

ARTICLE

Lake temperature and morphometry shape the thermal composition of recreational fishing catch

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Abstract

Objective: Managing freshwater fisheries in warming lakes is challenging because climate change impacts anglers, fish, and their interactions.

Methods: We integrated recent models of current and future lake temperatures with recreational fisheries catch data from 587 lakes in three north-central U.S. states (Michigan, Minnesota, and Wisconsin) to evaluate how the thermal composition of recreational fisheries catch varied as a function of temperature, ice coverage, and lake morphometry.

Result: We found that warmwater catch share (WCS), defined as the proportion of fish in recreational angling catch that belonged to the warmwater thermal guild (final temperature preferendum [FTP] > 25°C), increased with average annual lake surface temperature and decreased with survey ice coverage. However, we also found that WCS decreased with increased lake area and depth. Using mid-century (2040–2060) water temperature and ice projections while holding all other variables constant, we predicted that WCS will likely increase as the climate warms but that significant thermal heterogeneity will persist.

Conclusion: Lakes that are large (>100 ha) and deep (>10 m) and those with cooler (<3700 annual growing degree-days) predicted future temperatures will likely hold thermal refugia for coolwater (FTP = 19–25°C) and coldwater (FTP < 19°C) fish even as average lake temperatures rise, creating the potential for management actions to resist the shift from coolwater to warmwater fisheries. Managers of smaller and more rapidly warming lakes may want to consider strategies that accept or direct emerging warmwater fishing opportunities. We suggest that the most viable path to climate adaptation in landscapes of diverse lakes may be to resist warmwater shifts where possible and to accept or direct the rise of warmwater fishing opportunities where necessary.

KEYWORDS

fisheries, human dimensions, lake and reservoir, survey methods

INTRODUCTION

Freshwater anglers fish for numerous reasons, including recreation, time outdoors, strengthening social connections, and collecting food (Young et al. 2016; Cooke et al. 2018). Freshwater fisheries consequently provide many benefits in the form of food, recreation, economic development, and conservation funding (Embke et al. 2020; Lueck and Parker 2022; Federal-State Relationships 2024). The magnitude and variety of benefits provided by freshwater fisheries flow directly from the diversity of freshwater systems (Lynch et al. 2022). Freshwater anglers pursue diverse fish taxa in widely varying climates, landscapes, and water bodies, inspiring varying techniques, cultures, regulatory structures, and informal governance practices across regions (Arlinghaus et al. 2016; Cooke et al. 2018). However, a changing climate may require both fish and anglers to adapt to warming conditions across broad spatial extents (Hunt et al. 2016).

Many freshwater rivers, lakes, and streams in the United States are rapidly warming, thereby threatening the social–ecological diversity that has long fueled productive fisheries (Maberly et al. 2020; Woolway et al. 2020). Rising water temperatures impose physiological stress on coolwater (preferred temperature = 19–25°C; Coker et al. 2001) and coldwater (preferred temperature < 19°C) fishes and force changes in long-established community dynamics (Woodward et al. 2010; Comte et al. 2013; Whitney et al. 2016; Erickson et al. 2021). Increases in lake temperatures have been linked to decreased recruitment in coolwater and coldwater game fish populations and accelerated spread of invasive species (Mainka and Howard 2010; Junker et al. 2014; Rypel et al. 2018). Many smaller and more southerly lakes are already becoming unsuitable for important coolwater and coldwater fishes because rising water temperatures impose thermal stress on coolwater species and grant advantages to warmwater species (preferred temperature ≥ 25°C; Hansen et al. 2017, 2022).

The human communities and enterprises built around freshwater fishing may also be impacted by warming lake temperatures. Many northern communities have long ice fishing seasons in addition to the summer open-water season (Van Assche et al. 2013, 2014; Hunt et al. 2016; Lawrence et al. 2022). Rising and increasingly variable winter temperatures are reducing ice stability, shortening the winter fishing season, and rendering many traditional winter fishing practices less safe (e.g., driving or snowmobiling on frozen lakes and rivers, deploying winter fishing houses on the ice, and drilling or cutting multiple holes in the ice; Sharma et al. 2020). Hotter summer temperatures may also make fishing more difficult as environmental conditions become less favorable for outdoor recreation

Impact statement

Inland lakes are rapidly warming, creating novel coolwater management challenges and emerging warmwater opportunities. Warmwater fishing opportunities are likely to increase as the climate warms, but larger, deeper lakes will likely provide thermal refuges for coolwater fish and the anglers who pursue them.

(Wolf et al. 2017). If these patterns continue as the climate warms, then fishing opportunities for coolwater and coldwater species in temperate latitudes are likely to decline (e.g., Feiner et al. 2020). However, fishing opportunities for warmwater species may increase. The extent to which coolwater fishing opportunities will decline and the extent to which increasing warmwater opportunities may compensate for that decline are deeply uncertain. Fisheries managers are thus tasked with addressing the emerging needs of fish and fishers in a changing climate.

Freshwater fisheries managers who were already grappling with the ecological and social consequences of warming lakes are faced with the challenge of parsing climate change information into guidance that is applicable at a local scale. Climate change impacts on recreational fisheries are often addressed via independent models of fish or anglers (e.g., Hansen et al. 2017; Dundas and von Haefen 2020). However, freshwater recreational fisheries are complex social–ecological systems defined by feedback between people, fish, and climate (Midway et al. 2016; Arlinghaus et al. 2017; Nieman et al. 2021). Understanding and managing the effects of lake warming on freshwater recreational fisheries therefore require a joint understanding of how people and fish respond to warming waters.

Herein, we leverage the U.S. Inland Creel and Angler Survey Catalog (CreelCat; Lynch et al. 2021a; Sievert and Lynch 2023; Sievert et al. 2023), a database of freshwater fisheries recreational catch and harvest, in combination with recent hydroclimatological models (Corson-Dosch et al. 2023) to evaluate how warmwater catch share (WCS; i.e., the fraction of recreational fishing catch that belongs to the warmwater thermal guild) varies as a function of lake thermal conditions, survey ice coverage, and water body morphometry. We model current and mid-century WCS in Michigan, Minnesota, and Wisconsin—three U.S. states with avid open-water and ice angling participation, abundant catch surveys, high-resolution climate data, and rapidly warming lakes. Finally, we discuss how to develop climate-informed adaptation strategies for multiple thermal guilds at a regional scale in a warming 21st century.

METHODS

Questions and hypotheses

We integrated CreelCat with a recent, publicly available hydroclimatological model (Corson-Dosch et al. 2023) to ask how WCS varied in relation to lake surface temperature, survey ice coverage, and lake morphometry. Specifically, we tested the hypothesis that WCS was positively associated with correlates of warmwater fish habitat and negatively correlated with the proportion of creel survey effort during the entire creel survey period that was targeted at winter ice fishing. Creel survey periods were generally yearly increments, but their start and end dates varied per state research protocols. Some survey periods were calendar years (January 1–December 31 of a single year), whereas others included a summer season (e.g., May 1–August 31) and a winter season (e.g., December 1–March 31 of the following year) to capture open-water fishing and ice fishing; some captured only a summer season or a winter season. We consolidated the open-water and ice seasons when a given lake had multiple survey periods in the same 12-month period.

