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Review

Key Features and Context-Dependence of Fishery-Induced Trophic Cascades

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Abstract: *Trophic cascades triggered by fishing have profound implications for marine ecosystems and the socioeconomic systems that depend on them. With the number of reported cases quickly growing, key features and commonalities have emerged. Fishery-induced trophic cascades often display differential response times and nonlinear trajectories among trophic levels and can be accompanied by shifts in alternative states. Furthermore, their magnitude appears to be context dependent, varying as a function of species diversity, regional oceanography, local physical disturbance, habitat complexity, and the nature of the fishery itself. To conserve and manage exploited marine ecosystems, there is a pressing need for an improved understanding of the conditions that promote or inhibit the cascading consequences of fishing. Future research should investigate how the trophic effects of fishing interact with other human disturbances, identify strongly interacting species and ecosystem features that confer resilience to exploitation, determine ranges of predator depletion that elicit trophic cascades, pinpoint antecedents that signal ecosystem state shifts, and quantify variation in trophic rates across oceanographic conditions. This information will advance predictive models designed to forecast the trophic effects of fishing and will allow managers to better anticipate and avoid fishery-induced trophic cascades.*

Keywords: alternative states, fishing, food web, harvest, indirect effects, predation, trophic cascade

Atributos Clave y Dependencia del Contexto de Cascadas Tróficas Inducidas por Pesquerías

Resumen: *Las cascadas tróficas disparadas por la pesca tienen implicaciones profundas para los ecosistemas marinos y los sistemas socioeconómicos que dependen de ellos. Con el número de casos reportados incrementando rápidamente, han emergido atributos clave y similitudes. Las cascadas tróficas inducidas por pesquerías a menudo presentan tiempos de respuesta diferenciales y trayectorias no lineales entre los niveles tróficos y pueden ser acompañados por cambios en el estado de los ecosistemas. Más aun, su magnitud parece ser dependiente del contexto, variando como una función de la diversidad de especies, la oceanografía regional, la perturbación física local, la complejidad del hábitat y la naturaleza de la pesquería misma. Para conservar y manejar ecosistemas marinos explotados, existe una necesidad imperiosa por mejorar el entendimiento de las condiciones que promueven o inhiben las consecuencias en cascada de la pesca. Más aun, la investigación futura debe examinar la interacción de los efectos tróficos de la pesca con otras perturbaciones humanas, identificar especies estrechamente interactuantes y los atributos del ecosistema que confieren resiliencia a la explotación, determinar los rangos de disminución de depredadores que provoca las*

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cascadas tróficas, identificar antecedentes que indiquen cambios de estado de los ecosistemas y cuantificar la variación en las tasas tróficas en condiciones oceanográficas diferentes. Esta información mejorará los modelos predictivos diseñados para estimar los efectos tróficos de la pesca y permitirá que los manejadores anticipen y eviten las cascadas tróficas inducidas por pesquerías.

Palabras Clave: cascada trófica, depredación, efectos indirectos, estados alternativos, pesca, red alimenticia

Introduction

Mounting evidence suggests that overfishing can trigger a cascade of indirect effects throughout marine food webs, altering marine ecosystems and the social and economic systems that depend on them. What remains unclear is where, when, and under what conditions the cascading effects of fishing are likely to occur. Given emerging evidence of their context-dependent effects (Micheli et al. 2005; Frank et al. 2007; Shears et al. 2008), we asked, What conditions predictably drive the cascading consequences of fishing?

In the oceans, fishing has disproportionately targeted and reduced the abundance of apex predators (Jackson et al. 2001). Although debate exists over the magnitude of depletion, there is little doubt that major and persistent declines of exploited stocks are most often caused by the direct effects of fishing (Hutchings 2000; Scheffer et al. 2005). Now, growing evidence from a diversity of marine ecosystems suggests that the effects of fisheries extend well beyond exploited stocks. An increasing number of cases report that the reduction of dominant consumers from the sea can profoundly alter marine food webs and ecosystem dynamics via a cascade of trophic interactions.

Some of the earliest empirical evidence of trophic cascades—the indirect effect of predators on primary producers via a reduction in herbivores (Paine 1980)—comes from the depletion of predators in marine systems (Estes & Palmisano 1974). Here, we specifically define *fishery-induced trophic cascades* (FITCs) as the indirect effects of exploiting marine predators on the abundance, biomass, or productivity of species, or species assemblages, two or more trophic links below the exploited predator (Fig. 1). Because we considered community and individual species responses, our definition of FITCs includes both community- and species-level cascades. Our definition explicitly treats humans as an integral component of marine food webs and highlights the external factors known to drive human behavior and ultimately trigger FITCs. It also leads to the prediction that by reducing ocean predators and weakening their trophic role, the effects of fishing may propagate down food webs and drive alternating patterns of abundance at consecutively lower trophic levels.

Humans have been exploiting consumers from the sea and thereby modifying marine food webs for millennia (Jackson et al. 2001). Given that we continue to exploit ocean predators with accelerating efficiency, understanding how the role of consumer-driven forces vary as a function of productivity, management policies, and abiotic conditions deserves urgent attention. We evaluated early reports and recent evidence of FITCs, examined their key features and impacts, and identified factors that may alter their strength. We also identified vital information gaps and future research needs that will improve our ability to forecast FITCs, mitigate their effects, and inform management strategies that support resilient marine ecosystems.

Impacts of FITCs

Widespread evidence of the cascading effects of fishing exists from a diversity of marine ecosystems, from intertidal shores and subtidal kelp forests to tropical coral reefs and the open ocean (see Supporting Information). Equally, cases exist in which intense fishing has not triggered cascading effects (Supporting Information). By synthesizing cases across ecosystems, key features of FITCs emerged, including time lags and nonlinear responses among trophic levels; alternative state dynamics; size-mediated effects; prevalence of parasitism and disease; broad ecosystem-level consequences; and profound context-dependent effects.

