains (Sinclair and Arcese 1995). For this purpose, I will emphasize the Jamaican based fishery of the green turtle *Chelonia mydas* because the data are the best; but the same sort of story applies to sharks, rays, groupers, manatees and the extinct Caribbean monk seal. I will then depart from the general theme of overfishing to briefly consider inputs from the land. These have almost certainly been of comparable importance to overfishing but the data are less complete. Finally, I will return to Jamaica to examine the fishing history there since Columbus, which clearly shows that coral reef ecosystems had begun to fall apart in the eighteenth century.

Diadema, damselfish and overfishing

The conventional story (Hay 1984; Lessios 1988; Hughes 1994) is that intense overfishing allowed *Diadema* to increase because of reduced predation by fishes, and competitive release for algal food that was no longer consumed by larger herbivores. This increase in *Diadema* compensated for the loss of herbivorous fishes and kept down the growth of seaweeds on reefs. Then when the *Diadema* suddenly died, there were no other consumers capable of cropping the seaweeds which soon overgrew and killed most of the reef corals at depths down to about 50 m.

What are the facts and what is the inference in this story? The facts are that (1) overfishing was extreme by any standard, (2) *Diadema* was extremely abundant before the mass mortality in 1983, (3) mass mortality of *Diadema* allowed a dramatic increase in seaweeds which overgrew and smothered corals. The inference is that (1) decrease in large fish allowed a large increase in *Diadema*, (2) increase in people caused the decrease in fish in a roughly proportional fashion, and (3) the effects of people were relatively recent. Regarding the latter point, for example, Hughes' (1994) graph of human population increase starts in 1850 and is introduced within a section titled "Overfishing: 1960s to Present".

Let us examine some problems with this inference before reviewing the historical data. Hay's (1984) pioneering regional study of *Diadema* versus fish grazing confounds "overfished" and "less fished" with geography. Hay was very careful to avoid terms like "pristine" and "unfished", unlike many who have referred to his work subsequently. However, all of his "overfished" reefs are on islands in the central Caribbean, and all but one of his "less fished" reefs are on the mainland. Moreover, Levitan's (1992) ingenious study of *Diadema* nutrition over the last century shows an even greater geographic effect. Levitan (1991) showed experimentally that the ratio of the size of the feeding apparatus to the size of the animal test increases in inverse proportion to the food supply. He then examined changes in the ratio through time using museum specimens, and found a significant but surprisingly small increase over the past century when *Diadema* populations were inferred to have exploded due to overfishing. In contrast, geographic variation accounted for much more (23%) of the total variation observed than that due to time. Ordination of coral abundance data from reefs around the Caribbean compiled by Liddell and Ohlhorst (1988) also shows strong island-mainland differences in overall reef community structure (Jackson et al. 1996).

So is it possible that *Diadema* were abundant in the Caribbean before Columbus arrived? It turns out that *Diadema* has long attracted commentary because of its great abundance and reputation of being dangerous (Table 1). Moreover, all of the authors cited except Young were professional or amateur naturalists, with extensive experience dredging or (in the case of Beebe 1928) diving in tropical waters. All were well known for the reliability and accuracy of their observations and were not the type to mistake an occasional aggregation or hearsay for genuinely great abundance. These sources make it clear that *Diadema* was indeed very abundant in the seventeenth century when human populations were very small, and therefore long before overfishing could have caused their increase.

