Overexploiting marine ecosystem engineers: potential consequences for biodiversity

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Overfishing is a major environmental problem in the oceans. In addition to the direct loss of the exploited species, the very act of fishing, particularly with mobile bottom gear, destroys habitat and ultimately results in the loss of biodiversity. Furthermore, overfishing can create trophic cascades in marine communities that cause similar declines in species richness. These effects are compounded by indirect effects on habitat that occur through removal of ecological or ecosystem engineers. Mass removal of species that restructure the architecture of habitat and thus increase its complexity or influence the biogeochemistry of sediments could have devastating effects on local biodiversity and important water–sediment processes. The possible overexploitation of engineering species requires more attention because the consequences extend beyond their own decline to affect the rest of the ecosystem. This is particularly problematic in the deep ocean, where oil and gas exploration and fishing pressure are likely to increase.

Since Dayton *et al.*'s 1995 article [1] bemoaned the lack of attention paid to fishing effects on ecosystems, an avalanche of such material has appeared. Most of the papers that track the environmental impacts of fishing do so primarily along three lines: (1) those owing to BYCATCH (see Glossary) of nontargeted species [2]; (2) those owing to the impact of fishing gear on habitat [3–6]; and (3) those owing to trophic effects [7–9].

Bycatch was inarguably the first fishing effect to really capture the public's attention, because it involved high-profile marine animals, such as dolphins, whales, sea birds and sea turtles [1]. Bycatch of sharks, together with the REGULATORY DISCARDS common to fishing enterprises, drew somewhat less fire, but was also of interest. The issue was simple. The indirect effects of fishing could increase the risk of extinction for species of limited or no commercial value.

Public awareness rapidly expanded to include incidental effects of bottom TRAWLING on those noncharismatic suites of species that structure EPIBENTHIC communities, such as coral and sponges [10]. Initially, the focus was on the physical destruction of habitat caused by nets and other gear dragged across the bottom, rather than on the functional losses resulting from species removal, even though the organisms themselves lend more than just structural complexity to the benthos. Once Watling and Norse [3] drew the striking analogy between bottom trawling and forest clearcutting, this issue became a major concern to marine conservationists.

The complex nature of fishing effects on ecosystems became entrenched in the environmental consciousness when it became clear that fishing could cause imbalances in the most basic of species interactions – predator–prey relationships. Papers that describe these effects focus either on TROPHIC CASCADES or on FISHING DOWN FOOD WEBS. Trophic cascades result in significant changes in the composition and structure of communities. They can be envisioned as a domino effect ensuing from the removal of a predator, which results in fluxes in the prey populations and even populations at lower trophic levels. Of particular interest are the unexpected linkages revealed among species not directly interacting with one another. In the now famous sea otter–sea urchin–kelp example, for instance, interest focuses on the removal from the California coast of sea otters *Enhydra lutris*, and the resultant explosion populations of the sea urchin *Strongylocentrus franciscanus* (the primary prey) that led to the overgrazing and subsequent decline of kelp [11,12]. This is a straightforward cascading trophic effect resulting from the loss of a KEYSTONE SPECIES.

Sala *et al.* [13] linked trophic cascades effectively to fishing in their review of sea urchin population response to predator removal. However, it took Steneck's [9] coupling of trophic cascades with Pauly's [8] description of fishing down food webs to capture the enormity of the havoc played on ocean ecosystems by unsustainable fishing. Once top-level predators are removed, fishing cranks down a trophic notch to concentrate on the subsequently more abundant prey species of those predators. This decreases both the structural and functional diversity of ecosystems, presumably also decreasing their resilience. When compounded with trophic cascades, the picture is indeed bleak for maintaining any semblance of a natural system.

