REVIEW

Historical Overfishing and the Recent Collapse of Coastal Ecosystems

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Ecological extinction caused by overfishing precedes all other pervasive human disturbance to coastal ecosystems, including pollution, degradation of water quality, and anthropogenic climate change. Historical abundances of large consumer species were fantastically large in comparison with recent observations. Paleoecological, archaeological, and historical data show that time lags of decades to centuries occurred between the onset of overfishing and consequent changes in ecological communities, because unfished species of similar trophic level assumed the ecological roles of overfished species until they too were overfished or died of epidemic diseases related to overcrowding. Retrospective data not only help to clarify underlying causes and rates of ecological change, but they also demonstrate achievable goals for restoration and management of coastal ecosystems that could not even be contemplated based on the limited perspective of recent observations alone.

Few modern ecological studies take into account the former natural abundances of large marine vertebrates. There are dozens of places in the Caribbean named after large sea turtles whose adult populations now number in the tens of thousands rather than the tens of millions of a few centuries ago (*1*, *2*). Whales, manatees, dugongs, sea cows, monk seals, crocodiles, codfish, jewfish, swordfish, sharks, and rays are other large marine vertebrates that are now functionally or entirely extinct in most coastal ecosystems (*3*–*10*). Place names for oysters, pearls, and conches conjure up other ecological ghosts of marine invertebrates that were once so abundant as to pose hazards to navigation (*11*), but are witnessed now only by massive garbage heaps of empty shells.

Such ghosts represent a far more profound problem for ecological understanding and management than currently realized. Evidence from retrospective records strongly suggests that major structural and functional changes due to overfishing (*12*) occurred worldwide in coastal marine ecosystems over many centuries. Severe overfishing drives species to ecological extinction because overfished populations no longer interact significantly with other species in the community (*5*). Overfishing and ecological extinction predate and precondition modern ecological investigations and the collapse of marine ecosystems in recent times, raising the possibility that many more marine ecosystems may be vulnerable to collapse in the near future.

Importance of Historical Data

Most ecological research is based on local field studies lasting only a few years and conducted sometime after the 1950s without longer term historical perspective (*1*, *8*, *13*). Such observations fail to encompass the life-spans of many ecologically important species (*13*, *14*) and critically important environmental disturbances such as extreme cyclones or ENSO (El Niño–Southern Oscillation) events (*8*), as well as longer term cycles or shifts in oceanographic regimes and productivity (*15*–*17*). To help address this problem, we describe ecosystem structure predating modern ecological studies using well-dated time series based on biological (*18*, *19*), biogeochemical (*20*, *21*), physical (*22*), and historical (*23*) proxies that are informative over a variety of spatial scales and biogeographic realms (*24*). Although proxies vary in precision and clarity of the signals they measure, the use of multiple proxies that give the same ecological signal greatly increases confidence in results. Precision in age dating varies from centuries to a single year, season, or event in the exceptional case of varved sediments, ice cores, and written historical records (*25*). Precision decreases with the amount of biological or physical disturbance to the sediment analyzed (*26*).

We exploited data from many disciplines that span the period over which anthropogenic changes may have occurred. Because our hypothesis is that humans have been disturbing marine ecosystems since they first learned how to fish, our time periods need to begin well before the human occupation or European colonization of a coastal region. Broadly, our data fall into four categories and time periods:

1) Paleoecological records from marine sediments from about 125,000 years ago to the present, coinciding with the rise of modern *Homo sapiens*.

2) Archaeological records from human coastal settlements occupied after about 10,000 years before the present (yr B.P.) when worldwide sea level approached present levels. These document human exploitation of coastal resources for food and materials by past populations that range from small-scale aboriginal societies to towns, cities, and empires.

3) Historical records from documents, journals, and charts from the 15th century to the present that document the period from the first European trade-based colonial expansion and exploitation in the Americas and the South Pacific (*23*).

4) Ecological records from the scientific literature over the past century to the present covering the period of globalized exploitation of marine resources. These also help to calibrate the older records.

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Time Periods, Geography, and Analysis

We recognize three different but overlapping periods of human impact on marine ecosystems: aboriginal, colonial, and global. Aboriginal use refers to subsistence exploitation of near-shore, coastal ecosystems by human cultures with relatively simple watercraft and extractive technologies that varied widely in magnitude and geographic extent. Colonial use comprises systematic exploitation and depletion of coastal and shelf seas by foreign mercantile powers incorporating distant resources into a developing market economy. Global use involves more intense and geographically pervasive exploitation of coastal, shelf, and oceanic fisheries integrated into global patterns of resource consumption, with more frequent exhaustion and substitution of fisheries. In Africa, Europe, and Asia, these cultural stages are strongly confounded in time and space, so that their differential significance is difficult to establish. However, in the Americas, New Zealand, and Australia the different stages are well separated in time, and the aboriginal and colonial periods began at different times in the different regions. Thus, we can distinguish between cultural stages, as well as between human impacts and natural changes due to changing climate.

The addition of a deep historical dimension to analyze and interpret ecological problems requires that we sacrifice some of the apparent precision and analytical elegance prized by ecologists (*1*, *13*, *14*). Paleoecological, archaeological, and historical data were collected for many purposes, vary widely in methods of collection and quality, and are less amenable to many types of statistical analysis than well-controlled experiments. But none of these problems outweighs the benefits of a historical approach. Clearly, we cannot generate realistic null hypotheses about the composition and dynamics of ecosystems from our understanding of the present alone, since all ecosystems have almost certainly changed due to both human and natural environmental factors (*8*, *16*, *27*, *28*). Here, we briefly review long-term human impacts in several key marine ecosystems. These reconstructions provide insight into the nature and extent of degraded ecosystems that point to new strategies for mitigation and restoration that are unlikely to emerge from modern monitoring programs.

