

Unnatural Oceans*

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SUMMARY: Ecological understanding of the oceans is based on an unnatural mix of mostly small species whose trophic relations are distorted to an unknown degree by the overfishing of megafauna including sharks, sea turtles, sea cows, seals, and whales. Living habitats like seagrass beds, kelp forests, and coral reefs that once provided critical 3-dimensional habitats for refuge and reproduction of most of the biodiversity of the oceans are also greatly reduced by fishing and other factors. Successful restoration and conservation require a more realistic understanding of the ecology of pristine marine ecosystems that can only be obtained by a combination of retrospective analyses, modeling, and intensive studies of succession in very large marine reserves.

Key words: overfishing, food webs, biological habitat, body size, historical ecology.

INTRODUCTION

Like many others growing up in the 1950s, the senior author marveled at the books and films of Jacques Cousteau and watched television melodramas like *Sea Hunt*. Amongst the wonders of marine biology, underwater archeology, and intrigue were myriad renditions of frightening adventures with giant sharks, octopus, and “man-eating” clams that have indelibly permeated the popular culture of the oceans to this day. It was, therefore, a genuine personal surprise that he very rarely saw large sharks or large fishes of any kind when he began scientific diving around the Caribbean in 1968; and had to wait until a trip to Truk in the western Pacific the following year to see sharks in any abundance. Now, western Pacific coral reefs and seagrass meadows

look increasingly like the Caribbean and scientists are finally waking up to the extraordinary magnitude of the ecological changes on coral reefs and all other marine ecosystems that have been wrought by overfishing (Wilkinson 1992; Hughes 1994; Dayton *et al.*, 1995; Botsford *et al.*, 1997; Jackson, 1997, 2001; Dayton *et al.*, 1998; Jackson *et al.*, 2001; Ste-neck and Carlton, 2001).

Alarm about the collapse of coastal ecosystems worldwide and loss of marine biodiversity has brought about many promising initiatives for conservation and management (Palumbi, 2001; Peterson and Estes, 2001). However, our basic concepts about the ecology of pristine marine ecosystems have hardly been questioned, even though most of our textbook wisdom was obtained long after intensive fishing began. Margalef (1968) observed that fishing reverses ecological succession and explored theoretically the implications for the productivity of

*Received August 9, 2001. Accepted August 16, 2001.

ecosystems subjected to varying levels of exploitation. Today, Margalef's prescience is all too apparent in the replacement of Caribbean reef corals by benthic algae (Lessios, 1988; Hughes, 1994), of temperate kelp forests and other fleshy algal communities by "sea urchin barrens" of crustose coralline algae (Estes and Palmisano, 1974; Simenstad *et al.*, 1978; Dayton *et al.*, 1998; Sala *et al.*, 1998; Steneck and Carlton, 2001), the eutrophication of coastal estuaries (Officer *et al.* 1984; Elmgren, 1989; Nixon, 1995; Jonas, 1997), and the relentless global fishing down of marine food webs (Pauly *et al.*, 1998). However, we still lack the basic data for a general theory of the relationships between productivity, biomass, and the degree of exploitation in marine ecosystems that seems essential for rational conservation, restoration, and management.

An important step in the development of any theory is an examination of the basic assumptions. Here we briefly review our understanding of three basic themes in the ecology of marine ecosystems in the light of increased awareness of the magnitude and consequences of overfishing. The purpose is to question common generalizations about the composition and structure of pristine marine ecosystems that were formulated long after extensive exploitation began. Building more realistic models of pristine marine ecosystems, to the extent this is possible, will require detailed paleoecological, archeological, and historical analyses to determine what and how much was present, combined with observations and manipulations of succession due to the absolute cessation of human exploitation within very large marine protected areas. Such investigations have hardly begun for any marine ecosystem.

