Understanding inland recreational fisheries in a changing climate

by

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Abstract

Inland recreational fisheries are ecosystem service hotspots, providing disproportionate subsistence, economic, and cultural benefits to many communities. However, freshwaters are transforming at a rapid rate and are sensitive to multiple drivers including climate change and land-use change. Managing transforming inland systems presents challenges as some drivers, such as climate change, are beyond local control. Other influential factors including fisheries harvest and species assemblage are potentially under local control, but it is unclear the impact these drivers have on inland recreational fisheries. I sought to understand the role of harvest and species interactions on inland recreational dynamics to inform climate adaptation approaches. To do this, in chapters 1 and 2 I evaluated the role of harvest in inland recreational fisheries using multiple approaches. In chapter 1, I scaled-up waterbody-specific harvest estimates to estimate the statewide magnitude of harvest and consumption to understand the contribution of inland recreational fisheries to food security and the economy. I found that inland recreational fisheries consumption was likely an important food source for angling communities and contributed $63 million annually, which went unmeasured. In chapter 2, I took an in-depth analysis into the harvest dynamics of a single, multi-use fishery, walleye (*Sander vitreus*), by applying a novel production approach. I found prolonged and increasing production overharvest in the northern Wisconsin walleye fishery, likely contributing to species declines in combination with a complex of other factors including climate change, emphasizing the need for sensitive assessment metrics. Then in chapters 3 and 4, I evaluated the impact of species interactions on inland recreational fisheries through an intensive whole-lake fish removal experiment in a north temperate lake. I removed ~285,000 warmwater Centrarchidae spp. from a 33.1 ha lake and found a ~23% decline in centrarchid biomass. One coolwater species, walleye, did not respond, however another

coolwater species, yellow perch (*Perca flavescens*), biomass increased by ~900%, emphasizing

the contrasting responses thermally-similar fishes can have to changing food web interactions.

These studies demonstrated that harvest and species assemblages are influential drivers of

change for inland recreational fisheries.

Introduction

Inland recreational fisheries are ecosystem service hotspots, employing more than 60 million people and valued at $190B globally (World Bank 2012). However freshwater ecosystems and the fisheries they support are increasingly affected by global environmental change, including land use, habitat, climate, community assemblage, and harvest changes (Carpenter et al. 2011). Understanding the effects of these large-scale shifts on inland ecosystems is imperative to supporting self-sustaining fish populations. Knowledge gained from this understanding can inform potential conservation options by identifying factors fisheries managers can influence as well as factors they do not. These tradeoffs can be leveraged through the concept of a 'safe operating space' (SOS; Carpenter et al. 2017), wherein managers can work to maintain a fishery in acceptable limits of core factors (e.g., harvest, biotic interactions) while allowing for variation in external drivers to identify adaptive actions to protect inland fisheries given global change.

Key to developing a comprehensive understanding of drivers influencing freshwater fish populations is to identify the magnitude and role of influential factors (e.g., harvest, species interactions) on ecosystems. One of these drivers, harvest, is under the control of managers, but little is known regarding the magnitude and impact of recreational fisheries harvest due to challenges in reporting and assessing the high number of mobile and transient participants in relation to dynamic fish communities. In **chapter 1**, I quantified annual recreational harvest from lakes in Wisconsin and evaluated species-specific temporal dynamics to inform our understanding of the importance of recreational fisheries as a source of food as well as ecosystem service conservation and management (Embke et al. 2020). In **chapter 2**, I evaluated

the role of harvest in inland recreational fisheries using production dynamics of the walleye fishery of the Ceded Territory of Wisconsin (Embke et al. 2019).

In addition to harvest, species interactions may influence the SOS for a given species, but it is unclear how these interactions affect populations in relation to shifting abiotic conditions, for example between cool- and warm-species. In **chapter 3**, I tested if the removal of warm-water predators/competitors would result in an increase in natural walleye recruitment through an intensive whole-lake fish removal experiment (Embke et al. 2022). Additionally, from this whole-lake experimental fish removal, in **chapter 4** I quantified the influence of warmwater species in regulating coolwater fishes through food web interactions. These studies will further our understanding of the conditions necessary to support culturally, ecologically, and economically valuable inland recreational fisheries in a changing climate.

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Chapter 1: Fishing for food: quantifying recreational fisheries harvest in Wisconsin lakes

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Abstract

Recreational fisheries have high economic worth, valued at $190B globally. An important, but underappreciated, secondary value of recreational catch is its role as a source of food. This contribution is poorly understood due to difficulty in estimating recreational harvest at spatial scales beyond a single system, as traditionally estimated from individual creel surveys. Here, we address this gap using 28-year creel surveys of ~300 Wisconsin inland lakes. We develop a statistical model of recreational harvest for individual lakes and then scale-up to unsurveyed lakes (3,769 lakes; 73% of statewide lake surface area). We generate a statewide estimate of recreational lake harvest of ~4,200 t and an estimated annual angler consumption rate of ~1.1 kg, nearly equal to total estimated United States per capita freshwater fish consumption. An important ecosystem service, recreational harvest makes significant contributions to human diets and plays an often-unheralded role in food security.

1.1. Introduction

Globally, annual recreational fisheries expenditures are valued at $190B (World Bank 2012), with United States inland recreational fisheries expenditures estimated to have exceeded $29.9B in 2011 (U.S. Department of the Interior 2016). Recreational fisheries now constitute the dominant or sole use of inland fishes in developed nations (Arlinghaus et al. 2013). For many inland fish species in North America and Europe, recreational fisheries have replaced inland commercial fisheries landings, and therefore likely contribute significantly as a source of food, but the magnitude is not well understood (de Kerckhove et al. 2015, FAO 2016, Cooke et al.

2018). Studies have found that inland fisheries contribute far more to food security than previously recognized, with potential rates of harvest underreporting as high as 65% (Fluet-Chouinard et al. 2018). Given their immense economic value and role in food security, understanding the magnitude of inland recreational fisheries is vital to conserving and managing these resources as well as ensuring global food security.

Despite increasing evidence of the importance of inland recreational fisheries for food, these systems are rarely considered in food security discussions (Cooke et al. 2016). The United Nations Food and Agricultural Organization (FAO) defines food security as existing when "all people, at all times, have physical and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life (FAO 2016)." Fish have a crucial role in ensuring food security, as they provide valuable nutrients and micronutrients of central importance for healthy diets (FAO 2016). In some regions, such as Wisconsin, recreational fisheries are recognized as an important food source for anglers, as limited surveys have shown a high reliance on these resources for food, although the magnitude remains unclear (Christensen et al. 2016). Vital to understanding how inland recreational fisheries contribute to food security discussions is accurately quantifying harvest at a meaningful scale.

Inland recreational harvest is difficult to quantify as fisheries are dispersed across the landscape, there are many mobile and transitory anglers, and reporting and monitoring are limited. Although some recreational fisheries harvest estimates have been made, most were either performed at system-specific or global scales (Ryder 1965, de Kerckhove et al. 2015, Cooke et al. 2018). Although single-system estimates are useful for identifying potential drivers of harvest, they have rarely been used to understand the larger scale magnitude of recreational

fisheries harvest beyond a local system. Likewise, broad-scale estimates can provide global context as to overall fisheries harvest, but rarely emphasize quantifying recreational fisheries harvest and likely overlook important regional nuances necessary to inform an accurate understanding of the magnitude of recreational fisheries harvest.

In some developed regions, such as parts of the United States, recreational inland fish harvest data are available through time and across many sites. By understanding the implications of temporal and spatial variation in recreational harvest, we can inform the value of inland recreational fisheries given global environmental and social changes. Areas where data are available can be used to elucidate how recreational fisheries contribute to human consumption and overall fisheries harvest. In Wisconsin, over the past 28 years the Wisconsin Department of Natural Resources has conducted extensive creel surveys for 267 inland lakes distributed across the state. Here, we used comprehensive empirical data to develop a robust statistical model predicting Wisconsin lake-specific harvest based on lake predictor variables that includes abiotic and angler access information. We used this model to scale-up and estimate statewide recreational lake fisheries harvest. Such assessments will help guide science, policy, and fisheries management decisions to better balance consumptive use and conservation of fisheries resources.

1.2. Methods

Study area

The state of Wisconsin includes ~15,000 inland lakes ranging from 0.5 to 53,394 ha (Wisconsin Department of Natural Resources 2009). Most lakes occur in the northern and eastern part of the state as a result of glaciation. Approximately 3,620 lakes are > 20 ha and together comprise ~93% of the state's inland lake surface area (Wisconsin Department of Natural

Resources 2009). Wisconsin lakes constitute a wide range of physical and biological characteristics. Wisconsin inland lakes (not including the Great Lakes) support valuable recreational fisheries for a variety of species, including Walleye (*Sander vitreus*), Northern Pike (*Esox lucius*), Muskellunge (*Esox masquinongy*), Yellow Perch (*Perca flavescens*), Largemouth Bass (*Micropterus salmoides*), Smallmouth Bass (*Micropterus dolomieu*), Lake Sturgeon (*Acipenser fulvescens*), and a variety of sunfish species (*Lepomis spp.*).

Calculating empirical harvest

A standard angler creel survey was performed on a total of 267 inland lakes from 1990-2017 by the Wisconsin Department of Natural Resources (WDNR, unpublished data). Sampled lakes were selected using a rotating stratified randomized design therefore, most lakes were sampled once during 1990-2017, but some lakes were resampled during the study period. Total harvest was estimated as the product of angler effort and harvest rate (Rasmussen et al. 1998, Deroba et al. 2007). To estimate effort, instantaneous counts of anglers were conducted, while complete-trip interviews were conducted to estimate harvest rate (Rasmussen et al. 1998). During interviews, creel clerks recorded the number caught and length of fish for each species (Deroba et al. 2007). To estimate species-specific effort, anglers indicated how long they had been fishing and how much of their time was allocated to a particular species. Creel surveys were conducted beginning the first Saturday in May through March 1 of the following year, a period spanning the legal walleye angling season (Beard et al. 1997). Survey access points were randomly selected following a random stratified roving access design that was demonstrated to produce unbiased estimates of angling effort and harvest (Pollock et al. 1994, Rasmussen et al. 1998). Survey days were stratified into weekdays and weekend days, with 1-3 randomly selected weekdays and all weekend days sampled each week (Beard et al. 1997). Throughout the open-

water season, surveys were conducted during randomly selected periods. During the ice-fishing

season, complete days were sampled as daylight was shortened (Beard et al. 1997). Additionally,

creel surveys provided angler counts by type (e.g., boat, shore, ice) (Rasmussen et al. 1998).

Annual creel information including the total number of fish harvested per species (as

projected by WDNR based on angler effort and empirical harvest; n yr^{-1}) as well as species-

specific mean lengths were available for all harvested species for 267 lakes (573 lake-year

combinations). In addition to the number of fishes harvested annually, we were interested in

quantifying the mass of fishes harvested, therefore we compiled species-specific length-weight

regressions from multiple sources (Table S1). We applied these length-weight relationships to

convert species-specific mean length (mm) to mean weight (kg) for species in each lake-year

combination of harvested fish. We multiplied the total number of fish harvested per species by

the mean weight to estimate the species-specific total biomass harvested (kg) for that lake-year.

For each lake-year combination, we summed species-specific harvest values to calculate total

annual harvest (kg y^{-1}). This value was divided by the area of the lake to estimate total harvest

per unit area (kg ha^{-1}).

Lake Winnebago, the largest inland lake in Wisconsin, does not undergo a complete creel

survey similar to other lakes in the state, but does support Walleye, Lake Sturgeon, Yellow

Perch, and sunfish fisheries (Koenigs and Olynyk 2013, Koenigs et al. 2013, Koenigs 2017). We

estimated total annual harvest for this lake using a combination of data sources. A limited creel

was performed in 2012 from June-August, with a total of 35 days of angler interviews (Koenigs

and Olynyk 2013). This limited creel found that anglers harvested Black Crappie (*Pomoxis

nigromaculatus*), Bluegill (*Lepomis macrochirus*), Walleye, and Yellow Perch (Koenigs and

Olynyk 2013). From this information, we calculated the number of fish per species harvested

daily, which we multiplied by 365 to estimate the total number harvested for the year. We did this for Black Crappie, Bluegill, and Yellow Perch, but estimated Walleye harvest using more complete information. Mean lengths for Black Crappie and Bluegill were not available in the creel, therefore we calculated the mean length of all Black Crappie and Bluegill present in the statewide creel and used that information to estimate mean weights using species-specific length-weight regressions. Yellow Perch mean length was available from creel surveys and therefore this value was used to estimate mean weight using the species-specific length-weight relationship. Walleye are managed extensively in this system through annual surveys that estimate exploitation rate and other characteristics (Koenigs et al 2013). Mean abundance of adult (≥381 mm) Walleye as well as the mean exploitation rate from 1993-2012 were estimated (Koenigs et al. 2013). Mean lengths of males and females were also reported (Koenigs et al. 2013). From this information, we calculated the number of Walleye harvested annually using sex-specific abundances multiplied by sex-specific exploitation rates. Sex-specific mean length information was available from annual surveys, therefore we used this in combination with the species-specific length-weight regression to estimate mean weight and total Walleye harvest. The Lake Winnebago Lake Sturgeon fishery occurs annually and is highly regulated (Koenigs 2017). From available WDNR information, we calculated the mean number of Lake Sturgeon harvested between 2002-2016 as well as the mean length and weight of harvested individuals (Koenigs 2017).

Evaluating species harvest and angler effort trends

We evaluated temporal trends for overall combined harvest (kg ha^{-1}) and angler effort (hr ha^{-1}) from 1990-2017. Although 38 species contributed to overall harvest, we evaluated temporal trends for 10 species that comprise ~90% of harvest and were consistently present in creel

surveys. These species included Black Crappie, Bluegill, Largemouth Bass, Muskellunge, Northern Pike, Pumpkinseed (*Lepomis gibbosus*), Rock Bass (*Ambloplites rupestris*), Smallmouth Bass, Walleye, and Yellow Perch. To determine if species-specific harvest and angler effort changed over the study period, we developed species-specific linear mixed effects models for standardized harvest (kg ha^{-1}) and angler effort (hr ha^{-1}). We ran Shapiro-Wilk tests to determine whether the distributions for harvest (kg ha^{-1}) and effort (hr ha^{-1}) were normal. Based on findings, harvest and effort were log$_e$-transformed prior to analysis to meet assumptions of normality. For each model, log$_e$(harvest+1) or log$_e$(effort+1) was the dependent variable, year (centered around the mean) was an independent variable, and lake was a random effect. Models of best fit were first selected based on Akaike information criterion (AIC). If there was no difference between AIC values, the model of best fit was selected based on variance explained.

Evaluating angler license trend

To inform angler consumption information, we assessed the temporal trend of the number of fishing licenses purchased in Wisconsin (https://wsfrprograms.fws.gov/Subpages/LicenseInfo/Fishing.htm) using a linear model. For this model, the number of fishing licenses was the dependent variable and year (centered around the mean) was the independent variable. Using this information, we calculated the mean number of licenses over the study period.

1.2.5 Lake attributes

Lake surface area was available for all known lakes in the state (Wisconsin Department of Natural Resources 2009). To incorporate lake-specific abiotic characteristics to determine fish yield, we obtained Secchi depth (m) and conductance (uS) measurements from a statewide dataset that averaged measurements from multiple sources (Papes and Vander Zanden 2010). For

this analysis, only datasets developed since 1970 were used. To provide an index of angler access for each lake, we calculated the linear distance from the lake shoreline to the nearest mapped road. We did this by calculating the minimum distance from each waterbody to the nearest street in ESRI's map of detailed streets (ESRI 2011). Winslow et al. (2017) developed estimates of various thermal characteristics for 10,774 midwestern lakes, including 3,769 lakes in Wisconsin. We used two modeled characteristics from this dataset in the harvest prediction model: mean temperature at the bottom of the lake in June (°C) and annual growing degree days (base temperature 5°C) as these predictors contributed to the model of best fit. We evaluated numerous other variables which were not significant (e.g., no statistically significant relationship between angler effort and minimum distance to the nearest road) and did not provide the model of best fit (Table S2).

Modeling statewide annual harvest

To estimate statewide recreational annual fish harvest per unit area (areal harvest, kg ha^{-1}), we related areal harvest (summed species harvest in a given lake-year; kg ha^{-1}) to abiotic intrinsic lake characteristics as well as waterbody access information using a generalized additive model (GAM, using the "gam" function in R package "mgcv" version 1.8.17; Wood 2011, Wood 2017). GAMs are a flexible, nonparametric technique that employs penalized regression splines to fit smooth relationships between response and explanatory variables (Wood 2017). Distance to nearest road (m) and Secchi depth (m) exhibited linear relationships with harvest. Smooth curves were fit for mean temperature of the lake bottom in June (°C), annual growing degree days (base temperature 5°C), and conductance (uS) using thin plate spines with a null space penalty (Fig. S1). Although most lakes were sampled once during 1990-2017, some lakes were resampled, therefore lake and year were included as random effects (slope and intercept) in the model to

account for lake-specific and temporal variation during different sampling periods. Models were

fit using restricted maximum likelihood (REML).

Prior to model fitting, we assessed the statistical distribution of each predictor variable

and areal harvest (kg ha^{-1}) by constructing relative frequency histograms for each statistic and

ran Shapiro-Wilk tests to assess distribution normality. The model was fit using the 'Tweedie'

family such that a log-link function was used for non-normal statistics and zero values were

incorporated as potential predictions (Wood 2017). The model of best fit was selected based on

Akaike information criterion (AIC) and REML. We applied this model to 3,769 lakes that had

information available to predict lake-specific areal annual harvest (kg ha^{-1}). We multiplied these

values by lake area and summed lake-specific harvest values to calculate total annual harvest

(kg) and then converted total annual harvest to metric tonnes (t). We used an $\alpha = 0.05$ for all

statistical analyses. All calculations and statistical analyses were performed in R version 3.4.3 (R

Development Core Team 2017). All data have been made available as part of the Environmental

Data Initiative (Embke et al. 2020).

1.3. Results

Species composition of recreational harvest

Thirty-eight species were harvested, with median harvest values ranging from 0.01 to

0.95 kg ha^{-1} (Fig. 2). Walleye, Black Crappie, Lake Whitefish, Northern Pike, Bluegill, and

Yellow Perch had the largest median harvest values, all exceeding 0.25 kg ha^{-1} across all years

(Fig. 2). Five species accounted for the vast majority (90%) of overall harvest (kg): Walleye,

Black Crappie, Bluegill, Northern Pike, and Yellow Perch, although the relative importance of

species varied over time (Fig 3A, Fig. S2). For example, in 1990, Walleye comprised 25% of

overall annual harvest but by 2017 the contribution of Walleye fell to ~9% (Fig 3A). In contrast, the contribution of Black Crappie rose from ~11% to ~22% during the study period (Fig 3A).

1.3.2 Evaluating select species harvest, angler effort, and angler license trends

Overall combined harvest (kg ha^{-1}) and angler effort (hr ha^{-1}) for all species did not exhibit a significant change over the study period. Although 38 species contributed to overall harvest, five species (Black Crappie, Bluegill, Largemouth Bass, Muskellunge, and Walleye) showed significant temporal harvest trends (Fig. 3B; Table S3). Harvest of Muskellunge and Walleye declined over the study period (Fig. 3B). In contrast, Black Crappie, Bluegill, and Largemouth Bass showed harvest increases (Fig. 3B). Northern Pike, Pumpkinseed, Rock Bass, Smallmouth Bass, and Yellow Perch did not display significant temporal harvest trends. Seven species experienced significant changes in angler effort over time (Fig. 3C). Walleye, Muskellunge, and Rock Bass showed declines in effort (hr ha^{-1}), while Black Crappie, Largemouth Bass, Smallmouth Bass, and Pumpkinseed showed increases in effort (hr ha^{-1}) (Table S3, Fig 3C). Bluegill, Northern Pike, and Yellow Perch did not show significant changes in effort over the study period.

We found a slight declining relationship in the number of fishing licenses purchased over time (% change over the study period = -3.6%, p<0.01; Fig. S3). The mean number of fishing licenses during the study period was 1,405,262, which we used to estimate angler consumption rates.

Statewide harvest model results

From available creel information, areal annual lake-specific harvest (all species-specific harvest combined) ranged from 0.03 to 71.04 kg ha^{-1} with a median value of 5.29 kg ha^{-1} (mean(log(harvest)) = 1.57 +/- 0.05 (95% CI) kg ha^{-1}) (Table S4). Lake surface areas ranged

from 8.9 to 53,394 ha (median = 216 ha) and locations spanned the state (Fig. 1, Table S4).

Using the GAM (AIC = 2936, REML = 1589, $R^2_{adjusted}$ =0.78), total annual harvest (kg ha^{-1}) was

estimated for 3,769 lakes with surface areas ranging from 2-53,394 ha (median = 15 ha) (Table

S4). Harvest (kg ha^{-1}) decreased linearly as distance to the nearest road (m) and Secchi depth (m)

increased. Thermal predictor variables (i.e., mean bottom temperature of the lake in June (°C),

growing degree days$_{5°C}$) as well as conductance (uS) increased non-linearly with harvest (kg ha^{-1}; Fig. S1).

Estimated areal harvest ranged from 0-48.35 kg ha^{-1} with a mean harvest of 5.3 +/- 0.14

(95% CI; kg ha^{-1}) (Fig. 1). For 3,769 lakes (surface area of 305,693 ha), we estimated that 3,580

+/- 1,566 (95% CI) t of fishes were harvested annually by recreational anglers from Wisconsin

lakes. These lakes comprised 73% of the entire state's lake surface area. The remaining lakes for

which we were unable to estimate harvest due to data limitations were predominantly (80%)

small lakes (i.e., surface area < 5 ha). When we applied our median harvest estimate of 5.3 kg ha^{-1} to the remaining lakes for which we were unable to estimate harvest using the model (surface

area = 113,117 ha), this corresponded to ~4,200 t harvested annually by recreational anglers in

Wisconsin.

1.4. Discussion

Though interest in the importance of inland recreational fisheries is growing, information

relating to the scope, magnitude, and value of such fisheries is remarkably limited (Lynch et al.

2016, Cooke et al. 2018, Arlinghaus et al. 2019). As a result, major gaps remain in our

understanding of their social and economic value of inland recreational fisheries to humans

(Cooke et al. 2018, Arlinghaus et al. 2019). To address one aspect of this gap, we quantified the

magnitude of recreational fisheries harvest in Wisconsin to find high levels of harvest resulting

in angler consumption rates nearly equal that of the broader United States. Specifically, we developed a robust modeling approach that incorporated abiotic and angler access information to estimate the magnitude of inland recreational fisheries harvest for ~4,000 Wisconsin lakes. We estimated that anglers in Wisconsin annually harvest ~4,200 t of fishes from lakes, highlighting the important ecosystem service of recreational fisheries as a source of food.

We developed a model for estimating lake-specific recreational harvest, that we then used to approximate statewide recreational harvest. The model we developed incorporated information about angler accessibility, which improved our model predictions, without directly relying on angler effort information as a predictor variable, which restricted model prediction capacity due to data limitations. Other harvest estimation approaches have relied heavily on angler effort information (Deines et al. 2017), but this poses challenges when attempting to extrapolate estimates to a large number of systems as effort data is commonly lacking. Therefore, to incorporate angler access, we found that as lakes were farther from a road, predicted harvest declined (Fig. S1). Similar to previous analyses focusing on the interaction between thermal conditions and fish biomass (de Kerchhove et al. 2015), we found that warmer thermal conditions (higher summer bottom lake temperatures and higher annual growing degree days) corresponded with increased harvest (Fig. S1). Additionally, we found that valuable predictors of fish yield included indicators of the trophic status of the lake (i.e., Secchi depth, conductance). Both variables indicated that more productive systems (i.e., lower Secchi depth, higher conductance) resulted in higher levels of harvest, corresponding to literature predictors of fish harvest (Ryder 1965, Deines et al. 2017). Our approach leveraged robust empirical information across both time and space through the incorporation of random effects to account for temporal variability and among lake variation. Many of the lakes for which we estimated harvest were

small lakes (<10 ha, n=1,391), which comprise a portion of systems rarely considered in large-scale harvest analyses but contribute substantially to total harvest.

Our analyses do not extend beyond Wisconsin, but the approach we developed can be used to inform broad-scale analyses. Additionally, the majority of recreational fisheries occur within developed countries and therefore our estimates may be applicable to similar landscapes, if we assume recreational anglers harvest fish in similar fashion in other regions (Arlinghaus et al. 2013). This presents an opportunity for future evaluation, wherein if angler harvest patterns across varying landscapes were compared, it could be used to inform overall recreational harvest. Global estimates often overlook regional differences, but this variation may be substantial and therefore regional estimates like that performed in this study have the potential to inform data-poor scenarios.

We extrapolated empirical harvest information to estimate total statewide recreational harvest, however we acknowledge limitations of our approach. Firstly, we limited our analyses to inland lakes due to data limitations, even though other waterbodies, including ~51,500 river km (https://dnr.wi.gov/topic/Rivers/FactsResources.html) as well as wetlands and Laurentian Great Lakes contribute substantially to global harvest and food security (Lymer et al. 2016, McIntyre et al. 2016). Improved harvest estimates of these systems utilizing similar approaches to those we employed are greatly needed to more accurately understand the role of recreational fisheries in fisheries harvest.

Secondly, although we considered spatio-temporal creel sampling variation by incorporating lake and year as random effects in our model, there was additional variation in the empirical creel estimates we did not consider when scaling-up to the statewide level. As our intention was to understand broad-scale patterns in recreational fishing harvest in Wisconsin, we

used mean species-specific annual harvest estimates to inform our model but understand that these estimates were variable. This variation may influence our estimates and would be an avenue for further research in refining recreational harvest estimates. Finally, the lakes in our study were potentially biased towards lakes in northern Wisconsin, as these are much more commonly surveyed, where certain species (e.g., Walleye) are more selectively targeted (Cichosz 2017). However, the variables used to predict harvest were spatially independent and spanned the range of values used to estimate harvest. Lakes in southern Wisconsin are commonly warmer, more productive systems and thus likely contribute higher harvest in combination with the fact that anglers in southern lakes potentially target different species (e.g., *Lepomis* spp., that are viewed more consumptively) than those in northern lakes. Overall, our analysis provides a novel approach to estimate the contribution of inland recreational fisheries to overall fisheries harvest.

The creel survey revealed that 38 species were harvested over the past 28 years from lakes in Wisconsin (Fig. 2), a much larger number than those species actively managed by state agencies. Harvest was largely comprised of commonly targeted taxa, including Walleye, Northern Pike, Lake Whitefish, and sunfishes, but many other species contributed to overall harvest (Fig. 2). Additionally, our findings demonstrated species-specific harvest trends (Fig. 3). As harvest and angler effort of Muskellunge and Walleye declined, harvest and effort increased for other species, in this case Black Crappie and Largemouth Bass (Fig. 3). These species-specific trends align with species abundance shifts (Hansen et al. 2017). In contrast, Bluegill harvest increased but effort did not, indicating anglers may be choosing to keep additional Bluegill that they previously released (Fig 3). Some species, including Smallmouth Bass and Pumpkinseed showed significant changes in effort but no changes in harvest, indicating that

while these species may be important recreational target species, they may not be of interest to consumptive anglers (Fig. 3).

Overall pooled harvest and effort did not change over time even though species-specific shifts occurred, indicating anglers consistently harvested the same amount of fish, but the species that comprised that harvest did change. Additionally, total harvest and effort remained constant as the number of fishing licenses declined, potentially indicating that the dominant proportion of harvest is driven by a smaller group of highly skilled anglers who continued to harvest fish despite large-scale changes (e.g., species abundance shifts). We did not explore relationships between angler types (e.g., boat, bank, ice) but it would be an interesting area for future research to understand harvest dynamics of different consumptive anglers as they are known to target different species and how this relates to broad-scale ecosystem changes (Kaemingk et al. 2020). Although much management focus is put on specific species, consumptive anglers may target a variety of species and compensate to other species as a food source if they are primarily motivated by subsistence even if a preferred species declines. Harvest-switching by anglers to compensate and maintain overall harvest levels has significant implications for natural resource managers and our understanding of ensuring food security.

Few have assessed the magnitude of recreational fisheries harvest beyond individual systems, yet many have estimated global lake fisheries harvest (Welcomme 2011, Lymer et al. 2016, Deines et al. 2017). Employing a variety of extrapolation methods, including simple relationships between lake size and harvest and theoretical habitat-specific yields, global inland lake fisheries harvest was estimated to range between 20.7 to 93 million t (mt) annually (Welcomme 2011, Lymer et al. 2016). Others have used waterbody productivity and human populations to estimate that over 11 mt were harvested from inland lakes (Deines et al. 2017).

These broad-scale approaches overlook important fine-scale processes that influence the dynamics of specific fisheries sectors, such as recreational, that are not considered in these aggregated estimates. Others have focused exclusively on recreational fisheries harvest, using Canadian average harvest (4.5 kg ha^{-1}) to extrapolate global recreational harvest to be 10.86 mt annually, with recreationally harvested fish contributing 9.3% to total fish harvest (Cooke and Cowx 2004, Cooke et al. 2018). These estimates relied on significant assumptions, e.g., that Canadian harvest patterns apply globally, which is likely not the case given international variation in angler dynamics and fisheries ecology. Using our modeling approach that goes beyond applying a local average and considers small-scale dynamics, we estimated a slightly higher median harvest level (5.3 kg ha^{-1}), indicating that global recreational harvest estimates may be underestimating the contribution of recreational fisheries, although understanding regional harvest dynamics is critical to accurately estimating this magnitude.

We found that a substantial amount of fish, ~4,200 t, was recreationally harvested annually from lakes in Wisconsin. Although angler-specific consumption rates are highly uncertain given data limitations, assuming the people harvesting the fish are eating them, if we convert our harvest estimate to edible portion given an average filet yield of ~35% (Summerfelt et al. 2010, Lyons et al. 2017), this corresponds to ~1.1 kg per angler annually. For the United States, combined freshwater and estuarine annual finfish consumption rates were estimated to be ~1.8 kg per adult and ~0.4 kg per youth (50th percentile, edible portion; Environmental Protection Agency 2014). These consumption rates did not consider the source of consumed fishes (e.g., commercially versus recreationally harvested), but given that our coarse estimate stemming solely from recreational lake harvest is nearly equal to total freshwater fish consumption, it is clear that recreational fisheries contribute substantially to overall fish

consumption. Although precise consumption rates in the region are unclear, the sizeable contribution of recreational fisheries to overall per angler fish consumption highlights the significant and overlooked ecosystem service that the recreational fisheries sector provides as a source of food and highlights a critical avenue for future research.

Given the magnitude of harvest and consumption we estimated, these findings provide context for a potentially hidden and additional source of value that is not represented in these analyses. Much emphasis has been placed on quantifying the economic impact of the recreational fisheries sector as anglers contribute economically in a variety of ways, including purchasing fishing licenses, equipment, and chartering boats, generating $2.3B annually in Wisconsin alone (U.S. Department of the Interior 2016). Using our estimates, when we compare the average price of a kg of fish in a Wisconsin grocery store (~$15), it results in a value of ~$65 million annually that is contributed by recreational fisheries but goes unmeasured. More research is needed to accurately value inland recreational fisheries, but studies like ours can serve as starting points to begin to understand the hidden contribution this sector provides to many economies.

Our findings have implications for understanding the effect of recreational fisheries on local economies, ecosystems, and management, as well as a source of food. Recreational fisheries have the potential to greatly affect fish communities, therefore understanding the magnitude of harvest can inform the conservation and management of these populations (Post et al. 2002). Others have emphasized the nutritional value fishes contribute to fishing communities, therefore estimating the magnitude of recreational harvest can inform our understanding of the often-hidden role recreational fisheries play in food security issues (Cooke et al. 2018). Given that regional differences are highly influential in these harvest patterns, we suggest that a mosaic approach wherein harvest is estimated at smaller scales, such as was done in this study, and then

combined, can provide a greater understanding of the role recreational fisheries play in overall harvest. The approach we developed can be used to guide science, policy, and management decisions on harvest levels to satisfy consumption needs as well as conserve natural resources.