Time Lags, Nonlinearities, and Alternative States

Fishery-induced trophic cascades often display differential response times among trophic levels and nonlinear trajectories; moreover, they are commonly accompanied by wholesale changes in community structure. Consequently, FITCs have the potential to drive ecosystem-state shifts in which each state is maintained by internal feedback mechanisms and transitions between states are specifically defined by hysteresis: system recovery follows a different trajectory than that observed during decline (Scheffer et al. 2001). Although empirical evidence of hysteresis is scarce, many examples of profound changes in distinct ecosystem configurations triggered by fishing exist. Nonlinear shifts in community assemblages have been documented in conjunction with FITCs reported from New Zealand and Mediterranean subtidal reefs (Shears & Babcock 2002; Guidetti & Sala 2007), Chilean intertidal shores (Durán & Castilla 1989), Caribbean and African coral reefs (McClanahan & Shafir 1990; Hughes 1994), and the Gulf of Maine (Steneck et al. 2004).

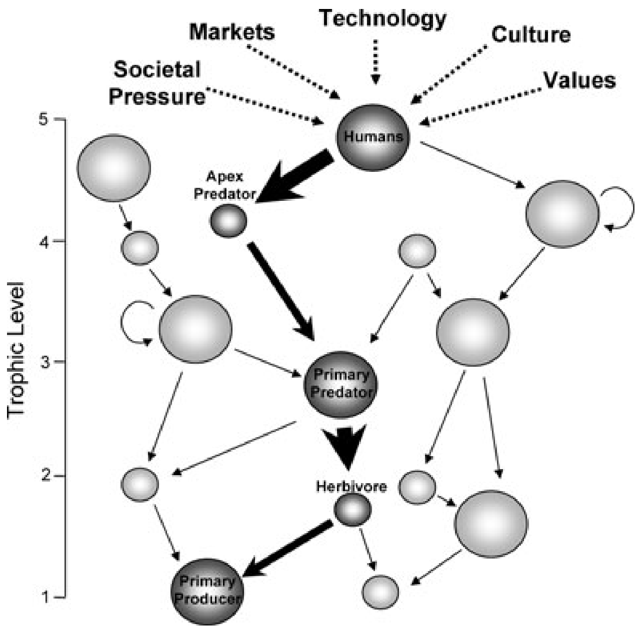

Figure 1. Trophic cascades are generated by strong interactions (thick solid arrows) embedded within complex food webs and result in an inverse pattern of abundance, biomass, or productivity across two or more trophic levels. Sphere size represents the relative biomass of each trophic group and the width of solid arrows represents the relative strength of trophic interactions. Human-induced cascades are influenced by social and economic forces (dashed arrows), their importance of which is typically overlooked or undervalued in current cascade research.

In northeastern New Zealand's two oldest marine reserves, predatory snappers (*Pagrus auratus*) and lobsters (*Jasus edwardsii*) have become 8.7 and 3.7 times more abundant compared with adjacent fished reefs (Babcock et al. 1999). As a result, predation rates on sea urchins (*Evechinus chloroticus*) are sevenfold greater within the reserves, which has reduced the density of actively grazing urchins and allowed kelp to increase significantly (Shears & Babcock 2002, 2003). Despite a quick recovery of previously fished predators following protection, it took 15–20 years of no fishing to reduce urchins below the threshold density required for kelp recovery (Babcock 2003) (Fig. 2). Once urchin densities were reduced below this threshold within the reserves, reefs formerly dominated by urchin barrens were replaced by kelp forests. This significant time lag in the manifestation of cascading effects has been attributed to size-specific predation by recovering reef predators that allowed large urchins to escape predation and changes in urchin behavior (from openly grazing to cryptic) (Babcock 2003). Similar shifts between urchin barrens and erect macroalgal assemblages have been reported in western Mediterranean reefs (Sala et al. 1998). Predator–prey relationships between predatory *Diplodus* fish and the sea urchins in this system also appear nonlinear, which suggests that the transition between states is driven by critical thresholds in the density of predatory fish (Guidetti & Sala 2007).

Similar community reconfigurations induced by fishing have been documented on coral reefs. In many cases, this has been in part the result of overfishing, under which nonselective fisheries remove both predators and herbivores. The loss of herbivory in these systems is believed to result in algal overgrowth of living coral. On Caribbean reefs, nonselective overfishing removes both predatory and herbivorous fishes, allowing sea urchins (*Diadema antillarum)* to become the dominant grazer (Sammarco et al. 1974). In the 1980s, *Diadema* suffered a massive disease-induced die-off that led to the proliferation of fleshy algae and a reduction in coral cover across the Caribbean (Hughes 1994). Some 25 years later there is little evidence that Caribbean reefs have recovered. Since the loss of *Diadema*, parrotfish have become the dominant grazer on these reefs. With establishment of marine reserves in areas such as the Bahamas and subsequent recovery of previously fished piscivores, there was a concern that parrotfish would be at higher risk of predation inside reserves. Mumby and colleagues (2006, 2007), however, did not find the expected trophic cascade. Instead, the effects of fishing overwhelm any indirect effects in this system because unfished areas have a greater abundance of both predators and herbivores. Thus, due to the nonselective nature of many coral reef fisheries, the physical removal of herbivores by fishing and the increase in herbivore abundance through the creation of no-take reserves seem to be among the most important drivers of what appears to be phase-shift formation and reversal.

Several cases of alternative state shifts associated with FITCs in pelagic ecosystems have revealed mechanisms driving hysteretic transitions between states. In the Black Sea, two sequential FITCs perpetuated two ecosystem-wide state shifts (Daskolov et al. 2007). The depletion of pelagic predators generated a cascade of indirect effects across four trophic levels, which in turn altered nutrient levels and oxygen concentrations in the surface water. This cascade also triggered a state shift in the 1970s. The reduction of planktivorous fish, eutrophication, and an outburst of jellyfish and an invasive ctenophore provoked a second state shift in the 1990s (Daskalov et al. 2007). Differences in forward and return paths of consumer and resource populations provide evidence of a hysteretic system. Although triggering factors in both state shifts appear to be excessive exploitation of consumers, evidence of possible stabilizing mechanisms, such as shifts in trophic control, or increased catchability or depensatory effects at low stock levels is lacking. In the Baltic Sea, where a multilevel trophic cascade has been

