

fold [19]. Moreover, recent attempts to re-engineer characterized homing endonucleases to bind and cleave unrelated sequences have revealed that few mutations are required to change DNA binding specificity [20]. Given the targeting of conserved sequences by both endonucleases and introns, it is perhaps not surprising then that mobile group I introns have independently evolved multiple times, creating extremely efficient and successful selfish genetic elements.

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Marine Conservation: Moving Beyond Malthus

A new study has shown that maximum overfishing of coral reefs occurs among countries at intermediate levels of socio-economic development; can managers and policy makers help countries dependent on these ecosystems avoid the resulting poverty traps?

Robert S. Steneck

It is an over-simplification to characterize countries as *developed* or *developing*. The latter is often a euphemism for poor countries with few economic opportunities. Nevertheless, most *developing* countries aspire to become *developed* with the associated lifestyles they have seen or heard about. From a paper in this issue by Cinner *et al.* [1], we learn that the socio-economic path developing countries take as they evolve towards the developed state can be critical to the sustainability of the ecosystem on which they depend. Specifically, socio-economic development can result in a social-ecological trap from

which escape will be difficult. Understanding the complex and non-linear path towards depletion is a necessary first step towards avoiding it.

In a sense, social ontogeny recapitulates social phylogeny. Humans began their social evolution as hunters and gathers and subsequently evolved, out of necessity, into farmers. With time and where resources allowed, city-states and social hierarchies emerged, with distinct classes ranging from workers to rulers as a pinnacle of social development [2]. Today, we can find this full spectrum of societies from Amazon rain forests to Beijing. Such gradients offer research possibilities for social scientists seeking to understand trajectories and consequences of human social

evolution. What we can learn from such studies is how societies alter their interaction strength with the natural ecosystems on which they depend. In effect, they go from initially being ‘passengers’ to ultimately being ‘drivers’ of these ecosystems.

Societies living close to coral reefs range from modest hunter-gatherers to major industrialized cities. Coral reef ecosystems are productive, fish-rich oases surrounded by nutrient-poor ocean deserts. Unfortunately, coral reefs are among the most endangered ecosystems in the world [3], which places their dependent human societies at risk. One reason why this coral reef crisis has been so difficult to confront [4] is because it is so multifaceted. While we know much about what drives complex biological systems, we know relatively little about what drives the associated social systems. More importantly, we know even less about how the two interact. Nowhere is this more obvious than for coral reef ecosystems and adjacent societies.

While the coral reef crisis is an interdisciplinary, social-ecological

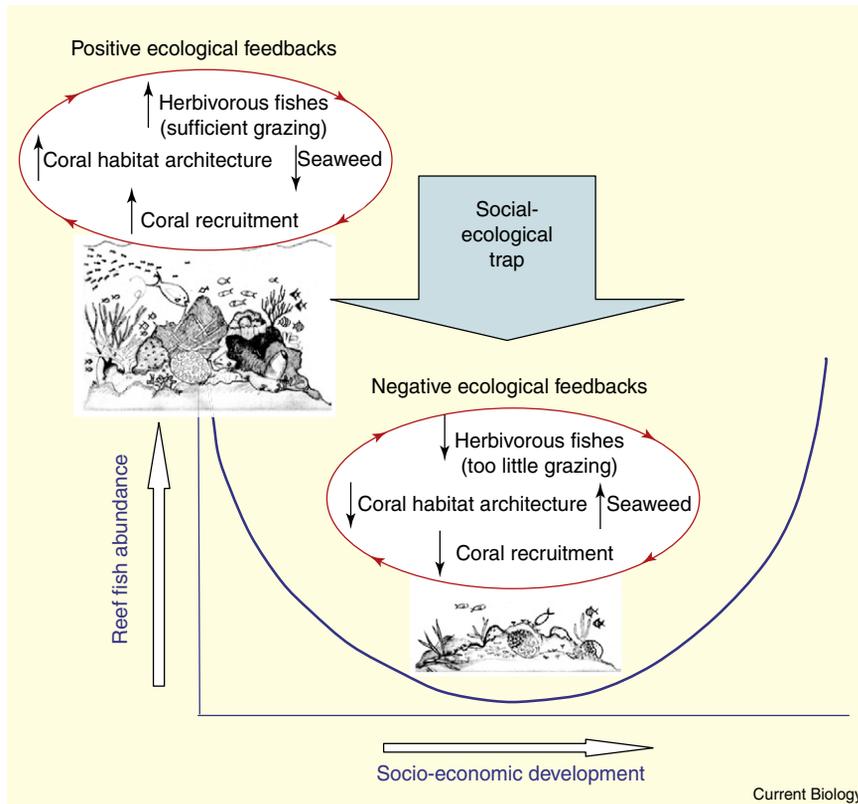


Figure 1. Reef fish abundance as a function of socio-economic development [1] drives negative ecological feedbacks that limit ecosystem recovery [6] and create a social-ecological trap.

problem, most research has failed to study it as such. Often missed is how social and ecological systems interact and the resulting conclusions can consequently oversimplify complex issues. For example, a common notion is that coral reefs suffer from too many people [5]. People can overfish coral reefs and, because some reef fish are key drivers of these ecosystems [6], as their abundance declines the risks of ecosystem collapse increase. The relationship between rates of population growth and rates of resource depletion is called 'Malthusian overfishing' because Malthus suggested in the 18th century that the geometric increase in human populations "would always outstrip the productive capacity of the resources available to them..." [7].

