

# Food-web theory provides guidelines for marine conservation

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## Introduction

Vast, unfathomable, and the major biome of our planet, the oceans had an assumed capacity that defied limitation. Unfortunately, this old presumption turned out to be terribly wrong as technological advancement reduced the world's oceans to mortal size by amplifying man's inputs (pollution) and magnifying his outputs (fishing). And the fact of this magnification combined with evidence of man's early impacts (Jackson and Sala 2001; Jackson et al. 2001; Pandolfi et al. 2003) has rapidly overtaken our historical myth of the infinite sea. The last couple of decades in particular have been hard on marine ecosystems and our myths about their robustness have all but faded. Witness the vast hypoxic zone (a 20,000 km<sup>2</sup> ecological desert in the Gulf of Mexico), the numerous other coastal fiascos (e.g. Dayton et al. 1998; Jackson et al. 2001), and the recently reported collapse of many major fisheries to 10% of preindustrialized fishing levels (Myers and Worm 2003).

Much to our dismay, ecological disasters in marine systems are in full bloom. These disasters are unintended and uncontrolled experiments, and can ironically, further our understanding of the functioning and structure of marine systems, and may eventually help to save them. Indeed examples of fisheries overexploitation can yield important ecological data that has been extremely useful to ecologists and marine fisheries scientists and may contribute to a general understanding of marine populations and food webs. These are valuable but costly data for marine science as some of these changes may not be easily reversible. Continuing on the negative side, this acceleration in environmental

misery careful the urgency for better understanding of marine ecosystems and for the need to connect this knowledge to conservation and better resource management. Given this background, it is the particular and immediate challenge of ecology and of food-web theory in general to contribute knowledge that can be used to assess, and ultimately manage, marine ecosystems toward desirable states and away from disaster. At the very least, one would like to have available some early quantitative indicators of when systems are being threatened.

Our objective here is to briefly review some of this very costly data with the aim of illustrating ecological generalities that should be useful as guidelines for detecting and understanding human impacts on marine ecosystems. That is, we shall attempt to summarize generalities concerning human impacts on marine food webs (broadly defined here to include properties of communities and ecosystems) as they relate to our theoretical understanding of these webs, and illustrate the generalities with specific examples. The time for scholasticism is past. It is time to step up, move beyond ivory tower theory, and state what we know (however humble that may be) in a way that can be useful for marine conservation.

Although the theme of this chapter concerns food webs, and the latest initiative in fisheries management is the ecosystems perspective, we wish to point out that it is important not to ignore the simple results from single-species management and conservation. For example, three simple patterns that occur regularly with overfishing and are emblematic of impacts in the fishery are: (1) a decrease in the

average size of fish caught, (2) a decrease in the average age of fish caught, and (3) a decrease in the percentage abundance of super-spawners. We emphasize that guidelines based on facts such as these coming from single-species management should not be ignored, while plans are being made to manage from the ecosystem and food-webs perspective. That is to say, although the current momentum in fisheries management is toward the ecosystems perspective, we should not lose sight of what we have uncovered from single-species studies.

### **Dynamically propagated effects in food webs: interaction strength, and cascades**

Simple cause and effect is comforting. Pull lever A and get result B. A world of simple direct effects is safe and knowable. Things get scary when the levers are connected with hidden wires. Marine ecosystems are known to contain such hidden wires, and the most well-studied configuration of wires is described by the so-called trophic cascade. This is a problem whose origins trace back to a classic paper by Hairston et al. (1960), which gave an explanation for why the earth is green, and not an overgrazed desert. Simply put, the idea is that overgrazing by herbivores is prevented by the action of predatory carnivores keeping herbivore numbers in check. This simple notion of the remote control of plants by top carnivores (via herbivores) was sharpened by Carpenter and Kitchell (1974) and became enshrined as the cascade effect. Typically, food chains with three or more nodes of odd length (length measured as the number of nodes starting with primary producers) are dominated by primary producers while chains of even length are not. Thus, in fresh waters, when secondary predatory fish are present in ponds (chains of even length (4)) the water tends to be clearer than when such top predators are removed leaving only primary producers, herbivores, and autotrophs (odd length (3)). Likewise, if predators-of-top-predators are introduced (e.g. fishing: producing chains of odd length with humans at the top), the water turns greener. These things seem to be true, both in models and in field experiments,

and in the marine cases to be discussed below. It is the remote-control aspect of this that is worrying in its ambiguity in complex networks where simple linear chains are the exception and not the rule. Nonetheless, when the very strongest interactions line up in a linear chain, food-web theory provides a reasonable cautionary guideline as to the expected propagation of indirect outcomes resulting from manipulation (harvesting) of some component. Thus, if a top predator is harvested, and there is a supporting linear chain of strong interactions below it, one should expect abundances in successive links in this chain to be alternatively augmented and reduced.