BODY SIZE

Most species of a higher taxon of free-living animals like mammals, birds, snails, and clams are small compared to the total range in size for the group (May, 1988, 1990, 1994; Brown, 1995). The number of species scales very approximately with decreasing characteristic body length, L , as L^{-2} , or for body mass, M , as $M^{-2/3}$. Moreover, the ancestral species in a clade are also generally small and lie near the apparent physiologically or biomechanically minimum functional body size for the group (Stanley, 1973). Thus, body size tends to increase over macroevolutionary time, whether by simple

evolutionary diffusion from smaller to larger size, or because of adaptive trends associated with evolutionary arms races that actually favor larger species (McShea, 1994, 2000; Vermeij, 1994).

Thus, ignoring for the moment the problems of bycatch and indirect ecological effects, selective fishing of large species should affect directly only a very small proportion of the total species diversity of a clade - although more evolutionarily derived species, to the extent that they are larger, should tend to be affected more than ancestral groups. If we look beyond diversity, however, to consider the ecological roles of species, the picture is dramatically different because large animals directly affect ecosystems in profoundly different ways than small animals that go well beyond Pieter Bruegel's famous pictorial maxim that "big fish eat little fish." Big animals not only eat much more than smaller animals, but they also physically disturb the habitat by their feeding and behavior in ways impossible for smaller species (Jackson, 1997, 2001). The best documented examples come from East Africa where elephants rip apart forests and vast herds of migrating wildebeest affect the abundance, composition, and nutritional value of the vegetation by their grazing and trampling in ways that affect all the other animals on the plains (Sinclair and Arcese, 1995).

Comparably detailed observations are unavailable for most marine ecosystems for the simple reason that most of the big animals were gone before marine ecology began; and that, tragically, there are no marine parks equivalent to the Serengeti where large animals live their entire lives in vast areas that are mostly well protected from human exploitation (Sinclair and Arcese, 1995). Nevertheless, we can still make a list of cases for which there is reasonable evidence that large marine species had comparably dramatic effects in coastal ecosystems (Jackson *et al.*, 2001, Table 1). In contrast, we have almost no idea of the magnitude of the ecological consequences in the open oceans of feeding by formerly abundant baleen whales, swordfish, tuna, and the like.

There is no clearer measure of our ecological ignorance of the animals in Table 1 than their virtual absence from the index of the most recent textbook on marine community ecology (Bertness *et al.*, 2001), except for discussions of the geological history of the biota or of human disturbance, conservation, and management. There is an enormous bias towards the study of small species that swell the index of the same textbook, even when larger

TABLE 1. – Some of the ecologically extinct large animals that were keystone species in pristine coastal ecosystems and their ecological effects. For more extensive discussion and references see Jackson *et al.* (2001).

Species	Ecological consequences	References
Seagrass meadows and soft sediments		
Green turtles	Closely crop turtlegrass and other seagrasses and reduce flux of organic matter to sediments	Jackson 1997
Manatees and dugongs	Excavate, break apart, and consume up to 96% of above ground biomass and 71% of below ground biomass of seagrasses	Preen 1995
Skates and rays	Excavate seagrass beds and sediments forming pits of bare sediment for feeding and camouflage	Orth 1975, VanBlaricom 1982
Coral reefs		
Tiger sharks	Consume large fishes and sea turtles, among others	De Crosta 1981
Monk seals	Consume fish	Polovina 1984
Parrotfish	Graze directly on coralline substrata including live corals and coralline algae	Steneck 1983
Hawksbill turtles	Feed upon and break apart large sponges	Meylan 1988, van Dam and Diez, 1997
Jewfish	Consume lobsters, other invertebrates, and fishes	Randall 1983
Kelp forests		
Cod, sheephead, and sea otters	Consume sea urchins, other benthic invertebrates, and fishes	Estes and Palmisano 1974, Steneck and Carlton 2001, Dayton <i>et al.</i> 1998
Seals and sea lions	Consume fish	Wells <i>et al.</i> 1999
Stellar's sea cow	Consumed kelp canopies or intertidal seaweeds	Jackson <i>et al.</i> 2001

species are still reasonably abundant as on the Great Barrier Reef in Australia. Yet, even in Australia, as for the Caribbean, almost all of the experiments on reef fish recruitment, and the ensuing controversy about the determinants of coral reef fish community structure, including the importance of chance events, competition, and predation, are based on short-term studies of fishes less than 10 cm long (Sale, 1991; Morgan, 2001); and the same is true of other benthic communities. The implications extend far beyond academic ecology, however, because our expectations about the potential recovery of larger species of reef fishes in marine reserves are heavily influenced by the only studies available (Dayton *et al.*, 1998; Palumbi, 2001).