1.5. Acknowledgements

1.6. References

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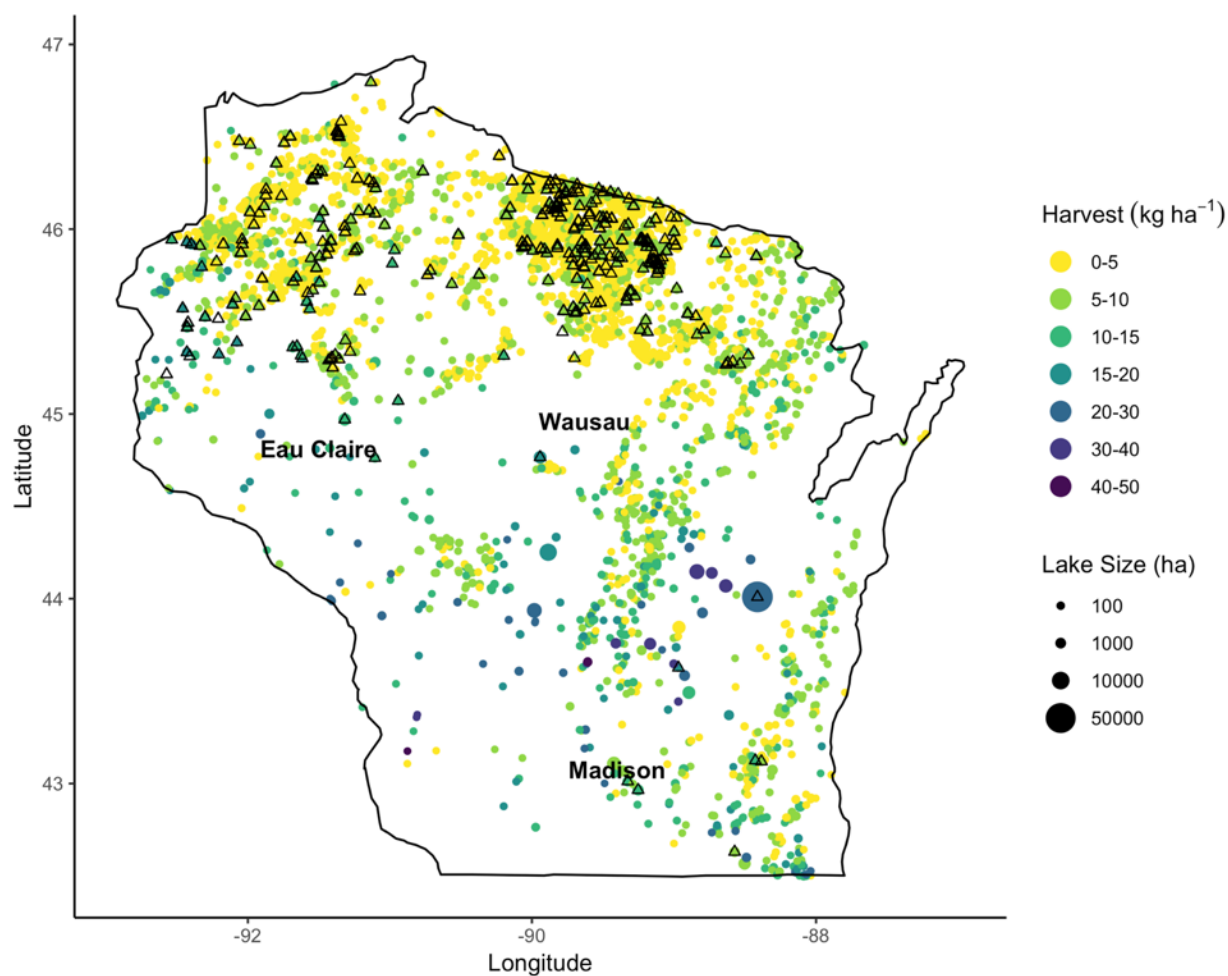
1.7. Figures

Figure 1. Predicted harvest (kg ha^{-1}) and waterbody size (ha) for lakes in Wisconsin predicted using a generalized additive model. Lakes with empirical data from 1990-2017 used to fit the model are marked with appts triangle. Reference cities (Madison, Eau Claire, and Wausau) are shown.
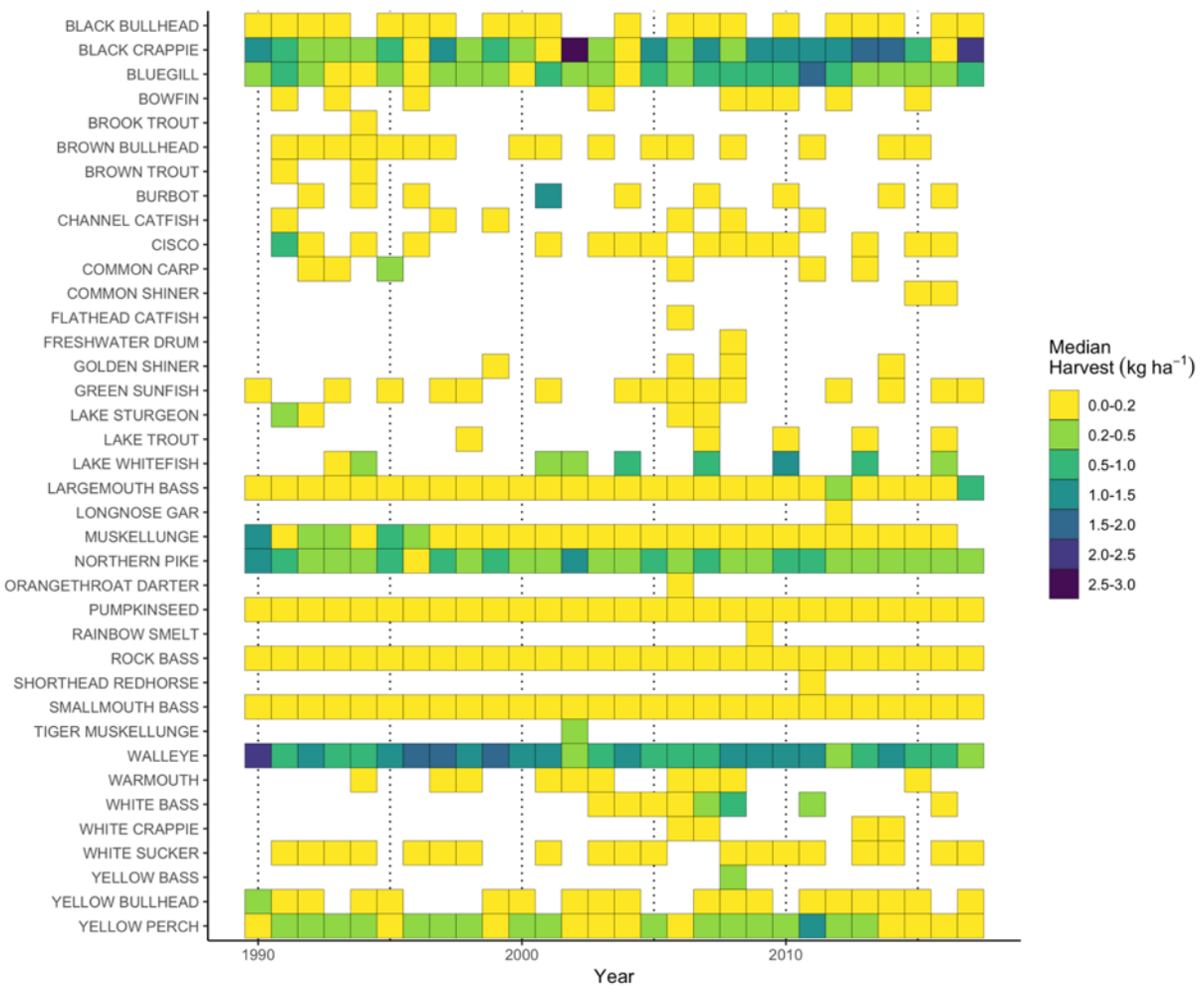
Figure 2. Species-specific annual median harvest (kg ha^{-1}) values for lakes in Wisconsin calculated from creel data from 1990-2017. Vertical dotted lines indicate 5-year intervals.
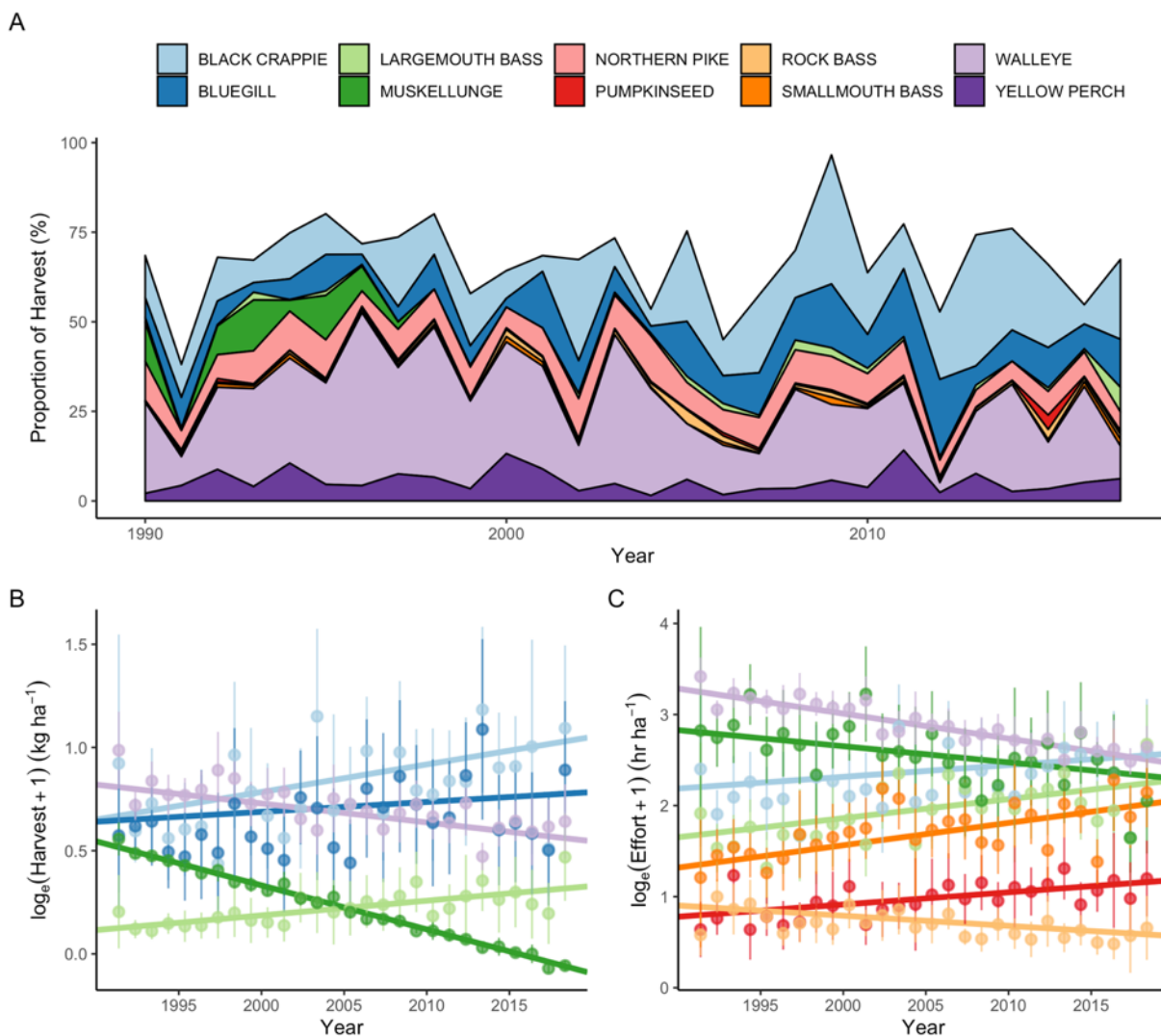
Figure 3. Species-specific proportion of harvest (%) (panel A), mean +/- 95% confidence intervals $\log_e$(harvest+1) (kg ha^{-1}) (panel B), mean +/- 95% confidence intervals $\log_e$(effort+1) (hr ha^{-1}) (panel C) from 1990-2017. Only statistically significant temporal harvest trends are shown in panel B and C, with trend lines corresponding to linear mixed effects models. Species include Black Crappie (*Pomoxis nigromaculatus*; light blue), Bluegill (*Lepomis machrochirus*; dark blue), Largemouth Bass (*Micropterus salmoides*; light green), Muskellunge (*Esox masquinongy*; dark green), Northern Pike (*Esox lucius*; light red), Pumpkinseed (*Lepomis gibbosus*; dark red), Rock Bass (*Ambloplites rupestris*; light orange), Smallmouth Bass (*Micropterus dolomieu*; dark orange), Walleye (*Sander vitreus*; light purple), and Yellow Perch (*Perca flavescens*; dark purple).

1.8. Appendix Tables and Figures

Table S1. Literature sources of taxa-specific length-weight regressions used to estimate taxa-specific mean weights from empirical creel data for Wisconsin lakes from 1990-2017.

Taxa	Scientific Name	Literature Source
Banded Darter	*Etheostoma zonale*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Black Bullhead	*Ameiurus melas*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Priegel, G.R., 1966. Age-length and length-weight relationship of bullheads from Little Lake Butte des Mortes, 1959. Wis. Conserv. Dept. Res. Rep. Fish. 17:6 p.
Black Crappie	*Pomoxis nigromaculatus*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.; Jennings, T., 1969. Age and growth of black crappie in Spirit Lake, Iowa. Iowa Q. Biol. Rep. 21(4):60-64.
Bluegill	*Lepomis macrochirus*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.; Parker, R.A., 1958. Some effects of thinning on a population of fishes. Ecology 39(2):304-317.
Bowfin	*Amia calva*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.
Brook Trout	*Salvelinus fontinalis*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Cooper, E.L., 1961. Growth of wild and hatchery strains of brook trout. Trans. Am. Fish. Soc. 90:424-438.
Brown Bullhead	*Ameiurus nebulosus*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Priegel, G.R., 1966. Age-length and length-weight relationship of bullheads from Little Lake Butte des Mortes, 1959. Wis. Conserv. Dept. Res. Rep. Fish. 17:6 p.
Brown Trout	*Salvelinus fontinalis*	Adams, P., C. James and C. Speas, 2008. Brown trout (Salmo trutta) species and conservation assessment: Prepared for the Grand Mesa, Uncompahgre, and Gunnison National Forests. Grand Mesa, Uncompahgre, and Gunnison National Forests, 28 p.
Bullhead Catfishes Unsp.	*Ameiurus spp.*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Burbot	*Lota lota*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Channel Catfish	*Ictalurus punctatus*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Muncy, R.J., 1959. Age and growth of channel catfish from the Des Moines River, Boone County, Iowa, 1955 and 1956. Ia. St. J. Sci. 34(2):127-137.
Cisco	*Coregonus artedi*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Common Carp	*Cyprinus carpio*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;

Common Shiner	*Luxilus cornutus*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Flathead Catfish	*Pylodictis olivaris*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Freshwater Drum	*Aplodinotus grunniens*	Velzquez-Velzquez, E., M. Maza-Cruz, A.E. G„mez-Gonz^lez and J.A. Navarro-Alberto, 2015. Length-weight relationships for 32 fish species in the Grijalva River Basin, M_xico. J. Appl. Ichthyol. 31:413-414.
Golden Shiner	*Notemigonus crysoleucas*	Chadwick, E.M.P., 1976. Ecological fish production in a small Precambrian shield lake. Environ. Biol. Fish. 1(1):13-60.
Greater Redhorse	*Moxostoma valenciennesi*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Green Sunfish	*Lepomis cyanellus*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.;
Lake Sturgeon	*Acipenser fulvescens*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Probst, R.T. and E.L. Cooper, 1955. Age, growth, and production of the lake sturgeon (Acipenser fulvescens) in the Lake Winnebago region, Wisconsin. Trans. Am. Fish. Soc. 84:207-227.
Lake Trout	*Salvelinus namaycush*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Lake Whitefish	*Coregonus clupeaformis*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Bjorklund, R.G., 1953. The lake whitefish,_Coregonus clupeaformis_(Mitchill), in Flathead Lake, Montana. Montana State University, Bozeman, Montana. 144 p. M.S. thesis.
Largemouth Bass	*Micropterus salmoides*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.
Longnose Gar	*Lepisosteus osseus*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Beckman, W.C., 1942. Length-weight relationship, age, sex ratio and food habits of the smelt (Osmerus mordax) from Crystal Lake, Benzie County, Michigan. Copeia 1942(2):120-124.
Mottled Sculpin	*Cottus bairdii*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Muskellunge	*Esox masquinongy*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Northern Pike	*Esox lucius*	Willis, D.W., 1989. Proposed standard length-weight equation for northern pike. Journal of Fisheries Manangement 9:203-208.
Orangethroat Darter	*Etheostoma spectabile*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Pumpkinseed	*Lepomis gibbosus*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.; Parker, R.A., 1958. Some effects of thinning on a population of fishes. Ecology 39(2):304-317.
Rainbow Smelt	*Osmerus mordax*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Beckman, W.C., 1942. Length-weight relationship, age, sex ratio and food habits of the

smelt (Osmerus mordax) from Crystal Lake, Benzie County, Michigan. Copeia 1942(2):120-124.

Rainbow Trout	*Oncorhynchus mykiss*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; van Woert, W.F., 1957. Time pattern of migration of adult salmon and steelhead into the upper Sacramento River steelhead. Calif. Inl. Fish. Admin. Rep. 57-19:1-5.
Redhorses Unsp.	*Moxostoma spp.*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
River Redhorse	*Moxostoma carinatum*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Rock Bass	*Ambloplites rupestris*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.; Parker, R.A., 1958. Some effects of thinning on a population of fishes. Ecology 39(2):304-317.
Shiners Unsp.	*Notropis spp.*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Shorthead Redhorse	*Moxostoma macrolepidotum*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Silver Redhorse	*Moxostoma anisurum*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.;
Smallmouth Bass	*Micropterus dolomieu*	Kolander, T.D., D.W. Willis and B.R. Murphy, 1993. Proposed revision of the standard weight (Ws) equation for smallmouth bass. N. Am. J. Fish. Manage. 13(2):398-400.
Suckers Unsp.	*Catostomus spp.*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Sunfishes Unsp.	*Lepomis spp.*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Tiger Muskellunge	*Esox masquinongy X Esox lucius*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Trouts Unsp.	*N/A*	Schneider, James C., P. W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 in Schneider, James C. (ed.) 2000. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor.
Walleye	*Sander vitreus*	Carlander, K.D., 1950. Handbook of freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. 427 p.; Carlander, K.D. and L.E. Hiner, 1943. Fisheries investigation and management report for Lake Vermilion, St. Louis County. Minn. Bur. Fish. Res. Invest. 54:1-175.

Warmouth	*Lepomis gulosus*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.; Hennemuth, R.C., 1955. Growth of crappies, bluegill, and warmouth in Lake Ahquabi. Iowa St. Coll. J. Sci. 30(1):119-137.
White Bass	*Morone chrysops*	van Oosten, J., 1942. The age and growth of the Lake Erie white bass,_Lepibema chrysops_(Rafinesque). Pap. Mich. Acad. Sci., Arts and Lett. 27:307-334.
White Crappie	*Pomoxis annularis*	Carlander, K.D., 1977. Handbook of freshwater fishery biology, volume 2. The Iowa State University Press, Ames, Iowa.
White Sucker	*Catostomus commersonii*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Parker, R.A., 1958. Some effects of thinning on a population of fishes. Ecology 39(2):304-317.
Yellow Bass	*Morone mississippiensis*	Priegel, G.R., 1975. Age and growth of the yellow bass in Lake Poygan, Wisconsin. Trans. Am. Fish. Soc. 104(3):513-515.
Yellow Bullhead	*Ameiurus natalis*	Carlander, K.D., 1969. Handbook of freshwater fishery biology, volume 1. The Iowa State University Press, Ames. Iowa. 752 p.; Priegel, G.R., 1966. Age-length and length-weight relationship of bullheads from Little Lake Butte des Mortes, 1959. Wis. Conserv. Dept. Res. Rep. Fish. 17:6 p.
Yellow Perch	*Perca flavescens*	Carlander, K.D., 1950. Handbook of freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. 427 p.; Smith, M.W., 1939. Fish population of Lake Jesse, Nova Scotia. Proc. Nova Scotian Inst. Sci. 19(4):389-427.

Table S2. Lake attributes considered to fit the generalized additive mixed effects model, but not ultimately used as predictor variables as they did not contribute to the model of best fit.

Attribute	Range	Median
Lake volume (m^3)	59300-$2.4x10^{10}$	$1.3x10^7$
Mean lake depth (m)	0.9-14.7	5.4
Max lake depth (m)	1.5-35.1	11.7
Shoreline Development Index (m)	1.037-14.947	2.062
Ice-on duration (n days)	94-184	144
Mean length of stratification (n days)	1-213	51.5
Growing Degree Days, base temperature 0ºC (n days)	2793-4567	3607
Watershed designated as wetland according to the National Land Cover Dataset (%)	0.008-0.52	0.32
Watershed designated as developed according to the National Land Cover Dataset (%)	0.016-0.54	0.05
100 m buffer designated as wetland according to the National Land Cover Dataset (%)	0-0.73	0.23
100 m buffer designated as developed according to the National Land Cover Dataset (%)	0-0.63	0.1
Public access (i.e., whether there was a public boat ramp present at the lake)	0-1	1
County population (n people)	4456-531273	21435
Linear distance from the lake shoreline to the nearest major road, determined in GIS by calculating minimum distance from each waterbody to the nearest road segment in ESRI's map of North America Major Roads, which include interstates, inter-metropolitan area, and intra-state highways and major roads mapped in 2010 (m)	0-270.7	5.8

Table S3. Model selection results for species-specific linear mixed effects models for harvest (H; kg ha^{-1}) for fish populations in Wisconsin lakes during 1990-2017 (n=613). Species include Black Crappie (*Pomoxis nigromaculatus*), Bluegill (*Lepomis machrochirus*), Largemouth Bass (*Micropterus salmoides*), Muskellunge (*Esox masquinongy*), Walleye (*Sander vitreus*). Random effects include lake, while fixed effects include year (centered around mean). Only models where all covariates were significant are shown. AIC (Akaike information criterion), R^2_m (pseudo-R^2 for fixed effects only), and R^2_c (pseudo-R^2 for both fixed and random effects) are presented. R^2_c for models with only fixed effects are also included. * denote optimal models used in Fig. 3.

Model	AIC	R^2_m	R^2_c
Black Crappie – Harvest (H)			
BCH1: $\log_e(y)$ ~ centered year	1351.38	N/A	0.02
BCH2: $\log_e(y)$ ~ centered year + (1 | lake)	1162.25	0.02	0.72
*BCH3: $\log_e(y)$ ~ centered year + (1 + centered year | lake)	1162.37	0.02	0.75
Bluegill – Harvest (H)			
BGH1: $\log_e(y)$ ~ centered year	1343.28	N/A	0.01
BGH2: $\log_e(y)$ ~ centered year + (1 | lake)	1072.72	0.01	0.80
*BGH3: $\log_e(y)$ ~ centered year + (1 + centered year | lake)	1068.08	0.01	0.80
Largemouth Bass – Harvest (H)			
LMBH1: $\log_e(y)$ ~ centered year	353.64	N/A	0.04
LMBH2: $\log_e(y)$ ~ centered year + (1 | lake)	191.35	0.03	0.64
*LMBH3: $\log_e(y)$ ~ centered year + (1 + centered year | lake)	147.25	0.03	0.70
Muskellunge – Harvest (H)			
MUSKH1: $\log_e(y)$ ~ centered year	568.80	N/A	0.14
MUSKH2: $\log_e(y)$ ~ centered year + (1 | lake)	583.66	0.14	0.23
*MUSKH3: $\log_e(y)$ ~ centered year + (1 + centered year | lake)	557.83	0.01	0.51
Walleye – Harvest (H)			
WH1: y ~ centered year	861.21	N/A	0.02
WH2: y ~ centered year + (1 | lake)	806.72	0.02	0.41
*WH3: y ~ centered year + (1 + centered year | lake)	806.37	0.02	0.48

Table S4. Lake attributes for variables used to fit the generalized additive mixed effects model as well as to predict total harvest (kg ha⁻¹).

| Variable	Empirical	Predicted
Latitude, Longitude	42.63-46.8, -92.57 - -88.38	42.50-46.8, -92.74 - -87.23
Number of lakes (n)	267 (573 populations)	3769
Lake size (ha)	8.9 - 53,394 (median = 216.1)	2.1 - 53,394 (median = 14.9)
Secchi (m)	0.1 - 9.3 (median = 2.53)	0.1 - 11.4 (median = 2.1)
Conductance (uS)	13.76 - 517.16 (median = 81)	2 - 1040.0 (median = 57.7)
Distance to nearest road (m)	0 - 270.67 (median = 5.65)	0 – 3662.5 (median = 27.1)
Mean bottom temperature in June (ºC)	4.07 - 23.17 (mean = 14.25)	4.03 - 24.34 (mean = 14.31)
Growing degree days (base temperature 5ºC; n days)	1731 - 3161 (mean = 2385)	2033 - 3482 (mean = 2526)
Total annual harvest (kg per lake)	0.9 - 374,580 (median = 1227)	0 - 1,196,166 (median = 64.5)
Areal harvest (kg ha⁻¹ in a lake)	0.03 - 71.04 (median = 5.24, mean = 7.91)	0 - 48.1 (median = 4.3, mean = 5.31)
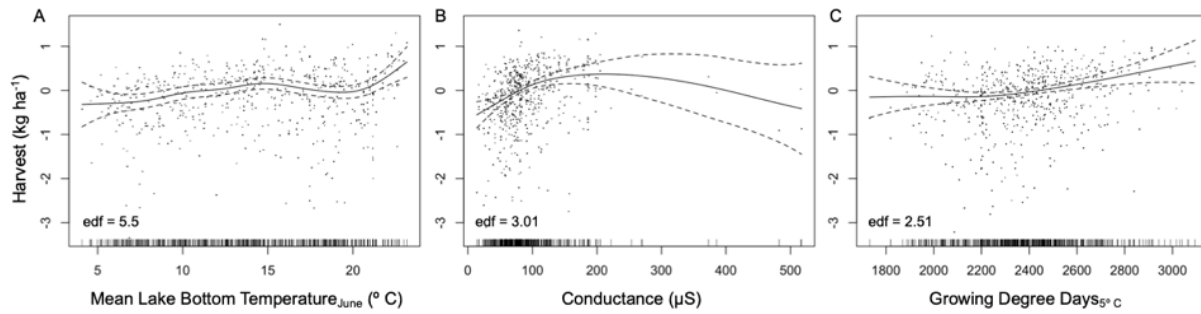
Figure S1. Estimated smooth curves for the effect of multiple predictor variables for a generalized additive mixed effects model used to predict total recreational fish harvest for Wisconsin lakes. Variables include: (A) Mean Lake Bottom Temperature in June (° C), (B) Conductance (µS), (C) Growing Degree Days (base temperature of 5° C). Solid lines represent the mean, and the dashed lines indicted ±2 standard errors. Mean and standard errors were generated using type = "iterms" in mgcv. such that standard errors returned for smooth components include uncertainty about the intercept/overall mean. edf represents effective degrees of freedom.
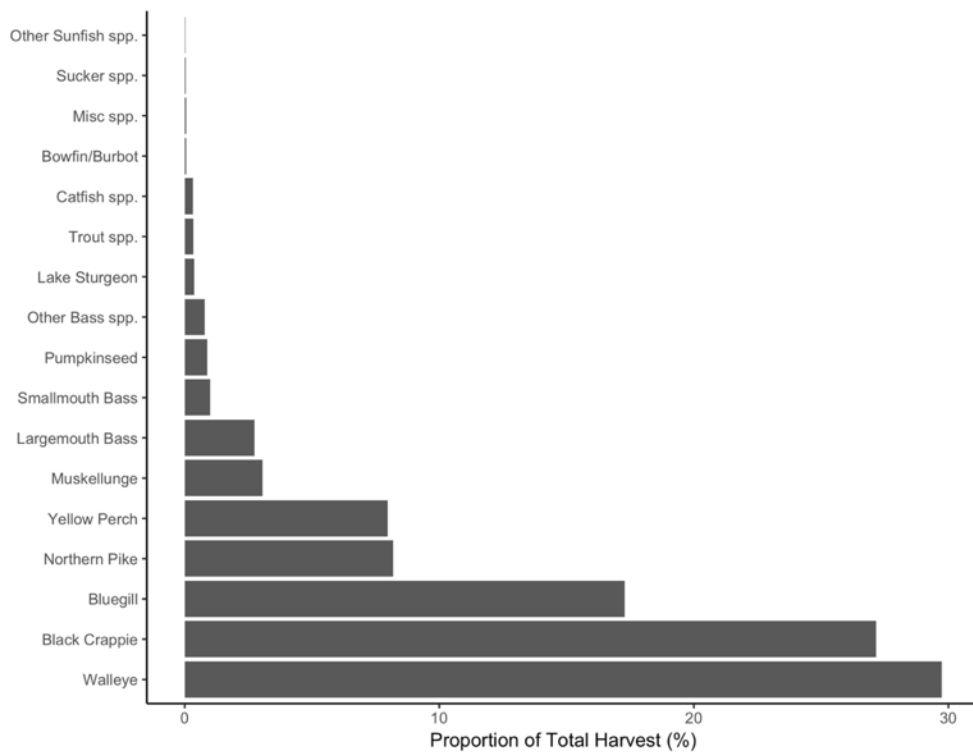
Figure S2. Taxa-specific contribution to total harvest pooled across all study years (1990-2017) for Wisconsin lakes with available creel information. The proportion of total harvest (%) refers to relative kg harvested.
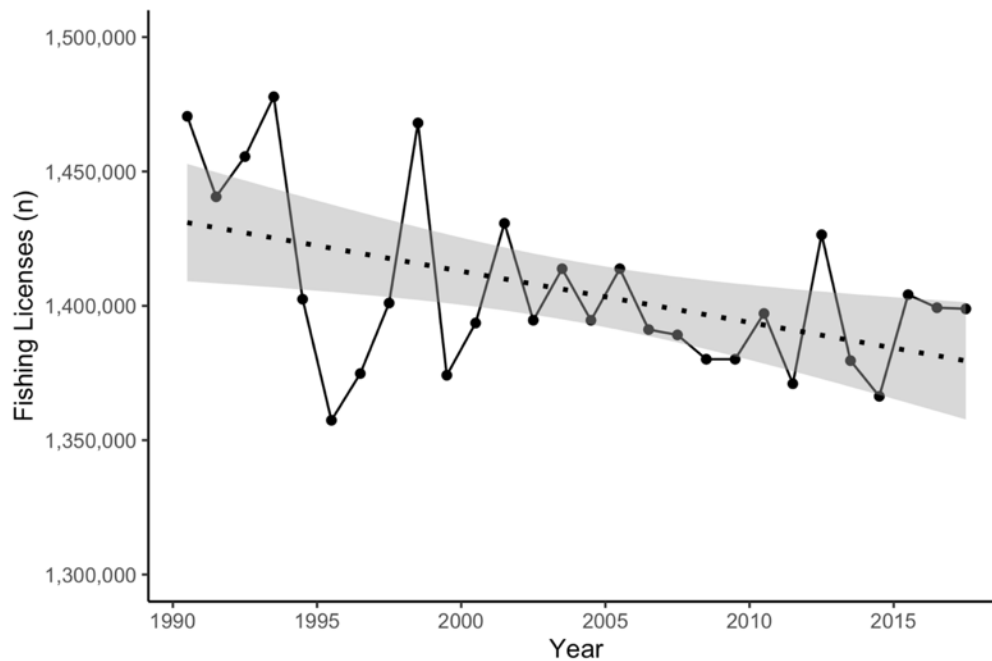
Figure S3. Total fishing licenses (number, n) sold in Wisconsin from 1990-2017. Dotted line indicates a fitted linear model and the shaded area corresponds to the 95% confidence interval.

Chapter 2: Production dynamics reveal hidden overharvest of inland recreational fisheries

Abstract

Recreational fisheries are valued at $190B globally and constitute the predominant way in which people use wild fish stocks in developed countries, with inland systems contributing the main fraction of recreational fisheries. Although inland recreational fisheries are thought to be highly resilient and self-regulating, the rapid pace of environmental change is increasing the vulnerability of these fisheries to overharvest and collapse. Here we directly evaluate angler harvest relative to the biomass production of individual stocks for a major inland recreational fishery. Using an extensive 28-y dataset of the walleye (*Sander vitreus*) fisheries in northern Wisconsin, United States, we compare empirical biomass harvest (Y) and calculated production (P) and biomass (B) for 390 lake year combinations. Pro- duction overharvest occurs when harvest exceeds production in that year. Biomass and biomass turnover (P/B) declined by ~30 and ~20%, respectively, over time, while biomass harvest did not change, causing overharvest to increase. Our analysis revealed that ~40% of populations were production-overharvested, a rate >10× higher than estimates based on population thresholds often used by fisheries managers. Our study highlights the need to adapt harvest to changes in production due to environmental change.