The role of rising lake temperatures in creating warmwater habitat—and thus fishing opportunities for warmwater fish—is well documented (e.g., Magnuson et al. 1990; Mohseni et al. 2003; Cline et al. 2013; Benoit et al. 2022; Wu et al. 2022). However, lakes are not homogeneous in temperature or structure. We therefore evaluated the effects of three lake morphometrics that may also affect WCS: lake surface area, maximum depth, and shoreline development index (SDI; a sinuosity index that reflects shoreline complexity; Hutchinson 1957). We additionally assessed the role of survey ice coverage, defined as the degree to which a creel survey targeted ice fishing. Lake area may affect WCS because coolwater and coldwater fishes often thrive in larger systems, taking advantage of open-water habitat, foraging opportunities, and pockets of cold water during stressful warm periods (Raabe and Bozek 2012). Walleye *Sander vitreus* in particular may be more abundant in large systems because large lakes provide a diverse prey base for adults and sufficient zooplankton resources for larval fish in addition to offering coolwater refuges (Bozek et al. 2011b; Hansen et al. 2015). We therefore predicted that WCS would be negatively associated with lake area. Lake depth plays an ecological role similar to that of lake area (although they were not strongly correlated in our data set; see [Supplemental Material](#) [available in the online version of this article]). Deeper lakes provide pockets of cool water that coolwater and coldwater fishes may use as thermal refugia during warm periods, and deeper lakes also facilitate the open-water foraging that is characteristic of many larger

coolwater species (Plumb et al. 2014). Consequently, we anticipated that lake depth would be negatively associated with WCS. Lakes with a higher SDI have a greater number of small bays and inlets that tend to hold pockets of warm water and vegetation, potentially providing more habitat for warmwater fishes (Azza et al. 2007). We therefore predicted that the SDI would be positively associated with WCS.

Finally, we sought to account for seasonal variation in angler behavior and geographic variation in fisheries agency objectives by calculating an ice fishing index that was scaled from 0 to 1, representing the proportion of each survey period during which the lake was covered in ice (e.g., 0=no ice days, 0.5=half ice days, 1=all ice days). Ice anglers display distinct patterns of targeting, catch, and harvest behavior, making it important to account for ice opportunity in creel catch models (Sass et al. 2023). Although ice period is correlated with lake temperature, the decision to survey ice anglers is often not correlated with lake temperature. Fisheries agencies may opt to only interview anglers during the open-water season due to management priorities or budget constraints, even when lakes freeze deeply and provide months of ice fishing opportunity. Conversely, states may take an interest in ice fishing and conduct their surveys only during the ice fishing period, leading to a catch thermal composition that is skewed toward coolwater and coldwater fish, which may have higher winter activity levels than warmwater fishes (Fernandes and McMeans 2019). The ice fishing index therefore accounts for how much of the total survey period was targeted at ice anglers. We anticipated that WCS would be negatively associated with the ice fishing index.

Study area

We focused our analysis on three north-central U.S. states with long-running angler survey programs and high-resolution lake temperature models: Michigan, Minnesota, and Wisconsin (Figure 1). This region is home to thousands of lakes, a pronounced climate gradient, and some of the nation's most avid recreational anglers (U.S. Fish and Wildlife Service 2023). Northern Minnesota, Wisconsin, and Michigan are characterized by a band of mixed deciduous–coniferous forests and glacial lakes, whereas southern Minnesota, Wisconsin, and Michigan are largely agricultural or urban, with a higher concentration of reservoirs (Jin et al. 2019; Homer et al. 2020). Climates in the region range from “continental–no dry season–warm summer” and “continental–dry winter–warm summer” in the north to “continental–no dry season–hot summer” in the south under the Köppen–Geiger climate classification (Beck et al. 2023).

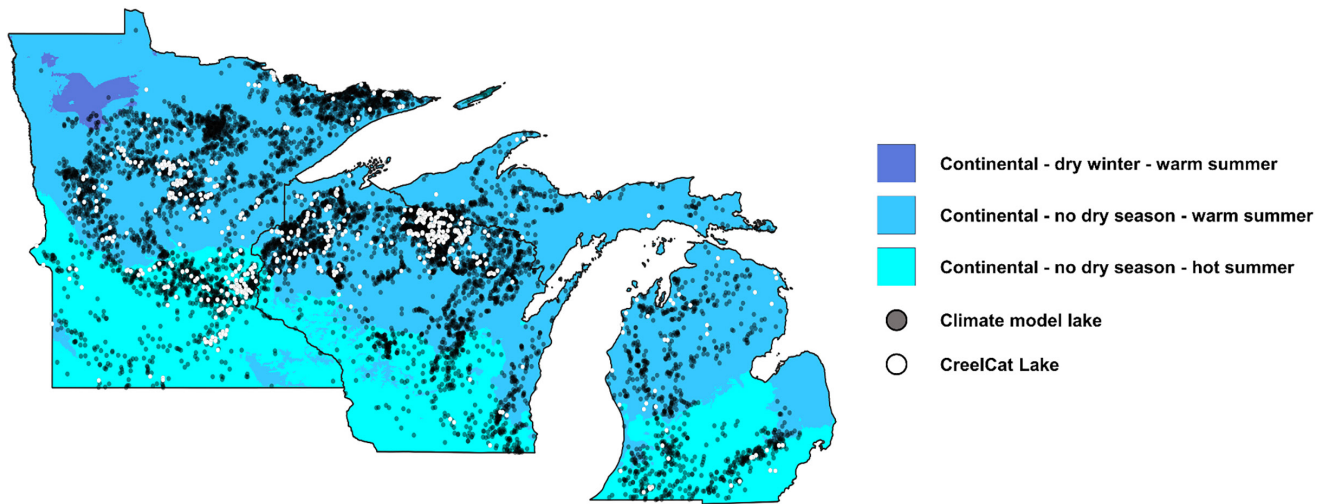


FIGURE 1 We modeled warmwater catch share (WCS) at 587 lakes across Michigan, Minnesota, and Wisconsin, United States. We then used current and mid-century lake temperature projections to predict current and mid-century WCS at 9538 lakes. The map shows the distribution of lakes in the three states. Lakes included in the temperature model are plotted in black, and data from the U.S. Inland Creel and Angler Survey Catalog (CreelCat; Sievert et al. 2023) are plotted in white. The map color scheme reflects the current Köppen–Geiger climate classification for the study region.

Creel data

We used CreelCat (Sievert and Lynch 2023; Table 1) to quantify fish catch and harvest by recreational anglers. CreelCat houses angler survey data provided by state natural resource management agencies from over 35 U.S. states and territories, including taxon-specific fish catch and harvest data as well as important metadata on survey methodology. We used only data collected via angler intercept surveys (Pollock et al. 1994) in which interviewers approached anglers during or at the completion of their fishing trip to quantify how many fish were caught and harvested. We accessed our data on November 15, 2023, and used the built-in features of CreelCat to extract our initial data set by filtering the data by geography (state), water body type (lakes, reservoirs, ponds, and tailraces), and survey type and then selecting the *Catch* and *Taxa* fields.