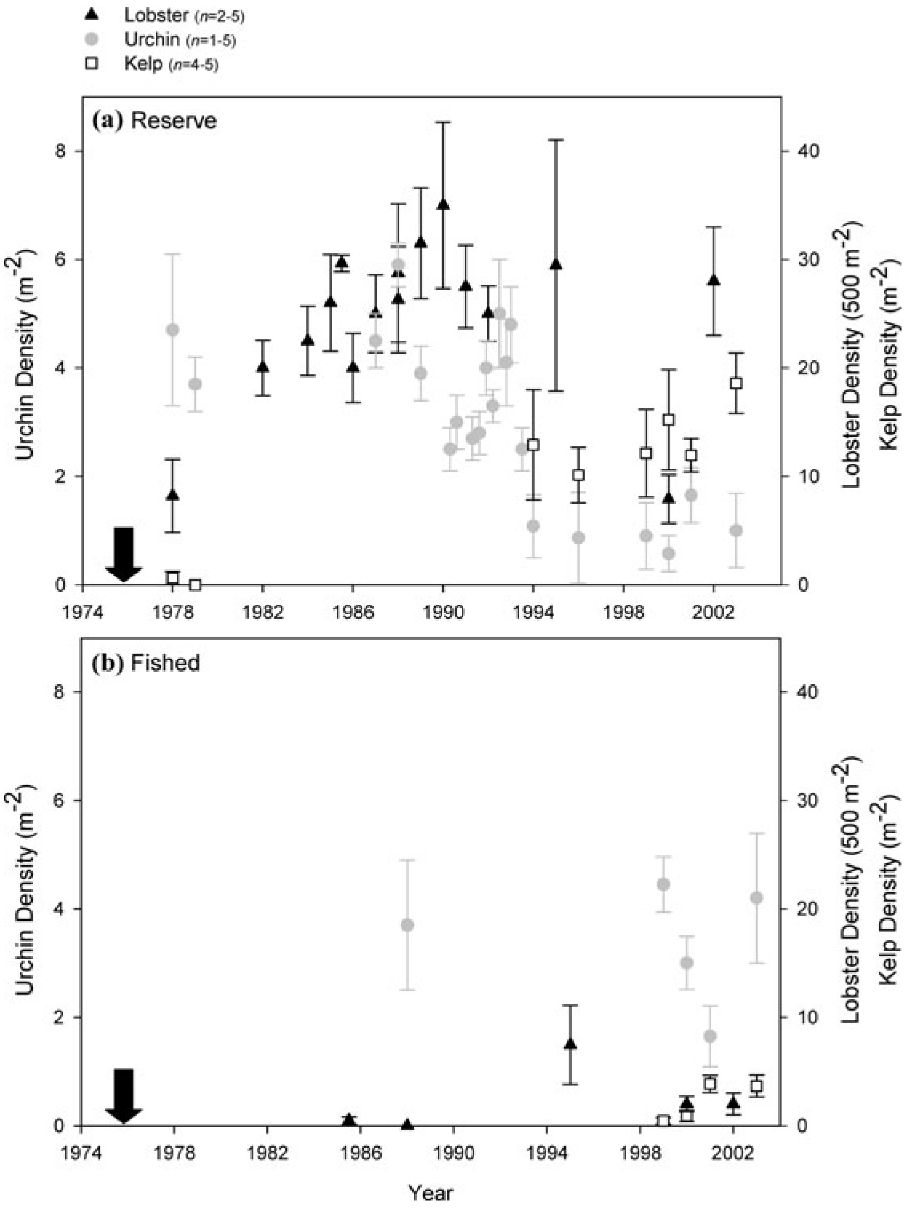

Figure 2. Trajectories of lobster, urchin, and kelp density in (a) the Leigh Marine Reserve and (b) adjacent fished sites on the basis of empirical data compiled from Ayling (1978), Choat and Schiel (1982), Cole et al. (1990), Cole and Keuskamp (1998), MacDiarmid and Breen (1993), Babcock et al. (1999), Babcock (2003), Shears and Babcock (2003), Langlois et al.(2005), and Salomon et al. (2008) (black arrows, date of reserve establishment [1976]; n, *number of sites surveyed).*

documented (Österblom et al. 2007; Casini et al. 2008), continued anthropogenic nutrient enrichment appears to be a stabilizing mechanism that is maintaining the current eutrophic state (Österblom et al. 2007). Moreover, by increasing predation on and competition with juvenile cod (*Gadus morhua*), the explosion of sprat (*Sprattus sprattus*) populations due to predator release and favorable climatic conditions after the collapse of the cod fishery, may also stabilize this new state and undermine both cod and ecosystem recovery.

Similarly, in the western North Atlantic, where intensely fished cod populations collapsed during the early 1990s, data spanning 4 decades showed that the decline in predatory fishes was associated with increases in small pelagic fish and benthic macroinvertebrates, declines in large herbivorous zooplankton, increases in phytoplankton, and a drop in nitrate concentrations (Frank et al. 2005). Despite a fishing moratorium since 1992, the recovery of cod has been slow, likely due to an increase in forage fish, which are both predators and competitors of juvenile cod. Elevated forage fish abundances may increase juvenile cod mortality, thereby delaying or even preventing cod recovery (Walters & Kitchell 2001). This feedback mechanism, known as compensation-depensation, can stabilize and promote the persistence of an alternative state.

Shifts in alternative states can be long lasting and difficult to reverse because the factors driving recovery of a system back to its original state need to be substantially stronger than those causing the initial shift. Although theoretical guidelines exist, detecting these shifts in real ecosystems is not a trivial task. In many cases, what remains unclear is the threshold density of predator reduction that will induce a trophic cascade and associated state shift and what feedback mechanisms cause ecosystem shifts to be irreversible. Insight into these questions, and their context-dependent nature, will help inform ecosystem-based management (EBM) and conservation policies designed to avoid unwanted state shifts and promote ecosystem resilience.

Size-Mediated Effects

Many examples of FITCs report size-mediated trophic interactions, such that FITCs may only manifest clearly among certain size classes of species within a trophic level. For example, in pelagic food webs of the North Atlantic, large zooplankton >2 mm declined in response to increased forage fish, whereas smaller species <2 mm did not (Frank et al. 2005). In some cases, prey of intermediate size are preferentially targeted because large size classes can escape predation simply due to predator gape limits, whereas smaller size classes have a high effort-to-calorie cost of consuming. For example, with the recovery of predator abundance and larger size classes within marine reserves, sea urchins in New Zealand and California reserves have a bimodal size-frequency distribution, in part because their predators preferentially target midrange size classes (Shears & Babcock 2002; Behrens & Lafferty 2004).