Significance

Despite the great economic and cultural importance of inland recreational fisheries, overharvest of inland fish stocks is rarely studied. We compared biomass harvest and biomass production in a unique 28-year, 179-lake dataset of a valuable inland fishery and found ~40% of stocks to be

overharvested – a rate >10x higher than population thresholds used to manage these fisheries. This is the first empirical example of recreational fisheries overharvest in a declining fishery revealed through a biomass production approach. The high level of production overharvest we found highlights the value of ecosystem approaches to inform recreational fisheries management in an era of rapid environmental change.

2.1. Introduction

Recreational fisheries are valued at $190B globally with nearly one billion people participating annually (1), constituting the predominant use of wild fish stocks in developed nations (2, 3). Recreational fisheries offer multiple benefits to diverse user groups (4), while also providing an important connection with nature in an era when people are more urbanized than ever (5, 6). Inland waters are hotspots for recreational fisheries – they comprise a significant component of these fisheries, despite making up only 0.01% of Earth's total water volume (1, 7, 8).

Inland recreational fisheries are thought to be highly resilient and self-regulating (9), but the rapid pace of environmental change is increasing their vulnerability to overharvest and collapse (10-14). Habitat loss due to climate change and lakeshore residential development in combination with other anthropogenic drivers (e.g., pollution, invasive species introductions) diminish the potential for freshwater ecosystems to support fisheries (14-17). Nonetheless, fishing effort is often constant across a range of fish densities while the contribution to fishing effort from highly-skilled anglers may actually increase, thereby increasing total harvest (18, 19). Given these trends, there is an urgent need to understand current and emerging threats to inland recreational fisheries, including the potential for excess harvest (11).

Here, we focus on the inland fisheries for walleye (*Sander vitreus*) in Northern Wisconsin, USA. Walleye are the most sought-after game fish in north-central North America (20) and support a robust recreational angler and tribal spearing fishery (21). Like many inland fisheries, the Wisconsin fishery is comprised of multiple discrete stocks associated with individual lake or river ecosystems. Over the past two decades, many walleye stocks have declined, on average by ~36% (Fig. 1*B*); however, the cause remains unclear (22-24). Conventional wisdom has been that overharvest is not contributing to walleye declines (25). In the current management regime, a stock is considered overharvested if >35% of the adult population is removed. Using this criterion, a small fraction (<3%) of stocks were overharvested over the past three decades (25, 26). There is growing awareness that lakes differ widely in terms of productivity and stocks may respond heterogeneously to harvest and other anthropogenic influences (24, 27). This heterogeneity highlights the need for a more biologically-grounded framework for assessing stock productivity and overharvest.

We extend previous research on production dynamics of inland walleye stocks (24, 28) by directly comparing estimated rates of biomass production and biomass harvest for individual walleye stocks to quantify overharvest. Using a unique and expansive 28-year standardized dataset of a valuable inland fishery, walleye in Northern Wisconsin, USA, we compare empirical annual biomass harvest (Y), empirically-estimated standing stock biomass (B), production (P; the annual rate of accumulation of new biomass), and biomass turnover rate (P/B) for 390 lake-year combinations. We examined the threshold at which annual biomass harvest (Y) exceeded annual production (P) (production overharvest; Y/P > 1) such that the stock exhibits depletion, referred to as the 'ecotrophic coefficient' (29, 30, 31). We found ~40% of walleye populations to be production-overharvested – a rate >10x higher than current population-based estimates. We

suggest that production could be measured along with harvest as a tool to assess the status of walleye populations of this region as well as for other inland fisheries (24, 28). Our study highlights the need for new approaches for managing and adapting harvest to changes in production in the face of global change (6).

2.2. Results

Age-0 relative abundance as well as adult density (N), P, B, and P/B have significantly declined over the past 28 years (Fig. 1*A-E*) in Northern Wisconsin walleye populations. Adult (≥5 yrs old, >381 mm) walleye (Fig. 1*B-E*) have experienced reductions of -36%, -35%, -30%, and -19%, respectively (all p < 0.001) (24). Water clarity (i.e., Secchi disk transparency), annual growing degree days, and conductivity explained very little of the variance among walleye populations (SI Appendix, Table S1). Declining trends were significant for all metrics (i.e., N, P, B, P/B) and provided models of best fit (SI Appendix, Table S1). For example, in 1990, mean P/B was 0.221 y^{-1} (biomass replacement time of ~4.52 y) but declined to 0.174 y^{-1} (biomass replacement time of ~5.74 y) by 2017. Thus, it takes more than an additional year for an average walleye population to replace its biomass now versus in 1990. Despite P, B, and P/B declines, annual biomass harvest (Y) has not changed significantly over this period (Fig. 2*A*). Angler harvest has been consistently higher than tribal harvest (Fig. 2*A*) (32). Over time, tribal harvest has remained relatively constant (Fig. 2*A*) (32). Relatively constant harvest coupled with declining production could lead to biomass harvest relative to production (Y/P) increasing over time. Overall, our Y/P metric indicated production overharvest in ~40% of lake-year combinations, representing an incidence of production overharvest >10 times higher than current estimates of numerical overharvest (Fig. 2*B*). Sustained Y/P above 1.0 may deplete biomass in populations where stocking is not able to replace excess biomass harvested (29, 31). When using

a more protective Y/P threshold of 0.75, the majority (52%) of populations would be classified as overharvested. The increasing trend in Y/P, although not statistically significant, is not being driven by increased biomass harvest. The combination of dwindling stock biomass (B) and decreasing biomass turnover rates (P/B) have caused similar harvest rates to remove larger proportions of available biomass.

We present modified "Kobe" plots, a tool commonly used in marine stock assessments (33, 34), to visualize changes in the incidence of production overharvest over time. Traditional Kobe plots track a single population or series of different species through time (34), but we modified this approach as we analyzed all walleye populations as a single fishery and therefore focus on regional temporal trends. When divided into three time periods of 9-10 years, median Y/P rose from 0.71 to 0.87 over the study period, with most of the change between the first and second decadal periods (Fig. 3). In 9 of 28 study years, biomass harvested exceeded production (i.e., Y/P>1.0) in more than half of populations (Fig. 2*B*). Median Y/P exceeded 0.75 in 18 of 28 study years, indicating sustained high levels of production harvest in this fishery.

We quantified the incidence of overharvest in select individual populations with >5 years of data (n=11) (SI Appendix, Figs. S1 and S2). Of these 11 stocks, 2 stocks had median levels of Y/P that exceeded 1.0 and experienced a decline in biomass while another 4 stocks had median levels of Y/P > 1 (SI Appendix, Fig. S1). Thus, the broad scale pattern of overharvest can also be observed for individual lakes where data are available.

2.3. Discussion

We found high rates of production overharvest when we compared harvest and production in an inland walleye fishery. Specifically, biomass harvest exceeded biomass production ~40% of the time among our 390 walleye harvest and production estimates over a 28-

year period, an overharvest rate >10x higher than estimates based on population harvest. While we found that overharvest has been frequent throughout this period, several observations were particularly revealing. First, walleye numerical abundance, biomass, and production all exhibited declines over this period – reflecting previously-described regional walleye population declines (24, 35). Meanwhile, walleye biomass harvest has remained constant. Constant harvest on a diminishing resource has led to frequent production overharvest through time due to removal of an ever-increasing proportion of available biomass. Finally, walleye biomass turnover rates (P/B) have also shown marked declines. Not only are walleye populations declining, but the rate at which walleye biomass is being replaced has also declined over the study period. On average, it now takes more than 1 year longer for the existing walleye biomass pool to fully replace itself. This decline in biomass turnover (P/B) is especially concerning as it is reflective of natural recruitment declines and thus the loss of productive capacity of this fishery.

Our analysis revealed high rates of walleye production overharvest – a pattern undetected in the fisheries management framework used over the past 30 years. In the current management framework, the management goal aims to ensure that no more than 35% of the total adult walleye population is harvested more than 1 time in 40 (25, 36). Because this 35% numerical limit reference point is rarely exceeded (~3% exceedance over 28 yrs (25, 26)) and average exploitation rates during the study period were ~15% (32), the widely-held view is that stock overharvest is minimal (25, 32). The fact that these two approaches generate such strongly contrasting conclusions regarding the extent of overharvest in this declining fishery warrants a more careful comparison of approaches and interpretation of existing data and analyses. It is important to recognize that population and biomass-based approaches have limitations, thus we recommend using both in concert to manage this fishery. First, by only considering fish

abundance and despite safety factors to account for numerical uncertainty, the current

management approach does not account for the contributions of fish of different ages and sizes to

future production. In contrast, assessing walleye populations in terms of biomass and production

accounts for the relative contribution of individual age classes to growth. Second, a 35%

numerical limit reference point to all populations does not recognize that stocks differ inherently

in their productivity and capacity to withstand harvest (24, 37). Recent inclusion of lake-specific

mixed effects models for setting safe harvest levels has attempted to address this shortcoming.

P/B values were highly variable among stocks, ranging from ~0.02 to 0.46. P/B is closely

correlated with natural mortality rates and therefore approximates the proportion of stock

biomass that can be harvested without depleting the population (38). Thus, depending on the

stock, anywhere from 2-46% of walleye biomass can be sustainably harvested. The fact that P/B

varies so widely highlights the difficulty of applying a single exploitation limit for all stocks.

Finally, our results indicate that a 35% reference point for population harvest is not protective of

many stocks (despite average exploitation rates of ~15%). While population and biomass limits

are not interchangeable, annual removal of 35% of either the adult population or standing

biomass would likely deplete any walleye stock. We found that only a very small fraction of

stocks had P/B values exceeding 0.35 or 0.15 (~3% and 71%, respectively) and could thus

sustain these levels of production-exploitation.

  In light of the limitations of the current and biomass-based management regimes

described above, our analysis provides an expanded management framework based on broader

ecosystem principles and informed by empirical data collected by fishery biologists. In this

framework, production, biomass, and P/B would be estimated, and management would aim to

limit annual harvest so as to not exceed the estimated productive capacity of the stock. Ideally,

such an approach would use a target Y/P < 1.0 (say 0.8) to be protective of walleye stocks in light of estimation error and biological variability. While the vast majority of Wisconsin's ~900 walleye stocks are not assessed in a given year, the broad findings of our study provide vital information on walleye populations and productivity that are useful for management. Key features of such a fisheries management regime are reliance on biomass in addition to abundance, and that harvest limits are biologically-grounded to better reflect heterogeneity in stock productivity. Under such a management regime, harvest limits would likely be lower for most walleye stocks but may increase for others (37). Balancing population and production parameters may improve overall stock management, not only in cases where harvest might be reduced, but also in cases where a certain level of production-overharvest may be desirable to reduce density and increase growth of individual fish to better achieve management objectives (39). Given that walleye stocks have undergone widespread declines (22-24) and that our assessment reveals that walleye stocks have been production-overharvested, we find that overharvest has contributed in part to the observed walleye declines. A production analysis using the same data adds new dimensions to existing management approaches to protect this valuable fishery.

Dwindling turnover rates (P/B) indicate an alarming trend in the productivity of these walleye populations. Due to slower biomass growth, it now takes an additional year for a given biomass to replace itself due to reduced production. There are multiple potential reasons for the declining turnover rates (P/B) observed in this fishery resulting from declining natural recruitment (Fig. 1*A*), including reduced habitat because of lakeshore development or climate change (23), invasive species introductions (40), biotic interactions with increasing warm-water species (22), as well as harvest. In contrast to many documented cases of overfishing found to be

due to rising harvest levels, the overharvest we found was due to a combination of declining populations (i.e., declining N, P, and B) and declining turnover (P/B, reflective of true declines in productivity) combined with unchanging harvest trends. Constant harvest as a proportion of a population does not necessarily result in sustainable exploitation, especially if underlying size structure, growth, and recruitment dynamics are shifting. We found that constant harvest of declining stocks led to production-overharvest. Given the prolonged production-overharvest we identified, harvest is part of a complex of factors that decrease the biomass available for removal. In the face of global environmental changes that impact freshwater ecosystems (41), it is imperative to understand trends in productivity such that conservation and management actions can be implemented swiftly if needed (42, 43).

Our findings have broad implications for recreational fisheries and natural resource management. Large-scale trends in climate or other factors may gradually undermine productivity in uncertain ways beyond the control of local managers. Carpenter et al. (27) developed a Safe Operating Space (SOS) framework that described how manageable and external factors interacted to affect the sustainability of a fishery. When viewed through this paradigm, our findings indicate an empirical example of constant harvest coupled with reduced productivity driven by changes in other factors such as habitat, climate, and biotic interactions (27, 44, 45) pushing a fishery outside of the bounds of the SOS. Local managers must compensate for unmanageable variables by adjusting the factors that directly influence growth and biomass of managed stocks, such as harvest and stocking in the case of walleye (28, 46, 47). Our production-based empirical approach, the SOS framework, and the existing numerical management system could be used to develop more robust management approaches capable of identifying management thresholds in the face of interacting population drivers.

The pattern of production overharvest we found is rarely assessed and may be widespread, particularly for harvest-oriented inland recreational fisheries. Early work by Post et al. (11) suggested that hidden collapse of recreational fisheries may be widespread. Over time, the weight of scientific evidence has supported this perspective (14, 48, 49). Management systems will need to adopt conservation measures to address the call for better governance of recreational fisheries (6, 50). There are many instances where fisheries are declining or have already collapsed, yet management systems may be relying on misleading metrics to evaluate fisheries currently considered sustainable due to hyperstability in catch rates, among other factors (18, 19, 51, 52, 53). Production-based metrics provide a system-specific measure of the productive capacity of a population to inform its harvest potential, adding to numerical assessment approaches. For many high-profile recreational fisheries, especially in developed countries, the data necessary to calculate these metrics are already being collected and should be leveraged to their full potential. Furthermore, in fisheries without the necessary data, production can be estimated from biomass using production-biomass relationships (28, 54) and potentially metabolic theory (55). Although data may never be available for all ecosystems, the merits of production raise a global question as to how best assess data-poor fisheries and underscores the need to develop a more thorough understanding of surrogates for inland fish production in relation to harvest. Incorporating production with other methods, such as Bayesian hierarchical models, could provide an opportunity to apply knowledge from well-studied populations to data-poor scenarios. Such insights would identify the limits to harvest and help inform strategies for strengthening the management of recreational fisheries.

There is growing recognition of the globally important role of inland recreational fisheries (6). Not only do these fisheries contribute significantly to overall fisheries harvest, but

they are a disproportionate economic contributor, while also providing multiple important ecosystem services and improving human well-being (6). Unfortunately, inland waters are subject to accelerating and often interacting anthropogenic impacts (15, 56), all of which can adversely affect fisheries (14, 17). Our study adds to this understanding by revealing widespread and persistent stock overharvest in a valuable and declining recreational walleye fishery using production dynamics. While the walleye decline cannot be fully attributed to fishing pressure, we conclude that the lack of management adaptation to productivity shifts has likely intensified the declines. When viewed in relation to biomass harvested, these metrics offer an assessment of freshwater fish population status founded in biomass flow dynamics that establishes system-specific harvest thresholds based on local productivity. While overharvest almost certainly interacts with other drivers in this regional fishery decline, our results highlight the urgent need for improved governance, assessment, and regulation of recreational fisheries in the face of rapid environmental change (6).

2.4 Methods Summary

Walleye data collection

Walleye in Wisconsin have been jointly managed by the Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) since reinstatement of tribal spearing rights in 1985 (36). This management strategy has involved an annual rotating stratified randomized sampling design to assess walleye populations in lakes in the Ceded Territory (~northern third of Wisconsin; 36, 57). Over the last ~28 years, population-specific data have been collected for ~900 walleye lakes, including demographic information (i.e., length, weight, sex, age), growth, size-structure, and adult population estimates. Additionally, to obtain an index of walleye recruitment, age-0 walleye

were collected from surveys conducted on all lakes where a population estimate was performed.

Further information on these surveys can be found in the supporting information. In addition,

angler and tribal harvest data are available, including the actual or estimated number of fish

harvested as well as a large subset of length measurements of harvested fish.

Production calculations

We calculated production using the instantaneous growth method, an application of a

standard model of secondary production for age-structured populations (29, 31, 58). This method

measures the production of new biomass from somatic growth and how that production is

affected by recruitment and mortality. This metric is distinct from surplus production which

specifically accounts for biomass gains from recruitment and losses from mortality in addition to

the gains from somatic growth. We show in the supporting information that somatic growth

production (i.e., the production estimated in this study) is a suitable, and more readily measured

proxy for surplus production for walleye in this region (SI Appendix, Fig. S5, Fig. S6).

Production was calculated for each lake and year combination with available data (n=566) by

applying the instantaneous growth method to fish from all age-classes from age 5 to a_{max}

(maximum age) (28, 29, 31, 58):

$$P_y = \sum_{a=5}^{a_{max}} G_{a,y} \bar{B}_{a,y} \qquad \text{(eqn. 1)}$$

Where a refers to an age class, P_y is total walleye production for year y (kg ha^{-1} y^{-1}), $G_{a,y}$ is the

instantaneous growth rate of cohort aged a in year y. Because we lacked measurements of

cohorts in repeated years, we estimated growth rate from consecutive cohorts in the same year

(i.e., $\log_e\left(\frac{\text{mean weight at age a+1,y}}{\text{mean weight at age a,y}}\right)$), $\bar{B}_{a,y}$ is the mean biomass (kg ha^{-1}) classes of cohort during the

year, also estimated by substituting age-classes for time. A detailed description and example

calculation of these estimates can be found in the supporting information (SI Appendix, Fig. S3, Table S3, Table S4). For all analyses, we did not include individuals <5 years old, as immature walleye of these sizes are not reliably vulnerable to capture by fyke nets (36).

Biomass harvest calculations

To calculate loss of biomass due to fishing imposed on northern Wisconsin walleye populations, we estimated age-specific harvest (harvested biomass) for each fishery in each lake-year with available data (n=390). For tribal harvest, the total number of fish harvested is known, but for angling harvest, the total number of fish harvested is projected by WDNR based on creel data. WDNR designates adult fish as all fish ≥381 mm and all sexable fish <381 mm, therefore we removed individuals <381 mm to maintain comparability between harvest and production estimates. These angler harvest estimates likely underestimate the number of adult fish harvested as it does not include sexable individuals <381 mm.

For both harvest types, a subsample of individual lengths of harvested fish was collected. To estimate angler harvest, for unmeasured fish in a lake-year, we randomly sampled with replacement from the available subset of length data for that lake-year combination, and then assigned those values as lengths to the unmeasured fish from that same lake-year combination. If the lake-year combination had no lengths available (number of lake-years = 2), we extrapolated length data from the nearest year from the same lake. According to management regulations for the tribal fishery, all harvested fish 508 mm or larger must be measured, therefore measured fish represent large individuals and unmeasured individuals are known to be <508 mm. Thus, to estimate tribal harvest, we randomly assigned lengths to unmeasured fish between 381 mm and 483 mm as this corresponds to the most likely adult size range for these individuals. Once all harvested fish had a corresponding length, we assigned ages and weights to all fish using the

age-length keys and length-weight regressions developed through production calculations. From

this information, we calculated the number of fish harvested for each age class (H_a) as well as

mean weight-at-age of harvested fish ($W_{ha,a}$; kg), which we used to calculate age-specific tribal

and angler biomass harvest ($Y_{t,a}$ and $Y_{f,a}$; kg):

$$Y_{t,a} \; or \; Y_{f,a} \; = \; H_a * W_{ha,a} \qquad \text{(eqn. 3)}$$

Total annual biomass harvest (Y_y; kg ha^{-1}) was calculated by summing $Y_{t,a,y}$ and $Y_{f,a,y}$ for each

lake. All biomass harvest estimates were divided by lake-specific surface area (kg ha^{-1}). We

evaluated harvest as biomass harvested relative to production as this represents the ecotrophic

coefficient, i.e., Y/P (29, 31).

Statistical analyses

　　　　We ran Shapiro-Wilk tests to determine whether distributions for P, B, P/B, Y, and Y/P

were normal. Based on findings, P, B, Y, and Y/P were log$_e$-transformed prior to analysis to

meet assumptions of normality. We developed mixed-effect regression models to test for

temporal trends in P, B, and P/B. For each model, the estimated metric (i.e., log$_e$(N), log$_e$(P),

log$_e$(B), P/B) was the dependent variable, year (centered around the mean) was an independent

variable, and lake was a random effect. The additional covariates of conductivity, water clarity

(i.e., Secchi disk transparency), and annual growing degree days (base temperature of 0°C;

GDD) were further assessed (SI Appendix, Table S1). Models of best fit were first selected

based on Akaike information criterion (AIC). If there was no difference between AIC values,

model of best fit was selected based on variance explained. For each model, we calculated

percent change over time based on model predictions in 1990 and 2017. Temporal yield and Y/P

trends were also assessed but were not significant. We used an $\alpha = 0.05$ for all statistical

analyses. All calculations and statistical analyses were performed in R version 3.4.3 (65). All

code detailing production and biomass calculations is open-source and freely available on GitHub (https://github.com/hembke/Production-and-Biomass-Calculation). All data have been made available at https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-ntl&identifier=373&revision=1.

2.5. Acknowledgements

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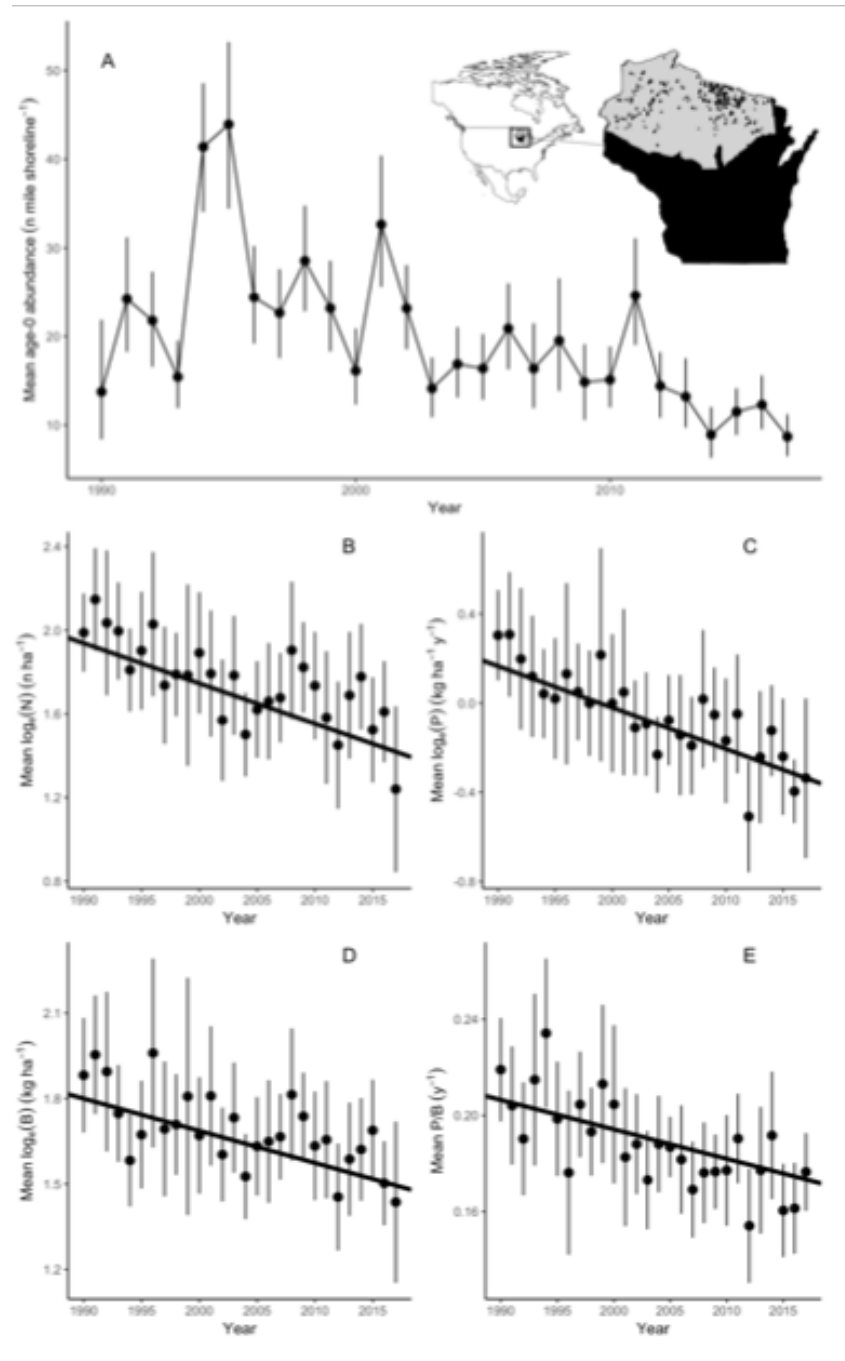
2.7. Figures

Figure 1. Inset map identifies the location of lake-year combinations as black dots used in this analysis in Northern Wisconsin, USA during 1990-2017 (n=566). Panels A-E show mean +/- 95% confidence intervals for annual walleye (*Sander vitreus*) age-0 abundance (number of age-0 individuals per mile shoreline), $\log_e$(adult density; N) (n ha^{-1}), $\log_e$(adult production; P) (kg ha^{-1} y^{-1}), $\log_e$ (adult biomass; B) (kg ha^{-1}), and adult biomass turnover rate (P/B) (y^{-1}). Trend lines in panels B-E correspond to linear mixed effects models.
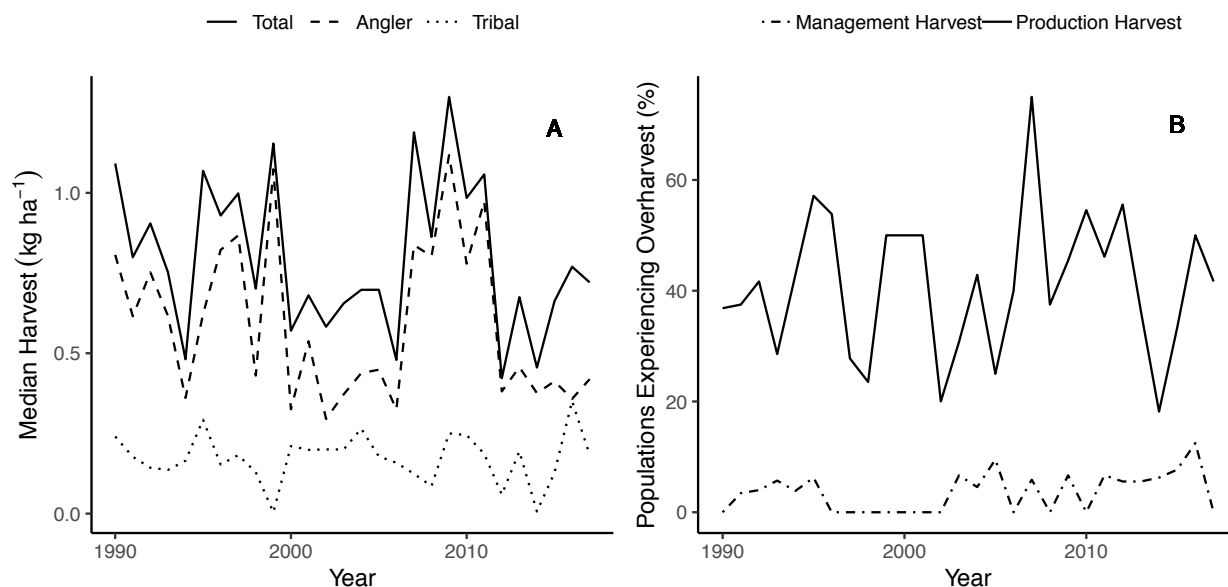
Figure 2. Panels correspond to walleye (*Sander vitreus*) populations in Northern Wisconsin, USA during 1990-2017 with harvest data (n=390). Panel A illustrates median biomass harvest (Y) (kg ha^{-1}) according to harvest type. Panel B shows the percentage of populations considered overharvested annually according to production computations (solid line) as well as management agency harvest computations of walleye exploitation rates exceeding 35% of the adult population in a given-lake year (dotdash line).
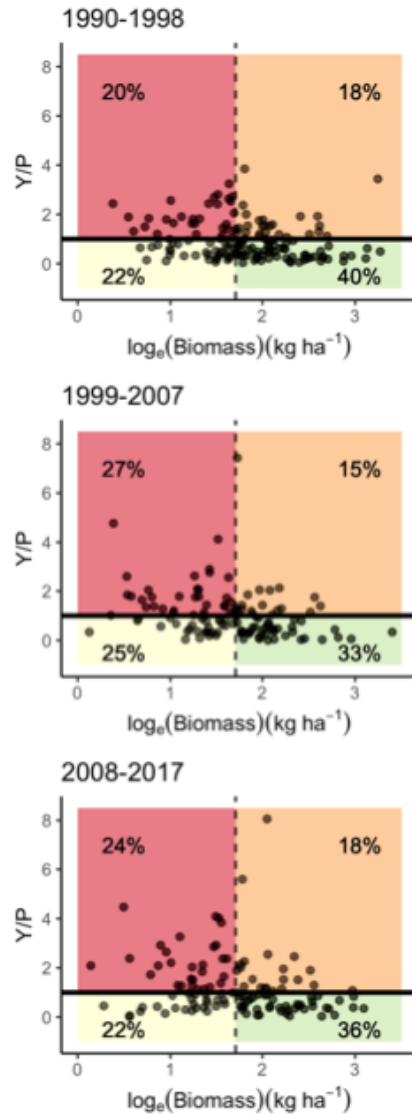
Figure 3. Modified Kobe plots for three time periods (9-10 year intervals) of walleye (*Sander vitreus)* Y/P (% production) relative to $\log_e$-transformed biomass (kg ha^{-1}) for each population with harvest data (n=390) for Northern Wisconsin, USA populations during 1990-2017. Each point represents one lake-year combination. Production (P) was measured immediately following spring ice-out and harvest (Y) was measured for the year following the P estimation. The horizontal solid line establishes the 1.0 harvest threshold, at which 100% of biomass produced is harvested. The vertical dashed line shows the overall median biomass level for the region over the entire time period. Points in the red indicate populations where production overharvest is occurring and biomass is low, points in the orange indicate populations where production overharvest is occurring but biomass is high. Points in the green indicate populations where production overharvest does not exceed 1.0 and biomass is high. Points in the yellow indicate populations where production overharvest does not exceed 1.0 but biomass is low. The percentage of populations in each quadrant is shown for each time period.

2.8. Supporting Information – Embke et al., Production dynamics reveal hidden overharvest of inland recreational fisheries

Detailed Methods

    a. Walleye data collection

Given its importance in the state, walleye have been actively managed following the legal affirmation of Native American off-reservation fishing treaty rights in the Ceded Territory (~ northern third of the state) in 1985 (1). To prevent overharvest, the Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) began a management strategy in 1990 that relied upon extensive stock assessments (1, 2). Population-specific data have been collected for ~900 walleye lakes over the last ~28 years, including demographic information (i.e., length, weight, sex, age), growth, size-structure, and adult population estimates. Managers use adult population estimates to establish safe harvest quotas on individual lakes such that combined angler and tribal harvest does not violate the limit reference point of 35% numerical harvest (% adult population estimate) in more than 1-in-40 instances (minus margins of error to account for population estimate variability) (1). Note that the original stock assessment strategy focused primarily on high abundance, naturally reproducing walleye populations and was modified in 1995 to incorporate lower profile and lower density stocked walleye populations. Increased sampling in lower density waters through time potentially influences the results of our study by partially contributing to noted declines in N, P and B, but in a manner that (like the sampling rotation itself) likely better represents the regional fishery as a whole.