### **Topology and dynamics**

The main caveat of the basic model result is that the chain is a simple linear one, rather than part of a more reticulated network. The latter describes a more realistic situation where the indirect effects are less clear. Studies with simple models that include omnivory links that bridge trophic levels and knit the simple chains into more complicated networks, confirm the intuitive hypothesis that these alternative pathways will tend to reduce the likelihood and magnitude of trophic cascades (e.g. McCann and Hastings 1997; McCann et al. 1998). These alternative pathways must be sufficiently weak so as to not be destabilizing in themselves, but strong enough to matter. This suggests that more highly connected systems with more omnivory links can be more resistant to trophic cascades. Note that this stabilizing effect of connectivity only superficially runs counter to classical dynamic arguments about stability-complexity (May 1973), where large numbers of species, higher connectivity, and strong interaction terms can be destabilizing. What harmonizes the result is the need for the secondary interactions to be sufficiently weak so as to not be destabilizing in themselves. That is, they cannot lead to Gershgorin disks with large radii. Recent analysis of the most detailed web to date for a Caribbean coral reef system (Bascompte et al. submitted) containing several hundred species and several thousand interaction coefficients shows that interaction strengths are often lognormally distributed so that

relatively few interactions are strong and the vast majority are weak (supporting previous results obtained from smaller webs; for example, Paine 1992; Wootton 1997). One can assume that most real ecological systems are built this way. That is, they are the product of dynamic selection, in that the configurations we see are ones that can persist long enough to be seen. Likewise, system configurations that are dynamically fragile are rarely if ever seen. Although not well publicized, this idea was demonstrated in models fairly early on (Sugihara 1982), where it was shown that dynamic selection is capable of reproducing some difficult food-web regularities, including rigid circuits (triangulation), intervality, and tree-like guild patterns. That is to say, more often than not, randomly assembled simple model systems (large, random, and initially unstable) tend to decay dynamically into nonrandom configurations having the peculiar topologies found in natural food webs. That random model assemblages settle down by dynamic selection (via extinctions) to smaller stable assemblages having many topological attributes (triangulation, etc.) that are seen in nature is not surprising perhaps. It is an example of self-organization.

In similar vein one may speculate that in real systems, potential trophic cascades (linear chains of strongly interacting species) would be rare, and would be more commonly associated with omnivory than otherwise expected. This was found to be true in the highly resolved Caribbean coral reef system cited above (Bascompte et al. in preparation). The cooccurrence of strong interactions in tri-trophic food chains (three trophic levels connected hierarchically by two strong predatory links) in this Caribbean coral reef food web was less frequent than expected by chance. Moreover, a significant proportion of these strongly interacting chains had a strong omnivory link between the top predator and the basal resource. That is, tri-trophic chains containing two successive strong predatory links were far rarer than expected by chance; and when they did occur, they had a much higher likelihood of being associated with omnivory than expected by chance. This, combined with the observation that marine food webs are thought to have a slightly higher degree of connectivity than webs from other biomes (Link 2002), suggests that

there may be some structural buffering operating against cascades in marine systems. This buffering may promote community persistence and stability (Fagan 1997; McCann and Hastings 1997; McCann et al. 1998). Nonetheless, as Bascompte et al. point out, the strong predatory chains or potential cascades that exist are nonrandomly associated with commercial top predators (sharks, in their Caribbean web), and thus cascades remain a concern for ecosystem management. This is, perhaps a heavier concern in temperate marine food webs as these webs have been shown to be simpler and have lower connectivity than tropical marine webs. Therefore, it is not surprising that trophic cascades appear to be more ubiquitous in temperate marine food webs as compared to tropical webs (such as those described in Hughes 1994; McClanahan 1995; Dulvy et al. 2004).

Thus, the configuration of the strongest interactions in natural food webs is not random, and although current information suggests that in general it is biased toward more stable configurations, the danger remains that human activity in marine webs can be selective in a way that targets fragile nodes and links. Awareness of known principles relating dynamics to the configuration of strong linkages in webs is essential to informed conservation and management, and speaks to the acknowledged need for the ecosystems perspective in marine fisheries management.

### Examples of dynamically propagated effects in marine food webs

We illustrate the relevance of these principles to marine conservation, with several cases of propagated effects involving strong interactors in marine food webs.

#### *Coastal-intertidal*

Starfishes (mostly *Pisaster*) in rocky intertidal food webs in the northeastern Pacific provide a paradigmatic example of cascades. They demonstrate the importance of strong interactors in the web and the consequences of their removal. In the coast of Washington, *Pisaster* is a top predator feeding mainly on the mussel *Mytilus californianus*, but also on barnacles and chitons. In the presence of

*Pisaster*, benthic dominance is shared among a number of species, including barnacles and algae. The classic experimental field work in this system conducted by Paine (1966, 1980) consisted of the removal of *Pisaster*, and showed that the removal of the top predator resulted in a successive replacement by more efficient occupiers of space. The endpoint of these successional changes was a community dominated overwhelmingly by *Mytilus*. Although the removal of the top predator was experimental, Paine's work was an early warning about the ecological risks and food-web impacts of species depletion.

Fishing provides many examples of propagated effects due to the removal of strong interactors from the web. A global-scale example is the often seen explosion in sea urchin populations that result from the commercial removal of a variety of large- and medium-sized sea urchin predators, such as sea otters and fishes. These cases show that following the removal of sea urchin predators, the abundant urchins can subsequently turn complex algal forests into marine barrens. Again, this is a global phenomenon which has happened, among other places, in the Mediterranean rocky sublittoral (Sala et al. 1998; Hereu 2004), and kelp forests in the north Atlantic (Witman and Sebens 1992; Vadas and Steneck 1995), Alaska (Estes and Duggins 1995; Estes et al. 1998), and New Zealand (Babcock et al. 1999; see also review by Pinnegar et al. 2000). In the relatively simple food webs in temperate seas, these trophic cascades generally result in a decrease of many other measures of ecological complexity (e.g. lower species richness and evenness).

Indeed, the hallmark example of trophic cascades in nature are the kelp forests in the Pacific northeast. In this system, sea otters are top predators, and these top predators feed upon benthic grazers, such as sea urchins and abalones. The consumption of sea urchins is especially important, since sea urchins are avid consumers of kelp. Kelps are the most important architectural species, providing a canopy that serves as refuge and provides microhabitats for an array of subordinate species. In the presence of sea otters, kelps will thrive and sea urchins generally shelter in crevices, feeding upon drift algae. The removal of the sea

otter by humans can result in increases of sea urchin abundance beyond a point where they leave shelter and eat the kelps themselves, eventually resulting in the destruction of the kelp canopy and the formation of a barren dominated by encrusting coralline algae (Estes and Duggins 1995).

