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MONTANA FIRST JUDICIAL DISTRICT COURT
LEWIS AND CLARK COUNTY

<p>RIKKI HELD, et al.,</p> <p>Plaintiffs,</p> <p>v.</p> <p>STATE OF MONTANA, et al.,</p> <p>Defendants.</p>	<p>No. CDV-2020-307</p> <p>Hon. Kathy Seeley</p> <p>NOTICE OF SUPPLEMENTING EXPERT DISCLOSURE</p>
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Pursuant to Rule 26 (e)(2), M.R.Civ.P., Plaintiffs hereby submit the following new sources to supplement the Expert Report of Jack A. Stanford which was filed and served on Defendants on September 30, 2022. On page 2 of the Report, it states: "Should additional relevant or pertinent information become available . . . I reserve the right to supplement the discussion and findings in this expert report" and these studies qualify as additional relevant information that have recently become available. The two new studies are as follows and are attached hereto at Bates Nos. P0043158-P0043167 and P0043149-P0043157.

- Cline, Timothy J., Clint C. Muhlfeld, Ryan Kovach, Robert Al-Chokhachy, David Schmetterling, Diane Whited, and Abigail J. Lynch. 2022. "Socioeconomic Resilience to Climatic Extremes in a Freshwater Fishery." *Science Advances* 8 (36): eabn1396. <https://doi.org/10.1126/sciadv.abn1396>. (Bates Nos. P0043158-P0043167).
- Elser, James J., Shawn P. Devlin, Jinlei Yu, Adam Baumann, Matthew J. Church, John E. Dore, Robert O. Hall Jr., Melody Hollar, Tyler Johnson, Trista Vick-Majors, and Cassidy White. 2022. "Sustained Stoichiometric Imbalance and its Ecological Consequences in a Large Oligotrophic Lake." *Proceedings of the National Academy of Sciences* 119 (30): e2202268119. <https://doi.org/10.1073/pnas.2202268119>. (Bates Nos. P0043149-P0043157).

Executed this 3rd day of November, 2022.

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I certify that a true and correct copy of the foregoing was delivered by email to the following on November 3rd, 2022:

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Sustained stoichiometric imbalance and its ecological consequences in a large oligotrophic lake

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Considerable attention is given to absolute nutrient levels in lakes, rivers, and oceans, but less is paid to their relative concentrations, their nitrogen:phosphorus (N:P) stoichiometry, and the consequences of imbalanced stoichiometry. Here, we report 38 y of nutrient dynamics in Flathead Lake, a large oligotrophic lake in Montana, and its inflows. While nutrient levels were low, the lake had sustained high total N: total P ratios (TN:TP: 60 to 90:1 molar) throughout the observation period. N and P loading to the lake as well as loading N:P ratios varied considerably among years but showed no systematic long-term trend. Surprisingly, TN:TP ratios in river inflows were consistently lower than in the lake, suggesting that forms of P in riverine loading are removed preferentially to N. In-lake processes, such as differential sedimentation of P relative to N or accumulation of fixed N in excess of denitrification, likely also operate to maintain the lake's high TN:TP ratios. Regardless of causes, the lake's stoichiometric imbalance is manifested in P limitation of phytoplankton growth during early and midsummer, resulting in high C:P and N:P ratios in suspended particulate matter that propagate P limitation to zooplankton. Finally, the lake's imbalanced N:P stoichiometry appears to raise the potential for aerobic methane production via metabolism of phosphonate compounds by P-limited microbes. These data highlight the importance of not only absolute N and P levels in aquatic ecosystems, but also their stoichiometric balance, and they call attention to potential management implications of high N:P ratios.

phosphorus | nitrogen | stoichiometry | limnology | ecosystem

The emergence of the Anthropocene era has been marked by major changes in all of Earth's major biogeochemical cycles (1). For example, fluxes of carbon (C) (as CO₂) to the atmosphere have increased by ~14% during the last 120 y largely due to fossil fuel combustion. Fluxes of nitrogen (N) into the biosphere have increased by at least 100% due to application of the Haber-Bosch reaction for fertilizer production, land use change favoring N-fixing legumes, and conversion of atmospheric N₂ to available forms (NO_x) by high temperature combustion of petroleum and fossil gas (2). Finally, large-scale mining of phosphorus (P)-rich geological deposits for production of fertilizers has amplified rates of P cycling in the biosphere by ~400% (1). Each of these perturbations has biophysical and ecological impacts at differing time and space scales. For C, its accumulation in the atmosphere has altered Earth's radiative balance, warming the planet and perturbing precipitation patterns globally. Amplified inputs of reactive N to the Earth system enter the hydrosphere and, thus, potentially lead to overenrichment of lakes, rivers, and coastal oceans across broad regions. Amplifications of P inputs often impair water quality at watershed and local scales (3), stimulating phytoplankton production and contributing, along with N, to harmful algal blooms, fish kills, and "dead zones" (4, 5). These differential amplifications and their contrasting spatial scales indicate that ecosystems are experiencing not only absolute changes in biogeochemical cycling, but also perturbations in the relative inputs and outputs of biologically important elements (6). Studies of elemental coupling and uncoupling in ecosystems are not yet widespread, but emerging work has shown how C, N, and P are differentially processed as they pass through watersheds (7).

The potential for differential alteration in supplies of N and P to aquatic ecosystems suggests that understanding the nutrient status of a water body requires knowledge of not only absolute supplies of limiting nutrients, but also their relative proportions (i.e., their N:P stoichiometry). This work has been facilitated in recent years by the emergence of the theory of ecological stoichiometry (8). For example, seminal work by Redfield (9) found that N:P ratios in marine organic matter were tightly constrained around 16:1 (molar, here and throughout), a value that may represent the central tendency for the N:P ratio of phytoplankton undergoing balanced growth in which major

Significance

Both nitrogen (N) and phosphorus (P) drive water quality and are heavily altered by human activities that amplify their supplies to lakes, rivers, and oceans. Considerable attention is given to management of absolute nutrient levels but less to their relative abundances, their N:P stoichiometry. This study documents high N:P ratios in low-nutrient Flathead Lake that persist despite considerably lower N:P ratios in river nutrient inputs. The lake's elevated N:P ratios are associated with phytoplankton P limitation, impaired food quality for zooplankton, and potential production of the greenhouse gas methane by P-limited microbes. These findings highlight the need to consider not only absolute levels of N and P in aquatic ecosystems, but also their stoichiometric balance.

Author contributions: J.J.E., J.Y., M.J.C., J.E.D., and T.V.-M. designed research; S.P.D., J.Y., A.B., M.J.C., J.E.D., M.H., T.J., T.V.-M., and C.W. performed research; A.B. contributed new reagents/analytic tools; J.J.E., S.P.D., J.Y., M.J.C., J.E.D., R.O.H., M.H., T.J., and C.W. analyzed data; J.J.E., S.P.D., J.Y., M.J.C., J.E.D., R.O.H., and T.V.-M. wrote the paper.

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The authors declare no competing interest.

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P-0043149

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pools of N (protein) and P (RNA) are produced at the same rate (10). In lakes, N:P ratios show much wider variation—around a value of ~ 30 —perhaps reflecting the biogeochemical connections of lakes to terrestrial systems where N:P ratios have a similar value and range of variation (11). Nevertheless, this classic “Redfield ratio” of 16:1 can be thought of as representing a balanced nutrient supply for primary producers in pelagic ecosystems. When the ratios of N and P supplied deviate from this balanced ratio, primary limitation of growth by N (when N:P is low) or by P (when N:P is high) can occur. For example, phytoplankton growth in lakes with imbalanced total N: total P (TN:TP) ratios that exceed 30:1 is generally P limited (12). Disproportionate inputs of N relative to P from atmospheric deposition can increase lake TN:TP ratios and shift lake phytoplankton from N to P limitation (13), inducing P limitation in zooplankton (14). Imbalanced N:P ratios in nutrient supplies can also shift the competitive advantage among phytoplankton and enhance production of potentially toxic compounds during harmful algal blooms. For example, skewed supplies of N relative to P can increase production of N-rich secondary compounds by phytoplankton, while disproportionate inputs of P relative to N can induce production of C-based toxins (15). High N:P ratios can also enhance proliferation of fungal parasites of phytoplankton (16).

Imbalanced N:P ratios can impact aquatic ecosystems in other ways. For example, they can alter the functioning of food webs. In particular, shifts in nutrient supply regimes that enhance P limitation can impede energy flow in trophic interactions because biomass of P-limited primary producers is of low quality for animals due to its low P content (8). Ecosystem shifts to high N:P ratios and more prevalent P limitation can also impact the cycling of the greenhouse-active gas methane (CH_4) because phosphate limitation can result in production of methane under aerobic conditions in both marine and freshwater phytoplankton and bacteria (17, 18). Both chemoheterotrophic and photoautotrophic bacteria (e.g., *Pseudomonas*, SAR11, *Trichodesmium*, *Synechococcus*) can metabolize organic P compounds, called phosphonates, to acquire P. Microbial cleavage of one type of phosphonate, methylphosphonic acid (MPn), to acquire P results in formation of methane (17). While it is likely that anaerobic methane production due to oxygen depletion in response to P-driven eutrophication is the dominant process connecting P to methane dynamics, the significance of aerobic phosphonate metabolism to global methane cycles remains to be assessed. However, contributions are potentially large, given the prevalence of P limitation in both freshwater and marine ecosystems. In light of emerging trends that suggest overall increases in ecosystem N:P ratios due to human impacts (6), these trophic and biogeochemical impacts of stoichiometric imbalance show that it is critical to consider not only absolute levels of nutrients, but also their stoichiometry. In particular, high N:P ratios can accentuate P limitation, causing a suite of ecological impacts that, currently, are poorly described.

In this paper, we illustrate the utility of stoichiometric approaches by combining analyses of long-term records of nutrient supply and dynamics, together with contemporary experiments, to examine how imbalances in N:P stoichiometry (e.g., strong divergence from classic Redfield proportions) influence plankton ecology and biogeochemistry across multiple scales in Flathead Lake, a large lake in western Montana. The lake is itself relatively unperturbed by human impacts and, thus, maintains low overall nutrient levels. However, the strong stoichiometric imbalance that we describe makes Flathead Lake appropriate for assessing ecosystem consequences of what

appear to be general trends of increasing N:P ratios in global ecosystems (6). Numerous limnological properties of the lake and its inflow rivers have been monitored continuously for several decades, including concentrations of various forms of N and P. Thus, these time-series data allow us not only to assess long-term variability or stability in the stoichiometry of N and P in the lake and its river inflows over decadal time scales, but also to connect its stoichiometry with potential consequences for nutrient limitation, food web dynamics, and biogeochemical cycling under low-nutrient conditions.

Results and Discussion

Lake-Scale Stoichiometry. To assess the long-term status of N and P in Flathead Lake, we summarized data for average concentrations of TN and TP and their stoichiometric ratio in the upper 30 m of Flathead Lake since 1983 (Fig. 1). While exhibiting considerable seasonal variability, TN and TP concentrations, as well as the TN:TP ratios, showed no long-term trends over the 38 y of observation (Fig. 1). Overall, concentrations of TN and TP were low, falling in the lower 2.5% and 1%, respectively, of observations in the US Environmental Protection Agency’s 2017 National Lakes Assessment (19). TN concentrations did decline

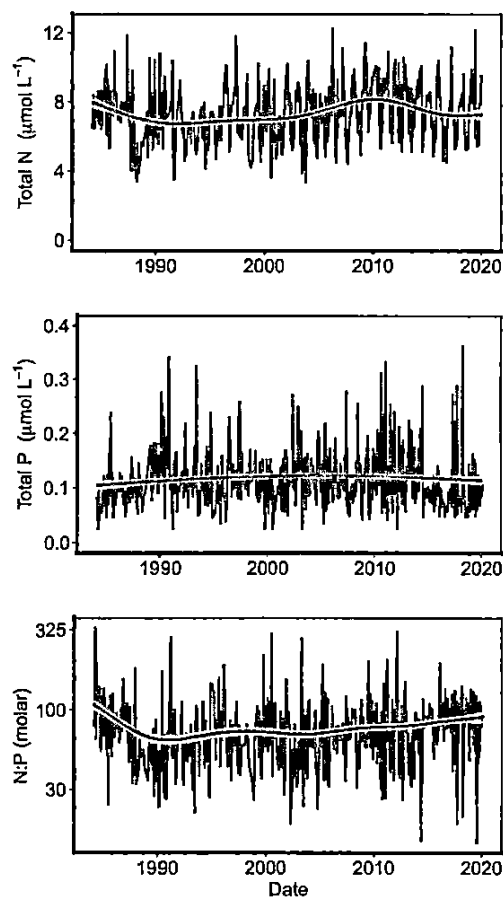


Fig. 1. (A–C) Biweekly or monthly concentrations of (A) TN, (B) TP, and (C) the TN:TP stoichiometric ratio (molar) in integrated samples of the upper 30 m of Flathead Lake from 1983 to 2019 (note natural log scale). GAMS were used to assess trends in the time series data, with solid black lines indicating the fitted model and gray shading indicating model error.