Since 1990, state and tribal fishery biologists have conducted spring surveys to estimate adult (all fish $\geq$ 381 mm plus all sexable fish <381 mm) walleye abundances in the Ceded Territory. Biologists use a rotating stratified randomized design to select survey lakes; therefore some lakes have been sampled multiple times during this period, while others have been surveyed less frequently (3; Fig. S4). Spring surveys began shortly after ice-out, when adult walleye moved into near-shore habitats to spawn (Fig. S4). To maximize catch, fyke nets were set overnight at likely spawning locations. Captured individuals were marked with a Floy® tag or fin clip and released. Boat electrofishing surveys were used to recapture individuals at the peak of the spawn. From the number of marked and recaptured individuals, population estimates (PEs) were calculated using Chapman's modification of the Petersen estimator (4). For all

captured walleye, total length (TL, mm) was recorded, as well as weights (kg) for some individuals; collection of weight data was primarily done prior to 2000. To estimate age, calcified hard structures (dorsal spines for walleye ≥508 mm TL, scales for walleye <508 mm TL) were collected from as many as 5 individuals per half-inch length bin per sex for each population.

To obtain an index of walleye recruitment, age-0 walleye surveys were conducted on all lakes where a population estimate was performed. Surveys began in autumn when water temperatures fell below 21°C. In most cases, the entire shoreline of each lake was sampled with 230-V AC electrofishing boats for one night (3). In some lakes where the entire shoreline could not be surveyed, randomly selected transects were sampled and the distance was recorded. Individual ages were verified from observed gaps in the length-frequency distribution between age-0 and age-1 fish and scale aging. We then calculated the total number of age-0 individuals sampled per mile of shoreline surveyed.

b. Production calculations

A more detailed derivation of production metrics is provided below, but here we summarize the specific procedures used to calculate production from the empirical data. Production was calculated for each lake and year combination with available data (n=566) by applying the instantaneous growth method to fish from all age-classes greater than age-4 (4, 5, 6, 7):

$$P_y = \sum_{a=5}^{a_{max}} G_{a,y} \, \bar{B}_{a,y} \qquad \text{(eqn. 1)}$$

P_y = annual production rate (kg ha^{-1} y^{-1}) in year y
$G_{a,y}$ = instantaneous growth rate (y^{-1}; see eqn. 2), of age a in year y
$\bar{B}_{a,y}$ = mean biomass of cohort age a during year y (kg ha^{-1}; see eqn. 4 and 5)
y = year
a = age
a_{max} = maximum age class

Because we did not have consecutive annual measurements at size at age of cohorts to estimate growth rate, we approximated this by the size-at-age of consecutively aged cohorts within a lake in a year:

$$G_{a,y} = \log_e\left(\frac{\overline{w_{a+1,y}}}{\overline{w_{a,y}}}\right) \qquad \text{(eqn. 2)}$$

$G_{a,y}$ = instantaneous growth rate (y^{-1}) of age a during year y

$w_{a,y}$ = individual mass (kg) of age a at start of year y

$$B_{a,y} = n_{a,y} * \bar{w}_{a,y} \qquad \text{(eqn. 3)}$$

$$\bar{B}_{a,y} = (B_{a+1,y} + B_{a,y})/\Delta y \qquad \text{(eqn. 4)}$$

$B_{a,y}$ = biomass (kg ha^{-1}) of cohort aged a at start of year y

$\bar{B}_{a,y}$ = mean biomass of cohort aged a over year y (kg ha^{-1})

   y = number of age classes over which mean biomass is calculated

n = number of fish

A detailed framework (Fig. S3), example calculation (Table S3), and table summarizing measured and calculated variables (Table S4) used in this methodology can be found in the supporting information. This method (known as the instantaneous growth method; 6) is the predominant production estimation method used for freshwater fishes (6). Nonetheless it provides a discrete "snapshot" of production as it does not measure mortality and biomass through time with multiple samples (8).

We calculated age-specific abundance and growth using empirical total length (TL) measurements and age estimations to develop a smoothed age-length key for each lake-year combination (9). If the lake-year age-length key was not sufficient (i.e., number of fish <30, and/or number of ages in the key <5), we developed a lake-specific (i.e., pooled across years) age-length key. If the lake-specific key was also insufficient, we classified lakes according to lake-class information (10) and calculated class-specific age-length keys (Table S2). We assigned ages for all unaged fish in a lake-year using the appropriate age-length key.

We developed lake-year-specific length-weight regressions to calculate total weight for each age class (kg), mean weight-at-age (kg), and biomass (kg ha^{-1}). We determined if a lake-year-specific regression was valid according to specific criteria: number of fish > 25, R^2 > 0.85, and 2 < b (length-weight regression slope) < 4. Froese (11) showed empirically that mean values of b by species were between 2.5 and 3.5. Individual lake-year values would likely exhibit a larger range, thus we included relationships with a broader range of slopes. Based on these criteria, if the lake-year specific regression did not meet these requirements, we developed a lake-specific length-weight regression. If the lake-specific regression also did not meet requirements, we calculated a regression according to lake class (10). We then applied the appropriate length-weight regression to all fish with unknown weights in a lake-year (Table S2).

We converted adult population estimates (PEs) to age-specific population estimates by calculating the proportion of fish present in each age class from age-structure data (5, 12). From this information, we calculated age-specific biomass divided by lake size (B_a, kg ha^{-1}) using eqn. 3. We calculated total biomass for each lake-year by summing age-specific biomass for each age class. We calculated annual production rates (P_t) for all age classes in each lake-year. Using eqn 1, we summed age-specific rates to estimate total adult walleye production for each lake-year (Fig. S3, Table S3). For all analyses, we did not include individuals <5 years old, as immature walleye of these sizes are not reliably vulnerable to capture by fyke nets (1).

Long-term trends in individual lakes

Our research provides a broad understanding of regional dynamics in the walleye fishery of Northern Wisconsin, USA and therefore reduced focus is placed on individual lake dynamics. However, some lakes in our dataset (n=11) have >5 years of data and therefore we were able to observe long-term trends (Fig. S1 and S2). While the majority of lakes experienced a median level of production harvest (Y/P) > 1, some lakes have shown consistent production overharvest without coincidental declines in abundance. Others have previously demonstrated the disconnect between production and density metrics (13) as well as described the factors influencing why this pattern may occur. Reasons contributing to the mismatch between production and density patterns include compensatory responses as a result of reduced densities, stochasticity in year classes, and slow population responses.

Numerical exploitation rates

Although the current management exploitation limit reference point protects walleye populations against exceeding 35% exploitation more than 1 in 40 times (3), a recent study estimated that an exploitation rate ≤ 20% would represent a more protective regionally optimal average exploitation rate of adult walleye, with acknowledgement that the level would vary with lake productivity (14). Additionally, given that mean numerical exploitation rates are estimated at ~15% (15), our results indicate that 71% of stocks had P/B ratios exceeding 15% and therefore could be expected to sustain this level of harvest. Compensatory responses to high levels of harvest may lead to hyperstability of production, biomass, and/or density across a range of harvest levels in some cases (13), adding a degree of uncertainty to the use of more biologically-based management approaches to define suitable harvest levels, particularly when models are developed using only data from a period of relatively modest harvest.

The effect of hatchery stocking

Stocking walleye in Wisconsin has been a consistent practice throughout the study period, although the size of stocked individuals has changed as recruitment has declined (3). Previously, it was common practice to stock fry and small fingerlings but as natural recruitment has declined, stocking of extended growth fingerlings has become increasingly common in an effort to improve survival and recruitment to the fishery (3). Overall, the proportion of naturally reproducing lakes has declined over time (5), thus the production overharvest we observed is not unexpected as stocking has not been able to match natural reproduction.

Simulation modelling comparison between somatic growth production and total population productivity

We aimed to determine how well empirically-derived measures of somatic growth production (i.e., what we estimated in this study) reflect total population productivity in a way that allows for direct comparison to fisheries yield. Broadly, fished populations can be conceived as being governed by:

$$\Delta B_y = P_y - Y_y \tag{eqn. 5}$$

Where B_y is population biomass in year y, P_y is surplus production, and Y_y is fishery harvest. Surplus production accounts for the gain of new biomass produced via recruitment and somatic growth and loss of biomass via mortality. Under this model, ratios of $Y_y/P_y > 1$ cause populations to decline (7).

Production in age structured populations can be calculated by accounting for individual body growth and mortality of individual cohorts (7). These processes operate continuously within each discrete yearly time step (y), governed by rates that are specific to each age class. If these rates are linear functions of abundance (mortality) and body size (growth), then the biomass of a cohort age a in year y at any time t within the year is:

$$B_{a,y}(t) = B_{a,y}(0)\exp\left((G_{a,y} - M_{a,y} - F_{a,y})t\right) \tag{eqn. 6}$$

Where $G_{a,y}$ is the instantaneous growth rate of age-a individuals $M_{a,y}$ is the age specific natural mortality rate $F_{a,y}$ is the age-specific fishing mortality rate (7).

Given this, the production gain from somatic growth and the production loss from mortality can be analytically derived over discrete annual time increments (7). Production from somatic growth during year y is simply the integral of $B_a(t) G_a$ over the year from $t=0$ to $t=1$. We replace $B_{a,y}(0)$ notation with $B_{a,y}$ to denote biomass at age a at start of year y:

$$P_{g,a,y} = B_{a,y} G_{a,y} \frac{1 - \exp(G_{a,y} - M_{a,y} - F_{a,y})}{-G_{a,y} + M_{a,y} + F_{a,y}} \qquad \text{(eqn. 7)}$$

This expression is the motivation for eqn. 1. Here instantaneous rates are indexed to year for generality but could be assumed constant. Similarly, production losses from mortality corresponds to the integral of $B_a(t) M_a$:

$$P_{g,a,y} = -B_{a,y} M_{a,y} \frac{1 - \exp(G_{a,y} - M_{a,y} - F_{a,y})}{-G_{a,y} + M_{a,y} + F_{a,y}} \qquad \text{(eqn. 8)}$$

Therefore the net of these two equations is equal to:

$$P_{net,a,y} = B_{a,y}(G_{a,y} - M_{a,y}) \frac{1 - \exp(G_{a,y} - M_{a,y} - F_{a,y})}{-G_{a,y} + M_{a,y} + F_{a,y}} \qquad \text{(eqn. 9)}$$

The above calculations apply to a given cohort. Total population production in year y is equal to $P_{net,a,y}$, summed over all age classes, plus the biomass of new recruits, $B_{ar,y}$, where a_r is age at recruitment:

$$P_y = B_{a_r,y+1} + \Sigma_a P_{net,a,y} \qquad \text{(eqn.10)}$$

Note here the discrete time window over which production is estimated presumes that recruits enter the population at the very end of the time interval, approximated by $B_{ar,y+1}$, but could also be written as $B_{ar, y}$.

We sought to determine how Pg is related to P. For the purposes here, where we aim to identify cases when fishing yield exceeds productivity, we aim to be conservative. Thus, Pg is a (conservative) proxy for P if it generally exceeds P. To that end, we simulated equilibrium population age structure under different fishing intensities and compared somatic growth production to surplus production over a range of equilibrium population biomass levels (Fig. S5). We applied a standard age-structured model to model abundance at age:

$$N_{a,y} = \begin{cases} R_y & if \ a = \ a_r \\ N_{a-1,y-1} exp \ (-M_{a-1,y-1} - F_{a-1,y-1}) & otherwise \end{cases}$$

Where R_y is a function of equilibrium age 5+ biomass. We used the equilibrium renewal method of Lawson and Hilborn (17), assuming a Beverton-Holt stock recruitment relationship with steepness parameter (h) equal to 0.8 (steepness is the recruitment relative to unfished state when spawning biomass is 20% of unfished level).

Biomass-at-age was calculated as the product of abundance-at-age and mass-at-age, the latter from a Von-Bertalanffy growth function and standard length-weight conversion function. We used the age-structured model to generate abundance, and biomass (kg ha^{-1}), and then applied two different production estimation routines to compare somatic growth production (i.e., what was empirically estimated in this study, P_g; kg ha^{-1} y^{-1}) and total population production (i.e., surplus production, P; kg ha^{-1} y^{-1}) (Fig. S6). Parameters used in these calculations can be found in table S5. Somatic growth production was estimated as an approximation using eqn. 7. Total population production was estimated as the full calculation of all components of production (eqn. 7-10).

From these simulations, we found that when a population was at least 30% of unfished levels, somatic growth production (Pg) was greater than production (P) and were roughly equivalent for population biomass densities between 3 – 4 kg ha^{-1} (Fig. S5). When biomass was sharply reduced by fishing, to less than one-third of unfished levels, Pg was generally less than P, likely because the former does not account for recruitment gains (Fig. S5). Therefore, P_g represents a suitable proxy for P under most conditions. When yield exceeds P_g (i.e., $Y_y/P_g > 1$), this likely indicates that yield exceeds total population production (P) or that the population has been reduced to very low levels compared to its unfished state.

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2.10. Supporting Information – Tables and Figures

Table S1. Model selection results for linear mixed effects models for density (N), production (P), biomass (B), and biomass turnover rate (P/B) of Northern Wisconsin, USA walleye (*Sander vitreus*) populations during 1990–2017 (n=566). Random effects include lake, while fixed effects include year (centered around mean), conductivity, Secchi disk transparency, annual growing degree days (base temperature of 0°C; GDD). Only models where all covariates were significant are shown. AIC (Akaike information criterion), R^2_m (pseudo-R^2 for fixed effects only), and R^2_c (pseudo-R^2 for both fixed and random effects) are presented. R^2_c for models with only fixed effects are also included. * denote optimal models used in Fig. 1.

Model	AIC	R^2_m	R^2_c
Density (*N*)			
N1: $\log_e(y)$ ~ centered year	1238.83	N/A	0.04
N2: $\log_e(y)$ ~ centered year + (1 | lake)	1100.59	0.04	0.66
*N3: $\log_e(y)$ ~ centered year + (1 + centered year | lake)	1085.06	0.04	0.74
N4: $\log_e(y)$ ~ centered year + GDD	1225.36	N/A	0.06
N5: $\log_e(y)$ ~ centered year + GDD + (1 | lake)	1111.72	0.05	0.65
N6: $\log_e(y)$ ~ centered year + GDD + (1 + centered year | lake)	1095.88	0.07	0.73
Production (*P*)			
P1: $\log_e(y)$ ~ centered year	1233.32	N/A	0.04
P2: $\log_e(y)$ ~ centered year + (1 | lake)	1088.46	0.04	0.64
*P3: $\log_e(y)$ ~ centered year + (1 + centered year | lake)	1086.74	0.04	0.70
P4: $\log_e(y)$ ~ centered year + GDD + $\log_e$(secchi)	1202.81	N/A	0.10
P5: $\log_e(y)$ ~ centered year + $\log_e$(secchi) + (1 | lake)	1083.18	0.07	0.64
P6: $\log_e(y)$ ~ centered year + $\log_e$(secchi) + (1 + centered year | lake)	1081.89	0.07	0.68
Biomass (*B*)			
B1: $\log_e(y)$ ~ centered year	1010.10	N/A	0.02
B2: $\log_e(y)$ ~ centered year + (1 | lake)	904.07	0.03	0.60
*B3: $\log_e(y)$ ~ centered year + (1 + centered year | lake)	901.06	0.03	0.67
B4: $\log_e(y)$ ~ centered year + GDD + $\log_e$(secchi)	990.11	N/A	0.06
B5: $\log_e(y)$ ~ centered year + $\log_e$(secchi) + (1 | lake)	903.83	0.05	0.60
B6: $\log_e(y)$ ~ centered year + $\log_e$(secchi) + (1 + centered year | lake)	900.88	0.04	0.66
Biomass turnover rate (*P/B*)			
PB1: y ~ centered year	-1369.50	N/A	0.04
PB2: y ~ centered year + (1 | lake)	-1553.37	0.02	0.69
*PB3: y ~ centered year + (1 + centered year | lake)	-1557.63	0.02	0.74
PB4: y ~ centered year + $\log_e$(conductivity) + $\log_e$(secchi)	-1383.04	N/A	0.06
PB5: y ~ centered year + $\log_e$(conductivity) * $\log_e$(secchi) + (1 | lake)	-1534.37	0.05	0.70
PB6: y ~ centered year + $\log_e$(conductivity) * $\log_e$(secchi) + (1 + centered year | lake)	-1538.58	0.05	0.74

Table S2. Classification of length-weight regression and smoothed age-length-key types used to estimate biomass and production for Northern Wisconsin, USA walleye (*Sander vitreus*) populations (n=566) from 1990-2017.

	All Lakes & Years	Lake Class	Lake	Lake-Year
Regression	9	198	242	117
Age-Length-Key	0	157	248	161

Table S3. Example calculation of biomass and secondary production for walleye (*Sander vitreus*) in Big Carr Lake, Wisconsin in 1999. Lake surface area is 85 ha. B corresponds to age-specific biomass, $\bar{B}$ is mean biomass between age classes, G represents the instantaneous growth rate, and P is the rate of secondary production.

Age	No.	Mean mass (kg)	B (kg ha⁻¹)	$\bar{B}$ (kg ha⁻¹)	G	P (kg ha⁻¹ year⁻¹)
5	10.8261	0.4018	0.0515			
				0.2651		0.2489
6	39.3676	1.0275	0.4787		0.9391	
				1.0483		0.3056
7	99.4032	1.3753	1.6178		0.2915	
				1.2932		0.1951
8	51.1779	1.5992	0.9686		0.1509	
				2.4228		0.7937
9	147.6285	2.2191	3.8770		0.3276	
				3.1741		-0.0458
10	95.4664	2.1874	2.4712		-0.0144	
				1.2916		0.4939
11	2.9526	3.2061	0.1120		0.3824	
				0.1910		-0.0193
12	7.8735	2.8974	0.2700		-0.1013	
				0.2583		-0.0537
13	8.8577	2.3533	0.2467		-0.2080	
				0.1725		0.0307
14	2.9526	2.8115	0.0982		0.1779	
				0.4547		0.1452
15	17.7154	3.8695	0.8112		0.3194	
				0.6071		0.1486
16	6.8893	4.9424	0.4030		0.2447	
				0.2940		-0.0644
17	3.9368	3.9705	0.1850		-0.2190	
				0.1501		-0.0278
18	2.9526	3.2996	0.1153		-0.1851	
Total			11.7062			2.1507

Table S4. Measured and calculated variables used to make annual production calculations. Subscripts: a = age, y = year. Examples of specific ages a=i, a+1=j.

Symbol	Units	Measured/Calculated	Definition	Equation (if applicable)
$n_{a,y}$	Individuals/ha	Measured	Population density of fish age a in year t	n/a
$w_{a,y}$	kg/individual	Measured	Individual mass for age a in year t	n/a
$B_{i,y}$	kg/ha	Calculated	Biomass of fish in age i in year t	$B_{i,y} = n_{i,y} * w_{i,y}$
$\bar{B}_{i,j,y}$	kg/ha	Calculated	Mean biomass of fish between age i and age j in year t	$\bar{B}_{i,j,y} = \dfrac{B_{i,y} + B_{j,y}}{2}$
$G_{i,j,y}$	year^{-1}	Calculated	Growth rate between ages i and j in year t	$G_{i,j,y} = log\,\dfrac{w_{j,y}}{w_{i,y}}$
$P_{i,j,y}$	kg/(ha*year)	Calculated	Annual production of fish between ages i and j in year t	$P_{i,j,y} = G_{i,j,y} * n_{i,j,y} * w_{i,j,y}$

Table S5. Parameters used to compare somatic growth production and surplus production estimations. Values come from empirical calculations based on the dataset used in this study or from Tsehaye et al. (14).

Parameter	Description	Units	Value
M	Natural Mortality	$year^{-1}$	0.24
L_∞	Asymptotic Length	cm	68.61
K	Growth coefficient	$year^{-1}$	0.13
a	Length-weight slope	cm/kg	0.0035
b	Length-weight intercept	cm/kg	3.28
$R_{b,5}$	Mean biomass recruitment at age-5	$kg\ ha^{-1}$	1.24
$R_{n,5}$	Mean recruitment at age-5	$n\ ha^{-1}$	2.61
$R_{b,5}$	Mean biomass recruitment at age-5	kg	558
$R_{n,5}$	Mean recruitment at age-5	n	1117
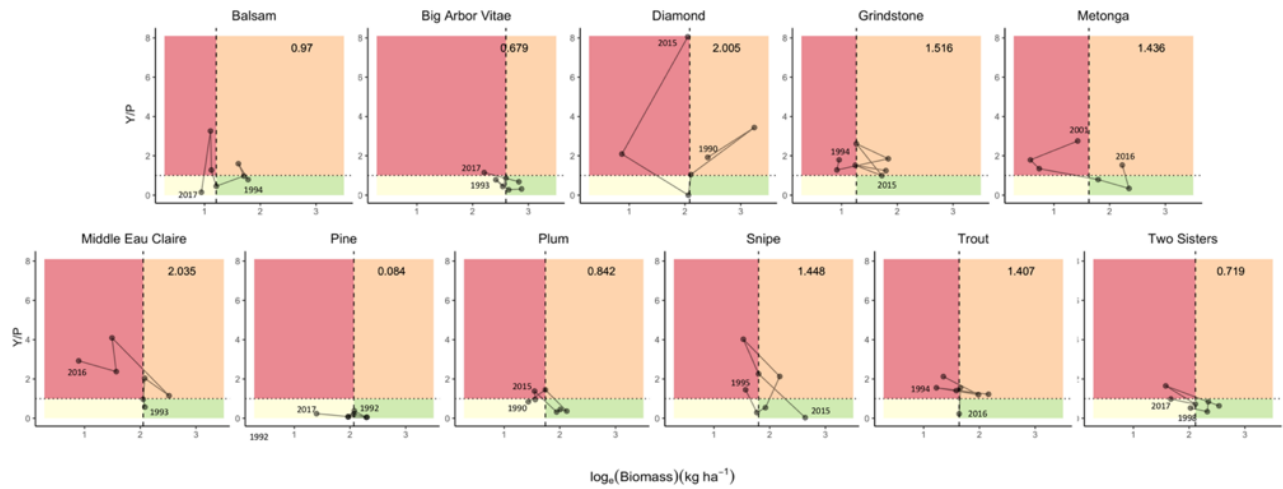
Figure S1. Modified Kobe plots of walleye (*Sander vitreus)* Y/P relative to $\log_e$-transformed biomass (kg ha^{-1}) for Northern Wisconsin, USA lakes with >5 years of sampling data (n=11). Each point corresponds to a sample year, with the first and last years identified. The horizontal dotted line establishes the 1.0 harvest threshold, at which 100% of biomass produced is being harvested. The vertical dashed line shows the lake-specific median biomass level over the study period. Reported proportions indicate the median Y/P value for the individual lake. Points in the red and orange indicate populations where production overharvest is occurring, while points in the green and yellow indicate populations that are not overharvested.
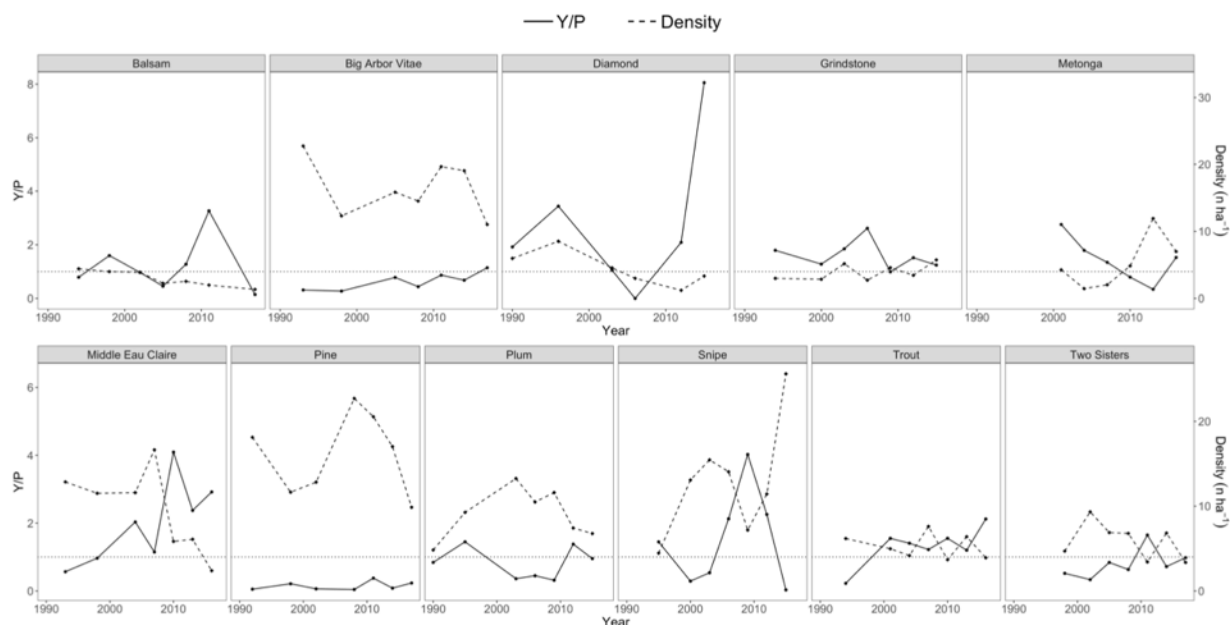
Figure S2. Time series plots of Y/P and density (n ha^{-1}) for walleye (*Sander vitreus*) populations in Northern Wisconsin, USA lakes with >5 years of sampling data (n=11) from 1990-2017. Production (P) was measured immediately following spring ice-out while harvest (Y) was measured for the year following the P estimation. Each panel corresponds to a single lake, with each point indicating a sample year. Y/P sample points are connected by a solid line and density (n ha^{-1}) sample points are connected via a dashed line. The left y axis corresponds to Y/P while the right y axis shows density (n ha^{-1}). The horizontal dotted line establishes the 1.0 harvest threshold, at which 100% of biomass produced is harvested.
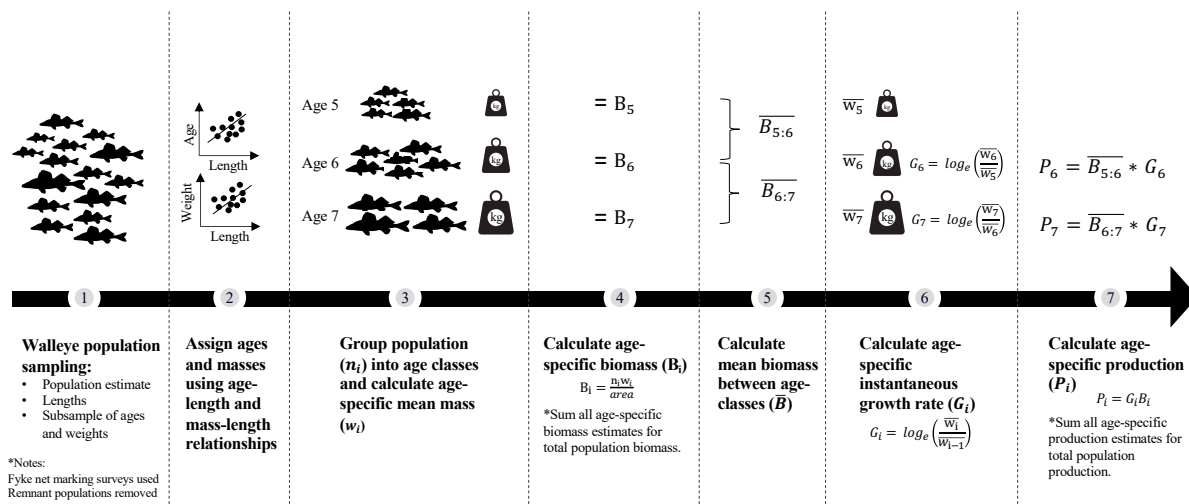
Figure S3. Flowchart illustrating the methodology used to estimate biomass and production for adult (≥5 year olds; ≥381 mm) walleye (*Sander vitreus*) populations in Northern Wisconsin, USA from 1990-2017. The example illustrates the methodology for hypothetical data from a single walleye population (i.e., single lake-year combination) with three age classes (5, 6, 7). A specific example calculation can be found in Table S3.
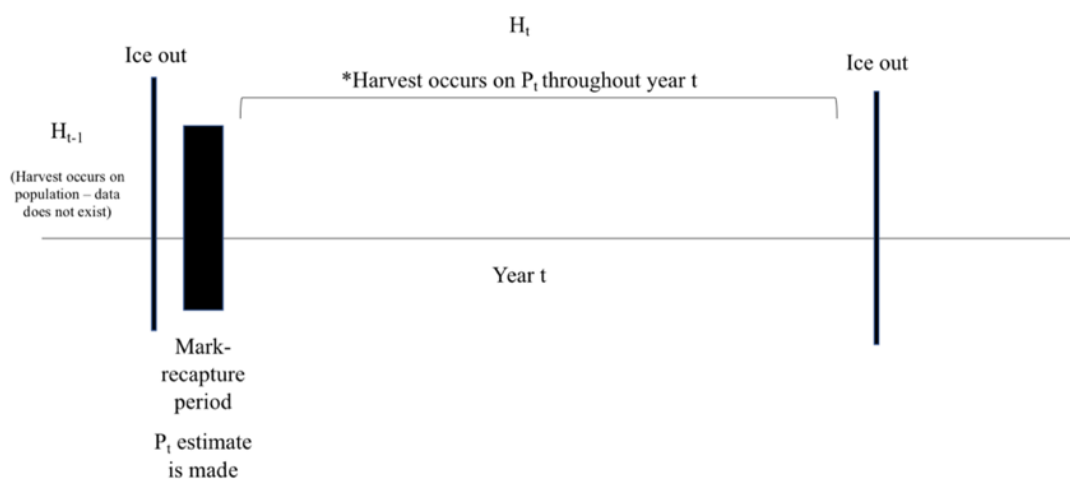
Figure S4. Illustration of sampling phenology for walleye (*Sander vitreus*) populations in Northern Wisconsin, USA. Populations are sampled immediately following ice-out using mark-recapture surveys. During this time, all data collected to make annual production estimates for year t (P_t) are sampled immediately following ice out in the spring of year t. Following these sampling events, harvest and measurements of harvest begin on this population. Although prior years' harvest would have affected the population, this influence on biomass is incorporated into the annual production estimate made at the start of the season prior to that year's harvest. Because we estimate annual production of the population immediately following the completion of the mark-recapture sampling period, harvest during population sampling is accounted for as follows. The recreational fishery is typically closed during the population sampling period. If tribal spearing harvest does occur when populations are sampled, this loss is accounted for in the population estimates because there is a compulsory creel census and any fish harvested between the mark and recapture period are subtracted from the population estimate. Likewise, state agency creel surveys begin on the first Saturday in May, which is opening day for walleye fishing in Ceded Territory lakes of Wisconsin. Therefore, projected harvest from the creel survey is also subtracted from the population estimate if this harvest occurred between the mark and recapture period (black rectangle).

