Symbiosis, fisheries and economic development on coral reefs

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Life-history traits of commercially important species, physiological attributes of the framework species, and characteristics of ecosystem processes make coral reefs especially vulnerable to export of biomass. Organisms in ecosystems driven by upwelling and terrestrial nutrient input are more amenable to biomass yield. Nonexportive approaches to resource management, exemplified by Palau, are compatible with the attributes of coral-reef ecosystems; they satisfy to a greater degree the economic demands and pressures of growing human populations, and they provide motivation to manage.

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Coral reefs have been touted as having the greatest gross primary productivity and highest standing stock biomass of marine ecosystems. It has been calculated that the coral reefs of the world can produce a sustainable fisheries yield of 20-35 million metric tonnes per year[1,2].

But high yields have not been sustained when the fisheries are exploited commercially. Although average annual fisheries yields have been documented to be as high as 26.6 metric tons per km^{-2} yr^{-1} for some coral reefs, the yields on these same coral reefs eventually demonstrate a decrease of up to 70% catch per unit effort, a decrease of 75% in number of fish per hectare, and a major shift in relative abundances among species, with a drastic decrease in the species preferred by fishermen[3]. There are a number of examples of coral-reef fisheries being found to be more vulnerable to commercial overexploitation than predicted by the initial standing stock or potential yield calculated for the system[4]. This special vulnerability is largely from the life-history characteristics of the important species (Table 1) and the characteristics of the ecosystem (Fig. 1).

Although pelagic fishes can also be overharvested[6], they can support a greater biomass yield per unit gross primary productivity of the ecosystem than can coral-reef fishes (Fig. 1). Tropical pelagic fishes search widely for dense concentrations of food, feeding intensely in 'foamers' or 'boils' when they find concentrations, consuming as much as 25% of their own body weight in one day. They can grow to 5kg (skipjack, *Katsuwonus pelamis),* 9kg (mahimahi, *Coryphaena hippuros)* or 14 kg (yellowfin, *Thunnus albacares)* within their first two years7, although they do tend to have short lifespans (skipjack and mahi-mahi live for a maximum of four or five years). When finding a dense patch of food, feeding activity by tunas is sometimes so intense that the body temperature can rise above that of the surrounding seawater and cause 'burns' in the muscle tissue that lower the market value of the catch. Thus, the tropical pelagic fishes that search out and feed on patchy concentrations of abundant resources are characterized by fast growth, early reproduction and rapid population turnover, traits that are relatively favorable for the adjustment of their populations to exploitation.

Although some coral-reef fishes can grow to a great size (the grouper *Epinephelus itajara* can grow to 300 kg and the wrasse *Cheilinus undulatus* to 87 kg). coral-reef fishes generally grow at a rate less than one kg per year in the diverse and highly competitive coral-reel ecosystem. The intensity of predation on coral reels is indicated by the disproportionate prevalence and diversity of predators in the community structure[8], and the ratio of juveniles to adults in populations on coral reels is much less than in neighboring mangroves or seagrass beds. Although even smaller coral-reef fishes can live for decades once they reach adulthood, the survivorship of juvenile fishes in their first year is as low as 0.007 *(Acanthurus lineatus* in American Samoa, central Pacific)[9] or 0.008 *(Haemulon Ilavolineatum* at St Croix, Caribbean)[10]. The uncertainty of survival in a tightly competitive system with high rates of predation probably contributes to selection for large size, longevity and multiple reproduction. These traits of coral-reel species reflect the low rates of population turnover and vulnerability to overharvest[11] in groupers, giant clams, spiny lobsters and sea turtles. These life-history traits of coral-reel animals have recently contributed to the conclusion that marine protected areas are the most practical and effective method for management of coral-reef fisheries[ll-13].

Ecosystem processes

There are also fundamental differences at the level of ecosystem processes between coral reefs and regions subjected to pulses of concentrated nutrient input. Oceanographic processes such as upwelling are the major driving forces in large-scale current ecosystems (Humboldt, Benguela, Oyashio, Kuroshio), while species interactions (e.g. predation) are a major controlling factor in coral-reef eco-systems[l4-16]. The complexity of these interactions has contributed to the conclusion that a holistic approach to fisheries management such as marine protected areas is the most practical and effective method for management of coral-reef fisheries[11-13].

Overfishing by humans does not influence the process of upwelling. On coral reefs, in contrast, overfishing can have large-scale, long-term. ecosystem-level effects[14-16]. In recent recognition of the

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importance of taking basic characteristics of the ecosystem into account, the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS) is presently establishing an advisory panel to explore the application of ecosystem principles in fishery conservation and management.

