

# Grassroots reserves rescue a river food web from cascading impacts of overharvest

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Intensive fishing is altering the functioning of aquatic ecosystems worldwide, threatening both biodiversity and food security. No-fishing reserves have proven effective at restoring food-web structure and enhancing fisheries in marine ecosystems, but remain virtually untested in freshwater systems. Using experiments inside and outside of community-created riverine reserves in Thailand, we describe a trophic cascade across six trophic levels, from humans to algal responses to nutrient availability. Protection from fishing profoundly reconfigures fish communities – greatly increasing biodiversity, biomass, and body size – yet mean trophic position was unaffected. Cascade dynamics from fish to algae were observed regardless of protection status, although fishing intensified trophic interactions through strong effects on grazing insect behavior. The marked effectiveness of these small, grassroots reserves offers an important conservation-planning model for protecting food webs and augmenting fishery yields in biodiverse tropical rivers.

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Overharvest of fisheries threatens biodiversity and food security in aquatic ecosystems worldwide (FAO 2018). Widespread fishery declines have led to the development of a broad range of ecosystem-based management strategies, the goals of which are to enhance harvest sustainability by ensuring ecosystem resilience (Halpern *et al.* 2010). Marine protected areas (MPAs) are central to conservation and management of coastal oceans, and have led to increased fish density, biomass, and species richness within their boundaries (Lester *et al.* 2009) that can spill over to augment fisheries in adjacent unprotected areas (Gell and Roberts 2003; Cabral *et al.* 2019). No-take reserves also offset selective depletion of large, predatory fishes, thereby re-establishing important trophic interactions that shape community assembly and ecosystem processes (Mumby 2006; Cheng *et al.* 2019).

Despite their success in marine ecosystems, no-take reserves remain rare in freshwater ecosystems, such as rivers and lakes (Abell *et al.* 2007), with the exception of Southeast Asia. Across Southeast Asia, hundreds of no-take areas along rivers have been designated and enforced by local communities in response to declining subsistence catches (Baird and Flaherty 2005). These inland fisheries provide critical food security to underresourced and undernourished populations (McIntyre *et al.* 2016); annual harvest from the Lower Mekong Basin alone is estimated to be 2.2 million metric tons, providing a major source of animal protein for over 70 million people (Hortle 2009). The sustainability of such heavy exploitation is questionable (Allan *et al.* 2005; Ngor *et al.* 2018), and the proliferation of riverine reserves throughout Southeast Asia indicates that communities are prepared to take substantive action to protect this critical resource. Yet principles of reserve design in oceanic and terrestrial ecosystems call into question the effectiveness of reserves that are small relative to the expected home range size of their target species (Gaines *et al.* 2010).

In ecosystems of all types, removal of particular animal species can have profound consequences for animals and primary producers at lower trophic levels (Estes et al. 2011). Marine reserves have played a key role in testing the strength of such trophic cascades, revealing that fishery impacts must be understood in a food-web context (Mumby 2006). The consequences for trophic dynamics of removing harvest pressures are less well known for freshwater systems, particularly biodiverse rivers and lakes (Allan et al. 2005). Theory suggests that high biodiversity and widespread omnivory among tropical fishes may buffer key ecosystem functions against intense harvest (Gellner and McCann 2012) while also reducing the strength of top-down trophic interactions (Shurin et al. 2010). Empirical tests of these predictions have proven challenging for inland fisheries but are essential for understanding whether community-initiated reserves offer a viable model for protecting fish diversity and food security in productive tropical freshwaters.