GEOMETRY OF FOOD WEBS

One large tiger shark weighs roughly the same as one hundred large groupers, snappers, or parrotfish; or ten thousand damselfish or small wrasses – the species that have been the overwhelmingly favorite subjects of study by coral reef ecologists (Sale, 1991). What percentage of the total free-living animal biomass of pristine ecosystems was comprised of megafauna, such as the species in Table 1, compared to smaller species like damselfish, wrasses, shrimps, and brittlestars? Moreover, what was the

effect of the removal of megafauna on lower trophic levels? Recent empirical studies of reefs subjected to varying degrees of fishing (but where the “large” predators are not really very large) suggest that the effects are minimal (Hixon, 1991; Russ and Alcala, 1998; Jennings and Polunin, 1997) whereas modeling studies strongly suggest the opposite (Polovina, 1984; Optiz, 1996; Aliñao *et al.*, 1993; Sala and Jackson, unpublished).

There are at least two great difficulties in trying to answer these questions. The first is that we cannot observe natural populations of marine megafauna today and will have to wait several decades to do so, even in well-managed, very large marine protected areas. The second problem is that the answers do not depend closely upon the ecological efficiency of energy transfer among trophic levels because of the great differences in generation times of larger and smaller species (Stevens *et al.*, 2000; Jackson, 2001). Ages of first reproduction of sea turtles and many large sharks are measured in decades and their longevity presumably in centuries. Large groupers, sheephead, cod, and other large groundfish mature more rapidly but still live for decades. In contrast, smaller species of fishes and free-living benthic invertebrates typically mature within 1-2 years and live only a few years; and the comparable statistics for most zooplankton are measured in months. Thus vertebrate megafauna could have collectively out-

TABLE 2. – Comparison of the vertebrate and invertebrate animal faunas of French Frigate Shoals and Bolinao (Polovina 1984, Aliñao *et al.* 1993). Biomass data are metric tons/km².

Faunal Component	French Frigate Shoals	Bolinao
Megafaunal vertebrates*	0.61	0
Other vertebrates	15.90	6.83
Total vertebrates	16.51	6.83
Invertebrates	171.35	351.95

* monk seals, green turtles, sharks, jacks, scombrids

weighed their prey and other species down the food chain by the long-term accumulation of biomass, but there are virtually no biomass data from pristine ecosystems to tell.

The only food web for a quasi-pristine coral reef ecosystem is from French Frigate Shoals in the remote western Hawaiian chain, which we compared with a heavily overfished site at Bolinao in the Philippines (Polovina, 1984; Aliñao *et al.*, 1993, Table 2). The total vertebrate biomass/km² at French Frigate Shoals is 2.4 times greater than at Bolinao. This difference is statistically significant (one sample test, $\chi^2 = 4.02$, $P < 0.05$), and is probably biologically meaningful despite the differences in methods, investigators and environments. Bolinao is very shallow compared to French Frigate Shoals and is dominated by abundant seagrasses. Nevertheless, there were no green turtles, rays, small sharks, or larger fishes characteristic of shallow seagrass habitats. Nearly 4% of the vertebrate fauna at French Frigate Shoals was megafauna (monk seals, sharks, and green turtles) as opposed to none at Bolinao, but this difference is not statistically significant ($\chi^2 = 0.26$). It is unclear whether this is because the megafauna of French Frigate Shoals have also been reduced by fishing (which seems likely because of the importance of migration for many megafauna and probable unreported fishing in the past), or that the numbers were always around 4%.