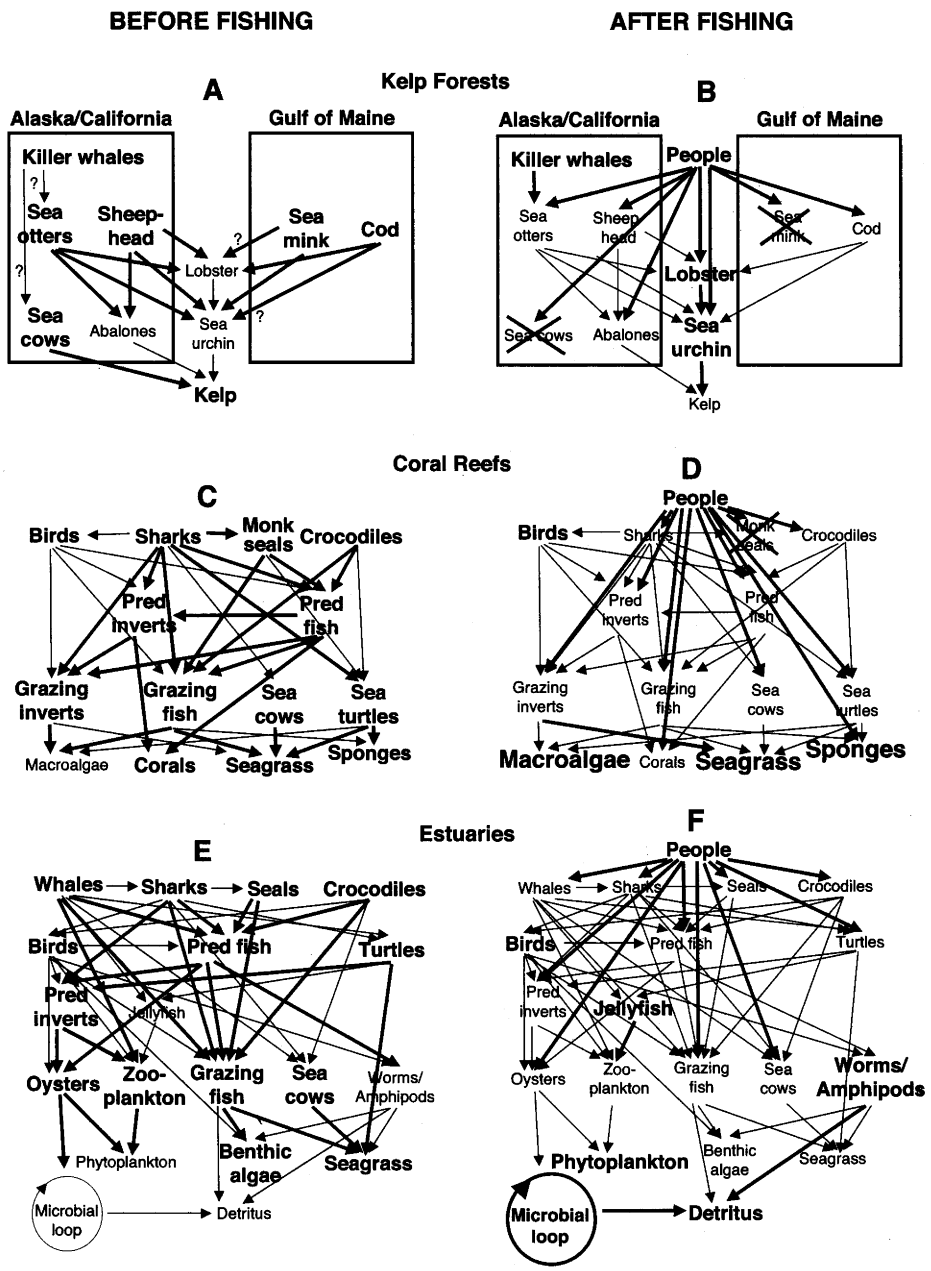

Fig. 1. Simplified coastal food webs showing changes in some of the important top-down interactions due to overfishing; before (left side) and after (right side) fishing. (**A** and **B**) Kelp forests for Alaska and southern California (left box), and Gulf of Maine (right box). (**C** and **D**) Tropical coral reefs and seagrass meadows. (**E** and **F**) Temperate estuaries. The representation of food webs after fishing is necessarily more arbitrary than those before fishing because of rapidly changing recent events. For example, sea urchins are once again rare in the Gulf of Maine, as they were before the overfishing of cod, due to the recent fishing of sea urchins that has also permitted the recovery of kelp. Bold font represents abundant; normal font represents rare; "crossed-out" represents extinct. Thick arrows represent strong interactions; thin arrows represent weak interactions.

Kelp Forests

Kelp forests characterize shallow, rocky habitats from warm temperate to subarctic regions worldwide and provide complex environments for many commercially important fishes and invertebrates (*29*). Northern Hemisphere kelp forests have experienced widespread reductions in the number of trophic levels and deforestation due to population explosions of herbivores following the removal of apex predators by fishing (Fig. 1, A and B). Phase shifts between forested and deforested states (the latter known as "sea urchin barrens") result from intense grazing due to increased abundance and altered foraging patterns of sea urchins made possible in turn by human removal of their predators and competitors (*7*, *8*, *30*–*32*).

The kelp forest ecosystem of the Northern Pacific arose during the last 20 million years with the evolution of kelps, strongylocentrotid sea urchins, sea otters, and the extinct Steller's sea cow (*6*). Sea cows were widely distributed across the northern Pacific Rim through the Late Pleistocene. They may have been eliminated from most of their range by aboriginal hunting at the end of the Pleistocene and in the early Holocene, because they survived thousands of years longer in the western Aleutian Islands that were not peopled until about 4000 yr B.P. (*6*). By the time of European contact in 1741, sea cows per-

sisted only in the Commander Islands, the only islands of the Aleutians unoccupied by aboriginal people. European fur traders killed the last sea cow 27 years later in 1768. We have no idea to what extent abundant sea cows grazed kelp forests, although their apparent inability to dive deeply probably limited their grazing to the surface canopy of kelps and to seaweeds lining the shore (*6*).

Northern Pacific kelp forests presumably flourished before human settlement because predation by sea otters on sea urchins prevented the urchins from overgrazing kelp (*30*). Aboriginal Aleuts greatly diminished sea otters beginning around 2500 yr B.P., with a concomitant increase in the size of sea urchins (*31*). Fur traders subsequently hunted otters to the brink of extinction in the 1800s with the attendant collapse of kelp forests grazed away by sea urchins released from sea otter predation. Legal protection of sea otters in the 20th century partially reversed this scenario. However, kelp forests are again being depleted in areas of Alaska because of increased predation on sea otters by killer whales (*33*). The whales shifted their diet to sea otters from seals and sea lions, which are in drastic decline.

A similar sequence of events occurred in kelp forests of the Gulf of Maine (*7*, *34*). Sea otters were never present, but Atlantic cod and other large ground fish are voracious predators of sea urchins. These fishes kept sea urchin populations small enough to allow persistence of kelp forests despite intensive aboriginal and early European hook-and-line fishing for at least 5000 years. New mechanized fishing technology in the 1920s set off a rapid decline in numbers and body size of coastal cod in the Gulf of Maine (*7*) (Fig. 2A and Table 1) that has extended offshore to Georges Bank (*35*). Formerly dominant predatory fish are now ecologically extinct and have been partially replaced by smaller and commercially less important species. Lobsters, crabs, and sea urchins rose in abundance accordingly (*7*). Kelp forests disappeared with the rise in sea urchins due to removal of predatory fish, and then reappeared when sea urchins were in turn reduced to low abundance by fishing.

The more diverse food web of southern California kelp forests historically included spiny lobsters and large sheephead labrid fish in addition to sea otters as predators of sea urchins, as well as numerous species of abalone that compete with sea urchins for kelps (Fig. 1, A and B) (*36*). Aboriginal exploitation began about 10,000 yr B.P. and may have had local effects on kelp communities (*37*). The fur trade effectively eliminated sea otters by the early 1800s (*38*), but kelp forests did not begin to disappear on a large scale until the intense exploitation and ecological extinction of sheephead, spiny lobsters, and abalone starting in the 1950s (*8*, *36*) (Table 1 and Fig. 1, A and B). Subsequent fishing of the largest sea urchin species in the 1970s and 1980s resulted in the return of well-developed kelp forests in many areas that, as in the Gulf of Maine, effectively lack trophic levels higher than that of primary producers (*36*, *39*).

Coral Reefs

Coral reefs are the most structurally complex and taxonomically diverse marine ecosystems, providing habitat for tens of thousands of associated fishes and invertebrates (*40*). Aboriginal fishing in coral reef environments began at least 35,000 to 40,000 years ago in the western Pacific (*41*) but appears to have had limited ecological impact. Recently, coral reefs have experienced dramatic phase shifts in dominant species due to intensified human disturbance beginning centuries ago (*1*) (Fig. 1, C and D). The effects are most pronounced in the Caribbean (*42*) but are also apparent on the Great Barrier Reef in Australia despite extensive protection over the past three decades (*43*).

Large species of branching *Acropora* corals dominated shallow reefs in the tropical western Atlantic for at least half a million years (*44*–*46*) until the 1980s when they declined dramatically (*42*, *47*) (Fig. 2B and Table 1). Patterns of community membership and dominance of coral species were also highly predictable (*44*), so that there is a clear baseline of pristine coral community composition before human impact.

Western Atlantic reef corals suffered sudden, catastrophic mortality in the 1980s due to overgrowth by macroalgae that exploded in abundance after mass mortality of the superabundant sea urchin *Diadema antillarum* that was the last remaining grazer of macroalgae (*42*, *47*). Early fisheries reports suggest that large herbivorous fishes were already rare before the 20th century (*48*). However, macroalgae were held in check until the last major herbivore, *Diadema*, was lost from the system through disease (*42*, *47*).

Corals on the Great Barrier Reef have experienced recurrent mass mortality since 1960 due to spectacular outbreaks of the crown-of-thorns starfish *Acanthaster planci* that feeds on coral (*49*). The causes of outbreaks are controversial, but they are almost certainly new phenomena. There are no early records of *Acanthaster* in undisturbed fossil deposits, in aboriginal folklore, or in accounts of European explorers and fishers. Now, in recent decades, the frequency and intensity of outbreaks have exceeded the capability of longer lived species to recover as outbreaks have become more chronic than episodic (*50*).