Survey aggregation and thermal guilds

We extracted the most recent survey year from each water body, combining ice and open-water surveys where applicable as described above. The resulting data set contained data from 587 lakes. We calculated WCS based on the taxon-specific final temperature preferendum (FTP) and recreational fishing catch estimates. The FTP is the temperature to which a fish will gravitate when given a wide range of choices (Beitinger and Fitzpatrick 1979). We followed the Coker et al. (2001) thermal guild classification

for Canadian freshwater fishes because many of our study sites were near the Canadian border and all species were shared between the United States and Canada (Table 1). Per Coker et al. (2001), fish taxa were assigned to (1) the coldwater guild if their FTP was less than 19°C, (2) the coolwater guild if their FTP was 19–25°C, or (3) the warmwater guild if their FTP was greater than 25°C. Because relatively few lakes had large catches of coldwater fish, we condensed the coolwater and coldwater guilds to simplify the model. All fish species that are typically caught using hook and line for which we could access FTP data were included. We excluded Rainbow Smelt *Osmerus mordax* because they are targeted during their spawning runs by using dip nets, a method that yields extremely large harvests (smelt regulations are written in units of gallons; Michigan Department of Natural Resources 2023).

Water temperature and lake morphometry

We extracted yearly temperature metrics for each survey year from a recent hydroclimatological machine learning model (Corson-Dosch et al. 2023). The machine learning model created daily water temperature predictions for each water body by using a downscaled regional climate model based on predictions for the present epoch (2000–2022) from the National Land Data Assimilation System and predictions for the mid-century epoch (2040–2060) from six global climate models (Australian Community Climate and Earth System Simulator, Centre National de Recherches Météorologiques Climate Model version 5, Geophysical Fluid Dynamics

TABLE 1 Inland recreational fish catch and harvest data for Michigan, Minnesota, and Wisconsin, accessed from the U.S. Inland Creel and Angler Survey Catalog (CreelCat database; Sievert et al. 2023) and organized by thermal guild and final temperature preferendum (FTP; Beitinger and Fitzpatrick 1979; Coker et al. 2001).

Thermal guild	Taxon	FTP (°C)	Catch (number of fish)	Harvest (number of fish)	Harvest (% of catch)
Cold	Lake Sturgeon <i>Acipenser fulvescens</i>	11.00	726	0	0
	Cisco <i>Coregonus artedii</i>	12.40	14,803	11,844	80
	Lake Whitefish <i>Coregonus clupeaformis</i>	12.70	6401	3275	51
	Burbot <i>Lota lota</i>	13.20	2716	683	25
	Rainbow Trout <i>Oncorhynchus mykiss</i>	15.50	17,972	15,552	87
	Yellow Perch <i>Perca flavescens</i>	17.60	4,670,876	1,551,247	33
	Brown Trout <i>Salmo trutta</i>	15.70	505	448	89
	Brook Trout <i>Salvelinus fontinalis</i>	14.80	1535	1103	72
	Lake Trout <i>Salvelinus namaycush</i>	11.80	11,667	8786	75
	Coldwater total			4,727,201	1,592,939
Cool	Rock Bass <i>Ambloplites rupestris</i>	24.90	626,398	105,601	17
	Freshwater Drum <i>Aplodinotus grunniens</i>	24.60	96,539	5940	6
	White Sucker <i>Catostomus commersonii</i>	23.40	2732	1117	41
	Northern Pike <i>Esox lucius</i>	20.70	1,085,507	225,903	21
	Hybrid Northern Pike × Muskellunge <i>E. masquinongy</i>	23.05	2816	0	0
	White Crappie <i>Pomoxis annularis</i>	19.10	16,499	14,065	85
	Black Crappie <i>Pomoxis nigromaculatus</i>	23.40	2,523,919	1,335,231	53
	Walleye <i>Sander vitreus</i>	22.50	1,465,384	546,014	37
Coolwater total			5,819,794	2,233,871	38
Warm	Black Bullhead <i>Ameiurus melas</i>	26.20	71,915	34,033	47
	Yellow Bullhead <i>Ameiurus natalis</i>	26.20	6215	2072	33
	Brown Bullhead <i>Ameiurus nebulosus</i>	26.20	2482	1136	46
	Bowfin <i>Amia calva</i>	30.30	6767	577	9
	Common Carp <i>Cyprinus carpio</i>	27.70	7592	2895	38
	Muskellunge <i>E. masquinongy</i>	25.40	37,564	632	2
	Channel Catfish <i>Ictalurus punctatus</i>	27.30	16,144	6949	43
	Longnose Gar <i>Lepisosteus osseus</i>	27.40	23	6	26
	Green Sunfish <i>Lepomis cyanellus</i>	25.40	6910	2603	38
	Pumpkinseed <i>Lepomis gibbosus</i>	27.70	435,935	177,971	41
	Warmouth <i>Lepomis gulosus</i>	25.00	240	26	11
	Bluegill <i>Lepomis macrochirus</i>	30.20	7,899,262	3,045,413	39
	Hybrid sunfish <i>Lepomis</i> spp.	25.00	20,020	6776	34
	Smallmouth Bass <i>Micropterus dolomieu</i>	25.00	612,240	34,131	6
	Largemouth Bass <i>Micropterus nigricans</i>	28.60	1,857,891	139,386	8
	White Bass <i>Morone chrysops</i>	27.30	29,823	5105	17
	Flathead Catfish <i>Pylodictis olivaris</i>	29.50	61	9	15
	Warmwater total			11,011,084	3,459,721

Laboratory Climate Model version 4, Institut Pierre Simon Laplace Climate Model version 6, Interdisciplinary Research on Climate version 5, and Meteorological Research Institute

Global Climate Model version 3). We quantified thermal condition as the total yearly number of growing degree-days (GDD) above 0°C (Venturelli et al. 2010) at the water's

surface. Growing degree-days are a measure of integrated temperature and therefore provide a more holistic measure of yearly thermal conditions than seasonal means. Finally, we extracted lake area and perimeter from the National Hydrography Dataset (NHD) Plus–High Resolution and calculated the SDI for each lake (Buto and Anderson 2020). The final data set included state, lake NHD identifier, lake area, GDD in the survey year, ice fishing index, maximum lake depth, lake SDI, total number of fish caught, the number of warmwater fish caught, and the number of harvested fish from each taxon.