*Note: each lake is rarely visited more than once during the study period, therefore annual production estimates correspond to discrete snapshots of the population for year t. Annual production calculations are based off empirical age and weight data, therefore our parameters are estimated empirically during this sampling snapshot. This approach corresponds to that developed by Ricker (7) and summarized by Hayes et al. (16).
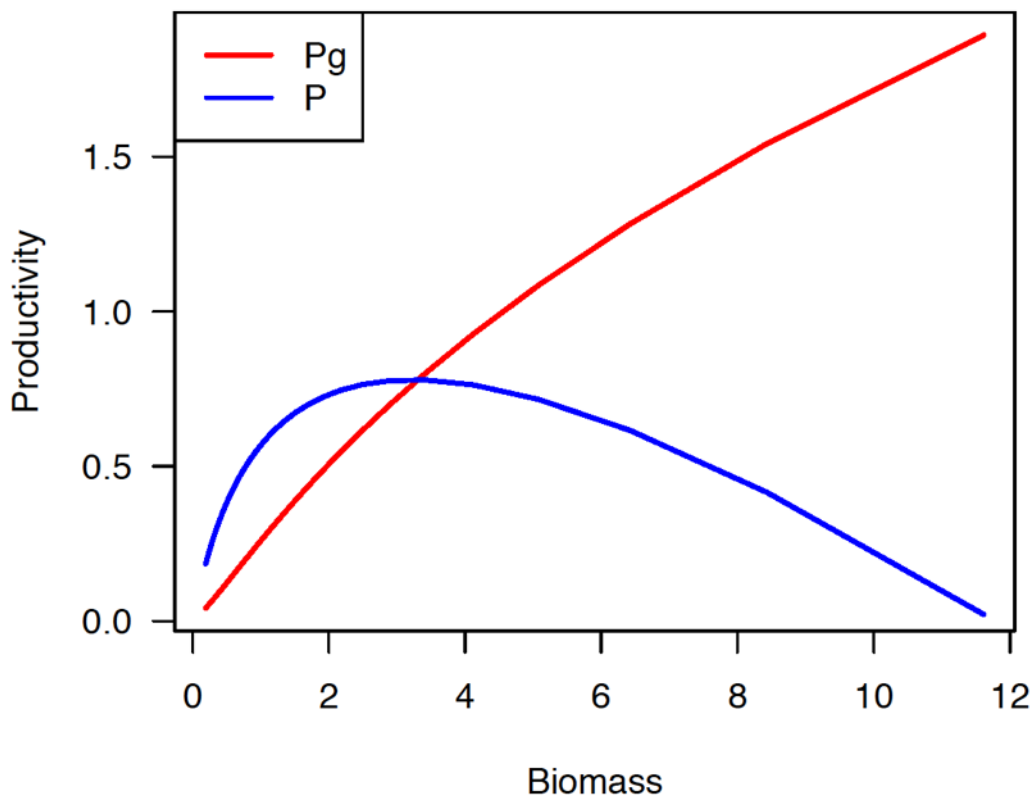
Figure S5. Equilibrium somatic growth production (Pg, red line; kg ha^{-1} y^{-1}) and surplus production (P, blue line; kg ha^{-1} y^{-1})) as a function of equilibrium population biomass for walleye (*Sander vitreus*) populations in Northern Wisconsin, USA. Parameters used to make these estimations are shown in table S5.
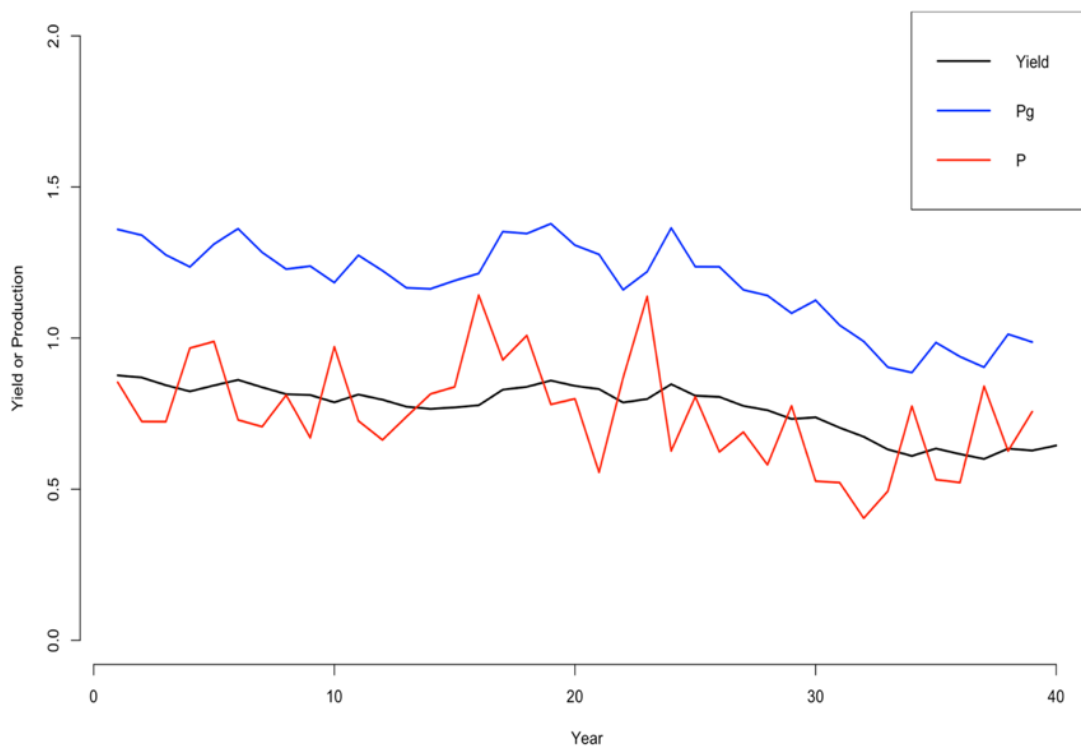
Figure S6. Simulated temporal yield (black line; kg ha^{-1}), somatic growth production (P$_g$, blue line; kg ha^{-1} y^{-1}) and total population production (P, red line; kg ha^{-1} y^{-1}) trends for walleye (*Sander vitreus*) populations in Northern Wisconsin, USA. Parameters used to make these estimations are shown in table S5.

Chapter 3: Resisting ecosystem transformation through an intensive whole-lake fish removal experiment

Abstract

Lake ecosystems are shifting due to many drivers including climate change and landscape-scale habitat disturbance, diminishing their potential to support some fisheries. Walleye Sander vitreus (Mitchill) populations, which support recreational and tribal fisheries across North America, have declined in some lakes. Climate change, harvest, invasive species, and concurrent increases in warm-water fishes (e.g., Centrarchidae) may have contributed to declines. To test the utility of an intensive management action to resist walleye loss, an experimental removal of ~285,000 centrarchids from a 33-ha lake over four years was conducted while monitoring the fish community response. Centrarchid abundance declined and yellow perch Perca flavescens (Mitchill) increased, yet no evidence of walleye recruitment was observed. These findings explore the feasibility of intensive resistance as a management strategy in supporting walleye facing environmental change and act as a segue for management discussions to move beyond resist strategies in the Resist-Accept-Direct (RAD) framework to navigate ecosystem change.

3.1. Introduction

Lake ecosystems are shifting due to unprecedented effects of climate change and landscape-scale disturbances (Carpenter et al. 2011, Lynch et al. 2016). An ecosystem transformation occurs when a system deviates from prior structure, processes, and uses by people, with climate often being a dominant driver (Thompson et al. 2021). As global

environmental change accelerates and interacts with anthropogenic stressors, such as habitat change and resource overharvest, ecosystems may be pushed across ecological thresholds (Jacobson et al. 2013, Thompson et al. 2021). Freshwater systems are sensitive to these synergistic threats due to their disproportionately high biodiversity and tight human-land-water linkages (Reid et al. 2019). North-temperate lakes, particularly those supporting important fish communities, are transforming at a rapid rate (Carpenter et al. 2011, Lynch et al. 2016). Habitat loss due to climate and land use change (Christensen et al. 1996, Marburg et al. 2006, Gaeta et al. 2014) in combination with other anthropogenic stressors (e.g., pollution, invasive species) diminish the potential for freshwater ecosystems to support fisheries (Jacobson et al. 2013, Post 2013).

Walleye *Sander vitreus* (Mitchill), the most sought-after game fish in north-central North America, supports important recreational and tribal fisheries (Nesper et al. 2002). Walleye populations in Wisconsin have declined in abundance by ~36% over the past two decades (Hansen et al. 2015a, Hansen et al. 2018, Rypel et al. 2018, Embke et al. 2019). Walleye recruitment (here defined as non-stocked age-0 relative abundance) failures have been identified as the key bottleneck leading to declines (Gostiaux et al. 2021). Multiple mechanisms have been proposed to explain recruitment failures. Climate change, leading to reduced optimal thermal and optical habitat (Hansen et al. 2019), as well as habitat degradation (Christensen et al. 1996) have been associated with declines and pose challenges for managers as they are abiotic drivers beyond local control. Other drivers potentially within the control of managers, including harvest (Embke et al. 2019), invasive species (Mercado-Silva et al. 2007, Kapuscinski et al. 2010, Hansen et al. 2020), and shifting ecological interactions resulting in increased competition/predation (Hansen et al. 2015b, Kelling et al. 2016, Hansen et al. 2018) have also

been implicated in walleye declines. Management interventions have largely sought to resist declines through extended growth fingerling stocking to supplement juvenile populations (Sass et al. 2022; Lawson et al. in press), regulation changes to limit adult walleye harvest, incentivizing harvest of potentially predatory species (e.g., largemouth bass *Micropterus salmoides* (Lacepède); Hansen et al. 2015b), and targeted species removals (Tingley et al. 2019, Sikora et al. 2021, Feiner et al., concurrent submission).

Coinciding with walleye declines, black bass and sunfish abundances are increasing (i.e., Centrarchidae species; hereafter centrarchids) leading to speculation that increasing warm-water species abundances may be contributing to walleye declines through increased predation and/or competition, especially during early life stages (Fayram et al. 2005, Hansen et al. 2015b, Kelling et al. 2016, Hansen et al. 2017). Removing centrarchids may reduce competition/predation pressure on walleye early life stages, alleviating the recruitment bottleneck observed in many walleye populations (Gostiaux et al. 2021). Managing walleye fisheries in a changing climate will require a better understanding of the role of species interactions as a factor in walleye declines and testing which adaptation options are viable for managers.

The Resist-Accept-Direct (RAD) framework can assist with the process of identifying adaptation options for such transforming ecosystems (Schuurman et al. 2021, Thompson et al. 2021, Lynch et al. 2021a, Rahel 2022). Decision options in RAD include resisting change to maintain historical conditions, accepting change without intervention, and directing the trajectory of change; therefore, it supports decisions that are effective and practically feasible (Lynch et al. 2021b). When one strategy is no longer feasible, the RAD framework can present alternative pathways to determine the viability of other management approaches. Interventions can be tested

through targeted monitoring, experimentation, and pilot studies to evaluate actions that may be considered at larger scales (Lynch et al. 2021a).

Fisheries managers can use a broad suite of RAD strategies to address transforming aquatic systems (see Lynch et al., concurrent submission, Table 1; Rahel 2022). Regional management of walleye declines have largely focused on resistance actions via stocking and harvest regulation, often with limited success (Feiner et al., concurrent submission). One of the few, and most intensive, resist actions that remains untested in its ability to rehabilitate walleye includes centrarchid removal, the efficacy of which could be best tested at the whole-lake scale because they incorporate complex interactions in a natural environment at the appropriate scale for management (Walters and Holling 1990, Carpenter et al. 1995, Carpenter 1998). In lakes, the discrete borders and relative ease for sampling provide a useful context to study whole ecosystem shifts in response to disturbance and intervention. Whole-lake manipulations have addressed community and biogeochemical responses to a variety of stressors and increased understanding of the capacity to manage ecosystem change (Carpenter et al. 1995). The focus of these experiments has spanned the effects of eutrophication to large-scale biomanipulations, ultimately informing freshwater policy and management (Schindler 1974, Carpenter et al. 1995, Bernes et al. 2015). Some whole-lake manipulations have revealed that intervention may need to be continuous, while others have successfully resulted in long-term regime shifts (Mehner 2002). Trade-offs in spatial extent and replication exist in ecosystem experiments; however, there is great value in conducting manipulations in a natural context where the experimental unit includes relevant physical, chemical, and biotic processes (Carpenter et al. 1995). Ecosystem experiments can provide incomparable insights regarding system responses to disturbance as well as the efficacy of a potential management intervention.

To test the utility of intensive resist actions, a whole-lake experimental removal of centrarchids was conducted. More than ~285,000 centrarchids were removed from an 33-ha Northern Wisconsin lake over four years while the walleye population and fish community response in the experimental lake and a reference lake were monitored. The primary objective of this research was to test whether removing centrarchids would result in quantifiable walleye natural recruitment. Additional study objectives included: a) testing whether it was possible to reduce the abundance and biomass of centrarchids; b) if possible, test for changes in abundance in the percid (i.e., walleye and yellow perch *Perca flavescens* Mitchill) community; and c) test for changes in the size-structure of the centrarchid community under intensive removal. More broadly, this manipulation was used to understand the role species interactions play in limiting natural walleye recruitment. These findings explore the feasibility of intensive resistance as a management strategy in supporting walleye fisheries facing environmental change and provide a platform for management discussions to move beyond resist actions when navigating ecosystem change. It is acknowledged that any fish community responses to the biomanipulation coincided with the removals, therefore our results represent short-term responses that may be stable or transient over time. Therefore, additional monitoring of the experimental and reference lakes will commence in the future to test for longer-term responses.

3.2. Materials and Methods

Study Area

Selecting the experimental lake where centrarchid removals occurred was a lengthy process that began with >50 candidate lakes and included extensive consultation with Wisconsin Department of Natural Resources (WDNR) and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) biologists, and public meetings with lakeshore property owners. In

addition to gaining necessary public and management support for site locations, the experimental

and reference lakes were selected based on a series of abiotic and biotic characteristics. Criteria

included: a history of self-sustaining, natural walleye recruitment, a population of adult walleye,

ample walleye spawning habitat, and an increase in centrarchid abundances. The experimental

(McDermott Lake; 46.00299280, -90.16081610) and reference (Sandy Beach Lake;

46.10614350, -89.97131020) lakes are in Iron County in Northern Wisconsin. The experimental

lake has a surface area of 33.1 ha, mean depth of 3.0 m, and maximum depth of 5.7 m. The

reference lake has a surface area of 44.5 ha, mean depth of 2.1 m, and maximum depth of 4.0 m.

Both lakes included a variety of substrates (e.g., rock, gravel, and sand) and areas of submerged

and emergent vegetation. At the start of the study, the experimental and reference lake fish

communities were similar with high centrarchid abundances (e.g., black crappie *Pomoxis*

nigromaculatus (Lesueur), bluegill *Lepomis macrochirus* Rafinesque, largemouth bass, and

pumpkinseed *Lepomis gibbosus* (Linnaeus)), few adult walleye, and a history of self-sustaining,

natural walleye recruitment. For Wisconsin lakes, natural recruitment of walleye is defined as the

relative abundance of non-stocked age-0 individuals collected in fall electrofishing surveys.

Natural recruitment was last detected in both lakes in 2003-2004, with higher age-0 catch per

unit effort (CPUE) in the reference lake (~6.51 ind/km) compared to the experimental lake

(~1.67 ind/km; see below for further information on recruitment survey methodology). Like

other walleye populations across the upper Midwest United States, both lakes have experienced

declines in adult walleye abundance and have been stocked with extended growth fingerlings

(~150-225 mm total length; TL) during the fall of every other year since at least 2011. Other

species present included yellow perch, northern pike *Esox lucius* Linnaeus, muskellunge *Esox*

masquinongy Mitchill, black bullhead *Ameiurus melas* Rafinesque, and golden shiner

Notemigonus crysoleucas (Mitchill).

Fish sampling

    Standardized surveys

        During 2017-2021, standardized monitoring surveys were conducted using numerous

sampling techniques to test for changes in the fish communities of both lakes. Sampling began

immediately after ice-out (~mid-April) with the deployment of five fyke nets (1.2 m x 1.8 m

frames, 1.9 cm bar mesh) for one week at nonrandom locations in lakes that were probable

walleye spawning sites (Hansen et al. 1991). The fyke-net surveys served two purposes: 1) to

capture walleye for marking as part of the mark-recapture survey to attain an adult population

estimate; and 2) to estimate relative abundances (fish per net night) of black crappie and yellow

perch. During these surveys, all collected walleye were measured (TL; mm), sexed, checked for

a uniquely-coded passive integrated transponder (PIT) and implanted with a PIT if one was not

present. Adult (mature) walleye were defined either as all fish ≥381 mm or for which sex could

be determined by extrusion of gametes (regardless of length). Walleye of unknown sex <381 mm

were classified as juvenile (immature). Both study lakes have had walleye population estimates

previously conducted by the WDNR. Therefore, WDNR protocols were followed where the goal

was to mark 10% of the anticipated spawning population (based on previous population

estimates; Cichosz 2017). Marking continued until the target number was reached or spent

females began appearing in fyke nets. Tagged walleye were recaptured using nighttime AC boat

electrofishing within one week (typically 1-4 days) after netting and marking were completed

(Beard et al. 1997). In each lake, the entire shoreline was electrofished. All walleye were

measured and examined for PITs. Population estimates (PEs) were calculated using Chapman's

modification of the Petersen estimator (Chapman 1951, Cichosz 2017). To determine black crappie and yellow perch relative abundances, all individuals were counted and a subsample of 30 fish per species per day for each lake was measured (TL; mm).

A combination of standardized surveys was performed to quantify centrarchid relative abundances of species other than black crappie (i.e., bluegill, largemouth bass, pumpkinseed, and rock bass *Ambloplites rupestris* (Rafinesque)). In early summer (May, water temperatures=13.0–21.0°C), surveys began with an AC boat electrofishing. During June-August, fish were sampled once monthly when lake surface water temperatures were ≥13.0°C in both lakes (water temperatures =18.3–26.7°C; Simonson et al. 2008). Both lakes were sampled for 1week each month using three gears (AC boat electrofishing, mini-fyke nets, cloverleaf traps). Lakes were sampled on consecutive nights in each 1-week period but only one gear type was used per night.

All gears sampled shallow littoral zones (0–5 m from bank, depth ≤2 m) and were deployed in fixed locations following standard approaches (Bonar et al. 2009). Sampling locations were evenly distributed along the lake shoreline, and all gears were deployed in similar habitat types. Five 10-min nighttime boat electrofishing (Wisconsin-style; AC; 2.0–3.0 amps, 200–350 V, 25% duty cycle) transects were conducted using two dipnetters covering the majority (>80%) of the shoreline and spanning a variety of habitat types (e.g., vegetation, sediment, gravel). Five mini-fyke nets (0.9-m × 0.61-m frames, 3.2-mm mesh [bar measure], 7.6-m-long lead, and a double throat) were deployed in areas where the net frames would be in 1.0–1.5 m of water, with leads fixed onshore. Five cloverleaf traps (three lobed, height = 41 cm, 50 cm diameter, 6.0-mm bar wire mesh with 12.7-mm-wide openings between lobes, and an attractant [beef liver]) were deployed in littoral habitats. Mini-fyke nets and cloverleaf traps were set in early afternoon, fished overnight, and retrieved the following afternoon (~24-h soak time).

All catches were standardized according to gear-specific effort. For boat electrofishing, CPUE was calculated as the number of individuals captured per hr. For mini-fyke nets and cloverleaf traps, CPUE was calculated as the number of individuals captured per net night or trap night.

To estimate walleye recruitment, multiple gears were used, including ichthyoplankton surface trawls, micromesh gillnets, beach seines, and boat electrofishing. A 1,000-μm mesh ichthyoplankton net was towed within 1 m of the water surface at five locations in each lake at night about every seven days beginning two weeks after the presumed walleye spawn until June (Isermann and Willis 2008). In late July/early August, four vertical gillnets (46-m x 1.2-m with 0.64-cm bar mesh) were deployed. Sampling locations were evenly distributed along the shoreline and locations were fixed each year. Gillnets were set at night and at depths ranging from 0-5 m. Set duration ranged from 1-2 hours to minimize bycatch (Boehm et al. 2020). In late August, 0.24-m long beach seines with 0.64-cm mesh were pulled at five sites in each lake. Sites were chosen to represent a variety of habitat types and based on ability to effectively use the seine. Seining sites remained fixed for the duration of the study. Seines were used during daylight hours on each lake. Catch per unit effort was calculated as the number of individuals per seine haul. When water temperatures fell below 21°C (early September), age-0 walleye were sampled using nighttime boat electrofishing of the entire shoreline of each lake (Wisconsin-style; AC; 2.0–3.0 amps, 200–350 V, two netters). Surveys were conducted prior to walleye fingerling stocking, meaning any collected age-0 walleye were produced via natural recruitment.

Removal efforts

In addition to standardized surveys, centrarchid removal efforts began in 2018 in the experimental lake using a variety of techniques including fyke nets, boat electrofishing, mini-fyke nets, and cloverleaf traps. Following spring fyke net surveys, fyke nets remained in the

experimental lake to remove centrarchids. In 2018, 10 fyke nets were used to remove fish from

May 14 to June 7 and in 2019, from May 9 to June 27. During 2018 and 2019 fyke netting ended

when centrarchid catches started to decline. In 2020 and 2021, only five fyke nets were used

from late spring (April 30 and May 10) until late-June (June 25 and June 11) due to personnel

limitations. Additionally, five mini-fyke nets and 21 cloverleaf traps were sampled from late-

May to mid-August each year. All gears were emptied every 1-2 days and sites were rotated to

maximize centrarchid catches. Collected fish were identified to species and up to 30 individuals

per species per gear were measured daily (TL, mm). Centrarchid species were retained while

other species were returned to the lake. Species removed included black crappie, bluegill, green

sunfish *Lepomis cyanellus* Rafinesque, pumpkinseed, rock bass, largemouth bass, and

smallmouth bass *Micropterus dolomieu* Lacepède (Fig. 1). Removed centrarchids were used for

aging purposes (see below) or donated to local wildlife health centers.

Fish processing

To understand demographic changes of the centrarchid and yellow perch populations in

the experimental and reference lakes, up to 20 individuals per ~25 mm interval were retained for

analyses from each lake. In the laboratory, individuals were dissected and species, TL (mm), and

weight (g) were recorded. Sagittal otoliths were removed to determine if an individual was age-0

or age-1+. Ages were estimated using a combination of whole and thin-sectioned otoliths. To

generalize across species, whole otoliths were typically used for fish <150 mm TL and sectioned

otoliths were always used for fish >150 mm TL (Hoyer and Maceina 1985, Schramm 1989).

Whole otoliths were submerged in water in a black dish and viewed using a Nikon 1500 SMZ

stereomicroscope under reflected light; images were projected to a 76 × 45 cm flat-screen LCD

monitor using via a Nikon DS-Fi2 or DS-Fi3 color camera connected to Nikon NIS-Elements

software (Schramm and Doerzbacher 1985). To section otoliths, one otolith was embedded in epoxy and a transverse section (1.2 mm) through the focus was obtained using a low-speed saw (Wegleitner & Isermann 2017). Otolith sections were glued to microscope slides with cyanoacrylic cement and were projected using the same microscope, camera, and software configuration but under transmitted light. Ages were assigned independently by two readers; when disagreements occurred, consensus ages were obtained by the two readers viewing the otoliths together. If a consensus age could not be reached, the fish was not used for age assignment.

Data analyses

The total biomass of centrarchids removed from the experimental lake over the study period was estimated via extrapolation of lengths and weights to unmeasured fish based on the measured samples. A subset of measured fish lengths (daily maximum = 30 per species per gear) was used to assign total length (mm) to unmeasured individuals. Available fish lengths were sampled with replacement and used to assign lengths to unmeasured fish according to the total number of individuals collected. To estimate centrarchid biomass (kg) removed from the experimental lake, species-specific weight-length regressions were developed for each year within each lake to predict weights (g) of fishes that were not weighed. Length (mm) was $\log_e$ transformed prior to analysis. Once all sampled fish had an assigned weight, centrarchid weights were summed from the experimental lake for years 2018-2021 to calculate total biomass removed from the lake.

Examination of temporal trends in the relative abundance and removed biomass of species focused on the species that collectively comprised the majority (>95%) of overall species abundances: black crappie, bluegill, pumpkinseed, rock bass, largemouth bass, walleye, and

yellow perch. To remain consistent across years, removal sampling dates were separated from survey sampling dates. Removal data were used to estimate the abundance (n) and biomass (kg) of centrarchids removed from the experimental lake. Standardized survey CPUE was compared across years to test for changes due to the removal experiment. Species susceptibility to gears varies across seasons. Therefore, depending on the species of interest, different (or a combination of) surveys were used to test for changes in abundance over time. To test for changes in black crappie and yellow perch relative abundances, spring fyke net survey CPUE was used, whereas boat electrofishing survey CPUE was used for largemouth bass, as these surveys best reflect adult relative abundance shifts. Further, once lengths had been assigned for all sampled fish during spring electrofishing surveys, largemouth bass <203 mm were removed, as they were not fully recruited to the sampling gear.

Bluegill, pumpkinseed, and rock bass were susceptible to multiple gears throughout the sampling season. Therefore, gear-specific CPUE from each standardized survey gear (cloverleaf trap, mini-fyke net, fyke net, boat electrofishing) was used. This research was primarily interested in understanding adult population dynamics of these species while avoiding the influence of highly variable age-0 recruitment dynamics. Therefore, otolith age data from 2017-2020 were used to develop lake-species minimum length-at-age-1 thresholds to designate fishes into two categories: age-1+ and age-0 (i.e., young-of-year). Based on assigned lengths, if a fish was below the age-1+ threshold, it was considered age-0. If the fish was equal to or exceeded the age-1+ threshold, it was considered age-1+ and included in the analyses. Once age-1+ fish were identified, mean CPUE was calculated for each lake-gear-species combination. For all data, Shapiro–Wilk tests were run to test whether CPUE were normally distributed. Based on findings, CPUE data were $\log_e$-transformed prior to analysis. To test for differences in mean annual CPUE

and mean length before and after the experiment, a one-way ANOVA was used. Gear-specific $\log_e$(CPUE) or total length (mm) was compared before and after the experiment. An $\alpha = 0.05$ (adjusted for multiple comparisons) was used for all statistical analyses. All calculations and statistical analyses were performed in R version 4.0.3 (R Core Team 2021). All data and accompanying metadata are freely available to the public supported by the U.S. Geological Survey (USGS) Climate Adaptation Science Centers (DOI in prep).

3.3. Results

Seven centrarchid species were among the ~285,100 fishes (~3190 kg) removed from the experimental lake during 2018-2021 (Fig. 1). Most individuals removed were bluegill (n=197,152) and largemouth bass (n=35,168), while the majority of biomass removed was bluegill (~64% of all removed biomass), in addition to black crappie and pumpkinseed (Fig. 1). Over the study duration, removal efforts in the experimental lake comprised 107 hours of electrofishing, 717 net nights of fyke nets, 908 net nights of mini-fyke nets, and 6942 traps nights of cloverleaf traps. When spread across individual nights, this effort totaled ~23 years of individual nightly effort.

After two years of centrarchid removals, adult walleye abundance temporarily increased in the experimental lake when ~120 (95%CI = 54-342) adults were estimated, but in the most recent sampling year (2021) abundance decreased to pre-removal levels (~30-40 (95%CI = 26-98) individuals; Fig. 2). In contrast, adult walleye abundance decreased in the reference system until the most recent year (2021) when the population increased to ~112 (95%CI=64-474) individuals (Fig. 2). Both lakes were stocked with extended growth walleye fingerlings (mean TL ~164mm) in late-September 2017, 2019, and 2021. Specifically, the experimental lake was stocked with ~840 individuals each stocking year and the reference system was stocked with

~1110 individuals each stocking year. No age-0 walleye were collected in either lake, indicating

that no detectable natural recruitment had occurred during the study period.

As fish were removed in the experimental lake, age-1+ CPUE decreased for most

centrarchid species (Table 1, Fig. 3). Black crappie relative abundance significantly declined

following the first year of removal efforts and has remained at lower relative abundances in

subsequent years, with an overall decline in CPUE from pre-removal to 2021 of ~83% (CPUE

change from ~13.25 to ~2.26 ind/net, $p<0.01$; Table 1, Fig. 3). Adult largemouth bass relative

abundance remained relatively constant throughout the study (Table 1, Fig. 3). Bluegill were the

most abundant species in the lake, with pre-removal CPUE in most gears of ~55 ind/net or per

trap (mean CPUE from cloverleaf traps, fyke nets, and mini-fyke nets; Table 1, Fig. 3). Bluegill

showed the largest declines through 2020, concurrent with an increase in adult walleye, but

bluegill CPUE was higher in the most recent sampling year (2021; Fig. 2, Fig. 3). Cloverleaf

traps, which sample smaller individuals (Sullivan et al. 2019*a*), showed the most variability (Fig.

3). Cloverleaf catches initially declined ~89% from pre-removal-2020 CPUE (CPUE change

from 75 to 8.5 ind/trap), but then increased ~241% from 2020-2021 CPUE (CPUE change from

8.5 to 29.1 ind/trap; Fig. 3). Other gears sampling larger bluegill relative abundances including

fyke nets and mini-fyke nets significantly declined throughout the study period ($p<0.01$, Table 1,

Fig. 3). Overall, pumpkinseed CPUE significantly declined in most gears aside from

electrofishing (which remained relatively constant) throughout the study period ($p<0.01$, Table 1,

Fig. 3). The CPUE of rock bass significantly declined after the first year of removal efforts, with

overall declines of ~75% ($p<0.01$, Table 1, Fig. 3). Fishes in the reference lake varied in CPUE

over time, with no statistically significant trends (Table 1, Fig. 3). Yellow perch showed the most

marked response to removal efforts, with a significant and steady CPUE increase of 788%

following fish removals (CPUE change from ~8.9 to ~79.11 ind/net, p<0.001; Table 1, Fig. 3). Although not statistically significant, yellow perch CPUE also increased by ~116% in the reference lake over the study period (CPUE change from ~17.61 to ~38.14 ind/net; Table 1, Fig. 3).

Yellow perch mean length significantly changed in both lakes over the study period, but in opposite directions (p<0.001, Table 2, Fig. 4). In the experimental lake, yellow perch mean length increased by ~ 17.9% from 156 mm to 184 mm (p<0.001, Table 2, Fig. 4). In the reference lake, yellow perch mean length slightly decreased by ~4% (p<0.001, Table 2, Fig. 4). In the experimental lake, all centrarchid species except for black crappie significantly decreased in mean length with overall declines of ~6-33% (p<0.01, Table 2, Fig. 4). Rock bass showed the largest decrease in mean length from 133 mm to 89 mm over the study period (p<0.01 Table 2, Fig. 4). In the reference lake, bluegill significantly increased by 14% in mean length from 77 mm to 87 mm (p<0.01 Table 2, Fig. 4).

3.4. Discussion

Whole-lake manipulation to resist walleye decline

An ecosystem experiment was performed where ~285,000 centrarchids were removed from an 33-ha north-temperate lake to understand the role of centrarchid species interactions in limiting walleye populations. Although intensive effort was applied and relative abundances of most centrarchids significantly declined by ~74% over the study period, adult walleye abundance did not appreciably change and there was no evidence of natural recruitment (Table 1). These findings indicate walleye were less influenced by centrarchid interactions (e.g., predation, competition) and may be more influenced by other drivers, such as climate and habitat change. However, in the experimental lake yellow perch relative abundance and mean length

significantly increased by ~788% and ~18%, respectively, demonstrating that yellow perch may

be more sensitive to reduced competition/predation and thus intervention (Fig. 3).

The whole-lake experiment that was conducted was used to test the efficacy of resistance

as a management approach in sustaining walleye populations given climate change and other

disturbances. Further, the value of management experiments was demonstrated as the removal

helped to define the extent to which managers can intervene in response to shifting ecosystems.

Despite intensive effort (more than 23 yrs of net-nights, trap-nights, and electrofishing), a

historical ecosystem condition restoring natural recruitment in the experimental lake was not

achieved during the study time frame. These results demonstrate that resistance may not be a

viable option in certain contexts, specifically in warming, centrarchid-dominated lakes where

fish community composition is also influenced by other non-climate change factors (e.g.,

voluntary release of centrarchids by anglers, Fig. 5; Gaeta et al. 2013, Hansen et al. 2015*b*, Shaw

and Sass 2020). As resistance efforts may be futile in certain contexts, transitions to different

approaches will be critical to adapt to transforming ecosystems (Lynch et al., *concurrent*

submission).

Fish species responses to the whole-lake fish removal experiment

In the experimental lake, an increase in adult walleye abundance was observed in 2020

relative to 2017-2019 and 2021 abundances, but this finding cannot be attributed to any

detectable natural recruitment. Given the increasing adult walleye population response in 2020,

stocked individuals from previous years may have contributed to the adult fishery at that point,

but this response may have been short-lived given the most recent (2021) return to pre-removal

abundances. In contrast, after declining for four consecutive years, the reference lake walleye

population showed increases in 2021 possibly due to a variety of factors including stocking, harvest variability, and natural population fluctuations.

The majority of dominant centrarchid species decreased in relative abundance in the experimental lake, except for largemouth bass, while no significant changes occurred in the reference lake throughout the study period. Black crappie and rock bass showed the largest declines following the first year of removals and have remained at relatively low relative abundances in subsequent years, indicating that these species may be effectively reduced through a single year of intensive removal efforts. Notably, rock bass mean length significantly decreased following removals, indicating compensatory recruitment may have occurred wherein remaining individuals reproduced and grew faster given increased resources (Ali et al. 2003, Gaeta et al. 2015, Sass and Shaw 2018, Sass et al. 2021*a*). Pumpkinseed showed slight declines in relative abundance and mean length over time while largemouth bass showed no change in abundance but a decrease in mean length, illustrating that these species may be more resistant to removal efforts. Largemouth bass, especially juveniles, are difficult to sample in lakes therefore gear evasion may have played a role in the ability to remove this species. Others have shown the limitations of largemouth bass removals via harvest (Gabelhouse 1987, Sullivan et al. 2019*b*), therefore controlling largemouth bass abundance may currently be beyond the reach of management efforts.

