

Incorporating Angler Behavior into Recreational Fisheries Management

By

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Abstract

Recreational fisheries are social ecological systems, where aquatic ecosystems, fish populations, anglers, and governing bodies interact across scales in complex and often unexpected ways. In the context of fisheries management, many of fishery systems' relevant dynamics occur at the level of human users. Recreational anglers are decentralized, mobile, and have different preferences and drivers for their behavior. The efficacy of fisheries management decisions frequently depend on the response of anglers to social, regulatory, and ecological change. In this dissertation, I investigate human behavior in two distinct recreational fishery systems: the Wisconsin inland lake fishery and the New Jersey bottom fishery. In Chapter 1 I develop and validate a method for estimating fishing effort across many lakes with limited data. Wisconsin is highly lake rich. This landscape provides a bounty of opportunities for recreational anglers, but their activities are difficult to monitor. I used generalized linear mixed effects models to share observations across lakes to estimate overall fishing effort. I was able to produce total summer fishing effort estimates for 44 lakes that were within 11% of the mean value of traditional data rich estimates. This result shows that existing intensive data collection could instead be spread across many lakes to achieve landscape-scale monitoring of inland lake fisheries.

In Chapter 2, I applied this model-based method to test the effect of the COVID-19 pandemic on fishing effort. Because I had collected observations of vehicle traffic at lake access points in 2018 and 2019, I was able to compare these values to a socially distanced roving count of vehicles at lake access sites in the summer of 2020. The pandemic was associated with increased interest in outdoor recreation, and I showed that this interest extended to recreational

fishing on northern inland lakes of Wisconsin. On average, vehicle counts at the same lakes were 29% higher during the pandemic than in previous years. These changes in vehicle counts corresponded with a surge in fishing license sales, particularly among first-time-buyers. Lake-specific differences in the effect of a pandemic year highlighted “hotspot” lakes that may require additional monitoring.

Chapter 3 shifts to New Jersey marine recreational fisheries to investigate anglers’ responses to regulatory changes. Popular bottomfish species have experienced increasingly strict regulation since 2001. Stakeholder groups, including private anglers, tackle shop owners, and for-hire vessel operators expressed deep concern regarding the social and economic effects of these changes in focus groups. By analyzing changes in fishing effort reported by vessel trip reports, I found that fishing effort was declining in response to reduced possession limits, but only among anglers aboard large party boats. These results show that anglers engaged in different sectors of the for-hire fishery engage in different degrees of substitution behavior when harvest of preferred species is restricted.

Chapter 4 looks towards the future of the Wisconsin inland lake fishery. These lakes are undergoing a shift in species composition as walleye production declines and warmwater species thrive. Using a stated preference method, I investigated how anglers would trade off travel time with catch rates and maximum sizes of walleye, largemouth bass, and bluegill. Respondents were motivated to travel considerable distances for walleye, but also for other species. Maintaining high-quality warmwater assemblages may therefore present greater net benefits to anglers than intensified walleye stocking.

Together, these chapters evaluate the response of human resource users to change in a complex social ecological system in a fisheries management context. Substitution behavior of

anglers emerged as a key dynamic to understand and anticipate for effective fisheries management under social and ecological change.

Introduction

Recreational fisheries are socially and economically important (Tufts, Holden, and DeMille 2015), globally widespread (Arlinghaus, Tillner, and Bork 2015), and responsible for considerable fishing mortality (Cooke and Cowx 2004; Ihde et al. 2011). Because recreational fisheries are decentralized and often dispersed across landscapes, monitoring fishing effort and harvest is costly (Pereira and Hansen 2003). Recreational fisheries managers therefore typically rely on limited data to achieve benefits to human resource users across complex social ecological systems. The social ecological system (SES) framework describes integrated resource, user, and governance systems interacting across scales to produce emergent outcomes (Ostrom 2007). Management actions therefore result in feedbacks and nonlinear effects that vary across systems, resulting in considerable uncertainty regarding outcomes. One key source of uncertainty is the response of users to changes in resource availability, management actions, and environmental change (Ward et al. 2016).

Because recreational fishers are motivated by the fishing experience rather than by only catching fish (Birdsong, Hunt, and Arlinghaus 2021), monitoring and predicting changes in recreational fishing effort is an important goal for managers to enact landscape-scale active adaptive management (van Poorten and Camp 2019; Olsson, Folke, and Berkes 2004). Fishing effort dynamics are one driver of feedbacks in fishery systems, responding to fishing quality (Askey and Johnston 2013), regulations (Beard, Cox, and Carpenter 2003), fishing site accessibility (Wilson et al. 2020), site congestion (Timmins and Murdock 2007), among other characteristics (Birdsong, Hunt, and Arlinghaus 2021). However, the actual responses of anglers to these changes are often unexpected. Catch rates, for example, are frequently subject to hyperstability, masking declines in fish density (Dassow et al. 2019; Erisman et al. 2011; Feiner,

Wolter, and Latzka 2020). In addition, recreational fishers are motivated to fish by factors other than catch (Hunt et al. 2019). Fishing effort may therefore not respond to declines in catch rate, putting recreational fisheries at risk of collapse (Hunt et al. 2011; Post 2013; Golden, van Poorten, and Jensen in review). Regulations such as season closures and bag limits are frequently used as levers to manage fishing effort and harvest. However, these actions can also have unintended consequences. For example, lower possession limits in the Wisconsin walleye (*Sander vitreus*) recreational fishery signaled to experienced anglers that walleye populations were robust enough to be targeted by Indigenous spearfishers (Beard, Cox, and Carpenter 2003), muddling the regulations' intended effects. As another example, where fishing seasons lengths have been severely reduced in the Gulf of Mexico, intensified fishing effort has reduced regulations' effectiveness at controlling fishing mortality (Powers and Anson 2018). Social ecological outcomes of fisheries undergoing change therefore pivot on the response of human resource users. Successful fisheries management requires effective monitoring of fishing effort across landscapes and proactive consideration of how angler behavior could respond to ongoing environmental and regulatory change.

This dissertation contributes to this knowledge gap by investigating fishing effort dynamics in two fisheries: the inland lake fishery of Wisconsin and the marine bottom fishery of New Jersey. Both fisheries include a variety of target species distributed across a large spatial area. In both of these fisheries, fishing opportunity has changed over time because of changes in species distribution, environmental change, and regulations (Bell et al. 2015; Hansen et al. 2017). In both of these systems, the future success of fisheries management decisions depends on understanding the response of human resource users, specifically recreational anglers, as these changes take place. Both systems have a long and complex history of contentious fisheries

management processes (Nesper 2002; Terceiro 2018). Conflicting values and goals between different resource users with different levels of institutional power have led to ongoing fractious debates about the efficacy of data collection on recreational fisheries, fish population assessments, and local and federal agency management decisions.

The lake-rich glacial landscape of northern Wisconsin was ceded to the United States through treaties with Ojibwe tribes in 1837, 1842, and 1854. The inland lake fishery of northern Wisconsin became a popular fishing tourism destination starting at the end of World War I. By 1996, Wisconsin was one of the top 5 destination states for fishing tourism in the US (Ditton 2002). Management of the state's recreational fisheries is overshadowed by a history of a disregard for Tribal treaty rights to hunt, fish, and gather, and this history has frequently left Ojibwe subsistence fishers, recreational anglers, and management agencies at odds (Nesper 2002). Because the sustainable co-management of walleye populations is federally mandated, walleye lakes are centered in fisheries data collection (Staggs 1989). As climate change progresses, however, walleye populations are declining (Hansen et al. 2017). Continued successful management of warmwater species is therefore an important goal for future angler satisfaction. Fishing effort, catch rates, and harvest data are collected through annual creel surveys on select lakes each year. Enormous numbers of person-hours are spent on these surveys, but due to the intensive nature of the data collection, relatively few lakes each year are surveyed. For example, although Vilas County, one of 24 counties in the Ceded Territory, has 175 publically accessible lakes. Since 1996, the Wisconsin Department of Natural Resources (WDNR) has surveyed 65 of them. These surveys yielded high-quality data, but they left substantial data vacuums for non-walleye lakes. Estimation methods that rely on lower volumes

of data collected from a broader selection of lakes are therefore a valuable step towards applying active adaptive management to a wider range of lakes, species, and anglers.

New Jersey is home to another socioeconomically important recreational fishery, generating nearly \$750 million of income for state residents in 2016 (National Marine Fisheries Service 2018). A source of conflict among fishery stakeholders in NJ is the allocation of safe harvest limits between recreational and commercial harvesters. New Jersey marine fisheries support numerous coastal businesses, including for-hire vessels, marinas, and tackle shops. Summer flounder (*Paralichthys dentatus*) is among the most sought-after species for marine recreational fishers, and strict regulations on recreational harvest has led to a strong sense of frustration among stakeholders (Terceiro 2001; 2011; 2018). Season lengths and possession limits have decreased, and minimum length limits have increased over time, leading to widespread concern about the social and economic effects that tight regulations will have on coastal communities. Understanding regulations' effects on recreational fishing effort will assist managers in balancing biological, social, and economic outcomes as they continue to maintain sustainable fish populations.

In this dissertation I first develop, validate, and field-test a model-based method for estimating fishing effort across a lake-rich fishery landscape in northern Wisconsin. I then leverage an underutilized source of data to infer angler response to regulations in the recreational bottomfish fishery of New Jersey. Last, I develop a stated preference method that predicts angler responses to ongoing tradeoffs in availability of walleye, largemouth bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*) in Wisconsin.

In Chapter 1, I developed and validated a method of estimating fishing effort at many lakes using extensive data collected through boat-based and aerial counts of anglers in Vilas County, WI. Traditional creel methods require full-time creel clerks stationed at one lake ten months of the year to generate precise estimates of fishing effort through mean expansion (Newman, Rasmussen, and Andrews 1997). We distributed our survey across many more lakes to collect counts of fishing effort at different times of day and throughout the summer fishing season. By sharing data across lakes, we could estimate seasonal and daily dynamics that stayed the same across the county. By collecting additional observations at similar times of day through aerial surveys, we were then able to improve estimates of lake-specific mean fishing effort. A generalized linear mixed effects model (GLMM) could then account for seasonal, daily, and weekend effects on fishing effort using fixed effects that did not vary by lake, and lake-specific mean effort was incorporated using random effects. I fit these models to our observations, predicted a summer of fishing effort, and then compared our model-based estimates to traditional mean expansion. I found that model-based estimates using limited data produced estimates within, on average, 11% of traditional data rich estimates. With modest tradeoffs of precision, more estimates of fishing effort can therefore be produced per year across a lake-rich landscape using extensive (rather than intensive) data collection.

For Chapter 2 I used this model-based method to compare vehicle counts at public lake access points between years to test the effect of the COVID-19 pandemic on fishing effort in Wisconsin. The pandemic has had far-reaching social, economic, and ecological effects globally (Searle, Turnbull, and Lorimer 2021). One effect of the widespread shutdowns and restrictions on indoor gatherings was increased participation in outdoor activities (Derks, Giessen, and Winkel 2020; Landry et al. 2020; Morse et al. 2020). Sustained increased participation in

recreational fishing would increase WDNR revenue from license sales but could also lead to increased harvest of freshwater species. Because we had collected counts of vehicles at lake access points in 2018 and 2019, we were able to complete a socially distanced bus route survey of the same lakes to compare vehicle traffic before and during the pandemic. Using the GLMM fixed effects to account for differences in time of day and day of year, we inferred that vehicle numbers at lakes entirely surrounded by public lands increased by 103% on average in 2020 compared to the previous two years. However, no significant effect of the COVID year on all lakes was detected. Rather, lakes with more public shoreline were more likely to experience increased vehicle numbers in 2020, suggesting that these “hotspots” should be subject to increased monitoring if this surge in participation continues.

In Chapter 3, I evaluated changes in angler behavior in a different system: the recreational marine bottom fishery of New Jersey. Since 2001, regulations for summer flounder (*Paralichthys dentatus*), black sea bass (*Centropristis striata*), tautog (*Tautoga onitis*), and scup (*Stenotomus chrysops*) have become increasingly restrictive. Fishery stakeholders, including private anglers, for-hire vessel operators, and tackle shop owners are concerned about the negative economic effects of these restrictions if they reduce fishing effort. Revealed preference methods are useful for evaluating the tradeoffs of changes in fishing effort versus reductions in harvest. I used vessel trip reports (VTRs) submitted by for-hire vessels between 2001 and 2017 to construct a time series of angler trips during each week of the year. I de-trended the seasonal patterns through dynamic harmonic regression (Young, Pedregal, and Tych 1999), which allowed me to then infer how the remaining changes in weekly fishing effort corresponded to changes in possession limit, the number of species open for harvest, and season lengths. I did not find any evidence of intensified fishing effort corresponding to shorter seasons. I did, however,

detect differences in substitution behavior between anglers aboard large party boats and anglers renting smaller charter boats. As long as at least one species was open for harvest, fishing effort in the charter sector stayed about the same regardless of possession limits for all species. Party boat anglers, in contrast, showed less willingness to switch species. Fishing effort declined in weeks with lower possession limits for summer flounder and black sea bass. Fisheries managers should therefore account for the economic effects of possession limits and season length reductions when developing new regulations to limit mortality to safe harvest thresholds.