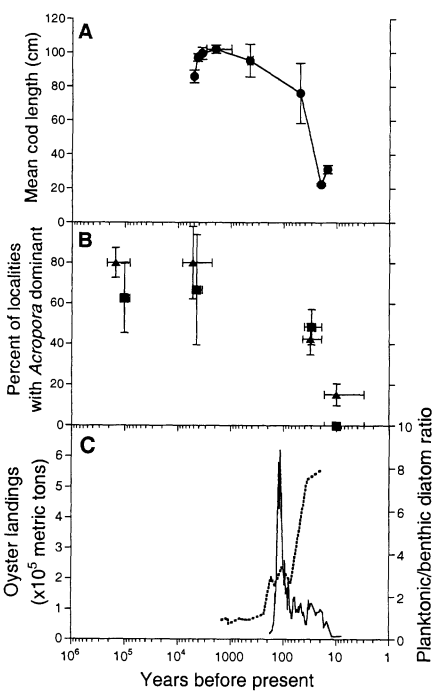

Fig. 2. Retrospective data showing baselines before ecosystem collapse. (**A**) Time series of mean body length of Atlantic cod from kelp forests in the coastal Gulf of Maine. The earlier five data points are derived from archaeological records, whereas the last three points are from fisheries data (*113*). Vertical bars represent the standard error. Horizontal bars represent the time range of data for a single interval of observations. (**B**) Paleoecological and ecological data showing the percentage of Caribbean localities with *Acropora palmata* (▲) or *A. cervicornis* (■) as the dominant shallow-water coral in the Late Pleistocene, Holocene, before 1983, and after 1983 (*114*). Percentages of localities are significantly different over the four time periods for *A. palmata* (χ^2 = 34.0, P <0.0001, df = 3) and *A. cervicornis* (χ^2 = 22.4, P <0.0001, df = 3). Vertical and horizontal bars are as in (A). (**C**) Paleoecological and fisheries data from Chesapeake Bay showing the ratio in abundance of planktonic to benthic diatoms (dotted line) (*77*) and landings of the oyster *Crassostrea virginica* (solid line) (*80*). The planktonic to benthic diatom ratio is a proxy for eutrophication that shows the relative amount of planktonic to benthic primary production (*77*). For over 1200 years this ratio remained fairly constant at about 1:1, but then increased threefold coincidentally with increased runoff of sediments and nutrients due to European agriculture after 1750. The ratio remained at about 3:1 between 1830 and 1930, after which it increased dramatically to about 8:1. Oyster landings show an initial increase in the early 19th century, peak in 1884, and subsequent collapse as deep channel reefs were destroyed by mechanical dredging (*80*). These data strongly imply that oysters were able to limit the potential for eutrophication induced by increased inputs of nutrients between 1750 and 1930 until oyster populations collapsed as a result of overfishing.

Table 1. Retrospective records from coastal ecosystems that offer baselines that contrast with recent observations. Data source: P, paleoecologial; A, archaeological; H, historical; F, fisheries; E, ecological. Inferred causes: 1, fishing; 2, mechanical habitat destruction by fishing; 3, inputs. Abbreviations: BSi, biologically bound silica; DOP, degree of pyritization of iron; dec., decrease; inc., increase. References after *115* are located on *Science* Online (www.sciencemag.org/cgi/content/full/293/5530/629/DC1).

Parameter of interest	Location	Data source	Proxy	Time of baseline (yr B.P.)	Baseline observation or estimate	Recent observation or estimate	Trend	Inferred cause	Ref.
Kelp forests									
Sea Otter	Pacific Ocean	H, E	Area estimates	260	>100,000 individuals	30,000 individuals	>3.3-fold dec.	1	*116*
Stellar's sea cow	Alaska	H	Herd size	259	<5,000 sea cows	0	Extinction	1	*117*
Atlantic cod	Gulf of Maine	A	Cod vertebrae	3550	Mean body length of 1.0 m	Mean body length of 0.3 m	3-fold dec.	1	*113*
White abalone	California	E	Number per area	30	>2,000 per ha	1.0 ± 0.4 per ha	>2,000-fold dec.	1	*118*
Coral reefs									
Coral	Caribbean Sea	P, E	% sites with *A. palmata* dominant	125,000	80% of Pleistocene sites	15% of post-1982 sites	5.3-fold dec.	1	*114*
Coral	Caribbean Sea	P, E	% sites with *A. cervicornis* dominant	125,000	63% of Pleistocene sites	0% of post-1982 sites	100% loss	1	*114*
Coral	Bahamas	P, E	Standardized abundance of *A. cervicornis*	125,000	12	1	12-fold dec.	1	*119*
Coral	Belize	P	Relative abundance	3,130	*A. cervicornis* dominant	*A. cervicornis* absent	100% loss	1	*45*
Coral	Netherlands Antilles	E	Coral cover at 10 m	27	54% coral cover	31% coral cover	1.7-fold dec.	1	*120*
Coral	Jamaica	E	Coral cover at 10 m	23	73% coral cover	4% coral cover	18-fold dec.	1	*42*
Monk seal	Caribbean Sea	H	Historical reports	>300	Abundant	0	Extinction	1	*4, 68*
Coral	Moreton Bay	P, E	*Acropora* dominance in fossil reefs	8,000	Dominated reefs throughout Bay	Only one small *Acropora* reef left	Decrease	3	*121*
Tropical and subtropical seagrass beds									
Green turtle	Caribbean Sea	E	Biomass estimates	>300	>16.1 × 10^6 50-kg turtles	>1.1 × 10^6 50-kg turtles	15-fold dec.	1	*2, 122*
Green turtle	Caribbean Sea	H	Hunting, biomass estimates	>300	>3.3 × 10^7 adult turtles	>1.1 × 10^6 50-kg turtles	30-fold dec.	1	*1, 122*
Seagrass beds	Tampa Bay	H	Area	121	30,970 ha	10,759 ha	3-fold dec.	1, 2, 3	*123, 124*
Dugong	Eastern Australia	H	Herd size	>100	>1.0 × 10^6 estimated dugongs	14,000 estimated dugongs	>74-fold dec.	1	*125, 126*
Dugong	Moreton Bay	H	Herd size	107	>104,000 estimated dugongs	500 estimated dugongs	>208-fold dec.	1	*125, 127*
Oysters and eutrophication in estuaries									
Inputs	Chesapeake Bay	P	Sedimentation rate	1,900	0.04 cm $year^{-1}$	0.2 cm $year^{-1}$	5-fold inc.	3	*77*
Eutrophication	Chesapeake Bay	P	Total organic carbon	1,900	0.26 mg cm^{-2} $year^{-1}$	2.3 mg cm^{-2} $year^{-1}$	9-fold inc.	2, 3	*77*
Eutrophication	Chesapeake Bay	P	Centric/pennate diatom ratio	1,450	1:1 ratio	8:1 ratio	8-fold inc.	2, 3	*77*
Eutrophication	Chesapeake Bay	P	Dinoflagellate cysts (*Spiniferites* spp.)	>300	50% relative abundance	80% relative abundance	1.6-fold inc.	2, 3	*128*

Table 1. (Continued)

Parameter of interest	Location	Data source	Proxy	Time of baseline (yr B.P.)	Baseline observation or estimate	Recent observation or estimate	Trend	Inferred cause	Ref.
Seagrass beds	Fleets Bay, CB	H	Area	63	273 ha	16 ha	17-fold dec.	1, 2, 3	*78*
Oyster reefs	Chesapeake Bay	F	Oyster landings	116	6.2×10^5 metric tons $year^{-1}$*	0.12×10^5 metric tons $year^{-1}$	52-fold dec.	2	*80*
Oyster reefs	Tangier Sound, CB	F	Area	122	44.6 km^2	0	100% loss	2	*129*
Anoxia	Cheapeake Bay	P	Degree of pyritization	1,900	0.32 DOP	0.51 DOP	2-fold inc.	2, 3	*77*
Seagrass beds	Botany Bay	H	Area of *Posidonia* beds	58	445 ha	188 ha	2.4-fold dec.	1, 2, 3	*130*
Eutrophication	Baltic Sea	P	Planktic diatom relative abundance	250	25% of total diatom abundance	80% of total diatom abundance	3-fold inc.	3	*131*
Eutrophication	Baltic Sea	P	Total organic carbon accumulation rate	138	3.2 $gC\ m^{-2}\ year^{-1}$	70 $g\ C\ m^{-2}\ year^{-1}$	22-fold inc.	3	*132*
Anoxia	Baltic Sea	P	Laminated sediments	100	5% of cores laminated	90% of cores laminated	18-fold inc.	3	*85*
Offshore benthic communities									
Oyster reefs	Foveaux Strait, NZ	F	Oyster landings	34	127×10^6 oysters/year*	15×10^6 oysters $year^{-1}$	8-fold dec.	2	*93*
Oyster reefs	Foveaux Strait, NZ	F	Reef by-catch per station	38	1 in 4 stations had reef by-catch	1 in 7 stations had reef by-catch	2-fold dec.	2	*93*
Eutrophication	Gulf of Mexico	P	Biologically bound silica	295	0.29% BSi	1.00% BSi	3.4-fold inc.	3	*106*
Eutrophication	Gulf of Mexico	P	Total organic carbon accumulation rate	100	2.4 mg C $cm^{-2}\ year^{-1}$	7.8 mg C $cm^{-2}\ year^{-1}$	3.3-fold inc.	3	*133*
Hypoxia	Gulf of Mexico	P	Benthic foraminifera	295	71 *Ammonia–Elphidium* Index	85 *Ammonia–Elphidium* Index	1.2-fold inc.	3	*134*
Eutrophication	Adriatic Sea	P	Eutrophic benthic foraminifera *Nonionella turgida*	170	6% relative abundance	38% relative abundance	6-fold inc.	3	*135*
Eutrophication	Adriatic Sea	P	Coccolithophorids	286	100 cells/g of sediment	1.6×10^6 cells/g of sediment	15,700-fold inc.	3	*136*

*Baseline taken from peak in landings.