The most abundant fish species in the lake, bluegill, showed relative abundance declines in response to fish removals, especially for gears sampling smaller fishes, however this trend was reversed in 2021. Large-bodied bluegill relative abundance, best indicated by fyke net CPUE, declined throughout the study period, until remaining consistent in 2021. In combination with smaller-bodied bluegill CPUE increases in 2021, increasing bluegill relative abundances as well

as reduced mean length potentially indicating a density-dependent compensatory response occurred. Prior to fish removals, the bluegill population was characterized by many small-bodied individuals (i.e., a stunted population), therefore it is not entirely surprising that reduced population densities resulted in increased abundances and reduced mean length (Beard and Essington 2000). However, it is notable that this potential compensatory response did not occur until ~228,000 fishes had been removed from the lake. In contrast, bluegill in the reference lake showed a ~14% increase in mean length. Overall, with the decline in abundance of younger age classes (i.e., smaller fishes) due to removals, it is unsurprising older ages (i.e., larger fishes) also declined over the study period, until a compensatory response was observed. As is emphasized by these results, bluegill are a highly resilient species with remarkably flexible life-history characteristics making them challenging to control in predictable ways (Mittelbach 1986, Beard and Essington 2000).

Yellow perch significantly increased in relative abundance and mean length following the first year of fish removals and maintained high levels for the remainder of the study period, overall increasing in abundance by ~788% and in length by ~18%. Although the ecosystem was not pushed back to its historical state supporting natural walleye recruitment, centrarchid relative abundances were reduced such that a window may have been opened for yellow perch to increase and maintain high relative abundances and increase in mean length. It is possible this response was driven by a very strong year-class emerging soon after initial removals, therefore monitoring will be critical to disentangle the effect of species interactions driving yellow perch population dynamics. Yellow perch are a highly popular cool-water gamefish in north-temperate lakes and a close taxonomic relative to walleye (Embke et al. 2020, Feiner et al. 2020, Brandt et al. 2022). Based on these findings and others (Sikora et al. 2021), yellow perch may be more

responsive to changes in community dynamics, revealing potential management intervention avenues to support self-sustaining populations in the future (Fig. 5). Increased yellow perch relative abundances present potential fishery opportunities that may satisfy resource user needs given climate change limitations for walleye.

Approach limitations and considerations

This experiment was performed on a single lake; therefore, the results may not adequately represent the variety of conditions and suite of responses when scaled up to other locations with variable habitat or species assemblages. For example, Sikora et al. (2021) found remarkable rebounds in natural walleye recruitment following single-year intensive bullhead (*Ameiurus* spp.) removals in north-temperate lakes, indicating predator/competitor life-history strategies greatly influence intervention success (Weidel et al. 2007). Further, a significant reduction in centrarchid abundance may not align with a comparable ecological effect for walleye. Perhaps the threshold where enough resources are released for walleye to become dominant was not reached and therefore any observed responses may be short-lived. It is acknowledged that a critical threshold may not have been passed but future research may show if the manipulation achieved a new state of the food web as well as if the intensive removal and ongoing stocking could shift the walleye population from depensation to compensation (Mehner 2002, Walters and Kitchell 2001, Sass et al. 2021*b*). Therefore, despite uncertainty with regards to reaching a critical threshold, these findings still indicate it is unrealistic to use this intensity of removal efforts as a management measure in broader contexts.

Although the experimental lake did have a history of natural walleye recruitment, no natural recruitment has been detected since 2004. It is possible the experimental lake was never a robust natural population; therefore, this lake may represent a more marginal population like

many of those in the region. However, the research presented here represents a highly intensive

removal effort for centrarchid species and therefore is likely representative of the efficacy of

less-intensive management approaches that may be undertaken. Large-scale management

experiments such as this are necessary to understand which approaches are feasible given

ecological, economic, and social constraints (Lynch et al. 2021*b*).

This study was performed over five years and many organisms including walleye are

slow-growing (average age-at-maturity = 4yrs for males, 5yrs for females; Cichosz 2017), thus

changes underway may not have been detected due to response time-lags. Yellow perch relative

abundance increased in both lakes, however the magnitude of increase in the experimental lake

was significant and suggestive of a centrarchid removal manipulation effect. Given the

abundance and mean length response of yellow perch to the centrarchid removal, it is possible

that walleye natural recruitment and adult abundance responses may be lagged. Yellow perch are

a major prey item of walleye (Forney 1974), and indices of yellow perch abundance have been

shown to be significant predictors of walleye recruitment (Hansen et al. 1998, Beard et al. 2003).

Monitoring will be essential to track the ecosystem trajectory and detect when/if the system

reaches a new state, specifically if reduced centrarchid populations rebound once removal efforts

subside or if walleye and other species, such as yellow perch, further increase.

Alternative management approaches and future thoughts

Given the effects of global environmental change, it is necessary to consider alternative

strategies to *resisting* ecosystem transformation (Lynch et al. *concurrent submission*).

Alternative *accept* and *direct* approaches can be used simultaneously. In this context, managers

could *accept* that walleye fisheries may not persist in all ecosystems where they once thrived,

especially in warming, centrarchid-dominated systems (Fig. 5). At the same time, managers

could identify ecosystems most likely to support walleye in the future (e.g., lakes with lower

centrarchid abundances; Tingley et al. 2019) and allocate management resources accordingly

(Fig. 5; Dassow et al. *concurrent submission*). However, for north-temperate lakes with multi-

species fisheries, acknowledging expected walleye declines in certain systems has great

implications for the management of other species and human expectations (Hansen et al. 2015*b*,

Tingley et al. 2019, Feiner et al., *concurrent submission*). For example, when resistance is no

longer feasible and managers *accept* that some ecosystems may turn to centrarchid dominance,

they could then *direct* certain fisheries towards different species to provide alternative

ecologically viable, socially acceptable opportunities (Fig. 5). Overall, lake districts – regions

with many lakes such as those in Northern Wisconsin – provide the option to distribute RAD

approaches across the landscape. For instance, some walleye population managers can *resist*

transformation by limiting invasive species or removing bullheads or other predators, while

others can *accept* warm-water fisheries that emerge, or others may *direct* the systems by

introducing new fisheries (Fig. 5).

The heterogeneity of lakes on the landscape provides a great context to apply the RAD

decision framework. Management decision pathways such as these will be necessary to manage

transforming ecosystems that are likely unable to transition back to historical states given

changing climates (Dassow et al. *concurrent submission*, Feiner et al. *concurrent submission*).

Further shifts to inland systems are likely as complex lake food webs yield to a changing climate

(Jackson 2021). As observed in the large-scale experiment, ecosystem responses are

unpredictable and non-stationary. Even in the reference system which was only influenced by

abiotic effects and current management approaches (e.g., stocking, harvest regulations),

community responses were non-stationary. To effectively manage transforming ecosystems,

decisions must consider the inherent uncertainty in future outcomes to account for unexpected shifts (Lynch et al. 2021*b*). For inland recreational fisheries, several assessment methods exist that consider stochastic dynamics and critical thresholds (Carpenter et al. 2017, Embke et al. 2019, Cahill et al. 2021). To increase management resilience to ecosystem transformation, it will be vital to use approaches such as these that directly consider system thresholds in combination with iteratively evaluating management options in the RAD framework to move beyond traditional resistance when this approach is no longer viable.

3.5. Conclusion

Global environmental change is transforming ecosystems at unprecedented rates. Freshwater systems and the fisheries they support are particularly vulnerable to these changes given their sensitivity to anthropogenic stressors. Although some fishes are negatively influenced by climate change and have declined in some areas (e.g., walleye), others are positively affected and abundances have increased (e.g., centrarchids). These shifting community dynamics present novel challenges for natural resource managers, who have generally resisted change by attempting to maintain historical conditions. The RAD framework provides alternative decision pathways to consider, especially when resistance is no longer an ecologically, economically, or socially feasible option (Schuurman et al. 2021, Thompson et al. 2021, Lynch et al. 2021*a*). The efficacy of resistance as a strategy in supporting self-sustaining walleye populations was tested through a whole-lake centrarchid removal experiment. Although centrarchid abundances were reduced and yellow perch abundance significantly increased, natural walleye recruitment was not detected indicating resistance may not be a viable approach in warming, centrarchid-dominated systems also influenced by other drivers. Managers may need to consider alternative *accept* and *direct* pathways, which open the door to new fishery opportunities (e.g., centrarchids and/or

yellow perch in the region of this study). Large-scale management experiments such as the one undertaken here are vital to better understand the capacity to manage ecosystem change. To increase resilience to ecosystem transformation, managers can incorporate uncertainty into assessments while iteratively evaluating management options within the RAD framework.

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3.7. Tables

Table 1. Species-gear-specific age-1+ relative abundance (CPUE; n/gear) for the experimental (McDermott) and reference (Sandy Beach) lakes before (2017) and after (2021) Centrarchidae species were removed from the experimental lake. If no individuals were collected in given gear in 2017, 2018 values are shown. Modelled predictions are presented for statistically significant trends and empirical estimates are presented for statistically insignificant trends. Colors represent statistical significance and different colors represent positive or negative % change.

Lake	Species	Gear	Pre-removal mean CPUE	Post-removal mean CPUE	% Change	Statistically Significant
Experimental (McDermott)	Black Crappie	Fyke net	13.25	2.26	-82.94	Yes
	Bluegill	Cloverleaf Trap	76.62	29.07	-62.06	No
		Electrofishing	1.83	1.87	2.19	No
		Fyke net	43.72	21.00	-51.97	Yes
		Mini-Fyke net	20.85	3.13	-84.99	Yes
	Largemouth Bass	Electrofishing	8.26	8.81	6.66	No
	Pumpkinseed	Cloverleaf Trap	1.2	0.14	-88.33	No
		Electrofishing	0.32	0.49	53.13	No
		Fyke net	1.61	3.30	104.97	No
		Mini-Fyke net	3.81	1.06	-72.18	Yes
	Rock Bass	Cloverleaf Trap	0.05	0.20	294.00	No
		Electrofishing	0.19	0.03	-84.21	Yes
		Fyke net	1.21	0.40	-66.94	Yes
		Mini-Fyke net	0.69	0.75	8.70	No
	Yellow Perch	Fyke net	8.9	79.11	788.88	Yes
Reference (Sandy Beach)	Black Crappie	Fyke net	9.95	38.97	291.66	No
	Bluegill	Cloverleaf Trap	29.34	4.63	-84.22	No
		Electrofishing	0.13	0.13	0.00	No
		Fyke net	1.21	2.19	80.99	No
		Mini-Fyke net	2.47	2.37	-4.05	No
	Largemouth Bass	Electrofishing	0.75	1.65	120.00	No
	Pumpkinseed	Cloverleaf Trap	1.2	0.40	-66.67	No
		Electrofishing	0.02	0.18	800.00	No
		Fyke net	0.29	0.31	6.90	No
	Yellow Perch	Fyke net	17.61	38.14	116.58	No

Table 2. Species-specific annual mean length (mm) for the experimental (McDermott) and reference (Sandy Beach) lakes before (2017) and after (2021) Centrarchidae species were removed from the experimental lake. If no individuals were collected in given gear in 2017, 2018 values are shown. Modelled predictions are presented for statistically significant trends and empirical estimates are presented for statistically insignificant trends. Colors represent statistical significance and different colors represent positive or negative % change.

Lake	Species	Pre-removal mean length (mm)	Post-removal mean length (mm)	% Change	Statistically Significant
Experimental (McDermott)	Black Crappie	196.78	196.38	-0.20	No
	Bluegill	75.21	70.89	-5.74	Yes
	Largemouth Bass	248.65	218.30	-12.21	Yes
	Pumpkinseed	99.55	78.62	-21.02	Yes
	Rock Bass	133.48	88.78	-33.49	Yes
	Yellow Perch	156.14	184.03	17.88	Yes
Reference (Sandy Beach)	Black Crappie	202.32	203.67	0.67	No
	Bluegill	76.83	87.44	13.81	Yes
	Largemouth Bass	419.86	355.00	-15.44	No
	Pumpkinseed	107.62	75.91	-29.46	No
	Yellow Perch	167.09	160.51	-3.94	Yes

3.8. Figures
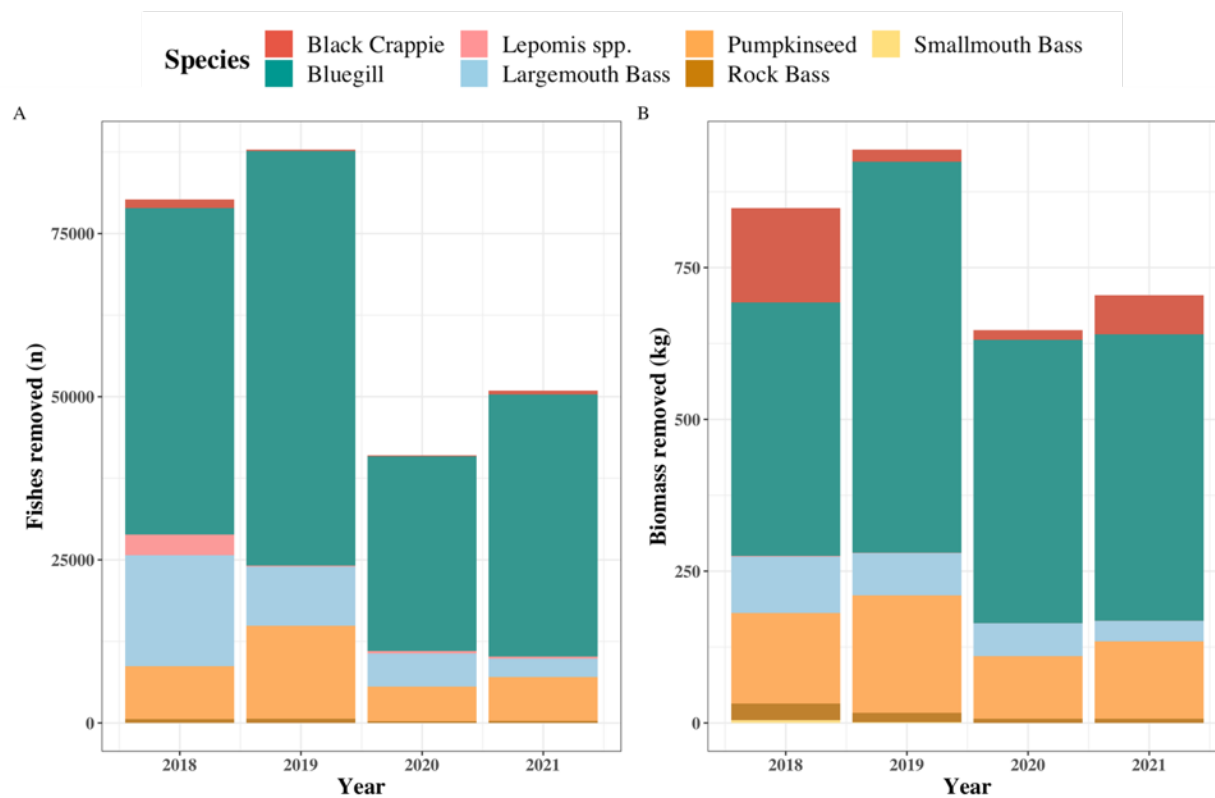
Figure 1. Centrarchidae species removed from the experimental lake, McDermott Lake, Wisconsin, during 2018-2021. Panel A shows the abundance (n) of fishes removed and panel B shows biomass (kg) of fishes removed. Colors indicate species.
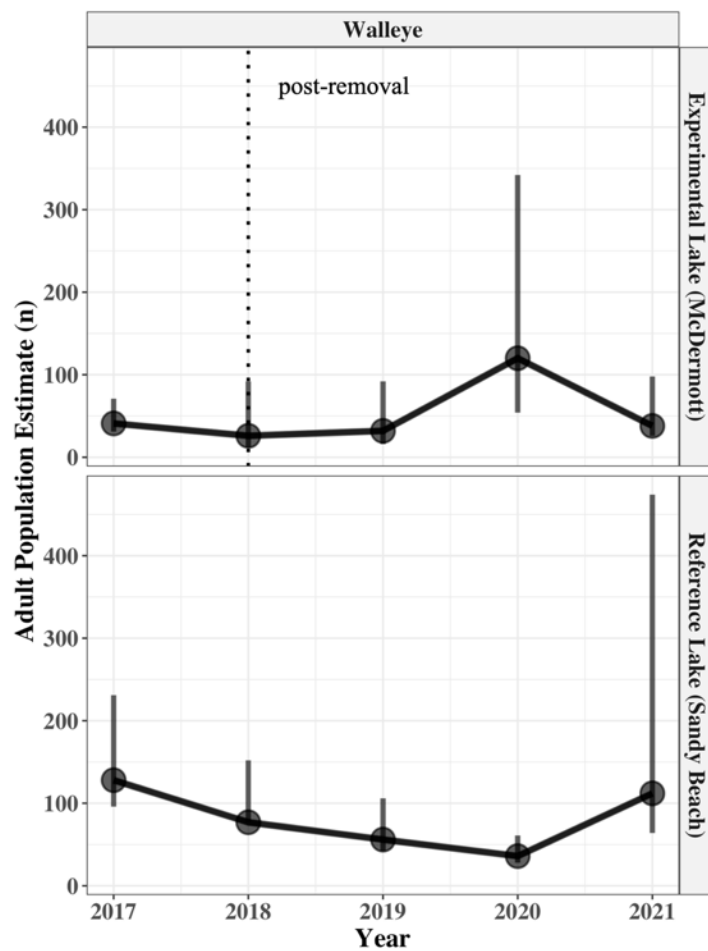
Figure 2. Adult walleye (*Sander vitreus*) population estimates (n) for the experimental (McDermott) and reference (Sandy Beach) lakes during 2017-2021. The upper row corresponds to the experimental lake and the lower row corresponds to the reference lake. Error bars represent 95% confidence intervals. The vertical dotted line indicates when Centrarchidae species removals began from the experimental lake in 2018.
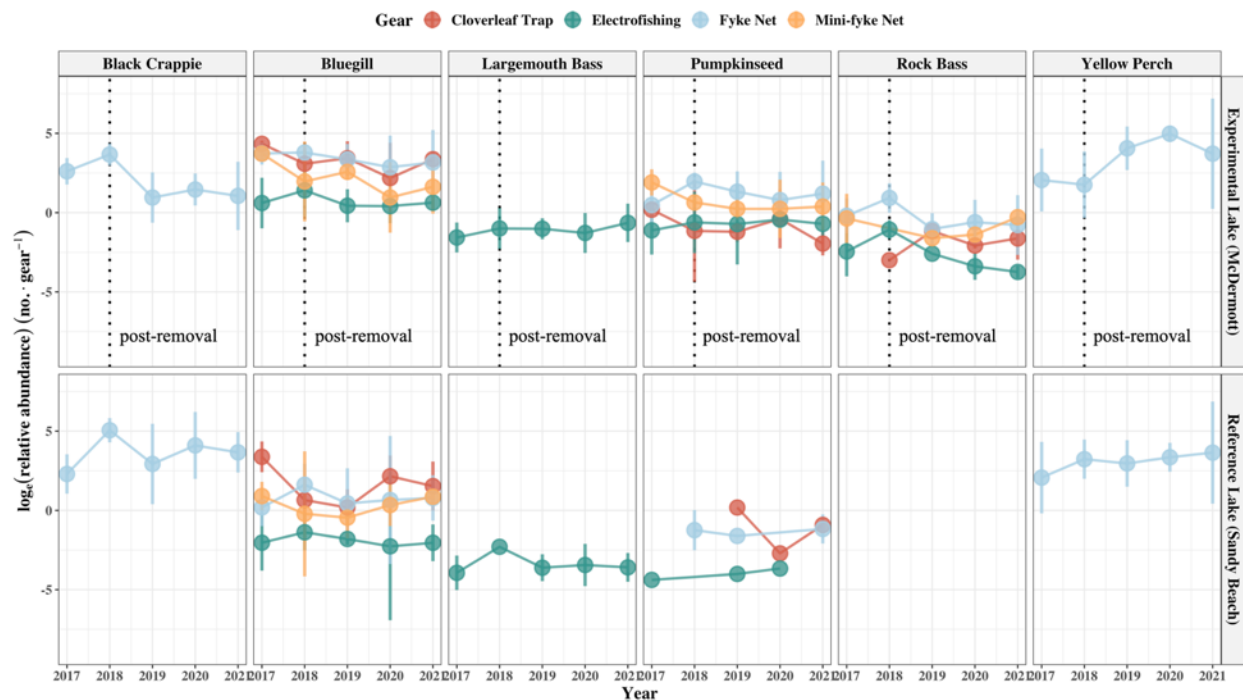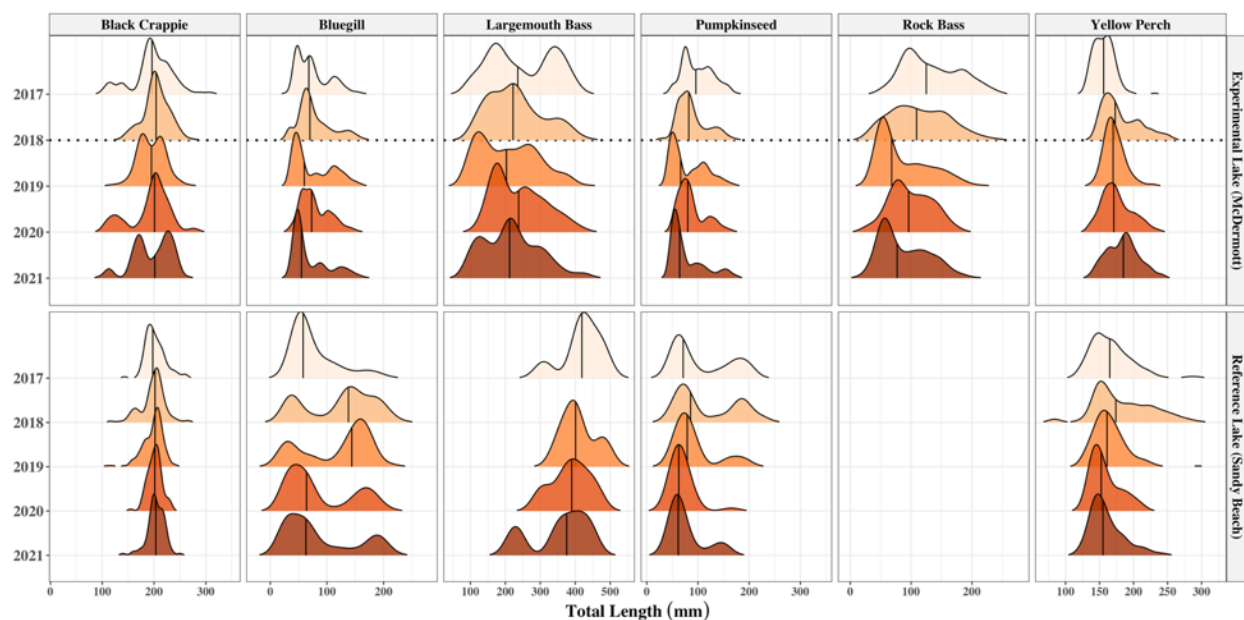
Figure 3. Species-specific relative abundance $\log_e$(age-1+ catch per unit effort) (n/gear) for the experimental (McDermott) and reference (Sandy Beach) lakes during 2017-2021. Columns correspond to species, with names identified at the top. The upper row corresponds to the experimental lake and the lower row corresponds to the reference lake. Error bars represent 95% confidence intervals. Point and line color correspond to gear type. Vertical dotted lines indicate when Centrarchidae species removals began from the experimental lake in 2018.

Figure 4. Species-specific total length (mm) density distributions for the experimental (McDermott) and reference (Sandy Beach) lakes during 2017-2021. Columns correspond to species, with names identified at the top. The upper row corresponds to the experimental lake and the lower row corresponds to the reference lake. Vertical black lines in each distribution correspond to the median value. Color corresponds to year. Horizontal dotted lines indicate when Centrarchidae species removals began from the experimental lake in 2018.
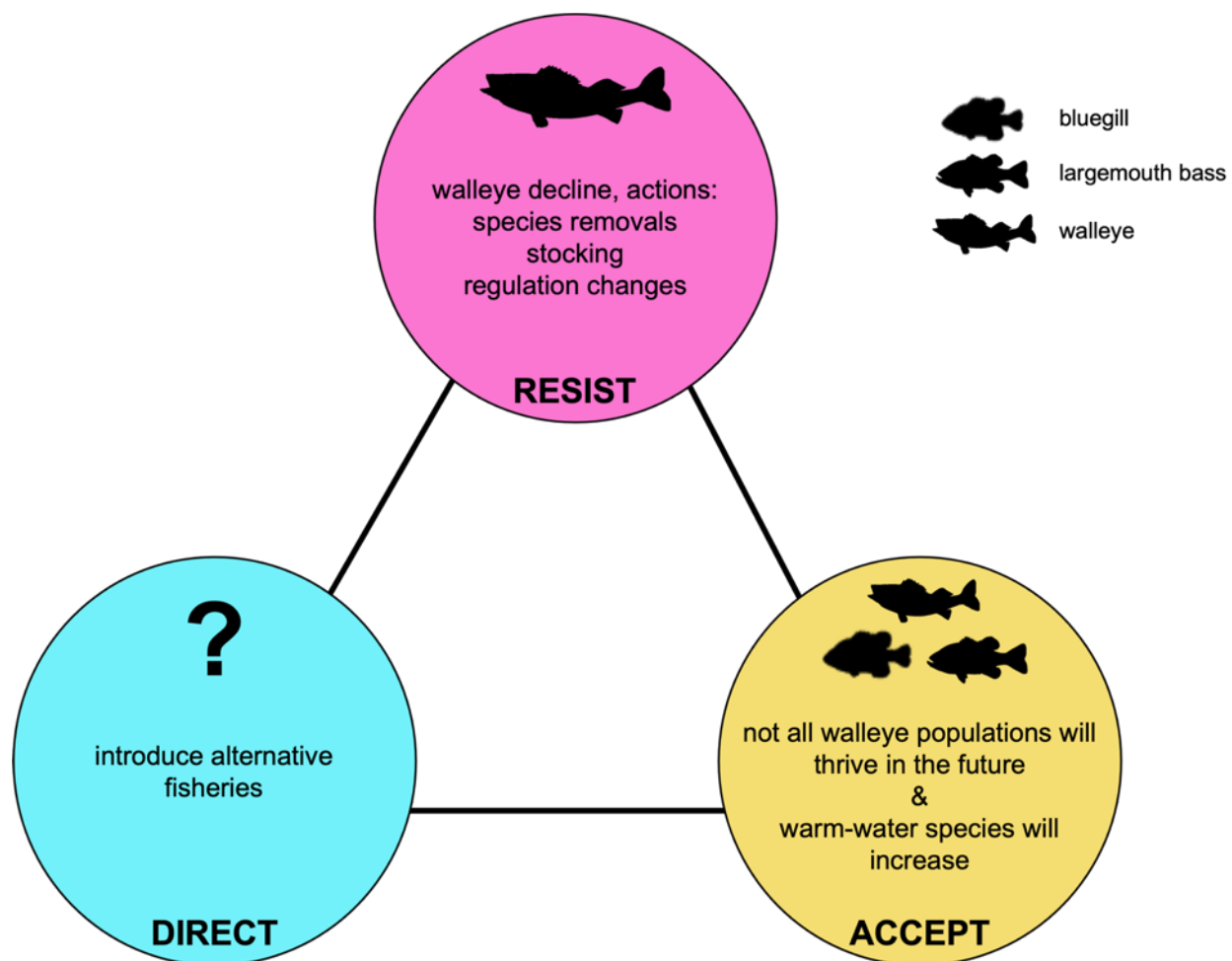
Figure 5. Conceptual diagram illustrating potential Resist-Accept-Direct decision pathways for managers reconciling ecosystem transformation in heterogeneous lake districts, such as Northern Wisconsin, USA.

Chapter 4: A whole-ecosystem experimental test of interactions among thermal guilds of fishes: does warmwater fish removal benefit coolwater fishes?

Abstract

Climate change is transforming lakes at a rapid pace, leading to rising and variable thermal regimes. Cool- and warmwater habitats are essential to the life-history of diverse fishes, but climate change is shifting lakes towards warmwater-dominant habitats. As a result, warmwater fishes are expanding into new lakes and increasingly dominating ecological communities, creating novel species interactions. Understanding how changing thermal regimes alter biotic interactions will be critical to developing more essential conservation plans. We present a 5-yr experimental removal of ~285,000 warmwater fishes from a north-temperate lake as an experimental test of the hypothesis that shifting warmwater-coolwater species interactions regulate coolwater fisheries. Overall, warmwater fish biomass declined by 23% and species were omnivorous. Among coolwater fishes, piscivorous walleye showed no biomass or recruitment response, while omnivorous yellow perch biomass increased by ~914%. Effects of biomass change cascaded to lower trophic levels, including a decrease in zooplankton and increase in zoobenthos abundance. Our results highlight a complexity in the dynamic biotic interactions that underlie shifting thermal regimes under climate change. For fisheries managers, climate adaptation cannot be a 'one-size-fits-all' approach despite species having similar thermal tolerances given the importance of biotic interactions.

4.1. Introduction

Climate change is transforming lakes at a rapid rate, leading to rising and increasingly variable water temperatures (O'Reilly et al. 2015, Woolway and Maberly 2020). Many lakes have complex bathymetries; therefore, they often support multiple thermal guilds of fishes,

including warm-, cold- and coolwater species. Current climate warming is shifting thermal habitats towards increased suitability for warmwater fishes while decreasing suitability for cold- and coolwater fishes (Hansen et al. 2017). Yet while there is much known on distributional and abundance shifts of fishes in response to climate warming, little is known on how shifting thermal regimes affect species interactions, especially among thermal guilds.

In lakes, global change is shifting thermal regimes toward warmwater habitat, which can manifest in multiple ways depending on the lake characteristics such as landscape position, morphometry, and type (e.g., seepage versus drainage; Kraemer et al. 2021). Thus historically cool lakes may become more suitable for warmwater fish, resulting in an expansion of warmwater fishes and increased interactions of warm- and coolwater guilds (Fig. 1; Robillard & Fox 2006, Hansen et al. 2015, Hansen et al. 2017). In lakes where warm- and coolwater fishes are sympatric, warming may confer an advantage to warmwater fishes, resulting in novel interactions between species and thermal guilds (Fig. 1; Robillard & Fox 2006). Further, some lakes with both warm- and cold- or coolwater thermal habitat (i.e., 'two-story' lakes) may lose all coolwater and thus result in a complete loss of coolwater fishes (Fig. 1; Hansen et al. 2017). Warming mediates the interactions between warm- and coolwater fishes and in lakes where thermal guilds increasingly coexist, biotic interactions may play a more regulatory role but is it unknown how these novel biotic interactions affect certain guilds and species, especially in freshwater ecosystems (Klanderud 2005, Suttle et al. 2007, Hellmann et al. 2012).

In north-temperate lakes, coolwater fishes (e.g., Percidae species) have declined (Rypel et al. 2018, Holbrook et al. 2021, Brandt et al. 2022), while warmwater fishes (e.g., Centrarchidae species; hereafter centrarchids) have increased in abundance in many lakes (Hansen et al. 2015, Hansen et al. 2017, Rypel et al. 2016). Coolwater fish declines accompanied by warmwater fish

increases may produce novel species interactions wherein coolwater fishes experience increased predation and/or competition creating additional and unexpected constraints for vulnerable species. Further, the relative dominance of a species hinges on a combination of abiotic and biotic factors (Suttle et al. 2007, Hellman et al. 2012), thus understanding the importance of food web interactions relative to habitat is key to informing adaptation approaches for coolwater fishes in a changing climate.

Here, we present a 5-yr experimental removal of warmwater fishes from a north temperate lake as a method of testing the hypothesis that shifting warmwater-coolwater biotic interactions regulate coolwater fishes. From 2017-2021, we removed ~285,000 warmwater centrarchids from a 33.1 ha northern Wisconsin, USA lake while monitoring a nearby reference lake. We quantified cool- and warmwater fish population dynamics, fish diets, as well as lower trophic level (i.e., zooplankton, zoobenthos) abundances. Additionally, we measured thermal conditions of the experimental and reference lakes to understand the relative influence of abiotic and biotic interactions between warm- and coolwater fishes.

