A network of grassroots reserves protects tropical river fish diversity

https://doi.org/10.1038/s41586-020-2944-y

Received: 14 January 2020

Accepted: 5 October 2020

Published online: 25 November 2020

Check for updates

Aaron A. Koning[1,2,3]✉, K. Martin Perales[1], Etienne Fluet-Chouinard[1,4] & Peter B. McIntyre[1,5]

Intensive fisheries have reduced fish biodiversity and abundance in aquatic ecosystems worldwide[1–3]. 'No-take' marine reserves have become a cornerstone of marine ecosystem-based fisheries management[4–6], and their benefits for adjacent fisheries are maximized when reserve design fosters synergies among nearby reserves[7,8]. The applicability of this marine reserve network paradigm to riverine biodiversity and inland fisheries remains largely untested. Here we show that reserves created by 23 separate communities in Thailand's Salween basin have markedly increased fish richness, density, and biomass relative to adjacent areas. Moreover, key correlates of the success of protected areas in marine ecosystems—particularly reserve size and enforcement—predict differences in ecological benefits among riverine reserves. Occupying a central position in the network confers additional gains, underscoring the importance of connectivity within dendritic river systems. The emergence of network-based benefits is remarkable given that these reserves are young (less than 25 years old) and arose without formal coordination. Freshwater ecosystems are under-represented among the world's protected areas[9], and our findings suggest that networks of small, community-based reserves offer a generalizable model for protecting biodiversity and augmenting fisheries as the world's rivers face unprecedented pressures[10,11].

Overharvesting of fisheries threatens thousands of species and the food and nutrition security of hundreds of millions of people around the world[12–14]. Over the past several decades, no-take marine reserves have become central management tools for conserving marine ecosystems and sustaining local fisheries[5,7]. The widespread success of marine reserves in enhancing the abundance, size, and biomass of fishes[4] has guided the distillation of design principles that maximize both conservation efficacy within reserves[8,15] and the export of harvestable biomass across their boundaries[7,16,17]. The success of individual marine reserves in providing ecological benefits varies widely[18], but typically increases with vigorous enforcement, complete bans on harvest, time since establishment, large size, and high degree of isolation[8,15]. As catchable fish disperse across reserve borders, they can augment nearby fisheries and local livelihoods, thereby providing an incentive to respect reserve boundaries[16]. Furthermore, gains in diversity and biomass within a reserve can be amplified by exchange among nearby reserves[7,16], which has motivated the expansion of reserve networks worldwide. To date, the reserve network paradigm remains untested for halting high rates of biodiversity loss[11] and bolstering human food supplies from the world's freshwater ecosystems.

Despite holding roughly half of all fish species and providing accessible sources of animal protein and critical micronutrients to many poor and undernourished populations[12–14], freshwater ecosystems are not well represented by existing protected areas[9]. Indeed, formal protection of rivers and lakes has been largely limited to their incidental inclusion within terrestrial reserves[19,20]. Although terrestrial reserves can provide watershed-level benefits, they often inadequately represent freshwater biodiversity[21] and rarely address overfishing[3]. By contrast, recent marine reserve paradigms have explicitly aimed to balance protection of biodiversity inside reserve boundaries with sustainable harvests beyond them[7]. Although the effectiveness of reserves as a large-scale management strategy continues to be debated[18,22], there is widespread evidence that small, community-based reserves can improve the sustainability of coastal fisheries[23], particularly for nations with limited fisheries management capacity[24]. Such an approach offers great potential to address human and ecosystem needs in low-income countries where biodiverse rivers contribute disproportionately to inland fisheries[12,13], frequently suffer from overharvesting[3], and defy efforts to apply traditional fisheries management strategies[12].

Southeast Asia is the only region of the world where riverine reserves are commonplace; hundreds of communities have designated no-fishing zones that together form de facto reserve networks in rivers throughout the region[25,26]. Here, we use one such network of small, community-based reserves located within the Salween River basin in northern Thailand (Fig. 1) to test how fish communities respond to protection. We studied 23 reserves that, despite a common cultural context (see Supplementary Information), represent gradients in age, size, enforcement, isolation, and network connectivity. Each of these factors contributes to the success of marine reserves[7,8,17], so we tested their influence on the responses of fish species richness, density, and

[1]Center for Limnology, University of Wisconsin-Madison, Madison, WI, USA. [2]Cornell Atkinson Center for Sustainability, Cornell University, Ithaca, NY, USA. [3]Global Water Center, Department of Biology, University of Nevada, Reno, Reno, NV, USA. [4]Department of Earth System Science, Stanford University, Stanford, CA, USA. [5]Department of Natural Resources, Cornell University, Ithaca, NY, USA. ✉e-mail: akoning@unr.edu

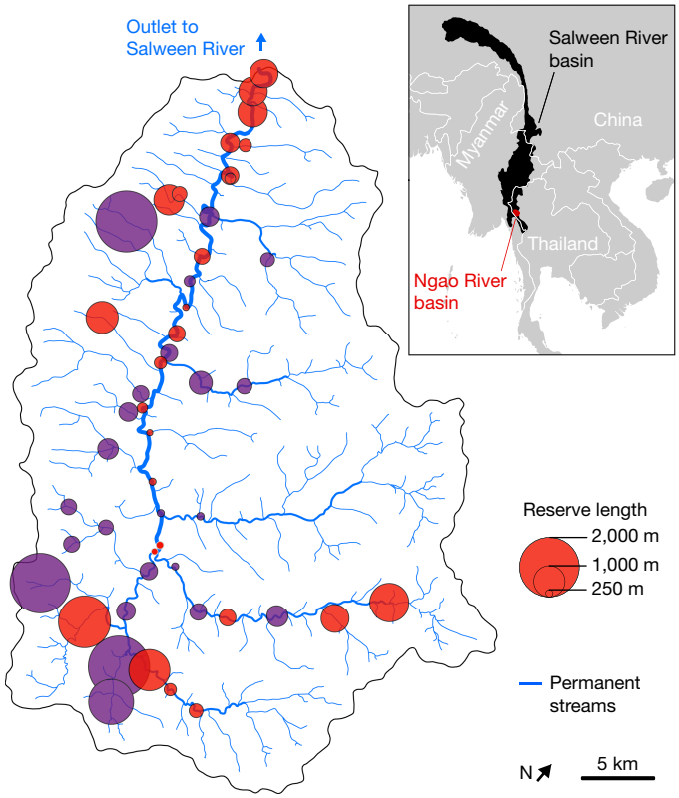


Fig. 1 | Riverine reserve network within the Mae Ngao basin. Network of 52 community-based reserves documented in 2018 within the 1,000-km^2 Mae Ngao River, a tributary of the Salween River in northern Thailand (inset). Reserves are depicted by circles scaled according to reserve length. Purple denotes the 23 reserves where fish communities were profiled for this study, which represent a stratified subset of all known reserves. River basin and stream delineation are detailed in the Methods.

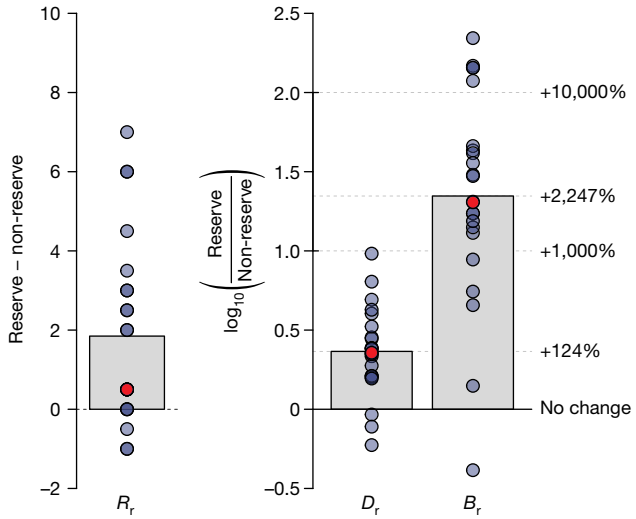


Fig. 2 | Fish responses to protection in reserves. Responses of fish communities to protection from fishing, in terms of species richness (R_r), density (D_r), and biomass (B_r). Points are mean pairwise comparisons (R_r is the arithmetic difference between reserve and non-reserve species richness; D_r and B_r are $\log_{10}$ response ratios comparing reserve and non-reserve areas). Grey rectangles, response means; red circles, response medians.

biomass to protection from fishing in rivers. These reserves are surrounded by reaches in which intensive harvests discriminate little among fish species, sizes, or trophic positions[27], providing a strong test of the overall effectiveness of community-based reserves as well as the design principles that can maximize their ecological benefits.