However, the most striking difference between the two sites is in the proportions of total vertebrate to total invertebrate biomass. Vertebrates comprise 9.6% of the total animal biomass/km² at French Frigate Shoals compared to 1.9% at Bolinao ($\chi^2 = 14.3$, $P < 0.01$). The data are limited and we need more examples from sites subjected to varying intensity of fishing. Nevertheless, they are consistent with the general impression that both the absolute and proportional abundance of vertebrates are declining greatly in tropical coastal environments, while that of invertebrates is rising. Increase in

abundance of sea urchins is especially characteristic of overfished coral reefs (Hay, 1984; Hughes, 1994; McClanahan, 1994; McClanahan and Muthiga, 1998; Knowlton and Jackson, 2001). Sea urchins were very abundant in the survey at Bolinao but were not singled out for description in the food web from French Frigate Shoals. Fishing is also still the best explanation for the extraordinary outbreaks of the crown-of-thorns starfish *Acanthaster planci* that have decimated Pacific reef corals since the 1960s (Ormond *et al.*, 1990, Jackson *et al.*, 2001). It is a measure of our ignorance of the trophic ecology of coral reefs that we still cannot explain the most spectacular anthropogenic phenomenon to afflict coral reefs in the past 50 years (Sapp, 1999).

We know considerably more about the effects of the removal of top predators on the abundance of lower tropic levels in kelp forests and other subtidal communities in higher latitudes (Simenstad *et al.*, 1978; Dayton *et al.*, 1998; Estes *et al.*, 1998; Sala *et al.*, 1998; Steneck and Carlton, 2001; Jackson *et al.*, 2001). Loss of sea otters, cod, and other predatory fishes results in an increase in free-living benthic invertebrates, especially sea urchins, that are notable for their virtual elimination of fleshy benthic algae, and lobsters that are notable for their value as fisheries. Here again, however, we lack quantitative estimates of the changes in relative abundance and biomass of the bigger fishes, smaller fishes, and invertebrates respectively.

One very promising approach is to compare the species composition and sizes of the preservable remains of species with hard parts from sediments and archeological sites deposited before and after intensive fishing (Jackson *et al.*, 2001). Calcareous skeletons of stony corals, bryozoans, and mollusks are particularly well preserved, and sharks' teeth, the otoliths and teeth of teleost fishes, and the teeth and bones of sea turtles and marine mammals are also commonly but more sporadically well preserved. The greatest problem of interpretation is due to bioturbation of sediments and other forms of "time averaging" that commonly mix up remains varying in age by many hundreds to a few thousand years (Kidwell and Flessa, 1996). However, these problems can be largely avoided by exploiting sites that were uplifted or closed off from the sea tectonically some time before intensive fishing began (Pandolfi, 1996), and then comparing analyses of skeletal remains from these uplifted deposits with modern faunas. In contrast, a big problem with archeological remains for ecological analysis is

human selectivity of species (Davis, 1987), although changes over time in the size and composition of species in garbage heaps at the same sites may be revealing (Simenstad *et al.*, 1978).

Changes in species composition and size frequencies from deposits before and after fishing can provide strong circumstantial evidence of the extent to which removal of megafauna and other large fishes may have cascaded down food webs to affect the abundance of smaller species. For example, bivalve mollusks that are a favorite food of skates, rays, puffer fishes, and octopus may be larger now than before, and less commonly fractured and broken into pieces. Comparison of the food webs of French Frigate Shoals and Bolinao also suggests that the same may be true of otoliths of damselfish, small wrasses, cardinal fish, and squirrel fishes; although there are good paleontological data showing that algal gardening by the three-spot damsel fish was common on Pleistocene Jamaican reefs 125,000 years ago (Kaufman, 1981).

LIVING IN GROUPS

Sedentary and sessile animals and plants commonly form dense aggregations that create, modify, and maintain biological habitats that are more physically stable and more topologically complex and 3-dimensional than are the same environments in their absence (Jackson, 1977, 2001; Jones *et al.*, 1994; Bruno and Bertness, 2001). These biological habitats are the forests and savannas of the oceans, from which they differ principally in their generally lower stature (due to the greater viscosity of seawater than air) and in the more equal representation of structurally important animals as well as plants. The most important organisms that form biological habitats are marsh grasses, mangroves, seagrasses, fleshy and calcareous macroalgae (seaweeds), sponges, stony corals, soft corals, bryozoans, oysters, mussels, and tube-building polychaete worms, among others (Bruno and Bertness, 2001). These organisms are the foundation species of most coastal benthic communities, including the rocky intertidal, soft sediments, salt marshes, seagrass meadows, rocky subtidal communities, coral reefs, and mangroves.