Two major patterns that emerge for coastal marine food webs following the removal of strong interactors are as follows. Dramatic food-web-wide effects can ensue if: (1) the strong interactor is a predator on a food chain feeding upon a strong interactor which in turn feeds upon an architectural species (such as kelp), or (2) if the strong interactor is a predator feeding upon the dominant primary producer or architectural species. This should occur even though the strong interactor has low abundance.

#### *Coastal–Pelagic*

In some cases, dramatic changes in the abundance of the strongest interactors may not be caused by fisheries targeting them directly, but may result more indirectly from harvest of their prey. Here the effects may not be seen immediately and can involve significant time lags, especially with the tendency for longer response times (e.g. longer generation times) at higher trophic levels. An intriguing example is the delayed effect of the dramatic depletion (removal) of gray whales by oceanic fishing fleets in the 1960s and 1970s. These whales are a major prey item of transient orcas, both of which normally reside in the open ocean of the north Pacific. Decades after intensive hunting of gray whales, transient orcas moved to nearshore areas and shifted their feeding behavior to other marine mammals including sea otters (Estes et al. 1998; Springer et al. 2003). The reduction of sea otters are believed to have triggered the trophic cascade described above where kelp forests were eliminated and replaced by barrens (Estes et al. 1998).

#### *Some generalities*

When the food web contains an embedded three-species food chain (defined by two strong links) there is a higher likelihood of trophic cascades. For example, in a recent study of a Caribbean coral reef food web, where the top predators are sharks,

groupers, and jacks; medium consumers are groupers; and basal species are herbivorous fishes, such as parrotfish and surgeonfish (Bascompte et al. in preparation), it was found that sharks and other top predators are overrepresented in strongly interacting food chains. Humans tend to selectively target these strong interactors first, because of their higher economic value (e.g. Pauly et al. 1998; Sala et al. 2004); and this has implications for food web structure and dynamics. The removal of sharks may have resulted in a decline of the parrotfish populations via trophic cascade (Bascompte et al. in preparation). The decline of the parrotfish has been implicated in the ecological shift of Caribbean reefs from coral to algal dominated (Hughes 1994). Thus the removal of reef sharks by fishing may have contributed to a trophic cascade that extends to lower trophic levels and involves competitive interactions between algae and corals. In this example, the selective depletion of the strongest interactors increased the likelihood of propagating trophic cascades (Bascompte et al. in preparation). Thus, although as a group marine food webs may have some structural buffering (higher connectance and omnivory), fishing remains a threat that promotes instability by virtue of its tendency toward targeted removal of species at higher trophic levels.

As previously mentioned, the effects of removing a strongly interacting species is more evident and immediate in simpler, less connected food webs (specifically webs having lower connectance). The intuitive explanation for the vulnerability of simple webs is their lack of ecological redundancy, with the caveat that the redundant secondary interactions cannot be too strong. This most likely accounts for the relative ubiquity of trophic cascades in temperate marine food webs as compared to tropical food webs.

Not all food web components are equally important with regard to web dynamics. Strong interactors can maintain food-web stability, and their removal should be averted if the goal is to preserve complex food webs. Experimental work in the eastern Pacific intertidal dealing with only four species interactions suggests that non-keystone species have only minor effects on the food web, although after keystone species removal

they can partly compensate for the reduced predation (Navarrete and Menge 1996). Other experimental work has indicated the potential importance of non-keystone predators in the absence of the keystone species (Dayton 1971; Paine 1971). Indeed, some weak interactors may have strong effects due to great field densities or to their link frequency, and their removal could also cause food-web instability (McCann et al. 1998; Kokkoris et al. 1999). How to distinguish these weak interactors with potentially destabilizing effects is another question. No matter what, pretending that the removal of small, seemingly insignificant species will have no significant effects on food webs is, at this point, an act of hubris and eventually risky. More studies are needed that explore the role of weak interactors in real, speciose food webs.

The effects of the removal of weak interactors are not as predictable as the effects of the removal of strong interactors (Paine 1980). On a per capita basis, the absence of a weak interactor in a species-rich food web should not have a significant effect on the web. From a real-world perspective and on a population basis, the removal of weak interactors can have unpredictable effects, these being basically a function of numbers. This uncertainty is enhanced by the fact that weak interactions generally show greater variance than strong interactions (Berlow 1999). Moreover, there is consensus that weak interactors may have important stabilizing roles in food webs (e.g. McCann et al. 1998). Although small species often have per capita interaction strengths similar or smaller than larger species, their tendency to have greater densities in the field increases their potential food-web impacts (Sala and Graham 2002). There is clear evidence of significant food-web-wide impacts due to striking increase in the population of weak interactors. Such increase can be caused by release from predation after the elimination of a strong predator, or to other factors such as environmental fluctuations. For example, amphipods are weak interactors in California kelp forests, and under usual densities their grazing has insignificant effects on the kelps (Sala and Graham 2002), but during El Niño events amphipod populations can exhibit explosive increases and eat out entire sections of the kelp

forest (Graham 2000). Another example of the key role of species with relatively low biomass and weak per capita interaction strength is symbiotic zooxanthellae in reef corals (Knowlton and Rorer 2003). The loss of just a few species could enhance coral bleaching during prolonged warming events and shift the ecological state of coral reefs. Although these examples do not involve trophic cascades, they highlight the potential for trophic cascades when a species interacting with an architectural species is not a strong interactor but has a strong impact on the basis of extraordinary abundance.