Instead of examining previous changes in angler behavior, Chapter 4 attempts to predict angler behavioral response to future changes in species composition in an experimental context. By mid-century, Wisconsin is predicted to lose around 46% of its naturally recruiting walleye populations (Hansen et al. 2017). Simultaneously, warmwater species such as largemouth bass and bluegill are expected to flourish. Wisconsin supports a diverse array of species targeted by recreational anglers, which is a strong predictor of angler satisfaction (Beardmore et al. 2015). Walleye anglers could therefore target alternative species in the face of these declines. It is also, however, possible that committed walleye anglers would instead travel greater distances to maintain their catch rates at remaining walleye lakes. This behavior could result in an intensification of fishing effort per lake as the number of walleye-producing lakes declines. We investigated these potential responses using a stated preference approach, where WI resident anglers choose hypothetical fishing sites that varied in travel time, catch rates, and maximum sizes for walleye, largemouth bass, and bluegill. We did not find evidence that anglers would travel greater distances to maintain walleye catch rates. Nor, however, did we find that anglers were substituting bluegill and largemouth bass as second-best species when walleye was unavailable. Instead, anglers were inclined to fish for a variety of species, particularly when

catch rates and maximum sizes were high. This result suggests that anglers may be willing to adapt their fishing behavior to the new reality of dominance by warmwater assemblages. Instead of only increasing stocking of walleye to resist this change in species composition, additionally prioritizing high quality centrarchid fisheries may result in greater net benefits to anglers.

Although monitoring the response of human resource users to system change presents a number of challenges, this dissertation demonstrates that landscape-scale monitoring of recreational fishery systems is feasible. Incorporating multiple data sources, including the local knowledge of resource users, is an effective approach for both monitoring changes in resource use and quantifying socioeconomic tradeoffs of social, ecological, and regulatory change. Finally, understanding and anticipating substitution behavior of anglers in response to these changes emerged as a key strategy for effective management of fisheries undergoing change.

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Chapter 1: Estimating fishing effort across the landscape: a spatially extensive approach using models to integrate multiple data sources

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Abstract

Measuring fishing effort is one important element for effective management of recreational fisheries. Traditional intensive angler intercept survey methods collect many observations on a few water bodies per year to produce highly accurate estimates of fishing effort. However, scaling up this approach to understand landscapes with many systems, such as lake districts, is problematic. In these situations, spatially extensive sampling might be preferable to the traditional intensive sampling method. Here we validate a model-based approach that uses a smaller number of observations collected using multiple methods from many fishing sites to estimate total fishing effort across a fisheries landscape. We distributed on-site and aerial observations of fishing effort across 44 lakes in Vilas County, Wisconsin and then used generalized linear mixed models (GLMMs) to account for seasonal and daily trends as well as lake-specific differences in mean fishing effort. Estimates of total summer fishing effort predicted by GLMMs were on average within 11% of those produced by traditional mean expansion. These estimates required less sampling effort per lake and can be produced for many more lakes per year. In spite of the higher uncertainty associated with model-based estimates

from fewer observations, the improvements associated with the addition of only three aerial observations per lake highlighted the potential for improved precision with relatively few additional observations. Thus, the combination of GLMMs and extensive data collection from multiple sources could be used to estimate fishing effort in regions where intensive data collection for all fishing sites is infeasible, such as lake-rich landscapes. By using these methods of extensive data collection and model-based analysis, managers can produce frequently updated assessments of system states, which are important in developing proactive and dynamic management policies.

Introduction

Recreational fisheries are widespread and socioeconomically important, with about 118 million estimated participants in North America, Europe, and Oceania (Arlinghaus et al., 2015; Tufts et al., 2015). Inland and marine recreational fisheries are responsible for substantial removal of biomass, but in many systems, insufficient data are available to make proactive management decisions with the goal of maintaining sustainable harvest (Cooke and Cowx, 2004; Ihde et al., 2011). In addition, these fisheries are frequently open-access, leaving them particularly vulnerable to overfishing (Cooke and Cowx, 2004; Cox et al., 2002; Post and Parkinson, 2012). Anglers exhibit heterogeneous preferences, which leads them to adjust the location and intensity of their fishing effort in response to changing conditions. This complicates managers' ability to predict fish population dynamics (Carruthers et al., 2018; Wilson et al., 2020). Successful management of recreational fisheries therefore requires understanding fishing effort dynamics across different spatial and temporal scales.

Recreational fisheries are diverse in their spatial extent; their distribution across the landscape; and their availability of catch, effort, and harvest data (FAO, 2012; Kaemingk et al., 2019). Different systems therefore rely on different methods for quantifying fishing effort dynamics, which can include intensive and/or extensive observations of water bodies or access points. The number of water bodies surveyed depends on the abundance of water bodies present in the region as well as the budget limitations of the managing agency (e.g. Cass-Calay and Schmidt, 2009; Chizinski et al., 2014; Malvestuto et al., 1978). Intensive data collection on relatively few locations permits more in-depth sampling of these locations over a wide range of conditions. For example, access point creel surveys assign clerks to select water bodies or access points for stratified-random shifts over much of the year. During these shifts, clerks interview anglers and collect instantaneous counts of angler effort (Newman et al., 1997; Pollock, 1994). For landscapes where water bodies are relatively scarce, intensive data collection satisfactorily balances costs of data collection with accuracy of fishing effort and catch rate estimates. However, intensive data collection regimens can also leave many water bodies with no available data describing fishing effort, catch rates or harvest (Post et al., 2002). Many fisheries landscapes could therefore benefit from extensive data collection, where fewer observations are collected per site, but more water bodies or access points are surveyed (Beard et al., 2011). Fisheries already applying these methods tend to rely on multiple data sources to find the right balance between collecting sufficient observations per site while also surveying as many sites as possible (e.g. Steffe et al., 2008). In contrast, many fisheries that have historically been classified as “small scale” are surveyed through intensive methods in spite of their large spatial extent and/or their high number of access points or fishing sites, such as lake districts (Deroba et al., 2007) and river systems (West and Gordon, 1994). The pool of harvesters within a recreational fisheries

landscape is mobile and heterogeneous, and their fishing effort dynamics cannot always be understood by treating small water bodies and fishing sites as independent fisheries (Matsumura et al., 2017; Martin et al., 2017). Many of these fisheries landscapes therefore benefit from a more extensive form of data collection and the integration of multiple data sources (e.g. Smallwood et al., 2012, Askey et al., 2018).

Redistributing data collection to sample all water bodies or access points is not a trivial issue, particularly in lake-rich landscapes or for very large water bodies. For large water bodies with many access points, roving creel survey methods are used to cover more area (Roop et al., 2018; West and Gordon, 1994). Additional extensive survey methods include the use of aerial surveys (Askey et al., 2018; Smucker et al., 2010), cameras (van Poorten et al., 2015), and vehicle counters (Simpson, 2018; van Poorten and Brydle, 2018), often in combination with intensive creel methods (Hartill et al., 2016; van Poorten and MacKenzie 2020). However, when adapting these mixed methods for a particular system, it will not always be possible to produce data compatible with design-based estimates of fishing effort. Traditional methods of estimating fishing effort rely on specific creel designs intended to accommodate variation in fishing effort by temporal strata, such as month or day of the week. Mean effort of a stratum is a mean of means: the mean of daily total effort means within the stratum (Newman et al., 1997). This mean expansion process leverages the central limit theorem to allow Gaussian error propagation to estimate confidence intervals around total fishing effort estimates (Särndal et al., 1978). Disparate systems use different creel designs to achieve this goal (e.g. Chizinski et al., 2014; Lockwood and Rakoczy, 2005; Smallwood et al., 2012), and they are difficult to adapt to non-standard data from supplemental sources.

In contrast, model-based estimation of fishing effort can more easily accommodate multiple data sources and is flexible to system-specific sampling methods. An example of earlier model-based approaches includes a regression method predicting on-site estimates of total fishing effort from instantaneous observations collected by aerial surveys in British Columbia (Tredger, 1992). Askey et al. (2018) demonstrated that the previously employed regression method produced biased estimates and rigorously demonstrated the effectiveness of a generalized linear mixed model-based estimation approach using aerial surveys and on-site data collection from time-lapse cameras. Model-based approaches to estimating fishing effort across multiple fishing sites or water bodies are therefore not new methods, but they have generally been applied to test for differences in fishing effort dynamics among groups (Merten et al., 2018), or to understand ecological and fishery influences on fish growth and productivity (Varkey et al., 2018). Similar models could instead be applied to extensively collected data from multiple sources to estimate waterbody-specific fishing effort over many potential fishing sites.

Despite the availability of multiple data sources for estimating fishing effort, it is not always feasible to survey all fishing sites across a landscape. Models used to estimate total fishing effort could therefore be extended to predict angling effort based on empirical relationships between fishing effort and abiotic and biotic lake variables. Studies of stated and revealed angler preferences have already identified lake characteristics that are particularly attractive to anglers. For example, large lakes that are easily accessible and present high-quality fishing opportunities are more likely to be chosen as angling sites (Hunt, 2005; Reed-Andersen et al., 2000; Hunt and Dyck, 2011). However, anglers have heterogeneous preferences, so it is not immediately clear whether these differences in characteristics among lakes may influence the overall distribution of angling effort (Beardmore et al., 2013; Breffle and Morey, 2000; Curtis

and Breen, 2016, Kane et al., 2020). Lake-specific predictors could include some of the many lake morphometric and landscape variables known to influence fishing effort either directly or indirectly through their influence on fish community composition and abundance. In a study estimating total harvest across Wisconsin, Embke et al. (2020) used generalized linear mixed models (GLMMs) with lake characteristics as predictors to estimate harvest on unobserved lakes. If lake characteristics as well as the confounding effects of weather, time of day, and seasonality are also consistent predictors of fishing effort among lakes (i.e. Deroba et al., 2007), at least coarse estimates of fishing effort at unobserved lakes can be produced based on observed lake characteristics.

We tested a model-based approach to estimating fishing effort using extensive data collected in Vilas County, Wisconsin. To accomplish this goal, we examined annual summer fishing effort predictions of GLMMs fit to three datasets. These datasets were collected using different methods that demonstrated tradeoffs between the number of observations per lake and the number of lakes surveyed (Table 1). One dataset was classified as intensive because it included many observations of fewer lakes per year. The second and third datasets were extensive because they contained fewer observations per lake, but many more lakes were surveyed each year. The third dataset additionally included aerial survey observations of the same lakes to test for the value of including a supplemental data source. We completed a series of tests using these datasets to address the following questions: 1) When fit to extensive data, can models detect annual, seasonal, and daily changes in fishing effort? 2) How do fishing effort estimates derived from extensive observations compare to those derived from intensive observations? 3) How well can models fit to extensive data predict total fishing effort on

unobserved lakes? 4) How can these model-based methods be applied to predict fishing effort across a fisheries landscape?

Methods

Study area

All observations of angling effort took place in Vilas County, Wisconsin. Vilas County is part of the Northern Highlands Lake District (NHLD), a highly forested, lake-rich region known for its fishing tourism (Peterson et al., 2003). With increasing shoreline residential development and the continued effects of global climate change, the NHLD lake fisheries have shown marked changes in species composition and size structure (Christensen et al., 1996; Sass et al., 2006; G. J. A. Hansen et al., 2015; J. F. Hansen et al., 2015; Embke et al., 2019). The high density of lakes in this region means that intensive creel data are collected infrequently for each surveyed lake. If accurate estimates of fishing effort could instead be derived from extensive data collected over more lakes, managers' understanding of effort dynamics at many lakes of interest could be updated more frequently. Vilas County has 1318 lakes, of which 175 have public access points maintained by the WDNR (Wisconsin Department of Natural Resources, 2009). Since 1995, the Wisconsin Department of Natural Resources (WDNR) has conducted intensive creel surveys on 65 Vilas county lakes (Figure 1, Table 1). Intensive data collection on lakes inhabited by walleye (*Sander vitreus*) in the Ceded Territory (the northern third of Wisconsin) was initiated by the WDNR and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) in 1987 after the US Seventh Circuit Court of Appeals affirmed the off-reservation hunting, fishing, and gathering rights of Ojibwe tribal members. The WDNR annually selects among all lakes containing walleye using a stratified random design to complete adult walleye population estimates, age-0 walleye relative abundance surveys, and nine-month creel surveys. In addition, each year four

“trend” lakes are selected, which are sampled every three years, and most other lakes are surveyed about once every ten years (Cichosz, 2019). The data collected from these surveys are used to manage the joint tribal spearing and recreational angling fishery for walleye in the Ceded Territory of Wisconsin (Hansen et al., 1991).

Data collection

Intensive observations of instantaneous boat counts were collected by the WDNR during 1995-2019 across 65 lakes using a stratified random survey design. On average, five Vilas County lakes were surveyed per year (Tables 1 and A1), and only lakes containing walleye were surveyed (Cichosz, 2019). Survey dates and times were stratified by month, weekend, and mornings and evenings. A creel clerk’s 40-hour workweek was randomly assigned to days and times based on these strata. In general, lakes were surveyed for nine months each and visited for about 20 creel shifts per month. November, March, and April were usually omitted from sampling due to perilous ice conditions. Instantaneous counts were completed at two randomly selected times during each shift. Creel clerks circled the lake by boat, counting the number of anglers that were either actively fishing or known to be moving between fishing locations (Gilbert et al., 2013; Rasmussen et al., 1998).

For our extensive experimental creel survey, we completed on-site, instantaneous counts of fishing activity at 38 lakes in Vilas County, WI from mid-May to mid-August of 2018 and 2019 (Figure 1, Supplementary Material A1). Sixty creel shifts in 2018 and 120 shifts in 2019 were stratified by weekends and weekdays as well as by morning (5:30 to 13:30) and evening (13:30 to 21:30) shifts. We randomly assigned at least four of these shifts to each lake, with the restriction that each lake needed to be surveyed at least once on a weekend or holiday. In addition, morning and evening shifts were required to take place at each lake. During each creel

shift, we completed three instantaneous boat counts at randomly selected times. If randomly selected count times were less than one hour apart, count times were re-drawn until this criterion was met. If a count was selected to take place before sunrise or after dark, the count was instead completed at sunrise or sunset, respectively, and the new count time was recorded. On average, 13 instantaneous counts were completed per lake during the 6 months total of experimental creel surveys from 2018 and 2019 (Tables A1 and A2). We completed on-site instantaneous counts of fishing effort from a boat, counting the number of fishing boats and shore anglers who were actively fishing at the count time. For each boat or shore angler observed, we recorded whether or not they were angling, the number of passengers, and whether the boats were moving or stationary. Because we counted fishing vessels while the intensive creel survey counted anglers, we converted the intensive raw counts to an approximate number of fishing boats based on the mean number of passengers per boat observed during our extensive on-site counts ($\mu=2.04$, $\sigma=0.95$).