One possible explanation for *Acanthaster* outbreaks is that overfishing of species that prevy upon larval or juvenile stages of crown-of-thorns starfish is responsible for massive recruitment of the starfish (*51*). The highly cryptic, predator-avoiding behavior of juvenile starfish, their formidable antipredator defenses as subadults and adults, and the reduction of some generalized predatory fishes on the Great Barrier Reef all point to such a "top-down" explanation. Commercial and recreational fishing, as well as indirect effects of intensive trawling for prawns, are likely explanations for decreased abundance of predators of crown-of-thorns starfish (*52*). Massive recruitment of starfish may also be due to "bottom-up" increases in productivity due to increased runoff of nutrients from the land (*53*). In either case, the explanation is almost certainly historical and anthropogenic, and cannot be resolved by recent observations alone.

Expeditions occurred annually to northern Australia from the Malay Archipelago throughout the 18th and 19th centuries to harvest an estimated 6 million sea cucumbers each season (*54*). After European colonization, industrial-scale fishing developed along the Great Barrier Reef and subtropical east Australian coast in the early to mid–19th century (*55*). Whales, dugongs, turtles, pearl oysters, and *Trochus* shell were each heavily exploited only to rapidly collapse, and all have failed to regain more than a small fraction of their former abundance (*55–57*). Fishing of pelagic and reef fishes, sharks, and prawns has continued to the present, although catch per unit effort has declined greatly (*58*).

Tropical and Subtropical Seagrass Beds

Seagrass beds cover vast areas of tropical and subtropical bays, lagoons, and continental shelves (*59*). Seagrasses provide forage and habitat for formerly enormous numbers of large sirenians (dugong and manatee) and sea turtles, as well as diverse assemblages of fishes, sharks, rays, and invertebrates, including many commercially important species (*59–62*) (Fig. 1, C and D). Like coral reefs, seagrass beds seemed to be highly resilient to human disturbance until recent decades when mass mortality of seagrasses became common and widespread (*63–65*). Examples include the die-off of turtlegrass in Florida Bay and the Gulf of Mexico in the 1980s (*65*) and the near disappearance of subtidal seagrasses in the offshore half of Moreton Bay near Brisbane, Australia, over the past 20 to 30 years (*63*, *64*). Proximate causes of these losses include recent increases in sedimentation, turbidity, or disease (*63–65*). However, extirpation of large herbivorous vertebrates beginning centuries ago had already profoundly altered the ecology of

seagrass beds in ways that increased their vulnerability to recent events.

Vast populations of very large green turtles were eliminated from the Americas before the 19th century (*1*, *2*) (Table 1). Formerly great populations of green turtles in Moreton Bay, Australia, also were greatly reduced by the early 20th century (*66*). Moreover, there are no estimates of abundances of turtles in Australia at the dawn of European exploitation, so that reported reductions must be only a small fraction of the total numbers lost. All turtle species continue to decline at unsustainable rates along the Great Barrier Reef today (*67*).

Abundant green turtles closely crop turtlegrass and greatly reduce the flux of organic matter and nutrients to sediments (*59–62*, *68*). In the near absence of green turtles today, turtlegrass beds grow longer blades that baffle currents, shade the bottom, start to decompose in situ, and provide suitable substrate for colonization by the slime molds that cause turtlegrass wasting disease (*65*). Deposition within the beds of vastly more plant detritus also fuels microbial populations, increases the oxygen demand of sediments, and promotes hypoxia (*65*). Thus, all the factors that have been linked with recent die-off of turtlegrass beds in Florida Bay (*65*), except for changes in temperature and salinity, can be attributed to the ecological extinction of green turtles (*27*).

European colonists did not exploit tropical American manatees as systematically as they exploited green turtles, so the data related to fisheries are poor. We know, however, that manatees were extensively fished by aboriginal people and by early colonists (*68*). In Australia, aboriginal people also harvested dugongs extensively long before European colonization (*3*), yet the numbers reported by early colonists were vast. Three- or four-mile-long herds comprising tens of thousands of large individuals were observed in Wide Bay in about 1870 (*69*) and in Moreton Bay as recently as 1893 (*70*). Widespread colonial exploitation of dugongs for their flesh and oil along the southern Queensland coast resulted in the crash of the dugong fishery by the beginning of the 20th century (*3*) (Table 1). Ironically, scientists recently reported the "discovery of a large population" of dugongs in Moreton Bay—a mere 300 individuals (*71*). Further north, numbers of dugongs in the vast southern half of the Great Barrier Reef had dwindled to fewer than 4000 when they were first accurately counted in 1986–87, with a further 50 to 80% decline in recent years (*72*). These increasingly fragmented populations represent the last remnants of the vast herds of the early 19th century and before.

The ecological implications of these reductions are at least as impressive as those for green turtles. Moderate sized herds of dugongs remove up to 96% of above-ground biomass and 71% of below-ground biomass of seagrasses (*73*). Their grazing rips up large areas of seagrass beds, providing space for colonization by competitively inferior species of seagrasses. Dugong grazing also produces massive amounts of floating debris and dung that are exported to adjacent ecosystems. The decline in seagrasses in Moreton Bay is certainly due in large part to the dramatic decline in water quality due to eutrophication and runoff of sediment (*63*, *64*). Nevertheless, as noted for green turtles and turtlegrass in Florida Bay, the cessation of systematic plowing of the bay floor by once abundant dugongs must also have been a major factor.

Oysters and Eutrophication in Estuaries

Temperate estuaries worldwide are undergoing profound changes in oceanography and ecology due to human exploitation and pollution, rendering them the most degraded of marine ecosystems (*74–76*) (Fig. 1, E and F). The litany of changes includes increased sedimentation and turbidity (*77*); enhanced episodes of hypoxia or anoxia (*74*, *75*, *77*); loss of seagrasses (*78*) and dominant suspension feeders (*79*), with a general loss of oyster reef habitat (*80*); shifts from ecosystems once dominated by benthic primary production to those dominated by planktonic primary production (*77*); eutrophication (*74–76*) and enhanced microbial production (*81*); and higher frequency and duration of nuisance algal and toxic dinoflagellate blooms (*82*, *83*), outbreaks of jellyfish (*79*), and fish kills (*83*). Most explanations for these phenomena emphasize "bottom-up" increases in nutrients like nitrogen and phosphorus as causes of phytoplankton blooms and eutrophication (*74–76*), an interpretation consistent with the role of estuaries as the focal point and sewer for many land-based, human activities. Nevertheless, long-term records demonstrate that reduced "top-down" control resulting from losses in benthic suspension feeders predated eutrophication.

The oldest and longest records come from cores in sediments from Chesapeake Bay (*77*) and Pamlico Sound (*84*) in the eastern United States and from the Baltic Sea (*85*) that extend back as far as 2500 yr B.P. (Fig. 2C and Table 1). A general sequence of ecological change is apparent in all three cases, but the timing of specific ecological transitions differs among estuaries in keeping with their unique histories of land use, exploitation, and human population growth—a difference that rules out a simple climatic explanation. Increased sedimentation and burial of organic carbon began in the mid–18th century in Chesapeake Bay, coincident with widespread land clearance for agriculture by European colonists (*77*). The main ecological response was a gradual shift in the taxa responsible for primary production that began in the late 18th century. Seagrasses and benthic diatoms on the bay floor declined, while planktonic diatoms and other phytoplankton in the water column correspondingly increased. However, anoxia and hypoxia were not widespread until the 1930s when phytoplankton populations and the flux of organic matter to the bay floor increased dramatically with concomitant loss of benthic fauna (*75*, *77*) (Fig. 2C and Table 1). Similar changes began in the 1950s in the Baltic Sea, with widespread expansion of the extent of anoxic laminated sediments (*74*, *85*), and in the 1950s to 1970s in Pamlico Sound (*84*).

Vast oyster reefs were once prominent structures in Chesapeake Bay (*11*), where they may have filtered the equivalent of the entire water column every 3 days (*79*). Despite intensive harvesting by aboriginal and early colonial populations spanning several millennia, it was not until the introduction of mechanical harvesting with dredges in the 1870s that deep channel reefs were seriously affected (*79*, *80*). Oyster catch was rapidly reduced to a few percent of peak values by the early 20th century (*79*, *80*) (Fig. 2C and Table 1). Only then, after the oyster fishery had collapsed, did hypoxia, anoxia, and other symptoms of eutrophication begin to occur in the 1930s (*75*, *77*), and outbreaks of oyster parasites became prevalent only in the 1950s (*80*). Thus, fishing explains the bulk of the decline, whereas decline in water quality and disease were secondary factors (*80*). However, now that oyster reefs are destroyed, the effects of eutrophication, disease, hypoxia, and continued dredging interact to prevent the recovery of oysters and associated communities (*86*). Field experiments in Pamlico Sound demonstrate that oysters grow well, survive to maturity, and resist oyster disease when elevated above the zone of summer hypoxia—even in the presence of modern levels of eutrophication and pollution (*87*).