### Humans versus other marine top predators

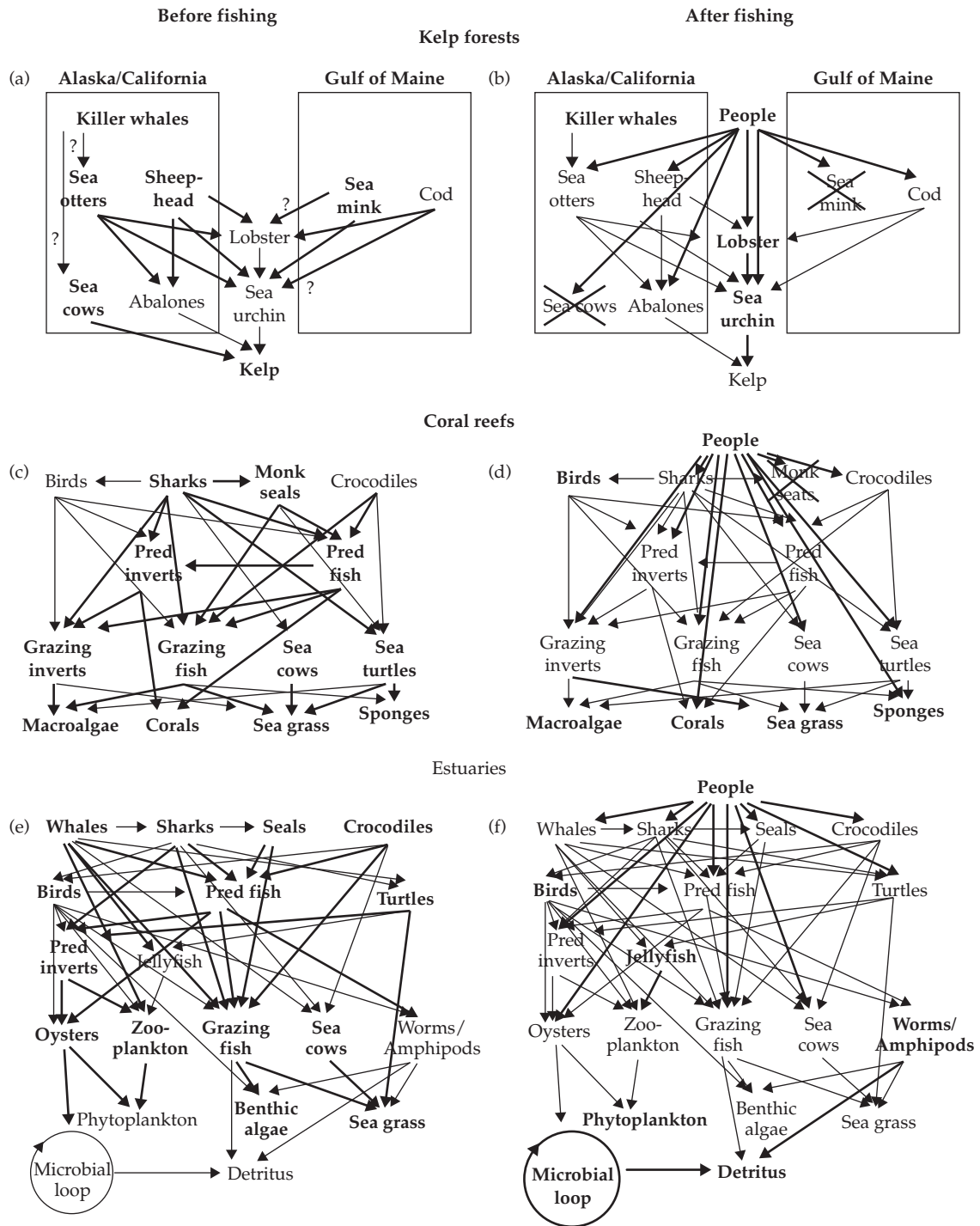
In the northwest Mediterranean subtidal, it has been estimated that humans account for 11% of the trophic links for a food web with relatively low taxonomic resolution (Sala 2004). In the same web, top predators such as monk seals and sharks account for 24% of the links. Unlike other top predators, however, humans have the capability to reduce the complexity of food webs by (1) effectively eliminating other top predators, (2) reducing the abundance of many other species as a consequence of direct trophic effects, and (3) reducing the number of functional trophic levels (i.e. trophic levels containing species at abundances such that they still perform their ecological roles) (e.g. Dayton et al. 1998; Jackson et al. 2001; Pandolfi et al. 2003). Indeed, trophic levels are reduced to the point where even fish parasites are less diverse and abundant in fished areas than in marine reserves (C. F. Boudouresque, personal communication).

Food webs in the presence of marine top predators generally exhibit greater complexity than in their absence (e.g. Estes et al. 1998; Sala et al. 1998). Food webs that have been degraded by overfishing have lost the top-down regulation exerted by other predators and are increasingly influenced by bottom-up factors (Figure 13.1) (Jackson et al. 2001). Although humans exercise a formidable top-down control on marine food webs, unlike other top predators we increase the likelihood of large fluctuations and instability in food-web structure. For instance, the removal of herbivores in estuarine food webs subject to eutrophication can result in

planktonic algal blooms, and the removal of large herbivores in tropical coastal food webs can facilitate the appearance of sea grass disease (Jackson et al. 2001). One of the few examples of another top predator reducing the complexity of a food web is that of transient orcas in the north Pacific which, by reducing the abundance of sea otters, enhance an increase in sea urchin abundance and, by cascading effects, a decrease in kelp cover and a reduction of overall food-web complexity (Estes et al. 1998). Perhaps the reason in this case is that transient orcas, like humans, moved into coastal ecosystems relatively recently (Springer et al. 2003). Humans also have the advantage of agricultural subsidies, in turn subsidized by oil. This might be the single most important reason why humans are unlike marine top predators and their effects on food webs are remarkably different. Lotka-Volterra dynamics and population regulation can operate for low-mobility marine predators, but human populations so far do not appear to be regulated by changes in the abundance of lower trophic level marine prey. Ironically, humans are using fossil food webs to exploit present marine food webs.