P-0043150

somewhat during a 5- to 6-y period during the late 1980s and had a temporary increase around 2010 (Fig. 1A), while TP concentrations were constant throughout (Fig. 1B). Following a modest decline at the start of the record (Fig. 1C), TN:TP ratios, while quite variable at short time scales, have held steady at high values (80 to 90:1) for the 30 y since 1990. Current TN:TP ratios of ~90:1 place Flathead Lake in the upper 87th percentile for TN:TP ratio in lakes of the United States (19). Thus, Flathead Lake has sustained a strong and steady stoichiometric imbalance for decades. This constancy of nutrient levels and ratios is notable, given that during the period of our observations, human population in the watershed—while still at relatively low density—doubled, and wildfires have burned sizable portions of the lake's watershed.

To connect the stoichiometric status of the lake to external inputs of N and P, we analyzed long-term data on river nutrient concentrations and discharge to estimate rates of nutrient loading and the N:P stoichiometry of that loading for the past 38 y. While highly variable, annual TN loading (Fig. 2A) has declined slightly during the study period. Annual loading of TP also displayed considerable year-to-year variability, declining modestly (~10%) over the study period (Fig. 2B). Reflecting this long-term stability in TN and TP loading, the TN:TP ratio of annual nutrient loading, while variable (range: 5 to 60 around an overall geometric mean of 21.5), showed no long-term trend (Fig. 2C). We note that the average loading N:P ratio from Flathead Lake's rivers is somewhat lower than national values of river and stream TN:TP ratios (median value

of 31:1; ref. 20). This relatively low N:P of loading likely reflects the status of the lake's watershed. Manning et al. (20) report that rivers and streams in forested watersheds generally have lower TN:TP ratios than those draining developed or agricultural watersheds. This is consistent with the relatively low TN:TP of loading to Flathead Lake, as the watershed is heavily forested with limited developed or agricultural land areas. Furthermore, much of this landscape lies within federally protected areas, including Glacier National Park, and federally designated wilderness areas. While there was no long-term trend in loading N:P, interannual variability in loading N:P ratios (Fig. 2C) was notable and appeared to be driven by changes in P loading (Fig. 2B). We hypothesized that this variation was driven by interannual changes in discharge. Indeed, loading N:P ratios (log-transformed) negatively correlated with annual discharge ($P < 0.001$, $r = -0.65$). That is, years when the loading N:P ratios were particularly low correspond to years with high absolute loading rates of N and, especially, P (see Fig. 2; 1990 to 1991, 1996 to 1997, 2002). This hydrologic variation itself may be due to decadal-scale climate variation (e.g., El Niño/La Niña cycles), as annual discharge into Flathead Lake is negatively correlated ($P = 0.03$, $r = -0.34$) with the Oceanic Niño Index. (Note that in western Montana, strong El Niño produces dry conditions, while La Niña is associated with wet conditions; ref. 21.) Following previous work (20, 22), we hypothesize that years of high discharge in the Flathead watershed include flood events in spring and early summer that mobilize and transport low N:P sediments from in-river or near-channel deposits in the floodplain.

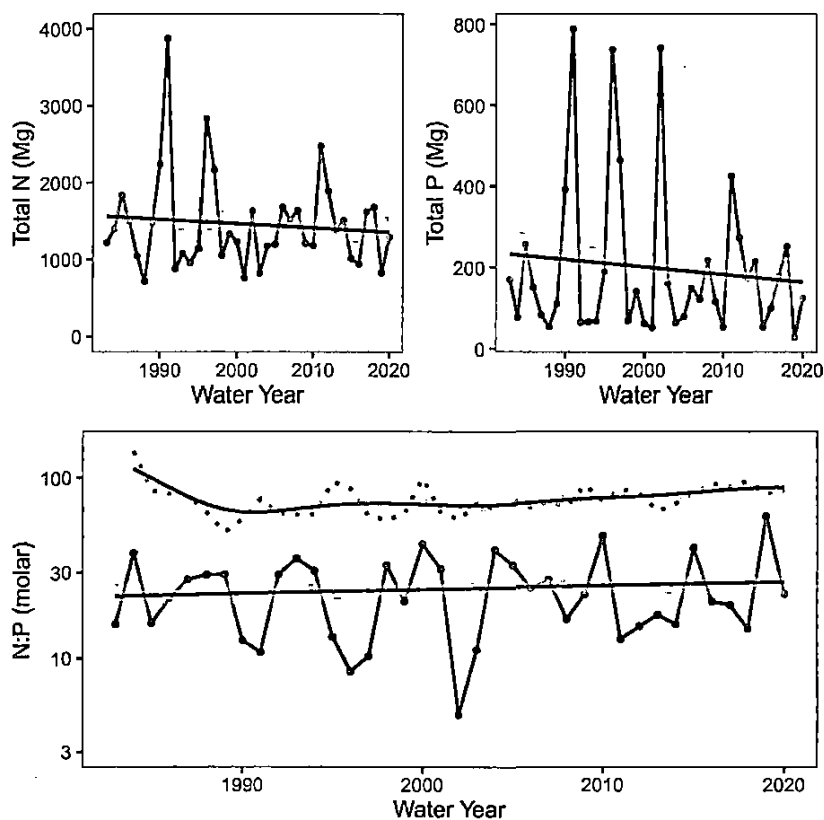


Fig. 2. (A–C) Annual riverine loading for (A) TN, (B) TP, and (C) TN:TP loading ratios (molar) since 1983. Inputs from the Flathead River dominate both the riverine hydrologic and nutrient loading to the lake. The dynamics of lake TN:TP ratio and associated GAM are shown in the upper dotted line to ease comparison.

Thus, a notable feature that emerges from this analysis of the long-term status of N:P stoichiometry in this coupled lake-watershed ecosystem is that the lake maintains unusually high N:P ratios (90:1) despite loading N:P ratios that are relatively low (~21:1). Various mechanisms might produce this discrepancy between N:P of the lake and its river inflows. One possible contributor is that river loading N:P ratios might not reflect what nutrients are available for biological use and subsequent processing in the lake water column. For example, based on measurements of nutrient pools in river inflows since 2016, at least ~50% of TP concentrations in river water are in particulate form versus only ~23% for N. This observation is consistent with earlier studies in the Flathead River showing that much P carried to Flathead Lake is in nonlabile forms associated with inorganic sediments (23). Thus, much inflowing P appears particle associated, entering Flathead Lake during periods of elevated spring and early summer runoff that is high in suspended particles. Much of this particulate load is likely lost to sedimentation soon after it enters the lake. Alternatively, low bioavailability of dissolved organic N (DON) may also increase TN:TP ratios. In a large study (348 watersheds) of organic N in runoff, 50% of exported N from forested watersheds was in the form of DON, and the bioavailability of this DON was only ~20% (24). Given that the Flathead Lake watershed is mostly forested, we expect DON to represent a large fraction of TN loading as well. While data needed to estimate DON contributions are lacking in the long-term record, assessments from spring 2021 indicate that DON contributed 49% to TN concentrations in river water, higher than nitrate (37%), a highly bioavailable form of N. Furthermore, dissolved organic P (DOP) carried by Flathead's inflows may be more bioavailable than its DON, as for rivers entering the Baltic Sea (75% of DOP bioavailable vs. 30% for DON) (25). Thus, riverine inputs of relatively refractory DON may allow N to accumulate in the lake. Unfortunately, long-term data on the relative bioavailability of DON and DOP in river loading to Flathead Lake are not available. High lake TN:TP ratios, despite comparatively low N:P ratios in river discharge, may also be explained if low river N:P ratios are offset by contributions from high N:P nutrient sources, such as atmospheric deposition to the lake surface. Atmospheric deposition in this region does have a high N:P ratio (~50:1) and has been an increasing contributor to the lake's nutrient budget (26). Furthermore, most of the deposited N is in the form of highly available NH_4^+ , and direct aerosol deposition to lake surface waters may make it an important nutrient source of N during summer periods of low river discharge (26). Nevertheless, this direct deposition constitutes <10 and 4% to the lake's overall N and P inputs, respectively (26), and thus is unlikely to have a major influence on the overall nutrient regime. Thus, we hypothesize that in-lake processes are primarily responsible for the maintenance of Flathead Lake's imbalanced N:P stoichiometry.

These in-lake processes might include N_2 fixation. While taxa of cyanobacteria capable of N fixation are present in both the phytoplankton and periphyton of Flathead Lake (27), direct measurements of N fixation for the lake are lacking. Nevertheless, even relatively low rates of N fixation would accumulate in the lake's N inventory if rates of denitrification are also low, as would be expected, given that the entire water column and even upper sediment layers are well oxygenated year-round. Sedimentation processes might also contribute to high TN:TP in the water column of Flathead Lake, as particulate P contributes a greater fraction (~39 to 49%) of water column TP than particulate N contributes to TN (18%). Since particle-bound

nutrients sink but dissolved forms do not, sedimentation might differentially remove P relative to N from the water column, raising overall TN:TP ratios. Another internal process that might amplify or mitigate stoichiometric imbalance is eddy diffusion of nutrients from the hypolimnion into surface waters during stratified periods. To assess this, we examined N:P ratios in hypolimnetic (90 m) pools during summer for 2018 to 2020. These ratios were also high (TN:TP of 137:1 and dissolved inorganic nitrogen: soluble reactive phosphorus of at least 190:1), implying that internal resupply of nutrients to surface waters would further reinforce stoichiometric imbalance and potential P limitation in the lake. These hypothesized internal processes contributing to the high TN:TP ratios observed in Flathead Lake require investigation but are consistent with a recent global analysis of 573 lakes (28) indicating that deep lakes (in which mean depth exceeds summer mixing depth) such as Flathead Lake have high TN:TP ratios and, thus, more potential for P limitation of phytoplankton growth because of increased efficiency of P sedimentation and diminished influence of benthic denitrification.