4.2. Results and Discussion

We removed ~285,000 warmwater fishes consisting of seven Centrarchidae species from a 33.1 ha north temperate lake however warmwater species biomasses declined only 23%. Coolwater species showed sharply contrasting responses to warmwater fihs removals: walleye recruitment and biomass did not respond but yellow perch biomass increased nearly ten-fold. Effects of fish community changes cascaded to lower trophic levels, where we observed decreases in zooplankton abundance and increases in zoobenthos abundances. The whole-lake experimental removal of warmwater species we performed highlights the importance of biotic interactions in regulating thermally-similar species.

Both lakes had suitable optical and thermal habitat for coolwater fishes but were projected to become centrarchid dominant by the mid-century (Fig. 2; Hansen et al. 2017). Mean annual growing degree days (base water temperature 5°C; $GDD_{5°C}$) increased from 1980-2015 for both the experimental and reference lakes (Fig. 2; Winslow et al. 2017). In 2007, both the experimental and reference lakes reached maximum $GDD_{5°C}$ of 2606 and 2673, respectively, exceeding the turning point between walleye and bass suitability identified by Hansen et al. (2017; Fig. 2). Thus although these lakes are currently thermally suitable, they are likely on the cusp of optimal conditions for coolwater fishes.

Annual littoral and pelagic temperature profiles (~1m depth) were variable, with peak water temperatures increasing over the study years (Fig. 3A). Littoral temperatures were more variable and were significantly warmer than pelagic temperatures, reaching a maximum temperature of ~28.8°C in 2020 and ~27.8°C in 2021, in the experimental and reference lakes respectively, and occasionally exceeding optimal thermal conditions for coolwater fishes (Fig. 3A, Mandeville et al. 2019). Overall, warmwater fishes had a maximum optimal mean daily water temperature ~4.43°C higher than coolwater fishes (Fig. 3, Mandeville et al. 2019), although there was species-specific variation within the warmwater guild (Fig. 3B). Water temperature variability indicates that although these lakes currently provide suitable thermal conditions for coolwater species in some habitats (i.e., pelagic), others (i.e., littoral) are already becoming too warm to support the life-cycle of coolwater species, a trend likely to continue with climate change. Overall, changing thermal regimes in the study lake is consistent with others on the landscape that are increasingly warming (O'Reilly et al. 2015). As climate change accelerates (Woolway and Maberly 2020), it is likely more lake habitat will resemble these study lakes, becoming more limiting for coolwater species while also more suitable for warmwater species.

We removed ~285,100 warmwater fishes (~3190 kg) comprising seven centrarchid species from the experimental lake during 2018-2021, with a mean annual removal of 23.74 kg/ha (Embke et al. 2022; Fig. 4). The majority of biomass removed was bluegill *Lepomis macrochirus* (~64% of total), in addition to black crappie *Pomoxis nigromaculatus* and pumpkinseed *Lepomis gibbosus* (Fig. 4). In response to removals, some warmwater species relative biomass declined significantly, including bluegill, black crappie, and rock bass *Ambloplites rupestris* by ~53%, ~88%, and ~91%, respectively ($p < 0.001$; Fig. 5, Table S1). However, other wamwater species including largemouth bass *Micropterus salmoides* and pumpkinseed relative biomass remained relatively constant and somewhat increased (Fig. 5, Table S1), illustrating that these species may be more resistant to control efforts. The fluctuation of warmwater species biomass over time reveals population flexibility and density dependence to reproductively adapt to shifting conditions (Mittlebach 1986). Further, it reveals a persistent challenge in trying to control fisheries in any predictable way more generally when density-dependent effects are pronounced (Beard and Essington 2000).

A coolwater species, yellow perch, showed the most marked response to warmwater species removals, with a significant and steady relative biomass increase of 914% (biomass per unit effort change from ~0.46 to ~4.63 kg/net night, $p < 0.001$; Fig. 5, Table S1). Over the course of the removal, warmwater species were reduced such that a window may have been opened for yellow perch to increase and maintain elevated abundances. Size distribution information (Embke et al. 2022) indicate this response may have been driven by a strong year-class emerging soon after initial removals, therefore monitoring will be critical to disentangle the effect of species interactions driving yellow perch population dynamics.

The other coolwater species, walleye, did not show a response to warmwater species removals in any detectable way. No natural walleye recruitment occurred during the study in either study lake as no age-0 walleye were collected, indicating the experimental removal of centrarchids did not result in a detectable release for early walleye life stages. Adult walleye biomass did not significantly change in either lake (experimental lake mean biomass = 0.84 kg/ha), however in the reference lake adult walleye biomass declined by 69% during 2017-2021, possibly due to a variety of factors including harvest variability (Embke et al. 2019) and natural population fluctuations (Fig. 5, Table S1).

Species feeding strategies can influence an organism's ability to adapt to change, with more omnivorous species having more flexibility (Wooton 2017). Therefore, to understand if there were differences among thermal guild feeding strategies, we quantified adult fish diet compositions (Fig. 6, Fig. S2). Regardless of thermal guild, fish diets were dominated by benthic items (i.e., benthic invertebrates, crayfish) and fishes in both lakes, emphasizing the importance of benthic resources in supporting higher trophic levels as well as fishes as links between benthic and pelagic habitats (Fig. 6, Fig. S2; Vander Zanden and Vadeboncoeur 2002, Vander Zanden et al. 2011). Warmwater fishes were highly omnivorous, with largemouth bass showing the most variability in diet (Fig. 6, Fig. S2). Of the two coolwater species, yellow perch were also omnivorous (5-yr mean = 36% benthic invertebrates, 7% crayfish, 31% fishes, 4% terrestrial invertebrate, 14% vegetation, 12% zooplankton; Fig. 6) while walleye were much more piscivorous (5-yr mean=27% benthic invertebrates, 65% fishes, 8% terrestrial invertebrate; Fig. 6, Fig. S2). Reliance on zooplankton decreased over time for most species, although very small individuals (<100 mm) were not well represented in diet samples which likely comprised the largest consumers of zooplankton, therefore overall zooplankton consumption may have been

underestimated (Fig. 6). We recognize there are biases in fish diet analyses as certain items including benthic invertebrates and fishes are retained better in samples (Preston et al. 2017). Flexibility in yellow perch feeding strategies in comparison to the reliance on higher trophic levels by walleye may have contributed to each species ability to shift to abiotic and biotic changes, emphasizing the important role food web interactions have in regulating species dynamics.

In the experimental lake, we observed significant declines in dominant zooplankton taxa abundance (i.e., Calanoida, Cyclopoida, *Daphnia*, p<0.001; Fig. 7A), likely in response to predation pressure from increasing coolwater yellow perch. In contrast, dominant zoobenthos taxa abundance (i.e., Chironomidae, Gastropoda, Sphaeridae) significantly increased over time (p<0.001; Fig. 7), potentially in response to a predation release from declining warmwater littoral species. The habitat-specific food web shifts we observed highlight the significant direct and indirect effects species interactions can have on trophic dynamics in lakes.

We observed strongly contrasting responses of two coolwater fishes to the experimental reduction of predation/competition under the same abiotic conditions, whereby walleye did not change but yellow perch greatly increased. Although both species have similar thermal tolerances (Christie and Regier 1988, Fig. 3B), walleye are more sensitive to light (Lester et al. 2004), take longer to reach maturity (average age-at-maturity = 4-5yrs; Cichosz 2017), and more sensitive spawning requirements (Christie and Regier 1988). Walleye were also more piscivorous, thus dependent on higher trophic levels, while yellow perch were omnivorous and capable of flexibility in their feeding strategies (Fig. 6). Our results highlight that selective feeding strategies, despite higher energetic benefits, may become more limiting when habitat is suboptimal, especially for species with additional life history constraints.

Thermal conditions may have been more limiting for walleye in comparison to yellow perch, who may be less sensitive to abiotic constraints when biotic pressure is reduced. We recognize ecological changes underway may not have been detected due to response time-lags, especially for slow-growing species like walleye, therefore continued monitoring will be key to better understanding long-term responses. Our work emphasizes that the relative importance of abiotic and biotic drivers for coolwater species is not uniform but depends on many factors including species life history, biological constraints, and food web interactions.

Despite highly intensive removal efforts, warmwater centrarchids were not easily controlled, highlighting a capacity for these species to handle massive mortality events. In addition to their flexible thermal tolerance, centrarchids can spawn continuously and are thus relatively independent of abiotic spawning limitations, increasing their capacity to reproduce despite climate variability (Beard and Essington 2000). Further, centrarchids have nest spawning behavior and some parental care, therefore are potentially able to reduce competition/predation of their offspring (Mittlebach 1986, Winemiller and Rose 1992) – a strategy in direct contrast to coolwater broadcast spawners with short, sensitive spawning strategies (Winemiller and Rose 1992). Overall, warmwater species such as centrarchids seem to be heavily favored over coolwater species in a changing climate, thus trying to maintain coolwater populations in suboptimal habitats heavily dominated by warmwater fishes may not be a viable climate adaptation.

Understanding relative importance of thermal conditions versus biotic drivers in regulating fish dynamics will become even more important as we try to navigate climate change and develop climate adaptation approaches. Others have identified the critical importance of biotic interactions in regulating population dynamics in a changing climate (Suttle et al. 2007,

Hellmann et al. 2012), however direct understanding of these relationships in freshwaters was unclear. In developing strategies, it will be key not only to consider species habitat requirements, but also biotic interactions and the indirect food web implications of these shifts. Further, species life history strategies will likely play a key role in a species' ability to adapt to climate change. For example, particularly sensitive species such as walleye will likely need different adaptation approaches than other coolwater species such as yellow perch, despite similar thermal tolerances. In ecosystems projected to shift towards suboptimal conditions under climate change, it will be critical to consider the governing influence of species interactions in fragile ecosystems. We found that responses are flexible to a degree for some species, but also depend on factors such as life history strategies of both the warmwater and coolwater species.

Species interactions are notoriously complex and may be largely beyond the control of managers, especially when thermal habitat availability is increasingly limited (Carpenter et al. 2017). We highlight that climate change strongly favors warmwater species, which are resilient and flexible, while coolwater fishes may be more sensitive and dependent on specific habitat characteristics. However species responses were not uniform within thermal guild. Because climate change will have unmanageable impacts on important coolwater species, it is necessary to consider a portfolio of adaptation approaches (Hellman et al. 2012, Dudney et al. 2022). There will be a conflict between biotic and abiotic drivers in regulating population dynamics and these dynamics will advantage certain species under certain conditions. Given this high level of context-dependence, it is necessary to develop a better system-specific understanding of climate adaptation approaches. Time-scale and context are critically important in understanding the impacts of climate change on certain species – in ecosystems with less-than-optimal conditions, which will become more common with climate change, species interactions may play a larger

role, but that is dependent on species life-history traits and sensitivities. In a changing climate,

coolwater species adaptation needs to consider the current and future habitat trajectory of the

ecosystem, species assemblage life history strategies, and potential indirect biotic interactions, as

all of these factors interact to generate complex and variable outcomes.

4.3. Methods

Study area

Selecting the experimental lake where centrarchid removals occurred was a lengthy

evaluation and community outreach process that began with >50 candidate lakes and included

extensive consultation with Wisconsin Department of Natural Resources (WDNR) and Great

Lakes Indian Fish and Wildlife Commission (GLIFWC) biologists, and public meetings with

lakeshore property owners. In addition to gaining necessary public and management support for

site locations, the experimental and reference lakes were selected based on a series of abiotic and

biotic characteristics. Criteria included: a history of self-sustaining, natural walleye recruitment,

a population of adult walleye, ample walleye spawning habitat, and an increase in centrarchid

abundances. The experimental (McDermott Lake; 46.00299280, -90.16081610) and reference

(Sandy Beach Lake; 46.10614350, -89.97131020) lakes are in Iron County in Northern

Wisconsin. The experimental lake has a surface area of 33.1 ha, mean depth of 3.0 m, and

maximum depth of 5.7 m. The reference lake has a surface area of 44.5 ha, mean depth of 2.1 m,

and maximum depth of 4.0 m. Both lakes included a variety of substrates (e.g., rock, gravel, and

sand) and areas of submerged and emergent vegetation. At the start of the study, the

experimental and reference lake fish communities were similar with high centrarchid abundances

(e.g., black crappie, bluegill, largemouth bass, and pumpkinseed) few adult walleye, and a

history of self-sustaining, natural walleye recruitment. For Wisconsin lakes, natural recruitment

of walleye is defined as the relative abundance of non-stocked age-0 individuals collected in fall electrofishing surveys. Natural recruitment was last detected in both lakes in 2003-2004, with higher age-0 catch per unit effort (CPUE) in the reference lake (~6.51 ind/km) compared to the experimental lake (~1.67 ind/km; see below for further information on recruitment survey methodology). Like other walleye populations across the upper Midwest United States, both lakes have experienced declines in adult walleye abundance and have been stocked with extended growth fingerlings (~150-225 mm TL) during the fall of every other year since at least 2011. Other species present included yellow perch, northern pike *Esox lucius*, muskellunge *Esox masquinongy*, black bullhead *Ameiurus melas*, and golden shiner *Notemigonus crysoleucas*.

Limnological sampling

Each year, we deployed continuously recording HOBO© temperature loggers at three sites in the littoral zone and four loggers spaced evenly along a rope anchored at the deepest point of the lake from early May until mid-September. Water temperature was recorded every 30 min. From this data, we calculated mean daily littoral and pelagic water temperatures.

Fish sampling

Standardized surveys

During 2017-2021, standardized monitoring surveys were conducted using numerous sampling techniques to test for changes in the fish communities of both lakes. Sampling began immediately after ice-out (~mid-April) with deployment of five fyke nets (1.2 m x 1.8 m frames, 1.9 cm bar mesh) for one week at nonrandom locations in habitats that were probable walleye spawning sites (Hansen et al. 1991). The fyke-net surveys served two purposes: 1) to capture walleye for marking as part of the mark-recapture survey to attain an adult population estimate; and 2) to estimate relative abundances (fish per net night) of black crappie and yellow perch.

During these surveys, all collected walleye were measured (total length (TL); mm), sexed, checked for a uniquely-coded passive integrated transponder (PIT) and implanted with a PIT if one was not present. Adult (mature) walleye were defined either as all fish ≥381 mm or for which sex could be determined by extrusion of gametes (regardless of length; Cichosz 2017). Walleye of unknown sex <381 mm were classified as juvenile (immature). Both study lakes have had walleye population estimates previously conducted by the WDNR. Therefore, WDNR protocols were followed where the goal was to mark 10% of the anticipated spawning population (based on previous population estimates; Cichosz 2017). Marking continued until the target number was reached or spent females began appearing in fyke nets. Tagged walleye were recaptured using nighttime AC boat electrofishing within one week (typically 1-4 days) after netting and marking were completed (Beard et al. 1997). In each lake, the entire shoreline was electrofished. All walleye were measured and examined for PITs. Population estimates (PEs) were calculated using Chapman's modification of the Petersen estimator (Chapman 1951, Cichosz 2017). To determine black crappie and yellow perch relative abundances, all individuals were counted and a subsample of 30 fish per species per day for each lake was measured (total length; mm).

We used a combination of standardized surveys to quantify centrarchid relative abundances of species other than black crappie (i.e., bluegill, largemouth bass, pumpkinseed, and rock bass). In early summer (May, water temperatures=13.0–21.0°C), we began surveys with an AC boat electrofishing. During June-August, we sampled fish once monthly when lake surface water temperatures were ≥13.0°C in both lakes (water temperatures =18.3–26.7°C; Simonson et al. 2008). Both lakes were sampled for 1week each month using three gears (AC boat electrofishing, mini-fyke nets, cloverleaf traps). Lakes were sampled on consecutive nights in

each 1-week period but only one gear type was used per night. All gears sampled shallow littoral zones (0–5 m from bank, depth ≤2 m) and were deployed in fixed locations following standard approaches (Bonar et al. 2009). Sampling locations were evenly distributed along the lake shoreline, and all gears were deployed in similar habitat types. Five 10-min nighttime boat electrofishing (Wisconsin-style; AC; 2.0–3.0 amps, 200–350 V, 25% duty cycle) transects were conducted using two dipnetters covering the majority (>80%) of the shoreline and spanning a variety of habitat types (e.g., vegetation, sediment, gravel). Five mini-fyke nets (0.9-m × 0.61-m frames, 3.2-mm mesh [bar measure], 7.6-m-long lead, and a double throat) were deployed in areas where the net frames would be in 1.0–1.5 m of water, with leads fixed onshore. Five cloverleaf traps (three lobed, height = 41 cm, 50 cm diameter, 6.0-mm bar wire mesh with 12.7-mm-wide openings between lobes, and an attractant [beef liver]) were deployed in littoral habitats. Mini-fyke nets and cloverleaf traps were set in early afternoon, fished overnight, and retrieved the following afternoon (~24-h soak time). All catches were standardized according to gear-specific effort. For boat electrofishing, CPUE was calculated as the number of individuals captured per hr. For mini-fyke nets and cloverleaf traps, CPUE was calculated as the number of individuals captured per net night or trap night.

To estimate walleye recruitment, we used multiple gears including ichthyoplankton surface trawls, micromesh gillnets, beach seines, and boat electrofishing. A 1,000-μm mesh ichthyoplankton net was towed within 1 m of the water surface at five locations in each lake at night about every seven days beginning two weeks after the presumed walleye spawn until June (Isermann and Willis 2008). In late July/early August, four vertical gillnets (46-m x 1.2-m with 0.64-cm bar mesh) were deployed. Sampling locations were evenly distributed along the shoreline and locations were fixed each year. Gillnets were set at night and at depths ranging

from 0-5 m. Set duration ranged from 1-2 hours to minimize bycatch (Boehm et al. 2020). In late August, 0.24-m long beach seines with 0.64-cm mesh were pulled at five sites in each lake. Sites were chosen to represent a variety of habitat types and based on ability to effectively use the seine. Seining sites remained fixed for the duration of the study. Seines were used during daylight hours on each lake. Catch per unit effort was calculated as the number of individuals per seine haul. When water temperatures fell below 21°C (early September), age-0 walleye were sampled using nighttime boat electrofishing of the entire shoreline of each lake (Wisconsin-style; AC; 2.0–3.0 amps, 200–350 V, two netters). Surveys were conducted prior to walleye fingerling stocking, meaning any collected age-0 walleye were produced via natural recruitment.

Warmwater fish removals

In addition to standardized surveys, centrarchid removal efforts began in 2018 in the experimental lake using a variety of techniques including fyke nets, boat electrofishing, mini-fyke nets, and cloverleaf traps. Following spring fyke net surveys, fyke nets remained in the experimental lake to remove centrarchids. In 2018, 10 fyke nets were used to remove fish daily from May 14 to June 7 and in 2019, from May 9 to June 27. During 2018 and 2019 fyke netting ended when centrarchid catches started to decline. In 2020 and 2021, only five fyke nets were used from late spring (April 30 and May 10) until late-June (June 25 and June 11) due to personnel limitations. Additionally, five mini-fyke nets and 21 cloverleaf traps were sampled from late-May to mid-August each year. All gears were emptied every 1-2 days and sites were rotated to maximize centrarchid catches. Collected fish were identified to species and up to 30 individuals per species per gear were measured daily (TL, mm). Centrarchid species were retained while other species were returned to the lake. Species removed included black crappie, bluegill, green sunfish *Lepomis cyanellus*, pumpkinseed, rock bass, largemouth bass, and

smallmouth bass *Micropterus dolomieu.* Removed centrarchids were used for aging purposes (see below) or donated to local wildlife health centers.

Fish processing

To understand demographic changes of centrarchid and yellow perch populations in the experimental and reference lakes, up to 20 individuals per ~25 mm interval were retained for analyses from each lake. In the lab, individuals were dissected and species, TL (mm), weight (g), and stomach contents (% wet weight) were recorded. Stomach contents were weighed, then components were identified to the lowest taxonomic resolution possible and recorded as % wet weight. Sagittal otoliths were removed to determine if an individual was age-0 or age-1+. Ages were estimated using a combination of whole and thin-sectioned otoliths. To generalize across species, whole otoliths were typically used for fish <150 mm TL and sectioned otoliths were always used for fish >150 mm TL (Hoyer and Maceina 1985, Schramm 1989). Whole otoliths were submerged in water in a black dish and viewed using a Nikon 1500 SMZ stereomicroscope under reflected light; images were projected to a 76 × 45 cm flat-screen LCD monitor using via a Nikon DS-Fi2 or DS-Fi3 color camera connected to Nikon NIS-Elements software (Schramm and Doerzbacher 1985). To section otoliths, one otolith was embedded in epoxy and a transverse section (1.2 mm) through the focus was obtained using a low-speed saw (Wegleitner & Isermann 2017). Otolith sections were glued to microscope slides with cyanoacrylic cement and were projected using the same microscope, camera, and software configuration but under transmitted light. Ages were assigned independently by two readers; when disagreements occurred, consensus ages were obtained by the two readers viewing the otoliths together. If a consensus age could not be reached, the fish was not used for age assignment.

Zooplankton and zoobenthos sampling

In the experimental and reference lakes, each year we sampled the invertebrate community (e.g., zooplankton, zoobenthos). From May to mid-August, we sampled zooplankton during the day and night at bi-weekly intervals. In each lake, zooplankton samples were taken at the deepest point by pulling a conical net (15 cm diameter, 80 μm mesh) vertically through the water column (i.e., vertical tow sample). After the net was raised and the sides rinsed, the sample was transferred to a bottle and preserved in 90% ethanol. Each sample was standardized to a sample volume of 100mL, organisms were identified to family and enumerated in three separate 1-mL subsamples obtained by a Hensen-Stemple pipette. Abundances for each sample were standardized to the volume of water sampled based on the sampling depth and net opening area (ind/L).

Twice each summer (late-June and early-August) we sampled zoobenthos using an Ekman sampler (3L, 0.02 m^2) along three transects per lake. At each transect, we took three samples at depths of 0.5-1m, 2m, and 3-4m. Ekman samples were transferred into a sieving bucket (500 μm). All material remaining on the sieve was transferred into sampling bottles and preserved in 90% ethanol. In the laboratory, macroinvertebrates were identified from the samples using a dissecting microscope and Merritt & Cummins (1996). We identified most orders to a family level of taxonomy (i.e., Amphipoda, Bivalvia, Coleoptera, Diptera, Ephemeroptera, Gastropoda, Odonata, Oligochaeta, and Trichoptera). A few groups were classified to class (i.e., Hirudinae and Ostracoda). Nematoda was identified to phylum. Samples were standardized to the number of individuals per square meter (ind./m^2).

Data analyses

Water temperature

Winslow et al. (2017) estimated annual growing degree days (base temperature 5°C; GDD$_{5°C}$) for both study lakes from 1980-2015, therefore we used this information to assess the thermal characteristics of the study lakes (Fig. 2B). From these predictions, it was found that for lakes with ~2400 GDD$_{5°C}$, the probability of largemouth bass versus walleye dominance is relatively equal (Hansen et al. 2017).

Fish population dynamics

Walleye biomass (kg/ha) was estimated by sampling the weight (kg) distribution with replacement corresponding to a given lake-year population estimate. Individual weights were then summed. For centrarchids and yellow perch, we estimated trends in biomass per unit effort (BPUE) over the study period by extrapolating lengths and weights to unmeasured fish based on the measured sampled. A subset of measured fish lengths (daily maximum = 30 per species per gear) was used to assign total length (mm) to unmeasured individuals. Available fish lengths were sampled with replacement and used to assign lengths to unmeasured fish according to the total number of individuals collected. To estimate species-specific biomass (kg), species-specific weight-length regressions were developed for each year within each lake to predict weights (g) of fishes that were not weighed. Length (mm) was log$_e$ transformed prior to analysis. Once all sampled fish had an assigned weight, we calculated species-specific daily BPUE for each lake-gear combination.

We focused our examination of temporal trends in the relative abundance and removed biomass on the species that collectively comprised the majority (>95%) of overall species abundances: black crappie, bluegill, pumpkinseed, rock bass, largemouth bass, walleye, and yellow perch. To remain consistent across years, removal sampling dates were separated from survey sampling dates. Removal data were used to estimate the abundance (n) and biomass (kg)

of centrarchids removed from the experimental lake. Standardized survey BPUE was compared across years to test for changes due to the removal experiment. Species susceptibility to gears varies across seasons. Therefore, depending on the species of interest, different (or a combination of) surveys were used to test for changes in abundance over time. To test for changes in black crappie and yellow perch relative abundances, spring fyke net survey catches were used, whereas boat electrofishing survey catches were used for largemouth bass, as these surveys best reflect adult relative abundance shifts. Further, once lengths had been assigned for all sampled fish during spring electrofishing surveys, largemouth bass <203 mm were removed, as they were not fully recruited to the sampling gear.

Bluegill, pumpkinseed, and rock bass were susceptible to multiple gears throughout the sampling season. Therefore, gear-specific BPUE from each standardized survey gear (cloverleaf trap, mini-fyke net, fyke net, boat electrofishing) was used. This research was primarily interested in understanding adult population dynamics of these species while avoiding the influence of highly variable age-0 recruitment dynamics. Therefore, we used otolith age data from 2017-2020 to develop lake-species minimum length-at-age-1 thresholds to designate fishes into two categories: age-1+ and age-0 (i.e., young-of-year). Based on assigned lengths, if a fish was below the age-1+ threshold, it was considered age-0. If the fish was equal to or exceeded the age-1+ threshold, it was considered age-1+ and included in the analyses. Once age-1+ fish were identified, BPUE was calculated for each lake-gear-species combination. For all data, Shapiro–Wilk tests were run to test whether BPUE were normally distributed. Based on findings, BPUE data were $\log_e$-transformed prior to analysis. To test for differences in mean annual BPUE during the study period, we fit linear regressions where $\log_e$(BPUE) was the dependent variable and year was the independent variable.

Lower trophic levels – zooplankton and zoobenthos

We quantified taxa-specific mean abundance of zooplankton (ind/L) and zoobenthos (ind/m^2) for each lake over the study period. For all data, we ran Shapiro–Wilk tests to test whether densities were normally distributed. Based on findings, data were log$_e$-transformed prior to analysis. To test for differences in abundances before and after the experiment, we fit linear regressions where log$_e$(relative abundance) was the dependent variable and year was the independent variable. An $\alpha = 0.05$ (adjusted for multiple comparisons) was used for all statistical analyses. All calculations and statistical analyses were performed in R version 4.0.3 (R Core Team 2021).

4.4. Acknowledgements

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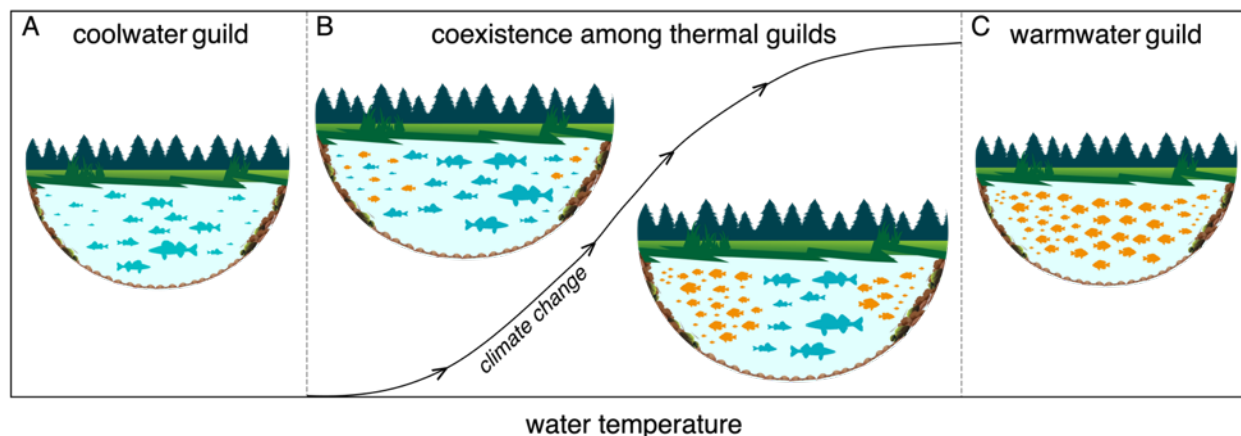
4.6. Figures

Figure 1. The roles of biotic and abiotic drivers of lake fish communities. For abiotic drivers, in lakes with low water temperatures, thermal habitat necessitates a coolwater fish guild (A). For lakes with high water temperatures, thermal habitat necessitates a warmwater fish guild (C). Many lakes are intermediate and have both cool- and warmwater thermal habitats (C), especially deeper lakes which undergo thermal stratification. This allows sympatry of the two thermal guilds. In these lakes, cool- and warmwater fishes loosely partition thermal habitat. But given that lake habitats are closely coupled, there is strong potential for ecological interactions (predation and competition) between cool- and warmwater guilds.