Despite their small size, grassroots reserves enhanced the species richness, density, and biomass of protected fish communities enormously (Fig. 2). Relative to adjacent fished areas with comparable water depth and substrate composition (see Methods), reserves held an average of 27% more fish species (95% confidence interval (CI), 9–47%), 124% higher fish density (118–130%), and 2,247% higher biomass (1,460–3,433%). Whereas richness and density responses at our study sites were similar to those reported for marine reserves, mean biomass differences were six times higher than those typically observed in marine protected areas[4]. These large biomass responses reflect defaunation of the majority of the river by fishers, which creates such stark disparities that unmarked reserve boundaries can be readily discerned by eye because the visibility of large fishes from above water shifts sharply (Supplementary Fig. 1).

The strength of responses to reserves varied among fish species according to body size and trophic guild. Relatively large fishes (maximum length 200 mm or more; Extended Data Fig. 1) disproportionately benefited from protection; their species richness increased by 59% (31–93%), density by 245% (234–257%), and biomass by 4,326% (2,490–7,463%). By contrast, reserves had no effect on the richness, density, or biomass of smaller-bodied fish species (maximum length less than 200 mm; $P > 0.05$). Among trophic guilds, herbivores (trophic position (TP) ≤ 2.5) had the highest gains in richness (96% (22–221%)), density (117% (105–128%)), and biomass (3,536% (1,688–7,293%)) inside reserves. Omnivores (2.5 < TP ≤ 3.5) also benefited substantially; their richness increased 18% (1–39%), density 132% (125–140%), and biomass 2,327% (1,527–3,522%) relative to adjacent fished areas. Although predators (TP > 3.5) increased in density by 179% (58–421%) and biomass by 136% (26–340%), we found no change in their richness ($P > 0.05$).

The responses of river fish to protection accord well with several principles of marine reserve design, but the degree of benefit was also mediated by functional traits. For instance, the richness response (R_r) across all species was rarely correlated with reserve characteristics, but size, enforcement, and connectivity were all associated with higher R_r for particular functional groups (Fig. 3). Increasing reserve area increased R_r for all fishes, large fishes, and omnivores (Fig. 4), suggesting that species–area relationships apply even to these small habitat patches. For predatory and herbivorous fishes, reserves in high-discharge reaches were particularly important for richness gains (Fig. 4), probably owing to the greater availability of deep-water habitats favoured by large species in these trophic guilds.

Density responses (D_r) to reserves were strongly influenced by enforcement metrics. Specifically, D_r for all fishes and large fishes decreased with increased isolation, suggesting that village proximity encourages community vigilance against illegal harvest (Figs. 3, 4). The boundaries of several reserves corresponded with the most upstream and downstream homes in the village, allowing near-constant surveillance while minimizing travel distances to adjacent fishing areas. Although close proximity to a village could increase fishing intensity outside reserves, village size—another proxy for potential fishing intensity—had little effect on observed outcomes (Fig. 3). The D_r for small fish was higher in reserves that had explicitly stated penalties for illegal harvest, regardless of severity, than in those that lacked such community-imposed penalties (Fig. 4). Thus, it appears that merely having an agreed-upon enforcement policy can bolster reserve protection for some functional groups of river fishes[28].

Reserve size was among the best predictors of reserve biomass response (B_r) across all categories except for small fishes (Fig. 3), and village proximity remained important for B_r of large fishes and herbivores (Fig. 4). Biomass gains are particularly important for fisheries, as larger fish may be expected to provide both greater yields on fishing effort and disproportionately high reproductive capacity to

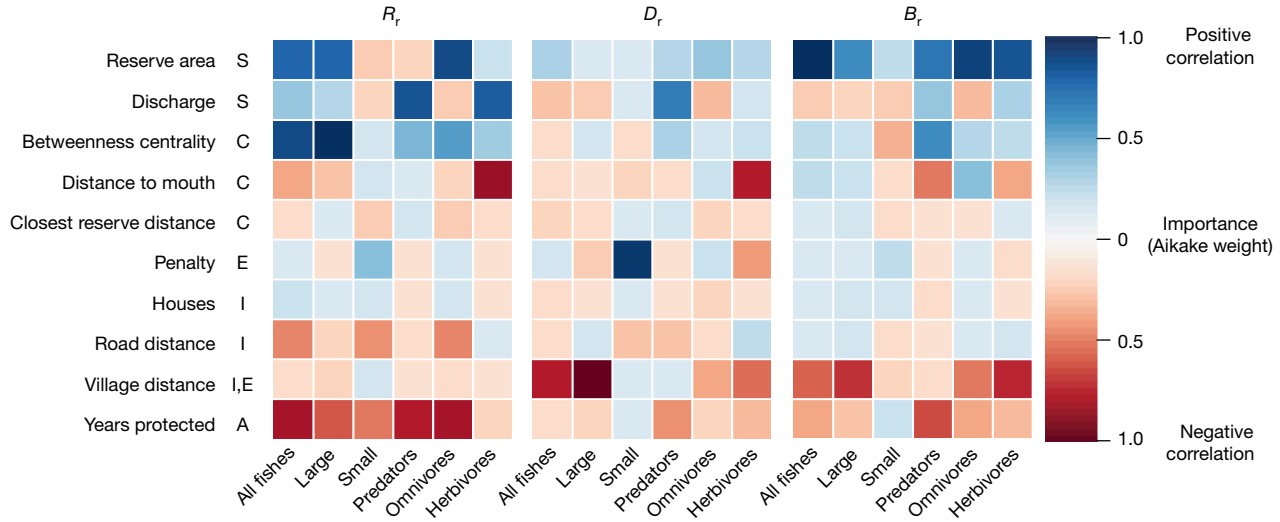


Fig. 3 | Reserve features vary in benefits for fish. Richness (R_r), density (D_r), and biomass (B_r) gains for all fishes and particular functional groups in best averaged models. Cell colour identifies positive (blue) or negative (red) model coefficients and deeper colour saturation signifies greater importance as Akaike weight summed across models. Letters on the left indicate the major categories of reserve features: S, size; C, connectivity; E, enforcement; I, isolation; A, age.

sustain reserve populations and seed unprotected areas by exporting juveniles[16,17].

Our results demonstrate that small reserves have great benefits for intensively harvested fishes in this tropical river, even though their collective area encompasses only 2% of the channel in our study catchment. The areas of individual reserves ranged from just 0.2 to 2.2 Ha (2,003–21,629 m^2), but both fish richness and biomass outcomes scaled with reserve size. The increase in B_r with area may result from greater resource availability provided by larger reserves[7] (Fig. 4), and the strong area dependence of R_r for large fishes suggests a role for the scaling of home range requirements with body size[29]. Notably, the linear scaling of gains in richness and biomass with reserve area (Fig. 4) suggest that modest expansions of the boundaries of existing small reserves might yield considerable ecological benefits.

The success of this reserve network has emerged through the voluntary actions of numerous communities. In return for creating and enforcing a reserve, the local population stands to benefit directly from enhanced fish populations, thereby completing a virtuous cycle that encourages continued community action[30]. Successful community-based inland fishery management efforts have been documented in the Amazon[31–33], Bangladesh[34], and elsewhere in Southeast Asia[25], but our systematic analysis across replicate reserves in the Salween basin elucidates how decisions regarding size, location, and enforcement affect the ecological outcomes of protection. In particular, two aspects of community enforcement maximize reserve benefits: close proximity between reserve and village, which increased density and biomass outcomes (Fig. 4), and explicit penalties, whether monetary (about $15–$300 per offence) or non-monetary (animal sacrifice or libations). These findings underscore the fact that empowering communities to manage local resources can achieve conservation and ecosystem service outcomes more effectively than top-down, centralized management[32,35,36]. Indeed, the grassroots reserves of the Salween basin, individually and collectively, exemplify the critical human dimensions of achieving ecological, economic, and social success in natural resource management[23].