By removing the largest size classes of predators, which typically have the greatest predatory impact on prey, the effects of fishing can be further magnified through reef food webs. On Bahamian coral reefs, large-bodied parrotfish escape predation inside of marine reserves due to the gape limitations of their predators, and this limitation has prevented an FITC (Mumby et al. 2006). Such size escapes may in part explain time lags and nonlinear trajectories associated with FITCs because large-bodied individuals may avoid natural predation and persist for many years.

Parasitism and Disease

In association with FITCs, emerging evidence suggests that intense exploitation of predators can indirectly alter parasite dynamics throughout food webs. By fishing a parasite's host to low densities, parasite transmission efficiency may be reduced. Adding to the classic work of Durán and Castilla (1989), documenting the indirect effects of harvesting the predatory gastropod *Concolepas concolepas* on Chilean rocky shores, Loot et al. (2005) show that prohibiting exploitation of a clingfish, the final host of a parasitic trematode, can lead to increased parasite loads in the protected clingfish. Infection rates were greater in the absence of fishing probably because of elevated densities and larger sizes of the clingfish. Higher parasite levels in the absence of fishing, however, do not have pathogenic effects on clingfish and do not translate into lower fecundity of the intermediate host, keyhole limpets, which supports the notion that parasitism can indicate ecosystem health (Hudson et al. 2006).

Disease outbreaks among dense prey populations released from predation are also associated with FITCs. In addition to releasing kelp from grazing pressure, the presence of urchin predators within a southern Californian marine reserve prevents urchins from exceeding the host-density threshold for epidemics (Lafferty 2004). At fished sites, dense urchin populations are more likely to experience epidemics and suffer higher mortality. Pathogens of sea urchins represent a critical mechanism controlling urchin populations on temperate and tropical reefs (e.g., Hughes 1994; Sala et al. 1998; Tegner & Dayton 2000). Increased frequency of such outbreaks may be a feature of fishing urchin predators; consequently, when urchin disease is prevalent, the occurrence of FITC effects may be less evident or even reversed.

Ecosystem Consequences

Only recently have the cascading effects of fishing on ecosystem processes been explored in marine systems. Evidence from temperate reefs in northeastern New Zealand suggests that the indirect effects of reducing reef predators (snapper and lobster) on kelp biomass can alter kelp carbon flux through reef food webs (Salomon et al. 2008). Stable carbon isotope ratios of filter feeders (oysters and mussels) transplanted in reserve and fished sites revealed that fishing can indirectly reduce the proportion of kelp-derived organic carbon assimilated by these bivalves where kelp biomass is an order of magnitude lower than reserve sites. This result highlights the importance of predators in mediating benthic primary production and organic carbon flux and that their depletion can fundamentally alter crucial ecosystem processes.

Context-Dependent Effects

The magnitude of trophic cascades can vary with biotic and abiotic factors such as system productivity and consumer efficiency (Power 1992). Nevertheless, the processes that regulate the expression and magnitude of cascades in natural systems remain largely unknown (Borer et al. 2005). Although the evidence for FITCs is mounting, results of many studies show no evidence of such effects (Supporting Information) and suggest that top-down control is not evident across all systems. In fact, in many systems where FITCs had been documented initially, continued investigation into the generality of these effects has identified their intricacies and context-dependent nature (Frank et al. 2006, 2007; Shears et al. 2008). Given that a multitude of factors can influence the abundance, size, behavior, and spatial distribution of populations and species interaction strength, it is clear that the magnitude of FITCs depends on the context in which the interactions take place. The strength of species interactions and

Table 1. Factors that alter the occurrence and magnitude of fishery-induced trophic cascades by either dissipating or amplifying the transmission of indirect fishing effects throughout marine food webs.

Context-dependent factors	*Effect*	*Explanation*
Species diversity and trophic complexity	dissipate	High species diversity facilitates the replacement of overfished species.
Top-down control	amplify	Marine ecosystems under strong top-down control are less resilient to the exploitation of top predators and more susceptible to FITCs.
Regional oceanography	dissipate or amplify	Factor mediates rates of recruitment, primary production, growth and maturation, predation, and herbivory.
Recruitment limitation and variability	dissipate	Low or sporadic recruitment at intermediate trophic levels can slow the recovery rate of prey following predator depletion.
Local physical disturbances	dissipate	Physical disturbance can decouple the trophic links between predators, herbivores, and primary producers.
Multitrophic-level fisheries	dissipate	Prey release that may have occurred following the exploitation of predators is offset by the harvest of prey.
Disease	dissipate	A dramatic depletion in predators may cause prey to exceed their host density threshold for epidemics.
Predator-avoidance behavior by prey	amplify	Because most organisms behave in ways that moderate their exposure to predation risk, often at the cost of reduced food intake, predator depletion can also lead to increased prey foraging effort or efficiency.
Habitat complexity and spatial refuges	dissipate	Predator effectiveness can be dampened by prey-avoidance behavior and the availability of safe hiding spots.

their cascading effects can vary as a function of species diversity and trophic complexity, regional oceanographic conditions, local physical disturbance, recruitment variability, and habitat complexity (Table 1).

Susceptibility to FITCs

Species Diversity and Trophic Complexity

High species diversity and food-web complexity can reduce the trophic impacts of predators and prevent strong cascading effects (Strong 1992; Polis et al. 2000). For example, highly diverse ecosystems with reticulate food webs are more likely to dissipate the effects of predator loss due to dietary flexibility and overlap, omnivory, and functional redundancy, and thereby undergo "trophic trickles" rather than true cascades. Minimal evidence of FITCs in highly diverse coral reefs supports this notion despite intensive fishing effort in these systems.

On Fijian coral reefs, Jennings and Polunin (1997) found that a fishery that selectively targets piscivorous fishes reduces piscivore biomass but does not result in increased prey biomass. Additionally, fishing has significantly reduced the biomass of predatory reef fishes in parts of the central Pacific's northern Line Islands, but the biomass of herbivorous fishes is relatively constant across the islands (Sandin et al. 2008). In contrast to FITC expectations from temperate reefs with tritrophic food chains, unfished islands in this system, with their full compliment of top predators, have lower fleshy algal cover and higher live coral cover. In a theoretical model of a Caribbean marine food web, Bascompte et al. (2005) showed that strong omnivory often accompanies strong interactions and reduces the likelihood of FITCs.