To this list of fishing effects can be added the indirect effects on both habitat and biodiversity of fishing that actively target marine habitat engineers, or ECOSYSTEM ENGINEERS. In the simplest form, ecosystem engineers are species that either morphologically or behaviorally create more complex habitat. This is a woefully understudied phenomenon, given the importance of structure (both abiotic and biotic) to fisheries productivity [1], and the declines of so many species resulting from intense fishing pressure. OVERFISHING marine ecosystem engineers is a potentially serious problem as disturbing as any other fishing consequence so far examined because engineering activity influences both biological diversity and ecosystem function. Given

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Box 1. Examples of marine ecosystem engineers categorized by structures formed

The following examples of widespread marine ecosystem engineers all increase the structural complexity of the habitat, the local biomass, and the local biodiversity, with additional ecological influences distinctive to each category.

- Corals, oysters, vermetid gastropods, sabellid worms and crustose coralline algae construct large solid mineralized reefs [a–d]. These provide settlement substratum for other organisms and provide refuge from predation.
- Marine plants (e.g. seagrasses and kelps) [a] form canopies of vegetation in nearshore waters. They modify water flow, entrain larvae and provide refuge from predation.
- Bivalve molluscs (e.g. mussels and clams) [a] build thick shellfish beds and mats on rocky shores and in soft sediments. The structure provided by shells and by byssal threads of molluscs serve to ameliorate environmental extremes, deposit organic matter, fertilize sediments and promote growth of marine plants [e,f].
- Tilefish, groupers, clams, amphipods, specific types of shrimps (callianassid, alpheid), sea cucumbers, fiddler crabs and worms form excavations and burrows [g], sometimes meters deep.
- While foraging, herbivorous sea turtles [h] and dugongs [i] create large gaps in seagrass beds. Dugongs 'bulldoze' through vegetation and sediments.

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recent shifts in fishing pressure from inshore to offshore waters as shallower sites are fished out [14], and the current political climate to increase oil and gas exploration and development [15], our concerns are not unwarranted and it is likely that deep water species and habitats are at particular risk. We present examples of ecosystem engineering by fishes living on the continental shelf and highlight the perils that they face as a result of these shifts.

Ecosystem engineers

The concept of ecosystem engineering gained considerable attention in the early 1990s when Jones *et al.* published an article [16] elucidating the evolutionary and ecological importance of organisms that structure the physical and biological components of their environment to create habitat. Most engineering feats, according to the authors, separate along two lines: those produced by autogenic engineers whose morphological features alone precipitate local environmental change, and those produced by allogenic engineers, whose behaviors transform biotic or abiotic materials from one physical state to another (Box 1).

The framework provided in the Jones *et al.* [16] paper is of particular conceptual importance because it provides a unifying theory that explains how species influence the abundance and distribution of associated populations within their communities mediated through interactions with their abiotic environments. Furthermore, it provides a counterbalance to related theories involving trophically mediated pathways.

Although the authors lamented that their efforts might result in a body of work characterized as 'just so

stories' – interesting descriptions of engineering feats that lacked empirical underpinnings – this clearly has not been the case. Indeed, scientists responded to their challenge with field experiments on terrestrial mammals (e.g. gophers [17]), freshwater organisms (e.g. crayfish [18] and detritivorous fishes [19]) and marine invertebrates (e.g. callianassid shrimp [20]). But the point brought home by Lawton and Jones [21] that ecologists '…have failed to recognize the role of ecosystem engineers as keystone species' is still valid. Perhaps, too, we have failed to recognize the consequences of their loss.