Notably, reserve age was nearly always negatively associated with the magnitude of richness, density, and biomass benefits (Fig. 3). However, our data give no indication that the positive effects of reserves eventually wane. Negative responses were found in only six reserves (Fig. 2), each of which was relatively newly established (mean age, 5.3 years; median, 5.0 years), and simple linear regressions showed that age had no independent effect on any reserve response. In the best averaged models, age was strongly important only in conjunction with other variables that had higher importance scores, such as size, connectivity, or enforcement variables (Fig. 3, Extended Data Tables 1–3). Thus, we infer that the gradual decline in reserve benefits with time reflects improvements in fish communities in unprotected areas adjacent to reserves of sufficient size, connectivity, and enforcement. The mechanism that underlies the reduced disparities between adjacent protected and fished areas is presumably a rise in density-dependent spillover with reserve age (Extended Data Fig. 2). This is a critical insight with regard to both conservation and local food security in tropical rivers. Growing evidence from marine reserves suggests that spillover effects are greatest among networks of many small reserves, akin to our study system, rather than fewer large ones[7,37]. Furthermore, estimates of spillover distance from marine reserve boundaries range from 10^2 to 10^3 m (ref. [37]), which broadly matches the distances over which intensive fishing pressure occurs between reserves among our study sites. There is also circumstantial evidence that spillover of fish from our study reserves enhances local fisheries: fishers regularly harvest fish of many species that are larger than we have observed outside reserves during years of field work. The ongoing proliferation of new reserves suggests that subsistence fishing communities expect this conservation approach to improve their own food security.

Network-level benefits have emerged across our study reserves despite a lack of formal planning or coordination among communities during creation of this de facto reserve network (see Supplementary Information). Connectivity, measured as how central a reserve is within the network, was important for R_r of all fishes and large species, suggesting the importance of dispersal among protected areas for maintaining metapopulations (Fig. 3, Extended Data Fig. 3). In dendritic river networks, dispersal pathways are effectively one-dimensional, but centrally located reserves can link populations in multiple tributaries, thereby stabilizing metapopulations through time[38]. Nonetheless, certain rare predators were found only in downstream reserves that had high discharge (Fig. 4). For large-bodied (>1 m) and far-ranging species, persistence may depend on immigration from larger rivers downstream, and individual reserves are likely to be too small to sustain a viable population.

Despite the apparent effectiveness of small reserves for protecting the richness, density, and biomass of river fishes, questions about

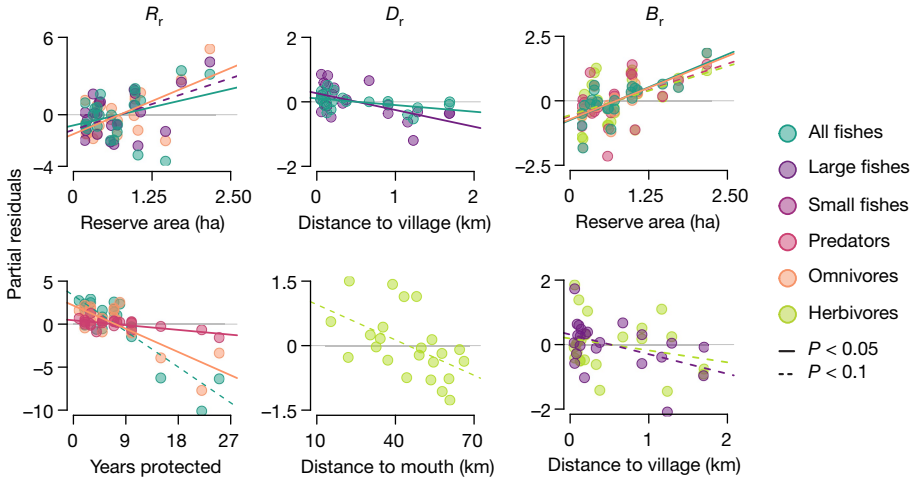


Fig. 4 | Scaling of benefits with key reserve features. Partial residual plots illustrating relationships between important predictors of richness (R_r), density (D_r), and biomass (B_r) responses to no-take reserves in best averaged models. Symbology indicates alternative groupings of fish species by body size and trophic group. Full model results are reported in Extended Data Tables 1–3.

their long-term impact remain. If protected sub-populations become isolated by intensive fishing between reserves, metapopulation persistence is unlikely[39]. In highly seasonal rivers such as the Salween—tropical Asia's longest remaining free-flowing river[10]—connectivity between reserves is most likely during the wet season, when rising water levels simultaneously cue spawning migrations by some species and decrease the efficacy of all fishing methods. Relaxing these constraints on movement may enable a critical influx of individuals and alleles, alleviating demographic bottlenecks and inbreeding[39]. It remains unclear, however, whether seasonal movement among reserves can overcome the likelihood of extinction debts when each individual protected area is so small[40]. Additionally, for long-distance migrants such as catadromous eels (*Anguilla bengalensis*), reserves can offer only partial protection in the face of proposed hydropower and water diversion projects throughout the Salween basin.

The demonstrable benefits of reserve size, enforcement, and connectivity in this growing network of grassroots riverine reserves show that many principles that were developed for marine reserves are applicable to rivers. However, our findings also reveal the need for care in adapting marine reserve designs to suit the physical structure of river networks, the distinctive life history requirements of their fauna, and the cultures of local communities and fishers. For example, large reserves are clearly important, but maximizing area by exclusively creating reserves in wide downstream river reaches would leave unique headwater species unprotected. Rather, riverine reserve networks should be designed to encompass both high- and low-order segments[38]. Additionally, while explicit fines did improve reserve outcomes, communal surveillance resulting from close village proximity may be even more important for deterring poaching, because enforcement is so challenging in remote areas within large watersheds. More generally, cultural context must be accounted for in the design of effective enforcement strategies. Although communities in northwestern Thailand have created riverine reserves of their own accord, such grassroots networks may require encouragement and even subsidies in other locations. From an ecological perspective, reserves located centrally within networks may benefit many resident species and functional groups, but upstream–downstream connectivity along the entire river continuum will be required to conserve the migratory species that are critical in many river fisheries[10,41].

While surely not a panacea for all that ails the world's rivers, the reserves of the Salween basin demonstrate the benefits of a community-based model for protecting the biodiversity that underpins ecosystem resilience and local subsistence fisheries. Like many rivers worldwide, the Salween is threatened by a combination of land use change, intensifying agricultural practices, non-native species, flow modification, and intensive and indiscriminate fishing pressure[11,42]. Networks of riverine reserves directly address only one stressor, but the biological diversity and ecological processes that they protect are likely to augment local ecosystem resilience and moderate the impacts of other stressors[43].

Given the variety and magnitude of positive outcomes observed in each of these small reserves, as well as the emergent benefits of position within the ad hoc network, we expect that even greater fishery and conservation gains could be achieved through a more deliberate approach. Many of the principles that have been distilled from successful marine reserves appear to apply to rivers, and further lessons from marine and terrestrial networks of protected areas should be sought in order to strengthen ecosystem-based protection for freshwater systems. Accounting for both local and network-based features will be critical for planning an optimal portfolio of riverine reserves. Perhaps even more central to conservation success are the human motivations for establishing, enforcing, and harvesting from reserves. Our findings from the Salween prove that riverine reserves, when embedded in a conducive cultural context, can yield impressive benefits for the imperilled freshwater ecosystems upon which hundreds of millions of people depend worldwide.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-020-2944-y.