Nevertheless, FITCs have been documented on highly diverse tropical reefs. Most researchers report an increase in the abundance of a strongly interacting invertebrate, typically an echinoderm, following predator exploitation and subsequent declines in coral cover. For example, overfishing of predatory fishes in Kenya resulted in the proliferation of the bioeroding sea urchin, *Echinometra mathaei* (McClanahan & Shafir 1990; McClanahan & Muthiga 1998; McClanahan 2000) that consumes algae living on or in the reef matrix. High *Echinometra* abundances reduce coral cover and increase the success of opportunistic turf algae. When fishing is excluded, predatory triggerfish density increases, urchin abundance declines, and coral cover increases. In Fiji, as subsistence fishing increases, predator abundance declines, the coral-eating seastar *Acanthaster planci* increases, and reef-building corals and coralline algae are replaced by fleshy algae (Dulvy et al. 2004). Lastly, Burkepile and Hay (2007) found that in the Florida Keys, removal or reductions in predator abundance coincides with an increase in the density of a gorgonian-eating snail (*Cyphoma gibbosum*) and a decline in the abundance of their prey. The variable trophic outcomes of fishing predators on highly diverse coral reefs imply that multiple mechanisms driving community dynamics are at play.

An ecosystem's resilience to FITCs may depend on whether communities contain species capable of compensating for depleted species. For example, in the

Gulf of Maine, where kelp forest species diversity is low relative to similar latitudes in the northeast Pacific, rapid phase shifts in nearshore reef ecosystems occur, likely due to low functional redundancy within trophic levels and compensatory dynamics (Steneck et al. 2004). Before industrial-scale fishing, a system replete with apex predators (cod, haddock, and wolfish) persisted for over 4000 years. A fisheries-induced phase shift caused this predator assemblage to be replaced by a system dominated by green sea urchins that persisted from the 1970s to the 1990s. Urchins were quickly depleted by the mid 1990s by overfishing, and a second phase shift to a system dominated by macroalgae occurred in which invertebrate predators (large crabs and lobster) became the top-level predator. Although the lobster fishery in Maine is now one of the world's largest, no large decapod crabs or lobster have been reported in shell middens dating between 5000 and 400 years before present, and historical records documenting the existence of lobster date back only to the 1600s (Steneck et al. 2004).

Regional Oceanography

Recent evidence suggests that large-scale oceanographic factors may influence a system's susceptibility to FITCs. Time-series analysis from 26 heavily exploited regions in the North Atlantic reveals pronounced spatial variation in trophic forcing; top-down control dominated in northern areas, where species diversity and ocean temperatures were low, whereas bottom-up control dominated in warmer, more speciose southern areas (Frank et al. 2006, 2007). Southern ecosystems may be more resilient to overfishing because high species diversity facilitates replacement of the overfished species and warmer temperatures support higher demographic rates. These context-dependent findings help reconcile the inconsistencies in trophic control observed in midlatitude pelagic food webs and illustrate that marine ecosystems under top-down control are less resilient to the exploitation of top predators and more susceptible to FITCs.

By expanding the spatial scope of FITC research, the role of regional oceanography in altering key rates that mediate the cascading consequences of fishing is becoming increasingly clear. For example, in northeastern New Zealand, the occurrence of FITCs in kelp forest ecosystems varies across geographic locations (Salomon et al. 2008; Shears et al. 2008). Although clear FITCs have occurred on the coast, the cascading effects of fishing have been variable among offshore island reefs. This can in part be explained by regional current patterns and upwelling regimes. Bathed by clear, subtropical water of the East Auckland Current, reefs surrounding the offshore islands experience low phytoplankton concentrations and high light levels, which likely promote high kelp production. At some sites, the exploitation of urchin predators appears to have had minimal effect on kelp biomass, perhaps because urchin grazing rates cannot offset high kelp production rates. Ultimately, the strength of FITCs depends on the relative magnitude of predation, herbivory, primary production, and recruitment rates. Quantifying regional variation in these population and per capita rates will allow forecasting of the occurrence and relative magnitude of FITCs given various predator exploitation rates.

Recruitment Limitation and Variability

The supply of larval recruits to a population is an essential component of population persistence and ultimately determines whether species will play an important trophic role in a food web (Roughgarden et al. 1988). Inherent variability in recruitment can influence the effects of fishing on lower trophic levels and the extent to which communities recover following the cessation of fishing. Population and community recovery may occur with lags of decades, especially for long-lived species with sporadic recruitment, because larval supply and postrecruitment settlement success are essential for recovery of previously fished populations and reestablishment of lost trophic interactions. For example, lack of suitable habitat for recruitment of predatory sea breams in an Italian marine reserve is thought to be responsible for lack of recovery of these species (Guidetti & Sala 2007).

Recruitment limitation and variability at intermediate trophic levels also has the potential to decouple trophic linkages and alter the magnitude of FITCs. For example, on sheltered reefs in New Zealand, where sea urchin recruitment and postsettlement survival is limited by high levels of sedimentation, FITCs are not observed (Shears et al. 2008). In this case, urchins remain rare and macroalgae predominate regardless of predator abundance and fishing intensity. Similarly, it is plausible that under consistently high levels of sea urchin recruitment, high abundances of predators may not be sufficient to control urchin populations. Accordingly, the rate and variability of recruitment will be important in determining the response times of lower trophic levels relative to changes in predator abundance brought about by fishing.

Local Physical Disturbances

Physical disturbance provides another potential mechanism to decouple the trophic links between predators, herbivores, and primary producers (Menge & Sutherland 1987) and thereby alter the occurrence and strength of FITCs. For example, wave exposure can reduce sea urchin grazing rates in shallow water; thus, the indirect effects of fishing on macroalgal-urchin interactions can be reduced in physically stressful environments. Correlative data from two Mediterranean islands in Italy suggest that although marine reserves have had a direct positive effect on fish assemblages, the indirect effects on benthic assemblages mediated by urchins are observed only at sites of lower wave exposure (Micheli et al. 2005).

