PERSPECTIVE NOTE

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Perspective review of the impacts of overfishing on coral reef food web linkages

Introduction

Overfishing is increasingly understood to result in indirect alterations of habitat structure and function (McClanahan et al. 1995; Bowen 1997; Jackson 2001; Jackson et al. 2001; Gardner et al. 2003). The intense harvesting of sea otters from kelp forests, for example, created "low- predation refuges" for their sea urchin prey. Following otter removal, sea urchin grazing exploded resulting in large regional losses of kelp (Estes and Palmisano 1974; Duggins 1980). Further support for the impacts of large consumers was found in Alaskan embayments where inshore migration of killer whales changed the strength of interactions between sea otters and their herbivorous sea urchin prey, again resulting in local losses of kelp forests (Estes et al. 1998). Similarly, McClanahan et al. (1995) found that intense harvesting of predatory trigger fishes promoted large-scale habitat changes as their sea urchin prey, once released from predation, increased. More urchins subsequently led to more coral reef erosion and the eventual replacement of corals by seagrasses (McClanahan and Kurtis 1991). Moreover, the intense harvesting of both large piscivo-

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rous and herbivorous fishes, coupled with the die-off of herbivorous sea urchins, is thought to be responsible for widespread macroalgal overgrowth of coral reefs in Jamaica (Hughes 1994 but see Aronson and Precht 2001).

Given that the dramatic impacts of fishing on marine food webs preceded the development of most theory in marine ecology, it is understandable that management agencies have predominantly focused their efforts on the role of bottom-up processes (nutrient concentration) in regulating the productivity of coastal ecosystems. But given the increasing evidence that food web alterations have figured prominently in the collapse of marine ecosystems, it seems clear that new studies are urgently needed to assess the degree to which large-scale food web alterations have changed the structure and function of marine ecosystems (Estes and Peterson 2000; Jackson 2001; Pandolfi et al. 2003).

Habitat linkages: has overfishing altered the strength of trophic transfers among habitats?

The passive and active transport of materials (via currents or foraging migrations, respectively) link communities across distinct habitat boundaries. Passive movements of nutrients, detritus, and prey between habitats (also called spatial subsidies or cross-habitat exchanges) can have major 'bottom-up' effects on food web productivity, especially in places with little or no in situ primary production [e.g., caves, mountaintops, stream banks, central ocean gyres, and the deep sea (Vetter 1994, 1995, 1998; Polis and Hurd 1996; Polis and Strong 1996; Persson et al. 1996; Harrold et al. 1998; Rose and Polis 1998; Hilderbrand et al. 1999)]. Such trophic links between terrestrial and freshwater habitats and between marine and terrestrial habitats are commonplace (Polis and Hurd 1996; Polis and Strong 1996; Fagan et al. 1999; Nakano and Murakami 2001). These subsidies of food and nutrients sustain greater densities of large predators than could otherwise exist if feeding was limited to prey produced in

a single habitat (Moore 1998; Vetter 1998; Huxel and McCann 1998; Rose and Polis 1998).

Great numbers of large consumers (e.g., groupers, snappers, tuna, sharks, and whales), so widely reported in the earlier literature (cf. Safina 1995, 1998; Parfit 1995; Dayton et al. 1995; Block et al. 2001), appear to have relied on the production of multiple habitats to meet their nutritional needs. Where abundant, these large consumers probably represented important vehicles for the transfer of energy and nutrients across habitat boundaries.

Early studies of coral reefs, for example, found that most reef fishes were carnivores and that carnivorous fish biomass was three to four times greater than that of herbivore biomass (Goldman and Talbot 1976; Parrish and Zimmerman 1977; Grigg et al. 1984; Polunin 1996), and that herbivorous fish biomass was usually much higher than plant biomass. Such an inverted biomass pyramid suggests that cross-habitat exchanges of energy must have played a key role in sustaining large reef consumers. In fact, many "reef" consumers were observed to hide in structurally complex coral reefs to avoid predators, but foraged in nearby structurally simple seagrass meadows (e.g., Randall 1965; Ogden and Zieman 1977; Zieman et al. 1984; McAfee and Morgan 1996; but see Nagelkerken et al. 2000; Cocheret de la Moriniére et al. 2003). Thus evidence suggests that coral reefs were once characterized by much greater cross-habitat trophic exchanges than is reported in the current literature (Ogden 1980; Valentine and Heck 1999).

In some locations, fish and in some cases sea urchin, grazing is so intense that unvegetated 'halos' are created and maintained within seagrass meadows adjacent to coral reefs (Randall 1965; Ogden and Zieman 1977; Hay 1984; Carpenter 1986; McAfee and Morgan 1996). Not all foraging in and on seagrasses is near coral reefs, however. While many herbivorous fishes shelter on reefs at night, they commonly forage throughout seagrass habitats during the day (Randall 1965; Ogden and Zieman 1977; Zieman et al. 1984; McAfee and Morgan 1996). For example, *Scarus guacamaia* and *S. coelestinus* are reported to move up to 500 m from the reef to feeding areas (Winn and Bardach 1960; Winn et al. 1964). Away from the reef, juvenile and smaller species of resident parrotfishes, those that are found in the diets of many reef-resident predators, also feed heavily on seagrasses and their epiphytes (Randall 1965; Ogden and Zieman 1977; Handley 1984; McGlathery 1995; McAfee and Morgan 1996; Valentine and Heck 1999; Kirsch et al. 2002). Once large enough, many species of parrotfish abandon structurally simpler seagrass habitats for more complex coral reefs, where it is believed they find protection from large piscivorous fishes (Ogden and Zieman 1977; Handley 1984; Carpenter 1986; Sweatman and Robertson 1994; Nagelkerken et al. 2001, 2002; Cocheret de la Morinière et al. 2003). Similarly, reef-resident lower order carnivores (e.g., grunts and lobsters) forage in vegetated habitats at night (e.g., Burke 1995; Cox et al. 1997). All of these qualitative observations strongly point to an important transfer of seagrass meadow production to coral reef food webs.