1. Worm, B. et al. Rebuilding global fisheries. *Science* **325**, 578–585 (2009).
2. Costello, C. et al. Global fishery prospects under contrasting management regimes. *Proc. Natl Acad. Sci. USA* **113**, 5125–5129 (2016).
3. Allan, J. D. et al. Overfishing of inland waters. *Bioscience* **55**, 1041–1051 (2005).
4. Lester, S. E. et al. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* **384**, 33–46 (2009).
5. Halpern, B. S., Lester, S. E. & McLeod, K. L. Placing marine protected areas onto the ecosystem-based management seascape. *Proc. Natl Acad. Sci. USA* **107**, 18312–18317 (2010).
6. Carr, M. H. et al. Marine protected areas exemplify the evolution of science and policy. *Oceanography (Wash. D.C.)* **32**, 94–103 (2019).
7. Gaines, S. D., White, C., Carr, M. H. & Palumbi, S. R. Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl Acad. Sci. USA* **107**, 18286–18293 (2010).

8. Edgar, G. J. et al. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220 (2014).
9. Abell, R., Lehner, B., Thieme, M. & Linke, S. Looking beyond the fenceline: assessing protection gaps for the world's rivers. *Conserv. Lett*. **10**, 384–394 (2017).
10. Grill, G. et al. Mapping the world's free-flowing rivers. *Nature* **569**, 215–221 (2019).
11. Vörösmarty, C. J. et al. Global threats to human water security and river biodiversity. *Nature* **467**, 555–561 (2010).
12. McIntyre, P. B., Reidy Liermann, C. A. & Revenga, C. Linking freshwater fishery management to global food security and biodiversity conservation. *Proc. Natl Acad. Sci. USA* **113**, 12880–12885 (2016).
13. Fluet-Chouinard, E., Funge-Smith, S. & McIntyre, P. B. Global hidden harvest of freshwater fish revealed by household surveys. *Proc. Natl Acad. Sci. USA* **115**, 7623–7628 (2018).
14. Golden, C. D. et al. Nutrition: Fall in fish catch threatens human health. *Nature* **534**, 317–320 (2016).
15. Botsford, L. W., Micheli, F. & Hastings, A. Principles for the design of marine reserves. *Ecol. Appl*. **13**, 25–31 (2003).
16. Gell, F. R. & Roberts, C. M. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol*. **18**, 448–455 (2003).
17. Hastings, A. & Botsford, L. W. Comparing designs of marine reserves for fisheries and for biodiversity. *Ecol. Appl*. **13**, 65–70 (2003).
18. Pendleton, L. H. et al. Debating the effectiveness of marine protected areas. *ICES J. Mar. Sci*. **75**, 1156–1159 (2018).
19. Chessman, B. C. Do protected areas benefit freshwater species? A broad-scale assessment for fish in Australia's Murray–Darling Basin. *J. Appl. Ecol*. **50**, 969–976 (2013).
20. Lawrence, D. J. et al. National parks as protected areas for U.S. freshwater fish diversity. *Conserv. Lett*. **4**, 364–371 (2011).
21. Abell, R. et al. Concordance of freshwater and terrestrial biodiversity. *Conserv. Lett*. **4**, 127–136 (2011).
22. Hilborn, R. Policy: Marine biodiversity needs more than protection. *Nature* **535**, 224–226 (2016).
23. Halpern, B. S. et al. Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. *Proc. Natl Acad. Sci. USA* **110**, 6229–6234 (2013).
24. Gill, D. A. et al. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* **543**, 665–669 (2017).
25. Baird, I. G., Flaherty, M. S. & Baird, I. G. Mekong River fish conservation zones in southern Laos: assessing effectiveness using local ecological knowledge. *Environ. Manage*. **36**, 439–454 (2005).
26. Loury, E. K. et al. Salty stories, fresh spaces: lessons for aquatic protected areas from marine and freshwater experiences. *Aquat. Conserv*. **28**, 485–500 (2018).
27. McCann, K. S. et al. Food webs and the sustainability of indiscriminate fisheries. *Can. J. Fish. Aquat. Sci*. **73**, 656–665 (2016).
28. Gutiérrez, N. L., Hilborn, R. & Defeo, O. Leadership, social capital and incentives promote successful fisheries. *Nature* **470**, 386–389 (2011).
29. Kramer, D. L. & Chapman, M. R. Implications of fish home range size and relocation for marine reserve function. *Environ. Biol. Fishes* **55**, 65–79 (1999).
30. Morrison, S. A. A framework for conservation in a human-dominated world. *Conserv. Biol*. **29**, 960–964 (2015).
31. Campos-Silva, J. V. & Peres, C. A. Community-based management induces rapid recovery of a high-value tropical freshwater fishery. *Sci. Rep*. **6**, 34745 (2016).
32. Castello, L., Viana, J. P., Watkins, G., Pinedo-Vasquez, M. & Luzadis, V. A. Lessons from integrating fishers of arapaima in small-scale fisheries management at the Mamirauá Reserve, Amazon. *Environ. Manage*. **43**, 197–209 (2009).
33. Pinho, P. F., Orlove, B. & Lubell, M. Overcoming barriers to collective action in community-based fisheries management in the Amazon. *Hum. Organ*. **71**, 99–109 (2012).
34. Thompson, P. M., Sultana, P. & Islam, N. Lessons from community based management of floodplain fisheries in Bangladesh. *J. Environ. Manage*. **69**, 307–321 (2003).
35. Alexander, S. M., Epstein, G., Bodin, Ö., Armitage, D. & Campbell, D. Participation in planning and social networks increase social monitoring in community-based conservation. *Conserv. Lett*. **11**, e12562 (2018).
36. Ostrom, E. A general framework for analyzing sustainability of social-ecological systems. *Science* **325**, 419–422 (2009).
37. Halpern, B. S., Lester, S. E. & Kellner, J. B. Spillover from marine reserves and the replenishment of fished stocks. *Environ. Conserv*. **36**, 268–276 (2009).
38. Campbell Grant, E. H., Lowe, W. H. & Fagan, W. F. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecol. Lett*. **10**, 165–175 (2007).
39. Palumbi, S. R. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl*. **13**, 146–158 (2003).
40. Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994).
41. McIntyre, P. B. et al. in *Conservation of Freshwater Fishes* (eds Closs, G. P. et al.) 324–360 (Cambridge Univ. Press, 2015).
42. Dudgeon, D. et al. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev. Camb. Philos. Soc*. **81**, 163–182 (2006).
43. Roberts, C. M. et al. Marine reserves can mitigate and promote adaptation to climate change. *Proc. Natl Acad. Sci. USA* **114**, 6167–6175 (2017).

Methods

Study site

We surveyed fish assemblages within the Mae Ngao tributary of the Salween River, the largest free-flowing river in Southeast Asia (Fig. 1). The Mae Ngao River basin of northwestern Thailand encompasses approximately 1,000 km^2 of mixed deciduous secondary forest, swidden and lowland agricultural lands, and over 80 villages (>8,000 people) of predominately ethnic Karen people. A land use survey conducted by the Land Development Department of Thailand in 2009 estimated basin-wide forest cover to be 70%, with agriculture comprising approximately 27% of the land, though there has been substantial forest clearing for intensified forms of agriculture within the basin over the past decade[44]. During this time communities have moved from diversified, low-input swidden agricultural practices to row crops, predominately soy, requiring substantial chemical herbicide and pesticide inputs. The Mae Ngao River has a strongly seasonal hydrograph, with a single rainy season extending from May to October and a dry season from November to April. During the rainy season, the depth of the Ngao River increases by over 4 m relative to dry season baseflows. During dry season, the river becomes clear, allowing census of fish using visual methods (with mask and snorkel). While fishing effort and gears used vary seasonally, the collective fishing effort of communities dispersed throughout the valley encompasses nearly all unprotected waters, access to which is facilitated by motorbikes and extensive streamside trails.