Similarly, a comparison of urchin abundance and macroalgal biomass across six marine reserves and fished sites in northeastern New Zealand showed that FITCs were apparent in only two of the six locations examined (Shears et al. 2008). Urchin abundance varied in relation to depth, wave exposure, and sedimentation, and these factors covaried at differing spatial scales. Only when environmental conditions facilitated overgrazing by sea urchins were the indirect effects of predator recovery on macroalgal biomass apparent.

Multitrophic-Level Fisheries

In addition to ecosystem characteristics and physical factors, the nature of the fishery itself may play a key role in preventing or attenuating FITCs. Fishing on coral reefs is often not selective, and multiple trophic levels are often harvested simultaneously. Consequently, prey release that may have occurred following the exploitation of predators is offset by its harvest. For example, although nonselective fishing on two Philippines islands alters total fish biomass, there is little evidence that predator reduction has led to either the numerical release of their prey or indirect effects on the benthic community (Russ & Alcala 1998). Despite a 40-fold range in total fish biomass across Caribbean reefs spanning a large range of nonselective fisheries, Newman et al. (2006) found no evidence of cascading effects of predator removal and cites the nonselective nature of the fisheries as the likely reason cascading effects were not observed. Indeed, humans exploit multiple trophic levels throughout marine food webs. A recent analysis of fishery landings from 48 large marine ecosystems worldwide suggests that the decline in mean trophic level of global landings can be explained by the serial addition of low-trophic-level fisheries (Essington et al. 2006). Akin to omnivory, this pattern of exploitation would weaken FITCs.

Predator Avoidance Behavior by Prey

Although FITCs typically involve numerical changes in prey density in the absence of fished predators, changes in prey foraging behavior can be an equally important driver of community-level trophic cascades. Because prey make themselves vulnerable to predation while foraging, a trade-off exists between eating and being eaten (Walters & Juanes 1993). Consequently, organisms that behave in ways that reduce their exposure to predation risk do so at the cost of reduced food intake. Beyond causing increases in prey, exploitation of predators could also lead to increased prey foraging effort and efficiency. In the presence of predators, prey foraging may be compromised simply due to the threat of predation.

Nonlethal predator effects can exacerbate cascades and shape entire marine ecosystems (Dill et al. 2003). Evidence from New Zealand and Mediterranean reefs suggests that total urchin numbers in unfished areas tend to be slightly lower than in fished areas, yet those urchins present in unfished areas tend to be cryptic, seeking refuge from predators in crevices (Sala et al. 1998; Shears & Babcock 2002). Enhanced kelp survival is thus more a function of the density of exposed, grazing urchins than total urchins. Behaviorally mediated indirect interactions can also cause FITCs to attenuate or vary in magnitude across space. For example, when prey respond to predators by preferentially foraging in “safe” over “risky” areas, they can create a mosaic of their resource. Consequently, complex habitats offering spatial refuges may reduce the strength of FITCs.

Habitat Complexity and Spatial Refuges

Predator effectiveness can be dampened by prey-avoidance behavior and the availability of spatial refuges. Because hiding spots grant prey immunity, complex habitat should weaken FITCs by reducing a predator’s search-and-capture efficiency. For example, in temperate reefs, where shelters are abundant, urchins can coexist with predators resulting in patchy, intensively grazed coralline patches surrounding refugia (Sala et al. 1998). So-called halo effects are also common on coral reefs. Complex habitat, therefore, can reduce the propensity for consumer-driven effects to propagate through food webs by allowing predator and prey coexistence.

By contrast, destructive fishing practices that reduce habitat complexity, such as bottom trawling, can increase vulnerability of prey to predation and thus decrease resilience of a system to the cascading effects of fishing. In the Northwest Atlantic, bottom trawling may have magnified effects of the cod decline by reducing habitat complexity and increasing juvenile mortality (Fogarty & Murawski 1998). This in turn may have accelerated the cascading effects of overexploiting predatory cod.

In theoretical trophic models, where prey are completely vulnerable to predation, strong top-down control is exhibited, resulting in unstable predator-dependent interactions. When these models account for antipredator behavior by prey (e.g., via spatial refuges), ratio-dependent interactions occur in which prey mortality is proportional to the ratio of vulnerable prey to predators and systems are more likely to exhibit stable equilibria (Walters & Martell 2004). When prey vulnerability is low due to an abundance of hiding spots, top-down effects are dampened (Fig. 3). Models exploring the trophic effects of marine reserves illustrate how exchange rates between being safe (hiding) and vulnerable (foraging) that occurs over small spatial scales can modify the strength of FITCs and can therefore have gradual yet profound ecosystem-scale implications (Walters et al. 1999; Salomon et al. 2002). Fast dynamics at small spatial scales can translate into gradual changes at large spatial scales and can lead to nonlinear dynamics and system-wide collapse (Carpenter & Gunderson 2001).