Overfishing of oysters to the point of ecological extinction is just one example in a general pattern of removal of species capable of top-down control of community structure in estuaries. Dense populations of oysters and other suspension-feeding bivalves graze plankton so efficiently that they limit blooms of phytoplankton and prevent symptoms of eutrophication (*88*, *89*), just as occurs with grazing by zooplankton in freshwater ecosystems (*90*). The ecological consequences of uncounted other losses are unknown. Gray whales (now extinct in the Atlantic), dolphins, manatees, river otters, sea turtles, alligators, giant sturgeon, sheepshead, sharks, and rays were all once abundant inhabitants of Chesapeake Bay but are now virtually eliminated.

Offshore Benthic Communities

Continental shelves cover more of the ocean floor than all previously discussed environments combined. Commercially important cod, halibut, haddock, turbot, flounder, plaice, rays, and a host of other ground fishes, scallops, cockles, and oysters have been fished intensively for centuries from continental shelves of Europe and North America, and more recently throughout the world (*5*, *7*, *10*, *91*). Hook-and-line fishing was replaced by intensive use of the beam trawl during the 18th century, and industrialized fishing was further intensified with the advent of large steam- and diesel-powered vessels and the otter trawl at the end of the 19th century. Reports of severely depleted fish stocks and shifting of fishing grounds farther and farther from home ports into the North Sea and the outer Grand Banks were commonplace by the beginning of the 19th century. Scientific investigation consistently lagged behind economic realities of depleted stocks and inexorable exploitation of more-distant fishing grounds. As late as 1883, Thomas Huxley claimed that fish stocks were inexhaustible (*92*), a view discredited by the beginning of the 20th century (*5*). Today, several formerly abundant, large fish as well as formerly dense assemblages of suspension feeders are ecologically extinct over vast areas (*7–10*, *93*).

The Primacy of Overfishing in Human Disturbance to Marine Ecosystems

Overfishing of large vertebrates and shellfish was the first major human disturbance to all coastal ecosystems examined (Table 1). Ecological changes due to overfishing are strikingly similar across ecosystems despite the obvious differences in detail (Fig. 1, A to F). Everywhere, the magnitude of losses was enormous in terms of biomass and abundance of large animals that are now effectively absent from most coastal ecosystems worldwide. These changes predated ecological investigations and cannot be understood except by historical analysis. Their timing in the Americas and Pacific closely tracks European colonization and exploitation in most cases. However, aboriginal overfishing also had effects, as exemplified by the decline of sea otters (and possibly sea cows) in the northeast Pacific thousands of years ago.

There are three important corollaries to the primacy of overfishing. The first is that pollution, eutrophication, physical destruction of habitats, outbreaks of disease, invasions of introduced species, and human-induced climate change all come much later than overfishing in the standard sequence of historical events (Fig. 3). The pattern holds regardless of the initial timing of colonial overfishing that began in the Americas in the 16th and 17th centuries and in Australia and New Zealand in the 19th century. The full sequence of events is most characteristic of temperate estuaries like Chesapeake Bay. Not all the human disturbances illustrated in Fig. 3 have affected all ecosystems yet. But wherever these events have occurred, the standard chronological sequence of human disturbance and modification of ecosystems is recognizable.

The second important corollary is that overfishing may often be a necessary precondition for eutrophication, outbreaks of disease, or species introductions to occur (*27*). For example, eutrophication and hypoxia did not occur in Chesapeake Bay until the 1930s, nearly two centuries after clearing of land for agriculture greatly increased runoff of sediments and nutrients into the estuary (*77*). Suspension feeding by still enormous populations of oysters was sufficient to remove most of the increased production of phytoplankton and enhanced turbidity until mechanical harvesting progressively decimated oyster beds from the 1870s to the 1920s (*77*, *80*) (Fig. 2C).

The consequences of overfishing for outbreaks of disease in the next lower trophic level fall into two categories. The most straightforward is that populations in the lower level become so dense that they are much more susceptible to disease as a result of greatly increased rates of transmission (*94*). This was presumably the case for the sea urchin *Diadema* on Caribbean reefs and the seagrass *Thalassia* in Florida Bay. In contrast, among oysters disease did not become important in Chesapeake Bay until oysters had been reduced to a few percent of their original abundance (*80*), a pattern repeated in Pamlico Sound (*86*, *87*) and Foveaux Strait, New Zealand (*93*). Two factors may be responsible. First, oysters may have become less fit owing to stresses like hypoxia or sedimentation, making them less resistant to disease (*87*). Alternatively, suspension feeding by dense populations of oysters and associated species on oyster reefs may have indirectly limited populations of pathogens by favoring other plankton—an explanation that may extend to blooms of toxic plankton and most other outbreaks of microbial populations (*88*).

The third important corollary is that changes in climate are unlikely to be the primary reason for microbial outbreaks and disease. The rise of microbes has occurred at different times and under different climatic conditions in different places, as exemplified by the time lag between events in Chesapeake Bay and Pamlico Sound (*77*, *79*, *80*, *84*). Anthropogenic climate change may now be an important confounding factor, but it was not the original cause. Rapid expansion of introduced species in recent decades (*95*) may have a similar explanation, in addition to increase in frequency and modes of transport. Massive removal of suspension feeders, grazers, and predators must inevitably leave marine ecosystems more vulnerable to invasion (*96*, *97*).

Synergistic Effects of Human Disturbance

Ecological extinction of entire trophic levels makes ecosystems more vulnerable to other natural and human disturbances such as nutrient loading and eutrophication, hypoxia, disease, storms, and climate change. Expansion and intensification of different forms of human disturbance and their ecological effects on coastal ecosystems have increased and accelerated with human population growth, unchecked exploitation of biological resources, technological advance, and the increased geographic scale of exploitation through globalization of markets. Moreover, the effects are synergistic, so that the whole response is much greater than the sum of individual disturbances (*98*). This is perhaps most apparent in the rise of eutrophication, hypoxia, and the outbreak of toxic blooms and disease following the destruction of oyster reefs by mechanical harvesting of oysters (*79*, *80*, *86*). Other possible examples are outbreaks of seagrass wasting disease due to the removal of grazers of seagrasses like the green turtle (*27*).

A striking feature of such synergistic effects is the suddenness of the transition in abundance

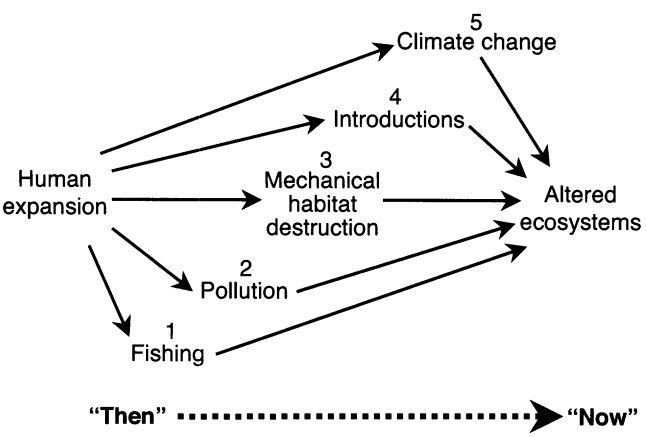

Fig. 3. Historical sequence of human disturbances affecting coastal ecosystems. Fishing (step 1) always preceded other human disturbance in all cases examined. This is the basis for our hypothesis of the primacy of overfishing in the deterioration of coastal ecosystems worldwide. Subsequent steps 2 through 5 have not been observed in every example and may vary in order.

of different kinds of organisms and community composition due to threshold effects (*99*). Ecological diversity and redundancy within trophic levels is probably the most important reason for the delay or time lag between the onset of fishing and the subsequent threshold response (*42*, *100*). The importance of biodiversity in the form of ecological redundancy is clearly apparent for the delay in the collapse of kelp forests in southern California compared with Alaska after the extirpation of sea otters. Sheephead fish, spiny lobsters, and abalone in the more diverse Californian kelp forests kept sea urchin populations in check until these predators and competitors of sea urchins had also been effectively eliminated (*8*, *36*). Similarly, the sea urchin *Diadema* kept macroalgae in check long after the extreme overfishing of herbivorous fishes on Caribbean coral reefs (*42*).

A second potentially important mechanism for the suddenness of ecosystem collapse is the elimination of previously unfished refuges that were protected historically because of distance or expense of access. For example, reef fishes all around Jamaica in the 1960s rarely reached reproductive maturity so that the abundant recruits of fishes on Jamaican reefs at that time must have come from undiscovered populations in Jamaica or elsewhere (*101*). But as more and more reefs have been overfished, the potential sources of such recruits must have effectively disappeared over wider areas (*102*). A similar scenario has been proposed for the American lobster with regard to loss of larvae from deep-water offshore stocks (*103*).