Fish surveys

To estimate the potential for reserves to increase fish richness, density, and biomass, we surveyed 23 paired reserve and non-reserve locations during a single dry season between December 2017 and March 2018. Individual reserves were selected to represent a range in age, size, isolation, size of nearest village, stream order (first to fifth), and network position. Non-reserve surveys were conducted downstream of reserves at all locations except one, to which there was only upstream access. Where stream segments were sufficiently narrow and shallow (19 of 23 sites), two researchers wearing dive masks and snorkels carried out fish censuses by swimming or crawling along 50-m transects from downstream to upstream and enumerating all fish within a 2-m band centred on each observer.

In the four large mainstem sites (mean width >20 m), one researcher surveyed 50-m-long reaches by systematically counting fish while moving from bank to bank in an upstream direction. Each survey lasted 20 min, which approximated the average survey duration for shallow reaches. Additionally, to account for benthic or cryptic species in shallow water (<80 cm) at these four sites, a second researcher conducted four lateral belt transects at each survey reach. Belt transects were demarcated with a chain placed on the substrate perpendicular to flow. To allow disturbance effects to dissipate, we waited for 15 min after chain placement to begin surveys, then enumerated all fish within a 2-m band centred on the chain for up to 20 m of stream width. For each reserve–non-reserve site, a total of four surveys were conducted at two reserve and two non-reserve reaches.

To estimate site-specific biomass, each researcher estimated fish total lengths during each transect. When fewer than ten individuals of a species were observed, lengths were estimated for each individual. For species with more than ten observations in a survey, researchers estimated ten lengths representing the size distribution observed for that survey. Estimated lengths were cross-validated between researchers in the field using submerged measuring tapes as reference. We estimated site-specific biomass for reserve and non-reserve fish by evaluating the mean observed length for each site with a length–weight relationship developed from previous work in the Ngao River (A.A.K., unpublished data) and supplemented with literature values[45]. For the four large mainstem sites, we combined density estimates using count-weighted averages of both survey techniques for each survey location.

Ethics oversight for the handling of animals was provided and the methods approved by the University of Wisconsin Research Animals Resources and Compliance and the Institutional Animal Care and Use Committee under protocol number L00447-0-02-12.

Habitat variables

At each survey site we measured key aspects of reach habitats that could affect fish communities, then tested for habitat differences within (reserve vs. non-reserve) and among areas. At each transect location, we measured depth and substrate composition at six lateral transects corresponding to 0, 10, 20, 30, 40, and 50 m marks. Depth and substrate type were recorded at ten evenly spaced locations across the stream width. Substrate types followed the Wentworth classification: silt (<62.5 μm); sand (62.5 μm–2 mm); pea gravel (2–8 mm); gravel (8–32 mm); pebble (32–64 mm); cobble (64–256 mm); boulder (>256 mm); bedrock (>4,000 cm). For mainstem sites where both snorkel and benthic counts were employed, we conducted five lateral transects from the chain counts and snorkel surveys for a total of ten transects and 100 benthic point samples. To calculate median particle size at each site, we used the median size of each particle class for each observation, then calculated the median across all 60 point-samples. We also measured discharge at each reserve–non-reserve location to account for the effect of segment size on reserve outcomes using standard methods[46].

From these measurements we calculated mean depth, maximum depth, mean width, median substrate particle size, and three metrics of substrate diversity: Simpson's diversity index of substrate types, and the loading scores for the first two axes of a principal component analysis of substrate types by site. Simpson's diversity index and principal component analyses were conducted in the 'vegan'[47] package in R[48]. We tested for differences in each habitat variable using mixed effects models with reserve protection as a fixed categorical variable and each reserve–non-reserve location as a random term. Across all variables, reserve habitats did not differ from non-reserves for our study transects ($P > 0.05$). On the basis of these results, we ruled out any potential contribution of habitat differences to our analysis of reserve–non-reserve effects.

Reserve features

To quantify those reserve features we considered potentially important for predicting reserve success, we either made direct field measurements, extracted data from digitized maps, or interviewed community members at each survey site. River size quantified as discharge ($m^3 s^{-1}$) was measured in the field using standard methods. Reserve size was quantified using field measurements of river width, multiplied by reserve length determined as river length between upstream and downstream reserve boundaries.

To evaluate the spatial metrics of the reserve network, we digitized the Mae Ngao River network from a Google Earth[49] satellite imagery base map in ArcGIS 10.3[50] and mapped all potential stream courses regardless of the presence of visible surface water, as no existing hydrological maps were at sufficient resolution for our study region. We used field observations to constrain the digitized stream network based on in situ observation of the presence of water in 20 tributaries during the height of dry season (early May 2016). Using our digital river network and a hydrologically conditioned digital elevation model of 90-m resolution[51], we extracted the upstream catchment area, then estimated an upstream area threshold that best separated wet from dry locations (pROC package[52]). We estimated an upstream extent of 1.02 km^2 to best delineate perennial flows (receiver operating characteristic area under the curve (ROC-AUC) = 0.89, $n = 20$) and trimmed our digitized stream network accordingly to a total length of 827 km of perennial rivers. We also delineated all roads and villages within the Ngao River Valley from the same satellite imagery, which allowed us to calculate Euclidean distances between each reserve and the nearest road and the nearest village as metrics of reserve isolation.

Considering these reserves as a network, we calculated three additional parameters from our stream network that could influence ecological responses: river distance to the nearest reserve, river distance to mainstem confluence, and betweenness centrality. Distances among reserves and to the river confluence were calculated from reserve boundaries and measured along the perennial river network. Betweenness centrality (BC) is an index used in network analysis that describes the relative importance of each node (that is, reserve) to overall connectivity within the network. Specifically, the standardized betweenness centrality for a node i is calculated as:

$$\mathrm{BC}_i = \frac{2 \times \sum_{j<k} g_{jk}(i)/g_{jk}}{(N-1)(N-2)}$$

where $i \neq j \neq k$, g_{jk} is the number of equally shortest paths between nodes j and k, $g_{jk}(i)$ is the number of these paths that include node i, and the denominator represents twice the total number of node pairs without node i[53].

We determined the reserve age (numbers of years since establishment), enforcement (explicit penalty for illegal harvest: yes or no), and village size (number of households in sponsoring village) from more than 35 interviews with village leaders and community members.

Data analysis

To test for differences in species richness and abundance between reserves and unprotected areas, we used mixed-effects Poisson regression to model species counts, accounting for area surveyed using an offset. We tested biomass differences between reserves and non-reserves by modelled biomass per unit area using a mixed-effects linear model, again with reserve as the lone predictor and site as a random effect. Mixed-effect models were analysed using the 'lme4' package[54] in R[48].

To test the effects of reserve features on fish species richness, density, and biomass, we calculated a reserve response index for each outcome variable. For species richness (S), we calculated a reserve response index (R_r) as $R_{\text{reserve}} - R_{\text{non-reserve}}$, where R is the mean number of species observed during two surveys[55]. We calculated the reserve response indices for fish density (D_r) and biomass (B_r) as: $\log_{10}$(reserve mean/non-reserve mean).

In addition to testing the significance of overall reserve responses across sites, we used functional trait categorization of species to test for differential responses by size and trophic position. Both the magnitude and direction (±) of organismal responses to reserve protection have been shown to vary with life history and ecological traits[56]. We divided fish into larger-bodied and smaller-bodied categories using a threshold of 20 cm maximum length from observations across all 23 reserves. This cutoff was derived empirically from the size frequency distribution across all species observed (Supplementary Fig. 1). Trophic positions were estimated using our own nitrogen stable isotope data from the study area when available, supplemented with literature data for 10 of 38 species[45].

We regressed the reserve response indices for richness (R_r), density (D_r), and biomass (B_r) against all predictor variables. We standardized all model coefficients, then evaluated all factorial models (n = 1,024) and quantitatively compared the subset of models whose cumulative sum was 0.95 of the total Aikake weight, which corresponds to a 95% credible interval for best models[57]. For the subset of best-fitting models, we summed Aikake weights (w_i) for each predictor and used them to estimate their relative importance[57]. All analyses and model fitting were conducted using the 'MuMIn' package in R[58]. Full model results are reported in Extended Data Tables 1–3.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

The datasets used and/or analysed during the current study are available in the Environmental Data Initiative repository (https://portal.edirepository.org/nis/mapbrowse?packageid=edi.513.1).