Table 1. Caribbean *Diadema* lore

Source	Location	Quoted text
Beebe 1928	Haiti	Under every bit of coral … in great abundance
Clark 1919	Jamaica and Dry Tortugas	On and about the coral reefs, the dreaded poisonous "black sea egg" (*Centrechinus antillarum*) is common and on certain areas it is so numerous that a person can scarcely move about without touching one.
Nutting 1919	Barbados Antigua and Bahamas	No one goes bathing or into the water for any purpose in this region without being warned against the danger of being wounded by the cruel black spines of this ubiquitous sea-urchin. It is found almost everywhere in shallow water, both on sandy and rocky bottom. The all too familiar black sea-egg *Diadema antillarum* is abundant here, as it is everywhere that I have collected in the West Indies (therefore includes his 1895 expedition to the Bahamas, not seen)
Henderson 1914	Cuba	We were then upon the inner edge of the main reef upon which any further progress would have been difficult on account of the rapidly increasing numbers of the long black-spined sea urchins, the diademas … … the usual presence of the net [dredging] of the diadema sea-urchin … During the hours of bright sunshine the diademas seek cover under the rocks … In the late afternoon … they issue forth en masse in search of food and probably continue their slow wanderings throughout the night. In localities where hiding places are few, such as upon sandy patches in or near a reef, the diademas are always more or less in evidence.
Field 1891	Jamaica	The most strikingly conspicuous of all the creatures about the coral reefs. As one approaches the cay, far down in the water are seen numerous irregularly shaped black patches of varying extent. … around and under its branches (elkhorn coral) are crowded together great numbers of this large black urchin. … what formidable defense against attack they present when crowded so closely together.
Aggasiz 1883	Dry Tortugas	… on somewhat deeper regions (of the reef) we find pockets filled with large Diadematidae.
Young 1847 (writing of his observations in 1839)	Nicaragua and Honduras	… they were both badly cut by the coral and sea eggs in diving for the things that had been upset. Numbers of sea eggs were seen in all directions, and we well knew the danger of getting amongst them, as they have long and sharp pointed spines, which inflict deep and dangerous wounds on those who chance to tread on them. … the handsome sea-eggs inviting but to betray …
Sloane 1725 (writing of his observations in 1688)	Jamaica	The great, long prickled Sea Egg … set about on every hand with prickles, the largest being three or four inches long, with membrane round their setting on to the shell … purple deep coloured … The prickles of this Sea Echinus are very rough and considered poisonous. I have found them in great numbers on the reef by Gun-Key, or, Cayos off the Port Royal Harbour in great numbers.

There is also strong paleontological evidence that *Diadema* were abundant on Jamaican reefs long before any humans arrived there (Gordon and Donovan 1992). Diadematoid plates and spines are the most abundant echinoid remains in the 125 000 year old Falmouth Formation, constituting 90% of all identified echinoid fragments. These are almost, certainly of *Diadema antillarum* because the only other Caribbean Pleistocene diadematoid is *Astropyga magnifica* which occurs today in deeper water than the backreef environment of the Falmouth Formation (Donovan and Gordon 1993).

In conclusion, *Diadema* apparently has been the most abundant sea urchin on Caribbean reefs for at least 125 000 years. Its abundance still may have increased historically due to overfishing, but we lack the quantitative data to tell. However, it now seems unlikely that any such increase was as great as that, for example, of *Echinometra mathaei* in response to over-fishing in

Kenyan lagoons (McClanahan and Muthiga 1988; McClanahan et al. 1996). Thus *Diadema* abundance is at best a secondary consequence of the degradation of Caribbean reefs, and we need to look for other indicators of faunal change in response to human interference. For this purpose, let us now turn to changes in the abundance of the really large consumers in reef environments, such as green turtles.

How many turtles in 1492?

Big animals are ecologically important, not only because of the amount of plants or animals each individual consumes, but also because of the physical and biological disturbance they cause, which fundamentally alters their environment and affects other species. Perhaps the best studied example is the Serengeti ecosystem of east Africa (Sinclair 1995a; Sinclair and Arcese 1995). Long distance migration (wildebeeste) and growth to very large size (elephant, hippopotamus, rhinoceros and buffalo) result in virtual escape from predation, so that such herbivores are "bottom up" regulated by food limitation rather than "top down" by predators (Sinclair 1995a). The enormously abundant wildebeeste is a keystone species because its grazing and migration directly or indirectly affect almost everything else. Wildebeeste grazing alters the protein content of the grass and stimulates growth of new shoots, increasing the available food supply for smaller grazers, and possibly also for themselves (McNaughton and Banyikwa 1995). There is also strong evidence for alternate stable states of vegetation (woodland versus grassland), maintained by grazing and disturbance by elephants and by fire (Dublin 1995; Sinclair 1995b).