We analyzed existing riverine reserves in Thailand as a manipulation of the top predator (humans) and used multi-scale experiments to quantify the cascading effects of intensive fishing on the food web that supports fishery productivity (Figure 1a). We compared fish diversity, abundance, and biomass within two small reserves (<1 km in length) to adjacent upstream and downstream reaches in the Ngao River, a medium-sized, clear-water tributary of the Salween River, the longest free-flowing river remaining in southern Asia (Grill *et al.* 2019). Having been under continuous protection since 1993 and 2003, our study reserves are among the oldest of over 50 community-based reserves in the basin, and therefore provide

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Figure 1. (a) Sampling framework and experimental design across spatial scales. Fish were surveyed along transects (dashed arrows) at four sites within each reserve (RR), at four sites within each upstream (UP) reach, and at four sites within each downstream (DN) reach. Macroinvertebrates and algae were sampled within paired full fish exclosures (right) and twosided exclosure controls (left) from trays of natural cobbles, and nutrient-diffusing substrates (NDS) were used to compare algal accrual on control versus nitrogen and phosphorus (NP) amended tiles. (b-g) Mean effects of reserve zone and exclosure treatment by trophic level. To summarize the mean (± standard error [SE]) effect of reserve zone (colored bars) and exclosure treatment (gray bars) on each trophic level, we calculated (b) human harvest effort as number of fishing gears observed; (c) larger (median length > 15 cm) fish density; (d) smaller (median length  $\leq$ 15 cm) fish density; (e) mean macroinvertebrate density by functional feeding group (grazer [GR], suspension feeder [SF], collector-gatherer [CG]); (f) ash-free dry mass (AFDM) of algae collected from rocks (in [e] through [g], white and gray bars are control [Cont] and exclosure [Excl] treatments, respectively; inset in [f] shows zone-exclosure interaction); and (g) AFDM from NDS tiles, displayed as the log<sub>10</sub> response ratio of algae on nutrientenriched and unenriched tiles. Letters denote significant group differences ( $\alpha = 0.05$ ). NS = no significant difference.

a relatively long-term perspective on ecological responses to reserve protection. We then manipulated fish densities and nutrient availability to examine whether harvest-induced changes to fish assemblages were sufficiently strong to alter trophic interactions among large and small fishes, macroinvertebrates, benthic algae, and algal response to nutrient enrichment (Figure 1a). Conducting experiments both within and outside of reserves allowed us to assess the robustness of trophic cascades, as well as elucidate whether shifts in food-web dynamics could extend the benefits of no-take reserves beyond harvested species themselves. If these reserves are sufficient to restore ecosystem structure and functioning to a pre-fishing state, they could offer a new model for safeguarding both aquatic biodiversity and future fisheries in imperiled tropical freshwaters.

## Methods

Our two study reserves were located on mainstem river reaches and had upstream drainages of 739.7 km<sup>2</sup> and 771.1 km<sup>2</sup> (WebFigure 1). At each reserve, we selected 12 sites for our fish surveys and paired experimental manipulations, consisting of four sites spaced evenly within the reserve, as well as four sites extending upstream and four sites extending downstream from its boundaries (50 m, 100 m, 300 m, 700 m; Figure 1a). To test whether reserves were effective in eliminating fishing, we counted pieces of fishing gear encountered along the entire study reach (~2.5 km). Types of fishing gear used during the dry season include gillnets and fishing lines, which are supported by rock piles and bamboo poles that make enumeration straightforward. Conventional fish survey techniques (nets, electrofishing) are prohibited within reserves, and therefore visual surveys were used to profile fish communities throughout each study reach. We counted all fish observed by a snorkeler within three 50-m longitudinal transects (2-m width) in deeper water (>60 cm) and six bank-tobank belt transects (2-m width) in shallower water ( $\leq 60$  cm) at each site in each reach. The maximum river depth encountered during observations was 3.6 m, the river bottom was visible throughout each survey, and horizontal visibility was typically >4 m. These survey methods captured the major habitats and most fish species in the study reaches.

We categorized fish species as large-bodied (>15 cm) or small-bodied ( $\leq$ 15 cm) based on natural groupings of fish species by median body length (WebPanel 1; WebFigure 2). Typical body mass and trophic position (inferred from nitrogen stable isotopes) of each fish species were measured from fish collections outside of reserves or based on literature values for larger species we were unable to sample representatively (WebPanel 1; www.fishbase.org).