Consequences at the Ecological Level: Phytoplankton Nutrient Limitation. Regardless of its underlying causes, what are the ecological consequences of Flathead Lake's sustained highly imbalanced TN:TP ratios? We do not have continuous long-term data on summer phytoplankton nutrient limitation or C:N:P stoichiometry of seston (suspended particulate matter) in Flathead Lake. However, high in-lake TN:TP ratios could cause phytoplankton P limitation (12), at least in summer when light intensities are high, potentially leading to high C:P and N:P ratios in lake seston. Consistent with this possibility, nutrient enrichment bioassays performed in early to midsummer 2018 and 2019 show evidence of phytoplankton growth response to addition of P alone, with larger responses to combined N and P enrichment but no significant response to the addition of N alone (Fig. 3). According to a taxonomy of $\text{N} \times \text{P}$ enrichment experiment outcomes (29), these results would be consistent with serial N&P limitation, with P as the primary limiting nutrient during these summer months. Unfortunately, experiments testing N versus P limitation of phytoplankton in Flathead Lake are quite limited for earlier periods relevant to our study. Nevertheless, a set of $\text{N} \times \text{P}$ enrichment experiments similar to ours were performed in 1987 and 1988 (30, 31). While these found no response of chlorophyll-*a* concentrations to enrichment with P alone (in contrast to our results for three of six experiments; Fig. 3A), they did demonstrate significant stimulation by combined N&P enrichment, consistent with the strong response to combined N&P enrichment that we observed in all six of our experiments. These midsummer bioassays support a primary P limitation of phytoplankton during this period; however, we note that the N:P ratio of dissolved organic nutrients in lake must be quite high since particulate N:P is generally lower than TN:TP, even after inorganic N (nitrate) is depleted as summer progresses (*SI Appendix*, Fig. S1). This observation suggests differential accumulation of organic N pools (relative to P) that are not bioavailable. Thus, N&P colimitation or even N limitation of phytoplankton growth seems possible once pools of available N (NO_3^-) are depleted by late summer (see Fig. S1 in *SI Appendix*). That N can colimit phytoplankton growth is supported by our experimental results that show a consistent secondary stimulation when N is added along with P (Fig. 3), suggesting that, concordant with our inferences about river-borne DON, much of the lake's DON is also not readily bioavailable. In fact, during

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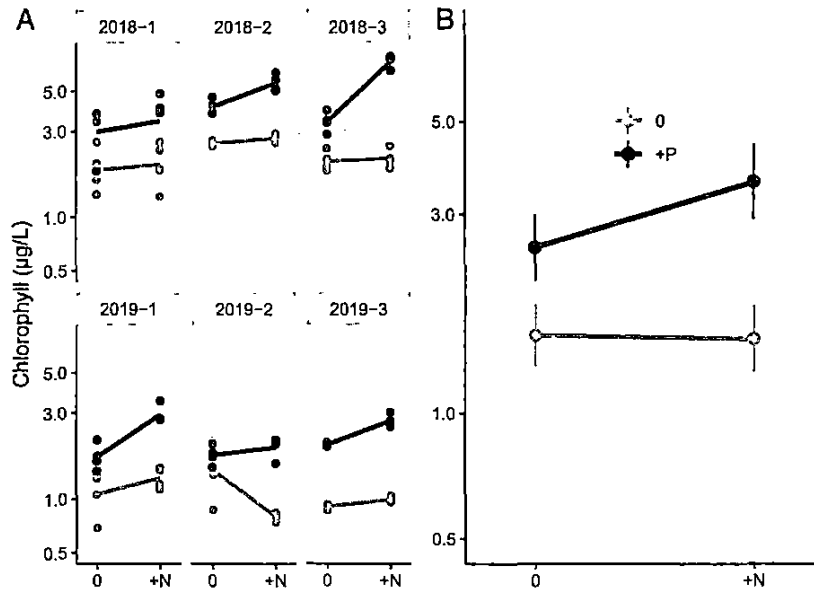


Fig. 3. P primarily limited Flathead Lake phytoplankton growth during summer, as estimated from factorial enrichment of N and P in six 5-d experiments testing response of chlorophyll-*a* concentration. (A) Raw data for three experiments in 2018 (Expt 1: 18 June; Expt 2: 2 July; Expt 3: 9 July) and 2019 (Expt 4: 24 June; Expt 5: 1 July; Expt 6: 8 July) (note log transformation of y axis). Lines connect means of the +P treatments. (B) Predicted values based on a mixed-effects linear model, with intercept as a random effect and N and P effects as fixed for all data combined. Model structure is $Y_{ij} = \beta_0 + \beta_1 N_{ij} + \beta_2 P_{ij} + \beta_3 N_{ij} P_{ij} + e_{ij}$ where Y_{ij} is ln (chlorophyll-*a* concentration) in replicate i in experiment j . N_{ij} and P_{ij} are dummy variables for N and P addition, and e_{ij} is independent and identically distributed error. Parameter estimates (\pm SE) are P effect, $\beta_2 = 0.49 \pm 0.067$; N effect, $\beta_1 = 0.02 \pm 0.067$; and NP interaction, $\beta_3 = 0.39 \pm 0.096$. Overall, P addition increased chlorophyll-*a* when added alone or with N, but N addition only had an effect when added with P (B).

summer (June to September 2016 to 2021), DON contributed an average of 68% of TN in lake surface waters (DOP contributed 56% of TP). A contributing role of N in colimiting phytoplankton growth in oligotrophic Flathead Lake, despite its high TN:TP ratios, is consistent with earlier comparative analysis indicating that the N:P ratio at which phytoplankton growth shifts to primary P limitation is higher at low nutrient levels (32). Consistent with the lake's overall high TN:TP ratios and our bioassay data indicating that early to midsummer (June to July) phytoplankton growth is P limited, seston C:P and N:P ratios (Fig. 4) were also consistently high (>300:1 and >30:1, respectively) in the lake's surface layers during summer. Indeed, epilimnetic seston C:P ratios reached as high as 490, consistently surpassing the threshold elemental ratio for P limitation of the important herbivore *Daphnia* (~200 to 300; ref. 33).

Consequences for Trophic Interactions: Food Quality for Zooplankton. High C:P and N:P ratios such as those in Flathead Lake seston indicate potential P limitation of animal growth (34), but it remains unclear if such stoichiometric food quality limitations operate at low food concentrations (35) such as those in Flathead Lake (Fig. 4A). To test to what extent these high seston C:P ratios impose P limitation on *Daphnia* despite low overall food concentrations, we performed growth experiments involving manipulations of both lake seston concentration and C:P ratio (see *SI Appendix* for details) in summer 2019. In short, we incubated seston from the epilimnion of Flathead Lake (after screening out zooplankton as well as phytoplankton larger than 45 µm that are less edible for *Daphnia*) with or without PO_4^{3-} enrichment for several days, allowing P uptake to lower seston C:P ratios and to increase seston biomass concentrations above low ambient levels. On a daily basis, we then diluted (using filtered lake water) or

concentrated subsamples of that seston to achieve a wide gradient of food concentrations for both control (high C:P ratio) and +P treatments (low C:P ratio). Juvenile *Daphnia* were then grown in these various food concentration and P enrichment treatments using daily transfers for 5 d, after which body growth rate of each animal was recorded. P enrichment of lake seston lowered seston C:P ratios (from ~280 to 591 in control seston to ~83 to 104 in enriched seston) and improved growth of *Daphnia* across all food concentrations (Fig. 5). While vertical migration into deeper water to feed on seston with lower C:P ratios (Fig. 4B) might ameliorate this food quality effect, the current dominant daphnid in the lake, *Daphnia thorata*, prefers warmer waters and tends to remain in the upper 5 to 10 m (36). Together with phytoplankton bioassay results, these findings support the idea that imbalanced N and P ratios in Flathead Lake are associated with P limitation in the food web at both the first and second trophic levels, affecting filter-feeding *Daphnia* with potential impacts on its roles in modulating water quality (37) and transferring primary production to higher trophic levels. One implication of our data is that a more stoichiometrically balanced nutrient regime in the lake, achieved perhaps by adding N removal to wastewater treatment in the basin or by mitigating atmospheric N deposition, might alleviate P limitation; lower seston C:P ratios; and, thus, increase *Daphnia* abundances, imposing stronger water column filtering and further increasing the lake's already considerable water transparency.

Biogeochemical Consequences: Aerobic Methane Production. We also assessed whether the strong stoichiometric imbalance in Flathead Lake was associated with potential for aerobic production of methane via metabolic processing of methylphosphonates by P-limited lake microbes. Consistent with these mechanisms, experimental addition of MPn (together with nitrate and glucose)

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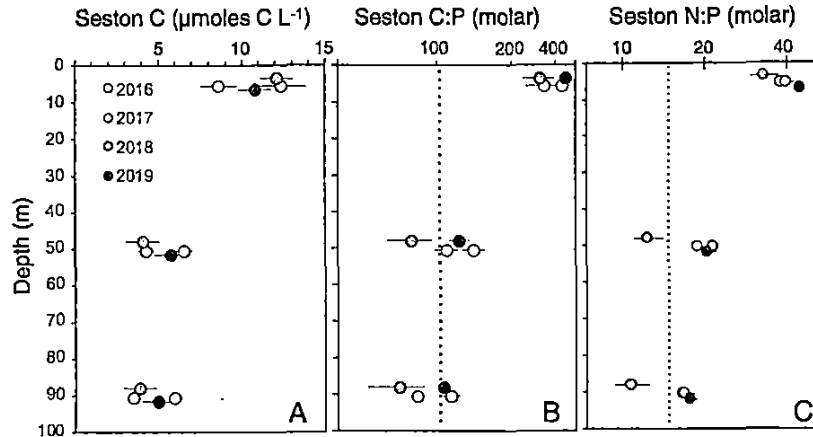


Fig. 4. (A–C) Average (A) seston C concentrations and (B) C:P and (C) N:P ratios (molar) at 5-, 50-, and 90-m depth during summer (June to mid-September) 2016 to 2019. Error bars indicate one SEM of five sampling dates within each year. Note that x axes in B and C are natural log-transformed. The gray bar in B indicates the range of values (200 to 300) for the threshold elemental ratio, above which *Daphnia* P limitation is predicted to occur. The dotted lines in B and C indicate the Redfield ratios for C:P (106) and N:P (16), respectively.

to epilimnetic water from Flathead Lake strongly stimulated methane production (Fig. 6), but this stimulation was suppressed when PO_4^{3-} was added to satisfy microbial P demand. These findings support the view that the high N:P stoichiometric ratios in Flathead Lake and associated P limitation could induce aerobic methane production, providing a feedback between lake nutrient stoichiometry and dynamics of this greenhouse gas. While P-sensitive aerobic methane production via phosphonate metabolism has been observed in oligotrophic Lake Saiko in Japan (18) and in mesotrophic Yellowstone Lake in the United States (38), data are needed from eutrophic lakes to establish the broader significance of our findings from oligotrophic Flathead Lake. However, it is likely that conventional anaerobic pathways of methane production dominate in eutrophic lakes due to oxygen depletion driven by high rates of organic matter production and burial.

Implications. Taken together, our observations indicate that strong imbalances in lake N:P stoichiometry can be sustained over long periods and that this imbalance can have a variety of ecological consequences. While high N:P ratios in Flathead Lake primarily reflect natural processes occurring in the lake

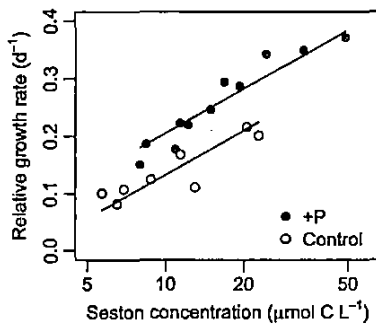


Fig. 5. *Daphnia* relative growth rate (g) response to seston concentration depended on both seston concentration and seston C:P ratio in Flathead Lake. Regression model was $g = -0.123 + 0.256 \ln(C) + 0.073P$ ($R^2 = 0.92$), where C is the seston concentration, and P is a categorical value contrasting the control and P-enriched treatments. That is, this model showed that P enrichment of seston increased growth rate by 0.073 d^{-1} (CI 0.40 to 0.98 d^{-1}) compared to unenriched seston, independent of food quantity. Note log-scaled x axis.

and in its relatively undisturbed watershed, our findings are timely given that various human activities can also accentuate or attenuate stoichiometric imbalances in aquatic ecosystems. For example, rapid population expansion, sewage inputs, and fertilizer use in China during recent decades lowered N:P ratios in its freshwater ecosystems (39). However, subsequent implementation of advanced wastewater treatment in China has counteracted those tendencies, leading to increasing TN:TP ratios (40). Increases in TN concurrent with decreases in TP have occurred in the Laurentian Great Lakes in recent decades and are attributed to implementation of P controls within the 1978 Great Lakes Water Quality Agreement (41). Similar processes also affect nutrient regimes in coastal oceans. Burson and colleagues (42) demonstrated strong declines in inorganic N:P ratios as well as seston N:P ratios moving offshore as phytoplankton nutrient limitation shifted from P limitation inshore to N limitation offshore in the North Sea. They attributed this pattern of inshore P limitation to high N:P ratios in river inflows due to anti-eutrophication efforts in northern Europe, which together have differentially reduced P relative to N supply to this ecosystem. In particular, PO_4^{3-} detergent bans and advanced wastewater treatment have effectively removed P, while N inputs from agricultural fertilizers have increased, and those from atmospheric deposition have declined only modestly. These shifts have likely affected phytoplankton community composition, toxin production during harmful algal blooms, and trophic interactions in coastal areas of the North Sea (42). Finlay et al. (43) have also linked P reduction to accumulation of N in lakes, resulting in stoichiometric imbalance in lake N:P ratios. While the mechanisms of this outcome are not completely established, Finlay et al. hypothesized that decreases in P availability (possibly due to mitigation of P pollution) weaken the ability of lakes to assimilate N and convey it to microhabitats (such as benthic sediments) for denitrification.