None of these topics have been studied as well on coral reefs and surrounding seagrass environments, but what we do know strongly suggests similarly important ecosystem effects of large species (Heinsohn et al. 1977; Ogden 1980; Thayer et al. 1984; Lanyon et al. 1989; Sheppard et al. 1992). Green turtles crop "turtlegrass" *Thalassia testudinum* to only a few centimeters above the bottom, and cause erosion and pits in the rhizomal mat of turtlegrass beds. Manatees and dugongs do much the same, sometimes ripping up entire beds of seagrasses and other aquatic vegetation, and thereby causing even greater physical disturbance. Stingrays excavate pits in seagrass beds foraging for mollusks beneath the rhizome mat, hawksbill turtles rip up sponges, and large parrotfishes occasionally bite to pieces entire coral colonies for unknown reasons.

I have nothing new to add to such observations, except the comment that I have not even seen most of these large animals underwater for twenty years or more, and some of them never at all, despite thousands of hours SCUBA diving on and around coral reefs. Instead, I want to dwell on the past enormity of the populations of such creatures using green turtles as an example. My calculations are rough in ways that responsible turtle biologists have shied away from, and the data are 15 to 300 years old. Nevertheless, it is essential to try, because we have no conception of the way things were. Why, after all, are so many hundreds of sites around the Caribbean, such as the Dry *Tortugas*, named after turtles that almost no living person has ever seen?

Calculations based on old hunting data from the Cayman Islands

Estimates of the size of pre-columbian human populations in the Caribbean are controversial and depend on differing interpretations of archeological and historical sources (Roberts 1989). Nevertheless, populations of Hispaniola, Jamaica and Cuba certainly ranged in the hundreds of thousands, perhaps even in the millions, and were sustained by a highly productive agricultural system supplemented by fishing and hunting (Sauer 1966; Rouse 1992). These early Americans were reduced by conquest, slavery and disease to only a few thousand by 1600. Subsequent Spanish colonization was slow, so that there were only about five thousand people in Jamaica when the English captured the island in 1655 (Long 1774). There was also no effective agricultural base, so the English turned immediately for food to the vast populations of green turtles that nested on Grand Cayman Island (Table 2). These abundant turtles were essential to the rapid growth and success of Jamaica as England's most important colony of the time, and indeed provided most of the meat consumed there until the 1730s (Sloane 1707, 1725; Long 1774; Lewis 1940; King 1982).

Thirty years later, the Cayman Islands fishery had grown to approximately 40 sloops and 120 to 150 men who brought back to Jamaica some 13 000 turtles per year between 1688 and 1730. Let us assume that the sex ratio and migration interval (time between years that females reproduce) were 1 : 1 and 2.5 years respectively, just as they are today (Bjorndal 1982). Thus, the proportion of the adult population (N_A) that are nesting females (N_{NF}) is given by

$$N_A = N_{NF}/0.5 \text{ (sex ratio)} \times 0.4 \text{ (migration interval)} = 5N_{NF}.$$

Let us further assume that hunters in 1688 captured only 1% of the nesting female turtles per year. This is an arbitrary but almost certainly conservative guess for the purpose of illustration, based on the impression from the early descriptions that the beaches all around Grand Cayman were literally covered by turtles, so that 13 000 would have been a very small fraction of the total. Moreover, female green turtles require 40–60 years to reach reproductive maturity (Bjorndal and Zug 1995), so that harvested females could not have been replaced for half the century-long duration of the fishery. Despite this, however, 13 000 reproductively mature females were harvested annually over 42 y, for a total (with the above correction) of more than 2.5 million on this basis alone. Based on the assumption of an initial catch rate of 1%, the estimated total adult population (N_A) based on the early hunting data is

$$\begin{aligned} N_A &= 5 \times 13\,000 \text{ (number harvested)}/0.01 \text{ (\% } N_{NF} \text{ caught)} \\ &= 6.5 \text{ million.} \end{aligned}$$