Although coral reefs have high gross primary productivity, the fisheries yield and net system productivity are relatively low (Fig. 1). Fisheries yield per unit gross primary productivity for the Peruvian upwelling is about 10 to 60 times greater than this ratio for coral reefs (Fig. 1). For coral-reef systems, the net system productivity averages very close to zero[2]. Far less than one percent of the gross primary productivity is converted to production that is meaningful for human consumption[2]. This is partially a result of the proportion of energy lost in transfers among trophic levels.

The concentration of standing stock biomass is lower in food webs characterized by high rates of nutrient input. The major increase in the world fisheries yield of the 1950s and 1960s was largely a result of concentrated harvesting effort on fishes lower on the food web, such as herring and anchovies. On coral reefs, the presently rampant live coral-reef fish trade of over a billion dollars a year[17], is concentrated on serranids and other large fishes such as *Cheilinus undulatus,* high in the food web. Upwelling regions of the world have short food-webs with only one or two steps between phytoplankton and a major source of food for man, while there are up to six substantial trophic levels in coral reefs.

Constraints of physiological complexity

Complex interactions at the physiological level also put constraints on the yield of the ecosystem. In systems of abundant nutrient input (such as in areas of upwelling), relatively simple, free-floating, phytoplankters such as diatoms and naked flagellates can respond rapidly and increase in population density. Feeding rates of herbivorous copepods increase as phytoplankton becomes densely available, and the gross growth efficiencies of herbivorous marine plankton in upwelling regions are at least twice the 10% usually quoted for terrestrial communities.

In contrast to the swift and large-scale response of free-floating single-celled algae to nutrient input in upwelling regions, the response of single-celled algae within the tissues of corals and other animals is inhibited by the complex physiological accommodations between the host and the symbiont. There is some indication that levels of dissolved nitrogen exceeding

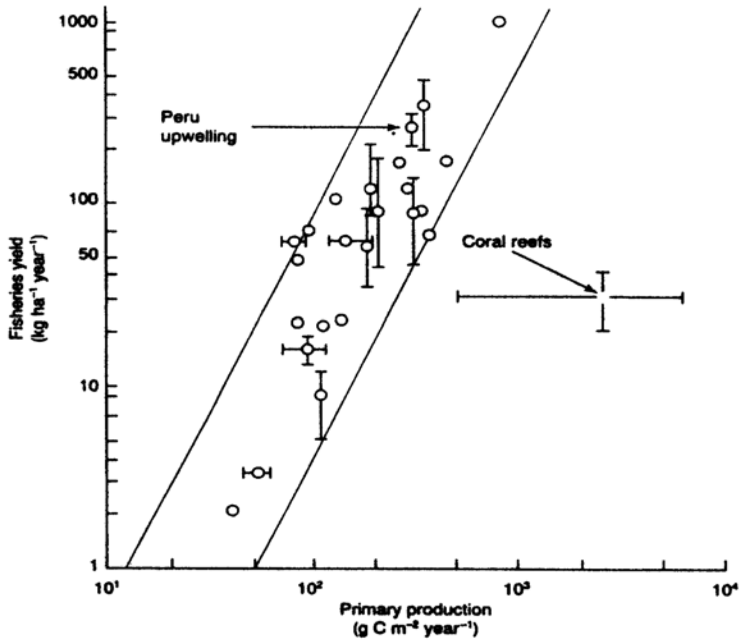

Fig. 1. The ratio of fisheries yield to gross primary productivity is substantially less for coral-reef ecosystems than for other marine systems. The data were compiled from 51 studies at 25 sites. *Reproduced, with permission, from Ref. 5.*

about 10μM destabilize the symbiosis of corals and intracellular algae by enhancing the growth rates of the zooxanthellae[18]. The corals may respond to this physiologically destabilizing rapid increase in intracellular algal density by expelling 'excess' plant cells. Furthermore, the intracellular algae within a single species of coral may be a complex of species in which the host coral may expel some and allow the establishment of others in response to light, temperature or other factors[19]. In contrast to the free-floating single-celled algae in the water column of upwelling areas, regulatory processes within the complex physiological adaptations of reef animals tend to dampen the responses of intracellular algae to pulses of nutrient input.

Physiological symbioses between animals and the algae within their tissues are

Table 1. Comparison of life-history traits of large tropical pelagic fishes and coral-reef fishes