Model

We built a Bayesian generalized linear mixed model (Bolker et al. 2009) that described WCS at each lake via a binomial structure wherein the number of trials was $C_{s,l}$ (the total number of fish caught in state s at lake l) and the number of successes was $W_{s,l}$ (the total number of warmwater fish caught in state s at lake l). The model employed a state-level random effect to create a random intercept model that accounted for methodological differences in creel study design and data collection among states. The probability that a given fish from the sample was a warmwater fish was given by a logistic function of state-specific intercept β_{0s} and the effects of GDD (β_T), area (β_A), lake depth (β_D), lake SDI (β_{SDI}), and ice index (β_I) multiplied by their respective scaled and centered values at lake l (T_l , A_l , D_l , SDI_l , and I_l). The model used an inverse logit function to ensure that the probabilities supplied to the binomial distribution were confined between 0 and 1:

$$W_{s,l} \sim B(p = p_{s,l}, n = C_{s,l}),$$

$$p_{s,l} = \text{ilogit}(\beta_{0s} + T_l\beta_T + A_l\beta_A + D_l\beta_D + SDI_l\beta_{SDI} + I_l\beta_I).$$

The random effect was implemented using dynamic indexing. An intercept was calculated for each state based on the state associated with lake l rather than comparing intercept parameter estimates of a reference state to that of the other states. All parameters were assigned normal prior distributions with a mean of 0 and a variance of 1000, and all predictor values except the ice index were scaled using z-scores. The ice index was not scaled because it was already bounded between 0 and 1 and thus was already regularized. The model ran for a total of 660,000 iterations, with a burn-in of 60,000 iterations and a thin of 60, resulting in 10,000 sampled iterations per chain. The model was fitted using the NIMBLE package in R, which uses a BUGS-like syntax but runs faster than previous BUGS-based languages due to an innovative C++ compiler (de Valpine et al. 2017, 2023). We ran three chains using different randomly generated initial

values, and we checked for convergence using trace plots, Gelman–Rubin statistics, and effective sample sizes.

We predicted current and mid-century (2040–2060) WCS for 9538 lakes in the climate model data set using predicted average GDD and ice coverage for each epoch while assuming that each lake's area, depth, and SDI were constant over time. We built predictive rasters to create thematic maps of WCS under current and mid-century GDD and ice coverage conditions using the inverse distance weighting function in the SpatStat package (Baddeley et al. 2015) and plotted the resulting rasters using QGIS (QGIS 2023). More details about the model, its performance, and the plotting methods are provided in the [Supplemental Material](#), code, and data.

RESULTS

We accessed CreelCat data from 587 surveys including 21,558,079 total fish from 34 taxa (Table 1). Survey years ranged from 1986 to 2021, and 86% of the surveys were conducted during or after the year 1995 (100% of Michigan surveys, 75% of Minnesota surveys, and 95% of Wisconsin surveys). Creel-surveyed lakes averaged 747 ha (standard deviation [SD] = 3481) in area and 15 m (SD = 13) in depth, and average SDI was 2.24 (SD = 1.35). Lakes in the larger hydroclimatological data set averaged 143 ha (SD = 1801) in area and 9 m (SD = 8) in depth, with an average SDI of 1.73 (SD = 0.89).

Current (2000–2021) GDD used for predictions at the creel-surveyed lakes ranged from 2848 to 5010 GDD, averaging 3948 GDD (SD = 380), and were predicted to rise by a mean of 193 GDD (SD = 119) by mid-century. Creel-surveyed lakes experienced an average of 132 ice days/year (SD = 14) and were predicted to lose 8 days (SD = 5) of ice coverage per year by mid-century. The creel survey ice index ranged from 0 to 1, averaging 0.24 (SD = 0.27). Lakes in the large climate model data set were predicted to experience an average increase of 168 GDD (SD = 122) and to lose a mean of 7 days (SD = 5) of ice coverage by mid-century (Figures 2 and 3). Warmwater catch share ranged from 0% to 100%, averaging 49% (SD = 29). Thirty-one percent of warmwater fish were harvested, and 36% of coolwater and coldwater fish were harvested.

All model parameters yielded a Gelman–Rubin statistic of 1, indicating that the model converged successfully (Brooks and Gelman 1998; [Supplemental Material](#)). Warmwater catch share was positively associated with lake GDD and SDI and was negatively associated with depth, area, and ice coverage (Table 2). The 95% credible intervals did not overlap 0 for any of the parameters, and predictions had a root mean square error of 0.25 ([Supplemental Material](#)).