Further assume that there were five additional precolumbian green turtle rookeries roughly equal to Grand Cay-

Table 2. Historical accounts of the early great abundance of green turtles in the Caribbean

Andres Bernaldez, writing about Columbus' 2nd voyage in 1494	Southeastern Cuba	But in those twenty leagues, they saw very many more, for the sea was thick with them, and they were of the very largest, so numerous that it seemed that the ships would run aground on them and were as if bathing in them.
Ferdinand Columbus, writing about the 4th voyage in 1503[a]	Cayman Islands	… in sight of two very small and low islands, full of tortoises, as was all the sea about, insomuch that they looked like little rocks …
Edward Long (1774), writing of the late 1600s	West of the Cayman Islands	… it is affirmed, that vessels, which have lost their latitude in hazy weather, have steered entirely by the noise which these creatures make in swimming, to attain the Cayman isles.

[a] not seen, cited in Lewis 1940

man including Bermuda, Bahamas, Florida Keys, Costa Rica, and Isla Aves (now less than a mile long but historically much larger). Then the estimated total adult population for the entire precolumbian Caribbean is five to six times the Grand Cayman estimate, or about 33 to 39 million. This is about 15 to 20 times the abundance and biomass of large ungulates in the Serengeti today (Sinclair 1995a)!

Calculations based on carrying capacity

The following is based on Bjorndal's (1982) study of green turtle nutrition and life history. There is apparently no reliable compilation of the total area of seagrasses in the wider Caribbean. However, we can assume that roughly ten percent of the total shelf area, which is 660 000 km^2 excluding south Florida (Munroe 1983), is covered by seagrasses for a total of 66 000 km^2. This is probably conservative, since the mapped area of seagrasses for south Florida alone is 5500 km^2 (Ziemann 1982). Bjorndal (1982) calculated that the carrying capacity of closely cropped (2.5 cm) *Thalassia* is one 100 kg adult female per 72 m^2 per year, which rounding up to one turtle per 100 m^2, gives 10 000 adult females per km^2. Assume further that the carrying capacity is the same for males as for females. Then the estimated total adult population (N_A) for the entire Caribbean is

$$N_A = 10\,000 \times 66\,000 = 660 \text{ million},$$

which is about 20 times the estimate based on the old hunting data. Of course, sharks and other predators of principally juvenile turtles were also very much more abundant. However, Sinclair's (1995a) generalization about the predominantly "bottom up" regulation of large, migratory herbivores suggests that the abundance of large, migrating adult green turtles would have approached carrying capacity even in the face of intense predation on juveniles.

Differences in feeding between green turtles and other herbivores

One adult green turtle consumes roughly the same amount of turtlegrass as 500 large sea urchins like *Diadema antillarum* or *Tripneustes ventricosus*, which works out to a potential increase of about 5 sea urchins per m^2 of seagrass beds throughout the Caribbean (calculations based on data in Thayer et al. 1984). Much more significantly, however, there are profound differences in the ways turtles versus sea urchins and herbivorous fishes graze on turtlegrass, and how well they process what they eat, with important consequences for the structure and function of the entire turtlegrass ecosystem (Ogden 1980; Thayer et al. 1982, 1984; Ogden et al. 1983). Sea urchins and fishes tend to feed indiscriminantly on turtlegrass, or on the older parts of the blades, whereas green turtles crop blades close to their base. They also return repeatedly to the same discrete grazing plots which may be maintained for a year or more. Moreover, grazing sea urchins and fishes feed principally on the cell contents of seagrass blades, due to lack of appropriate enzymes or microflora to digest cell walls, whereas green turtles rely on microbial fermentation in the hindgut to digest cell walls as well as their contents (Thayer et al. 1984).