To test food-web responses to protecting fishes within reserves, we used experimental cages to isolate consumptive and non-consumptive effects of fish on benthic macroinvertebrates and algae (Figure 1a). We paired  $1-m^2$  full exclosures (7-mm mesh) with open-sided controls that allowed fish access to substrates from downstream yet created flow obstruction and sedimentation comparable to the full exclosures. At each site, we placed one complete exclosure and one opensided cage control side-by-side in randomized position relative to the riverbank. To quantify fish use of experimental substrates, we deployed underwater time-lapse cameras in each exclosure, which captured images every 5 seconds during morning (08:00–10:00) and evening (16:00–18:00) hours on 2 days ( $n = \sim 5000$  photos per cage). For each image, all fish were counted and identified.

We placed standardized rock substrates inside each cage to measure the response of benthic macroinvertebrates and attached algae to fish. Two replicate trays ( $20 \text{ cm} \times 30 \text{ cm} \times$ 10 cm) made of rebar and large plastic mesh (15 mm), each holding ten size-matched rocks (4–12 cm diameter) with comparable initial biofilms, were embedded in the natural substrate of each exclosure cage. After 18–19-day incubations, we quantified macroinvertebrates and algal biomass (ash-free dry mass [AFDM] per square centimeter) in each rock tray.

We assessed the relative strength of bottom-up (nutrient limitation) and top-down (grazing) regulation of attached algae using nutrient-diffusing substrates (NDS). Unglazed ceramic tiles covered nutrient-enriched (both nitrogen and phosphorus) or unenriched agar (n = 2 per site). Tile dimensions (length, width, depth) were 82 mm × 82 mm × 17 mm, and each had a wall thickness of 2 mm and held approximately 115 mL of agar solution. We measured AFDM after 20–25 days and compared the effects of nutrient enrichment and exclosure type on algal accrual to infer the relative response to release from nutrient limitation and grazing.

# Results

Community-created reserves and our manipulations revealed that profound effects of fishing extended across the entire food web of the Ngao River. Intensive fishing exerted sufficient top-down pressure to influence algal response to nutrients across five trophic links involving over 75 animal taxa (Figures 1 and 2). Despite strong local dependence on fish for food, reserves effectively eliminated fishing effort (Figure 1b), creating a stark contrast between protected (fishing gear present) and unprotected (fishing gear absent) areas. Elimination of fishing pressure resulted in 14–28 times higher densities of large-bodied fish species (median length >15 cm) in reserves compared to adjacent harvested areas (Figure 1c). Conversely, relatively small (median length  $\leq$ 15 cm), commercially lower-value fishes had 39–74% higher



**Figure 2.** Cascade dynamics in (a) fished and (b) reserve areas. Solid and dashed arrows indicate direct effects and indirect effects, respectively. Inequalities represent the effect of harvest on biomass at each trophic level in fished versus reserve areas. Additional non-consumptive effects (red arrows) of smaller fishes augment the consumptive effects of comparable macroinvertebrate densities to propagate cascading interactions from humans to nutrients.

densities (ie number of fish per hectare) in fished areas outside of reserves (Figure 1d). Although protection led to only moderate increases in aggregate fish density, total fish biomass within reserves was 15 times that contained in harvested areas.

Reserve protection also resulted in comprehensive shifts in fish assemblages, reflecting a harvest-induced, size-based trophic cascade. Reserve assemblages were diverse (Shannon's H = 2.30) and dominated by large-bodied *Tor* spp, *Neolissochilus stracheyi*, and *Hypsibarbus salweenensis* that are prized for consumption by local communities. In contrast, unprotected sites had low diversity (Shannon's H =1.40) assemblages featuring small nemacheiline loaches, glass perch (*Parambassis vollmeri*), and spiny eel (*Mastacembelus armatus*) (Figure 3a). Multivariate analysis of fish assemblage structure supported significant differences between reserves and non-reserves ( $F_{[4,21]} = 4.63$ , P = 0.001). Greater average maximum length of fishes in reserves was the key trait underlying the assemblage differences (P < 0.001; Figure 3a).



