

Trade-offs between fisheries and the conservation of ecosystem function are defined by management strategy

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Efforts to conserve marine biodiversity must move beyond conserving individual species within protected areas and seek to preserve the functional roles that species perform in ecosystems across seascapes. For instance, herbivorous and predatory (including invertebrate-feeding) fish are critical for maintaining coral-reef habitat and the diversity of dependent fish assemblages. However, increasing the biomasses of fished species may come at a cost to fisheries. Using coral reefs as an example, we examined critical functional roles and model trade-offs between fishery profits and the spatial extent of functional fish communities. The nature of the trade-off depended on the management scenario: protecting functions in small areas could be achieved with marine reserves at minimal cost to fisheries, whereas reducing fishing effort was a more effective method for protecting functional communities across a seascape. An appropriate choice of management actions can alter the trade-off and, in doing so, ameliorate potential for conflict with resource users.

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Within ecosystems, the maintenance of key habitats, biodiversity, and productive fisheries may critically depend on the functions performed by only a few species (Jennings and Polunin 1996; Cadotte *et al.* 2011). Species that contribute disproportionately to the maintenance of biodiversity and ecosystem function reside within a variety of marine ecosystems, including temperate kelp forests (Steneck *et al.* 2002) and coral reefs (Mumby and Harborne 2010). On coral reefs, grazing by parrotfish (Scaridae) can control algal competitors of corals, facilitating recovery of coral-reef habitat after disturbance (Steneck 1988); large predators can suppress mesopredators and maintain reef fish diversity (Stallings 2009); and invertivorous (invertebrate-feeding) fish can control sea urchin populations, the grazing of which reduces habitat complexity (McClanahan and Shafir 1990). Conserving these functional roles is important for fisheries and biodiversity, because both depend on healthy ecosystems.

The integrity of ecosystems is threatened by fishing, which reduces the biomass and density of functionally important species (Jennings and Polunin 1996). Overfishing of parrotfish, large predators, and invertivores on coral reefs can have major effects on ecosystem function, ultimately leading to reduced coral abundance and lower fish diversity (Jennings and Polunin 1996). Maintaining non-target species and preventing degradation of habitats and biodiversity are primary goals of ecosystem-based fishery management (EBFM; Pikitch *et al.* 2004; Palumbi *et al.* 2008). For instance, parrotfish fishing is banned in some countries to conserve grazing

on reefs (see section below on “Functional roles of fished species on coral reefs” and Choat *et al.* 2012). Goals for conserving ecosystem function are expected to trade-off with fishery harvests and profits (Cheung and Sumaila 2008; Smith *et al.* 2011). As such, fisheries stakeholders may oppose conservation efforts (eg White *et al.* 2013). Thus, balancing the conservation of functional roles with fishery objectives is central to effective EBFM.

The balance between conservation and fishery objectives has been investigated through models of direct controls on fishery harvest and models of marine reserves. Studies on direct control typically suggest precautionary reference points for a species’ biomass that are necessary for maintaining functional roles (Pikitch *et al.* 2004). For instance, harvest limits for forage fish should be conservative to make food available for predators (Smith *et al.* 2011), and fisheries should try to balance their impact across size classes of targeted species to avoid large oscillations in ecosystems (Rochet and Benoît 2012). The models that were used to make these recommendations focus on resolving functional relationships but simplify spatial dynamics within seascapes. In many cases, models of spatial dynamics may be crucial for quantifying ecosystem function (eg herbivory rates depend on fish biomass at individual reefs, rather than population biomass). Although applied in studies of marine reserve design, spatial models have tended to rely on traditional conservation goals. Studies on the marine protected area network along the coast of California, for example, have used habitat representation and target species biomass as conservation goals (White *et al.* 2013), neither of which is explicitly linked to a functional role.

What is not known is whether the proper management approach could ameliorate the trade-off between fisheries

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and conservation, such that conservation of ecosystem function would be faced with less opposition from fishing industries. This requires comparing the effectiveness of direct controls and reserves in a spatial context. Direct controls on harvest are expected to reduce fishing effort across a seascape, whereas marine reserves reduce effort locally but increase effort offsite (Hilborn *et al.* 2004). Therefore, to implement EBFM, managers need to know if it is better to have many habitat patches with moderate local biomass of a species, or a few habitat patches with very high local biomass.