Biological habitats become established, grow, and are maintained against natural physical and biological disturbances by a combination of processes, including larval habitat selection to settle on, or nearby, conspecific or associated individuals; short-

distance dispersal (philopatry) of larvae, spores, and seeds; asexual (vegetative) budding; and patterns of growth that are both extensive and tenacious (Jackson, 1977; 1986; Bruno and Bertness, 2001; Morgan, 2001). Examples of physical tenacity and toughness include the varyingly dense rhizome mats of seagrass beds (Orth, 1977), the “mangal” of mangrove forests (Ellison and Farnsworth, 2001), oyster reefs (Newell, 1988; Rothschild *et al.*, 1994), and the ways that branching sponges hold themselves and corals together by their anatomizing growth and fusion of branches (Wulff, 1997). Many of these biological habitats are, of course, very well known. What is not appreciated, however, is the vast extent of dense tangles of sponges, bryozoans, azooxanthellate corals, bivalve mollusks, and algae that once covered vast areas of the continental shelves around the Gulf of Mexico and still persist off South Australia and southeast New Zealand (Probert and Batham, 1979; Bradstock and Gordon, 1983; Hageman *et al.*, 1995; Watling and Norse, 1998; Carlton *et al.*, 1999; McKinney and Jaklin, 2000).

Biological habitats harbor the greatest biodiversity of associated species per unit area of habitat in the oceans (Bruno and Bertness, 2001; Jackson, 2001; Knowlton, 2001; Williams and Heck, 2001). Numbers of associated species of coral reefs, seagrass meadows, oyster reefs, and sponge-bryozoan tangles, to the poor extent that they have been collected, documented, and described taxonomically, easily exceed the diversity of adjacent non-biological habitats by 10-fold or more. Biological habitats are well established as important nursing grounds for larval and juvenile fish, crustaceans, and other commercially important species (Bradstock and Gordon, 1983; Ogden, 1997; Bruno and Bertness, 2001; Lenihan and Micheli, 2001; Williams and Heck, 2001).

Biological habitats are also extremely vulnerable to human disturbance because we can actually kill the habitat. This was dramatically evident following a major oil spill in Panama, when residual oil in sediments continued to kill mangroves and seagrasses along the shore and the coastline actually receded several meters by erosion over several years (Jackson *et al.*, 1989; Keller and Jackson, 1993). In contrast, oil spills on rocky shores may kill the entire biota, but the oil does not kill the rocks that comprise the shore. Thus recovery is potentially much more rapid on a rocky shore, other things being equal, than on the unstable bare sediments where mangroves, salt marshes, or seagrass beds used to be

before an oil spill. Increased sedimentation due to deforestation and agriculture may have similarly greater effects on biological habitats. Fishing also devastates biological habitats, through the direct effects of trawling and dredging (Dayton *et al.*, 1995; Watling and Norse, 1998), or indirectly by altering the relative abundance of predators and prey and different competitors for space. Well known examples include Caribbean reef fishes, sea urchins, algae, and corals (Hughes, 1994); cod, sea urchins, and kelp forests (Steneck and Carlton, 2001); green turtles and turtlegrass beds (Jackson, 1997, 2001); and oysters and eutrophication in Chesapeake Bay (Officer *et al.*, 1984; Newell, 1988; Rothschild *et al.*, 1994; Jackson *et al.*, 2001).

The geographic extent, depth range, and total area of biological habitats in the coastal oceans has been greatly reduced, but we do not know by how much because there were so few studies before trawling, dredging, mining, and other human disturbances to the sea floor began. In some cases, such as the wasting disease of the eelgrass *Spartina alterniflora*, the deforestation of mangroves for shrimp farms and coastal development, and the collapse of Caribbean reef corals, the changes were obvious and were documented while they were happening. Changes may also be more subtle, as in the case of the slow shallowing of *Posidonia oceanica* beds in coastal areas of the Mediterranean that have become more turbid due to anthropogenic activities (Boudouresque *et al.*, 1994). Still other biological habitats, however, such as the tangles of sponges, bryozoans, azooxanthellate corals, and associated species on continental shelves were lost to trawling and dredging almost before we knew they were there; and their extent was never properly mapped in a systematic fashion. Such ignorance greatly diminishes the goals of conservation and management.