Code availability

The R code used for the analyses presented here is available from GitHub (https://github.com/aakoning/riv_res_2020).

44. Koning, A. A., Moore, J., Suttidate, N., Hannigan, R. & McIntyre, P. B. Aquatic ecosystem impacts of land sharing versus sparing: nutrient loading to Southeast Asian rivers. *Ecosystems (N. Y.)* **20**, 393–405 (2017).
45. Froese, R. & Pauly, D. (eds) *FishBase* http://www.fishbase.org (2019).
46. Lamberti, G. A. & Hauer, F. R. *Methods in Stream Ecology* (Academic, 2017).
47. Jari Oksanen, F. et al. vegan: Community Ecology Package. R package version 2.5-6 https://CRAN.R-project.org/package=vegan (2019).
48. R Core Team. *R: A Language and Environment for Statistical Computing* https://www.R-project.org/ (R Foundation for Statistical Computing, 2019).
49. Google Earth (November, 2015). Mae Ngao, Thailand. https://www.google.co.uk/earth/ (2020).
50. Environmental Systems Research Institute (ESRI). *ArcGIS Release 10.3* (2015).
51. Yamazaki, D. et al. A high-accuracy map of global terrain elevations. *Geophys. Res. Lett.* **44**, 5844–5853 (2017).
52. Robin, X. et al. pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics* **12**, 77 (2011).
53. Jordán, F., Liu, W. C. & Andrew, J. D. Topological keystone species: measures of positional importance in food webs. *Oikos* **112**, 535–546 (2006).
54. Bates, D., Maechler, M. & Ben Bolker, S. W. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
55. Claudet, J. et al. Marine reserves: size and age do matter. *Ecol. Lett.* **11**, 481–489 (2008).
56. Claudet, J. et al. Marine reserves: fish life history and ecological traits matter. *Ecol. Appl.* **20**, 830–839 (2010).
57. Johnson, J. B. & Omland, K. S. Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**, 101–108 (2004).
58. Barton, K. MuMIn: Multi-Model Inference. R package version 1.43.6 https://CRAN.R-project.org/package=MuMIn (2019).

Acknowledgements We thank the communities of the Mae Ngao River basin for their participation in and support of this research, and the International Sustainable Development Studies Institute (Chiang Mai) for logistical support. Earlier drafts of the manuscript were improved by the McIntyre laboratory groups at the University of Wisconsin-Madison and Cornell University, and by comments from I. Baird, B. Peckarsky, K. Winemiller, E. Stanley, T. Ives, R. Abell and M. Thieme. Funding was provided by National Science Foundation grants DGE-0718123, DGE-1144752, and DEB-15011836 to A.A.K. and DGE-1144752 to K.M.P., a Harvey Fellowship and a Cornell Atkinson Center for Sustainability Postdoctoral Fellowship to A.A.K., and a David and Lucille Packard Fellowship to P.B.M. Additional funding provided by USAID's 'Wonders of the Mekong' Cooperative Agreement No: AID-OAA-A-16-00057.

Author contributions A.A.K. conceptualized the research, acquired funding, performed fieldwork, conducted analyses, and wrote the manuscript. K.M.P. performed fieldwork, assisted in methodological development, and edited the manuscript. E.F.-C. conducted analyses, contributed to creating figures, and edited the manuscript. P.B.M. contributed to research conceptualization and methodological development, and edited the manuscript.

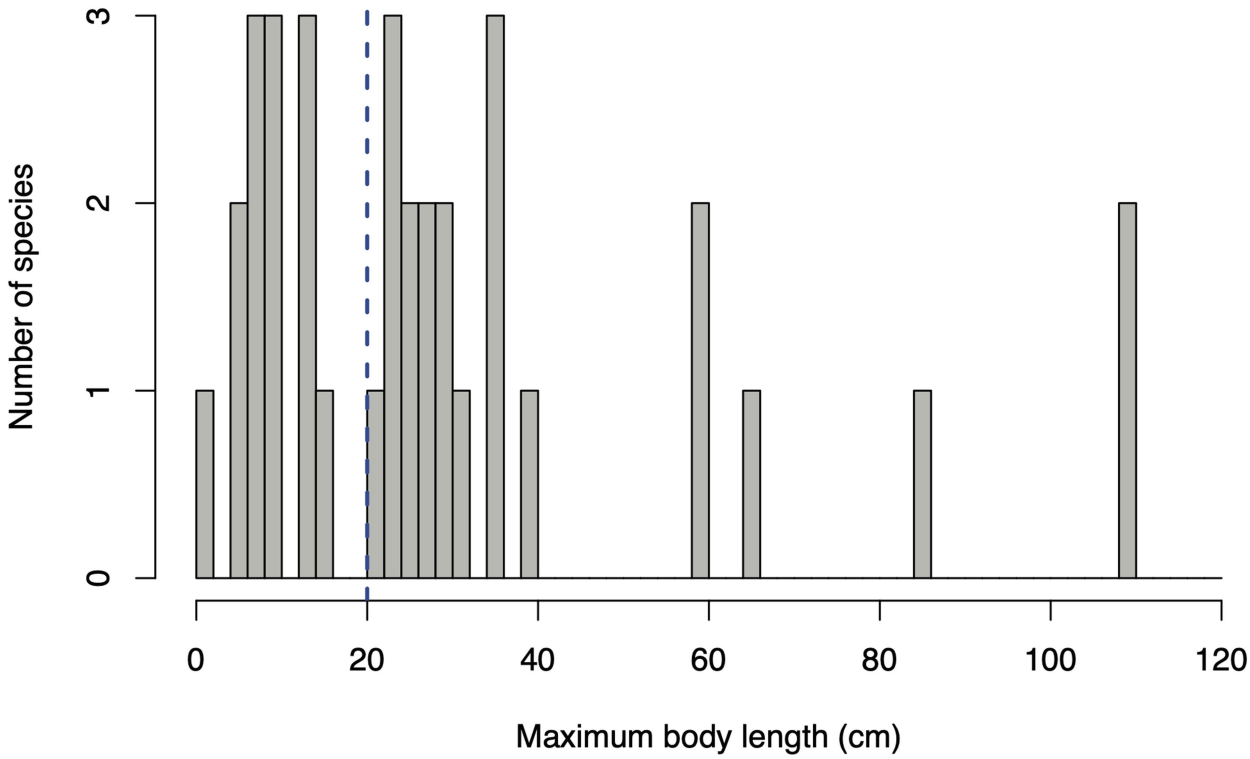
Competing interests The authors declare no competing interests.