Repeated grazing of the same plots of turtlegrass by green turtles temporarily increases the nutritional quality of the blades for the turtles (Thayer et al. 1984). However, it also stresses the plants and eventually reduces turtlegrass productivity, when turtles presumably move on to feed elsewhere. Turtle grazing also results in a roughly 15-fold decrease in the supply of nitrogen to seagrass roots and rhizomes, due to greatly decreased accumulation of detritus and digestion of cell walls (Thayer et al. 1984). Nitrogen in turtle feces and urine is also released over a much wider area with resulting net export to adjacent coral reefs and other adjacent ecosystems.

These differences in the effects of grazing by small and large herbivores extend to dugongs and manatees that also possess hindgut microflora that digest cell walls (Thayer et al. 1984), and were also formerly very abundant throughout tropical seas (Dampier 1729, Sheppard et al. 1992). Similar ecosystem effects almost certainly transpired on coral reefs due to the virtual disappearance of large predators such as hawksbill turtles, groupers, and sharks that were also extremely abundant historically (Ibid, King 1982; Limpus 1995). For example, the hawksbill turtle, *Eretmochelys imbricata*, feeds almost exclusively on sponges which commonly display large, characteristic feeding scars in areas where the turtles are still common (Meylan 1985, 1988; van Dam and Diez, in press). Hawksbills can rip big sponges apart, and in the process facilitate predation by other sponge feeders that cannot penetrate the heavy armor of many sponges such as *Geodia*; unlike the much smaller angelfishes that also feed almost exclusively on reef sponges (Randall and Hartman 1968). Hawksbills feed today mostly on non-toxic astrophorid and hadromerid sponges, but this may not have been true in the past when, by analogy to green turtles (King 1982; Limpus 1995; this study), hawksbills almost certainly numbered in the tens of millions. Thus non-toxic sponges may have been proportionally rarer before hawksbills were intensely harvested.

Large herbivores and carnivores are ecologically extinct on Caribbean coral reefs and seagrass beds, where food chains are now dominated by small fishes and invertebrates (Hay 1984, 1991; Knowlton et al. 1990). Moreover, similar depletion of megavertebrates is almost complete throughout the Indo-Pacific (Sheppard et al. 1992; Limpus 1995). Small consumers cannot fully compensate for the loss of megavertebrates because they cannot capture, consume or process their prey in the same ways as larger species. Many small herbivores are also feeding specialists, and live commonly on prey that are chemically defended against the much larger consumers that have now disappeared (Hay 1991, in press). Thus coral reef ecosystems must function in fundamentally different ways than only a few centuries ago. Similarly great changes are going on right now in east Africa (Sinclair and Arcese 1995). They also occurred 10 000 years ago in neotropical forests when over 15 genera of large herbivores became extinct (Janzen and Martin 1982), before which forests were probably more of a mixture of open forest and grassland than the dense tropical forest we imagine as more natural (Janzen and Wilson 1983). As a result, neotropical herbivorous food chains are now dominated by insects and small mammals, except where free-ranging livestock may have partially redressed the balance. But there are no such livestock on coral reefs!

Effects from the land

Sedimentation caused by deforestation and poor agricultural practice, eutrophication, and oil pollution have greatly increased along Caribbean coasts during the past few decades (Rodriguez 1981; Lugo et al. 1981), causing widespread and dramatic decline of coral reefs and associated marine communities throughout the region (Cortés and Risk 1985; Rogers 1985, 1990; Tomascik and Sander 1985, 1987a, b; Bak 1987; Jackson et al. 1989; Guzmán et al. 1991). A common assumption in such studies is that most reefs were not seriously affected by runoff from the land before the observations began. This allows the investigator to designate "unaffected" reefs or corals that can be used as a baseline to measure the effects of a particular source of pollution, such as an oil spill.