In addition, we completed three aerial surveys of the same 38 lakes (plus 6 others) on June 6, July 10, and July 27, 2019. Flights were scheduled based on pilot availability and weather conditions. Volunteer pilots flew a pre-planned flight path in low-wing, single-engine aircraft. The pilot circled each of the target lakes at an altitude of 760 m while the counts took place. Two passengers were present for data collection: one identifying lakes and recording counts and the second locating and counting boats. When conditions allowed, we used binoculars to identify boats containing anglers. We could not always visually identify fishing boats, so unassigned stationary or slow-moving boats were therefore probabilistically classified as fishing or non-fishing based on the proportion of fishing boats among all stationary and slow-moving boats observed during on-site counts. We observed 62% of stationary boats and 80% of slow-

moving boats to be fishing during our on-site counts, so each unassigned stationary and slow-moving boat was randomly assigned a classification with a 0.62 or 0.80 probability, respectively, of being classified as a fishing boat.

Traditional mean expansion estimates of fishing effort

Mean expansion estimates of total fishing effort from intensive data compute the sum of mean fishing effort over several strata. Every month of observations makes up one level, and then each month is subdivided into weekday and weekend/holiday strata. Two counts of fishing effort were collected every shift, and these were averaged to estimate each day's mean effort. Daily mean effort was multiplied by the number of daylight hours to estimate that day's total boat hours. The mean of this daily mean total effort was then calculated separately by month and weekday strata, and the sum of these grand means estimated the lake year's total fishing effort. The standard deviation (SD) of angler counts within a stratum was completed according to Rasmussen et al., (1998), and summer fishing effort SD for each lake was calculated as the square root of the summed variance of all strata. This protocol of mean expansion has been demonstrated to accurately estimate total annual fishing effort relative to a census count (Newman et al., 1997). We calculated fishing effort from intensive data only for summer months between May and August. Seven lakes were surveyed intensively and extensively on different years. This overlap allowed us to compare the accuracy and precision of mean-expansion total summer fishing effort estimates with our model-based estimates from extensive data.

When fit to extensive data, can models detect annual, seasonal, and daily changes in fishing effort?

We modeled instantaneous boat counts as a response to the effects of lake, year, day of year, and time of day using GLMMs. We tested the fit of different distributions to our count data

using the R package “fitdistrplus”(Delignette-Muller and Dutang, 2015) in R version 3.6.1 (R Core Team, 2019). Because the count data were overdispersed, we fit negative binomial regressions with a log link function. We used autocorrelation function (ACF) plots of standardized residuals to detect significant temporal autocorrelation. Random intercepts incorporated variation due to lake identity that was not accounted for in the explanatory variables (Zuur et al., 2009). By including random intercepts to accommodate lake-specific variation in fishing effort, we allowed the model to pool information across lakes in order to detect general patterns in seasonal and daily fishing effort dynamics. This model was then used to predict hourly instantaneous counts across a summer for each lake. The area under the curve of these predictions then provide estimates of annual summer fishing effort that can be compared to estimates obtained by mean expansion of intensive data.

We used two datasets, the intensive WDNR observations and the extensive experimental data, and compared the ability of GLMMs to detect changes in fishing effort on three subsets of this data: (1) the intensive observations, (2) the extensive on-site observations, and (3) our combined extensive on-site and aerial survey observations. We completed forward model selection of a pre-specified set of increasingly specific predictors by comparing Akaike Information Criterion (AIC) of candidate models. We used a ΔAIC cutoff of -2 for selecting the best-fitting model. The simplest model consisted of only a random intercept by lake. We sequentially added in effects for year, day of year, and hour of day. Seasonality and time of day are already well known predictors of fishing effort (e.g. Mann and Mann-Lang, 2020; Powers and Anson, 2016). By completing forward-selection of nested models, we were able to compare the ability of different datasets to detect increasingly granular dynamics of fishing effort. For the models fit to intensive observations, the year effect was a second random intercept. For the two

extensive datasets conducted only over two years, we included a year fixed effect using a dummy variable. To aid convergence, all continuous predictor variables were centered and scaled. We fit these models using the lme4 package version 1.21 (Bates et al., 2015, p. 4). Validity of the models was assessed using the DHARMA package v.0.2.6 (Hartig, 2019), and marginal and conditional r^2 were estimated using the trigamma method with the MuMIn package v.1.43.15 (Barton, 2019).

How do fishing effort estimates derived from extensive observations compare to those derived from intensive observations?

Before comparing model-based to mean expansion predictions, we first validated that generalized linear models fit separately to each lake year of intensive data produced total fishing effort estimates comparable with those produced through mean expansion (Appendix A2, Figures A1 and A2, Tables A3 and A4). After this validation, we then tested the accuracy and precision of total summer fishing effort estimates derived from each of the candidate GLMMs fit in section 2.4. We compared predictions generated by each GLMM with the estimates calculated by mean expansion for the seven lakes surveyed in both datasets. Hourly predictions of instantaneous boat counts from May 1 to August 31 for these lakes were obtained by predicting boat counts at each daylight hour of each day. Continuous prediction variables were centered and scaled according to the mean and standard deviation of the original fit data. Predictions for all models and datasets were produced for all daylight hours of summer, conditional on a mean year effect using the merTools v.0.5.0 R package (Knowles and Frederick, 2019). The area under the curve of each lake's summer predictions was then calculated using the trapezoidal rule, which produced an estimate of total summer fishing effort for each lake. By bootstrapping the model predictions for 5,000 iterations, we obtained a mean estimate of total fishing effort as well as

upper and lower 95% prediction intervals. This process was repeated for each of the candidate models. These prediction intervals of model-based estimates of fishing effort were then compared to fishing effort estimates calculated through mean expansion of intensive data. To summarize correspondence between predicted and observed fishing effort for each dataset and model, we compared indices of relative accuracy and precision (I_{RA} and I_{RP} , defined below) of each model's predicted total summer fishing effort versus expanded mean estimates as in Steffe et al. (2008). Some lakes were intensively surveyed over several years. For these lakes, we compared model-based total effort estimates to the mean of all years' mean expansion estimates. The I_{RA} specifies the similarity of two estimates relative to the magnitude of the estimate of interest. A positive I_{RA} indicates that the model-based estimate is higher than that of the mean expansion by some proportion of its overall value, while a negative value indicates a lower estimate.

$$I_{RA} = \frac{GLMM \text{ estimate} - \text{Mean expansion estimate}}{\text{Mean expansion estimate}} \times 100$$

The I_{RP} describes the similarity of each estimates' relative standard error (RSE) as a percentage of the RSE of the estimate of interest. A positive I_{RP} value indicates that the model-based estimate is more precise than that of the mean expansion, or in other words, its standard error is a smaller proportion of its estimate.

$$RSE = \frac{SE_{Estimate}}{Estimate} \times 100$$

$$I_{RP} = \frac{RSE_{Mean\ expansion} - RSE_{GLMM\ estimate}}{RSE_{Mean\ expansion}} \times 100$$

Mean I_{RA} and I_{RP} were then calculated for all lakes surveyed intensively and extensively.

How well can models fit to extensive data predict total fishing effort on unobserved lakes?

We chose the most accurate predictive model from section 2.5 and added covariates describing lake characteristics. We chose variables representing landscape predictors of boating density as described by Hunt et al. (2019). Hunt et al. (2019) modeled the distribution of boating activity in Ontario, Canada as a function of lake surface area, accessibility, human development, and fishing quality. We restricted ourselves to data that were easily obtained for all lakes in a fisheries landscape. Lake surface area is a well-established predictor of fishing effort (e.g. Hunt, 2005), and it is available for all Wisconsin lakes. We also had access to lake-specific availability of public boat ramps and presence of walleye, a popular target species. Each of these variables were obtained from the WDNR lake database. Distance from a resident pool of anglers, either from a nearby urban center or from lake residents, has also been demonstrated to predict fishing effort (Hunt et al., 2011; Wilson et al., 2020). However, given the low and relatively homogeneous population density of Vilas County (Peterson et al., 2003; U.S. Census Bureau, 2010), we judged housing density of the lakeshore to be a more influential source of nearby anglers. We calculated building density (buildings per km shoreline) within 200 m of each lake's shoreline using GIS data obtained from the WDNR and Vilas County. As an additional measure of accessibility, distance to the nearest secondary road was calculated as Euclidean distance from the centroid of a lake to the closest point of the road. Latitude and longitude of each lake was obtained from the WDNR 24K Hydro Geodatabase ("24K Hydro Full Geodatabase for Download," 2017), and road data came from the United States Geological Survey National

Transportation Dataset for Wisconsin (“USGS National Transportation Dataset Downloadable Data Collection,” 2017). Continuous variables were scaled and centered. These models were fit as described in section 2.4, and p-values were estimated based on Wald tests with the null hypothesis that the predictors have no effect on fishing effort and an $\alpha=0.05$.

Models’ ability to predict total effort on unobserved lakes was tested using leave-one-group-out (LOGO) cross validation for models fit to intensive and extensive datasets. All observations from each lake were iteratively removed from the dataset, the models were refit, and the missing values predicted. These predictions were bootstrapped for 5000 iterations to obtain upper and lower 95% prediction intervals for the effort estimates. The I_{RA} and I_{RP} of these estimates were then estimated relative to those produced by mean expansion of intensive data.

How can these methods be applied to predict fishing effort across a fisheries landscape?

The best-performing predictive GLMM was used to estimate total summer fishing effort across all lakes and years surveyed either intensively or extensively in Vilas County. We fit the model to the combined intensive and extensive datasets, including random lake and year effects and fixed effects of weekend, day of year, and a dummy variable indicating the survey method. A full summer of fishing effort was then predicted for each lake over each year represented in the full combined dataset. We obtained 95% prediction intervals by bootstrapping the model predictions for 5000 iterations. Predictions were completed for 100 lakes over 25 years.

Results

When fit to extensive data, models detect presence and shape of annual, seasonal, and daily changes in fishing effort, but underestimate their magnitude.

The best-fit models included a year effect and quadratic effects of day of year and hour of day, which suggests that seasonal and daily patterns of fishing effort were detected by models fit

even with few observations per lake (Table 2). The quadratic effect of time of day was the best fitting of all of the functional forms tested for this variable (Tables A5-A7). Weekends and holidays had a consistently positive effect on fishing effort for all datasets. However, the models fit to the intensive dataset were the only models to detect significant quadratic effects of day of year and hour of day on fishing effort (Tables A8-A10). Therefore, while including annual, daily, and hourly effects improved model fit for all of the data sets, it was only the annual and weekend effects that were detectable in the models fit to extensive data. Fixed effects such as day of year, weekend/weekday, and hour of day, explained very little variance in fishing effort (Table 3). Although lake and year random effects consistently explained around 40% of the variance in fishing effort, marginal r^2 values for hourly and daily fixed effects were very low, indicating that they explained < 5% of the variance in instantaneous fishing effort.

Models fit to extensive data produce similar estimates to mean expansion of intensive data, with some reduction in accuracy and precision.

With the exception of Irving Lake (IV), all models fit to the extensive data produced fishing effort estimates with prediction intervals that overlapped with those produced by mean expansion of intensive data (Figure 2). These models all produced mean estimates of fishing effort within 20% of the value of those produced by mean expansion of intensive data (Table 4). The best performing model for the extensive dataset, which included day of year and weekend fixed effects, produced estimates that were, on average, within 11% of the mean expansion estimate. As expected, when the models were fit to intensive data, they produced estimates of fishing effort that were nearly identical to those produced by mean expansion (Table 4, Figure 2).

On an individual lake basis, the effects on accuracy of increasing model complexity were relatively subtle and depended on lake identity. Fishing effort on Irving Lake (IV), for example, was continuously underestimated by all models fit to extensive data. Estimates for Little Arbor Vitae Lake (LV), however, were quite accurate for simple models but became more negatively biased as more parameters were added. Note the differences in total fishing effort predictions for this lake between Figures 2A and 2D. The addition of aerial survey data tended to marginally improve the mean accuracy of predictions for all lakes. More notably, aerial survey data on average improved the precision of fishing effort estimates as measured by I_{RP} (Table 4). Prediction intervals of model estimates based only on on-site extensive observations tended to be, on average, 7 to 10 times wider than the confidence intervals associated with mean expansion. Adding only 3 aerial observations per lake reduced the average width of estimate prediction intervals by nearly half. This improvement in precision suggests that a moderate number of additional samples could result in a substantial reduction in uncertainty associated with these estimates of fishing effort. An exaggerated version of this change can be seen in the predictions for Oxbow Lake (OB), on which fewer on-site observations were recorded. When three aerial observations were added for this lake, the span of the estimate's prediction interval decreased from a width of 16,147 boat hours to 7,724 boat hours, or over 50% (Figure 2C).

Intensive and extensive datasets were collected on different years, potentially limiting our ability to compare estimates of fishing effort. To investigate the influence of year effects on our estimates, we calculated estimates of total fishing effort for each year surveyed using our best-performing model. Fishing effort estimates varied substantially between years, especially for Little Arbor Vitae and Oxbow lakes (Figure 3). These two lakes had produced the least accurate model-based predictions conditional on a mean year effect, but for each of these lakes, the total

effort prediction produced for one year was substantially closer to the mean expansion estimates. Much of the difference between mean expansion and model-based fishing effort estimates could therefore be a result of the mismatch in years between intensive and extensive sampling.