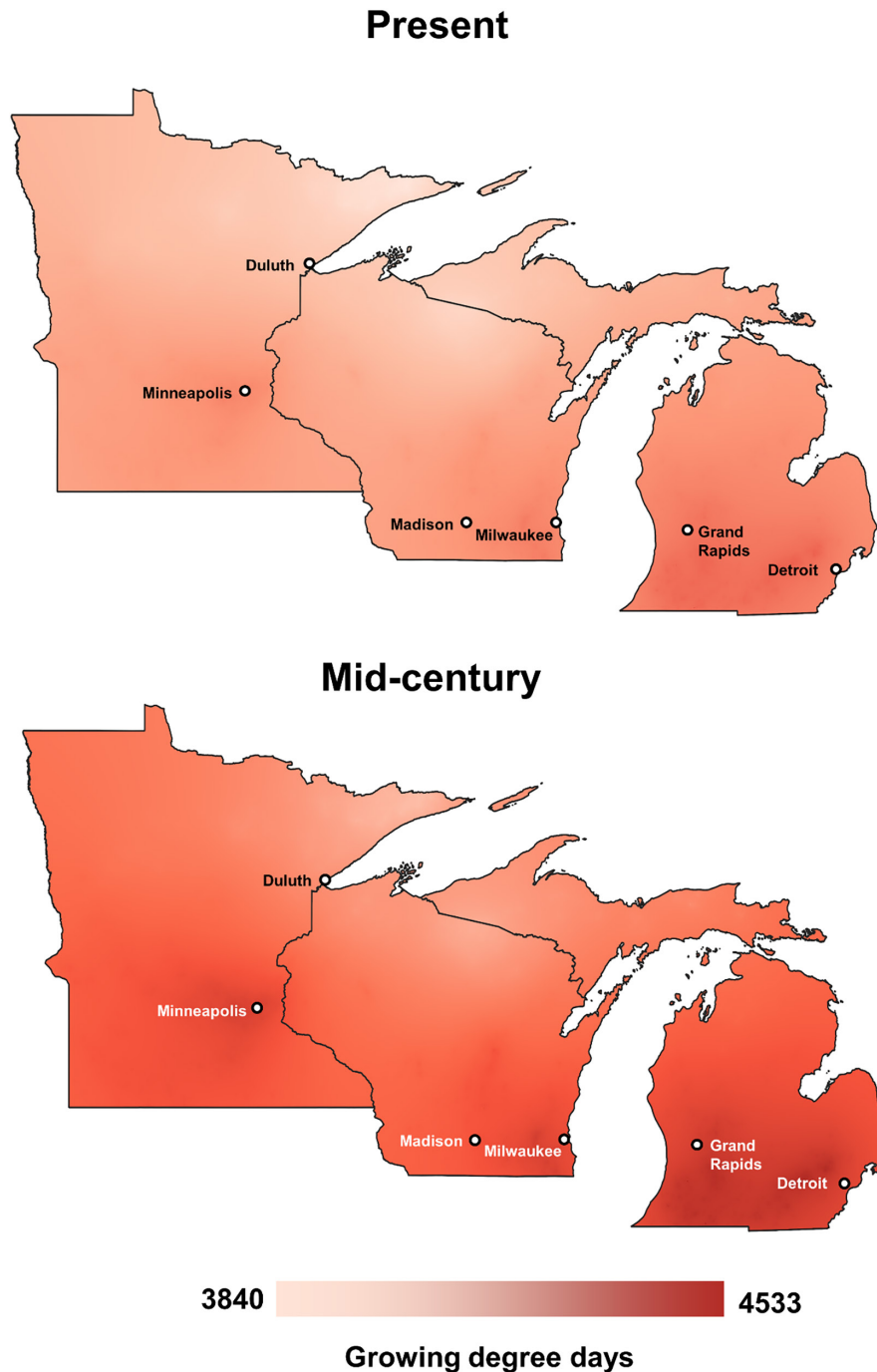


FIGURE 2 The top panel shows the spatial distribution of lake growing degree-days in the present climate epoch (2000–2021) for lakes in Minnesota, Michigan, and Wisconsin, United States. The bottom panel shows the spatial distribution of predicted lake growing degree-days in the mid-century epoch (2040–2060). Lake growing degree-days were greatest at more southerly latitudes and around urban centers. Lakes in the climate model data set were predicted to increase in temperature by an average of 168 growing degree-days/year (standard deviation = 122) by mid-century.

The model predicted that WCS within creel-surveyed lakes averaged 54% (SD = 16) and ranged from 8% to 89%. We linked the WCS model with the climate model to predict that WCS would rise to a mean of 59% (SD = 16; range = 11–93%) by mid-century within creel-surveyed

lakes. The predicted mean WCS in the larger regional lake group under current climatic conditions averaged 69% (SD = 17; range = 5–98%). The mean WCS in the larger lake group was predicted to rise to 73% (SD = 16) by mid-century (Figure 4).

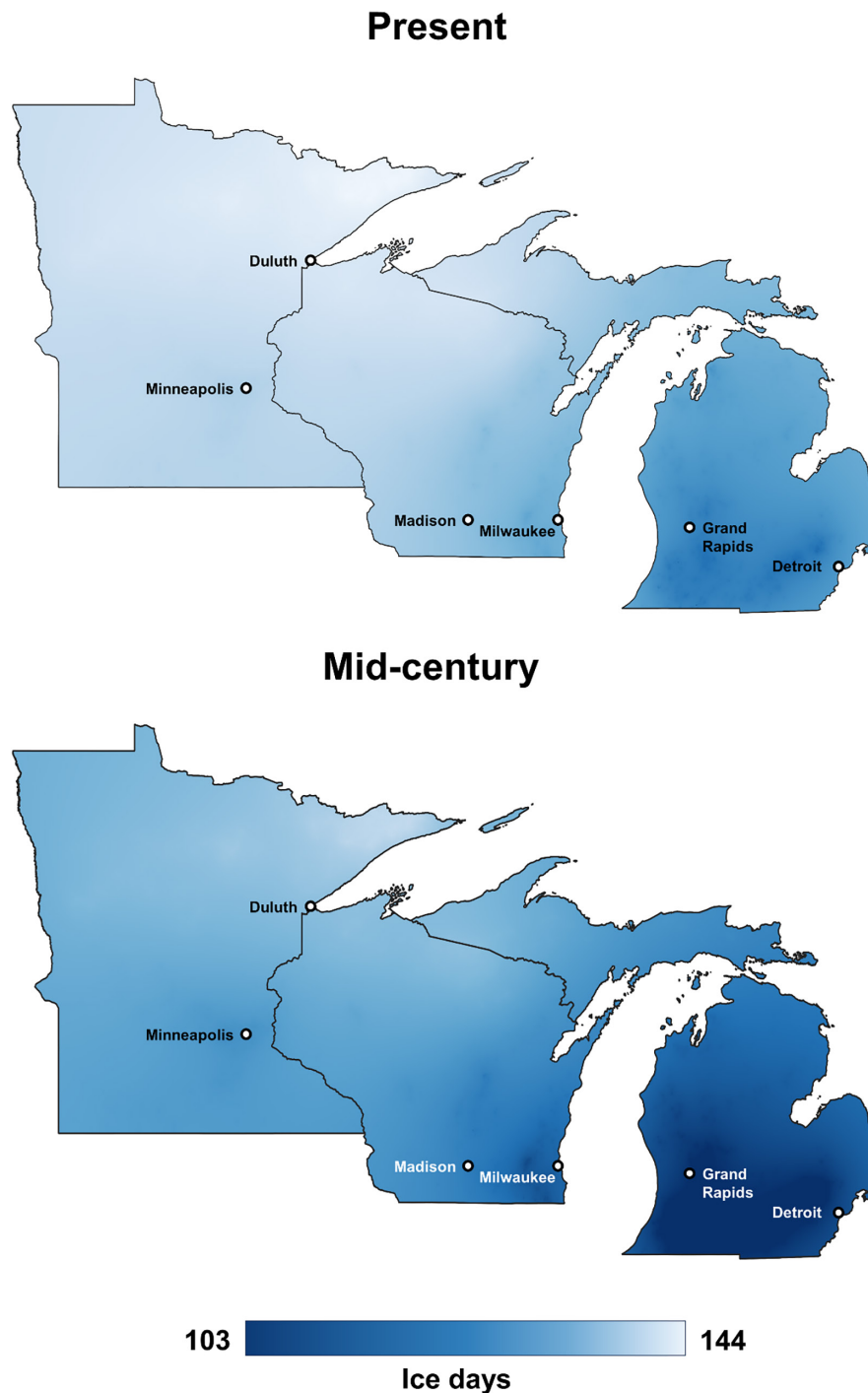


FIGURE 3 The top panel shows the spatial distribution of lake ice coverage in the present climate epoch (2000–2021) for Michigan, Minnesota, and Wisconsin, United States. The bottom panel shows the spatial distribution of predicted ice coverage in the mid-century epoch (2040–2060). Ice coverage varied from 103 days/year in southern Michigan to 144 days/year in northern Minnesota and the western Upper Peninsula of Michigan. Lakes in the study area were predicted to lose a mean of 7 days (standard deviation = 5) of ice coverage by mid-century.

Case study

Within-region variation in future thermal conditions and lake morphometry created diverse landscapes of predicted WCS, even within relatively small areas. For example, Leech and Roosevelt lakes, both located in Cass

County, Minnesota, sit only 48 km apart, but they have markedly different current and future predicted WCS. Leech Lake is large (41,824 ha) and deep (41 m) and currently experiences an average of 3852 GDD and 139 ice days/year. Leech Lake is predicted to warm more slowly than many other lakes, with a predicted mid-century

TABLE 2 Parameter means and 95% credible intervals (CIs) for the catch thermal composition model. SDI, shoreline development index.