New evidence, however, suggests that great ecological changes due to runoff began long before modern ecological analyses of Caribbean reefs. For example, *Montastrea "annularis"* and *Porites* spp. were the dominant reef building corals around Barbados in the 1960s and 1970s (Lewis 1960; Macintyre 1968; Stearn et al. 1977). These began to decline dramatically in the 1970s and 1980s, due primarily to runoff and eutrophication caused by exponential increase in populations of residents and tourists (Tomascik and Sander 1985, 1987a, b; Bell and Tomascik 1993). However, extensive deforestation began in Barbados in 1627 for sugar plantations, after which the vegetation of the island was completely destroyed three times by hurricanes (references in Lewis 1984); with untold increases in runoff of sediments from the land. Moreover, shallow reefs at that time were dominated by the elkhorn coral *Acropora palmata*, which persisted in huge tracts all along the southern and western coasts of the island until the 1920s (Nutting 1919; Lewis 1984; Bell and Tomascik 1993), and the same was true throughout the Late Pleistocene (Mesolella 1957; Jackson 1992). Degradation of these reefs and seagrass beds was clearly visible in aerial photographs taken in the 1950s (Lewsey 1978) when elkhorn corals were rare (Lewis 1960).

Similar decline in *Acropora palmata* and *A. cervicornis* occurred all along the coast of lower Central America in the 1970s and 1980s due to disease, deforestation, algal overgrowth due to the decline of *Diadema*, coral bleaching, oil spills, and other factors (Cortés and Risk 1985; Cortés 1993; Guzmán et al. 1991; Ogden and Ogden 1993). Live coral cover along the Caribbean coast of central Panama has declined by 50–90% in the past ten years (Guzmán and Jackson, unpublished data). However, there were hidden signs of danger long before, as measured by a steady decline of nearly 50% in the growth rate of the massive coral *Siderastrea siderea* over the past century (H. Guzmán, unpublished data). This is all the more remarkable because *S. siderea* generally prospers in turbid coastal environments unsuitable to most other Caribbean coral species. Guzmán's work obviously needs to be replicated elsewhere, but it strongly suggests that reef environments had begun to deteriorate at least 100 years before coral cover began to seriously decline. Isotopic ratios provide excellent proxy records of climate change, but simple growth rates and incidence of injuries are measures of coral fitness through time (Jackson 1982). As such, they may be among the best available measures of coral reef health (Dodge and Vaisnys 1977; Guzmán et al. 1994; Jackson 1995).

Fishing and people in Jamaica and San Blas

The green turtle fishery in the Cayman Islands crashed in the latter half of the eighteenth century, and was entirely gone by 1800 when the Cayman islanders moved on to do the same thing to the turtles of the Moskito Coast (Long 1774; Lewis 1940; Carr 1956; Neitschmann 1973, 1982; King 1982). Fishing on Jamaican reefs was inadequate to make up for the loss of turtles. By 1881 locally caught fish accounted for only 15% of the total consumed in Jamaica, with imported dried and preserved fish from the temperate zone making up the balance (Duerden 1901). This was probably true by the early 1800s, but there are not enough quantitative data. Moreover, extensive trials had clearly demonstrated that there was little prospect for improvement of local fisheries by trawling or longline fishing which are unsuitable for areas of coral reefs (Duerden 1901).

Table 3. Excerpts from Ernest F. Thompson's 1945 report *The fisheries of Jamaica*

Locally caught fish represents less than 15% of the protein fish food consumed in Jamaica… There is little prospect of any large increase in this local catch. In fact the probability is that the local areas are already overfished (p. 5)

…the greatest need for Jamaican fishermen is more in the nature of *welfare* than *development* (p. 7, Thompson's italics).

In a great many countries, fishing has proved a very valuable asset as a tourist attraction. Development of the tourist potential would require that the present usages of some sections of the community must be controlled and restricted (p. 7).

The fishing situation in Jamaica can be very briefly summarised. There are too many men trying to catch too few fish. As there seems little prospect of increasing the number of fish available, the only thing to do, if a decent living standard is to be attained, is to reduce the number of fishermen. Thus the chief problem for Jamaican fishermen is to organize them, stabilise their economy and assist about four-fifths of them to drift back to agriculture from whence they came (p. 83)

Despite these realities, Duerden's (1901) official report was surprisingly optimistic and, in a still all too familiar tone, called for more "scientific investigations and encouragement" to improve the marine resources of the Caribbean region. Half a century later the fisheries of Jamaica had not improved and were clearly unimprovable (Thompson 1945, Table 3). Thompson was far ahead of his time in recognizing the need for greatly reducing the numbers of fishermen, helping them to find alternative livelihoods, and focusing instead on the economic opportunities of fishing for tourism. But his report was apparently ignored and overfishing continued unabated.