Model-based predictions of fishing effort on out-of-sample lakes showed mixed performance.

Predicting fishing effort for specific unobserved lakes required adding covariates describing lake characteristics that may influence fishing effort. Adding these lake variables caused marked changes to the model's conditional and marginal r^2 values (Table 5). Although the fixed effects in GLMMs predicting fishing effort from year, seasonal, and daily effects explained only around 5% of the variance in fishing effort, fixed effects in models containing lake variables explained between 20 and 30%. Because these lake variables took over some of the explanatory ability previously held by the random effects, these models could predict at least a portion of the variation in out-of-sample lakes, i.e. lakes without their own random intercept.

The effect size and significance of these lake variables depended on the dataset to which the model was fit (Table 5). Lake area had a significant positive effect on instantaneous fishing effort in models fit to all three datasets. Distance from lake to the nearest secondary road had no significant effect in any models. In the model fit to intensive data, all lake variables with the exception of distance to road and walleye presence have a significant effect on fishing effort. In the model fit to extensive data, however, lake area and walleye presence were the only significant predictors.

The accuracy of the total fishing effort predictions produced during LOGO cross validation were mixed (Figure 4). On average, the model fit to the extensive dataset containing aerial survey data produced estimates of fishing effort within 11% of those produced by mean

expansion (Table 6). However, this small I_{RA} value was largely due to the very high predictions for Black Oak Lake (BK) and the very low predictions for Little Arbor Vitae (LV) offsetting each other. Model-based predictions of fishing effort were similar to the mean expansion estimates for Irving (IV), Birch (BH), Oxbow (OB), and White Birch (WB) lakes. However, this model produced much less accurate predictions for Allequash (AQ), Black Oak, and Little Arbor Vitae lakes. These results could have stemmed from two problems: 1) no lake-specific random intercept was available for the out-of-sample lakes, or 2) the selected lake variables were inconsistent predictors of fishing effort.

To evaluate these two options, the LOGO cross validation process was repeated while retaining the aerial survey observations for the “out-of-sample” lake. This process simulated the scenario of predicting fishing effort based on limited observations as well as lake variable predictors. Retaining these observations, however, did not substantially improve the predictions of total fishing effort (Figure S4). The models fit to the intensive dataset had to be simplified due to an upper limit on computation time. Rather than including both year and daily covariates, the model included only a year random effect, in addition to the lake random effect and lake characteristics that were included in the other models. Out-of-sample predictions of models fit to intensive data tended to reflect those produced by extensive data, with the exception of Irving Lake (IV), where these predictions were much closer to the mean expansion value.

Model-based methods can integrate multiple data sources to predict fishing effort across a fisheries landscape.

By fitting a GLMM to the combined intensive and extensive datasets, we could fit a random intercept to each lake and year surveyed and then predict total summer fishing effort across all lakes for each of the years represented in the datasets. Average hourly fishing effort is

highly heterogeneous across the county (Figure 5A, Table S11). Several lakes stood out as having exceptionally high mean hourly fishing effort. For example, Lac Vieux Desert and Little Saint Germain Lake had 603% and 518% higher effort, respectively, than the mean. In addition, while fishing effort varied by year, no trend in overall fishing effort was evident (Figure 5B). Fishing effort in 1995, however, was very high compared to other years.

Discussion

Extensive data collection from multiple data sources is an effective tool for managers to understand fishing effort dynamics across a fisheries landscape. A model-based approach to analyzing this data allows managers to leverage multiple sources of extensive fishing effort data available within their system. By relying on extensively collected data, managers can estimate total fishing effort for many more fishing sites or water bodies than would be possible under an intensive sampling regimen. Further coverage of fisheries landscapes by spatially extensive approaches could be achieved through supplemental data sources such as aerial surveys, camera traps, and drones. With further understanding of predictors of lake use, out-of-sample estimates of fishing effort can further improve landscape coverage.

Evaluating the success of extensive data collection for model-based estimates

On average within the seven lakes evaluated, a model incorporating the effects of lake identity, year, day of year, and weekends predicted total summer fishing effort estimate values within 11% of the value of those obtained by mean expansion. Because the extensive dataset contained fewer observations per lake, some reduction in accuracy was expected. Further, the intensive and extensive observations took place on different years. We therefore remain encouraged that estimation methods using much less data produced similar results to data-rich mean expansion. Mean differences in accuracy among the seven lakes surveyed intensively and

extensively were primarily driven by a tendency to underestimate fishing effort on Irving and Little Arbor Vitae lakes and to overestimate fishing effort on Oxbow Lake. The underestimation of fishing effort for Irving Lake highlighted an important consideration for the use of extensively collected data. By chance, two out of four of our experimental creel survey shifts at this lake took place during inclement weather. As a result, the mean instantaneous boat counts collected for this site were not representative of typical fishing effort, and these predictions showed no overlap of prediction intervals with those of mean expansion. When fishing effort estimates were based only on aerial survey data, which by necessity took place during fair weather, predictions of a simple GLMM were very similar to those of mean expansion of intensive data (Figure S3). The effects of poor weather could be accounted for in future applications by including a covariate for severe weather effects in the GLMM. Weather conditions did not obviously influence observations on Little Arbor Vitae, but a higher variation in total annual effort for this large, busy lake may have contributed to the reduced accuracy and precision of its model-based total fishing effort estimates.

Oxbow Lake produced fishing effort estimates with extremely wide prediction intervals. Only 6 instantaneous counts of fishing effort (3 on-site, 3 aerial) took place on this lake, less than half the number of observations collected for other lakes, which likely explains the discrepancy in total effort estimates. Although it was only possible to evaluate predictions for a small number of lakes, these examples demonstrate some of the strengths and limitations of our spatially extensive, model-based method. An extensive data collection scheme can produce reasonably accurate estimates of total fishing effort, but lake specific fishery characteristics and chance conditions during the survey will influence the optimal distribution of observations.

Our results highlight the tradeoffs that managers face in designing surveys to estimate lake-specific fishing effort. For landscapes where potential fishing sites are numerous, conducting extensive rather than intensive surveys may allow improved understanding of fishery dynamics across a broader scale. If, for example, an agency is limited to 500 observations for one summer, there are tradeoffs to consider when deciding how many lakes over which to spread those observations. These data could be used to obtain a highly accurate estimate for three lakes by following the traditional mean expansion protocol. In this case, each of the three lakes would be surveyed on 80 days of the summer with 2 instantaneous boat counts on each day (i.e., 3 lakes x 80 days x 2 observations per day = 480 observations). Alternatively, the agency could survey 31 lakes, spending 8 days surveying each one and completing two instantaneous fishing effort counts per day (i.e. 31 lakes x 8 days x 2 observations per day = 496 observations). Based on our results, transitioning from an intensive sampling regime to extensive sampling should result in, on average, a 3x increase in the width of the prediction intervals, but, in this example, a more than order of magnitude increase in the total number of lakes for which effort estimates are available. The acceptability of these tradeoffs in accuracy and precision associated with greater water body coverage will depend on the management priorities for the region in question.

Some limitations exist in our ability to compare our estimates of fishing effort from extensive data collection to traditional mean expansion of intensive data. When evaluating the accuracy of model-based total fishing effort predictions, we compared prediction intervals for an average survey year with the confidence intervals of the expanded mean total effort calculations. There was no way to account for the effect of the year of the intensive survey when calculating indices of relative abundance and precision, and year effects appear to be the reason for much of the difference in total fishing effort estimates. An additional design-related limitation is the

relatively small number of lakes available for comparison of model-based with mean-expansion total effort estimates. Our summary statistics of I_{RA} and I_{RP} generalize the accuracy and precision of estimates within the seven lakes surveyed intensively and extensively, but we have no way of knowing the accuracy and precision of total fishing effort estimates for the other 31 lakes that were extensively surveyed. We can, however, compare our methods and results with those of Askey et al. (2018). Askey et al. (2018) rigorously validated the use of GLMM-based estimates of fishing effort with different sample sizes selected from a large dataset collected by aerial surveys and time-lapse cameras. The smallest sample sizes tested in their article were 10 and 20 observations. Within our limited selection of lakes with extensive and intensive data available, we found similar mean percent inaccuracies for our total effort estimates.

Opportunities for further landscape coverage

Total fishing effort estimates can be improved by integrating supplemental data sources, such as aerial surveys. By including only three additional aerial observations per lake, we substantially improved the accuracy and precision of our estimates. Even without including on-site observations, a small number of aerial observations per lake produced reasonably accurate, if coarse, estimates of total fishing effort (Figure S3). Aerial surveys are ideal for measuring the distribution of fishing effort across many lakes. This method is particularly useful for surveying fisheries with a large spatial extent, such as lake districts (Askey et al., 2018; Hunt et al., 2019; Tredger, 1992), major river systems, (Sindt, 2012) and marine and Great Lakes fisheries (Lockwood and Rakoczy, 2005; Zellmer et al., 2018). Despite its strengths, this method may be too expensive to implement consistently in many fisheries systems and can be limited by severe weather conditions.

Traffic counters and boat launch cameras have also been used to quantify fishing effort and boat traffic (Hunt and Dyck, 2011; Simpson, 2018; van Poorten et al., 2015; van Poorten and Brydle, 2018). These methods can passively collect effort data without the need for creel clerks, but cameras and counters are still expensive and prone to vandalism (van Poorten et al., 2015). The use of drones in fisheries science has been advocated (Kopaska, 2014), and they have been successfully used for identifying derelict or illegal fishing gear (Bloom et al., 2019), counting fish in shallow rivers (Tyler et al., 2018), and monitoring marine protected areas (Miller et al., 2013). Privacy concerns and aviation laws, however, complicate their use in monitoring angling activity for inland fisheries (Duncan, 2016; Lally et al., 2019). Although each of these methods has costs and benefits, they are all potentially fruitful supplemental data sources for model-based estimates of angler effort for different fishery systems.

As we demonstrated, fishing effort data collected through an extensive sampling scheme from multiple sources can be used to understand differences in fishing effort across a broad spatial and temporal scale. Through two years of extensive data collection using on-site and aerial observations, we added coverage of 44 lakes to the combined intensive and extensive fishing effort dataset describing Vilas County. Based on the year effects estimated from 25 years of intensive data, we were able to predict total fishing effort for all lake-year combinations. Although the empirical data does not exist to validate these estimates, this analysis remains a useful demonstration for the potential of extensive data collection and GLMM-based analysis for estimating fishing effort across a lake-rich landscape. Further annual extensive data collection would quickly expand this coverage, as well as allow for the direct comparison of fishing effort between years on a broader scale. These data also have promise for detecting seasonal and daily

patterns in fishing effort, which can assist fisheries managers in choosing optimal times for management interventions.

As we found, however, a granular understanding of shifts in angler effort dynamics requires more data than we collected in our extensive sampling scheme. By allowing partial pooling of observations between lakes using lake random intercepts, some generalizable patterns were observed, but more observations per year may be needed to estimate the magnitude of seasonal and daily effects. Alternatively, different lakes may have different diel and seasonal fishing effort patterns. Although the extensive creel survey included fewer lakes than the intensive survey, a wider variety of lakes were surveyed, including lakes with no walleye population, no boat ramp, and lakes with smaller surface areas. Because of this greater variation in lake characteristics, concurrent differences in diel and seasonal fishing effort patterns may have been washed out to non-significance when the GLMMs were fit. In this case, more intensive data collection with more observations per lake may be required to understand lake-specific seasonal and daily patterns. A hypothetical fisheries manager is therefore left to decide whether their goals are best served by investing their limited resources in extensive data collection over a wider spatial extent or intensive data collection within a limited number of systems.

This question of appropriate tradeoffs could be sidestepped if managers could effectively predict fishing effort for unobserved lakes based on lake characteristics. We attempted to predict unobserved fishing effort using easily obtained data, with mixed results. Model predictions overlapped with mean expansion estimates for five out of the seven lakes tested, but total fishing effort for the other two were substantially over- or underestimated. Lakes associated with inaccurate predictions did not have any obvious characteristics in common that could explain this

discrepancy. These results could be explained by our use of only easily obtained predictor variables, or they could be an indication that lake characteristics are not consistent, linear predictors of lake-specific fishing effort. We chose lake variables that aligned with characteristics found to predict recreational boating density by Hunt et al. (2019), including lake surface area, walleye presence, and indices of human development and accessibility. Differences in sampling frame between our intensive and extensive data collection resulted in differences in parameter values between models fit to different datasets. For example, intensive data collection in Wisconsin takes place only on lakes containing walleye. Because no contrast was available for this parameter, no walleye effect could be tested. In summer, walleye are also almost exclusively available to boat anglers, potentially explaining the presence of a boat ramp effect in the intensive but not the extensive dataset. Distance to secondary road had no effect on instantaneous fishing effort in any dataset. Most likely, this result stems from measuring distance to road from the centroid of each lake. This metric does not account for the location of boat launches, so the nearest secondary road as measured here may still be inconveniently far away from any access points. Potential explanations for the absence of a building density effect in the extensive data are less clear. The lakes surveyed for both datasets had a similar range in building density values (0-70 buildings per km in the intensive data and 0-80 buildings in the extensive data). It is possible that, similar to diel and seasonal patterns, housing density has a different effect on fishing effort for different lakes. Not all lake residents are interested in fishing, and the presence of some building types such as resorts may be a better predictor of resident fishing effort than the presence of family homes.