Microbialization of the Global Coastal Ocean

Most recent changes to coastal marine ecosystems subsequent to overfishing involve population explosions of microbes responsible for increasing eutrophication (*74–76*, *81*), diseases of marine species (*104*), toxic blooms (*82*, *83*), and even diseases such as cholera that affect human health (*104*, *105*). Chesapeake Bay (*81*) and the Baltic Sea (*74*) are now bacterially dominated ecosystems with a trophic structure totally different from that of a century ago. Microbial domination also has expanded to the open ocean off the mouth of the Mississippi River (*106*) and to the Adriatic Sea (*107*).

Nowhere is the lack of historical perspective more damaging to scientific understanding than for microbial outbreaks. Plans for remediation of eutrophication of estuaries are still based on the belief that eutrophication is caused only by increased nutrients without regard to overfishing of suspension feeders. Even more remarkable is the attribution of the rise in marine diseases to climate change and pollution (*104*) without regard to the pervasive removal of higher trophic levels and the asynchronous outbreaks of disease in different ecosystems that belie a simple climatic explanation.

Historical Perspectives for Ecosystem Restoration

The characteristic sequence of human disturbance to marine ecosystems (Fig. 3) provides a framework for remediation and restoration that is invisible without a historical perspective. More specific paleoecological, archaeological, and historical data should be obtained to refine the histories of specific ecosystems and as a tool for management, but the overall patterns are clear. The historical magnitudes of losses of large animals and oysters were so great as to seem unbelievable based on modern observations alone (Table 1). Even seemingly gloomy estimates of the global percentage of fish stocks that are overfished (*108*) are almost certainly far too low. The shifting baseline syndrome is thus even more insidious and ecologically widespread than is commonly realized.

On the other hand, recognition of these losses shows what coastal ecosystems could be like, and the extraordinary magnitude of economic resources that are retrievable if we are willing to act on the basis of historical knowledge. The central point for successful restoration is that loss of economically important fisheries, degradation of habitat attractive to landowners and tourists, and emergence of noxious, toxic, and life-threatening microbial diseases are all part of the same standard sequence of ecosystem deterioration that has deep historical roots (*27*). Responding only to current events on a case-by-case basis cannot solve these problems. Instead, they need to be addressed by a series of bold experiments to test the success of integrated management for multiple goals on the scale of entire ecosystems. With few exceptions, such as the Caribbean monk seal and Steller's sea cow, most species that are ecologically extinct probably survive in sufficient numbers for successful restoration. This optimism is in stark contrast with the state of many terrestrial ecosystems where many or most large animals are already extinct (*28*). Moreover, we now have the theoretical tools (*109*) to roughly estimate per capita interaction strengths of surviving individuals of now rare animals like sea turtles, sirenians, sharks, and large groupers. We can then use these data to build tentative models of the consequences of the renewed abundance of these species in their native environments that can in turn be used to design large-scale, adaptive experiments for ecosystem restoration, exploitation, and management (*96*, *108*, *110*).

One obviously timely and overdue experiment is to attempt the amelioration of eutrophication, hypoxia, and toxic blooms in Chesapeake Bay by massive restoration of oyster reefs (*79*). Experiments in Pamlico Sound show that this is possible (*86*, *87*, *96*), and modeling of food webs suggests that even partial restoration of oysters would reduce eutrophication substantially (*110*). Aquaculture of suspension-feeding bivalves like oysters might be promoted to reverse the effects of eutrophication and to restore water quality in degraded estuaries. Other important examples include the restoration of coral reefs and seagrass beds by protection of fishes, sharks, turtles, and sirenians in very large reserves on the scale of all of Florida Bay and the Florida Keys—an approach recently advocated for terrestrial ecosystems (*111*). Once again, small-scale grazing experiments with reef fishes (*112*) show that fishes could reverse the overgrowth of corals by macroalgae on a massive scale. The potential for reducing diseases of corals and turtlegrass by restoring natural levels of grazing is unproven but consistent with historical evidence (*27*).

In summary, historical documentation of the long-term effects of fishing provides a heretofore-missing perspective for successful management and restoration of coastal marine ecosystems. Previous attempts have failed because they have focused only on the most recent symptoms of the problem rather than on their deep historical causes. Contrary to romantic notions of the oceans as the "last frontier" and of the supposedly superior ecological wisdom of non-Western and precolonial societies, our analysis demonstrates that overfishing fundamentally altered coastal marine ecosystems during each of the cultural periods we examined. Changes in ecosystem structure and function occurred as early as the late aboriginal and early colonial stages, although these pale in comparison with subsequent events. Human impacts are also accelerating in their magnitude, rates of change, and in the diversity of processes responsible for changes over time. Early changes increased the sensitivity of coastal marine ecosystems to subsequent disturbance and thus preconditioned the collapse we are witnessing.

References and Notes

1. J. B. C. Jackson, *Coral Reefs* **16**, S23 (1997).
2. K. A. Bjorndal, A. B. Bolten, M. Y. Chaloupka, *Ecol. Appl.* **10**, 269 (2000).
3. G. C. L. Bertram, C. K. Ricardo Bertram, *Biol. J. Linn. Soc.* **5**, 297 (1973).
4. K. W. Kenyon, *J. Mammal.* **58**, 97 (1977).
5. D. H. Cushing, *The Provident Sea* (Cambridge Univ. Press, Cambridge, UK, 1988).
6. J. A. Estes, D. O. Duggins, G. B. Rathbun, *Conserv. Biol.* **3**, 252 (1989).
7. R. S. Steneck, in *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop* (RARGOM Report 91-1, Regional Association for Research in the Gulf of Maine, Hanover, NH, 1997), pp. 151–165.
8. P. K. Dayton, M. J. Tegner, P. B. Edwards, K. L. Riser, *Ecol. Appl.* **8**, 309 (1998).
9. J. M. Casey, R. A. Myers, *Science* **228**, 690 (1998).
10. J. A. Hutchings, *Nature* **406**, 882 (2000).