Parameter	Explanation	Mean	2.5% CI	97.5% CI
β_0 , MI	Michigan intercept	1.664	1.660	1.667
β_0 , MN	Minnesota intercept	1.180	1.177	1.183
β_0 , WI	Wisconsin intercept	1.866	1.863	1.868
β_A	Area coefficient	-0.492	-0.493	-0.491
β_D	Depth coefficient	-0.072	-0.073	-0.071
β_I	Ice index coefficient	-1.438	-1.443	-1.433
β_{SDI}	SDI coefficient	0.046	0.046	0.046
β_T	Temperature coefficient	0.775	0.773	0.777

mean of 4101 GDD and 132 ice days. Roosevelt Lake is smaller (609 ha) and slightly shallower (39 m) and currently experiences 3862 GDD/year (only 10 more GDD than Leech Lake) and 127 ice days. Roosevelt Lake is predicted to warm to 4232 GDD/year—over 100 GDD more than Leech Lake's mid-century projection—and is predicted to lose 9 ice days. The increasing climatic difference between the two lakes creates very different climate and fishing futures. Warmwater catch share at Roosevelt Lake was predicted to rise from 30% to 41%, whereas Leech Lake was predicted to experience a rise from 8% to 11%. We invite curious readers to consider the included code and data (see [Supplemental Material](#)) if they are interested in further comparisons of thermal or catch distribution for specific areas.

DISCUSSION

We found that WCS among recreational anglers was positively associated with lake GDD and negatively associated with survey ice coverage. We therefore suggest that WCS will likely increase as lakes warm and provide fewer days of ice fishing opportunity per year. However, increasing WCS will likely be moderated by lake morphometry. In particular, our finding that WCS decreased as a function of increasing lake surface area and depth suggests that coolwater and coldwater fishes may find refuge or even experience seasonal improvements in habitat availability in larger and deeper lakes that maintain pockets of cool water—an inference that is supported by abundant ecological evidence (Jacobson et al. 2010; Hayden et al. 2014; Herb et al. 2014; Guzzo et al. 2017; Campana et al. 2020). Most pertinently for conservation decision makers and fisheries managers, our findings suggest that the responses of fisheries to warming will likely be heterogeneous within regions. We suggest that understanding and adapting to this heterogeneity in climate and lake morphometry will facilitate climate-resilient fisheries management strategies.

Thermal guild alignment and lake morphometry

We observed that WCS increased as GDD increased, indicating a complementary decrease in the catch shares of coolwater and coldwater fishes. Consequently, we predicted that WCS would increase by an average of four percentage points by mid-century. This aligns with previous evidence based on fish population data that coolwater and coldwater species are being replaced by warmwater species via increased thermal stress, decreased recruitment success, and rising competition from warmwater species (Daufresne and Böet 2017; Hansen et al. 2017).

We also found that WCS decreased with increasing lake depth and area, indicating that angler-caught fish from larger and deeper lakes had a higher probability of belonging to the coolwater or coldwater guild than did fish from smaller and shallower lakes. Greater coolwater and coldwater representation in these lakes likely occurred because larger and deeper lakes may hold pockets of cool water through the hot summer months, easing thermal stress on coolwater and coldwater fishes (Guzzo et al. 2017; Corson-Dosch et al. 2023). Popular coolwater sport fishes such as Walleye also tend to thrive in larger systems that facilitate effective foraging and reproduction (Graeb et al. 2005; Bozek et al. 2011a; Raabe and Bozek 2012), whereas warmwater species like Largemouth Bass and sunfishes *Lepomis* spp. tend to forage, reproduce, and be caught in warm, shallow areas with well-developed structure for camouflage and nesting habitat (Ellerby and Gerry 2011; Lawson et al. 2011). We further observed that WCS increased with SDI. This is likely because lakes with high SDI values have many small bays and inlets that provide pockets of vegetation and warm water for warmwater fishes and offer easy access for warmwater anglers fishing from the bank or small boats (Feiner et al. 2020).

Our finding that lake morphometry may moderate the effects of increasing temperatures suggests that larger and deeper lakes can provide refuges for coolwater and

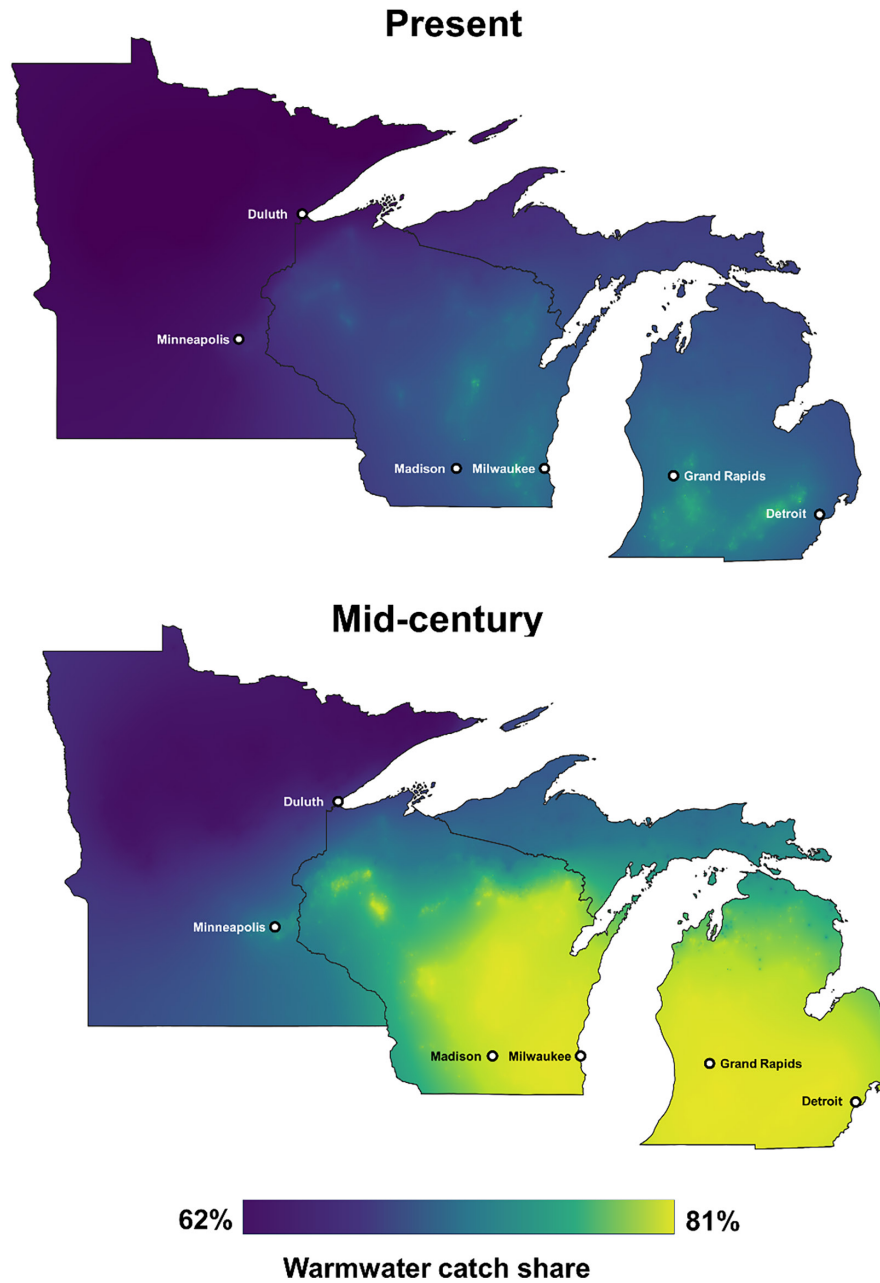


FIGURE 4 The top panel shows predicted warmwater catch share (WCS) in the present climate epoch (2000–2021) for lakes in Minnesota, Michigan, and Wisconsin, United States. The bottom panel shows predicted WCS in the mid-century epoch (2040–2060). Warmwater catch share was greatest in more southerly, agricultural areas with small lakes and around population centers. Predicted mean WCS rose from 69% in the current epoch to 73% in the mid-century epoch.

coldwater species even as average lake temperatures increase, whereas smaller, shallower lakes with complex shorelines will likely provide increasing warmwater opportunities. Fisheries managers that are invested in maintaining coolwater and coldwater fishing opportunities may therefore find it advantageous to consider not only lake surface temperature, but also a lake's ability to provide thermal refugia when surface conditions become unfavorable.