Potential cases of overexploitation in the marine realm

Although several commercially exploited marine invertebrate species are cited as ecosystem engineers, the consequences of their removal from ecosystems are unknown beyond the single-species or population level. A notable exception is Lenihan and Peterson's [22] work indicating that the harvesting of oysters and the consequent destruction of oyster reefs result in multiple ecosystem effects. We know of no published examples of marine vertebrate ecosystem engineers in spite of there being many species that burrow or otherwise substantially re-structure their habitats, including sea turtles, manatees, dugongs, tilefish (family Malacanthidae) and groupers in the genus *Epinephelus* (family Serranidae). Our concern is with allogenic engineers because of their active participation in structuring habitat. It is further limited to fish because they are commercially valuable and because, at least in the USA, there is no commercial exploitation of marine turtles or marine mammals.
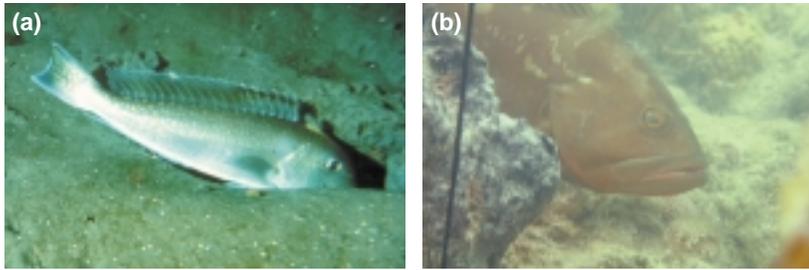
Fig. 1. Examples of ecosystem engineers. (a) tilefish *Lopholatilus chamaeleonticeps* and (b) red grouper *Epinephelus morio* . Photographs reproduced, with permission, from Ken Able and Churchill Grimes (a) and Kathy Scanlon (b).

As top-level predators, tilefish and grouper are integral components of the shelf-edge and slope environments that they inhabit. Thus, their biotic interactions are likely to influence the structure and function of their communities. As ecosystem engineers, their abiotic interactions leverage their ecological influence even further. This is particularly true if, by providing essential architectural structure in an otherwise less complex habitat, they support diverse communities of organisms. In addition, their burrowing behavior could potentially exert a major influence on sediment biogeochemistry and the breakdown and processing of deposited organic matter. With these dual trophic and engineering influences, they could have an extremely complex role in maintaining ecosystem structure and function.

These two families of fish represent two distinct groups of allogenic engineers, one that burrows in soft (clay) sediments along the continental shelf edge and upper slope (80–440 m depths), and one that excavates sandy substrata to expose carbonate rock at somewhat shallower depths (30–150 m). The first group includes tilefish *Lopholatilus chamaeleonticeps* (Fig. 1a), blueline tilefish *Caulolatilus microps* and the yellowedge grouper *Epinephelus flavolimbatus* [23–26] and the second, species such as red grouper

Epinephelus morio (Fig. 1b). Their excavations harbor suites of fish and invertebrate species whose abundances increase as a result, including the commercially important snowy grouper *Epinephelus niveatus*, vermilion snapper *Rhomboplites aurorubens,* black grouper *Mycteroperca bonaci* and spiny lobster *Panulirus argus* [27–29]. The burrows presumably function as refuges from predation for co-habitants [27] and, at least in the case of yellowedge grouper, serve as cleaning stations for the burrower [28], perhaps providing a positive feedback loop for the excavating activity. Tilefish build some of the larger burrows known in the ocean, ranging in size from 0.3 to 5 m in diameter and over a meter in depth [30]. The extreme manifestation of their engineering capacity is the formation of pueblos – virtual condominiums of burrows that are oriented horizontally in vertical cliffs [27,31,32]. Given the size and extent of these burrows, tilefish undoubtedly have a significant biogeochemical influence at the sediment–water interface (Box 2).

Potential problems resulting from fishing

Tilefish and grouper occupy habitat that is deep, often current-swept, and remote enough to make life-history information difficult to obtain. Thus, their ecology is poorly known. However, their association with discrete habitat features, coupled with advances in navigational equipment, such as global positioning systems, assures that fishermen can locate them with relative ease. In addition, their characteristic longevity and slow growth suggest that they are vulnerable to overexploitation and would need prolonged periods for recovery if overfished [33].