Climate change is shifting the abiotic conditions towards warmwater conditions. This can manifest in several ways depending on the lake type. 1) historically cool lakes may become suitable for warmwater fish, resulting in expansion of waterwater fish, and coexistence of warmwater and coolwater guilds (A to B); 2) In coexistence lakes, abiotic conditions shift to give an advantage to warmwater fishes (relative dominance of species shifts within B); or 3) lakes with warm- and coolwater thermal habitat lose coolwater thermal habitat and become only suitable for the waterwater guild (B to C).
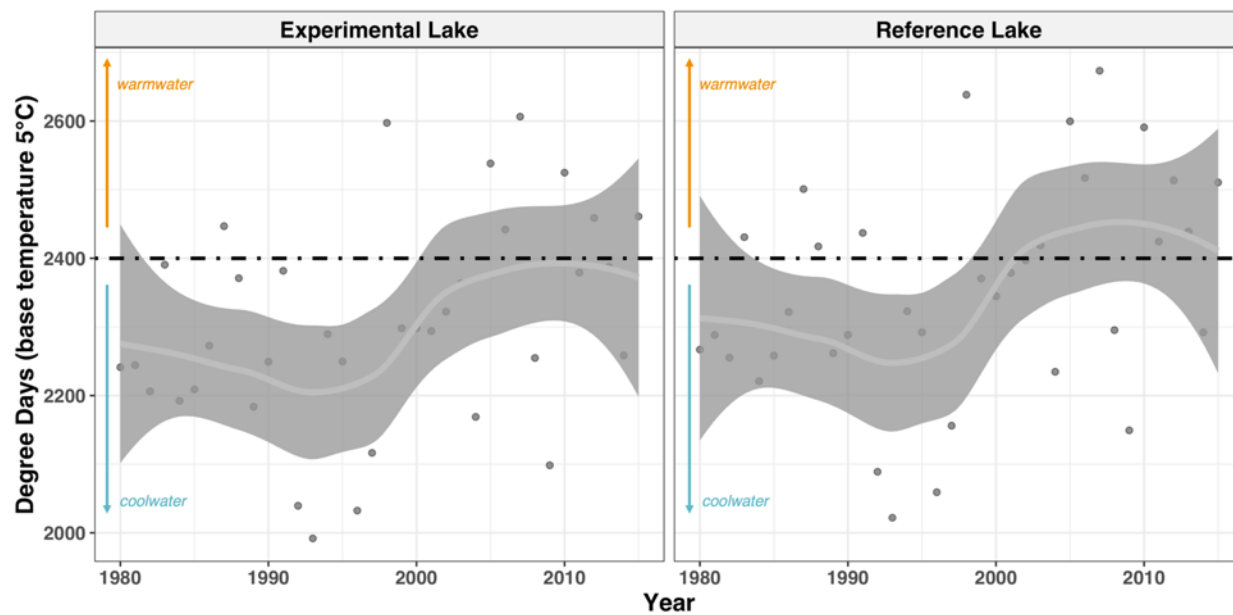
Figure 2. Estimated degree days (base water temperature 5°C, Winslow et al. 2017) for the experimental and reference lakes. Horizontal dotdash lines correspond to the approximate Hansen et al. (2017) degree day (base temperature 5°C) threshold between warm- and coolwater species dominance.
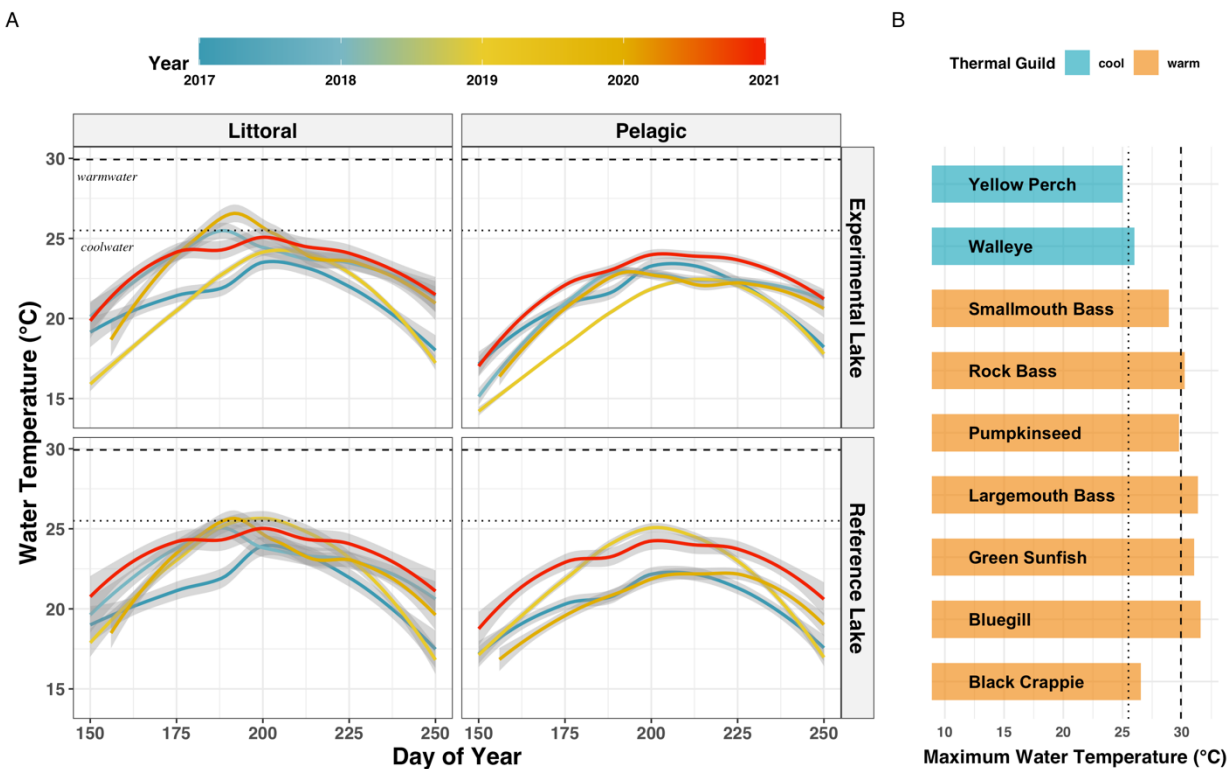
Figure 3. Littoral and pelagic water temperature (°C, 1m depth; A) for the experimental and reference lakes taken May-September (day of year 150-250) from 2017-2021. Horizontal dot- and dashed lines correspond to mean optimal maximum water temperature (°C) estimated from Mandeville et al. (2019) for cool- and warmwater fishes shown in panel B.
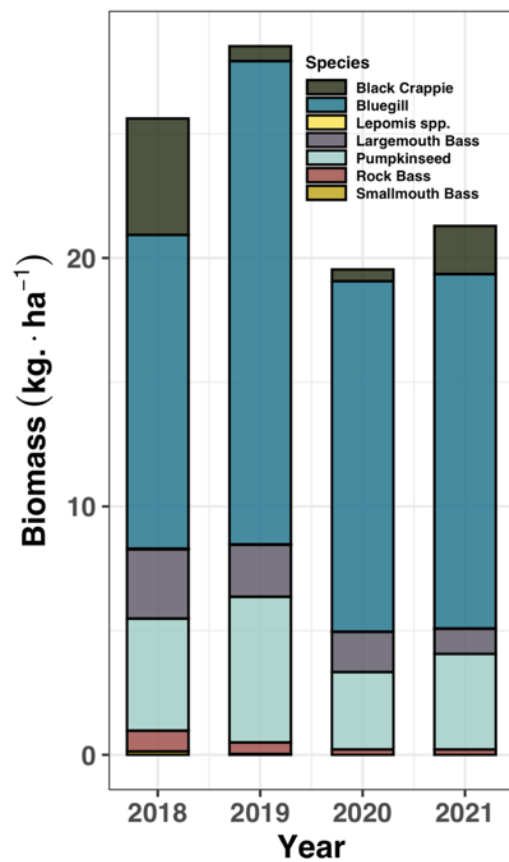
Figure 4. Centrarchidae biomass (kg/ha) removed from the experimental lake from 2017-2021.
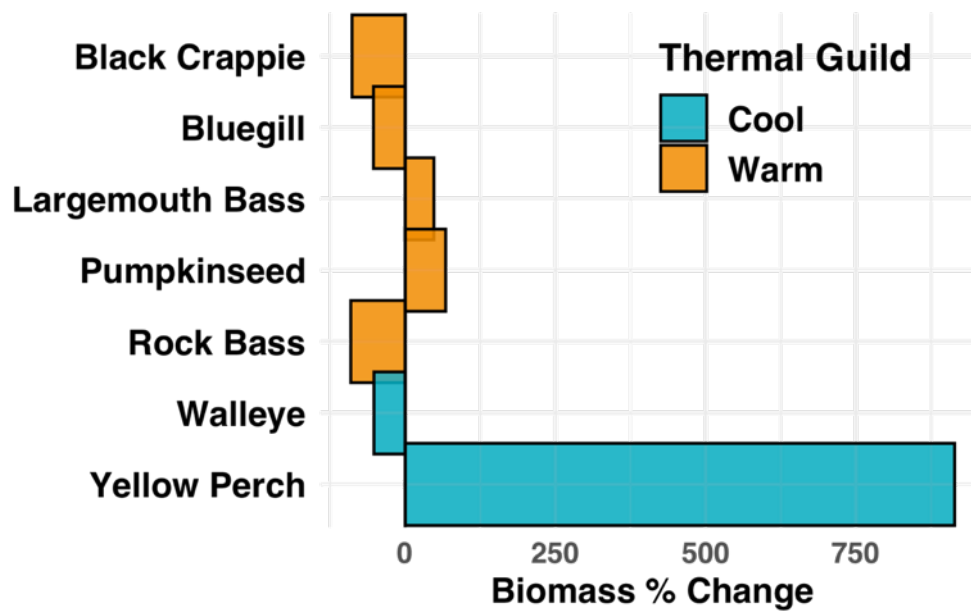
Figure 5. % change in catch per unit effort (CPUE, expressed as biomass; kg/gear) for warm- and coolwater fishes in the experimental lake from 2017 to 2021 following the removal of warmwater fishes. Note: for walleye, % change in total population biomass (kg/ha) is presented.
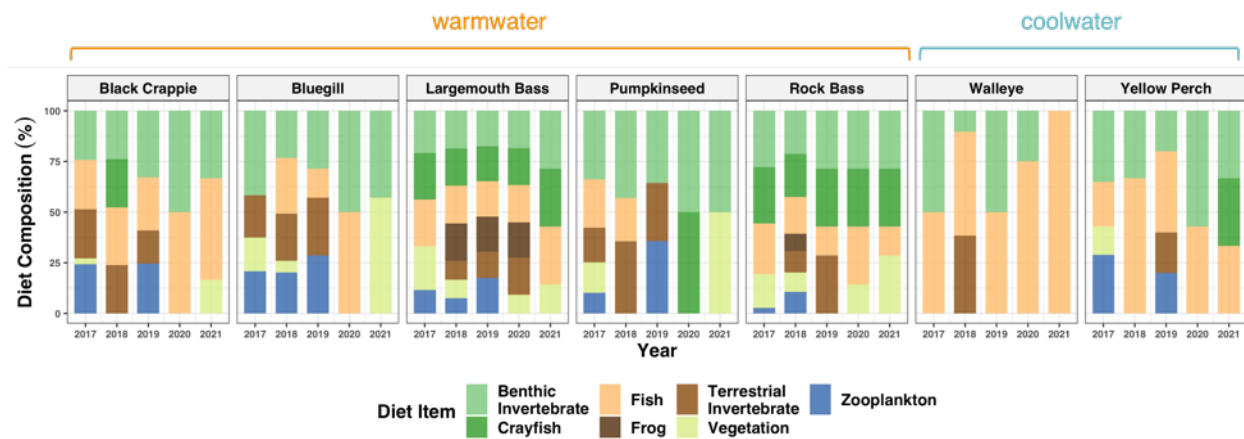
Figure 6. Fish diet compositions (%) for the experimental lake during 2017-2021.
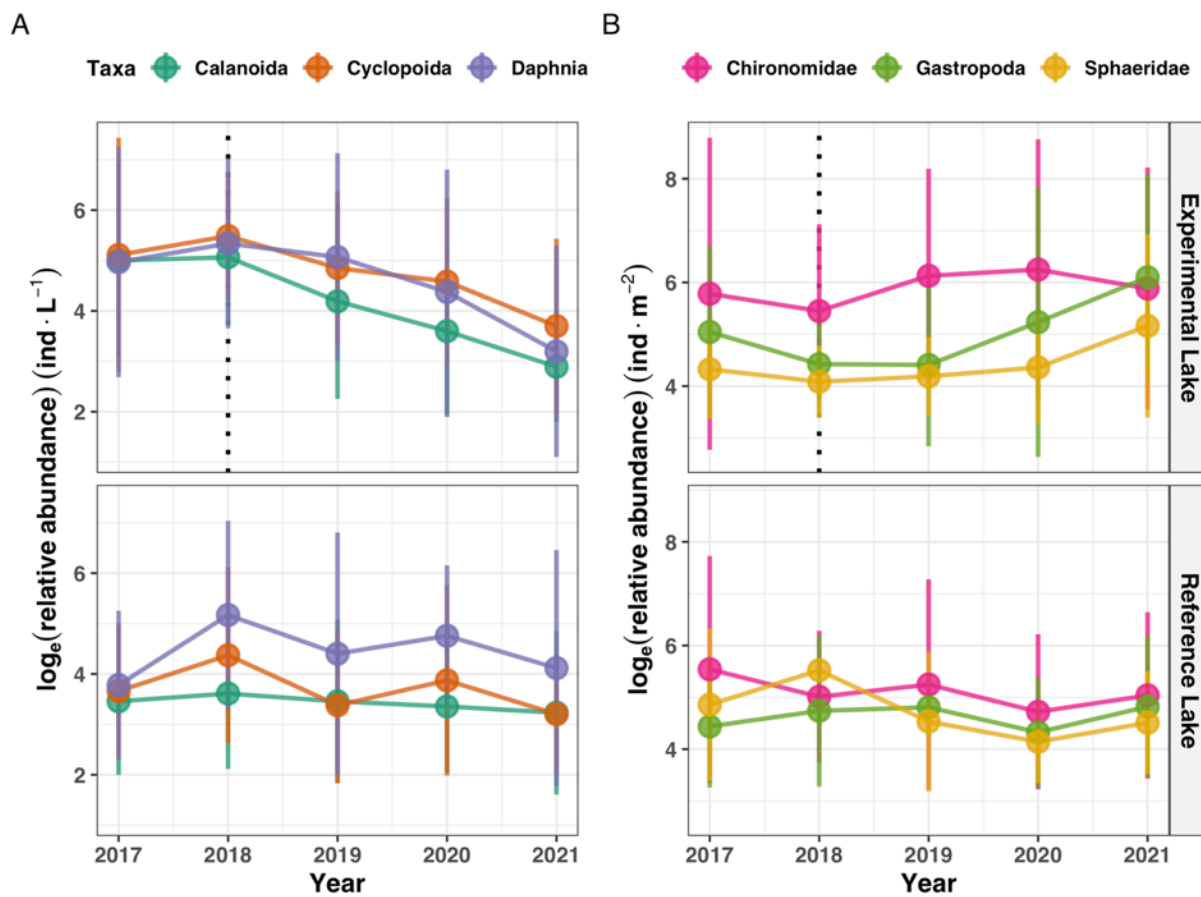
Figure 7. Mean (± 2 standard deviations) abundance of key zooplankton taxa log_e(ind/L; A) and zoobenthos taxa log_e(ind/m^2; B) in the experimental and reference lakes from 2017-2021. Vertical dotted lines indicate when warmwater Centrarchidae removals began from the experimental lake in 2018.

4.7. Supplemental Tables and Figures

Table S1. Age-1+ relative biomass (BPUE; kg/gear) for the experimental and reference lakes before (2017) and after (2021) warmwater fishes were removed from the experimental lake. If no individuals were collected in 2017, 2018 values are shown. Modeled predictions are presented for statistically significant trends and empirical estimates are presented for statistically insignificant trends. Note: for walleye, total population biomass (kg/ha) is presented.

| Lake	Thermal Guild	Species	Pre-removal Biomass per unit Effort	Post-removal Biomass per unit Effort	% Change	Statistically Significant
Experimental (McDermott)	Warm	Black Crappie	2.087	0.242	-88.42	Yes
		Bluegill	1.645	0.777	-52.79	Yes
		Largemouth Bass	0.046	0.068	47.783	No
		Pumpkinseed	0.055	0.092	67.27	No
		Rock Bass	0.134	0.013	-90.54	Yes
	Cool	Walleye*	1.455	0.698	-52.07	No
		Yellow Perch	0.456	4.627	914.06	Yes
Reference (Sandy Beach)	Warm	Black Crappie	1.239	4.776	285.551	No
		Bluegill	0.076	0.133	75.00	No
		Largemouth Bass	0.006	0.014	139.057	No
		Pumpkinseed	0.024	0.022	-8.91	No
	Cool	Walleye*	5.339	1.637	-69.33	No
		Yellow Perch	0.521	2.068	296.81	No
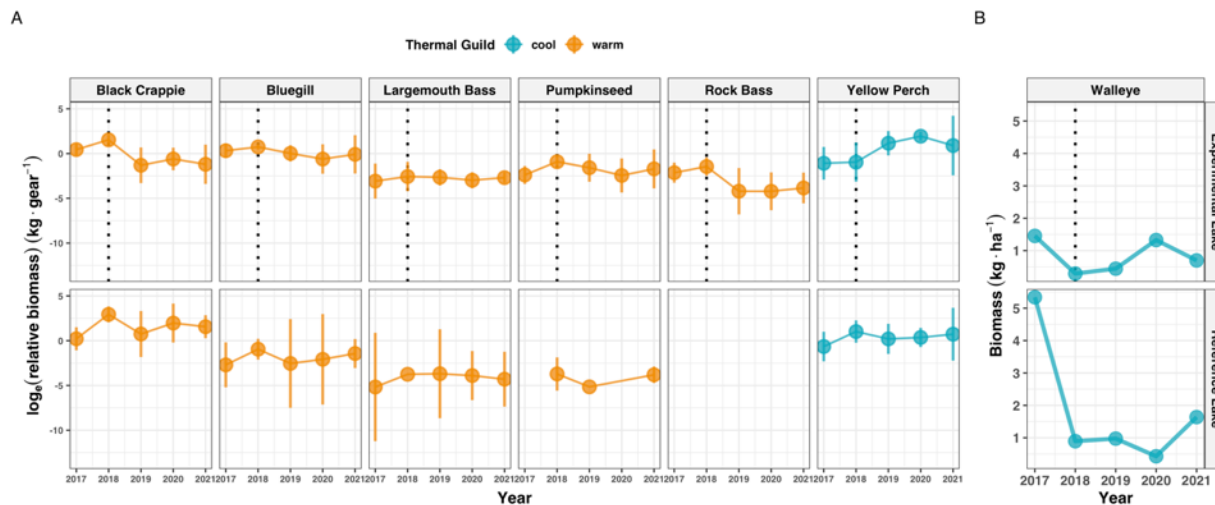
Figure S1. Species-specific biomass $\log_e$(age-1+ biomass per unit effort) (kg/gear: A) and adult walleye biomass (kg/ha: B) for the experimental and reference lakes during 2017-2021. Error bars in panel A represent 95% confidence intervals. Vertical dotted lines indicate when Centrarchidae species removals began from the experimental lake in 2018.
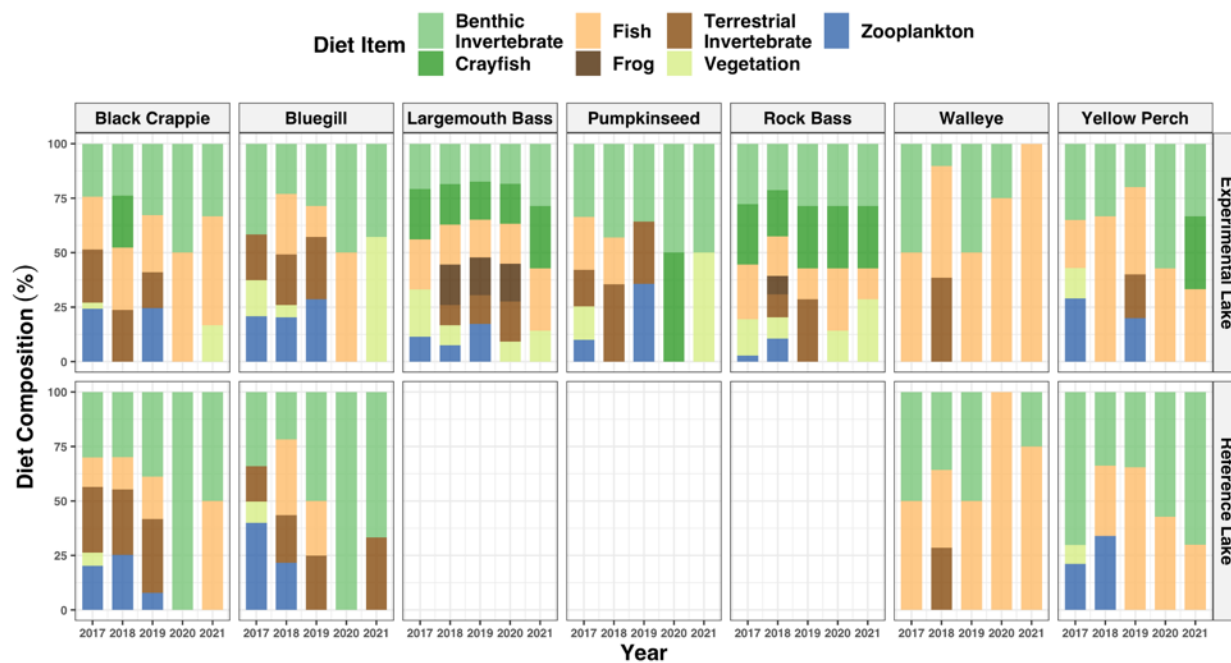
Figure S2. Fish diet compositions (%) for the experimental and reference lakes during 2017-2021.

Conclusion

Global environmental change is transforming ecosystems at unprecedented rates. Freshwater systems and the fisheries they support are vulnerable to these changes given their sensitivity to anthropogenic stressors. These shifting community dynamics present novel challenges for natural resource managers, as certain drivers including climate change are beyond local control. For inland recreational fisheries, potential manageable drivers of change include harvest and species assemblage, however the role of these factors in driving dynamics was unclear. In **chapters 1 and 2**, I evaluated the role of harvest in inland recreational fisheries and found that although harvest is a factor under local control, there are many social and political complications associated with shifting harvest practices. Further, I identified that we are just beginning to quantify the contribution of inland recreational fisheries to food security and economies, and it will be key to develop research to understand how these contributions shift under varying conditions (e.g., climate, angler decisions). Additionally, it is critical to use sensitive assessment tools to understand the magnitude of inland recreational fisheries harvest and detect shifts, especially given the increased uncertainty associated with climate change. In **chapters 3 and 4**, I tested the role of species interactions in regulating inland recreational fisheries dynamics through a whole-lake experiment. While relative species compositions are 'manageable,' complex interactions and species life histories make controlling assemblages in predictable ways challenging. Food web interactions play an important role in influencing species dynamics and the response was not uniform within thermal guild. Therefore, coolwater inland recreational fisheries adaptation will need to consider multiple factors, including the current and future habitat availability, species life history and feeding strategies, as well as potential indirect biotic indirect interactions.

Relevant authored/coauthored papers

Over my graduate studies, I was engaged with many projects beyond the scope of my dissertation. Here, I provide the context of other works I authored/co-authored. These works range in emphasis from national and global data syntheses to a lake food web literature review. Overall, these works contribute to our understanding of inland lake transformations given a changing climate.

Variation in Bluegill catch rates and total length distributions among four sampling gears used in two Wisconsin lakes dominated by small fish

Sullivan, C.J., **H.S**. **Embke,** K.M. Perales, S.R. Carpenter, M.J. Vander Zanden, M.J., & D.A. Isermann, (2019) *North American Journal of Fisheries Management,* 39(4), 714–724.

This paper was an output from our first year of work on the whole-lake fish removal experiment.

Here, we evaluated the sampling efficacies of our different gears in catching bluegill.

Abstract
Many Bluegill Lepomis macrochirus populations are dominated by fish ≤125 mm total length (TL) that may be underrepresented when using standard sampling gears. To identify efficient sampling methods for these populations, we compared catch per unit effort (CPUE) and TL frequency distributions of Bluegill captured in cloverleaf traps, boat electrofishing, mini-fyke nets, and beach seine hauls from two northern Wisconsin lakes supporting populations dominated by fish ≤125 mm TL. Mean Bluegill CPUE ranged from 41 (SE = 11) fish per cloverleaf trap lift to 16 (SE = 8) fish per beach seine haul. Cloverleaf traps generally captured smaller Bluegill relative to other gears and were the only gear to consistently capture Bluegill ≤80 mm TL. Conversely, boat electrofishing captured the widest TL range of Bluegill, and fish ≥80 mm TL composed a greater proportion of catch (37%) relative to other gears. With few exceptions, the effort required to detect 10% or 25% changes in Bluegill CPUE was >100 units of effort regardless of lake, sampling gear, or month. Furthermore, there was no consistency between lakes or months in terms of which sampling gear required the fewest number of samples to detect a 50% change in CPUE. Estimated units of effort needed to detect 10% or 25% changes in mean Bluegill TL were ≤16 for all sampling gears on the lake with consistently higher CPUE (i.e., more fish to measure per unit). In the lake with lower CPUE, cloverleaf traps consistently required less effort to detect changes in mean TL. We note that comparing sample size requirements among gears is not straightforward because gears are sampling differing segments of the Bluegill population. Our study emphasizes the importance of evaluating gear biases and sampling efficiency so that fisheries managers can develop suitable sampling protocols.

Application of eDNA as a tool for assessing fish population abundance

Spear, M.J., **H.S. Embke**, P.J. Krysan, & M.J. Vander Zanden. (2020) *Environmental DNA*, edn3.94.

This work was a collaboration with Mike Spear, a former Vander Zanden lab mate, combining our respective expertise in eDNA (Mike) and fisheries (me) to relate eDNA abundance to fish population size.

Abstract
Estimating the abundance of organisms is fundamental to the study and management of ecological systems. However, accurately and precisely estimating organism abundance is challenging, especially in aquatic systems where organisms are hidden underwater. Estimating the abundance of fish is critical for the management of fisheries which relies on accurate assessment of population status to maximize yield without overharvesting populations. Monitoring population status is particularly challenging for inland fisheries in which populations are distributed among many individual waterbodies. Environmental DNA (eDNA) may offer a cost-effective way to rapidly estimate populations across a large number of systems if eDNA quantity correlates with the abundance of its source organisms. Here, we test the ability of quantities of eDNA recovered from surface water to estimate the abundance of walleye (*Sander vitreus*), a culturally and economically important sportfish, in lakes in north- ern Wisconsin (USA). We demonstrate a significant, positive relationship between traditional estimates of adult walleye populations (both number of individuals and biomass) and eDNA concentration ($R^2 = .81$; n = 22). Our results highlight the utility of eDNA as a population monitoring tool that can help guide and inform inland fisheries management.

Lake food webs

Embke, H.S. & M.J. Vander Zanden. (2021) *Encyclopedia of Inland Waters*, 2nd Edition.

This is a book chapter we wrote for the 2nd edition of the Encyclopedia of Inland Waters. We

synthesized relevant literature on lake food webs for a more general audience, highlighting

current areas of research interest.

Structured Abstract
Aim - The goal of this chapter is to provide a broad overview of the diverse range of approaches used to study lake food webs. We highlight seminal findings in the development of the field and also highlight current areas of research interest. A central theme is that considering lake food webs contributes to a better understanding of the functioning of lake ecosystems.
Main concepts covered – We highlight the fundamentals of food webs, then go on to detail energetic and dynamic approaches to lake food web studies. We discuss the trophic cascade concept, alternative stable states, and cross-habitat linkages. We also include integrative and applied perspectives and discuss the role of microbes, stoichiometry, contaminants, lake biomanipulation, and invasive species.
Main methods covered – The concepts we discuss stem from a variety of methods, including simulation modelling, long-term temporal and spatial comparative studies as well as whole-lake

experiments. Further, we discuss the use of organismal diet contents and stable isotope analysis to describe food web structure.

Conclusion/Outlook – Food webs are fundamentally a way of representing predator-prey (trophic) linkages among species in an ecosystem. Food web structure is influenced by both internal and external drivers in lakes. Moreover, a broad and ever-growing literature highlights how food web interactions affect community and ecosystem properties of lakes, including the generation of ecosystem services that benefit humans.

The U.S. Inland Creel and Angler Survey Catalog (CreelCat): Development, Applications, and Opportunities

Lynch, A.J., N. Sievert, **H.S. Embke**, A. Robertson, B.J.E. Myers, M.S. Allen, Z.S. Feiner, F. Hoogakker, S. Knoche, R.M. Krogman, S.R. Midway, C.L. Nieman, C.P. Paukert, K.L. Pope, M.W. Rogers, L. Wszola, T.D. Beard, Jr. (2021) *Fisheries*, 46, 574–583, doi: 10.1002/fsh.10671

This paper highlights a highly collaborative project where we developed a public national angler survey database and user interface, where I worked on the core development team to design and apply the database for researchers and managers.

Abstract
Inland recreational fishing, defined as primarily leisure-driven fishing in freshwaters, is a popular past-time in the United States. State natural agencies endeavor to provide high-quality and sustainable fishing opportunities for anglers. Managers often use creel and other angler-survey data to inform state- and waterbody-level management efforts. Despite the broad implementation of angler surveys and their importance to fisheries management at state scales, regional and national coordination among these activities is minimal, limiting data applicability to larger-scale management practices and research. Here, we introduce the U.S. Inland Creel and Angler Survey Catalog (CreelCat), highlight applications, and consider challenges and opportunities for implementation. CreelCat is a first-of-its-kind, publicly available national database of angler-survey data that establishes a baseline of national inland recreational fishing metrics. CreelCat will drive a suite of modeling for inland recreational fishing using environmental data that, collectively, can begin to tackle angling responses to global environmental change.

Resist-Accept-Direct (RAD) considerations for climate change adaptation in fisheries: the Wisconsin experience

Feiner, Z.S., A.D. Shultz, G.G. Sass, A. Trudeau, M.G. Mitro, M.A. Luehring, C.J. Dassow, A.W. Latzka, D.A. Isermann, B.M. Maitland, J.J. Homola, **H.S. Embke**, M. Preul. (2022) *Fisheries Management and Ecology*

This paper was an output of the Wisconsin Initiative on Climate Change Impacts fisheries working group, on which I served as a contributing member. From our WICCI report, we

synthesized Wisconsin fisheries management approaches within the Resist-Accept-Direct framework to develop potential climate adaptation strategies for Wisconsin fisheries.

Abstract

Decision-makers in inland fisheries management must balance ecologically and socially palatable objectives for ecosystem services within the constraints of financially or physically possible outcomes. Climate change has altered social-ecological tradeoffs and transformed the potential range of ecosystem services available. The Resist-Accept-Direct (RAD) framework offers a useful foundation for responding to climate-induced ecosystem modification; however, ecosystem trajectories and current practices must be better understood to improve future decisions. Using Wisconsin's diverse inland fisheries as a case study, current and future management strategies for recreational and subsistence fisheries in response to climate change were reviewed in the RAD framework. Current management strategies largely focus on *resistance*, while future strategies may need to shift toward *acceptance* or *direction*. Understanding social-ecological fishery dynamics, the co-production of policies between state and tribal agencies, and input from recreational and subsistence fishers will be crucial to devise satisfactory strategies for fisheries given global environmental change.

Global dataset of species-specific inland recreational fisheries harvest for consumption

Embke, H.S., E.A. Nyboer, A.M. Robertson, R. Arlinghaus, S.L. Akintola, T. Atessahin, L.M. Badr, C. Baigun, T.D. Beard, Jr., G. Boros, S. Bower, H. Clare, S. Cooke, I. Cowx, A. Franco, L. Grapci-Kotori, V.P. Grenada, R.J. Hart, C.R. Heinsohn, H. Henley, V. Jalabert, A. Kapusta, T. Krajc, J. Koehn, G. Lopes, R. Lyach, T. Magqina, M. Milardi, A. Nightingale, H. Nyaboke, W. Potts, R. Raghavan, F. Ribeiro, N. Silva-Mercado, N. Sreenivasan, T. Treer, D. Ustups, P. Vrána, M. Zengin, A.J. Lynch. (In review) *Scientific Data*

This was a data paper describing a highly collaborative, international project I led where we collated all available species-specific inland recreational fisheries harvest data from the literature and expert sources. This dataset can then be used to understand the contribution of inland recreational fisheries to human consumption, economies, and vulnerability to climate change.

Abstract

Inland recreational fisheries are important to livelihoods, food and nutrition, leisure, and other societal ecosystem services worldwide. Recreational fisheries constitute the dominant use of inland fishes in developed nations and are of increasing importance in developing regions. Although recreationally caught fish are frequently harvested and consumed by recreational fishers, their contribution to food and nutrition has not been adequately quantified due to lack of data, poor monitoring, and under-reporting, especially in developing countries. Beyond limited global harvest estimates, few have explored species-specific harvest patterns, although this variability has great implications for fisheries management and food security. Given the continued growth of the recreational fishery sector, understanding recreational fish harvest and consumption rates represents a critical knowledge gap. Based on a comprehensive literature search and expert knowledge review, we quantified multiple aspects of global inland recreational

fisheries for 81 countries spanning 190 species. For each country, we assembled recreational fishing participation rate and estimated species-specific harvest, harvest composition, and consumption rate. This dataset provides the foundation for future assessments, including understanding nutritional and economic contributions of inland recreational fisheries.

Overturning stereotypes: The fuzzy boundary between recreation and subsistence in inland fisheries.

E.A. Nyboer, **H.S. Embke**, A.M. Robertson, R. Arlinghaus, S. Bower, C. Baigun, T.D. Beard, Jr., S.J. Cooke, I.G. Cowx, J.D. Koehn, R. Lyach, M. Milardi, W. Potts, A.J. Lynch (In review) *Fish and Fisheries*

This was a perspective piece that arose as we were putting together the global inland recreational fisheries harvest dataset (above). As we were speaking to experts around the world, it became apparent a 'fuzzy' boundary existed between recreation and subsistence in inland fisheries, therefore we highlighted instances of that gray zone with global case studies.

Abstract

Inland recreational fisheries provide social, economic, and emotional benefits to fishers, families, and communities. These fisheries also supply an important but often undervalued food source and, in some cases, may provide affordable and sustainable contributions to human nutrition. It is known that recreationally harvested fish species are frequently consumed but quantifying the contribution of recreational harvest to nutrition or food security on a global scale is impeded by lack of data on harvest and how much of that harvest is reduced to consumption. Records tend to be limited to wealthy, food-secure countries with longer histories of recreational fishing, but even in those instances, the records often neglect components of recreational harvest, particularly among food-insecure anglers who are potentially more likely to have consumption as a motivation. Here, we highlight the "fuzzy boundary" that can exist between freshwater recreational and subsistence fisheries and argue that unreported consumption is likely to be a hidden contributor to food security in some populations. We draw on case studies from all inhabited continents to highlight instances where recreationally harvested fish species contribute food security benefits to participating communities. We use these examples to highlight the diversity of ways that inland recreational fisheries contribute to human nutrition and to highlight data gaps in the biomass that recreational fishing for food can extract from inland aquatic environments. This study has relevance to recreational fisheries in low- and middle-income countries where demonstrating the subsistence aspect of recreational fisheries can add a new dimension to conversations about the potential for intersectoral conflict and inequity in the recreational fisheries sector. Further, in higher income countries recreational fishing can provide food security, especially in lower income communities and when combined with traditional and cultural importance of fish in diets. The aim of this study is to draw the attention of resource managers and policy makers, create greater social awareness of the importance of recreational fisheries, and bring to light this hidden contribution of inland fisheries to global food security and subsistence.