Our data on nutrient limitation of phytoplankton, seston C:N:P stoichiometry, and food quality for *Daphnia* provide direct evidence for some of the potential consequences of sustained decoupling of P and N proposed by Finlay et al. (43). While our food quality experiment in Flathead Lake (Fig. 5) highlights the role of stoichiometric constraints in a low-nutrient system, as seen in previous experiments (14, 34), food quality impacts of high seston C:P likely operate also in

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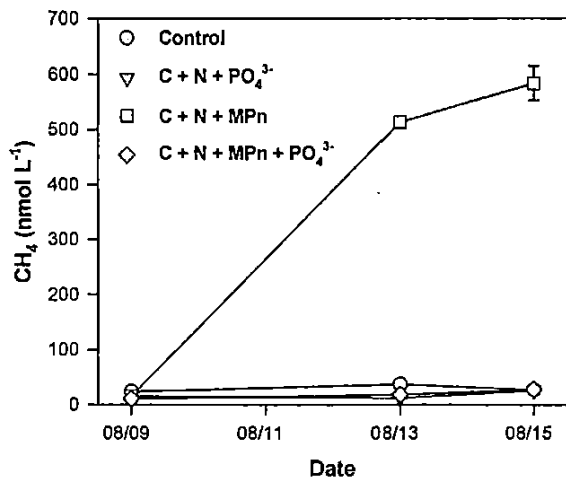


Fig. 6. Time-course experiment showing phosphate suppression of methane production by planktonic methylphosphonic acid use in Flathead Lake (August 2018). Experimental treatments were unamended (circles) or amended with 106 $\mu\text{mol C L}^{-1}$ as glucose, 16 $\mu\text{mol L}^{-1}$ nitrate (as a source of N), and either 1 $\mu\text{mol L}^{-1}$ PO_4^{3-} (triangles), 1 $\mu\text{mol L}^{-1}$ MPn (squares), or 0.5 $\mu\text{mol L}^{-1}$ PO_4^{3-} + 0.5 $\mu\text{mol L}^{-1}$ MPn (diamonds).

mesotrophic and eutrophic lakes, as shown in earlier work (44, 45). Furthermore, our finding that imbalanced N:P stoichiometry in Flathead Lake is accompanied by the potential for aerobic methane production is also important, given that inland waters contribute ~50% of global methane inputs to the atmosphere (46). While most aquatic methane flux derives from anaerobic processes that, themselves, are amplified by P-driven eutrophication (47), our data raise the possibility that aerobic methane production may be accentuated by establishment of high N:P ratios in lakes and other aquatic ecosystems. Overall, we propose that while much attention has been productively focused on processes that sustain or disrupt a lake's overall nutrient concentrations and thus its trophic status, aquatic scientists should also seek to better document and understand the stoichiometric status of aquatic ecosystems, given the various consequences that sustained imbalance in N:P stoichiometry can impose. Our data on impacts of high N:P ratios pertain to the oligotrophic conditions of Flathead Lake; the relevance of these impacts in more nutrient-rich lakes requires further assessment. Nevertheless, given that human interventions now dominate both the N and P cycles (1), we contend that management of nutrients informed by stoichiometric understanding will be of increasing importance during the Anthropocene (6, 43, 48, 49). Nutrient balance matters.

Materials and Methods

Study Site. Flathead Lake is located in northwestern Montana (47.902° N, -114.104° W). The lake is fed by the Flathead and Swan Rivers (along with other minor tributaries, <5% total load) and flows out to the Flathead River. The lake has a short residence time (~2.2 y). Lake water level is held at a stable elevation (881 m above sea level) throughout the summer months by operation of a dam at the outlet; however, lake elevation can vary by as much as 3 m on an annual cycle. At full pool, the mean depth is 39 m, and the maximum depth is 105 m. Much of Flathead Lake's watershed lies in Glacier National Park and adjacent wilderness areas (33%) and in managed national forest land in the United States and Canada (28%), while the remainder of the watershed (39%) lies in intermountain lowlands (prairie, pasture, farmlands, and expanding urban and suburban land use). The current year-round population in Flathead County (the largest in the watershed) is ~104,400. In addition, the area experiences considerable and expanding tourism visitation, especially in summer. Midsummer

water transparency (Secchi depth) ranges from 10 to 15 m, and epilimnetic chlorophyll-*a* concentrations are consistently less than 3 $\mu\text{g L}^{-1}$ during the period of record (37). Nutrient concentrations are summarized in the main text. The lake's upper food web is dominated by introduced fish species, especially lake trout (*Salvelinus namaycush*), whose abundance has increased following invasion by *Mysis diluviana* (opossum shrimp) in the early 1980s (37).

Lake Monitoring and Nutrient Loading.

Lake monitoring. The Flathead Lake Monitoring program has regularly measured physical, chemical, and biological parameters at the deepest point of the lake (Midlake Deep) and in tributaries since 1977. Dissolved and total nutrient concentrations were measured ~15 times per year at Midlake Deep and each of the major lake tributaries. Nutrient concentrations were determined using standard colorimetric segmented flow methods with alkaline persulfate digestions to assess organic pools. Samples for dissolved nutrient analyses (total dissolved P, $[\text{NO}_2^- + \text{NO}_3^-]\text{-N}$, $\text{NH}_4^+\text{-N}$) were filtered to 0.45 μm , while total nutrient concentrations were determined on unfiltered water samples. In addition, a limited set of samples were assessed for total dissolved N. Detailed methodology and metadata regarding the Flathead Lake Monitoring program's sampling and analysis protocols are available on the Flathead Lake Biological Station (FLBS) Public Data Portal (<https://flbs.umt.edu/PublicData>) and have been described previously in the literature (26, 37, 50). River discharge data were obtained from the United States Geological Survey's National Water Information System for both the Flathead River (USGS 12355500) and the Swan River (USGS 12370000) gauges.

Close inspection of the time series of nutrient chemistry in the lake called attention to a potentially anomalous period in the data for TP concentrations (beginning 2013); this period coincided with a change in the analytical methods used to measure the time series P pools. Beginning in July 2013, the colorimetric P determinations shifted to include a correction for potential silica interference (*SI Appendix*). The lack of silica correction in the pre-2013 analysis led to an overestimation of TP concentrations by 1.6 $\mu\text{g L}^{-1}$ (51.6 nmol L^{-1}) in lake samples and an Si-proportional overestimate of P in river samples. Hence, for this study, we transformed data prior to 2013 accordingly (see *SI Appendix* for details). Because TP levels in river samples were relatively high, the Si correction did not have a large effect on estimates of riverine TP loading, but the 51.6 nmol L^{-1} correction of lake TP concentrations for the early periods represented a ~25 to 30% reduction in values reported for this observation period. Corrected data are displayed in Figs. 1 and 2. See *SI Appendix* for additional information.

Nutrient concentration time series. Generalized additive models (GAMs) and mixed-effect models were used to identify trends for unaggregated Midlake Deep nutrient concentrations through time. Additive models are used because the Flathead Lake Monitoring program dataset time series contains missing data, has intermittent changes in the frequency of and intervals between sampling events, and likely has autoregressive tendencies that preclude standard linear models (51). Models included a random effect parameter accounting for the month sampled, thus preserving inherent variation due to seasonality or variable sampling frequencies throughout the dataset. To examine trends in the long-term time series data, GAMs were constructed with the R package *mgcv* structured with concentration as a function of date with a splining smoother term. Model optimization (i.e., the number of nodes used in the smoothing function) was based on a restricted maximum likelihood estimate approach. Models were assessed (52) using the package *mgcv* in R (53).

Nutrient loading time series. Annual loads of TP and TN were estimated using the *rloadest* and *loadflex* packages (54) in R (55). *rloadest* is based on the USGS LOADEST program (56), and *loadflex* allows for composite models accounting for variation in concentration to hydrograph relationships through time. These packages were used to estimate loads based on time series data of hydrologic regimes and nutrient concentrations. Total mass daily loadings were estimated and summed to calculate the annual load for the entirety of the Flathead Lake Monitoring program dataset. Models were automatically selected based on maximum likelihood estimation or least absolute deviation when residuals were not normally distributed. The TN:TP ratio was calculated daily and averaged annually. GAMs were then used to assess patterns of change in nutrient concentrations, loading, and stoichiometric balance through time as indicated above.

P-0043155

Nutrient Enrichment Experiments. Six *in situ* incubation experiments were performed to test for nutrient (N, P) limitation of phytoplankton growth via factorial enrichment of N and P in June and July of 2018 and 2019. All water samples were collected from Yellow Bay, a deep embayment on the eastern side of the lake. Water was collected along a 5-m column using an integrated tube sampler (2018) or a Kemmerer sampler (2019) at four random sites within Yellow Bay. All samples were filtered through a 125- μm Nitex mesh to remove macrozooplankton prior to enrichment. Initial water samples were reserved to determine the initial chlorophyll-*a* concentrations.

For each factorial N \times P experiment, 16 clear 500-mL bottles were rinsed and then filled with water from Yellow Bay, four each for a control (C), N, P, and a combined NP treatment. The N and P treatments were 8 $\mu\text{mol L}^{-1}$ N (equimolar as $\text{NH}_4\text{Cl} + \text{NaNO}_3$) and 0.5 $\mu\text{mol L}^{-1}$ P (as Na_2HPO_4), respectively, while the N&P treatment received both 8 $\mu\text{mol L}^{-1}$ N and 0.5 $\mu\text{mol L}^{-1}$ P enrichment (16:1 atomic ratio). In 2019, bottles used in experiments 2 and 3 all received the same level of potassium (K) as part of a separate study. All bottles were suspended at a depth of 1.5 m (equivalent to $\sim 50\%$ of incident light) in Yellow Bay. After 4 d, 250 mL from each bottle were filtered onto a glass fiber filter (Whatman GF/F) that was frozen until extraction. Chlorophyll-*a* was extracted by holding filters in the dark at 4 $^\circ\text{C}$ for 12 to 24 h in either methanol or 90% acetone. Extracts were analyzed following EPA method 445.0 (57) using a Turner Designs fluorometer and a hydrochloric acid correction for phaeophytin.

We estimated the effect of N, P, and N&P additions in multiple experiments by fitting a random intercept model predicting chlorophyll-*a* concentration for replicate *i* in experiment *j* (chl_{ij}) with slopes for N, P, and N&P as fixed effects. Values for N and P were 0 if not added and 1 if added. This model was

$$\log(\text{chl}_{ij}) = \beta_0 + \beta_1 N_{ij} + \beta_2 P_{ij} + \beta_3 N_{ij}P_{ij} + e_{ij}$$

where e_{ij} is normally distributed error. We fit this model using *lmer()* in package *lme4* in R.

Daphnia Food Quality Experiments.