Tropical pelagic fishes (e.g. *Thunnus albacares, Katsuwonus pelamis, Coryphaena hippurus*)	Coral-reef fishes (e.g. *Epinephelus cruentatus, Epinephelus itajara, Epinephelus guttatus, Cheilinus undulates, Sphyraena barracuda*)
Rapid growth 1-4.5 kg per year, 3-14 kg by the second year	Slow growth, rarely over 0.5 kg per year
Early sexual maturity	Postponed first reproduction
Periodically abundant recruitment	Irregular recruitment success
Relatively short life (*Coryphaena* and *Katsuwonus* have a life span of only about 4-5 years)	Long adult life (often decades) Life histories adapted to multiple reproduction
Live in schools or dense aggregations	Adults often territorial and solitary
Wide ranging: individuals can travel from the Philippines to Hawaii or further	Sedentary post-settlement life-history stages
Rapid population turnover	Low mortality of adults; high mortality of juveniles

fundamental to the characteristics of coral reefs at the ecosystem level. Coral reefs are often depicted as oases in nutrient-poor waters, and organisms characteristic of coral reefs are often involved in interactions that facilitate capture and recycling of materials. Symbiotic relationships of a variety of single-celled primary producers (e.g. dinoflagellates, chlorophytes, diatoms, cyanobacteria and *Pro-ch/oron)* with disparate classes of animals (e.g. ciliates, foraminiferans, radiolarians, demosponges, hydrocorals, actinians, scleractinians, octocorals, scyphozoans, turbellarians, bivalves, gastropods and ascidians) provide novel metabolic capabilities and mechanisms for the capture and recycling of nutrients[20]. Since a large proportion of primary production in coral-reef ecosystems is from intracellular symbioses (rather than phytoplankton), complex physiological responses probably lead to a dampening of a positive response of the coral-reef system to increased harvesting.

Bermuda and Palau

Coral reefs have supported subsistence fishing for hundreds or perhaps thousands of years[21]. However, as the Asian economy grows and the dollar value of reef resources overrides management, tradi- tion and law. as human populations grow beyond the carrying capacity of coral reefs, and as urbanization and immigration of people change the culture from subsistence to participation in the international cash economy, compelling and lucrative alternative sources of income must be found for the majority of fishermen living near coral reefs. The life-history characteristics of coral-reef organisms and the relatively closed nature of the ecosystem make it unrealistic to expect reef communities to continue to produce enough food to meet these increasing population and commercial demands. Radically new approaches to resource management have been initiated by Bermuda and Palau for sustainable income from coral reefs.

The number of people employed and the economics of extractive reef-fisheries were small in Bermuda compared to the economy supported by tourism. Tourism and recreation-related commerce in Bermuda grossed more than $9 million in 1988. There was widespread concern that because of commercial fishing the coral reefs in Bermuda were deteriorating and that algae were replacing living coral. The hotel owners, charter-boat fishermen, dive and tour-boat operators and other businesses concluded that the incomes of many were threatened by the activities of a few fishermen. In 1990, after considering evidence that the catches were declining substantially and that the reef communities were deteriorating. the Government of Bermuda offered payment of up to $75 000 per fisherman. in addition to compensation for hardware such as pots and winches. in order to close the coral reefs of Bermuda to pot fishing[22]. The fishermen were encouraged to use their boats for more lucrative endeavors in tourism.

It likewise became clear in Palau that exporting fishes was in competition with and far less profitable than subsistence fishing, recreational fishing, tourism and the sale of fishes to local restaurants and hotels. In view of the more sustainable economic use of resources in subsistence and tourism than in the export of biomass, the Government of Palau passed the 'Marine Protection Act of 1994' to phase out the export of fishes. Currently, the commercial export from Palau of fishes is illegal between the months of March and July, which corresponds to the spawning seasons for most species; invertebrates cannot be exported unless produced by aquaculture.

It takes at least an order of magnitude more fish to support a few commercial fishermen on oceanic islands than it does to support the same number of people by subsistence fishing. This is because most of the proceeds from the sale of fishes goes toward marketing and transportation costs. Coral-reef resources can sustain a much greater number of people or careers in the world economy if used in the nonextractive, service-oriented approaches of Bermuda and Palau. These approaches are compatible with the attributes of coral-reef species and ecosystems, and with the demands of the growing human populations, growing economies and urbanization.

The money exchanged in world tourism in 1992 was $1.9 trillion, over 27 times the $70 billion of the world marine fisheries revenue[23]. To participate in the world economy, the islands of Oceania can be highly competitive for the high spenders in tourism, while geography (transportation costs), ecology (low yield, effects of over fishing on ecosystem processes) and biology (life-history and physiological characteristics of the species) work against commercial export fisheries on coral reefs. The expenditures for commercial fisheries are more risky than the commitments to ecotourism. The cost of airfares are paid by the tourists themselves, in contrast to the costs of fisheries shipping and marketing which are subtracted from the profit on exported fish sales.

It is remarkable that coral reefs in regions of low nutrient input, such as on atolls in the Pacific gyre, are able to support such concentrations of high biomass and diversity .It is analogous that a greater number of people and diversity of careers can be supported sustainably by coral reefs if economies on tropical islands are based on the natural attributes of the species and ecosystem, i.e. recycling and low amounts of export. Seafood should be exported mainly from ecosystems with abundant nutrient input, such as upwelling, estuaries and continental shelves. where the populations of organisms are more amenable to being harvested.

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