### Overfishing and inverting food-web structure

Ecological textbooks portray the classic pyramidal food-web structure, where the biomass of a trophic level is always lower than the biomass of the trophic level immediately underneath. The reasons are purely energetic. While this seems to be a general pattern in terrestrial food webs, in aquatic food webs the biomass of an upper trophic level can be higher than the biomass of a lower trophic level upon which it feeds, if the lower trophic level has sufficiently rapid turnover. This is the case of the coral reef food web of the northwest Hawaiian archipelago, a large marine protected area where the biomass of top predatory fishes is 54% of total fish biomass (Friedlander and DeMartini 2002). In contrast, in the main Hawaiian Islands, subject to intense fishing, the biomass of top predators is only 3%. Top predatory fishes are not exclusively piscivorous, hence the differences in biomass between top predators and all prey will be smaller than those for fishes alone. An interesting result



**Figure 13.1** Schematic representation of selected marine food webs before and after intense fishing from Jackson et al. (2001).

from that study is that, although the biomass of top predators is overwhelmingly greater than that of lower trophic levels in the northwest Hawaiian archipelago, the biomass of its lower trophic levels is still greater than that in fished areas. This supports the idea that humans are often the strongest interactors in marine food webs. These extraordinary differences in food-web structure between areas with and without fishing suggest that our knowledge of marine food webs is probably biased toward simplified food webs, as our baselines for "pristine" systems shift. When top predators are eliminated, increases in abundance of weaker interacting prey may cause significant population impacts. The organization of the food web also shifts: the strength of top-down control is diminished and the importance of bottom-up control enhanced. We do not claim that this is necessarily a general pattern in marine food webs; nonetheless, it illustrates the danger of generalizing missing important functional components from webs.

### **Species relative abundance and evenness as an indicator of food-web complexity**

The distribution of species relative abundance in food webs can also provide a simple means of measuring the health and vulnerability of ecosystems. Species abundance distributions reflect the complexity of the underlying food web and its associated dendrogram of niche similarities (Sugihara et al. 2003). Simpler food webs (e.g. two trophic levels based on single ecological resources) are expected to have very uneven abundance distributions and are dominated by a few species; whereas more complex systems will have more equitable relative abundance distributions (Sugihara et al. 2003). This applies to both between- and within-system comparisons. Thus, the overlying abundance pattern is a reflection of the functional organization of food webs. Equitable abundances imply symmetrical dendrograms of niche similarity. Such symmetrical or evenly branched dendrograms correspond to an underlying niche space that is complex and has many different structuring forces (e.g. a diverse resource base) that give rise to a partial ordering of niche similarities (apples and

oranges). This reflects the many more-or-less independent ways of making a living, which is an expression of the underlying heterogeneity in the "realized" or "functional" structure of the food web. Thus, the connectivity of the "effective" linkages has a more spread-out look as in scale-free networks, as opposed to uniformly dense as in random networks. The heterogeneity implied by scale-free structure in food webs corresponds to more evenly branched niche similarity dendrograms. Using the approach advocated earlier, along succession and for a particular food web belonging to a relatively stable environment, we would expect dendrograms to become more evenly branched to reflect the partial ordering of niches (apples and oranges aspect), abundance distributions to become more equitable, and food webs to become more complex (less homogeneously connected). However, this may not be true for high-energy systems where the endpoint of succession is characterized by the dominance of one or few species.

Evenness declines when the underlying functional portrait simplifies, and the niches become homogenized in that they revert from a "partial ordering" to a simplified "perfect ordering." Such homogenization occurs when a single overwhelmingly strong factor is imposed on the system. Thus, if a previously complex system is subjected to a strong homogenizing force (e.g. intense pollution), a formerly complex partially ordered system can become a perfect ordering. Species can now be appropriately ranked in relation to how they respond to the single dominant structuring force.

The predicted decrease in equitability in abundances that comes from simplification of the underlying niche space via homogenization of niches is a phenomenon that has enormous empirical support. The reduction of evenness that accompanies human disturbance (such as nutrient enrichments or other forms of homogenizing stress) is one of the most robust generalizations in ecology.

### **Acceleration and homogenization of marine food webs**

Odum (1969) and Margalef (1997) suggested the general pattern that average growth rates of

organisms will decrease with successional maturity, and that mature communities will have smaller production:biomass (P:B) ratios. In this scheme, early successional stages, characterized by fast growing opportunistic species, are replaced by slower growing, tough competitors. There are exceptions of course, but this is a good generality. Fishing acts the opposite way, selectively removing the top predators first, and gradually moving down to target lower levels in the food web (Pauly et al. 1998; Sala et al. 2004). The removal of predators accelerates the turnover of food webs by (1) reducing the biomass in species with lower turnover (P:B ratio), and (2) eventually triggering an increase in the biomass of prey with higher turnover. The end result is an increase in the turnover of the entire food web.