Because these fish species are likely to have multiple ecological roles, their loss could have effects that extend beyond their own demise to resonate throughout the ecosystem. Their management, therefore, requires particular sensitivity to their

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Box 2. Burrows as recycling sites for organic matter in the ocean

Recycling organic matter deposited in seafloor sediments is a key biogeochemical process in the ocean. Microorganisms contribute by decomposing complex chemically reduced organic matter into dissolved inorganic forms of carbon, nitrogen, phosphorus and other minor elements through the processes known alternatively as mineralization, remineralization or early diagenesis [a,b]. Burrowing animals have marked influences on the process in a number of ways [b–d].

- Their burrows increase the surface area of the sediment in contact with the water column, thus increasing oxygen availability for efficient oxidation of organic matter.
- Their movement in burrows (entering, exiting or other actions) increases aeration of sediments by displacing burrow waters. This also establishes a nutrient concentration gradient between the burrow waters overlying the sediments and the water column. The greater the concentration difference between the sediments and water column, the higher the rate of diffusion. This functions both to return

nutrients to the water column, where they become available to primary producers, and to remove sulfide, which inhibits microbial activity.

- Their burrow sediments often have higher concentrations of microorganisms than do adjacent sediments; recycling of organic matter is rapid [e].

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Glossary

Bycatch: (incidental catch): catch of species other than those targeted by the fishery (e.g. dolphins in tuna nets and sea turtles in shrimp nets).

Ecosystem engineers: species that substantially modify the physical structure of the abiotic or biotic materials forming the habitat, and thus directly or indirectly change the availability of resources to other species (a type of keystone species).

Epibenthic: inhabiting the surface of the sea floor.

Fishing down food webs: describes a pattern of exploitation in which entire trophic levels are systematically removed from ecosystems.

Keystone species: species that have large effects on community structure and function that are disproportionate relative to their abundance.

Longline fishery: fishery involving stationary fishing gear composed of fishing line fitted with multiple baited hooks and either buoyed at the surface to catch pelagic species, such as sharks and swordfish, or anchored on the bottom to catch demersal species, such as grouper and tilefish. Longlines can be several miles long.

Overfishing: removing fish at a rate greater than that sustainable by the fished population.

Quota: the maximum number or pounds of fish that can be legally landed in a given time period.

Regulatory discards: catch of targeted species that is nonetheless thrown overboard because it does not conform to fishery regulations (e.g. individuals that fall outside of accepted size limits by virtue of being too big or too small, egg-bearing females when females are protected).

Trawling: fishing involving mobile fishing gear consisting of a net towed behind a vessel, fit with doors mounted ahead of and on each side of the net to spread the mouth of the net laterally across the sea floor. It is used in the capture of bottom-associated species, such as shrimp, scallops and flounder.

Trophic cascade: the chain reaction of events resulting from the removal of higher trophic levels from communities that shifts the dominance and impacts of consumers to lower trophic levels.

function in communities. Unfortunately, conventional management more typically tracks only the abundance and catch sizes of exploited stocks and management plans are bereft of information on crucial life-history characteristics, ecological interactions, such as predation or competition, and general behavior [34].

Tilefish and grouper are compelling candidate 'poster children' for elucidating the problem of ecosystem-engineer exploitation. Their removal is likely to have both direct and indirect effects on biodiversity and biogeochemistry, given their dual status as top predators and ecosystem engineers. They occur in deep-water habitats that are likely to face increased human activity from fishing and from oil and gas exploration. Moreover, they and virtually all related species for which anything is known are either overfished, headed in that direction, or are at risk of extinction [27,28,31,32,35]. In addition, tilefish and grouper are currently linked by seemingly unrelated events occurring in the mid-Atlantic region and the Gulf of Mexico. The Mid-Atlantic Fishery Management Council is about to impose a significant QUOTA reduction for tilefish in response to its overfished status. At the same time, the Gulf of Mexico Fishery Management Council is considering moving the LONGLINE FISHERY further offshore, to depths beyond 50 fathoms [29]. It is conceivable that, if the longline fishery moves, fishing pressure on tilefish will increase in the Gulf to fill mid-Atlantic demands in seafood markets for this species. This could result in rapid declines of both tilefish and yellowedge grouper, the only two species occurring at those depths in sufficient numbers to support a fishery. The fishery would be short-lived, however, based on available knowledge about their biology.