Indicators of fishing quality such as angler catch rates or fish population estimates, rather than indirect measurements of accessibility, may improve the predictive ability of these models,

but these data are labor-intensive to produce and therefore did not exist for every lake in our extensive dataset. By applying model-based fishing effort predictions over every lake-year combination in the combined intensive and extensive datasets, we identified a handful of extremely high fishing effort lakes, which allowed us to explore potential commonalities between them. The primary characteristic these lakes had in common was their surface area; the lakes with highest mean fishing effort ranged from 350 to over 1600 ha in surface area (Table S11). In contrast, no obvious correlation was found between fishing effort and population abundance or catch rates of popular target species. However, very high fishing effort lakes all tended to have moderate, rather than high or low, catch rates for panfish and muskellunge (Figures A5-A8). Most likely, predicting fishing effort based on lake characteristics would require accounting for nonlinear responses and interactions of lake characteristics, potentially using nonparametric methods such as random forests (e.g. van Poorten et al, 2013). Although out-of-sample predictions of fishing effort were not consistently accurate, we argue that extensive data collection for GLMM-based estimates of total fishing effort is a promising approach for understanding effort dynamics in highly distributed and/or data poor fisheries.

Applications to fisheries management

Our modeling approach proved effective for predicting angler effort across a fisheries landscape; however, other metrics derived from traditional angler intercept surveys, such as angler catch rates and estimates of total catch, are also important for fisheries management. That said, our approach could compliment existing efforts to address these important, additional aspects of fisheries. For example, recent research by Embke et al., (2020) used GLMMs to produce recreational harvest estimates for 267 lakes that were surveyed intensively as well as all unobserved inland lakes across Wisconsin based on abiotic variables and an angler access metric.

Coarse estimates of fishing effort based on spatially extensive observations could further refine harvest estimates on these otherwise unobserved lakes. Additional catch and harvest data can also be collected during spatially extensive sampling of fishing effort through angler intercept interviews (Iwicki et al., in prep). Perhaps most importantly, the different levels of variability associated with fishing effort and harvest estimates based on extensively collected data can identify lakes of greater uncertainty where additional sampling resources should be directed. For example, high-effort and high-variance lakes such as Little Arbor Vitae likely need to be allocated more sampling effort than lakes such as White Birch (Fig. 3).

In addition to its applicability to data-poor fisheries, a model-based approach to generating fishing effort estimates from fewer observations at more fishing sites could be a practical tool for managers who want to implement ecosystem-based management strategies that can respond to fast and slow changes across a fisheries landscape (*sensu* Walker et al., 2012). A transition from a one-size-fits-all management policy to a more diverse set of policies may contribute to a more persistent and resilient fisheries system (Carpenter and Brock, 2004; van Poorten and Camp, 2019). These policies would ideally be dynamic across space and time, which requires faster feedback from data collection describing how interventions have affected fishing effort, catch, and harvest. Although implementing highly dynamic and lake-specific policies is probably an unrealistic goal in lake-rich fisheries, tailored management of different categories of lakes may simultaneously improve system resilience and angler satisfaction by accommodating the preferences of heterogeneous groups of anglers. Strategic collection of fishing effort data over many lakes may therefore be an effective bridge between one-size-fits all policy and model-based implementation of diverse and dynamic policies.

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Tables

Table 1: Characteristics of the three datasets we evaluated when estimating lake-specific total fishing effort.

	Intensive dataset	Extensive dataset	Extensive dataset with aerial surveys
Sampling methods	On-site observations	On-site observations	On-site observations Aerial surveys
Number of years surveyed	25	2	2
Number of lakes surveyed	65	38	44
Mean number of lakes surveyed per year (SD)	4.9 (2.6)	21 (7.1)	29.5 (19.1)

Table 2: AIC values for each model fit to each dataset. Each model contains its listed predictors as well as all predictors listed for the models above it. Values for Δ AIC are the difference between that model's AIC and that of the model containing only a random lake effect. The best fit model for all datasets is in bold.

Model	Intensive data		On-site extensive data		On-site and aerial survey extensive data	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
(1 Lake)	90206		1360.1		1725.8	
+ Year	89883	-323	1350.2	-9.9	1713.3	-12.5
+ Day of year	88766	-1440	1346.6	-13.5	1708.5	-17.3
+ Day of year ²						
+ Weekend						
+ Hour of day	87948	-2258	1338.9	-21.2	1700.0	-25.8
+ Hour of day²						

Table 3: Marginal and conditional r^2 values for each model fit to each dataset. Each model contains its listed predictors as well as all predictors listed for the models above it.

Model	Intensive data		On-site extensive data		On-site and aerial extensive data	
	Marginal r^2	Conditional r^2	Marginal r^2	Conditional r^2	Marginal r^2	Conditional r^2
(1 Lake)		0.36		0.38		0.39
+ Year		0.39	0.035	0.46	0.021	0.43
+ Day of year	0.023	0.43	0.047	0.50	0.031	0.45
+ Day of year ²						
+ Weekend	0.044	0.46	0.065	0.52	0.044	0.46
+ Hour of day						
+ Hour of day ²						

Table 4: Mean indices of accuracy and precision for model-based estimates of total summer fishing boat hours relative to mean expansion estimates. (N=7) Each model contains its listed predictors as well as all predictors listed for the models above it.

Model	Intensive data		On-site extensive data		On-site and aerial extensive data	
	Mean I_{RA} (SD)	Mean I_{RP} (SD)	Mean I_{RA} (SD)	Mean I_{RP} (SD)	Mean I_{RA} (SD)	Mean I_{RP} (SD)
(1 Lake)	8.06 (6.48)	73.95 (5.51)	-5.50 (43.68)	-48.82 (61.24)	1.93 (42.57)	-7.67 (25.70)
+ Year	4.80 (12.03)	67.27 (7.44)	18.28 (58.46)	-51.57 (63.67)	11.98 (48.60)	-9.15 (25.46)
+ Day of year	-0.91 (11.73)	67.67 (7.24)	-8.13 (51.55)	-72.46 (67.02)	-10.86 (39.35)	-23.25 (24.22)
+ Weekend	-4.58 (12.35)	69.79 (8.93)	-11.31 (46.68)	-74.82 (61.75)	-13.71 (36.11)	-26.86 (24.88)
+ Hour of day						
+ Hour of day ²						

Table 5: Parameters of a GLMM predicting fishing effort from seasonality and lake variables as fit to each dataset. Parameters with significant effects are in bold.

Model parameters	Intensive data		On-site extensive data		On-site and aerial extensive data	
	Coefficient (SE)	P value	Coefficient (SE)	P value	Coefficient (SE)	P value
<i>Intercept</i>	-0.66 (0.55)	0.23	-1.51 (0.39)	0.0001	-1.35 (0.31)	<0.0001
<i>Lake area (ha)</i>	0.56 (0.12)	<0.0001	0.47 (0.13)	0.0002	0.50 (0.10)	<0.0001
<i>Building density</i>	0.25 (0.10)	0.01	0.09 (0.13)	0.50	0.06 (0.10)	0.55
<i>Boat ramp present</i>	0.71 (0.22)	0.001	0.14 (0.42)	0.74	0.19 (0.33)	0.56
<i>Walleye present</i>	0.72 (0.54)	0.18	1.40 (0.34)	<0.0001	1.23 (0.26)	<0.0001
<i>Distance to road</i>	-0.02 (0.09)	0.78	-0.06 (0.11)	0.61	-0.10 (0.09)	0.25
<i>Year 2018</i>			-0.25 (0.09)	0.006	-0.21 (0.06)	0.0009
<i>Day of year</i>	1.21 (0.09)	<0.0001	1.06 (0.78)	0.17	0.75 (0.58)	0.27
<i>Day of year²</i>	-1.22 (0.09)	<0.0001	-1.13 (0.77)	0.14	-0.85 (0.67)	0.21
<i>Weekend</i>	0.47 (0.01)	<0.0001	0.21 (0.11)	0.05	0.18 (0.09)	0.04
Marginal r^2		0.23		0.26		0.28
Conditional r^2		0.43		0.34		0.35

Table 6: Mean indices of relative accuracy and precision of out-of-sample model predictions relative to mean expansion estimates of intensive data. (N=7)

Model	Intensive data		On-site extensive data		On-site and aerial extensive data	
	Mean I_{RA} (SD)	Mean I_{RP} (SD)	Mean I_{RA} (SD)	Mean I_{RP} (SD)	Mean I_{RA} (SD)	Mean I_{RP} (SD)
(1 Lake) + Year	-26.17	987.31	-16.16	42.28	-10.66	88.11
+ Day of year	(76.46)	(400.09)	(64.71)	(63.90)	(58.99)	(76.00)
+ Day of year ²						
+ Weekend						
+ Lake area						
+ Building density						
+ Boat ramp						
+ Walleye presence						
+ Distance to road						

Figures

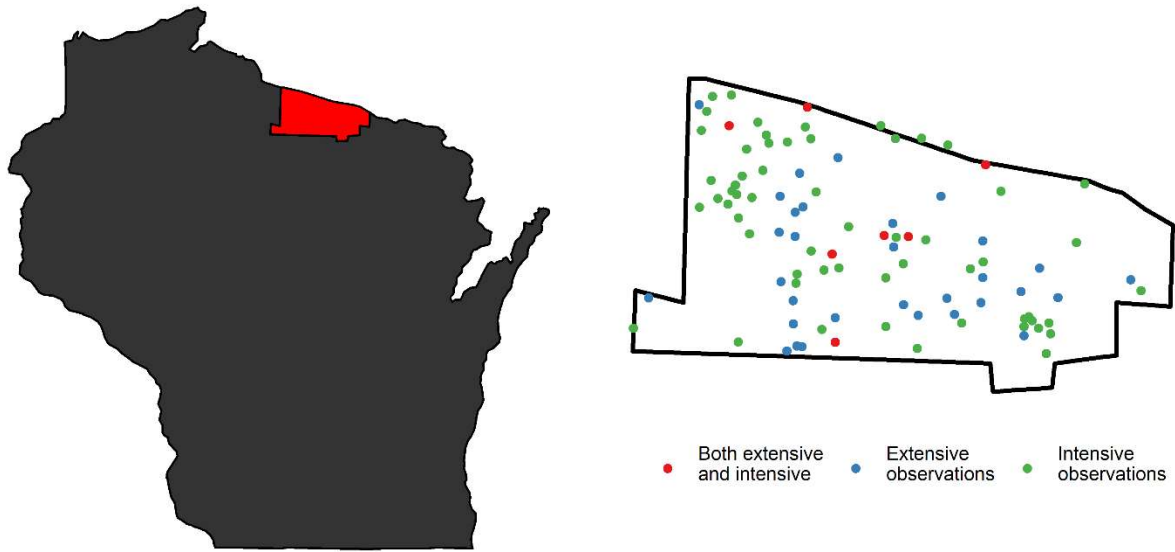


Figure 1: Map of Vilas County, WI showing location of lakes intensively surveyed by WDNR (green), extensively surveyed by our experimental creel survey (blue), and surveyed by both (red).

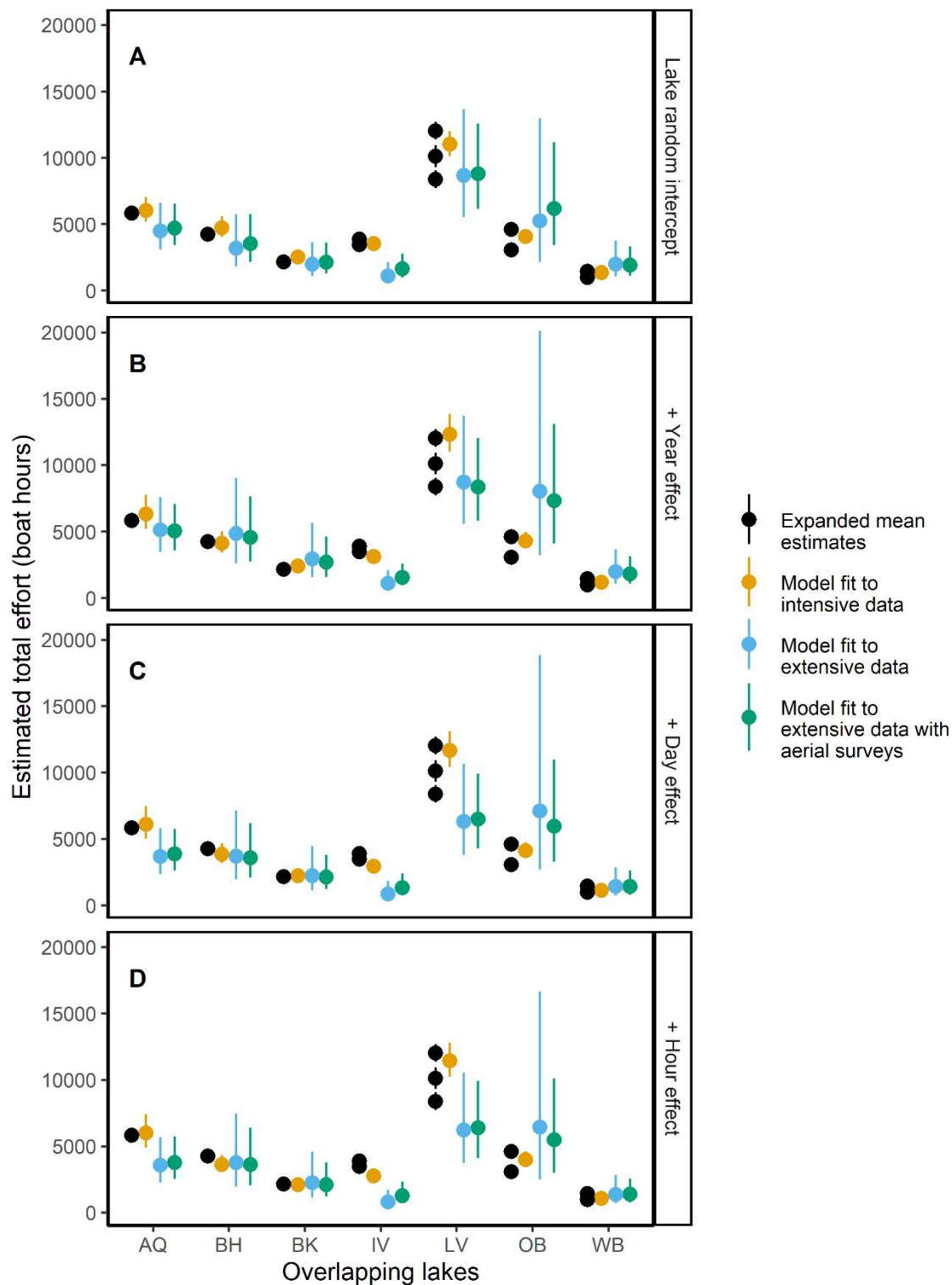


Figure 2: Comparison of total summer fishing effort estimates between mean expansion (black), and area under the curve of GLMM predictions fit to extensive data (colors). Parameters added to each model are indicated by the labels on the right. Points are mean estimates, and bars show 95% prediction intervals. Lakes that were intensively surveyed multiple years by the WDNR have multiple estimates depicted along with their 95% prediction intervals.