11. E. Ingersoll, in *The History and Present Condition of the Fishery Industries*, G. B. Goode, Ed. (U.S. Department of the Interior, Tenth Census of the United States, Washington, DC, 1881), pp. 1–252.
12. "Fishing" is the original and most general term in the English language for hunting and gathering all kinds of organisms in the oceans, including plants, invertebrates, and vertebrates ranging from sharks to true fishes to whales. "Overfishing" is the reduction of a species well below the sustainable yield or to such low abundance that it may not recover even if fishing ceases.
13. J. H. Brown, *Macroecology* (Univ. of Chicago Press, Chicago, IL, 1995).
14. J. B. C. Jackson, *BioScience* **41**, 475 (1991).
15. R. C. Francis, S. R. Hare, *Fish. Oceanogr.* **3**, 279 (1994).
16. A. D. MacCall, *Calif. Coop. Fish. Invest.* **37**, 100 (1996).
17. C. B. Lange, S. K. Burke, W. H. Berger *Clim. Change* **16**, 319 (1990).
18. J. B. C. Jackson, in *Biotic Interactions in Recent and Fossil Benthic Communities*, M. J. S. Tevesz, P. L. McCall, Eds. (Plenum, New York, 1983), pp. 39–120.
19. S. J. M. Davis, *The Archaeology of Animals* (Yale Univ. Press, New Haven, CT, 1987).
20. G. Wefer, W. H. Berger, J. Bijima, G. Fischer, in *Use of Proxies in Paleoceanography: Examples from the South Atlantic*, G. Fischer, G. Wefer, Eds. (Springer-Verlag, Berlin, 1999), pp. 1–68.
21. D. S. Jones, *Paleontol. Soc. Pap.* **4**, 37 (1998).
22. C. W. Finkl Jr., *J. Coast. Res. Spec. Iss.* **17**, 402 (1995).
23. A. W. Crosby, *Ecological Imperialism: The Biological Expansion of Europe 900-1900* (Cambridge Univ. Press, Cambridge, UK, 1986).
24. Biological proxies include fossils or archaeological remains that may indicate presence, abundance, age, growth rate, health, or body size, among other factors, of selected taxa. Biogeochemical proxies include concentrations of inorganic or organic constituents and isotopic ratios in sediments or skeletons that track former abundances of unpreserved organisms and variations in parameters such as temperature, salinity, oxygen, nutrient chemistry, and productivity. Physical proxies include sedimentary structures and composition that reflect water movements, runoff from the land, and rate of sedimentation. Historical proxies include demographic, customs, and commercial records, as well as explorers' and naturalists' descriptions of sights and events and nautical charts marking reefs, coastal wetlands, and other landmarks.
25. R. S. Bradley, *Paleoclimatology: Reconstructing Climates of the Quaternary* (Academic Press, San Diego, ed. 2, 1999).
26. S. M. Kidwell, K. W. Flessa, *Annu. Rev. Ecol. Syst.* **26**, 269 (1995).
27. J. B. C. Jackson, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 5411 (2001).
28. D. H. Janzen, P. S. Martin, *Science* **215**, 19 (1982).
29. P. K. Dayton, *Annu. Rev. Ecol. Syst.* **16**, 215 (1985).
30. J. A. Estes, J. F. Palmisano, *Science* **185**, 1058 (1974).
31. C. A. Simenstad, J. A. Estes, K. W. Kenyon, *Science* **200**, 403 (1978).
32. E. Sala, C. F. Boudouresque, M. Harmelin-Vivien, *Oikos* **82**, 425 (1998).
33. J. A. Estes, M. T. Tinker, T. M. Williams, D. F. Doak, *Science* **282**, 473 (1998).
34. B. J. Bourque, *Diversity and Complexity in Prehistoric Maritime Societies: A Gulf of Maine Perspective* (Plenum, New York, 1995).
35. K. Sherman, *Ecol. Appl.* **1**, 349 (1991).
36. M. J. Tegner, P. K. Dayton, *ICES (Int. Counc. Expl. Sea) J. Mar. Sci.* **57**, 579 (2000).
37. J. M. Erlandson *et al.*, *Radiocarbon* **38**, 355 (1996).
38. A. Ogden, *The California Sea Otter Trade* (Univ. of California Press, Berkeley, 1941).
39. M. J. Tegner, P. K. Dayton, *Mar. Ecol. Prog. Ser.* **77**, 49 (1991).
40. N. Knowlton, *Proc. Natl. Acad. Sci. U. S. A.* **98**, 5419 (2001).
41. J. Allen, C. Gosden, J. P. White, *Antiquity* **63**, 548 (1989).
42. T. P. Hughes, *Science* **265**, 1547 (1994).
43. R. A. Kenchington, *Managing Marine Environments* (Taylor and Francis, New York, 1990).
44. J. M. Pandolfi, J. B. C. Jackson, *Ecol. Monogr.* **71**, 49 (2001).
45. R. B. Aronson, W. F. Precht, I. G. MacIntyre, *Coral Reefs* **17**, 223 (1998).
46. J. Geister, *Proc. 3rd Int. Coral Reef Symp.* **1**, 23 (1977).
47. H. A. Lessios, *Annu. Rev. Ecol. Syst.* **19**, 371 (1988).
48. J. E. Duerden, *West Indian Bull.* **1901**, 121 (1901).
49. J. Sapp, *What Is Natural? Coral Reef Crisis* (Oxford Univ. Press, New York, 1999).
50. R. M. Seymour, R. H. Bradbury, *Mar. Ecol. Prog. Ser.* **176**, 1 (1999).
51. R. Ormond *et al.*, in Acanthaster *and the Coral Reef: A Theoretical Perspective*, R. H. Bradbury, Ed. (Springer-Verlag, Berlin, 1990), pp. 189–207.
52. A. Steven, *An Analysis of Fishing Activities on Possible Predators of the Crown of Thorns Starfish* (Acanthaster planci) *of the Great Barrier Reef* (Prepared for the Great Barrier Reef Marine Park Authority, Townsville, Australia, 1988).
53. C. Birkeland, *Mar. Biol.* **69**, 175 (1982).
54. C. C. MacKnight, *The Voyage to Marege: Macassan Trepangers in Northern Australia* (Melbourne Univ. Press, Melbourne, Australia, 1976).
55. D. T. Neil, in *Moreton Bay and Catchment*, I. R. Tibbetts, N. J. Hall, W. C. Dennison, Eds. (Univ. of Queensland, Brisbane, Australia, 1998), pp. 3–54.
56. D. Jones, *The Whalers of Tangalooma* (Nautical Association of Australia, Melbourne, 1980).
57. R. Ganter, *The Pearl-Shellers of Torres Strait: Resource Use, Development and Decline, 1860s–1960s* (Melbourne Univ. Press, Melbourne, Australia, 1994).
58. R. H. Quinn, *Fisheries Resources of the Moreton Bay Region* (Queensland Fish Management Authority, Brisbane, Australia, 1993).
59. J. C. Ogden, in *Handbook of Seagrass Biology: An Ecosystem Perspective*, R. C. Phillips, C. P. McRoy, Eds. (Garland STPM, New York, 1980), pp. 173–198.
60. G. W. Thayer, D. W. Engel, K. A. Bjorndal, *J. Exp. Mar. Biol. Ecol.* **62**, 173 (1982).
61. J. C. Ogden, L. Robinson, H. Whitlock, H. Daganhart, R. Cebula, *J. Exp. Mar. Biol. Ecol.* **66**, 199 (1983).
62. G. W. Thayer, K. A. Bjorndahl, J. C. Ogden, S. L. Williams, J. C. Zieman, *Estuaries* **7**, 351 (1984).
63. H. Kirkman, *Aquat. Bot.* **5**, 63 (1978).
64. E. G. Abal, W. C. Dennison, *Mar. Freshw. Res.* **47**, 763 (1996).
65. J. C. Zieman, J. W. Fourqurean, T. A. Frankovich, *Estuaries* **22**, 460 (1999).
66. C. J. Limpus, P. J. Couper, M. A. Read, *Mem. Queensland Mus.* **35**, 139 (1994).
67. C. J. Limpus, in *State of the Great Barrier Reef World Heritage Area Workshop*, D. Wachenfeld, J. Oliver, K. Davis, Eds. (Great Barrier Reef Marine Park Authority, Townsville, Australia, 1995), pp. 258–265.
68. W. Dampier, *A New Voyage around the World* (Dover, New York, 1968).
69. E. Thorne, *The Queen of the Colonies* (Sampson Low, Marson, Searle, and Rivington, London, 1876).
70. G. M. Allen, *Am. Comm. Int. Wildl. Protect. Spec. Pub.* **11**, 1 (1942).
71. G. E. Heinsohn, R. J. Lear, M. M. Bryden, H. Marsh, B. R. Gardner, *Environ. Conserv.* **5**, 91 (1978).
72. H. Marsh, P. Corkeron, I. Lawler, J. Lanyon, A. Preen, *Great Barrier Reef Marine Park Authority Rep.* **41**, 1 (1996).
73. A. Preen, *Mar. Ecol. Prog. Ser.* **124**, 201 (1995).
74. R. Elmgren, *Ambio* **18**, 326 (1989).
75. C. B. Officer *et al.*, *Science* **223**, 22 (1984).
76. S. W. Nixon, *Ophelia* **41**, 199 (1995).
77. S. R. Cooper, G. S. Brush, *Estuaries* **16**, 617 (1993).
78. R. J. Orth, K. A. Moore, *Science* **222**, 51 (1983).
79. R. I. E. Newell, in *Understanding the Estuary: Advances in Chesapeake Bay Research*, M. P. Lynch, E. C. Krome, Eds. (Chesapeake Bay Research Consortium, Baltimore, MD, 1988), pp. 536–546.
80. B. J. Rothschild, J. S. Ault, P. Goulletquer, M. Héral, *Mar. Ecol. Prog. Ser.* **111**, 29 (1994).
81. R. B. Jonas, *Am. Zool.* **37**, 612 (1997).
82. T. J. Smayda, in *Toxic Marine Phytoplankton*, E. Graneli *et al.*, Eds. (Elsevier Science, New York, 1990), pp. 29–40.
83. J. M. Burkholder *et al.*, *Nature* **358**, 407 (1992).
84. S. R. Cooper, *The History of Water Quality in North Carolina Estuarine Waters as Documented in the Stratigraphic Record* (Univ. of North Carolina Water Resources Research Institute, Raleigh, NC, 2000).
85. J. Persson, P. Jonsson, *Mar. Pollut. Bull.* **40**, 122 (2000).
86. H. S. Lenihan, C. H. Peterson, *Ecol. Appl.* **8**, 128 (1998).
87. H. S. Lenihan, F. Micheli, S. W. Shelton, C. H. Peterson, *Limnol. Oceanogr.* **44**, 910 (1999).
88. C. B. Officer, T. J. Smayda, R. Mann, *Mar. Ecol. Prog. Ser.* **9**, 203 (1982).
89. J. E. Cloern, *Mar. Ecol. Prog. Ser.* **9**, 191 (1982).
90. S. R. Carpenter *et al.*, *Ecol. Monogr.* **71**, 163 (2001).
91. D. Pauly, V. Christensen, J. Dalsgaard, R. Froese, F. Torres Jr., *Science* **279**, 860 (1998).
92. T. H. Huxley, *Fish. Exhib. Lit.* **4**, 1 (1884).
93. H. J. Cranfield, K. P. Michael, I. J. Doonan, *Aquatic Conserv. Mar. Freshw. Ecosyst.* **9**, 461 (1999).
94. W. M. Hochachka, A. A. Dhondt, *Proc. Natl. Acad. Sci. U. S. A.* **97**, 5303 (2000).
95. J. T. Carlton, J. B. Geller, *Science* **261**, 78 (1993).
96. H. S. Lenihan, *Ecol. Monogr.* **69**, 251 (1999).
97. J. J. Stachowicz, R. B. Whitlatch, R. W. Osman, *Science* **286**, 1577 (1999).
98. N. Myers, *Science* **269**, 358 (1995).
99. N. Knowlton, *Am. Zool.* **32**, 674 (1992).
100. S. Naeem, *Conserv. Biol.* **12**, 39 (1998).
101. J. Munro, *ICLARM (Int. Cent. Living Aquat. Resour. Manag.) Stud. Rev.* **7**, 1 (1983).
102. J. L. Munro, in *Fish and Fisheries Series; Reef Fisheries*, N. V. C. Polunin, C. M. Roberts, Eds. (Chapman & Hall, New York, 1996), pp. 1–14.
103. M. J. Fogarty, *Can. Spec. Publ. Fish. Aquat. Sci.* **125**, 273 (1998).
104. C. D. Harvell *et al.*, *Science* **285**, 1505 (1999).
105. R. R. Colwell, *Science* **274**, 2025 (1996).
106. R. E. Turner, N. N. Rabalais, *Nature* **368**, 619 (1994).
107. D. Justić, in *Modern and Ancient Continental Shelf Anoxia*, R. V. Tyson, T. H. Pearson, Eds. (Geological Society, London, 1991), pp. 95–105.
108. L. W. Botsford, J. C. Castilla, C. H. Peterson, *Science* **277**, 509 (1997).
109. R. T. Paine, *Nature* **355**, 73 (1992).
110. R. E. Ulanowicz, J. H. Tuttle, *Estuaries* **15**, 298 (1992).
111. M. E. Soulé, J. Terborgh, Eds., *Continental Conservation* (Island, Washington, DC, 1999).
112. S. M. Lewis, *Ecol. Monogr.* **56**, 183 (1986).
113. Cod body length for samples older than 50 years was derived from cod vertebrae collected at the Turner Farm shell midden, North Haven, Maine. Five occupations are recognized: Occupations 1 (5300 to 4900 yr B.P.), 2 (4500 to 4200 yr B.P.), 3 (3700 to 3500 yr B.P.), and 4 (= Ceramic Period, 3000 to 1000 yr B.P.), and Plow Zone (mixed from earlier occupations but mostly postdating 1000 yr B.P.). Regression of body length on vertebra diameter of living cod allowed estimation of body lengths from vertebrae of ancient cod [$y = 61.0 + 204.6\log(x)$]. This model assumes that we are using the largest vertebra for each fish, and will therefore tend to underestimate actual body size in cases where smaller vertebrae are used. Data from the past 50 years are actual body lengths reported from coastal zones [H. B. Bigelow, W. C. Schroeder, *Fish. Bull. Fish Wildl. Serv.* **53**, 1 (1953); J. S. Hacunda, *Fish. Bull.* **79**, 775 (1981); F. P. Ojeda, thesis (Univ. of Maine, 1987)].
114. Percent Caribbean localities with *A. palmata* or *A. cervicornis* as the dominant or codominant corals were derived from 50 studies from Antigua, Bahamas, Barbados, Belize, Bonaire, Cayman Islands, Colombia, Dominican Republic, Florida, Haiti, Jamaica, Mexico, Netherlands Antilles, Panama, Puerto Rico, and U.S. Virgin Islands. Studies contained either paleoecological data from outcrops of fossil reefs or from sediment cores, or ecological data. For *A. palmata*, only localities described as reef crest or between 0- and 10-m water depth were included (131 localities). For *A. cervicornis*, only localities described as forereef, reef slope, or between 10- and 20-m water depth were included (72 localities). Leeward and windward environments were not distinguished. The percentage of localities that contained *A. palmata* or *A. cervicornis* as the most abundant coral was estimated