Species assemblages and food potential

Angler catch rates are related to fish density and angling pressure, and anglers that seek specific taxa are typically more successful at harvesting those taxa (Mee et al. 2016; Pope et al. 2016; Caruthers et al. 2018). The shift from coolwater to warmwater species assemblages may therefore have consequences for the role of freshwater fisheries as food sources for people (Cowx et al. 2023). Indeed,

anglers in many U.S. states are already shifting their targeted species from coolwater to warmwater species (Hunt et al. 2016). Many coolwater species, particularly Walleye and Yellow Perch, are important food resources in northern communities and are harvested more frequently given capture than many warmwater species (Embke et al. 2020). Indeed, 37% of Walleye observed in our sample were harvested, compared to 8% of Largemouth Bass, a warmwater piscivore that is replacing Walleye in many systems. A shift from coolwater and coldwater fishing opportunities to warmwater fishing opportunities may therefore decrease the value of freshwater fisheries as food sources (Nyboer et al. 2022). However, the decision to harvest fish for food may not be based solely on the species caught but rather on a complex set of social–ecological interactions, making it difficult to predict the emergent consequences of climate change for fish as food (Kaemingk et al. 2019).

Although compensation for diminished production of coolwater species like Walleye and Yellow Perch may be possible with increased production of warmwater species like Largemouth Bass, Bluegill, and catfishes in some systems (indeed, anglers in our sample harvested 39% of captured Bluegill and 43% of Channel Catfish), the transition will likely pose new challenges for anglers and managers (Ojea et al. 2020). For example, many anglers increasingly value high-quality Bluegill fisheries, but some segments of the angling public persist in prioritizing high-yield Walleye fisheries, even in locations where Walleye are becoming less available (Tingley et al. 2019a). We predict that WCS will likely rise as the climate warms, but we cannot predict whether increasing warmwater opportunities will be enough to offset the loss of coldwater and coolwater species biomass. Some lakes in our study region already experience an overharvest of sunfishes, which has led to a diminished size structure and has limited the yield of harvested fish (Lyons et al. 2017; Rypel et al. 2018). Some fisheries management agencies are testing more assertive harvest regulations (e.g., reducing *Lepomis* spp. daily bag limits by half; Rypel et al. 2016) to facilitate robust size structure and harvest yields among sunfish populations that may replace formerly abundant coolwater species. As lake temperatures rise over the next century, managers and anglers alike will face the challenge of meeting angler expectations in changing fish communities (Hunt et al. 2016; Paukert et al. 2021).

Influence of angler behavior

In addition to elucidating the causes of variation in angler catch composition, our findings highlight the value and limitation of recreational fisheries creel data. Recreational angling outcomes are built on an ecological foundation; to

be caught, fish must be present in a system. However, catch composition is also a product of angler objectives and decisions (Tingley et al. 2019b; Arlinghaus et al. 2020). The positive relationship between lake GDD and WCS may be due in part to anglers targeting specific taxa in environments that they consider suitable for those taxa and using gears that they consider appropriate (Heermann et al. 2013; Hunt et al. 2016, 2019). In other words, coolwater and coldwater catch share might be higher in colder lakes in part because anglers and managers preferentially target those lakes for coolwater and coldwater fishing and research.

Our finding that WCS decreased with survey ice coverage demonstrates that both angler behavior and fish biology are essential to parsing creel data. We found that WCS was lower in surveys that included a larger proportion of days with ice coverage. The negative relationship between survey ice coverage and WCS makes sense biologically; coolwater and coldwater fishes may remain active in the winter, foraging and even spawning under the ice, so ice anglers are more likely to encounter them relative to warmwater fish, which are less active in winter (Shuter et al. 2012; Fernandes and McMeans 2019). However, increased coolwater and coldwater representation in surveys with more ice coverage is likely also a product of angler decisions. Ice anglers often target coolwater species, such as Yellow Perch and Northern Pike, and are much more likely to harvest these coolwater fishes than are open-water anglers (Sass et al. 2023). As lakes become warmer and ice fishing seasons become shorter, angler behavior may change in unpredictable ways. Any efforts to document changing fisheries populations, practices, and yields using recreational fishing data will therefore likely benefit from accounting for fish biology, human behavior, and their interaction.

Limitations

We developed our model using existing angler survey data that were not originally collected for this purpose; hence, those data reflect the informational needs of the three management agencies that collected them. We therefore advise managers seeking to use our findings—or future investigators seeking to use CreelCat data—to do so with an understanding of the full context of the data and their application here. We included a fairly limited suite of variables to focus the analysis on lake GDD and morphometry. Climate vulnerability, however, involves many factors beyond thermal conditions and lake morphometry. Because both temperature and dissolved oxygen profiles change seasonally, the volume of water with both suitable temperature and oxygen concentration (or “oxythermal habitat”) may be smaller

than the volume of suitable water temperatures (Jacobson et al. 2011; Magee et al. 2019). Even large, deep lakes must therefore maintain sufficient dissolved oxygen to effectively provide thermal refuges. Water levels may fluctuate greatly as a function of precipitation, especially in reservoirs used for irrigation or flood control, affecting recruitment success for many species and fishing opportunities for anglers (Siepker and Michaletz 2012). Additionally, climate change may increase the frequency of mass mortality events, like disease outbreaks or hypoxic crises, changing fish population dynamics in ways that we have not accounted for here (Paukert et al. 2021). Conversely, coolwater and coldwater fishes may adapt to rising temperatures, and managers may take action to maintain coolwater and coldwater habitat (Young et al. 2017).