Here we examine the efficacy of marine reserves and limits on fishing effort in meeting goals for functional persistence of three coral-reef fish species, not just inside reserves but across a seascape. We begin by identifying precautionary reference points, below which the biomasses of three fish species groups are inadequate for conserving their functional roles. We then model management scenarios where marine reserves and controls on fishing effort are used to manage for both the conservation of functional roles and fishery profits. The conservation objective is explicitly defined as maximizing the number of habitat patches where the fish community meets or exceeds the reference points. This simplification of system dynamics allows us to efficiently model trade-offs in a spatial context, and is transferable to other ecosystems.

■ Functional roles of fished species on coral reefs

Herbivorous parrotfish play important roles in maintaining suitable settlement habitat for coral larvae by preventing macroalgal blooms (Steneck 1988). Macroalgae can suppress the growth and recruitment of corals by competing with coral for space and light and by releasing secondary metabolites (Rasher and Hay 2010). Effective grazing requires relatively high fish densities, so we selected a biomass of 80% relative to unfished levels. This threshold was based on empirically tested simulation models for Caribbean reefs, which predicted the relationship between parrotfish grazing capacity and the resilience of coral populations (Mumby *et al.* 2007). Reductions of herbivore grazing by >80% have also been observed to trigger a reversal of the coral cover trajectory from one of recovery to one of decline (Mumby and Harborne 2010).

The second functional role is predation control of mesopredator abundance by large groupers (Serranidae). Trophic cascades can occur on reefs depleted of large groupers, where abundant mesopredators suppress abundances of other prey species, including small grazers (Stallings 2009). Although many decades of exploitation complicate estimating the true unfished biomass of large predators, an example of “fishing down a food web” from coral reefs suggests predator declines of ~90% are adequate for mesopredator release (Mumby *et al.* 2012). To be conservative, we therefore set the

minimum biomass of groupers required to perform their predation role at 20% of their unfished biomass (WebPanel 1).

The third functional role is predatory control of sea urchins. When released from sufficient predation, urchin populations in some regions can increase markedly, causing “urchin barrens” (habitat erosion due to extensive over-foraging; eg McClanahan and Shafir 1990). Triggerfish (Balistidae) are important predators that contribute to controlling urchin abundance. As compared with nearby no-take reserves, fished areas of Kenyan coral reefs had greater urchin densities and lower habitat complexity likely because they possessed 10% of the biomass of triggerfish (McClanahan and Shafir 1990). We set the minimum biomass for triggerfish to control urchin grazing at 20% of their unfished biomass.

■ Methods

Model of fishery and functional roles

We used a generic spatial model of three reef fish populations (grazing parrotfish, piscivorous grouper, and invertivorous triggerfish) to examine trade-offs between fisheries and conservation goals under four management scenarios. The model seascape was a linear coastline of 100 reef patches, each 1 km² in size. At each patch we tracked the age and size distribution for the three fish populations. Fecundity was size dependent, and there was density dependence among settling larvae arriving at a reef (WebPanel 1).

The conservation goal was the percentage of the seascape where the functional biomass thresholds were met for all three species groups, whereas the fishery goal was to maximize long-term profits aggregated across the three groups when the system was at equilibrium (eg White *et al.* 2013). We also ran simulations where we took the discounted net present profits, to represent fisheries driven by short-term demands (WebPanel 1). Higher discount rates increase the importance of short-term profits. The initial condition for model simulations was an overfished system, where a species' harvest and biomass were at equilibrium and the level of overfishing was in proportion to a species' relative sensitivity to fishing pressure (WebTable 1). Effort was aggregated on reefs where expected profits were greater, but total effort at a given time was limited to a constant level. The value per kilogram of grouper was four times as great as that of the other two groups (WebTable 1). The net result was that fishing effort for all species was relatively evenly distributed without marine reserves; if there were reserves, fishing effort was aggregated at reserve boundaries.