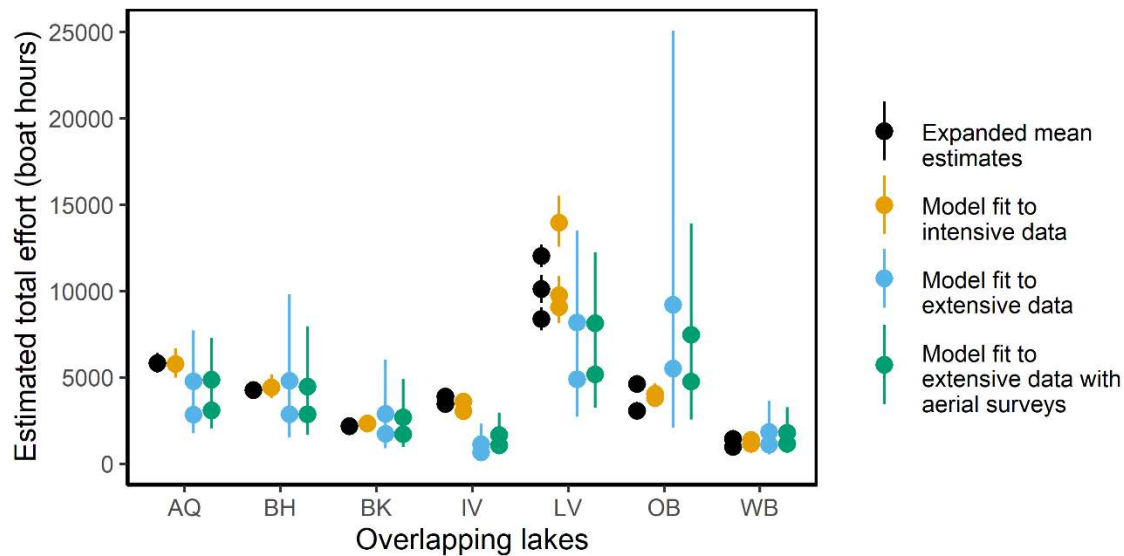


Figure 3: Total summer fishing effort estimates from mean expansion (black) and GLMM predictions incorporating lake, year, day of year, and weekend effects (colors) for every year the lake was surveyed. GLMM predictions from extensive data were always produced for the summers of 2018 and 2019, and mean-expansion estimates and GLMM predictions from intensive data are depicted for the years intensively surveyed. Points are mean estimates for each year observed by the dataset, and bars show 95% prediction intervals.

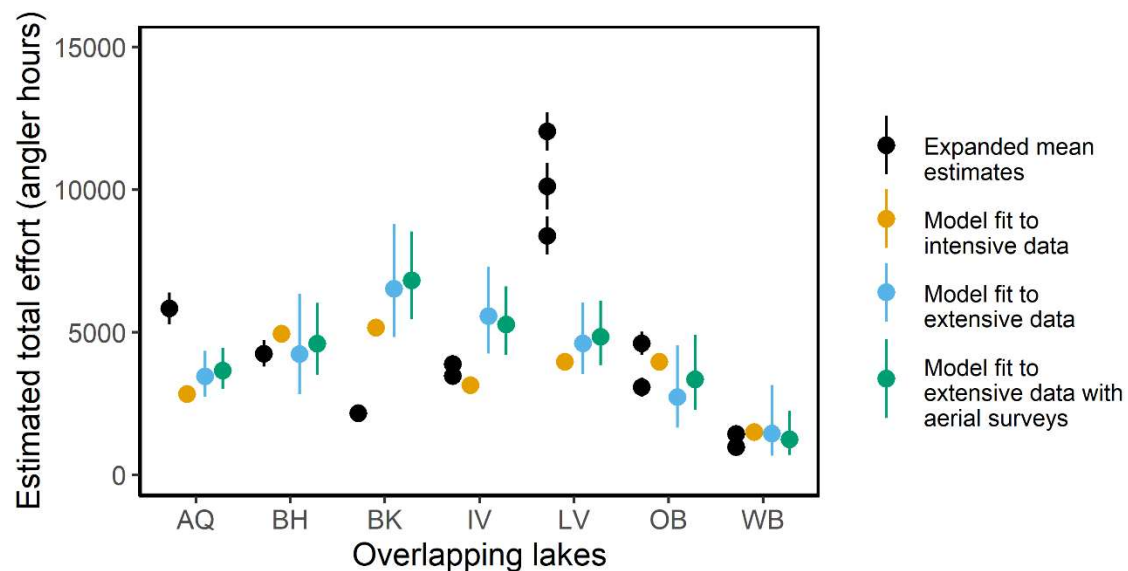


Figure 4: Out-of-sample total summer fishing effort predictions for lakes that were surveyed both extensively and intensively. Lakes that were intensively surveyed multiple years by the WDNR have multiple estimates depicted along with their 95% prediction intervals. Estimates were predicted based on lake characteristics, seasonality, and the grand mean random lake intercept through LOGO cross validation.

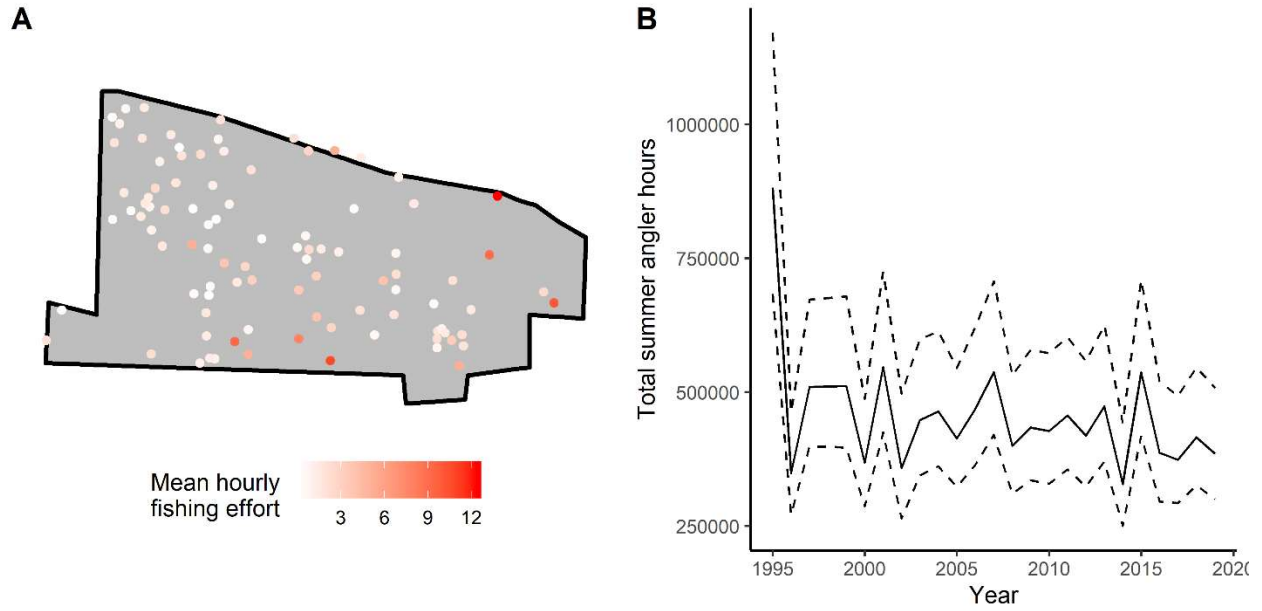


Figure 5: Lake-specific values of the random intercept for each of the 100 lakes surveyed either intensively or extensively in Vilas County, WI (A), and a time series of total annual summer fishing effort across each of these lakes for every year of observations (B).

Supplementary materials

Table S1: Summary of the observations collected intensively and extensively in Vilas county, WI. Standard deviation given in parentheses.

	Intensive dataset	Extensive dataset	Extensive dataset with aerial surveys
Number of lakes surveyed	65	38	44
Number of years surveyed	25	2	2
Mean number of observations per lake	337 (252)	12.4 (4.06)	13.3 (5.8)
Mean number of observations per year	374 (479)	235 (84.9)	294 (168)
Mean number of lakes per year	4.9 (2.6)	21 (7.1)	29.5 (19.1)
Mean number of observations per lake per year	182 (67.5)	11.2 (1.93)	10.5 (4.7)

Table S2: Years surveyed and number of observations for lakes surveyed by both intensively and extensively. Oxbow Lake only received 1 on-site visit (3 instantaneous counts) in 2018 for administrative reasons.

Lake name	Water body identification code (WBIC)	Lake ID	Years surveyed intensively	Number of instantaneous boat counts	Years surveyed extensively	Number of instantaneous boat counts (on-site and/or aerial)
Birch Lake	2311100	BH	1997	170	2018 2019	10 2
Oxbow Lake	2954800	OB	2008 2018	174 170	2018 2019	3 3
Allequash Lake	2332400	AQ	2010	176	2018 2019	10 14
Black Oak Lake	1630100	BK	2011	168	2018 2019	12 3
Irving Lake	2340900	IV	2001 2011	169 168	2019	17
Little Arbor Vitae Lake	1545300	LV	1996 2007 2017	172 170 168	2019	14
White Birch Lake	2340500	WB	2001 2011	170 168	2019	14

A1: Lake selection process

Lakes were selected as part of a larger, multi-objective study of lakes in this region. Initially, fifty lakes were randomly selected from all Vilas County lakes, 35 of which had lake associations, and 15 with no lake associations. All lakes fulfilled the following criteria based on WIDNR data:

- Lakes located completely within Vilas county, not crossing any county or state boundaries
- Have a public launch
- Contain largemouth bass
- Not directly connected to other lakes, so limited connectivity for fish and anglers (No “chained” lakes)
- Surface area less than 500 acres

Distributions of chemical, biological, and morphometric variables across lakes were visually checked using histograms comparing distributions of selected lakes with those of all Vilas county lakes.

Feedback from team members was solicited, and their suggestions were incorporated into an updated lake list based on availability of new data and consideration of logistical constraints.

All prior filtering criteria were retained, the maximum lake size was increased to 618 acres (250 hectares) to accommodate the largest sized lakes we could effectively electrofish.

The list of selected lakes was sent to colleagues affiliated with the WIDNR for consideration of a Scientific Collectors Permit. They provided feedback on this list indicating areas for revision.

Potentially problematic lakes were labeled for the following reasons:

- All smallmouth rather than largemouth bass

- No history of largemouth bass catches in creel data
- Extremely low fish populations
- Difficult to access by shock boat
- Connectivity to other lakes allowing movement of fish and anglers
- Negative encounters with residents

Because of this feedback, 19 lakes were removed from the previous selection. These lakes were replaced with lakes suggested by WIDNR colleagues. The final lake list therefore contained 22 lakes that were randomly selected and 19 lakes suggested as replacements because of their largemouth bass populations,

Note: Low density largemouth bass lakes were retained to achieve a continuum of bass densities and to retain representative low-bass lakes.

A2. Model validation

We needed to establish that, given the same intensive dataset, a generalized linear model-based estimate of total fishing effort is functionally equivalent to an expanded mean estimate. We therefore first compared the total summer fishing effort estimates derived from mean expansion to estimates of total summer fishing effort predicted by negative binomial generalized linear models (GLMs) fit separately to each lake year.

An equivalent model-based estimation approach to mean expansion was developed by fitting a negative binomial generalized linear model (GLM) separately to each lake year of intensive count data with the following parameterization:

$$\begin{aligned} \text{Count} \sim & \text{June} + \text{July} + \text{August} + \text{Weekend} + \text{June} * \text{Weekend} + \text{July} * \text{Weekend} \\ & + \text{August} * \text{Weekend} \end{aligned}$$

Instantaneous fishing effort was predicted by dummy variables categorizing the day as belonging to month and weekday strata, as in the mean expansion protocol. By including interaction effects between month and weekend, different weekend effects were estimated for each month. To estimate total summer fishing effort, counts of fishing effort were then predicted for each daylight hour between May 1 and August 31. By calculating the area under the curves of the predictions using the trapezoidal rule, we could then estimate total boat hours for the summer on a particular lake and year as well as upper and lower 95% prediction intervals. Because both sets of estimates were based on the same data and predictors, and because effort on all lakes was estimated separately, total summer fishing effort should be comparable as estimated by both methods.