Fully disentangling the ecological dynamics of fish populations from the effects of angler behavior requires additional data that we did not have because they are not collected at the same scale as catch and effort data. Most creel programs only ask anglers about catch, effort, and harvest. Of the three states included in our study, only Wisconsin consistently provided data on what species were targeted by anglers. This is a missed opportunity. Asking anglers about target species in a standard creel survey could help us begin to disentangle the social and ecological causes of variation in fishing outcomes and to facilitate more targeted ecological intervention and angler engagement (Jones and Pollock 2013). Additionally, creel programs may target the largest or most popular lakes, creating a nonrandom sample of angler behavior that is often not accounted for statistically (Chizinski et al. 2014). Future creel survey and modeling efforts will likely find it of interest to seek representative creel samples that can be used to develop explicit models of scale dependence in angler outcomes. Our study was based on existing data, and our findings are thus subject to any study design or sampling bias that was present in the original data. We advise readers to proceed with this limitation in mind, and we stress that a rigorous sampling design is important for the outcome of future creel survey efforts. Ultimately, we hope that the insights we have drawn here from nearly 600 lakes over three states may serve as a useful starting point for proactively adapting freshwater fisheries practices to a changing climate.

Management implications

We suggest that fisheries managers and anglers may need to adapt to warming temperatures if freshwater recreational fishing is to continue providing food and recreation benefits. The resist–accept–direct (RAD; Lynch et al. 2021b; Thompson et al. 2021; Schuurman et al. 2022) framework can help fisheries managers to navigate a changing climate.

The RAD framework proposes that decision makers faced with environmental change have three fundamental options. They may (1) *resist* the change, or try to stop it from happening; (2) *accept* the change and let it proceed without intervention; or (3) *direct* the change by managing the transition from one state to another. Our results suggest that conservation decision makers and managers may find value in a regional RAD approach (e.g., Dassow et al. 2022; Ward et al. 2023). Under such a program, lakes within a region are sorted into “resist,” “accept,” or “direct” pathways according to each lake's relative adaptive potential within the larger regional climate context. Such an approach will likely be facilitated by collaborative goal setting, climate evidence integration, and angler engagement.

Every management jurisdiction is likely to have some systems that may be better suited to “resist” strategies for coolwater and coldwater fish species and other systems where the “accept” and “direct” strategies are likely to be the most viable. Lakes that are predicted to stay cool throughout the year or provide thermal refuges during the hot months are likely to yield the best return on investments into resisting the shift from coolwater to warmwater fisheries, whereas systems that are likely to warm significantly may be better served by the accept and direct approaches. For example, Leech and Roosevelt lakes, the two Minnesota lakes highlighted in our case study, currently both provide fishing opportunities for coolwater species like Walleye, Yellow Perch, and Northern Pike (Minnesota Department of Natural Resources 2018; Pedersen 2020). However, Roosevelt Lake also provides robust fishing opportunities for warmwater species, such as Largemouth Bass and sunfishes, whereas Leech Lake is prized as a coolwater destination by anglers and managers. The difference in thermal guild composition between the two lakes is likely to increase as the climate warms; smaller, faster-warming Roosevelt Lake is likely to transition to a warmwater species assemblage more quickly than larger, slower-warming Leech Lake. Although the increases are proportionally similar when one considers the starting values, the increase in WCS will likely feel more drastic to anglers and managers at Roosevelt Lake than at Leech Lake. It will therefore likely be advantageous to prioritize Leech Lake and similar lakes for coolwater conservation in a warming climate while managing the transition to a warmwater species assemblage in smaller, faster warming lakes like Roosevelt Lake.

Strategic implementation of management actions based on anticipated climate conditions and lake morphometry can help anglers and agencies to adapt to a future in which coolwater and coldwater opportunities are scarcer. Systems that maintain a safe thermal operating space for species like Walleye and Yellow Perch may still require intensive management to maintain viable fisheries. Management

agencies may see benefits from proactively addressing threats like disease, invasive species, and harmful algal blooms that may be exacerbated by warming waters. If management objectives include anglers catching many fish per unit effort, stocking may be necessary when climate change undermines natural recruitment. If management objectives include anglers catching large fish, regulations with high minimum length limits or low daily bag limits may be required to protect large fish until they reach a preferred size—assuming that is possible in new climates. As coolwater and coldwater systems become less prevalent, it will become ever more important to proactively manage those that persist to conserve coolwater and coldwater species and fishing opportunities at a regional scale.

In systems where future climates are most suited to warmwater species, management agencies can work with scientists and anglers to determine an accept/direct threshold. This may be when the estimated cost of catching a coolwater fish rises above an acceptable limit or when natural recruitment falls below a viable threshold. At this point, managers may find that the most tenable strategy is to shift their focus toward proactively managing emerging warmwater fish communities. A managed shift to warmwater species assemblages will likely require an ongoing dialogue with anglers. If it is important to maintain freshwater fisheries as a food source, agencies could work with anglers to gently shift cultural norms (e.g., encouraging the idea that consuming black basses *Micropterus* spp. is acceptable) and foster enthusiasm for consuming warmwater species like catfishes. Youth events could target species with a range of thermal guilds to help prepare young anglers for the opportunities that they will encounter within their lifetimes. Efforts to manage invasive Silver Carp *Hypophthalmichthys molitrix* have already achieved some success in this arena by encouraging anglers to harvest and consume them (Varble and Secchi 2013; Morgan and Ho 2018; Keevin and Garvey 2019). Perhaps most importantly, in-person outreach, social media, and agency publications that cater to a public audience can share the science behind species assemblage shifts and management decisions. Public outreach efforts in person and online will be essential to keeping anglers engaged and helping them to set reasonable expectations for fishing in a warming world.

SUMMARY AND CONCLUSIONS

We predicted that WCS will increase as coldwater and coolwater fish catch shares decrease within the next 20–40 years, creating a heterogeneous landscape of future fishing opportunities. These findings are based on aggregated creel studies, an approach that comes with potential limitations and biases. The patterns and limitations that we have identified

elucidate a need for future research and management practices. Creel programs could start to disentangle social and ecological determinants of catch composition by examining angler objectives in addition to angler outcomes. Fisheries management agencies may find utility in considering lake structure and temperature jointly when making management plans. Overall, we suggest that scientists, anglers, and managers may find it advantageous to proactively address this heterogeneity in climate futures by implementing a regional RAD approach to maintain coolwater fishing opportunities where possible and to adapt to new warmwater fishing opportunities where necessary.

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Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. All data, metadata, and related materials are considered to satisfy the quality standards relative to the purpose for which the data were collected. Although these data have been processed successfully on a computer system at the U.S. Geological Survey (USGS), no warranty, expressed or implied, is made regarding the display or utility of the data for other purposes, nor on all computer systems, nor shall the act of distribution constitute any such warranty. The USGS or the U.S. Government shall not be held liable for improper or incorrect use of the data described and/or contained herein. First and foremost, we thank the state and territorial natural resources agencies that contributed data to CreelCat. Funding for this project was provided by the USGS National Climate Adaptation Science Center. The Missouri Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement among the USGS, Missouri Department of Conservation, University of Missouri, U.S. Fish and Wildlife Service, and Wildlife Management Institute. We thank D. Smith for his insightful feedback on this manuscript and its accompanying code. We furthermore thank two anonymous reviewers and the handling editor for their time and expertise, which have greatly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT



All code and data are available at https://osf.io/qrpjd/?view_only=5eebf9a37c2f4284afac9c014f947ccf.

ETHICS STATEMENT

There were no ethical guidelines applicable to this study.

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SUPPORTING INFORMATION

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