We considered different combinations of marine reserves and direct effort control in four management scenarios, which represented increasing requirements for sophisticated off-reserve management and enforcement (WebPanel 1):

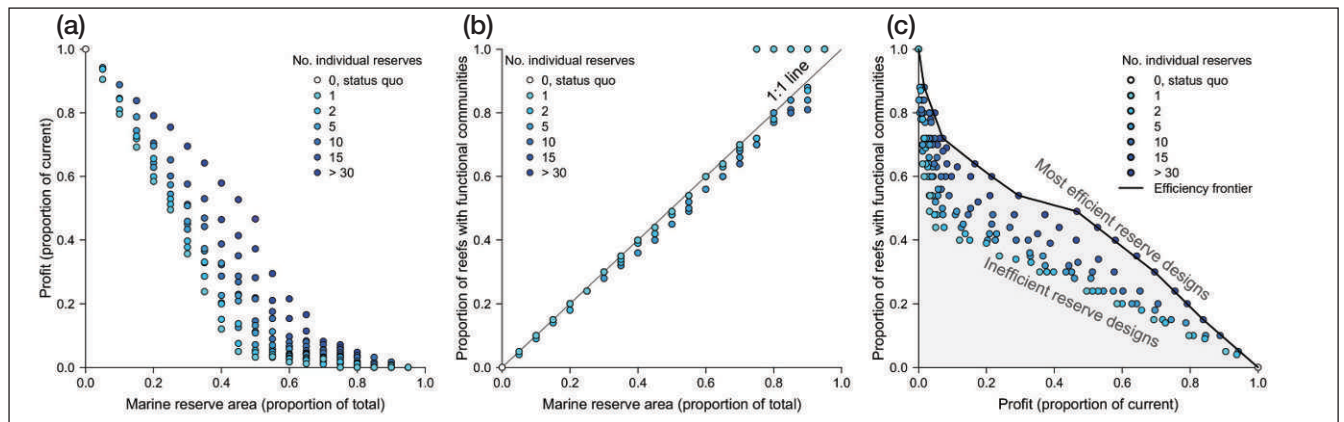


Figure 1. Trade-offs when using marine reserves for management in an overfished fishery (scenario 1). (a) Profits decreased for larger reserves but were higher if reserve area was split into many small reserves. (b) The proportion of functional communities increased linearly with reserve area (gray line – 1:1). (c) Profits and proportion of functional communities trade-off. Designs that split reserve area into many small reserves are the closest to the efficiency frontier (black line).

- (1) Marine reserve management only, where there was overfishing outside the reserve (eg McClanahan *et al.* 2008). Marine reserves could be declared on any or none of the reefs, and fishing did not occur inside marine reserves. We simulated all possible marine reserve designs that covered 0–95% of the seascape, ranged from 0–49 in number, and were evenly spaced across the seascape.
- (2) Mixed management, where marine reserves, designed as in (1), were present but overall effort was limited to the level that gave the maximum equilibrium profit.
- (3) Management that limits overall fishing effort (“effort management”) without marine reserves. The overall effort level was varied, but the catch rates per unit effort for the fish groups were fixed. This represents cases where the total number of fishers can be controlled, but not how they target individual species.
- (4) Multi-species effort management without marine reserves. Catch rates were varied by species. This represents cases where effort control across multiple species can be fine-tuned (eg in conjunction with gear restrictions or catch limits; Cheung and Sumaila 2008; McClanahan *et al.* 2008).

We displayed the trade-offs between profits and the conservation outcome by finding the most efficient options for each management scenario. For a given management scenario, the most efficient options were those where a gain in either goal cannot be made without a loss in the other goal. For instance, if reserve management was used, one option was to reserve 30% of the seascape. The model then predicted the conservation and profit outcome for this option, which is one point on the trade-off plot (Figure 1). We evaluated trade-offs across management scenarios by comparing the proportion of functional communities in each management scenario (1–4) for three management choices (“A”, “B”, and “C”), which were relative to the “status quo” profits (profits of: A = 72%, B = 90%, and C = 115%).

Results

Effect of marine reserves on fisheries and conservation of functional roles

Increasing reserve size without reducing effort decreased fishery profits but increased the number of functional communities (Figure 1, a and b). The net benefit of a marine reserve to fisheries was a balance between its benefits from the spillover of larvae from within the reserve and its costs through greater numbers of fishers operating in a smaller area. For reserve networks of similar areal extent, profits were greatest if individual reserves were small, because spillover that benefitted fisheries was greater. The high biomass threshold for parrotfish and the high susceptibility of grouper to overfishing meant that only areas inside marine reserves met their functional targets (WebFigure 1, a and b). Therefore, the proportion of the seascape with functional communities increased almost linearly with reserve size (Figure 1b). The functional biomass threshold for triggerfish was met without any marine reserves being present (WebFigure 1c). The net effect was that networks of smaller reserves had the highest areas of functional communities for a given profit level (Figure 1c).