A more efficient modeling approach may instead fit a quadratic effect of day of year and hour of day to estimate seasonal and daily changes in fishing effort. It would use fewer degrees of freedom than monthly dummy variables and would therefore be a more effective approach to modeling fishing effort using extensive data. Therefore, we additionally fit a negative binomial GLM to each lake year of intensive data with the following form:

$$Count \sim Day\ of\ year + Day\ of\ year^2 + Weekend + Hour\ of\ day + Hour\ of\ day^2$$

Each of these model-based estimates were compared to expanded mean estimates by calculating an index of relative accuracy (I_{RA}) and an index of relative precision (I_{RP}).

When fit to intensively sampled observations, model-based approaches produced very similar results to the standard approach of mean expansion. Negative binomial GLMs were fit to each lake-year of intensive observations, and the area under the curve of the predictions successfully matched the stratified mean total estimates for summer fishing effort (Figure S2). As expected, the model parameterization that more closely matched the stratification of the mean

expansion protocol generated nearly identical estimates (Figure S2A). When the monthly dummy variables were replaced by a quadratic effects of day of year and hour of day, some minor deviations from the mean expansion estimates were evident (Figure S2B). For the seven lakes that were surveyed both intensively and extensively, all estimates of total summer fishing effort were effectively the same, with some differences in the width of their confidence intervals (Figure S3).

Model-based estimates of total fishing effort that included month effects of a dummy variable produced estimates that were equally as accurate and precise relative to the expanded mean estimates (Table S3). When models instead included a quadratic effect of day of year, estimates of total effort tended to be lower but more precise than those produced by mean expansion (Table S4).

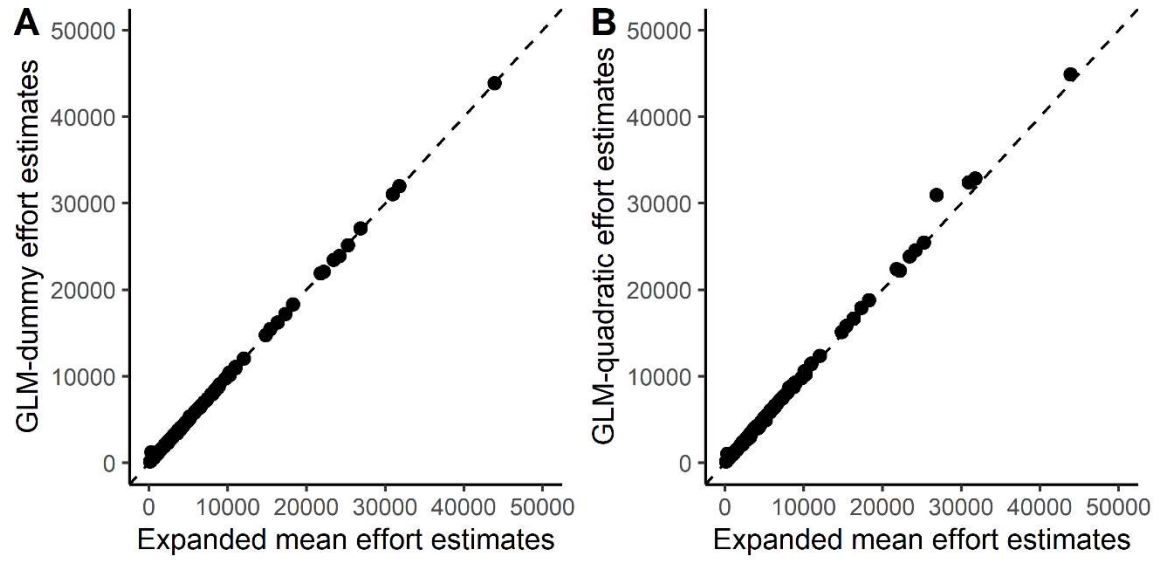


Figure S1: Comparison of model-based estimates of total fishing effort with WIDNR stratified mean estimates for all lake years.

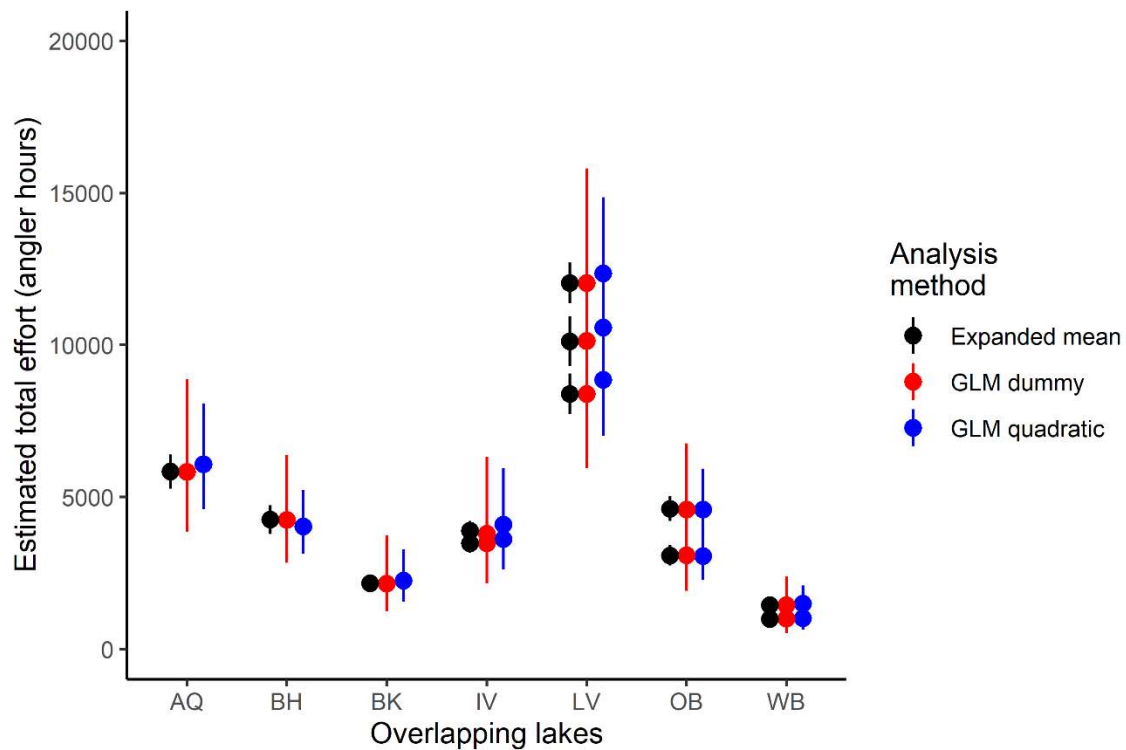


Figure S2: Comparison of total estimated fishing effort and 95% confidence intervals for expanded mean estimates and for two functional forms of a GLM. Lakes that were surveyed multiple years by the WIDNR have multiple estimates depicted along with their 95% confidence intervals. Confidence intervals are wider for GLM estimates, even though they used the same data as the expanded mean estimates. Including the quadratic effect somewhat reduces the width of the GLM confidence intervals.

Table S3: Indices of relative accuracy (I_{RA}) and precision (I_{RP}) for GLM predictions of total summer fishing boat hours day effects relative to expanded mean estimates.

Lake year	Expanded mean total estimate (SD)	GLM prediction (SE)	I_{RA} of GLM prediction	I_{RP} of GLM prediction
AQ 2010	5830.1 (284.5)	5828.8 (1551.5)	-0.02	-81.6667
BH 1997	4253.2 (239.8)	4247.6 (1089.5)	-0.13	-78.0189
BK 2011	2163.5 (111.1)	2142.5 (816.5)	-0.98	-86.5234
IV 2001	3886.6 (163.7)	3783.7 (1294.4)	-2.72	-87.6843
IV 2011	3470.4 (160.2)	3474.3 (1094.4)	0.11	-85.3432
LV 1996	12035.2 (340.0)	12032.5 (1926.1)	-0.02	-82.3508
LV 2007	8383.6 (341.3)	8389.5 (1777.8)	0.07	-80.7875
LV 2017	10118.0 (417.6)	10129.9 (2200.6)	0.12	-80.9993
OB 2008	4610.6 (208.5)	4585.8 (1107.6)	-0.54	-81.2776
OB 2018	3073.9 (169.7)	3077.5 (965.0)	0.12	-82.3964
WB 2001	1439.2 (76.5)	1439.8 (476.0)	0.05	-83.922
WB 2011	981.6 (80.4)	996.6 (513.0)	1.50	-84.0815

Table S4: Indices of relative accuracy (I_{RA}) and precision (I_{RP}) for GLM predictions of total summer fishing boat hours with quadratic day and hour of day effects relative to expanded mean estimates.

Lake year	Expanded mean total estimate (SD)	GLM quadratic prediction (SE)	I_{RA} of GLM quadratic prediction	I_{RP} of GLM quadratic prediction
AQ 2010	5830.1 (284.5)	6078.2 (1013.9)	4.08	-70.75
BH 1997	4253.2 (239.8)	4034.2 (601.2)	-5.43	-62.16
BK 2011	2163.5 (111.1)	2250.7 (523.3)	3.88	-77.91
IV 2001	3886.6 (163.7)	4088.6 (946.6)	4.94	-81.80
IV 2011	3470.4 (160.2)	3611.3 (708.7)	3.90	-76.47
LV 1996		12351.6		
	12035.2 (340.0)	(1275.7)	2.56	-72.65
LV 2007	8383.6 (341.3)	8852.3 (1208.4)	5.29	-70.18
LV 2017		10568.6		
	10118.0 (417.6)	(1439.5)	4.26	-69.70
OB 2008	4610.6 (208.5)	4591.0 (679.7)	-0.43	-69.46
OB 2018	3073.9 (169.7)	3054.0 (546.7)	-0.65	-69.16
WB 2001	1439.2 (76.5)	1489.4 (304.0)	3.37	-73.96
WB 2011	981.6 (80.4)	1006.9 (316.7)	2.51	-73.94
		Mean (SD)	2.36 (3.09)	-72.35 (5.04)
		Mean (SD)	0.02 (0.004)	-82.9 (2.71)

Table S5: Goodness-of-fit diagnostics for models fit to intensive fishing effort count data as additional parameters are added. Values of ΔAIC for alternate specifications for time of day are the difference between that model's AIC and that of model 3. The best-fit model is in bold.

	Predictors	AIC	ΔAIC	BIC	logLik	Deviance	df	Marginal r^2	Conditional r^2
1	(1 Lake)	90206		90230	-45100	90200	21873		0.36
2	+ (1 Year)	89883	-323	89914	-44937	89875	21872		0.39
3	+ <i>Day of year</i> + <i>Day of year</i> ² + <i>Weekend</i>	88766	-1440	88822	-44376	88752	21869	0.023	0.43
Alternate specifications for time of day:									
4	+ <i>Hours to</i> <i>/from dark</i> + <i>Hours to</i> <i>/from dark</i> ² + <i>Morning</i>	88393	-1813	88473	-44186	88373	21866	0.032	0.45
5	+ <i>Hours to</i> <i>/from dark</i> + <i>Morning</i>	88399	-1807	88471	-44190	88381	21867	0.032	0.45
6	+ <i>Hour of day</i> + <i>Hour of day</i> ²	87948	-2258	88020	-43965	87930	21867	0.044	0.46

Table S6: Goodness-of-fit diagnostics for models fit to extensive fishing effort count data. Values of Δ AIC for alternate specifications for time of day are the difference between that model's AIC and that of model 3. The best-fit model is in bold.

Model	Predictors	AIC	Δ AIC	BIC	logLik	deviance	df	Marginal r^2	Conditional r^2
1	(1 Lake)	1360.1		1372.5	-677.0	1354.1	467		0.38
2	+ year 2018	1350.2	-9.9	1366.8	-671.1	1342.2	466	0.035	0.46
3	+ Day of year + Day of year ² + Weekend	1346.6	-13.5	1375.7	-666.3	1332.6	463	0.047	0.50
Alternate specifications for time of day:									
4	+ Hours to /from dark + Hours to /from dark ² + Morning	1345.5	-14.6	1387.0	-662.8	1325.5	460	0.055	0.50
5	+ Hours to /from dark + Morning	1344.3	-15.8	1381.7	-663.2	1326.3	461	0.055	0.50
6	+ Hour of day + Hour of day ⁱ	1338.9	-21.2	1376.3	-660.4	1320.9	461	0.065	0.52

Table S7: Goodness-of-fit diagnostics for models fit to extensive creel and aerial survey effort count data. Values for Δ AIC for alternate specifications of time of day are the difference between that model's AIC and that of model 3. The best-fit model is in bold.

Model	Predictors	AIC	Δ AIC	BIC	logLik	deviance	df	Marginal r^2	Conditional r^2
1	(1 Lake)	1725.8		1739.0	-859.9	1719.8	588		0.39
2	+ year 2018	1713.3	-12.5	1730.9	-852.7	1705.3	587	0.021	0.43
3	+ Day of year + Day of year ² + Weekend	1708.5	-17.3	1739.2	-847.3	1694.5	584	0.031	0.45
Alternate specifications for time of day:									
4	+ Hours to /from dark + Hours to /from dark ² + Morning	1708.9	-16.9	1752.7	-844.4	1688.9	581	0.038	0.45
5	+ Hours to /from dark + Morning	1707.0	-18.8	1746.5	-844.5	1689.0	582	0.037	0.45
6	+ Hour of day + Hour of day	1700.0	-25.8	1739.4	-841	1682.0	582	0.044	0.46

Table S8: Parameter estimates for the best-fit model to intensive fishing effort count data.