**Figure 3.** Functional composition of fish assemblages within and outside of community reserves. (a) Transformation-based redundancy analysis (RDA) ordination of fish assemblages by zone (solid colored circles). Ellipses depict one standard deviation around the centroid of each zone. Gray arrows and black letters correspond to axis loadings for all observed fish species (n = 24; full names are provided in WebTable 5). Red arrows represent site correlations to density-weighted median length and trophic position (TP). (b) Trophic position and  $\log_{10}$  median body lengths for observed fish species labeled as in (a). Vertical and horizontal lines depict means of density-weighted  $\log_{10}$  median lengths and trophic position for fishes by zone.

Notably, the strong effects of fishing on fish assemblage structure did not change the mean trophic position of fishes within reserves (Figure 3b). Trophic position is an important functional trait, and is often correlated with fish size. However, body size and trophic position were not correlated in this food web (Pearson's r = 0.08; Figure 3b). In fact, densities of herbivores and omnivores showed the greatest response to protection within reserves, although predator biomass was also significantly enhanced by the presence of a large species of catfish (Sperata acicularis) within each reserve (WebFigure 3, a and b). Small-bodied species constituted 56% of all observed fish but only 7% of the total biomass in reserves (WebFigure 3c), yet accounted for 95% of fish density and 45% of biomass in fished areas. Patterns of both cumulative density and biomass of fishes across trophic positions were comparable inside and outside of reserves; each increased rapidly at a trophic position of ~3.0 (WebFigure 3c).

Experimental exclosures revealed cascading effects of fishing extending from fish to macroinvertebrates to algae (Figure 1, e–g; gray bars). In fishless exclosures, macroinvertebrate densities were higher (two-way analysis of variance [ANOVA], F = 5.06, P = 0.036; Figure 1e), and algal accrual was lower on both rocks (Figure 1f) and nutrient-diffusing clay tile substrates (Figure 1g). On the tile NDS, algal biomass increased with nutrients (three-way ANOVA, F = 151.45, P <0.001) and decreased when fish were excluded (F = 43.00, P <0.001) regardless of fishing pressure in the surrounding area. However, attached algae showed much weaker responses to nutrient supplementation (Hedge's  $d_N = 0.75$ ; WebPanel 1) than sheltering macroinvertebrate grazers from fish (Hedge's  $d_G$  = 1.25; WebPanel 1), indicating the primacy of top-down regulation of energy flow exerted by carnivorous fishes.

Although algal accrual on clay tiles was unaffected by reserves, algae on natural rock substrates exhibited a significant interaction between reach-scale fishing bans (via reserves) and local exclusion of fish via cages (Figure 1f, inset; two-way ANOVA, F = 3.99, P = 0.033). Rocks exposed to fish upstream and downstream of reserves developed higher algal biomasses than counterparts within reserves. In contrast, algal biomass was comparable in full exclosure cages inside and all exclosures outside of reserves (Figure 1f). Given similar macroinvertebrate grazer densities across sites (Figure 1e), the disparities in algal accrual on rocks suggest that behavioral responses of insects to high densities of small predatory fish outside of reserves plays a key role in mediating grazing intensity (Figure 2).

Analysis of 111,888 images from open-sided exclosures reveals that fish visited experimental substrates less frequently and for shorter peri-

ods of time inside reserves than in upstream and downstream areas. Although spiny eels were equally common everywhere, all other species occurred in images three times as often upstream (28% of images) and downstream (31%) as within reserves (9%). These differences reflected both the frequency and duration of visits by small, specialized invertivore fish species like glass perch and nemacheiline loaches.

A combination of consumptive and non-consumptive effects of predators therefore link the fishing-induced trophic cascade from humans to small fishes, with a second cascade from small fishes through macroinvertebrates to algal accrual, including top-down control on algae overwhelming the response to release from nutrient limitation (Figure 1g). Within reserves, however, these two cascades are decoupled by the alleviation of non-consumptive effects on macroinvertebrates due to the greater functional diversity of fish assemblages that resulted from effective fishery protection (Figure 2).