By far the most extensive coral reef fisheries research project in the Caribbean was carried out from 1969–1973 all around Jamaica and in the Pedro Cays (Munroe 1983). Overfishing was accepted as an established fact, and it was "shown that for most areas of the Jamaican Shelf, the fishing intensity is sufficient to ensure that extremely few fishes survive for more than a year after recruitment, and the proportion of fishes which survive to spawn must be extremely small." The report goes on to recommend a mesh size for fish traps of 6.60 cm maximum aperture that would provide a maximum yield of barely reproductive juveniles with a maximum fishing intensity of 1.5 canoes/km^2, without any consideration of the possible consequences for the health of the entire coral reef ecosystem. Of course, it is easy to be unfairly critical with the hindsight of the *Diadema* debacle and the collapse of Jamaican reefs (Hughes 1994), although even in the 1970s the consequences of not having any pretty reef fishes larger than sardines on lost tourist revenues were clear.

The situation in Jamaica is a story repeated everywhere throughout the Caribbean, including the traditional fisheries of indigenous peoples commonly romanticized for exhibiting wise restraint from overharvesting not observed by others. The Comarca Kuna Yala, for example, extends some 250 km along the eastern Caribbean coast of Panamá and contains extensive coral reefs, seagrass beds and mangroves (Porter 1972; Glynn 1973; Clifton et al. 1996). The population of Kuna people within the Comarca increased from less than 9000 in 1904 to less than 24 000 in 1970, when marine biological research intensified in the Comarca, and had climbed to 41 000 in 1989 (Francisco Herrera, personal communication). Kuna artesanal fishing has always been a small-scale enterprise, and the Comarca is closely guarded against outside exploitation. Nevertheless, reefs were severely overfished by the 1970s when large fishes were uncommon and branching acroporid and poritid corals had been mined extensively for landfill. Thus 250 km of coast were already insufficient for 24 000 Kuna, ten years before lobster fishing for external markets reduced lobster populations to critically low levels within only ten years (Chapin 1995; Ventocilla et al. 1995).

So let us now return to Jamaica to consider the history of Jamaican fisheries in light of human growth, much as Hughes (1994) did, but beginning 350 years before (Fig. 1). Depopulation by the Spaniards in the sixteenth century left the island almost uninhabited until the British invasion in 1655, when marine life may well have been at its apogee of the past 10 000 years. In 1688, when Sloane was in Jamaica, there were still only 40 000 Jamaicans and *Diadema* was the most abundant sea urchin on coral reefs. In 1793, there were 300 000 Jamaicans and breadfruit had just been introduced following extensive research by the Royal Society and the mutiny on the Bounty, to help stave off the starvation of Jamaican slaves. In 1881, there were 700 000 Jamaicans and local fish accounted for only 15% of the fish consumed. In 1945 there were 1 350 000 Jamaicans, and the 5 500 000 kg of fish caught locally was still only 15% of that consumed. In 1962 there were 1 700 000 Jamaicans and the fish harvest peaked at 11 000 000 kg. This was also when Goreau (1959) published his first famous paper about Jamaican coral reefs and the modern ecological perspective was born. By 1968, when I began my own research in Jamaica, there were 1 900 000 Jamaicans, and the harvest of minnow-sized fishes from Jamaican coastal waters was back down to 5 500 000 kg. Munroe's fisheries research project was only just beginning.