Seston manipulation. We used a 5-L Van Dorn horizontal water sampler to collect lake water from depths of 0.5, 3, 5, and 6 m in Yellow Bay. Water was combined into a single sample, passed through a 45- μm nylon net to remove zooplankton and phytoplankton inedible to *Daphnia*, and transferred to 20-L polycarbonate carboys. We conducted two experiments (21 August and 16 September 2019) to assess *Daphnia* growth at different food concentrations for ambient seston (high C:P ratio) and for P-enriched seston with low C:P ratio. In both experiments, food (seston) quantity and quality were manipulated by enriching N to 0.45 $\mu\text{mol L}^{-1}$ (as NaNO_3) to control carboys and P to +0.16 $\mu\text{mol L}^{-1}$ and +0.5 $\mu\text{mol L}^{-1}$ P (as K_2HPO_4) in the first experiment and +0.48 $\mu\text{mol L}^{-1}$ P in the second experiment to P-enriched carboys. Carboys were then placed in an outdoor incubator circulated with surface lake water to maintain temperature. The incubator reduced light intensity to 30% of ambient levels using blue Plexiglas shading. The carboys were held for 3 to 5 d to allow seston concentration to increase before the start of the *Daphnia* growth experiment, allowing us to examine animal growth with high and low seston C:P and covering a range of food concentrations after dilution (see below).

Seston C:P ratio and concentration. Seston C concentrations and C:P ratios in both the lake and the carboys were measured daily. Seston was filtered onto pre-combusted and acid-washed Whatman glass fiber filters (GF/F grade), dried for at least 24 h at 60 $^\circ\text{C}$, and then digested using modified persulfate oxidation followed by infrared detection (for C measurement) and the ascorbic acid method (for P measurement) (58). In the first experiment, seston concentration for each treatment carboy was measured daily by filtering seston onto a GF/F filter and measuring C concentration prior to dilution with filtered lake water (see below). In the second experiment, seston concentration in each individual jar used for animal growth was estimated daily by measuring turbidity (using a Hach 2100N turbidimeter) and then converting the turbidity measurement to C concentration based on a previous calibration.

Food concentration gradient preparation. In the first experiment, gradients of three food concentrations were established for seston from the control, +0.16 $\mu\text{mol L}^{-1}$ P, and +0.5 $\mu\text{mol L}^{-1}$ P treatments. For all the treatments, food concentrations were set at 25, 50, and 100% of the actual *in situ* concentration and prepared by diluting ambient seston (100%) with Whatman GF/F-filtered (nominal pore size: 0.7 μm) lake water. In the second experiment, gradients of five food concentrations were established for both control and P-enriched

(+0.5 $\mu\text{mol L}^{-1}$ P) seston. For the P-enriched treatments, food concentrations were set at 6.25, 12.5, 25, 50, and 100% of the initial concentration. For the control treatment, food concentrations were lower, and, thus, levels of seston were set at 12.5, 25, 50, 100, and 200% of the initial concentration in the carboy. To prepare these treatments, a 5- μm Nitex net was used to concentrate seston from the control carboy to 200% of the ambient level, and then the resulting concentrated seston preparation was diluted to different target concentrations with Whatman GF/F-filtered water. For the enriched treatment, food concentration gradients were prepared by diluting ambient seston (100%) with GF/F-filtered water. **Daphnia culture.** A population of *Daphnia pulex* isolated from Flathead Lake was maintained in the laboratory in modified COMBO media (59) on a diet of nutrient-sufficient *Scenedesmus acutus*. Adult *Daphnia* were separated from the main culture to produce offspring used in the experiments. Neonates were collected between 24 and 48 h in age, imaged for initial body size using a digital camera on a dissecting microscope, and placed individually into 60-mL glass vials with 60 mL prepared seston (see above). Each food treatment had eight replicate animals for the first experiment and seven replicates for the second experiment. Vials were kept on a rotating plankton wheel to prevent food particles from settling. The wheel was kept inside a growth chamber at 19 to 20 $^\circ\text{C}$ with continuous illumination. Every day, animals were transferred individually into freshly prepared seston. The experiments ran for 5 d, after which animals were individually reimaged. Relative growth rate (*g*) of each *Daphnia* was calculated from the pre- and postexperiment body sizes as $g (\text{d}^{-1}) = \ln(S_2/S_1)/\text{dt}$, where *S* is individual body area at beginning (S_1) and end (S_2) of the experiment, and dt is the duration of the experiment (5 d).

Data analysis. In the first experiment, daily measurements of seston concentration in each jar were averaged across all replicates for that food concentration treatment, and the resulting mean 5-d seston C concentration was used for analysis of *Daphnia* relative growth rate. In the second experiment, daily measurements of seston C concentrations of each treatment were averaged and used in analysis. Examination of data indicated that P enrichment resulted in similar C:P ratios in the two experiments and that growth rate data for the two experiments also collapsed onto a similar response function with seston C concentration. So, data for the two experiments were combined for comparison of growth rate of animals fed P-enriched seston with growth data for animals receiving unenriched seston, while controlling for seston concentration.

To do so, we fit the following regression model to the data:

$$g = \beta_0 + \beta_1 \log(C) + \beta_2 P + \varepsilon \quad [1]$$

where *g* is relative growth rate, *C* is seston concentration (log transformed to facilitate linearity), *P* is a dummy variable designating P-enriched or control treatments, and ε is normally distributed error. This model assumes a variable intercept and a common slope and is equivalent to an Analysis of Covariance without an interaction term. Models with an interaction term (i.e., $\beta_3 \log(C) \times P$) had $P = 0.07$ for β_3 and Akaike information criterion values three units higher than obtained for Eq. 1, indicating an overfitted model.

Methane Experiment. A time-course experiment to examine potential plankton production of CH_4 based on the use of MPn was conducted in August 2018. Near-surface Flathead Lake water was collected into four 20-L polycarbonate carboys and transported to the laboratory. In the laboratory, carboys were amended with treatment-specific nutrient substrates (glucose, N, P, and MPn). Experimental treatments were compared to unamended lake water controls. Nutrients (final concentrations) were added as C + N + $\text{PO}_4^{3-} = 106 \mu\text{mol L}^{-1}$ C (as glucose) + 16 $\mu\text{mol L}^{-1}$ NO_3^- (as NaNO_3) + 1 $\mu\text{mol L}^{-1}$ PO_4^{3-} (as Na_2PO_4); C + N + MPn = 106 $\mu\text{mol L}^{-1}$ C (as glucose) + 16 $\mu\text{mol L}^{-1}$ NO_3^- + 1 $\mu\text{mol L}^{-1}$ MPn; C + N + MPn + $\text{PO}_4^{3-} = 106 \mu\text{mol L}^{-1}$ C (as glucose) + 16 $\mu\text{mol L}^{-1}$ NO_3^- + 0.5 $\mu\text{mol L}^{-1}$ MPn + 0.5 $\mu\text{mol L}^{-1}$ PO_4^{3-} . Water was subsampled from each carboy into 160-mL glass serum bottles, and bottles were crimp-sealed with Teflon-lined silicone stoppers. Incubations were conducted at *in situ* temperatures in the dark. Triplicate serum bottles from each treatment (and control) were harvested at each sampling time point for quantification of CH_4 concentrations as described above. Samples were killed by injecting 200 μL of an 8 M NaOH solution and analyzed by gas chromatography via headspace (20 mL) gas introduction.

Data Availability. All observational and experimental data (water chemistry, loading, nutrient limitation, *Daphnia* growth, methane production) have been deposited via Dryad (<https://datadryad.org/>) at doi:10.5061/dryad.hdr7sqkw (60).

P-0043156

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Socioeconomic resilience to climatic extremes in a freshwater fishery

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Heterogeneity is a central feature of ecosystem resilience, but how this translates to socioeconomic resilience depends on people's ability to track shifting resources in space and time. Here, we quantify how climatic extremes have influenced how people (fishers) track economically valuable ecosystem services (fishing opportunities) across a range of spatial scales in rivers of the northern Rocky Mountains, USA, over the past three decades. Fishers opportunistically shifted from drought-sensitive to drought-resistant rivers during periods of low streamflows and warm temperatures. This adaptive behavior stabilized fishing pressure and expenditures by a factor of 2.6 at the scale of the regional fishery (i.e., portfolio effect). However, future warming is predicted to homogenize habitat options that enable adaptive behavior by fishers, putting ~30% of current spending at risk across the region. Maintaining a diverse portfolio of fishing opportunities that enable people to exploit shifting resources provides an important resilience mechanism for mitigating the socioeconomic impacts of climate change on fisheries.

INTRODUCTION

Ecological heterogeneity is critical for ecosystem resilience and the reliability of ecosystem services (1), especially under accelerating climate change and increasing frequency and intensity of extreme events. Biological and physical complexity within ecosystems and across landscapes (e.g., genes, populations, species, and habitats) have been shown to enhance ecosystem productivity (2), stabilize population dynamics (3–5), and mitigate against abrupt change in natural resource economies (6). In freshwater ecosystems, such heterogeneity interacts with changing environmental conditions to shift productive habitats across space and time, stabilizing the production of biological resources (i.e., fish) at the scale of entire landscapes (1). However, it remains unknown whether people using and benefitting from these dynamic resources adaptively track them across a range of spatial scales and whether such behavior translates to socioeconomic resilience in human communities reliant on fisheries for livelihoods and well-being.

Freshwater fisheries (commercial, subsistence, and recreational) have enormous social, ecological, and economic importance worldwide (7, 8), yet the natural systems that support them (e.g., climate, weather, and ecosystems) are being rapidly transformed by global climate change (9, 10). Shifts in species distributions in response to climate change have been documented for a broad range of organisms (11), especially ectothermic species like fishes that are strongly tied to water temperature (12). Such climate-induced range shifts may change the distribution of fishing opportunities across landscapes, requiring fishers to adapt by catching different species or fishing in new locations (13–15). Globally, extreme climatic events (e.g., droughts, storms, heat waves, and wildfires) are increasing in frequency and severity and may also affect fishing opportunities by affecting fishers' decisions on where and when to fish (16, 17). Although these climatic changes may have important ecological impacts on freshwater

fisheries (18, 19), how these dynamics influence the reliability of fishing opportunities and associated revenues has never been empirically quantified.

Here, we provide an empirical assessment of the impacts of climate change and climatic extremes on freshwater fisheries using an inland trout fishery as a case study. Trout (Salmonidae)—a group of cold-water fishes with substantial ecological and socioeconomic importance—are highly prized by fishers in many parts of the world (20). Fishers travel long distances to pursue trout in streams, rivers, and lakes, often generating substantial revenues for local and regional economies. The northern Rocky Mountains in Montana (USA) support some of North America's most popular trout fisheries, valued at more than US\$750 million year⁻¹ (21) representing more than 20% of the spending by tourism in the state (22). This economic value is primarily driven by nonresident fishers who spend, on average, US\$690 fisher-day⁻¹ compared to US\$90 fisher-day⁻¹ by resident fishers (21). However, the cold-water fisheries that support this substantial tourism industry may be at risk as this region warmed at twice the global average rate over the past century (23), contributing to warmer water temperatures (24), lower summer streamflows (25), and increasing frequency and severity of drought events. These climatic changes are shifting the abundance and distribution of trout species across the region (26–28). The combined effects of these climatic changes may significantly affect popular trout fisheries by shifting both fish and fishers across space, with potentially severe socioeconomic consequences. Therefore, understanding how climate change will affect social, economic, and ecological components of cold-water fisheries will be critical for enhancing resilience and adaptation of fisheries and local communities.

We used an extensive spatiotemporal dataset from more than 5000 km of popular trout rivers in the northern Rocky Mountains (1983 to 2017) to quantify trends and spatial patterns in fishing pressure in response to changing climatic conditions. First, we leveraged historical drought, temperature, and streamflow data to estimate how climate drivers directly affected fishing pressure at the river reach scale (8 to 190 km). We used dynamic factor analysis (DFA) (29) to account for common patterns in resident and nonresident fishing pressure over time that may be due to aggregate social and economic

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drivers while simultaneously estimating the interannual effects of past environmental conditions. Second, we quantified whether aggregating heterogeneous fishing pressure dynamics across river sections stabilized fishing pressure and spending at larger spatial scales (i.e., portfolio effects) (30). Third, we quantified the importance of cold-water habitat by comparing fishing pressure in river sections dominated by cold-water species (i.e., trout) to sections where fish communities were transitioning to cool-water species (e.g., black bass *Micropterus* spp. and walleye *Sander vitreus*). We then used predictions of current and future summer stream temperatures in 2040 and 2080 under an A1B emissions scenario [similar to the Representative Concentration Pathway (RCP) 6.0 emissions scenario] (31) to project how the spatial distributions of cold-water habitat may change and the potential effects on fishing pressure. Last, we estimated the potential economic impacts of future climatic change by combining estimates of current fisher spending with estimated changes in fishing pressure due to the combined impacts of future droughts and losses in cold-water habitats. Our analyses incorporate the direct impacts of climate drivers on fishers (i.e., streamflow and temperature) and the indirect effects of changing temperature on species distributions to comprehensively understand the potential consequences of climate change for these fisheries.