Combining marine reserves with a reduction in fishing effort (“mixed management”) meant the percentage of functional communities could be as high as 35% without reducing profit as compared with the status quo (Figure 2). Conversely, if management relied on marine reserves alone, profit had to be reduced from the status quo for there to be any functional communities.

Effect of effort management

With effort management, but without control on individual species, the trade-off was characterized by a severe threshold (Figure 2). With fishery profits >74%, no reefs had functional communities; alternatively, with fishery

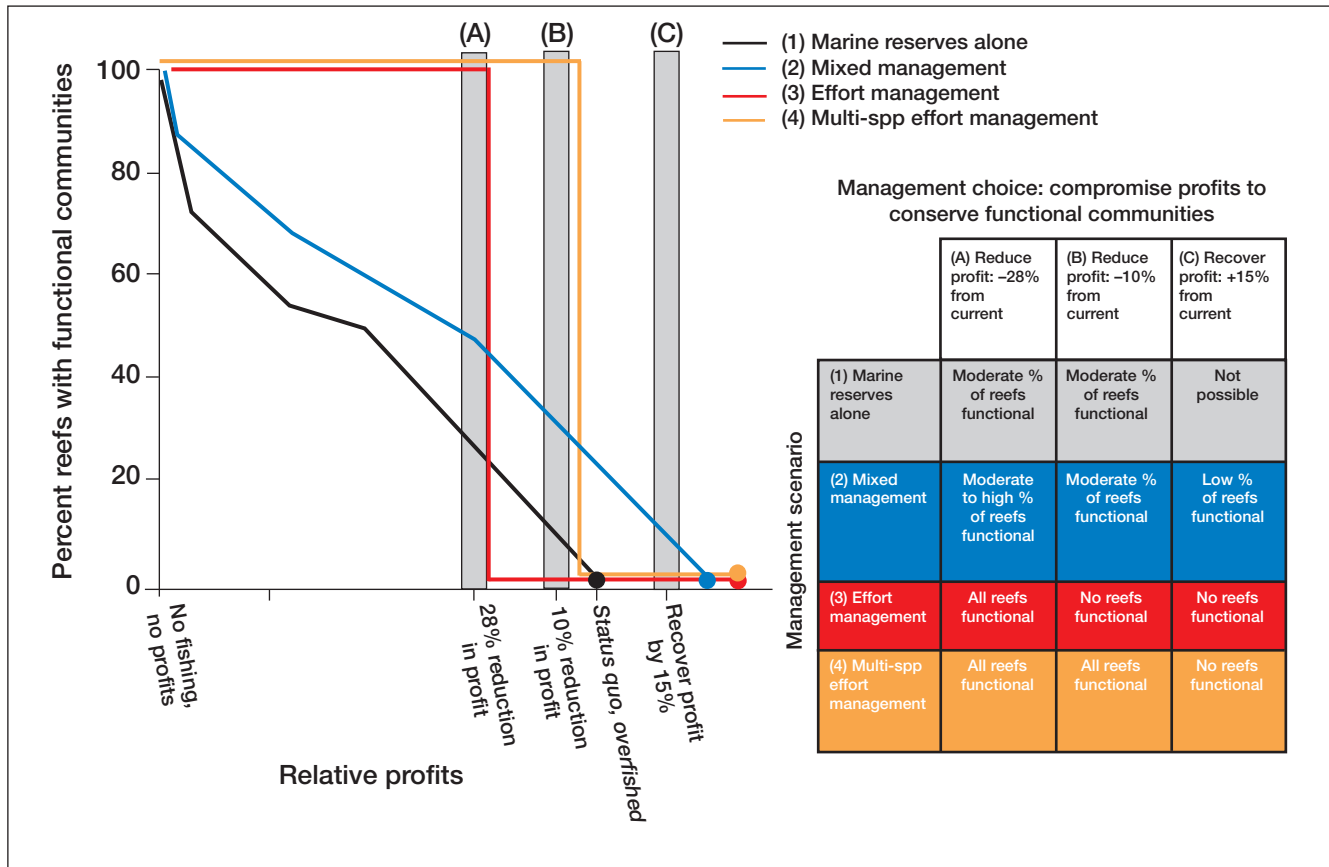


Figure 2. Management type affected the trade-off between multi-species profits and the percent of reefs with functional communities (ie reefs where all three species densities are greater than their functional thresholds). Profits are presented as differences from the overfished status quo. The colored points indicate the maximum attainable profits for a given management scenario. The inset table indicates how to read the trade-off; for a given profit level (management choices A–C), the conservation outcome can vary depending on the type of management used.