for four time intervals: Late Pleistocene (before humans arrived in the Americas), Holocene (when only aboriginal populations were present), pre-1983 (before the mass mortality of *Diadema antillarum*), and post-1983 (after the *Diadema* mortality).

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REVIEW

Noisy Clockwork: Time Series Analysis of Population Fluctuations in Animals

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Both biotic interactions and abiotic random forcing are crucial influences on population dynamics. This frequently leads to roughly equal importance of deterministic and stochastic forces. The resulting tension between noise and determinism makes ecological dynamics unique, with conceptual and methodological challenges distinctive from those in other dynamical systems. The theory for stochastic, nonlinear ecological dynamics has been developed alongside methods to test models. A range of dynamical components has been considered—density dependence, environmental and demographic stochasticity, and climatic forcing—as well as their often complex interactions. We discuss recent advances in understanding ecological dynamics and testing theory using long-term data and review how dynamical forces interact to generate some central field and laboratory time series.

The century of studies in population ecology has been dominated by a nested set of debates regarding the importance of various dynamical forces. The first controversy concerned the relative impact of biotic versus abiotic control of population fluctuations. The key question was the relative importance of "noise" (small-scale, high-frequency stochastic influences) versus climatic forcing (larger-scale, often lower-frequency signals) versus nonlinear interactions between individuals of the same or different species. The second question concerned the impact of intrinsic (i.e., intraspecific) processes, as opposed to extrinsic or community-level interactions, an argument that has been particularly heated with reference to population cycles. A third debate, nested within the latter, concerns the "dimensionality" of population fluctuations; given that most populations are embedded in rich communities and affected by numerous interspecific interactions, can simple (low-dimensional) models involving one or a few species capture the patterns of fluctuations? All these questions have been studied through a number of detailed analyses of specific systems in which theoretical models are linked with long-term studies (often 10 or more generations) through time series analysis.

There has been much parallel and intertwined development of these three dynamical themes, and history testifies to a succession of popularity of the various positions (*1*). Crudely summarized, early focus on extrinsic influences was replaced by the "density-dependent paradigm" (*2*) in the 1950s and 1960s. This accelerated in the late 1970s, with May's *cri de coeur* (*3*) about the potential of dynamical complexity even in simple models, leading to a focus in the 1980s on nonlinearity and the detection of deterministic chaos (Taken's embedology, Lyapunov exponents, etc.). Research has focused on two fronts in the past decade: (i) the impact of large-scale climatic forcing, coinciding with the rise in popularity of climate change studies through the early 1990s, and (ii) stochastic nonlinear models that combine the nonlinear deterministic and (largely) linear stochastic theories. The goal in synthesizing these approaches in recent years is to understand how population fluctuations arise from the interplay of noise, forcing, and nonlinear dynamics. The comparable importance of deterministic and stochastic forces makes ecological dynamics unique. In particular, the interaction between noise and nonlinear determinism in ecological dynamics adds an extra level of complexity compared with the largely stochastic dynamics of, say, economic systems or the largely deterministic dynamics of many physical and chemical processes.

The dynamics of marine stocks serve as an illustration of the current paradigm. Most commercial fish stocks vary greatly in abundance and the associated time series exhibit complex spectra, with combinations of high-frequency oscillations and longer term trends (*4*, *5*) (Fig. 1). High-frequency oscillations are thought to arise from environmental variability particularly affecting reproduction [through expatriation of eggs, temperature-induced mortality, etc. (*4*)], as well as interactions between individuals (competition and cannibalism) or between species (fish-fish or plankton-fish interactions). The low-frequency oscillations and trends are usually related to external forcing such as overfishing, climatic changes, and decadal, supra-, or super-decadal oscillations in climate. The most recent studies that combine theoretical modeling with time series analysis indicate that the full variability in marine stocks can only be explained by considering the interaction between nonlinear dynamics and stochastic forcing (*5*, *6*), often in the face of strong human influences (*7*, *8*) and obscured by measurement error (*5*, *7*).

The relative importance of different components of ecological dynamics differs somewhat between systems—notably between terrestrial versus marine, vertebrate versus invertebrate, simple versus complex life-cycle, etc. However, evidence is mounting that all components contribute and interact at particular spatial and temporal scales in most systems. Here we review the current understanding of the different forces that drive ecological dynamics.

Simple density-dependent interactions. Nonlinear, density-dependent interactions can potentially stabilize or promote fluctuations in abundance because such interactions can either result in stable equilibria (point attractors, namely "the carrying capacity") or cyclic or chaotic attractors, associated with strongly overcompensatory density dependence (*3*). About 25 years ago, Hassell *et al.* (*9*) and Gurney *et al.* (*10*) took the bold step of insisting that the then-qualitative, strategic theory ought to be testable by analyses of

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