It is obvious that any direct relationship between human population growth and fishing in Jamaica ended in the eighteenth century when human populations were only 10% of the present. Throughout this time, Jamaicans kept on eating fish courtesy of the now collapsed Grand Banks fisheries, and the same was true throughout the Caribbean. Thus, the causes of the present ecocatastrophe are deep and historical, not just the almost "current events" that have passed as history before.

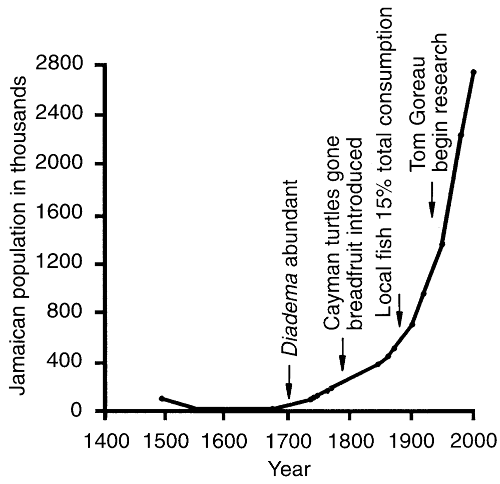

Fig. 1. Jamaican human population growth since Columbus and the depletion of local fisheries resources. Fisheries became inadequate some time in the mid nineteenth century when the local population was about 15% of that today. Value for 1492 arbitraily set at 100 000 which is almost certainly much too low (Sauer 1966). Sources for population size: 1658–1768 (Long 1774), 1844–1871 (Gardner 1909). 1901 (Duerden 1901), 1920–2000 (Hughes 1994), 1980 (National Geographic Society 1981)

Concluding remarks

I hope this brief discussion will put to rest two dangerous stupidities, at least within the scientific community. The first is the placebo of sustainable use for everyone and the second is the fallacy of a "pristine" coral reef. Forty thousand Kuna are too many fish eaters for 250 km of coastline (Ventocilla et al. 1995), just as a few hundred thousand Jamaicans were too many fish eaters for Jamaica. The same is true for reefs everywhere else, and not just the developing world (Wilkinson 1992). Even the Great Barrier Reef cannot be used sustainably at present levels, despite the best protection in the world (Bradbury et al. 1992), and virtually all other reefs are less sustainable.

There is nothing new about all this, as described so eloquently in Peter Matthiessen's (1975, 1986) eulogies to the turtle fishermen of Grand Cayman or the striped bass fishermen of the South Fork of Long Island. However, societies desperately need to set goals and priorities that reflect the realities of our lost and dying coral reef resources, and then follow them. For example, coral reef fishes may still provide sustainable luxury food and pleasure for tourists, just as Thompson (1945) proposed, and captive breeding of aquarium fishes is almost certainly a viable enterprise. Deciding on such options to the exclusion of others, and then enforcing them, involves extremely difficult economic, political and social issues beyond the bounds of ecological science. But some such decisions are long overdue, and no more research is required to get started, because the facts about "sustainability" have been clear for more than one hundred years.

Getting things straight is all the more important because, as far as we can tell, almost all the reef species are still there almost everywhere. The Caribbean monk seal is extinct and manatees are nearly gone, but even green turtles still number in the tens of thousands in the Caribbean. This means that it is still possible, at least in principle, to save Caribbean coral reefs; although continued human population growth makes this more and more unlikely. For example, all the species of corals encountered previously on Panamanian Caribbean reefs are still there, even on some of the most devastated reefs, despite huge decreases in coral abundance (Guzmán and Jackson, unpublished data). Thus the situation is like the East African savannas where large animals are more and more restricted and diminished, but the great majority of species alive during the Pleistocene still survive (Sinclair and Arcese 1995).

For this reason, and by analogy to the Serengeti, really large marine protected areas on the scale of hundreds to thousands of square kilometers are vital to any hope of conserving Caribbean coral reefs and coral reef species. Can we restore damaged reefs? Can we control inputs from the land and harvesting? Can we manage what we do decide to invest in and use? These are the questions that really do merit more research on a monumental scale (NRC 1995). The people trying to answer them are the heros of our discipline and the only chance we have got.

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