profits <74%, almost all reefs had functional communities. This threshold occurred because biomass increased evenly across the seascape when effort was reduced without reserves (Figure 3). The high biomass requirement for effective parrotfish grazing determined the profit level for the threshold.

Multi-species effort management moved the trade-off so that functional communities could be achieved across the seascape for a relatively small loss in fishery profits (Figure 2). Parrotfish were fished with low effort, whereas grouper and triggerfish, both of which had lower functional biomasses, could be fished at their species-specific optimum for profit.

Comparison of trade-offs across management scenarios

In our case study, if profit was reduced by 28% from its status quo overfished value (Figure 2, choice A), the marine reserve and mixed-management scenarios could achieve >25% coverage of functional communities (Figure 2, scenarios 1 and 2). However, almost all reefs had functional communities in the effort management scenarios (Figure 2, scenarios 3 and 4). If profit was reduced by 10% from

the status quo (Figure 2, choice B), multi-species effort management provided the best outcome; the marine reserve management scenario had moderate proportions of functional communities relative to choice A. However, no reefs had functional communities with effort management (Figure 2, scenario 3). Finally, profit could be increased through mixed, effort, or multi-species management (Figure 2, choice C, scenarios 2, 3, and 4). Yet only mixed management could increase profit and ensure that some reefs had functional communities.

Some ecological and economic traits vary regionally from the case study that we have analyzed here. Importantly, the additional benefit of multi-species effort management (scenario 4) over non-specific effort management (scenario 3) depended on there being a species with a low functional threshold but high value (WebFigure 2). For instance, if the value of parrotfish was four times as high as the value of the other fish groups, the effort and multi-species management scenarios had similar trade-offs. In many fisheries, the aim may be to maximize short-term profits. The trade-offs retained their shapes as discount rates were increased, although the reserve and mixed-management scenarios became more similar to each other (WebFigure 3).