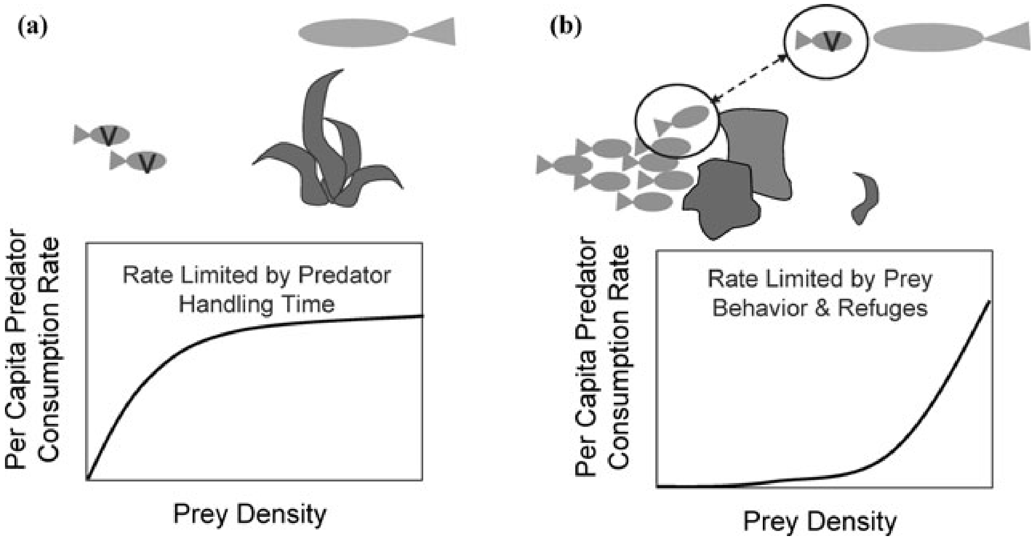

Figure 3. When prey (small herbivorous fish) are completely vulnerable (V) to predation (large piscivorous fish) (a), predation rates are only limited by predator handling time and top-down control dominates. Nevertheless, when spatial refuges (e.g., rocks) exist (b), some prey become invulnerable; predation rates become limited by prey-hiding behavior and the availability of hiding spots; and top-down effects are dampened. The exchange rate between being safe (hiding) and vulnerable (out foraging) that occurs over small spatial scales can modify the strength of FITCs and can therefore have gradual yet profound ecosystem-scale implications. (Diagram adapted from Walters & Juanes [1993] and Walters & Martell 2004).

Detecting and Predicting FITCs

Shifting Baselines

The long legacy of exploitation in the sea implies that FITCs could be widespread, yet our ability to detect them is hindered by our ignorance of consumers that may have once played key trophic roles but are now either extinct or severely depleted. Consequently, our current ability to evaluate the trophic effects of overfishing is crippled by the fact that marine systems worldwide have already suffered moderate-to-severe losses of top predators and other strongly interacting species (Dayton et al. 1998; Jackson et al. 2001). The syndrome of shifting baselines may thus reduce our expectations of FITCs occurrence. Although in some areas marine reserves have been highly valuable at providing an indication of what once might have been the norm, the role of extinct or severely depleted consumers in these systems in many cases remains unknown. One approach to remedy this quandary is to integrate historical data sets with contemporary assessments of multispecies trends (i.e., Salomon et al. 2007) because historical reconstructions can help reveal the indirect effects of past consumers.

Multiple Causation

Although fishing clearly can induce change in marine food webs, the causes of major community shifts are often complex and involve more than just top-down control. For example, cases of coral-algal phase shifts are likely the result of multiple interacting impacts. Nutrient pollution, sedimentation, disease, storm disturbance, warming, and acidification may all negatively affect coral abundance and allow benthic algae to proliferate (Hughes 1994). Similarly, on temperate reefs, factors besides fishing, such as recruitment variability, eutrophication, anomalous oceanographic events, disease, and availability of predator-safe habitats can alter the population dynamics of sea urchins and thus modify the strength of FITCs (Sala et al. 1998). Furthermore, the magnitude of FITCs can increase under eutrophic conditions (Daskalov et al. 2007).

Multiple stressors and the possibility of synergistic effects can complicate the prediction of FITCs and management of their drivers. Although phase shifts, for example, may ultimately be caused by fishing, reducing stocks to low levels makes them strongly dependent on annual recruitment and thus more vulnerable to environmental fluctuations, such that a change in climate may initiate a phase shift. Evidence from the Baltic Sea suggests that climate variability can influence the timing, magnitude, and persistence of fishery-induced regime shifts (Österblom et al. 2007). Consequently, it may appear that environmental fluctuations drive fisheries when originally they did not. In cases such as these, multiple causation can blur the picture and derail management when declines and phase shifts are attributed to climate variability rather than the primary anthropogenic cause.

Implications for EBM

Preventing undesirable and irreversible ecosystem state shifts associated with FITCs is a principle of EBM. Knowing threshold levels of predator abundance required to trigger trophic cascades and how they vary across systems would help inform EBM. Nevertheless, information on food-web dynamics is lacking for most exploited systems and to date there has been little emphasis on forecasting FITCs and the thresholds of consumer exploitation that may trigger them. Because marine ecosystems are fantastically complex in their spatial, temporal, and trophic organization, it may be arrogant and foolish to presume that scientists can make any useful predictions about the ecosystem ramifications of fishing at all. But, as we have shown above, there are some predictable regularities in the way populations and ecosystems respond to exploitation. Emphasis on identifying vulnerable ecosystems and processes within a risk-assessment framework to forecast FITCs may be most useful for EBM. For example, understanding the structural properties of food webs may indicate both key species (Fig. 4: Gaichas & Francis 2008) and strong interactions (Bascompte et al. 2005) with the highest risk for cascading effects. Identifying ecosystem features that confer resilience to exploitation will also help indicate high-risk ecosystems. Managers could then lower the risk of cascading effects of fishing by managing key species and prone ecosystems conservatively.

FITCs can be socially and economically hard on coastal communities. In the mid-Atlantic, when fisheries reduced multiple shark stocks over a 35-year period, 12 of 14 of their elasmobranch prey species increased (Myers et al. 2007). The rise of skates and rays led to elevated predation on commercially valuable bay scallops and the collapse of a century-old bay-scallop fishery. Managing for FITCs to ease economic hardships will require social and institutional flexibility, learning, and adaptive policies. Avoiding, anticipating, and preparing for FITCs will be essential.

Directions for Future Research

Thresholds and Ecosystem Resilience

One of the most fundamental challenges facing conservation biologists, given the possibility of nonlinearities in biological systems, is the ability to forecast how and when ecosystems will respond to human disturbances and if these responses are easily reversible. In marine systems for instance, it is unclear if predator thresholds, below which cascading events are triggered, are commonplace. Developing methods that can identify the prevalence of such thresholds and estimate the range of threshold consumer densities needed to initiate an FITC will help illuminate an ecosystem's resistance and resilience properties, thereby allowing managers to predict and avoid