RESULTS

Growth in freshwater trout fisheries

Fisheries across the region experienced rapid growth over the past three decades (Fig. 1A). From 1983 to 2017, total fishing pressure doubled from 0.8 million fisher-days year⁻¹ to more than 1.7 million fisher-days year⁻¹. This growth was primarily due to changes in non-resident fishing pressure, which increased from 0.2 to 0.8 million fisher-days year⁻¹ (280% increase), and, to a lesser degree, resident fishing pressure, which increased from 0.6 to 0.9 million fisher-days year⁻¹ (50% increase). These increases in fishing pressure were not distributed evenly across the region, varying considerably within and across major rivers (Fig. 1, B and C). Nonresident fishing pressure increased across 90% of river sections (~4500 km), and in some of the most popular rivers (i.e., Blackfoot, Bitterroot, and Madison rivers), fishing pressure increased up to 1600% (reaching 13,000 fisher-days km⁻¹ year⁻¹ in some sections), generating substantial spending across the region. Resident fishing pressure also increased in many sections (70%) but experienced pronounced declines across 30% (~1500 km) of river sections (Fig. 1B). This spatiotemporal variation in fishing pressure within and among rivers is the result of complex interactions between many socioeconomic, ecological, and environmental factors affecting fisher behavior.

Effects of changing environmental conditions on fishing pressure

Extreme climate events, particularly drought and its effects on streamflow, strongly influenced the spatiotemporal dynamics of resident and nonresident fishing pressure among rivers (Fig. 2 and fig. S1). Drought had a strong negative effect on fishing pressure for some river sections (herein referred to as drought-sensitive), most notably in the Big Hole River where fishing pressure declined by 127 (24%) and 252 (48%) fisher-days km⁻¹ year⁻¹ under moderate and severe drought conditions, respectively (Fig. 2, D and E). However, for other river sections, fishing pressure increased in drought years (herein referred to as drought-resistant), especially by resident fishers (Fig. 2D).

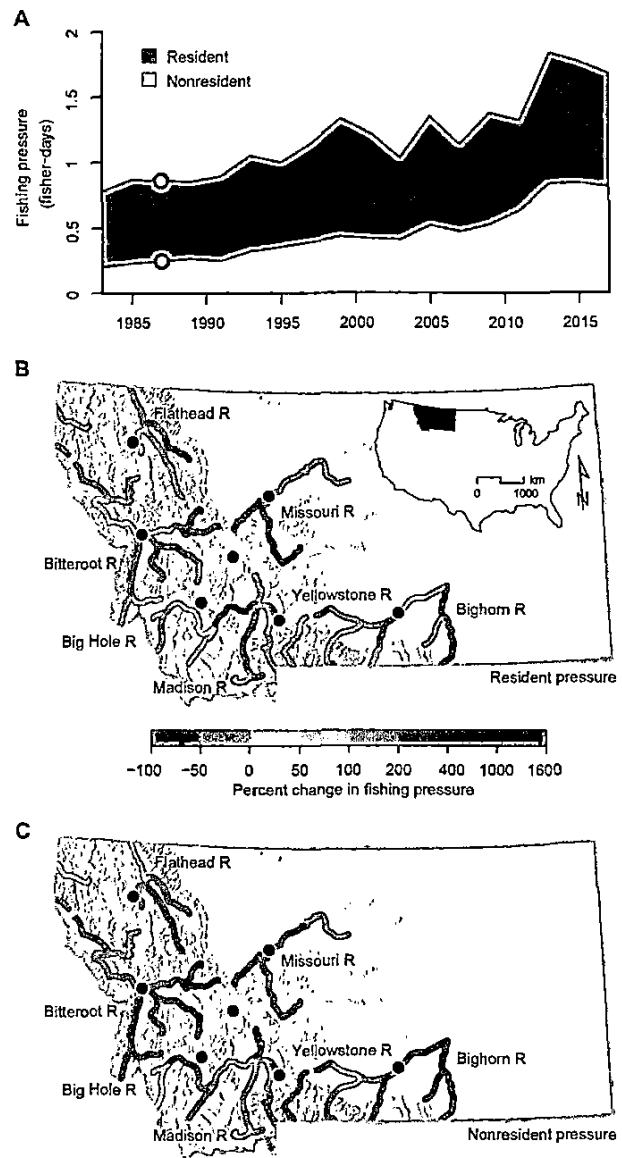


Fig. 1. Changing fishing pressure in freshwater trout fisheries across the northern Rocky Mountains. (A) Changes in total fishing pressure across popular trout rivers in Montana, USA between 1983 and 2017. No survey was conducted in 1987, indicated by open points. Estimates of change in resident (B) and nonresident (C) fishing pressure across river sections. Percent change is measured as the difference between the 1983–1989 surveys and 2013–2017 surveys. Black dots indicate regionally important cities with major airports. Hill shade has been added for geographic context. Note the nonlinear color scale.

Overall, there were more negative effects and greater variation in drought responses among sections for nonresident anglers than residents. The largest positive drought effects occurred in portions of the upper Yellowstone River and in tailwater sections of the Madison, Missouri, and Bighorn rivers (Fig. 2, D and E), where dams influence downstream water temperatures and streamflows. A substantial amount

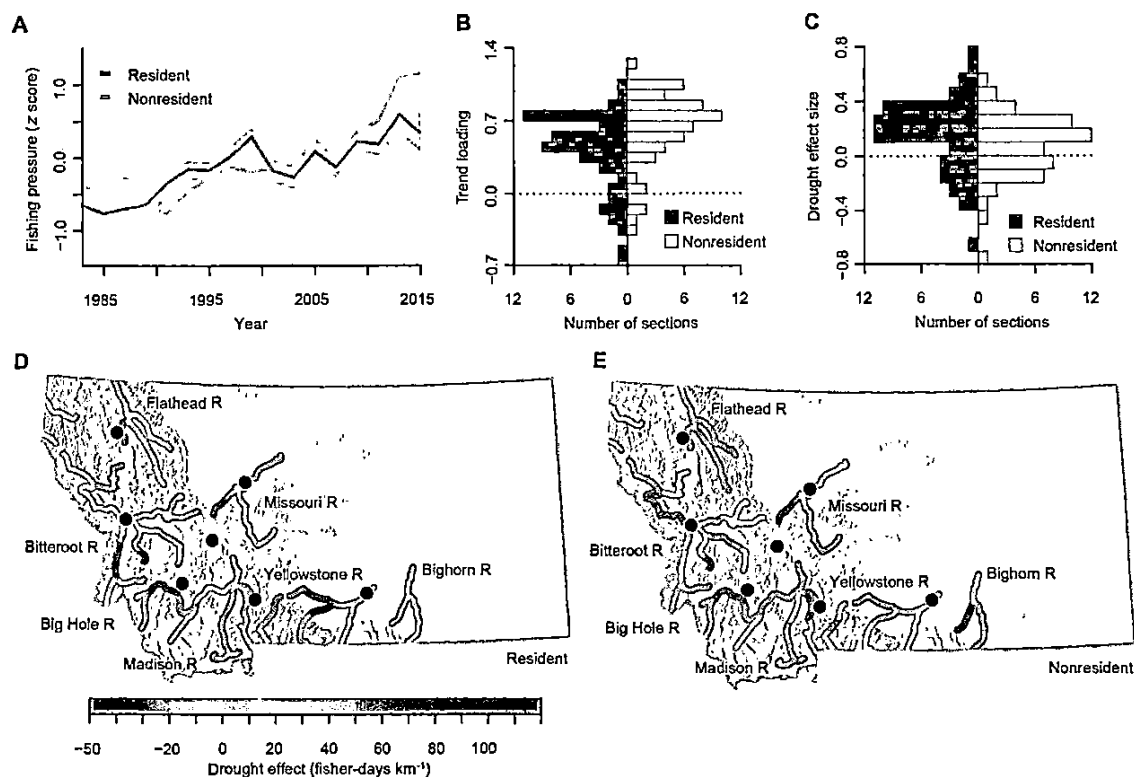


Fig. 2. The effects of drought on fishing pressure across popular trout rivers. (A) Common trends in resident (green) and nonresident (yellow) fishing pressure among river sections through time. Polygons represent 95% confidence intervals. Loadings of individual river sections on common trends. (B) Negative loadings indicate opposite trend. Effects of spring/summer PDSI (C) on resident and nonresident fishing pressure. Spatially explicit drought effects on resident (D) and nonresident (E) fishing pressure across rivers.

of variation in both resident and nonresident fishing pressure was explained by shared trends among river sections (Fig. 2A). These trends probably represent an aggregate of social (e.g., popularity of trout fisheries), economic (e.g., increase in disposable income), and other environmental factors (e.g., effective resource management) that are not explained by drought conditions through time.

Stabilizing portfolio effects

We calculated the stabilizing effect of shifting fishing pressure in space and time (i.e., portfolio effects) by comparing the average interannual variability [coefficient of variation (CV)] in fishing pressure across individual river sections (~60 km on average), rivers (multiple river sections; ~230 km), drainages (multiple rivers within a major river basin; ~770 km), and the region (full study area; ~5400 km; fig. S2). Interannual variation in fishing pressure and spending was greatest in individual river sections (Fig. 3A and fig. S3), but the dynamics among sections were asynchronous through time (synchrony = 0.49; fig. S3). Averaging across these dynamics at increasing spatial scales (i.e., sections, rivers, drainages, and region) dampened the interannual variability in fishing pressure and spending (Fig. 3A and fig. S3). Across the region, fishing pressure was 2.6 times more stable than the average of individual river sections and 3.2 times more stable for fisher spending (Fig. 3B). Furthermore, interannual variability and the strength of portfolio effects differed between nonresident

fishers (3.9) and resident fishers (2.7; Fig. 3B). Overall, these strong portfolio effects increased the reliability of fishing opportunities and fisher spending across the regional fishery. Aggregating fishing pressure at each successive spatial scale decreased interannual variability in fishing pressure and spending by about 25%, demonstrating the importance of portfolio effects occurring across a range of spatial scales.

Transitioning from cold- to cool-water habitats

Cold-water habitats (defined by trout dominance; see Methods) were disproportionately important for fisher use and economic value across the region compared to cool-water sections (defined by fewer trout and the presence of cool-water species; Fig. 4). In recent years, overall fishing pressure was four times higher in cold-water sections than in adjacent cool-water sections and was 10 times higher for nonresident fishers (Fig. 4A). Differences in fishing pressure between cold- and cool-water habitats amounted to substantial differences in fisher spending, with cold-water sections generating US\$500,000 km⁻¹ year⁻¹ and cool-water sections generating US\$60,000 km⁻¹ year⁻¹ (Fig. 4B), primarily due to the preference for cold-water by nonresident fishers.