#### Discussion

The disparity between fish assemblages separated by nothing more than an invisible boundary of fishing pressure supports the notion that humans act as super-predators (Darimont *et al.* 2015), having a disproportionate impact on fish species with one key functional trait: large size (Figure 3). The opposing shifts in densities of larger versus smaller bodied fishes across reserve boundaries – despite active harvest of all sizes and species of fish outside reserves – indicates that the benefits for small fish of removing their piscine predators exceeds that of protecting them from intensive fishing (Figure 1d). The strong size-based effects of harvest on fish assemblages, however, had no effect on macroinvertebrate densities, which were uniformly reduced when exposed to fish (Figure 1e). Yet algal accrual on rock substrates was lower outside reserves, where small, invertivorous fishes dominated and apparently reduced macroinvertebrate grazing effort relative to fish exclosures and reserves, where small fish were themselves subject to higher predation pressure from large-bodied fish (McIntosh *et al.* 2004).

Our replicated evidence of a trophic cascade from small fish to invertebrates to algae from both reserve and non-reserve exclosures contrasts with a frequent lack of detectable trophic cascades in tropical rivers (Flecker 1996; Pringle and Hamazaki 1998; but see Power 1984, 1987). Undetectable cascades have been interpreted as evidence that abundant omnivory and species diversity preclude the formation of strong cascading interactions in the tropics (Shurin *et al.* 2010). Our results therefore present an apparent paradox: a fish assemblage characterized by high local diversity and widespread omnivory – traits associated with weak species interactions (Gellner and McCann 2012) – clearly exhibits cascade-type dynamics that are expected to arise only from fewer, stronger species interactions (Shurin *et al.* 2010).

In contrast to the omnivores studied previously in tropical rivers, most of which show strong morphological adaptations for feeding effectively as both primary and secondary consumers (Flecker 1996; Pringle and Hamazaki 1998; Power 1984, 1987), the large-bodied omnivores that dominated reserves in our study river lack morphological specialization and readily eat fish in addition to algae and invertebrates (www.fishbase.org). The reduction in small invertivorous fishes (Figure 1d) and macroinvertebrates (Figure 1e), but not algae (Figure 1, f and g), in reserves suggests that omnivorous fishes preferentially fed on nutritious animal prey rather than algae (Marcarelli et al. 2011). Such trophic flexibility is the most plausible explanation for how strong top-down control emerges in reserves despite rampant omnivory and high fish diversity (Fahimipour et al. 2019). The result is a fish-driven cascade dynamic akin to that maintained by fewer, more specialized fishes outside of reserves, albeit without additional non-consumptive effects that intensify the cascade pattern.

The consistency of the fish-induced cascade dynamics in both depauperate fished zones and biodiverse reserves also challenges the assumption that no-take reserves invariably enhance ecosystem functioning (Halpern *et al.* 2010). Outside of reserves, high abundances of three specialist invertivore taxa (loaches, glass perch, spiny eels; 73% of observed fish) maintained cascade patterns that were comparable to those arising from more diverse fish assemblages in reserves. Despite the apparent robustness of the lower cascade dynamic across all zones, reduced fish species diversity in harvested areas may ultimately undermine community stability. Simplified, strongly interacting food chains can have complex and unstable dynamics between the coupled predator–consumer and consumer– resource trophic links (McCann *et al.* 1998). In contrast, reserve food webs were more taxonomically and functionally diverse, traits that are thought to buttress long-term ecosystem stability and resilience (Biggs *et al.* 2012; Gellner and McCann 2012).

#### Conservation and fishery implications of riverine reserves

Across many fisheries, a syndrome of intense pressure leading to decreased mean trophic position has emerged from decades of research on predator collapses ("fishing down the food web"; Pauly *et al.* 1998), and is often accompanied by increased harvest of species occupying lower trophic positions ("fishing through the food web"; Essington *et al.* 2006). These patterns are hard to apply to tropical subsistence fisheries, where food chain lengths are often short (Vander Zanden and Fetzer 2007) and harvest may be indiscriminate with respect to trophic position (McCann *et al.* 2015). Nonetheless, our findings show that intensive, indiscriminate fisheries can have a strong effect on trophic dynamics even without changing the mean trophic position of the fish community.