Additional information

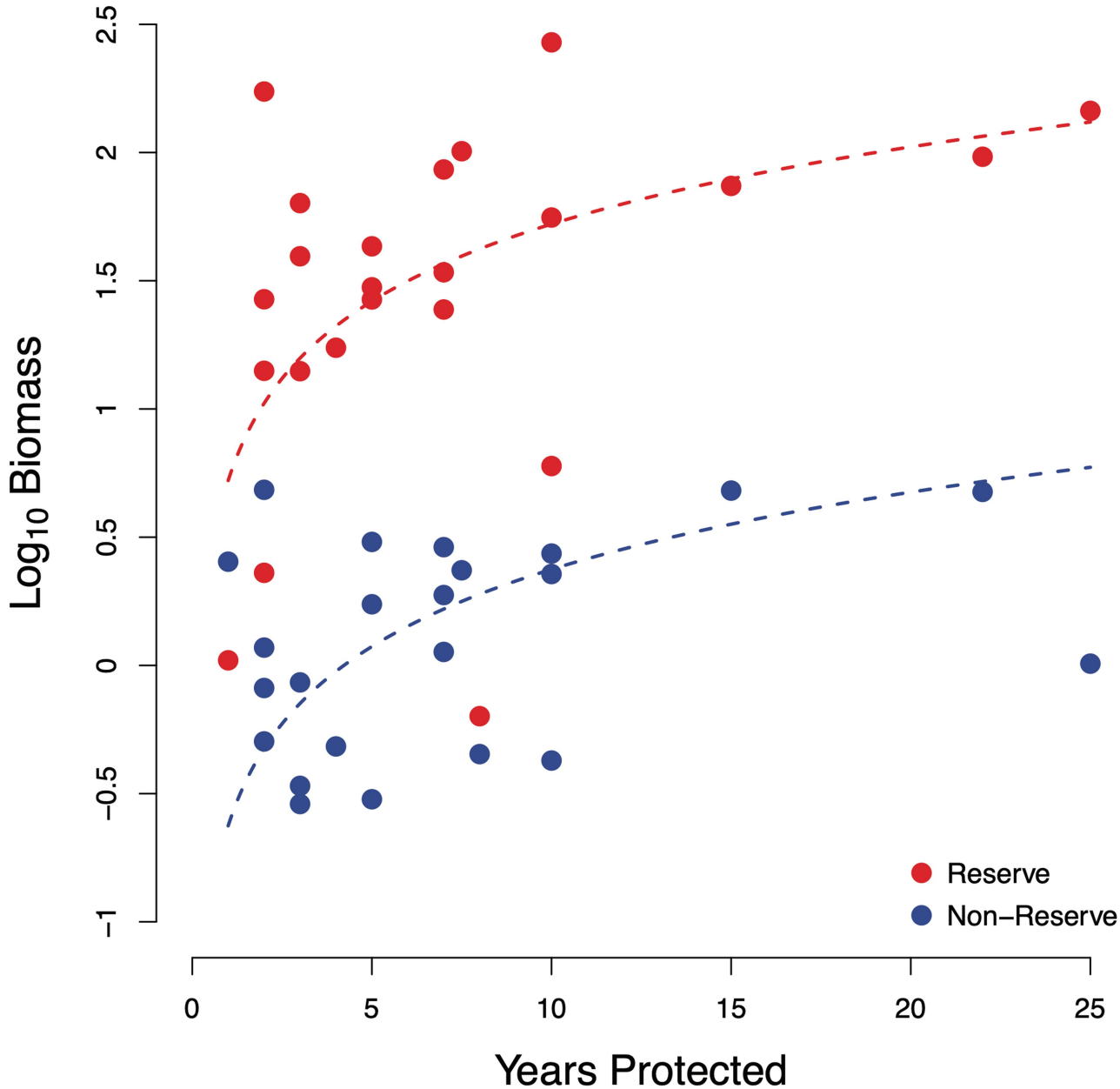
Supplementary information is available for this paper at https://doi.org/10.1038/s41586-020-2944-y.

Correspondence and requests for materials should be addressed to A.A.K.

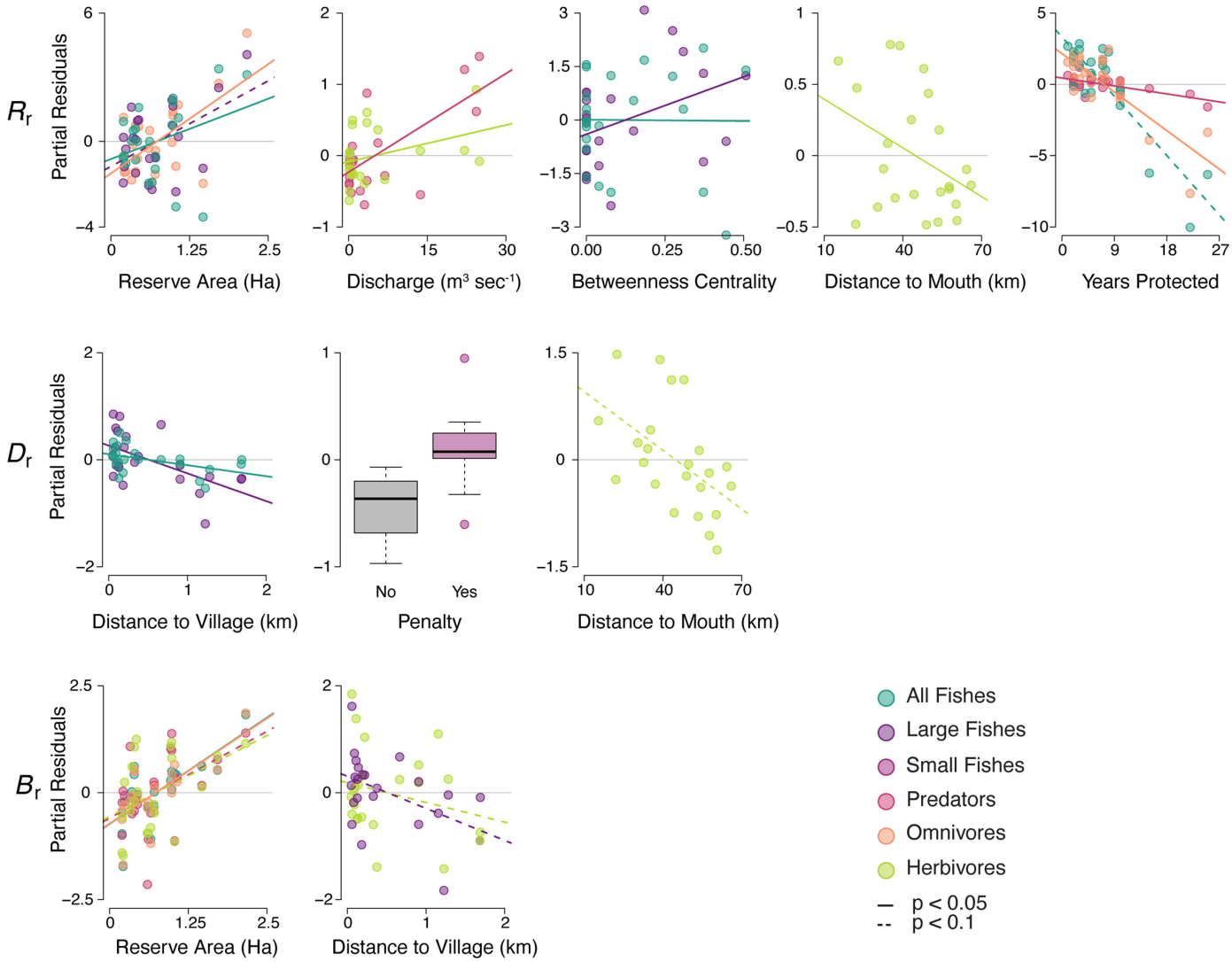
Peer review information *Nature* thanks Edward Allison and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.



Extended Data Fig. 1 | Frequency distribution of species-level maximum observed body length for the fish fauna of the study area of the Salween River basin. The natural break at 20 cm (blue dashed line) was used to classify each species as relatively large (≥20 cm) versus smaller (<20 cm).



Extended Data Fig. 2 | Average total fish biomass measures in paired reserve (red points) and non-reserve (blue points) of varying ages. Dotted lines correspond to nonlinear least squares estimates for reserves and non-reserves showing gains in both reserves and adjacent fished areas over time.



Extended Data Fig. 3 | Partial residual plots for all best averaged models of richness (R_r), density (D_r), and biomass (B_r) responses to no-take reserves. Symbology indicates alternative groupings of fish species by body size and trophic group at each site ($n = 23$). The box and whisker plot shows the minimum and maximum values (excluding outliers) as ends of hashed lines, upper and lower quartiles as the upper and lower bounds of the box, the median as the bold line, and outliers (values exceeding 1.5 times the interquartile range) as points for reserves having no explicit penalty (No; $n = 4$) and those with an explicit penalty (Yes; $n = 19$). Full model results are found in Extended Data Tables 1–3.