Accelerated growth rates often lead to destabilization of systems. A very general and robust result from ecological theory concerns the destabilizing effect of accelerating growth rates. This idea was discussed early on by Rosenzweig (1971) in his paradox of enrichment, and has emerged as one of the more robust generalities of ecological theory (May 1974). Resource enrichment (e.g. nutrient loading) provoke higher growth rates that destabilize the system and lead to species loss and reduced equitability. In the process of selectively culling species with lower growth rates, fishing increases the average growth rates in food webs, which are also more likely to be regulated by bottom-up processes, and exhibit greater fluctuation and instability. Chronic fishing pressure does not allow marine food webs to exhibit lengthy successional dynamics, and it can lock food-web structure into one dominated by high turnover species. The endpoint of the degradation dynamics may be (as it has been already observed in estuarine systems) a food web overwhelmingly dominated by planktonic organisms, such as jellyfish and protists (Jackson et al. 2001). The functional structure of the web is lost after the ecological extinction of entire trophic levels. While on land higher turnover means greater agricultural production, in the sea it is not clear whether higher turnover always means higher production available to humans. We believe that understanding the relationship between food web turnover and food

availability is going to be a crucial step in fisheries management and marine conservation in general.

The decline of top predators, the rise of high turnover species, and the microbial loop represent an acceleration and functional homogenization of the food web. An increasingly important factor in this homogenization of nature is the spread of invasive species. Biological invasions have the potential to homogenize entire food webs, and shift species abundance distributions to more skewed ones. Although connectivity and number of trophic links in an invaded food web might be maintained, the community-wide ecological effects of affected species can be dramatically altered. Invasive species including crabs (Grosholz et al. 2000), snails (Steneck and Carlton 2001), and algae (Meinesz 2002; Boudouresque and Verlaque 2002) can affect all trophic levels. An extreme example of the homogenization and acceleration of a marine food web after a biological invasion is the small planktonic ctenophore *Mnemiopsis* in the Black Sea. The introduction of this exotic species caused dramatic reductions in fish biomass and explosive increases of gelatinous zooplankton (Shiganova and Bulgakova 2000) resulting in overall reduced equitability in abundances in the web.

In conclusion, humans universally accelerate marine food webs by (1) eliminating food-web components with slow dynamics (low turnover) and enhancing dominance of high-turnover species, and (2) accelerating the dispersal of locally weak interactors (but potentially strong somewhere else), which probably would have failed to disperse and colonize on their own during ecological or evolutionary timescales. We are also accelerating evolution by increasing by several orders of magnitude the number of natural experiments on species interactions in ecological timescales (Palumbi 2002). In other words, enhancing the links between food webs entails the acceleration of the dynamics within the webs. Inevitably, the accretion of structure and information in human webs (mostly urban) has to cause an acceleration and homogenization of the biosphere, including marine food webs, besides the acceleration of the oxidation of the necrosphere (Margalef 1991). Such are the consequences of ecological globalization.

### Human impacts reverse successional trends

There are regularities commonly found in ecological successions. Some general changes occurring from early to mature successional stages are increases in species richness, number of trophic levels, biomass of higher trophic levels, total biomass, and three-dimensional biogenic structure (Margalef 1997). Although these regularities have been well documented in phytoplankton, we know very little for most other marine systems (but see Grigg and Maragos 1974; Grigg 1983). The old diversity concept, understood as the distributions of abundances into species in food webs (also called "ecodiversity," to distinguish it from "biodiversity"), often increases along terrestrial succession as well (Margalef 1997). In marine food webs, ecodiversity may show a unimodal relationship. In an underwater lava flow in Hawaii, ecodiversity of colonizing coral communities increased with time but decreased before reaching the successional endpoint, due to extreme competition for space, which led to monopolization by a few dominant species (Grigg and Maragos 1974). In any case, the increase in species richness in a food web over successional time will inevitably result in the multiplication of the number of species dependent or subordinate to those already present, and therefore in an increase of food-web complexity.

Although we know very little of changes in marine food-web properties in successions, there is evidence of short-term (annual) successions in planktonic and benthic communities. In a Mediterranean rocky sublittoral food web, algal assemblages undergo striking seasonal changes in structure (Ballesteros 1991; Sala and Boudouresque 1997). Although algal species composition does not change significantly, total biomass shifts from an annual low where biomass is partitioned quite evenly among a large number of species (high ecodiversity), to a peak where biomass is monopolized by a few large species (low ecodiversity) (Ballesteros 1991). These seasonal changes in algal biomass are immediately followed by similar changes in epifaunal invertebrates (Sala 1997). The biomass of sea urchins and fishes, in contrast, does

not exhibit significant seasonal changes, although their prey do (García-Rubies 1996; Sala and Zabala 1996). Although the species composition and topology of this food web does not change, the biomass of many of its components changes dramatically throughout the year. We would expect that changes in prey items cause subsequent changes in interaction strengths. Therefore the structure of the food web exhibits seasonal changes in structure and complexity. While these changes occur at a scale of months, longer-term changes can occur due to invasions of exotic species and interannual variations in recruitment of important species, such as sea urchins, among other factors (e.g. Sala 2004).

Similar changes in food-web structure occur at pluriannual scales in Californian giant kelp forests. The most mature successional stage of these kelp forests is virtually a monoculture of the giant kelp, *Macrocystis pyrifera* (Dayton et al. 1984, 1992). Every few years, strong storms or El Niño Southern Oscillation episodes virtually destroy the giant kelp canopy, resetting the food web to early successional stages dominated by undercanopy or turf algae (e.g. Dayton et al. 1992). In both the Mediterranean and Californian food webs, successional trajectories involve an increase in three-dimensional biogenic structure, a recreation of ecological niches that allows the recruitment of new species in the food web, and an increase in total biomass and total production. Regardless of what triggers these asymmetrical changes of food-web complexity (e.g. disturbances or seasonal environmental cycles), complexity clearly increases along succession.