Fishers in our study area invariably report decreasing catch mass due to declines in populations of large fishes, including both piscivorous and herbivorous species. Today, through much of southern Asia, use of multiple methods by several different groups of fishers yields indiscriminate fisheries in which all size classes of fish are harvested and consumed. This intensive fishing pressure appears to disproportionately impact slow-maturing, large-bodied species (Ngor *et al.* 2018), and the apparent resilience of some fisheries to these species losses arises from the capacity of smaller species to fully or partially replace collapsing catches of larger species (McCann *et al.* 2015; Szuwalski *et al.* 2017). However, in the Ngao River, fisher concerns suggest that intensive fishing apparently exceeds even the capacity of fast-growing, small-bodied fishes to support historical levels of catch.

Large fish are still caught in nets and on hooks near reserve boundaries, indicating that fish leave reserves at night. Such "spillover" is an essential aspect of the benefits of no-take reserves, boosting both the biomass and sustainability of fisheries across marine reserve networks (Gell and Roberts 2003). Presumably, spillover from riverine reserves is propping up local harvests throughout our study region, as enthusiasm arising from the increased size and biomass of fishes visible from the bank in reserve zones (WebFigure 4) has spurred the designation of over 50 reserves by communities in the Ngao catchment (Koning et al. 2020). Networks of reserves can have collective benefits that exceed expectations for individual protected areas, and such emergent effects have been enshrined in design principles for maximizing net benefits from marine reserve networks (Gaines et al. 2010). Our results demonstrate the potential for small riverine reserves to serve as effective refugia from fishing,

suggesting that adapting the tenets of MPA network design to river networks may be productive.

Decades of research on protected area design has emphasized the need for the size and spacing of reserves within a network to reflect the life-history requirements of target species, which differ for non-migratory and migratory species (Gaines et al. 2010; Halpern et al. 2010). Within our study network, individual reserves are typically large enough to include representation of all major habitat types and provide potential feeding, spawning, and nursery habitats for non-migratory species (WebPanel 1). For example, Hypsibarbus salweenensis typically occupy deeper reserve pools throughout the year, feed in run habitats, and have been observed spawning in the same reserve riffle habitats over several dry seasons. For resident species with similar life histories, reserves have the potential to maintain localized subpopulations, yet long-term persistence may still depend on inter-reserve movements.

Highly mobile and migratory fishes pose challenges to protection by individual reserves, but they may benefit from the addition of reserves nearby (Gaines et al. 2010). Individual Ngao River reserves are typically small, but their relatively close spacing throughout the river system may confer outsized protection, even for more mobile species (WebFigure 1). The migratory habits of most Salween River fishes are undocumented, but Ngao River fishers report long-distance movements of several local species, including N stracheyi and Tor spp during the rainy season (June-October). Although such movements out of reserves put these large fish species at higher risk of harvest, the greatly increased river height (up to 6 m), flow velocity, area of inundation, and turbidity combine to reduce local fishing effort and its efficacy. Thus, while highly mobile and migratory species are protected by the network of 50+ reserves basin-wide, seasonal conditions likely provide important additional protection during longer migrations.

There is plenty of cause for concern over the future of inland fisheries (McIntyre et al. 2016), and there remains a great need for identifying effective solutions for highly resource-dependent, lower-income nations worldwide. Our intensive assessment demonstrates that food-web dynamics respond strongly to eliminating fishing pressure from even small reaches of river, but it is unclear whether these small reserves can maintain fish diversity or food security in the longer term. Given the gauntlet of fishing pressures that separate reserves, the isolation of small populations within any single no-take area may ultimately undermine their continued success. Nevertheless, the grassroots reserves profiled here offer a potentially transferable model for conserving biodiversity while enhancing the sustainability of tropical river fisheries. The fact that more than 50 communities basin-wide have found the success of these small reserves sufficiently compelling to create and enforce their own protections further demonstrates the importance of the resource and the benefits of collective action. Such reserves offset the

cascading effects of intense, indiscriminate fishing by conserving the diversity of species, size classes, and trophic strategies that underlie a dynamic and resilient food web.

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# Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10. 1002/fee.2293/suppinfo