In cool-water river sections, August water temperatures exceeded 18°C along 90% of their extent (Fig. 4C), a threshold that is consistent with previous research on thermal extremes for trout (32). Using

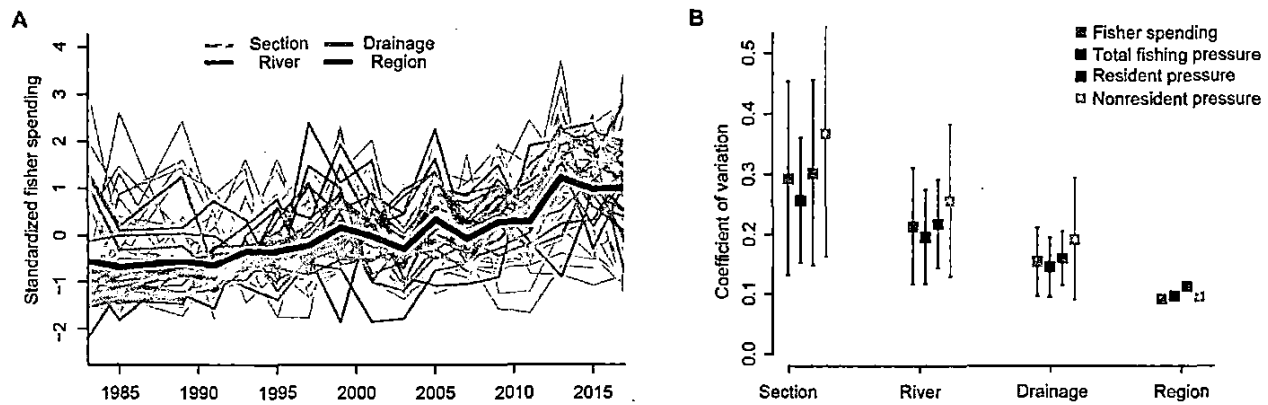


Fig. 3. Portfolio effects stabilize fishing pressure and fisher spending across spatial scales. (A) Estimated fisher spending through time among sections (gray), rivers (blue), drainages (orange), and the region (black). (B) Interannual variability (as measured by the CV; ± 1 SD) in fisher spending (red), total fishing pressure (black), resident fishing pressure (green), and nonresident fishing pressure (yellow) at four spatial scales. See Methods for description of spatial scales.

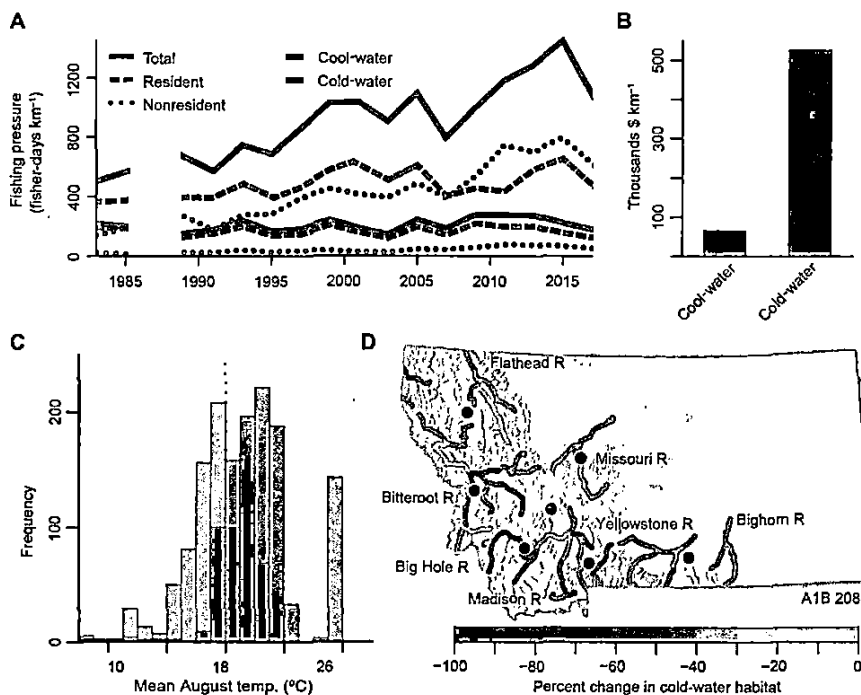


Fig. 4. Cold-water habitats are critical for fishers and economic value. Resident and nonresident fishing pressure over time (A) and economic value (B) of cold- and cool-water habitats (see fig. S7 for map of cold- and cool-water habitats). (C) Water temperature distributions in cold-water (blue) and cool-water (red) habitats. (D) Predicted losses in cold-water habitat by 2080 under A1B emissions scenarios. Dollar values are in 2018 US\$.
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this 18°C threshold to delineate cold- and cool-water habitat, we projected substantial losses in cold-water for most river sections across the region (Fig. 4D). Overall, 17 and 35% of the current cold-water habitat are projected to be warmer than 18°C by 2040 and 2080, respectively (Fig. 4D and fig. S4). However, losses in cold-water habitat were spatially heterogeneous, where some river sections exhibited little change and other sections exhibited losses in excess of 80% by 2080 (e.g., Bitterroot, Big Hole, and Yellowstone rivers; Fig. 4D). Given current fishing pressure distributions and preferences for cold-water

fisheries (Fig. 4A), losses in cold-water habitat availability could reduce fishing pressure by 100 to 800 fisher-days km^{-2} (~20 to 80% reduction in current fishing pressure) in many rivers by 2080 (fig. S5).

Economic impacts of future climate change

The effects of cold-water habitat loss and increased frequency and severity of drought on fishing pressure could result in substantial economic impacts across the region (Fig. 5). Spatial shifts in fishing pressure during past extreme droughts decreased spending in some

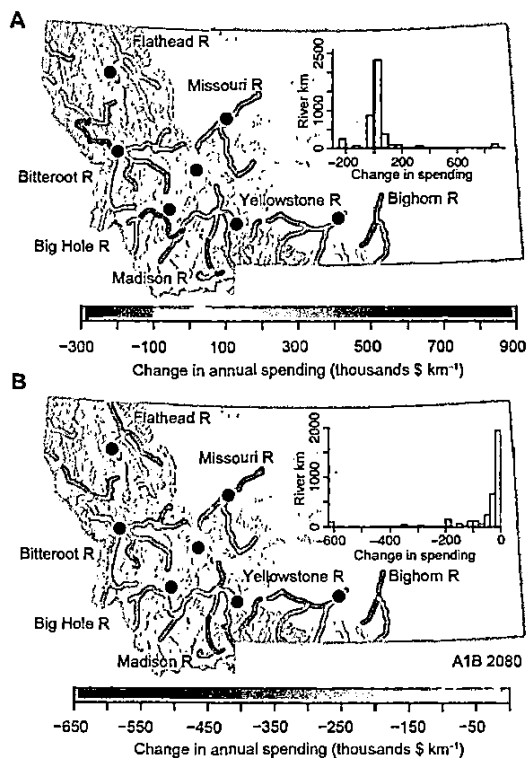


Fig. 5. Economic impacts of extreme drought and future range shifts on cold-water fisheries. (A) Potential shifts in fisher spending across rivers under extreme drought. (B) Changes in annual spending by fishers in response to cold-water habitat losses by 2080 under A1B emissions scenarios. Histograms summarize the distributions presented in each map. Dollar values are in 2018 US\$.

river sections (e.g., US\$150,000 km⁻¹ year⁻¹ in the Big Hole River) and increased spending in others (e.g., US\$600,000 km⁻¹ year⁻¹ in the Madison River; Fig. 5A). In contrast to these variable economic impacts of drought, loss of cold-water habitat is projected to cause widespread economic impacts across this region, with spending projected to decline in 64 and 76% of river sections by 2040 and 2080, respectively (Fig. 5B and fig. S6). Economic impacts were concentrated in southwestern rivers, with sections of the Yellowstone, Madison, Big Hole, and Bitterroot rivers having the largest potential changes in spending as large changes in cold-water habitat intersect with popular fishing areas for nonresident fishers. Decreases in spending of US\$50,000 to US\$100,000 km⁻¹ year⁻¹ were projected across many river sections, with some sections as high as US\$600,000 km⁻¹ year⁻¹. The cumulative impacts of these changes in spending across these rivers could put a total of US\$103 million year⁻¹ (16% of 2017 spending in these rivers) and US\$192 million year⁻¹ (30% of 2017 spending) at risk by 2040 and 2080, respectively.

DISCUSSION

Heterogeneity is a central feature of ecosystem resilience (1, 3, 33), but how this translates into socioeconomic resilience depends on people's ability to track shifting resources in space and time. By integrating long-term fishing surveys and bioclimatic data, we captured

emergent fisher behavior in response to past climate extremes, demonstrating that fishers adaptively moved across the landscape to exploit shifting fishing opportunities, resulting in negligible or even positive changes in regional fishing pressure and expenditures. Heterogeneity in drought responses across riverscapes provided opportunities for fishers to find cold-water fishing refuges in drought-resistant rivers, ultimately stabilizing social and economic components of the regional fishery. However, future climate warming may reduce the diversity of habitats that enable this adaptive behavior. Thus, conserving a diversity of habitats and biological communities across landscapes would promote adaptation and socioeconomic resilience in freshwater fisheries.

Our results indicate that the future loss of cold-water habitats could have substantial impacts on the local and regional economies supported by freshwater fisheries. Projected losses in cold-water habitat under future climate warming may put 30% of current spending at risk by 2080 (US\$192 million year⁻¹), representing 21% of the total annual fishing economy in the region (21). These findings are similar to climate projections from other studies in commercial and recreational fisheries (13, 14, 16, 18). Droughts and associated extreme events (e.g., wildfires and heat waves) will likely exacerbate these impacts for some local economies as fishers avoid poor fishing conditions and management closures. Although there is substantial uncertainty in future climate, adaptation by fishers to changing species distributions, emergence of novel fishing opportunities, and extreme drought conditions, as shown here, may help mitigate future socioeconomic losses in freshwater fisheries.

Despite evidence of socioeconomic resilience to recent climatic variation and extremes, future climate change may erode stabilizing portfolio effects that sustain freshwater fisheries and the livelihoods and well-being they support. Droughts are predicted to increase in frequency, severity, duration, and extent in the future (9, 34), leading to more widespread impacts on freshwater fisheries, including reductions in streamflow, increases in water temperature, altered water quality, and habitat fragmentation (35). The combined impacts of severe drought and losses in cold-water habitats are likely to negatively affect trout populations (e.g., size structure, abundance, and production) and thus may reduce fishing opportunities and the potential for fishers to exploit alternative habitats during poor environmental conditions. Maintaining a diversity of fishing opportunities across the landscape would help to stabilize the ecosystem services that freshwater fisheries provide.

Enhancing socioeconomic resilience in freshwater fisheries under climate change will require a broad suite of proactive and innovative management strategies that conserve habitats and fish populations while simultaneously allowing people to adaptively exploit shifting resources. This will require coordinated efforts at multiple spatial and temporal scales to protect and restore habitat and biological complexity and the processes that generate and maintain it across landscapes (1). In riverine ecosystems, this may include reconnecting rivers with floodplains, restoring geomorphic complexity and connectivity, and sustaining streamflows and cold-water inputs that support productive trout fisheries (36, 37). With increasing demands for diminishing water supplies (38), coordinated and multifaceted water management plans and policies that consider trade-offs among multiple ecological, social, and economic goals would help to improve system resiliency. In some cases, incentivizing water users to maintain in-stream flows may provide cold-water to sustain socioeconomically important trout fisheries, especially during periods of drought.

Equally important, effective climate adaptation may also require new ways of managing people. Fishing restrictions, such as closures or permitting, are often used to help protect vulnerable fish populations during periods of extreme drought and to regulate increasing fishing pressure. However, traditional paradigms that focus on restricting fishing effort to protect biological resources may have unintended consequences for social portfolio effects as they limit people's ability to opportunistically adapt to climatic extremes and shifting resources. Moreover, movement of anglers to fishing refuges during periods of drought will challenge managers to mitigate the potential ecological impacts of increased fishing pressure on underlying populations. In situations where climate change effects become so severe that mitigating impacts is untenable, managers may need to help people and communities adapt to new ecological and socioeconomic states (39, 40), such as transitioning from cold-water to cool-water fisheries. Climate change will thus pose complex and challenging dilemmas for freshwater fisheries management in the future.

Worldwide, trout fishing has grown markedly in popularity, and fishers travel to all parts of the globe to fish highly prized cold-water fisheries, including Montana's world-renowned trout rivers (20). We found that nonresident fishing pressure was more variable across space and time than resident fishers, indicating that nonresident fishers were more flexible to adapt to climate-induced changes in fishing conditions and management closures. This behavioral flexibility contributed to more robust portfolio effects that stabilized regional spending. Conversely, we found reduced variation in fishing pressure by resident fishers, suggesting that they may have been less willing to travel to find better conditions during periods of drought and thus may be more sensitive to management closures and potential crowding effects. As fishing pressure continues to increase and cold-water habitats become more limited, the potential for fisher conflicts is likely to increase, thereby reducing the quality fishing experiences for both nonresident and resident fishers and the economic benefits they provide to local and regional economies.