Human impacts (as well as other kinds of catastrophic disturbance) nearly always reverse successional trends. In the temperate food webs described above, fishing can cause sea urchin population explosions and the virtual elimination of complex algal forests (Estes et al. 1998; Sala et al. 1998; Steneck 1998). In the Mediterranean food web, increased sea urchin grazing reduces the biomass and diversity of the benthic community, and reduces the differences between the endpoints of the annual succession: less total algal biomass, less structural complexity, and much smaller epifaunal biomasses (Verlaque 1987; Hereu 2004).

Most of the benthic dynamics in sea urchin barrens lay on a turf of microscopic primary producers, such as benthic diatoms, which is continuously grazed by the urchins. Fishing marine food webs thus accelerates the system by increasing the global P:B ratio. The number of species, the number of trophic links, and complexity in general also decrease with increased fishing. In addition, three-dimensional biogenic structure can drop dramatically because of trophic cascades. These cascades have the strongest food-web-side impacts when the removal of a predator results in the elimination of architectural species. The removal of the architectural species in turn has effects on the recruitment and feeding behavior of many other species. In the case of coral reefs, a decline in coral cover has been shown to cause striking declines in reef fish species richness and abundance (Jones et al. 2004).

Invasive species homogenize food webs by truncating the frequency distribution of species abundance, eventually turning it into an extremely skewed distribution dominated by the invader. Despite the introduction of one more species, changes arising from invasion generally end up in local extinctions and decline in species richness. A paradigmatic example is the transformation of Mediterranean sublittoral habitats after the introduction of the tropical green alga *Caulerpa taxifolia*. In the absence of the invader, Mediterranean sublittoral food webs are composed of an extremely diverse (up to >100 algal species in only 400 cm<sup>2</sup>) and dynamic benthos, exhibiting annual and pluriannual successional dynamics (see above). After the invasion, the same habitats become a green carpet, and diversity plummets to very low values (Meinesz 2002). The dominance of space inhibits significant successional changes on the local communities. Finally, because *C. taxifolia* is a chemically defended species, the number and the diversity of trophic links also decreases.

The difference between nonanthropogenic and anthropogenic disturbance is that the former are generally pulse disturbances and seldom cause local extinctions, allowing the food web to restart ecological succession post-disturbance. In contrast, most human disturbances are chronic and cause local and even global extinctions. In many cases, this chronic pressure does not allow the ecological

communities to move along succession and locks them in early successional states as long as pressure is applied. But the removal of the disturbance may not be sufficient to allow the community to exhibit significant successional changes. This is a key point that has tremendous consequences for the conservation of marine food webs, as we will discuss below.

### Environmental gradients and human impacts

Environmental gradients can also produce changes in the structure and dynamics of marine food webs and hence determine the strength and scale of human impacts. We would expect the complexity of food webs to be greater in oligotrophic systems (e.g. coral reefs) than in systems subject to high-energy/nutrient inputs (e.g. upwelling areas). The number of species and trophic levels, and thus the number of trophic links and functional subwebs are expected to be greater in low-energy systems, while the likelihood of monocultures or dominance of a few architectural species is greater in high-energy systems. Food-web structural diversity and evenness will hence be higher in low-energy systems. For example, food web complexity is lower in a high-nutrient Californian kelp forest overwhelmingly dominated by the biomass of one species, the giant kelp, than in an oligotrophic Mediterranean algal community with greater species richness and equitability (Graham 2004; Sala 2004). There also exist differences within systems. For instance, the lower trophic levels of Caribbean coral reefs were dominated by single species of *Acropora* (a coral with relatively high growth rate) in shallow habitats subject to strong wave energy, whereas in deeper, calmer habitats coral abundance was shared more evenly among tens of species (e.g. Goreau 1959). Anthropogenic disturbances have turned the shallow reefs previously dominated by *Acropora* into algal beds also dominated by a few species with yet higher turnover (Hughes 1994; Knowlton 2001). In the Mediterranean sublittoral, benthic communities exhibit an amazing gradient in structure and dynamics over a mere 30-m distance along a vertical wall. Shallow food webs are dominated by a few species of algae with strong seasonal dynamics, while deeper webs

are dominated by a diverse community of suspension feeders (including sponges, ascidians, and cnidarians) with slow, pluriannual dynamics (Garrabou et al. 2002). This strong biological gradient is explained by a strong gradient in physico-chemical conditions: shallow communities are exposed to higher-energy inputs (more light and wave motion) than deeper ones.

Fluctuations in food-web complexity are expected to be higher in high-energy systems. The above differences in food-web structure, specially for benthic webs, partly occur because high-energy systems allow for dominance of species with high turnover, whereas in low-energy systems surface-dependent strategies are based mainly on the slow accretion of biomass and nonfunctional structures, such as the biogenic matrix of a coral reef (Zabala and Ballesteros 1989). Food webs in higher-energy systems have a faster turnover (P:B ratio) than these in low-energy systems. This links structure and dynamics of food webs within a particular set of environmental conditions: complex food webs are “decelerated” and exhibit slow dynamics, while degraded food webs have simpler structure and are “accelerated” (higher turnover and instability).