Such Malthusian overfishing was not, however, what Cinner *et al.* [1] found. Their study of coral reef ecosystems and associated countries in the eastern Indian Ocean revealed that the interactions between social and ecological drivers are critically important. They show that, while nearby human population densities and the habitat architecture of coral

reefs are statistically significant factors, the strongest single determinant of reef-fish biomass is an index of socio-economic development. By far the greatest determinant of reef fish biomass, however, was the *interaction* between habitat complexity and socio-economic development. Further, the relationship between socio-economic development and reef fish was a quadratic (U-shaped) function, with the highest fish biomass at both the lowest and highest levels of socio-economic development (Figure 1).

It is well known that the abundance of certain groups of reef fishes is essential to reef health [8,9]. What is new and exciting about the Cinner *et al.* [1] study is that they describe complex, nonlinear impacts of social evolution resulting from changes in fishing efficiency and motivation. As countries develop, their capacity to fish improves with access to advanced boats, engines and fishing gear. This inevitably results in significant declines in the abundance, and body size of reef fish and in critical ecological functions such as grazing from herbivorous reef fishes [4,10]. This not only degrades the

structure and functioning of the reef ecosystem, it slows its capacity to recover following disturbances (Figure 1) [6,9]. On the other side of the socio-economic valley in reef fish abundance, however, are countries with higher economic diversity, greater awareness of how the ecosystem works and a lower reliance on reef fish for food or profit. The ultimate challenge for managers, policy makers and concerned citizens will be to find a way to avoid this valley of depletion (Figure 1) [1].

The results of this new study are cause for both optimism and pessimism. The optimism stems from the idea that Malthusian overfishing may not be inevitable. It may be possible to avoid past mistakes with subtle, but effective, changes in how people fish. Cinner *et al.* [1] observed that, as socio-economic development progresses, fishing methods change. They found that spear guns, which can efficiently extirpate important large-bodied reef fish, were available and used primarily in countries at intermediate levels of social-economic development. At higher levels of development, greater economic diversity reduces local fishing pressure. Further, boats with engines allow fishing to target more distant and more sustainable pelagic fishes that are not part of reef ecosystems [11].

The pessimism relates to the unfortunate synergistic interactions between strong social and biological drivers, which result in a social-ecological trap of low abundance of coral reef fishes (Figure 1). Recent biological studies found important positive and negative feedback relationships that hinge on the ecological functions related to reef fish and habitat complexity [6,8,12]. For example, large herbivorous fishes such as parrotfish keep coral reefs free of seaweed (algae) that can smother live coral, and render reef ecosystems hostile to recruiting juvenile corals (Figure 1). As a result, fewer coral species persist and the complex three-dimensional coral habitat structure declines. Because reef habitat architecture is critical for some species of recruiting parrotfish, as it declines, it slows the recovery of reef herbivores and ultimately the ability of corals themselves to recover. This negative biological feedback creates an alternate stable state that sustains fewer fish.

The big danger resulting from combined negative feedbacks in the reef ecosystem and dependent societies is their inability to recover ecologically and economically. The latter can create a very stable social-economic condition called a 'poverty trap'. This occurs when people become so poor that short-term need to survive outweighs any long-term advantages to conservation or sustainable management.

Sadly, the paths into these social-ecological traps are much clearer than are the paths of escape. Ideally, developing countries should be managed to avoid such traps but this is difficult. Simple solutions, such as infusion of funds, rarely work because they fail to stop or reduce the impetus for, or efficiency of, fishing. Often such infusion of money feeds local corruption. Corruption is high in countries having limited socio-economic development (for example, see values in The Human Development Index [13] and the independently derived Corruption Perception Index [14]). Alternative economic drivers are difficult to establish. Coral reefs can be developed for ecotourism but this requires infrastructure such as airports, roads and hotels, which often have deleterious footprints. Furthermore, the limited pool of 'ecotourists' limits the spatial extent of economic benefits from this approach [15].

Cinner *et al.* [1] suggest that local customs be understood, so that complementary sustainable practices can be developed. Simple, locally acceptable management actions have had excellent success in some developing countries. For example, the

people of Palau prefer to eat ecologically important parrotfish; however, because their reef is large relative to their local population, they only had to ban the export of reef fish in order to harvest parrotfish sustainably for their customary meals [16]. R.E. Johannes' very effective work with local cultures suggests a way to use scientific information together with local practices to avoid the developing valley of depletion of fish on coral reefs.

Finally, Cinner *et al.* [1] establish a new analytical standard for the social sciences. They show quantitatively how to integrate ecological and social science data. Their research shows statistically why fishing capabilities of coastal resource users change as a function of their socio-economic development. They demonstrate why it is the social-economic index rather than some other regional factors causing the pattern in reef-fish biomass by presenting the results from unfished marine reserves from each of the regions as controls against spurious correlations among countries. Importantly, they identify which of the changes are statistically significant. Their approach can be replicated and scientifically evaluated by others. Significantly, it provides clear scientifically based advice to managers and policy makers about a very complex but important social-ecological problem.

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Evolution: Replacing Genes and Traits through Hybridization

The role of hybridization in evolution has been debated for over a century. Recent molecular genetic studies indicate that hybridization is surprisingly frequent in natural populations, and that it may allow populations to regain traits that have been lost and possibly to replace damaged alleles with functional copies from related species.

Loren H. Rieseberg

Botanists have long speculated that plant species may swap valuable genes

or traits through hybridization and backcrossing (i.e., introgression). The hybridization enthusiast Edgar Anderson [1] went so far as to argue

that, in hybridizing species, the "raw material for evolution brought in by introgression must greatly exceed the new genes produced directly by mutation." Similarly, Harlan and DeWet [2] attributed the aggressive nature of some of the world's worst weeds to the "plundering of related species of their hereditaries." However, the early evidence used to support these claims often had other possible interpretations, and botanists were accused of 'seeing hybrids under every bush'. Only with the application of molecular biology tools to the