Conclusion

During the past 25 years of critical attention paid to the consequences of fishing, there have been such significant lags between descriptive and empirical studies on the one hand, and public awareness on the other, that political responses to important issues have been small and, more often than not, late. But times are changing. The public's current understanding of fishing effects is such that it no longer dwells simply on population declines of fished species. It looks beyond single-species effects and simple gear-induced habitat damage to how these impacts ultimately affect the health of ecosystems.

We wish to bring to the public's consciousness the indirect consequences on habitat and biodiversity of overexploiting ecosystem engineers. We offer tilefish and grouper as cases in point, particularly relating to ocean habitats beyond the coast. Although the deeper regions of the ocean have special significance with regard to marine biodiversity, as noted by the National Research Council [36], the coastal and shallow regions more familiar to us still garner the most conservation support.

Ecosystem engineers, no matter what ocean realm they inhabit, merit increased scientific and conservation emphasis, because of the fundamental role that they play in shaping habitat and the dependent communities from microbes to predators. These fish provide wonderful examples of the astonishingly intricate relationships of the biotic and abiotic realms that were the focus of the celebration of biodiversity in 2001 [37]. They offer yet another compelling rationale for precautionary management that errs on the side of conservation rather than exploitation. Their loss, and the loss of other as yet unidentified ecosystem engineers, could well remove oases of structural and biological diversity from the ocean floor that cannot be restored in any meaningful way. Thus, we urge that policy makers and resource managers do not plunge ahead with policies unfettered by knowledge, but rather rethink their move to extend fishing and other kinds of resource extraction further offshore until they develop sustainable practices in the coastal ocean and better knowledge of the deep.

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The role of pocket gophers as subterranean ecosystem engineers

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Pocket gophers (Geomyidae) and their ecological cognates worldwide have profound impacts on ecosystems, from consuming vegetation to altering the soil physically. The rodents excavate vast burrow systems and deposit tailings in abandoned tunnels and on the ground surface. Energetic costs of excavations are extremely high, placing a premium on optimizing the location of burrows. The resulting disturbance patterns alter physical and biotic processes fundamentally. Recent studies reveal that the extensive excavations and their associated impacts generate a dynamic mosaic of nutrients and soil conditions that promotes diversity and maintains disturbance-dependent components of plant communities. Furthermore, these disturbances significantly accelerate erosion and downslope soil movement on shallow slopes and inhibit them on steep slopes.

Ecosystem engineers are those organisms that modify, maintain and create habitats [1]. The discussions about ecosystem engineering have become complex and, perhaps, trivialized by characterizing any influence on the environment as a form of engineering. Because all plants and animals affect the physical environment in some way, from their simple presence (autogenic; e.g. tree branches as habitats) to altering a substrate (allogenic; e.g. footprints on the surface of the soil), little is gained by classifying all organism–environment interactions as engineering.

Clearly, however, there are organisms that alter the physical environment significantly in nonincidental ways that strongly affect other organisms. Some – such as beavers, which construct dams to flood areas, providing protection and resources for themselves and generating a complex, diverse habitat for other organisms – truly engineer their environment [2]. If the concept of ecosystem engineers is to be useful, then biologically mediated change to the physical environment should be distinctive from processes that are strictly abiotic (e.g. soil movement resulting from rainsplash) and large relative to the purely physical processes operating in the system. Here, we show that subterranean mammals meet both of these criteria.

We focus on the ways in which subterranean herbivorous mammals (concentrating primarily on North American pocket gophers *Thomomys bottae*)