Retrospective analyses of the previous extent of biological habitats can refine our expectations. Paleocological analyses of Holocene and Late Pleistocene coral reefs have demonstrated that the species composition of coral reef communities is predictable and persistent over long time scales (Pandolfi, 1996), and that the coral reef communities that disappeared in the Caribbean in the late 1970s and 1980s were the characteristic communities of the region before human disturbance intensified (Aronson and Precht, 2000; Jackson *et al.*, 2001; Pandolfi and Jackson, 2001). Paleocological analyses provided a baseline for coral communities, but not for associated species of invertebrates and

vertebrates that are generally poorly preserved in fossil reef deposits.

A similar approach could be extended to determine the previous extent of other biological habitats. Molluscan assemblages of seagrass communities are distinctive and diagnostic in tropical and temperate seagrass beds (Jackson, 1968; 1972, 1973; Orth, 1973). Thus dead shell assemblages can be used to reconstruct the presence of seagrass beds where they have been lost. For example, abundant shells of species collected live from seagrass beds in Kingston Harbor, Jamaica in the 1960s (Jackson, 1973) are still present in the sediments although the seagrasses disappeared entirely sometime thereafter (Peter Roopnarine, pers. comm.). Similar studies could establish the former presence of seagrasses in areas that had not been studied before seagrasses had disappeared. Likewise, the bryozoan species characteristic of the dense tangle of sponges, bryozoans and other species on continental shelves are also characteristic of these assemblages (Probert and Batham, 1979; Bradstock and Gordon, 1983; Hageman *et al.*, 1995; McKinney and Jaklin, 2000). Bryozoan skeletons are normally well preserved in sediments although intensive trawling could reduce them to unidentifiable bits of sand. However, these species were also commonly dredged in early surveys of the continental shelves in the 19th century (Canu and Bassler, 1928), so that examination of museum collections could provide compelling evidence as well.

DISCUSSION

Colinvaux (1980) explained “*Why Big Fierce Animals Are Rare*” in terms of basic ecological principles, including most importantly the constraints on size imposed by the mechanics of feeding relationships and by the efficiency of assimilation of energy among trophic levels. Another explanation, however, is that we ate all the big animals before we studied them so therefore they are rare. This is perhaps unlikely on the land where top carnivores were never an important component of the human diet (Diamond, 1997), and one suspects they would have been eaten in proportion to their abundance along with everything else. In striking contrast, top and middle level carnivores have been and continue to be a major component of our food from the oceans, which is perhaps the strongest evidence available that these large animals comprised a much larger

proportion of the total pristine animal biomass than has been generally assumed.

We are witnessing an extraordinary transformation of the coastal oceans from complex and diverse 3-dimensional biological habitats to simple 2-dimensional sediments and rocky surfaces populated by scattered organisms and thin skins of biological cement (Jackson, 2001; Jackson *et al.*, 2001). Likewise, the size of animals is falling precipitously, not just in the loss of megafauna, but also in the slow, unrelenting decrease in average size and trophic level of the species that remain. Vertebrates are disappearing rapidly and being replaced by smaller and smaller invertebrates and superabundant microbes. The old “fish stories” may take on a postmodern twist: “You should have seen the ocean that got away.”

We badly need an historical ecology of sea monsters to determine the pristine abundances and sizes of megafauna before they were fished, and to provide the basic data for modeling their former ecological interactions with other, smaller species and their effects on biological habitats so that we can figure out what we have lost and decide what to do about it if we want to. We still have that chance.

ACKNOWLEDGEMENTS

We thank the members of the Marine Records Working Group of the National Center for Ecological Analysis and Synthesis (NCEAS) for valuable discussions, NCEAS for financial support, and Ken McKinney for the references to bryozoan-sponge communities.

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