What systems are thus more susceptible to greater rates of change and acceleration due to human activities? We would expect that human activities of similar intensity cause greater damage in systems with less complexity because they have reduced functional redundancy. Therefore, tropical oligotrophic food webs such as coral reefs would be more resistant to disturbance and less prone to fluctuation due to the reasons explained above. For instance, tropical systems would be less likely to exhibit trophic cascades. However, based on the environmental constraints, low-energy systems will suffer a greater rate of change than high-energy systems under a similar disturbance. In other words, the loss of complexity and information will be relatively greater in a “decelerated” system. Therefore, it seems that the best question to ask is not what food webs can we exploit, but “how are food webs going to respond to human activities on the basis of their intrinsic and environmental constraints?” The answer to this question will help determine

potential impacts of human activities and help prevent them.

### Conservation of marine food webs

It should be said that conservation (or management) is a value-laden concept. Nonexploitative uses of marine ecosystems are optimal with complex food webs (e.g. a diver will spend a vacation in an unfished coral reef rather than in an overfished reef). In contrast, social groups with sole interest in industrial exploitative activities, such as fishing, may aim at less complex food webs in order to target single species with large P:B ratios. The simplest approach is to eliminate marine top predators to reduce competition for prey (Yodzis 2001), following the disastrous example of previous wildlife management in the continental US. A downside is that simpler food webs are also more prone to instability and fluctuations. Moreover, even though simplified webs may not be a goal in itself, under current fishing practices marine food webs will inevitably be simplified and degraded. It is still not clear which food-web complexity levels produce optimal catches. Will fishing be more productive by exploiting accelerated food webs or decelerated ones? Accelerated food webs are dominated by high P:B ratios, but total production available to humans may be lower, than in complex webs composed of more trophic levels. This is an unexplored area that deserves serious attention.

Do we want to preserve homogeneous ecosystems with complex food webs, or mosaics of patches at different successional stages? Conservation could be interpreted as the preservation of something stable, but food webs may be stable only at short temporal scales. Thus the goal of marine conservation should not be the preservation of a particular food-web structure, because this structure will inevitably change over time, and the cost:benefit expectations of the public may be lowered. For instance, a coral reef can be restored to former levels of complexity by an expensive and time consuming management process, with the involvement of local communities whose goal is to enjoy both the intrinsic and instrumental values of the reef. However, the reef can be torn to pieces by a hurricane, and unless the local species pool and

the environmental conditions are right, it will not recover without further intervention. The public may be disappointed, blame managers and scientists, and be skeptical of further restoration efforts. Regardless of the goals of conservation efforts, the public and the decisionmakers need to understand the dynamic nature of ecological communities.

A better, albeit complex, approach for identifying marine conservation goals is to integrate ecological succession and food-web dynamics, as we have attempted here. Anthropogenic degradation of food webs is similar to catastrophic disturbances, although anthropogenic disturbances are chronic. In any event, anthropogenic disturbances disassemble marine food webs, and conservation efforts that reduce or eliminate these disturbances eventually result in the reassembly of the webs. The process can be viewed as a typical ecological succession where a food web acquires complexity over long-time periods, asymptotically decreasing the rate of change, to lose it more or less catastrophically, following anthropogenic disturbance in shorter timescales. When the disturbance is past, the food web slowly regains complexity, the time-scale depending on the post-disturbance starting point. A good example is the changes in fish biomass in the presence and the absence of fishing. The recovery of predatory fish involves much longer timescales than their removal by fishing (Russ and Alcala 1996). And, although small species with fast turnover can recover to former unexploited biomass in coastal reserves within a few years, the complete recovery of higher trophic level predators can take more than 25 years (Micheli et al. in press). Marine conservation science, as successional dynamics, is asymmetrical: we know a great deal about the loss of complexity, but relatively little about the slow recovery of that complexity.

*The goal of marine conservation should therefore be to preserve the global initial conditions so that food webs can self-organize and respond naturally to environmental change.* Global initial conditions include availability of subsidies, favorable environments, and low level of chronic disturbance, among others. Food webs isolated from all possible subsidies are less resistant to disturbance and indeed more likely to be simplified. These subsidies include trophic subsidies as well as the availability of

species for colonization at the right successional time, including strong interactors and keystone species. For instance, species with relatively low dispersal cannot recover locally (e.g. in a marine reserve) after being eliminated if the regional pool is exhausted. However, this simple fact has been ignored in many conservation works, and used as an argument by marine reserve opponents to conclude that reserves do not work and should be eliminated. The metapopulation and metacommunity aspects of marine food webs are essential for understanding successional dynamics in degraded webs. In some specific cases, the recovery of top predators can be enhanced through human intervention (e.g. sea otter reintroductions in central California), but in many others these interventions will not prove cost-effective. Future studies should explore the rates of recovery of marine food webs, not just single species, embedded in a spatial mosaic of webs at varying levels of complexity. Meanwhile, we should aim at ensuring that strong interactors are available, and to preserve functional trophic levels or food-web modules (*sensu* Paine 1980). Diagnosing health and measuring success of management can be carried out using simple measures of food-web complexity. We believe developing a restoration ecology based on successional dynamics, and with practical implications at relevant scales, is an important challenge for food-web students and conservation biologists.

### **Future directions: the linkage between marine food webs and human networks**

Science alone will not solve the conservation problems of marine ecosystems. Food-web theory and practice can provide decisionmakers with useful information and recommendations vis-à-vis the impacts of anthropogenic activities on marine ecosystems. However, these data and recommendations will be weighted against socioeconomic considerations before decisions are made. A major problem, which in many cases has resulted in counterproductive actions, is that food webs and human societal networks have seldom been analyzed in an integrated way. In most food-web studies which include humans, the socioeconomic

intricacies that regulate the interaction strength among humans tend to be ignored. In other words, although economies and marine food webs are linked, food-web models and economic models are not linked. We urgently need to develop an integrated network science that links human dynamic actions and sociopolitical networks to ecological networks and other earth science systems.

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