Fisheries are coupled social-ecological systems that are affected by not only physical and biological changes in ecosystems but also human responses to changes and associated feedbacks on ecosystems (41). As species and fishing opportunities shift under climate change, fishers will either need to travel farther in pursuit of specific species (13, 15) or fish in different habitats, such as protected areas or head-water streams that serve as critical thermal refugia for trout during the warm summer months (42), which may increase costs to fishers. Fishers seeking cold-water fishing refuges during drought may intensify fishing pressure in specific rivers, potentially increasing crowding among anglers and overfishing on fish populations already facing climate-induced stress, a pattern that will be exacerbated as demand for limited cold-water fisheries increases. Furthermore, with extended duration of warm summer temperatures and low streamflows (24, 43), fishers may shift seasonally by fishing in the spring and fall to avoid stressful conditions and associated management closures during the summer months. Last, fishers may ultimately need to adapt to fish for new species, yet shifts to cool-water fisheries may not compensate for lost revenue as they are currently less popular than cold-water fisheries, especially among nonresident fishers. Potential decreases in fishing pressure may reduce funding available for management and mitigation through losses in license fees and excise taxes. Better understanding the social dynamics of fishers, such as where, when, and what species fishers target, especially during extreme climatic

events, will be critical for developing effective climate mitigation and management strategies (13, 44, 45).

Accelerating climate change and increasing extreme weather events pose potentially serious socioeconomic consequences for fisheries (46). These impending impacts motivate a need to enhance ecological, social, and economic resilience, as climatic changes become more severe and unpredictable (47). More work is needed to understand the adaptive potential of different components of fisheries (e.g., biological communities, fishers, institutions, and economies) in the face of uncertain but inevitable environmental and social change. Maintaining a diverse portfolio of adaptive fishing opportunities across broad spatial scales provides an important resilience mechanism for mitigating the potentially severe socioeconomic impacts of climate change on fisheries and the well-being and livelihoods they support.

METHODS

Fisher survey and environmental data

We used fishing pressure data from individual river sections across the region to quantify shifts in fishing pressure in response to changing environmental conditions and future shifts in thermally suitable trout habitat. Montana Fish, Wildlife & Parks (MFWP) has been conducting a mail-based survey of all licensed fishers every other year since 1983 (no survey was conducted in 1987). All anglers using waters in the state of Montana are required to have a fishing license. Licenses for resident and nonresident anglers differ in cost but grant anglers the same access and privileges. Although we do not have information on licensing compliance among groups, this number of unlicensed anglers (or angler-days) is likely to be small and is probably not biasing the results and conclusions presented here. Fishers responded with residency status (resident or nonresident) and days fished on specific river sections (delineated on maps included in the survey). Fishing pressure estimates (i.e., fisher-days) were computed by MFWP for each water body or river section, including variance estimates to account for the survey-related errors (48). Between 67,000 and 97,000 surveys were used in most years, and response rates ranged from 40 to 60%. A small number of river reporting sections have changed over time (i.e., larger sections were divided); therefore, we combined annual fishing estimates in these sections to integrate over these changes in survey methodology. While we used annual fishing pressure, it is important to note that the majority of fishing pressure (69% in 2015) occurred during the summer period (May to September).

Trout fisheries in this region are predominately catch-and-release sport fisheries. Catch-and-release is regulated for some species in specific waterbodies (e.g., bull trout *Salvelinus confluentus* and westslope cutthroat trout *Oncorhynchus clarkii lewisi*), but commonly practiced by most fishers. There are no commercial harvest fisheries for trout in the region, but a small proportion of fishers harvest trout for food.

To characterize historical climate conditions, we used annual and seasonal estimates of air temperature, streamflow, and Palmer Drought Severity Index (PDSI) calculated for each river reach. Daily air temperature (49) and the 10-day PDSI data (www.climatologylab.org/gridmet.html) were downloaded for the years ranging from 1980 to 2017 for our study area. Individual yearly Geotifs were generated in R (50) to represent mean maximum daily August temperature, 7-day maximum temperature for summer months (July, August, and September), annual PDSI, and spring/summer PDSI (April to

September). For each water code reach, yearly mean temperatures (August and 7-day max) and mean PDSIs (annual and spring/summer) were calculated using zonal statistics in ArcGIS 10.6.1.

Monthly natural streamflow data from 1980 to 2015 (51) were summarized to calculate mean August and mean annual streamflow estimates. For rivers that originate in Canada (i.e., Flathead and Kootenai rivers), streamflow predictions were not available; therefore, we used U.S. Geological Survey discharge data accessed from <https://waterdata.usgs.gov/nwis/rt> (51).

Analyzing drivers of fishing pressure

We used DFA to evaluate common patterns in fishing pressure and its sensitivity to changes in environmental conditions. DFA is a dimension reduction technique, similar to principal components analysis, designed specifically for time series analysis. DFA characterizes common trends among N time series with many fewer M common trends.

More specifically, following (29), we can write the DFA model as

$$x_t = Z u_t + D d_t + v_t \quad (1)$$

$$u_t = u_{t-1} + w_t \quad (2)$$

The $N \times 1$ vector of data observed at time t (x_t) is modeled as a linear combination of the M latent trends (u_t), a $P \times 1$ vector of explanatory variables (d_t), and an $N \times 1$ vector of observation errors (v_t), which are distributed as a multivariate normal with mean $\mathbf{0}$ and $N \times N$ variance-covariance matrix \mathbf{R} . The $N \times M$ vector \mathbf{Z} and $N \times P$ matrix \mathbf{D} contain the stream-specific loadings on the trend and explanatory effects of environmental covariates, respectively. We incorporated error estimates from the survey methodology by adding an additional observation process

$$y_t \sim \text{normal}(x_t, s_t) \quad (3)$$

where the vector of observations of fishing pressure (y_t) is distributed as normal with mean equal to the latent “true” estimate of fishing pressure (x_t) and survey error variance (s_t).

Here, the common trend(s) is not simply a straight line but rather a random walk through time such that the value of x at time t is simply equal to its value at time $t - 1$ plus some random error w_t , which is distributed normally with mean $\mathbf{0}$ and variance-covariance matrix \mathbf{Q} . These common trend(s) can be thought of as an aggregate of unknown environmental, social, and economic drivers not captured by the explanatory environmental variables included in the model. To make the model identifiable, we set \mathbf{Q} to a diagonal matrix with value 1 (29). All data were z-scored to account for differences in the mean of fishing pressure among the river sections.

We fit separate models for resident and nonresident fishing pressure with two types of observation error structures (i) where all sections share a single observation variance (diagonal and equal) and no covariance (ii) where each section has an independent observation variance with no covariance (diagonal and unequal). Candidate models (i.e., models with different combinations of trends, error structures, and covariate terms) can be viewed as different hypotheses describing how fishing pressure dynamics are structured and were compared using corrected Akaike information criteria (52). We assessed the significance of environmental covariates (i.e., air temperature, streamflow, and drought) in these models by comparing

effect size estimates and 95% confidence intervals to zero across river sections. For statistical analyses presented in figures and text, we retransformed these effect sizes to represent changes in fisher-days per kilometer per year to understand the fisher and economic effects.

Calculating portfolio effects across spatial scales

We calculated the magnitude of portfolio effects in fishing pressure (or spending) by dividing the average CV in fishing pressure (or spending) over time in individual river sections to the CV of aggregate fishing pressure across the region (4). We assessed the scale dependence of portfolio effects by calculating the CV at different spatial scales (individual sections, rivers, and drainages). To remove the potential effects of different rates of increase in fishing pressure among sections and to isolate how the interannual and other short-term dynamics among sections may stabilize fishing pressure and spending, we used a loess smoother with a span of 0.7 to detrend all time series before calculating the CV. Estimated portfolio effects were not sensitive to the choice of span parameters in the loess smoother. We also calculated synchrony among individual river sections using the “synchrony” package in R. The synchrony metric ranges from 0 (completely asynchronous) to 1 (perfectly synchronous). Asynchrony is calculated as $(1 - \text{synchrony})$.

Characterizing cool- and cold-water habitats

To assess how changes in fish communities may affect fishing pressure, we compared fishing pressure by resident and nonresident fishers in sections dominated by cold-water species (e.g., brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, and cutthroat trout *Oncorhynchus clarkii*) to sections that are transitioning cool-water species (e.g., black bass *Micropterus* spp. and walleye *S. vitreus*). Cool-water sections were identified using species composition data from electrofishing surveys conducted by MFWP and expert knowledge from state biologists. We delineated 14 cool-water sections across the Yellowstone, Bitterroot, Smith, Missouri, Bighorn, Jefferson, Clark Fork, and Madison rivers. Twelve cold-water sections adjacent to the cool-water sections were chosen for comparison to account for distance to population centers and river popularity (fig. S7). Differences in fishing pressure among these habitat types are qualitatively unchanged if cool-water sections are compared to all cold-water sections across the region.

To characterize future changes in cold-water habitat, we compared baseline (1993 to 2011) and future mean August water temperatures under the A1B scenario (31). We used existing temperature predictions that were developed under the A1B scenario, which is comparable to the RCP 6.0 scenario. Baseline mean August water temperatures (mean, 1993 to 2011) were significantly warmer in cool-water sections than in cold-water sections ($t = -27.558, P < 2.2 \times 10^{-16}$) and were consistently in excess of 18°C (Fig. 4C), which is similar to previous research on tolerance thresholds for cold-water trout species in the region (32). We used this 18°C threshold to project future distributions of cold-water habitat by quantifying where August water temperatures were currently less than 18°C but were predicted to be greater than 18°C in 2040 and 2080. Water temperature predictions were available at a finer spatial resolution than fishing pressure data; therefore, we calculated a percent loss of cold-water habitat for each fishing pressure reporting section.

In fishing sections that were currently less than 18°C but were projected to be warmer than 18°C in 2040 or 2080, we reduced fishing pressure in proportion to the percentage of habitat that transitioned

from cold-water to cool-water. To estimate changes in fishing pressure by resident and nonresident fishers due to shifts in cold- and cool-water habitat, we compared the average fishing pressure per kilometer per year in cool-water and cold-water sections over the past 3 years. Specifically, fishing pressure in cool-water sections was 10 and 35% of pressure in comparable cold-water sections for non-residents and residents, respectively (Fig. 4A). To project changes in fishing pressure, we reduced fishing pressure in proportion to these current preferences for cold- and cool-water habitats by resident and nonresident fishers.

Estimating the economic impacts of drought and shifts in cold-water habitat

We estimated the potential economic impacts of future drought and shifts from cold-water to cool-water habitat by calculating changes in spending by resident and nonresident fishers. We do not have data to determine differences in per diem spending by anglers targeting cold- versus cool-water fisheries. Therefore, we assumed that spending was the same across these target fisheries and all projected economic impacts are the result of only changes in angler pressure for resident and nonresident groups. To estimate the socioeconomic impacts of drought, we transformed effect sizes of PDSI to fisher-days per PDSI from DFA models for resident and nonresident fishers (Fig. 2, D and E). We combined these coefficients with current estimates of spending by fisher-day and fisher demographics (resident or nonresident) from MFWP (21) to calculate the cumulative effect of moderate, severe, or extreme drought on spending in each river section. To calculate the changes in spending in response to changes in cold-water habitat, we combined projected changes in fishing pressure as a result of cold-water habitat transitioning to cool-water habitat (see above) with spending by resident and nonresident fishers. These calculations are not intended to be specific projections and do not account for future valuation (i.e., they are not a net present value calculation), but rather provide an estimate of the scope of potential economic impacts.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <https://science.org/doi/10.1126/sciadv.abn1396>

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Socioeconomic resilience to climatic extremes in a freshwater fishery

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