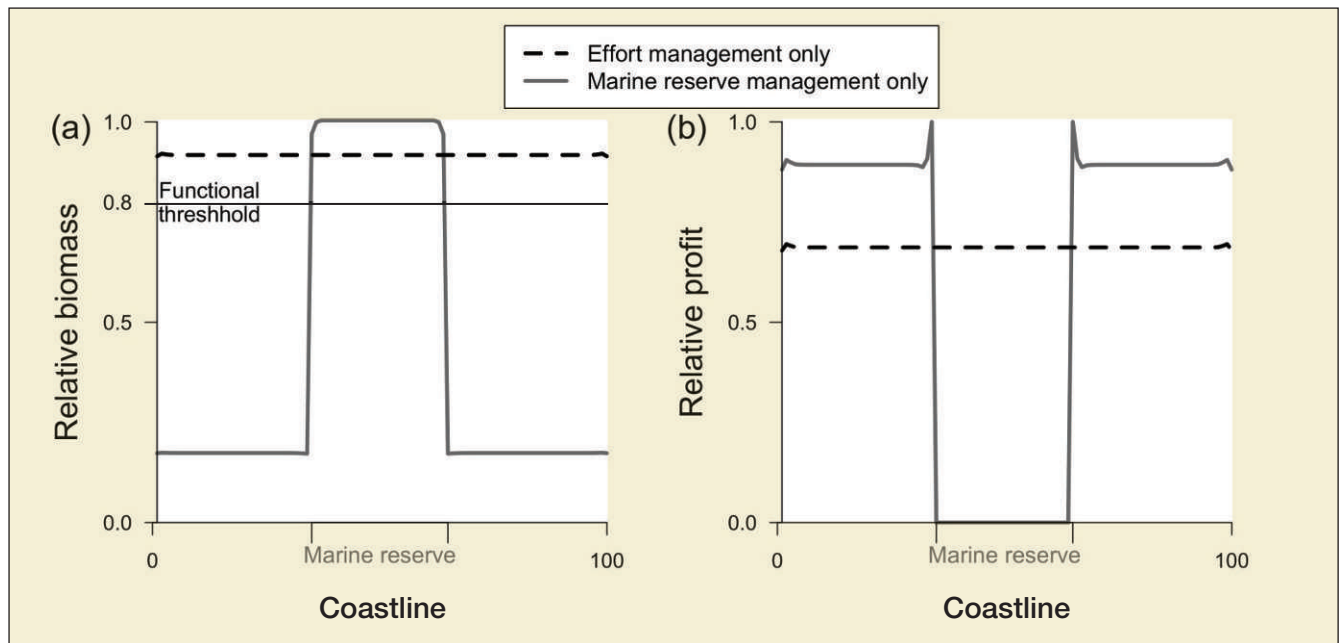


Figure 3. Parrotfish (a) biomass and (b) profits over space with marine reserves (solid gray lines) and with effort management (dashed lines). Both marine reserve and effort management scenarios had equivalent fishery profits. In the marine reserve scenario, biomass on habitat patches inside the reserve was above the minimum biomass threshold for functional persistence of parrotfish (black line). However, competition among fishers was greater, because much of the catch was concentrated at the edges of the marine reserve. Conversely, in the effort scenario, the threshold was exceeded on all reef patches.

Discussion

In redefining the conservation goal based on a biomass threshold, we show that the nature of trade-offs between conservation and fisheries goals depends on the approach to management. These trade-offs represent potential for conflict between different interests (Cheung and Sumaila 2008). Our results suggest ways in which such conflicts may be ameliorated or overcome.

The feasibility of our management scenarios depends on social context. Given the proper context, the management scenarios could be applied to both small and industrial-scale fisheries, because they are consistent with existing management (Smith *et al.* 2011; White *et al.* 2013). Likewise, our general result is applicable whether the goal for fisheries is short- or long-term profits. Marine reserves are often considered to be effective management options within regions that have low capacity to regulate effort directly, or for low-value and bycatch species (Hilborn *et al.* 2004). Therefore, an effective solution for conserving functional roles in such fisheries is to combine management that reduces effort, such as restricting access by non-local fishers, with marine reserves (McClanahan *et al.* 2008). Direct controls on fishing effort and harvest are often used in regions with enhanced capacity for enforcement. While having potential for conserving entire seascapes, such approaches also come with substantial risk. If effort is not reduced adequately, then species' functional roles may not be conserved at any sites because of the threshold effect. In contrast, marine reserves can be effective at ensuring that some locations maintain functional roles.

We estimated biomass thresholds for the conservation of functional roles based on the best available information, which necessarily came from multiple regions. Thresholds are likely to be context-dependent and to vary regionally. For example, the level of grazing required to prevent an algal bloom will differ according to interactions with predators (Madin *et al.* 2010). Further empirical and modeling studies will allow these thresholds to be refined both in terms of the species considered and the biomass reference points. For instance, fish biomass and habitat status could be compared across reserve boundaries, in similar fashion to existing syntheses of reserve effects on fish biomass (eg Edgar *et al.* 2014). Likewise, the effectiveness of effort management could be quantified by making comparisons within regions that have both limited and open-access fishing zones.

In the long term we predict synergies, rather than trade-offs, between the conservation of functional roles across the seascape and fisheries profits. Healthy coral reefs provide crucial habitat and refugia for juvenile fish, and productive fisheries depend on the persistence of such key habitats (Jennings and Polunin 1996). Future studies should consider the dependence of fisheries on ecosystem function. Our management scenarios, for example, could be compared within models of biomass size-spectra (Rochet and Benoît 2012), which account for habitat dependencies (Wilson *et al.* 2010).

In conclusion, our simulations suggest that the conservation of ecosystem function across seascapes can be most efficiently achieved by directly managing fishing effort, whereas marine reserves are effective for conserving small

areas of a seascape. The proper choice of management action may therefore reduce the potential for conflict between conservation and fisheries goals. Quantifying feedbacks between ecosystem function and fisheries profits is a crucial next step; in the long term, functioning ecosystems may support the most productive fisheries.

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