It is noteworthy, however, that many of the existing reports are from heavily fished areas, namely, the Virgin Islands and Jamaica (Ogden et al. 1973; Hay 1984; Thayer et al. 1984; Hughes 1994; Greenway 1995). In such overfished areas, in the absence of higher order consumers, lower order consumer biomass may have increased to such a point that food has become limited for them and they are forced to forage in seagrass beds to obtain adequate food. In addition, the reduced risk of predation from overfished predators may allow lower order consumers to forage at will in nearby seagrass habitats.

Marine reserves: opportunities for testing whether overfishing has altered trophic connections between seagrass and coral reef habitats

There is a critical need to rigorously assess the impacts of the human removal of large consumers on marine ecosystem structure and function (USNSF 1998; John Heinz Center 1998). Most information about the impacts of higher order consumers on lower trophic levels comes from experimental manipulations conducted at the scale of one to tens of meters. Processes operating at such small spatial scales often differ from those operating at larger spatial scales (Thrush et al. 1995; Carpenter 1996; Crowder et al. 1997; Sih et al. 1998; Diehl et al. 2000; Estes and Peterson 2000). Thus, conclusions from small-scale experiments should not be extrapolated to a larger scale without validation (Walters and Holling 1990; Eberhardt and Thomas 1991; Menge 1992; Carpenter 1996). However, controlled manipulation of larger consumers (e.g., a suitable cage size) conducted at an ecologically meaningful spatial scale would likely involve unacceptable artifacts.

Instead, whole ecosystem manipulation (Carpenter 1996) is a rigorous way to test the hypothesis that the overharvesting of piscivores has altered the abundance of lower order consumers and the entire structure of food webs on many coral reefs. The whole-system experimental approach was pioneered in freshwater and terrestrial systems with distinct natural borders (NSF 1998). While some predictions have been made about the role of large marine consumers on lower trophic levels (e.g., Jackson 1997; Bowen 1997), based on the results from small-scale experiments, lessons derived from whole ecosystem manipulations of lake and forest food webs show that surprising results are likely to occur.

The creation of replicated 'no take' zones around the world effectively represents a whole ecosystem manipulation in which enforcement of 'no take' regulations should allow the recovery of higher order consumers to nearshore waters. The restoration of the higher trophic levels on coral reefs, when studied in conjunction with nearby reference (fished) areas (cf., Underwood 1993),

allows study of the degree to which fishing has altered food webs in coral reef ecosystems.

In recent review, Halpern and colleagues (Halpern and Warner 2002; Halpern 2003) found that protection from fishing usually led to substantial increases in the density, average body size, and biomass of fishes found within marine reserves around the world. This indicates that the establishment of marine reserves can and does lead to increased densities of higher order consumers. The increased density of fishes within these reserves has also been positively correlated with more and larger fishes in nearby fished areas (the spillover effect) (Holland et al. 1996a, 1996b; Russ and Alcala 1996; McClanahan and Mangi 2000; Roberts et al. 2001; but see Shipp 2003). This documented increase in the size and density of fishes outside reserves may be the result of the increasing large number of consumers in reserves, who must rely on the production of adjacent habitats to meet their nutritional needs.

The newly created marine reserves of the Florida Keys National Marine Sanctuary (known as Special Protected Areas or SPAs) represent one example of a replicated whole ecosystem manipulation that provides an unparalleled opportunity to assess the impacts of large piscivorous fish removals on the strength of interactions among organisms in differing habitats. The Florida Reef Tract is one of the most heavily fished areas in Florida (Bohnsack et al. 1994), with seasonal peaks during the winter tourist season and summer months. Fishing pressure on reef fishes has historically focussed on several species of large predatory fishes including snappers, amberjacks, and groupers (Bohnsack et al. 1994; Ault et al. 1998).

Through an extensive 6 + year process, a system of 23 small no-take marine reserves was established in 1997 in the Florida Keys. Trap fishing was banned within state (3 n. mi.) and federal waters (to a depth of 30 m) in 1980 by the Florida Legislature (Bohnsack et al. 1989). These management actions limit the losses of large piscivorous fishes to recreational harvests on unprotected inshore reefs.

Significance to marine conservation

Developing an improved understanding of the degree to which higher consumers rely on the production of multiple habitats is vital to the successful restoration of marine food webs. Specifically, it is important to know how large marine reserves should be to include all the habitats required to sustain high levels of productivity. Unfortunately, there has been a very narrow politically-based focus on building marine reserves around single habitat types, which sometimes amounts to little more than conservation of isolated coral outcrops. To date, there has been less consideration of the importance of habitat connectivity in a functional seascape; a connectivity whose importance seems similar to that recognized in terrestrial and riverine ecosystems (e.g., Poiani et al.

2000). This issue is significant, because marine species have great potential for movement and dispersal. We believe that our best opportunity to assess the impacts of overfishing large piscivorous fishes on food web structure and function, and the importance of trophic interactions across habitat boundaries, can only come from controlled experiments in replicated ''no-take'' zones such as those found in the Florida Keys National Marine Sanctuary.

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