Extended Data Table 1 | Results of model averaging for richness reserve response (R_r)

	Reserve Area (Ha)			Discharge (m^3 sec^{-1})			Years Protected			Penalty (Y/N)			Distance to Village (km)		
	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p
All Fish	0.67	3.04	0.05	0.32	2.20	0.33	0.70	-3.62	0.05	0.14	0.71	0.53	0.15	-0.42	0.72
Large Fish	0.69	2.56	0.06	0.25	1.37	0.54	0.54	-2.60	0.11	0.12	-0.20	0.84	0.18	-0.67	0.45
Small Fish	0.21	-0.36	0.55	0.19	-0.16	0.83	0.44	-0.78	0.15	0.37	0.80	0.18	0.15	0.04	0.95
Predators	0.18	-0.14	0.66	0.73	1.02	0.02	0.67	-0.68	0.04	0.13	-0.05	0.85	0.13	0.00	0.99
Omnivores	0.76	2.95	0.03	0.22	-0.01	0.99	0.71	-3.00	0.04	0.15	0.71	0.51	0.15	-0.50	0.63
Herbivores	0.18	0.12	0.70	0.70	0.65	0.04	0.20	-0.22	0.54	0.13	-0.03	0.92	0.14	-0.07	0.72

	Distance to Road (km)			No. Houses in Village			Betweenness Centrality (normalized)			Distance to Mouth (km)			Closest Reserve Distance (km)			# Models
	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	
All Fish	0.42	-1.30	0.13	0.18	0.73	0.40	0.74	2.60	0.02	0.32	-1.51	0.26	0.14	-0.62	0.56	295
Large Fish	0.20	-0.70	0.37	0.14	0.41	0.60	0.86	2.61	0.01	0.25	-1.03	0.38	0.12	0.02	0.98	228
Small Fish	0.38	-0.64	0.18	0.15	0.20	0.67	0.15	0.00	1.00	0.16	0.11	0.85	0.21	-0.38	0.43	327
Predators	0.17	0.13	0.54	0.13	0.00	0.99	0.39	0.54	0.15	0.14	0.00	0.99	0.15	0.10	0.40	212
Omnivores	0.42	-1.23	0.13	0.16	0.60	0.47	0.46	1.70	0.15	0.20	-0.55	0.68	0.21	-0.81	0.35	353
Herbivores	0.14	0.05	0.83	0.14	-0.01	0.95	0.30	0.29	0.39	0.72	-0.50	0.04	0.15	-0.07	0.77	236

Aikake weight (w_i), coefficient (β), and p-value (p) for two-sided z-test of predictors from best averaged models. All factorial models were fit (n = 1,024). The results reported are for the best averaged model obtained from the subset of models (# Models) having highest Akaike weights (w_i), corresponding to a 95% credible interval for best fitting models.

Extended Data Table 2 | Results of model averaging for density reserve response (D_r)

	Reserve Area (Ha)			Discharge (m^3 sec^{-1})			Years Protected			Penalty (Y/N)			Distance to Village (km)		
	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p
All Fish	0.28	0.18	0.32	0.26	-0.18	0.36	0.17	-0.07	0.74	0.17	0.09	0.57	0.72	-0.27	0.04
Large Fish	0.15	0.03	0.93	0.23	-0.28	0.43	0.20	-0.19	0.50	0.23	-0.26	0.35	0.92	-0.58	0.01
Small Fish	0.14	0.00	0.99	0.15	0.04	0.87	0.14	0.01	0.97	0.89	0.54	0.01	0.15	0.03	0.88
Predators	0.25	0.28	0.39	0.63	0.62	0.11	0.41	-0.50	0.19	0.15	-0.11	0.70	0.14	0.00	0.99
Omnivores	0.37	0.22	0.22	0.29	-0.20	0.32	0.20	-0.12	0.58	0.20	0.12	0.47	0.35	-0.17	0.20
Herbivores	0.28	0.75	0.28	0.18	0.28	0.64	0.28	-0.83	0.33	0.39	-0.65	0.15	0.50	-0.67	0.10

	Distance to Road (km)			No. Houses in Village			Betweenness Centrality (normalized)			Distance to Mouth (km)			Closest Reserve Distance (km)			# Models
	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	
All Fish	0.16	-0.03	0.85	0.16	-0.06	0.64	0.17	-0.06	0.72	0.15	-0.02	0.90	0.19	-0.09	0.53	306
Large Fish	0.16	0.09	0.74	0.14	-0.06	0.79	0.18	0.18	0.63	0.15	-0.01	0.98	0.18	-0.15	0.55	238
Small Fish	0.27	-0.19	0.29	0.15	0.04	0.83	0.17	-0.11	0.63	0.21	-0.15	0.43	0.14	0.01	0.96	212
Predators	0.27	-0.23	0.28	0.13	-0.03	0.87	0.29	0.21	0.58	0.17	-0.11	0.70	0.16	0.04	0.86	317
Omnivores	0.16	-0.06	0.68	0.20	-0.09	0.47	0.16	0.03	0.89	0.19	0.08	0.58	0.19	-0.09	0.52	340
Herbivores	0.23	0.39	0.38	0.13	-0.04	0.93	0.19	0.37	0.43	0.73	-0.90	0.06	0.15	-0.22	0.56	349

Aikake weight (w_i), coefficient (β), and p-value (p) for two-sided z-test of predictors from best averaged models. All factorial models were fit (n = 1,024). The results reported are for the best averaged model obtained from the subset of models (# Models) having highest Akaike weights (w_i), corresponding to a 95% credible interval for best fitting models.

Extended Data Table 3 | Results of model averaging for biomass reserve response (B_r)

	Reserve Area (Ha)			Discharge (m^3 sec^{-1})			Years Protected			Penalty (Y/N)			Distance to Village (km)		
	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p
All Fish	0.87	0.83	0.03	0.21	-0.37	0.53	0.33	-0.48	0.31	0.13	0.02	0.95	0.49	-0.47	0.11
Large Fish	0.54	0.75	0.12	0.19	-0.31	0.63	0.24	-0.39	0.54	0.13	0.01	0.99	0.63	-0.68	0.06
Small Fish	0.21	0.15	0.47	0.21	-0.12	0.66	0.18	0.10	0.67	0.22	0.17	0.42	0.19	-0.10	0.56
Predators	0.64	1.36	0.07	0.35	0.85	0.25	0.57	-1.54	0.08	0.13	-0.15	0.75	0.16	-0.20	0.67
Omnivores	0.80	0.79	0.04	0.29	-0.62	0.32	0.34	-0.49	0.36	0.13	0.11	0.76	0.46	-0.45	0.12
Herbivores	0.75	1.23	0.07	0.27	0.69	0.29	0.27	-0.64	0.56	0.17	-0.38	0.50	0.65	-0.89	0.06

	Distance to Road (km)			No. Houses in Village			Betweenness Centrality (normalized)			Distance to Mouth (km)			Closest Reserve Distance (km)			# Models
	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	w_i	β	p	
All Fish	0.14	0.05	0.88	0.13	0.02	0.93	0.23	0.39	0.38	0.22	0.25	0.43	0.13	0.00	0.99	269
Large Fish	0.16	0.14	0.73	0.16	0.18	0.61	0.19	0.35	0.50	0.20	0.28	0.48	0.15	0.08	0.83	299
Small Fish	0.16	-0.06	0.72	0.15	0.04	0.80	0.30	-0.21	0.31	0.15	-0.03	0.88	0.16	-0.02	0.44	271
Predators	0.12	-0.01	0.97	0.16	-0.26	0.51	0.54	0.86	0.08	0.45	-0.89	0.12	0.14	-0.08	0.87	292
Omnivores	0.14	0.05	0.88	0.13	0.04	0.90	0.26	0.50	0.32	0.35	0.41	0.19	0.13	-0.03	0.93	305
Herbivores	0.15	0.17	0.74	0.13	-0.05	0.91	0.22	0.50	0.39	0.33	-0.74	0.23	0.14	0.04	0.94	305

Aikake weight (w_i), coefficient (β), and p-value (p) for two-sided z-test of predictors from best averaged models. All factorial models were fit (n = 1,024). The results reported are for the best averaged model obtained from the subset of models (# Models) having highest Akaike weights (w_i), corresponding to a 95% credible interval for best fitting models.