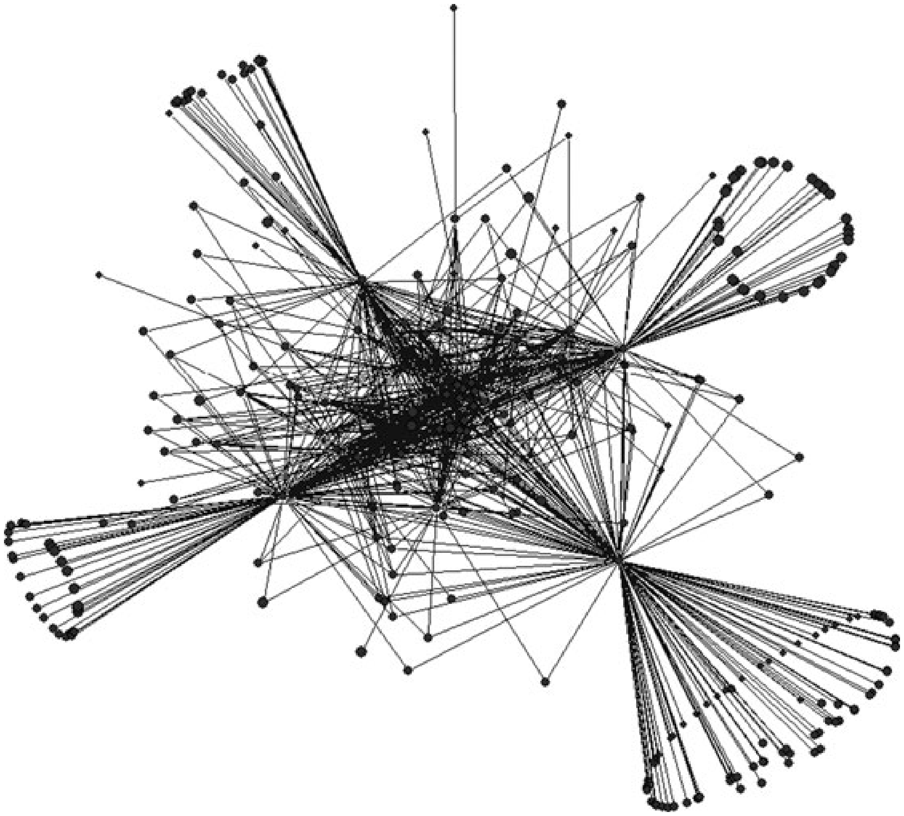

Figure 4. Model of the food-web network of the Gulf of Alaska continental shelf ecosystem built with detailed quantitative information on the stomach contents of 57 predator (fish) species collected between 1981 and 2002. The model displays scale-free network properties and suggests that impacts on one species might spread to many through short interaction chains and that although most food-web connections are not critical, a small set of fished species support critical structural connections. In this figure, four key species are revealed as critical structural "hubs" that connect prey at the edges of the food web with the rest of the food web at the center (diagram from Gaichas & Francis 2008).

FITCs and set ecosystem-based targets for conservation. For example, Mumby et al. (2007) used a simulation model in conjunction with analytical methods to determine critical thresholds of grazing pressure and coral cover on Caribbean reefs required to maintain system resilience. These estimates could guide an ecosystem approach to the exploitation of parrotfish, a dominant reef grazer.

Critically, research into the symptoms that herald ecosystem state shifts accompanying FITCs will increase our ability to anticipate and prevent them. Simulation models and analyses of ecological time series suggest that increased variability and changing skewness in ecosystem attributes can foreshadow impending shifts up to a decade in advance (Carpenter & Brock 2006; Guttal & Jayaprakash 2008). Nevertheless, the generality of such antecedents and the range of conditions and ecosystems for which they are useful warning signals remain largely unknown. Additionally, identifying the positive feedback mechanisms that maintain alternative states will provide insight into what restoration activities may reverse unintended state shifts. Where ecosystems have shifted to an undesirable state, restoration experiments could help reveal threshold consumer densities required to promote system recovery to a favored state.

Cumulative and Synergistic Effects

The challenge of predicting the occurrence and magnitude of FITCs is further complicated by the reality that multiple anthropogenic stressors can modify marine ecosystems simultaneously and have the potential to interact, leading to complex and possibly synergistic effects. The extent to which the trophic effects of fishing interact with changing sea temperatures, ocean acidification, eutrophication, sedimentation, and invasive species needs to be further explored if conservation policies are to be adequately informed. For example, with the forecasted increase in storm severity and ocean acidification associated with climate change, biogenic calcium carbonate structures, such as coral and oyster reefs, may become damaged either through structural weakening of materials or by a reduction in biomineralization. A decrease in habitat complexity may enhance FITCs where predators have been overexploited. Additionally, invertebrate consumers themselves may be compromised by ocean acidification, potentially rendering them more vulnerable to vertebrate predators and modifying their grazing rates. Investigations into these possible cumulative effects will clarify fundamental ecological processes and become increasingly necessary to incorporate into conservation and restoration strategies.

Strong Interactions and Variation in Trophic Rates

In less-well-studied ecosystems strongly interacting species still need to be identified. Combining fishery management experiments in the field with computer-model simulations will help elucidate key species and their potential indirect effects. Management strategies could then be tailored to maintain critical species interactions. Furthermore, quantifying variation in predation, grazing, and primary production rates across a range of oceanographic and consumer density gradients will allow the development of predictive models that can be used to forecast where FITCs are likely to occur.

Ecosystem Feedbacks

In some cases the recovery of apex predators can magnify secondary production (Duggins et al. 1989). Ecosystem feedbacks such as these, where the deletion or reduction of trophic groups can modify the productivity of entire food webs, should be further examined. For instance, under what conditions does the presence of top predators increase fishery yields by enhancing overall ecosystem productivity? Furthermore, quantifying fishery-induced alterations of material flux, such as carbon and nitrogen flux, could serve as an ecosystem-based currency by which to evaluate EBM policies. Finally, research into the feedbacks within coupled social-ecological systems and key socioeconomic inhibitors of overfishing (i.e., flexible economic markets and institutions, designated access privileges) will improve our ability to avoid FITCs.

Conclusions

In the coming decades humans will continue to exploit the world's oceans for protein. Consequently, there is an urgent need to assess how the reduction of major consumers from the sea alters marine food webs, productivity, and resilience. Fortunately, our current understanding provides a valuable start. Forecasting when, where, and under what conditions FITCs may occur will inform our ability to anticipate, prevent, and if necessary reverse the cascading consequences of fishing and accompanying state shifts that may ensue. Ultimately, fisheries management strategies and society will need to balance short-term yield with long-term ecosystem function to navigate toward ecological and social resilience.

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Supporting Information

Tables listing all peer-reviewed studies that report evidence of fishery-induced trophic cascades (Appendix S1), a lack of evidence for FITCs, or describe spatial variation in the magnitude of FITCs (Appendix S2) are available as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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