Model	Random effects	Variance of random intercept (SD)	Fixed effects	Fixed effect coefficients (SE)	Z value	P value
(1 <i>Lake</i>)	<i>Lake</i>	1.06 (1.03)	<i>Intercept</i>	0.43 (0.14)	3.11	0.0019*
+ (1 <i>year</i>)	<i>Year</i>	0.065 (0.25)	<i>Day of year</i>	1.25 (0.086)	14.44	<0.0001*
+ <i>Day of year</i> ²			<i>Day of year</i> ²	-1.25 (0.086)	-14.48	<0.0001*
+ <i>Weekend</i>						
+ <i>Hour of day</i>			<i>Hour of day</i>	1.42 (0.05)	26.75	<0.0001*
+ <i>Hour of day</i> ²			<i>Hour of day</i> ²	-1.31 (0.052)	-24.94	<0.0001*
			<i>Weekend or holiday</i>	0.48 (0.015)	32.63	<0.0001*

Table S9: Parameter estimates for the best-fit model to extensive fishing effort count data.

Model	Random effects	Variance of random intercept (SD)	Fixed effects	Fixed effect coefficients (SE)	Z value	P value
(1 <i>Lake</i>)	<i>Lake</i>	1.271	<i>Intercept</i>	-0.41 (0.21)	-1.99	0.047*
+ <i>year</i> 2018		(1.127)				
+ <i>Day of year</i>			<i>Day of year</i>	1.24 (0.78)	1.58	0.11
+ <i>Day of year</i> ²			<i>Day of year</i> ²	-1.32 (0.77)	-1.71	0.087
+ <i>Weekend</i>						
+ <i>Hour of day</i>			<i>Hour of day</i>	0.55 (0.37)	1.50	0.13
+ <i>Hour of day</i> ²			<i>Hour of day</i> ²	-0.37 (0.36)	-1.04	0.30
			<i>Year</i> 2018	-0.36 (0.10)	-3.74	0.0002*
			<i>Weekend or holiday</i>	0.27 (0.11)	2.52	0.012*

Table S10: Parameter estimates for best-fit model to extensive creel and aerial survey fishing effort count data.

Model	Random effects	Variance of random intercept (SD)	Fixed effects	Fixed effect coefficients (SE)	Z value	P value
(1 Lake)	Lake	0.98	Intercept	-0.31 (0.17)	-1.80	0.072
+ year 2018		(0.98)				
+ Day of year			Day of year	0.74 (0.69)	1.07	0.28
+ Day of year ²			Day of year ²	-0.86 (0.68)	-1.26	0.21
+ Weekend						
+ Hour of day						
+ Hour of day ²			Hour of day	0.48 (0.31)	1.52	0.13
			Hour of day ²	-0.32 (0.31)	-1.06	0.29
			Year 2018	-0.26 (0.07)	-3.91	<0.0001*
			Weekend or holiday	0.20	2.217	0.027*
				(0.088)		

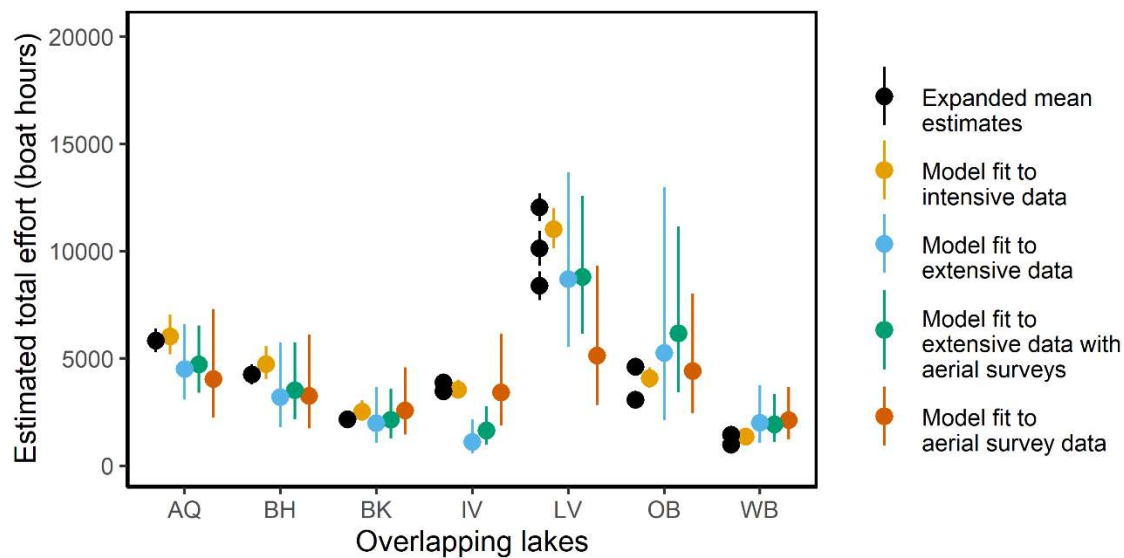


Figure S3: Comparison of total summer fishing effort estimates between traditional mean expansion of intensive data (black), and GLMM-based estimates (colors). Lakes that were intensively surveyed multiple years by the WDNR have multiple estimates depicted along with their 95% confidence intervals. Each dataset was fit to a simple GLMM containing only a lake-specific random intercept. Aerial survey data alone produced similar fishing effort estimates as larger datasets.

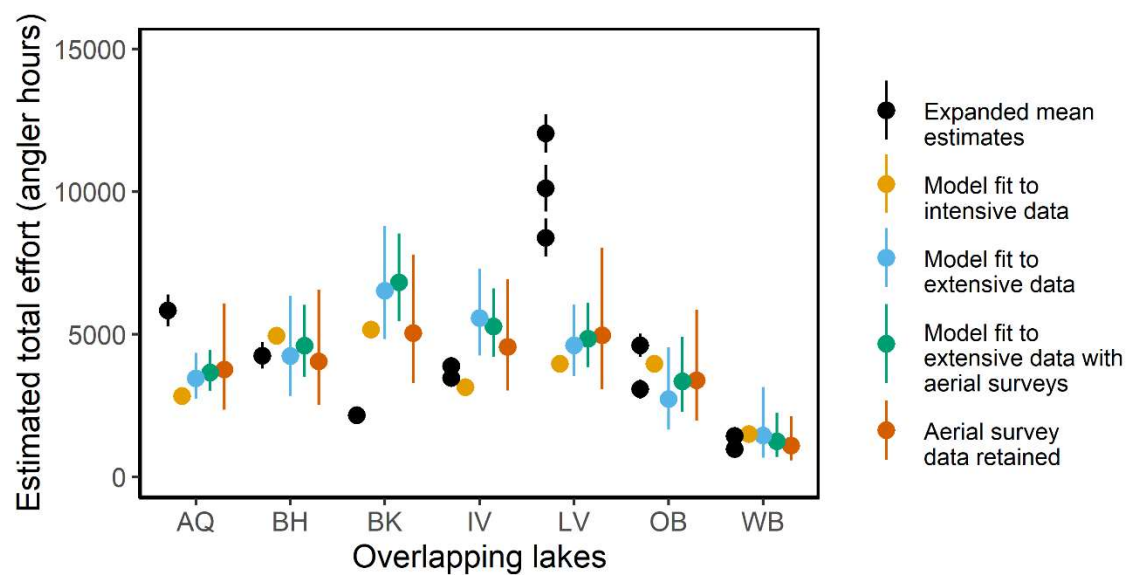


Figure S4: Total fishing effort estimates for out-of-sample lakes obtained by LOGO cross validation. Fishing effort estimates labeled “Aerial survey data retained” were obtained by leaving out on-site observations from the model fit but retaining three aerial survey observations.

Table S11: Random intercept values for all lake year combinations from a GLMM fit to the combined intensive and extensive datasets.

Lake name	WBIC	Random intercept: Mean hourly fishing effort	Surface area (hectares)	Years surveyed
Lac Vieux Desert	1631900	12.36316	1626.885	2013, 2006
Little Saint Germain Lake	1596300	10.61531	393.66	1997, 2015
Kentuck Lake	716800	10.05069	405.405	1998
Big Arbor Vitae Lake	1545600	9.223575	433.35	2008, 1998, 2005, 2011, 2014, 2017
Twin Lakes	1623800	8.957309	1162.755	2007, 1996, 2017
Big Saint Germain Lake	1591100	7.693141	656.91	2011
Catfish Lake	1603700	5.212021	396.09	2000, 2013
Upper Gresham Lake	2330800	5.078966	146.61	2019, 2015
Big Lake	2963800	5.056214	315.9	2008
Little Arbor Vitae Lake	1545300	5.03757	194.4	2019, 2015, 1996, 2007, 2017
Upper Buckatabon Lake	1621800	4.004153	199.665	2010
Lost Lake	1593400	3.95955	218.295	2019, 2015
Trout Lake	2331600	3.804271	1564.92	2001, 2004, 2007, 2010, 2013, 2016, 2019
Plum Lake	1592400	3.498538	428.085	1995, 2003, 2006, 2009, 2012, 2015, 2018
Eagle Lake	1600200	3.280705	232.875	2000, 2013
Star Lake	1593100	3.073703	493.695	1997, 2005
Big Muskellunge Lake	1835300	3.013383	363.285	1996
Palmer Lake	2962900	2.740117	260.82	2019, 2009
Found Lake	1593800	2.629966	136.08	2018, 2019, 2015
Allequash Lake	2332400	2.565629	164.43	2018, 2019, 2015, 2010
Spectacle Lake	717400	2.544978	67.23	2019, 2015
Clear Lake	2329000	2.415536	208.575	1999, 2004
Ballard Lake	2340700	2.318722	203.715	2019, 2015, 2001, 2011

Crab Lake	2953500	2.209385	368.145	2000, 2002
Gunlock Lake	1539700	2.20889	106.92	2002
Lower Buckatabon Lake	1621000	2.201147	153.09	2010
Island Lake	2334400	2.161185	350.325	1999, 2004
Scattering Rice Lake	1600300	2.145238	106.515	2000, 2013
Yellow Birch Lake	1599600	2.097776	77.76	2000, 2013
Pioneer Lake	1623400	2.026316	173.745	2019, 2015
Tenderfoot Lake	2962400	1.952217	183.465	2009
South Turtle Lake	2310200	1.905668	188.73	2010
Wildcat Lake	2336800	1.901813	118.665	2018, 2019, 2015
Oxbow Lake	2954800	1.863795	211.815	2018, 2019, 2015, 2008
Pickeral Lake	1619700	1.854283	109.35	2019, 2015
Boot Lake	1619100	1.828323	115.83	2019, 2015
Van Vliet Lake	2956800	1.821236	93.15	2015, 2012
Voyageur Lake	1603400	1.813109	57.915	2013
Amik Lake	2268600	1.799903	57.105	1998, 2005, 2018
Duck Lake	1599900	1.724904	42.93	2000, 2013
Muskellunge Lake	1595600	1.70102	116.235	2018, 2019, 2015
Anvil Lake	968800	1.649552	152.685	2019, 2015
Big Lake	2334700	1.631623	334.935	1995
Birch Lake	2311100	1.620301	204.93	2018, 2019, 2015, 1997
Little Spider Lake	1540400	1.551719	90.315	2018, 2019, 2015
Little John Lake	2332300	1.477845	61.155	2019
Wild Rice Lake	2329800	1.472612	155.52	1999, 2004
Rest Lake	2327500	1.471456	265.275	1999, 2004
Stone Lake	2328800	1.435453	55.89	2004, 1999
Big Portage Lake	1629500	1.407541	237.33	2006
Deerskin Lake	1601300	1.401943	121.905	2019, 2015
Manitowish Lake	2329400	1.386719	200.88	2016, 1999, 2004
Otter Lake	1600100	1.365467	70.47	2000, 2013
Harris Lake	2958500	1.312162	216.27	1997, 2019
Towanda Lake	1022900	1.2963	56.295	2018, 2019, 2015
Mamie Lake	2964100	1.288534	136.485	2008
Landing Lake	1630700	1.285178	82.215	2019
Presque Isle Lake	2956500	1.276282	471.825	2012

Fawn Lake	2328900	1.258813	28.35	2004
Irving Lake	2340900	1.235148	169.695	2019, 2015, 2001, 2011
Lynx Lake	2954500	1.174211	124.335	1998
Brandy Lake	1541300	1.144568	45.765	2019, 2015
Little Crooked Lake	2335500	1.046359	62.37	2018, 2019, 2015
Arrowhead Lake	1541500	1.011037	38.88	2018, 2019, 2015
Rainbow Lake	2310800	1.000412	59.94	2019, 2015
Big Kitten Lake	2336700	0.972799	20.25	2019
Black Oak Lake	1630100	0.969767	228.42	2018, 2019, 2015, 2011
Papoose Lake	2328700	0.969182	170.91	1997, 2012
North Turtle Lake	2310400	0.939383	145.395	2010
Johnson Lake	1541100	0.898655	34.425	2018, 2019, 2015
Lake Laura	995200	0.897062	254.34	1998
Alder Lake	2329600	0.853639	106.92	1999, 2004
Lynx Lake	1600000	0.821144	12.555	2000, 2013
Boulder Lake	2338300	0.794834	208.98	1999, 1995
Spider Lake	2329300	0.781624	112.59	1999, 2004
Silver Lake	1599800	0.681033	23.085	2019, 2015
Stormy Lake	1020300	0.671659	211.815	2019, 2015
Erickson Lake	983600	0.642838	44.55	2019, 2015
Partridge Lake	2341500	0.587026	95.175	2019, 2015
Annabelle Lake	2953800	0.577419	78.57	1996, 2019
Hunter Lake	991700	0.52965	70.875	2018, 2019, 2015
Snipe Lake	1018500	0.529036	87.48	1995, 2000, 2003, 2006, 2009, 2012, 2015, 2018
Rock Lake	2311700	0.504688	48.6	2010
White Birch Lake	2340500	0.486677	45.765	2019, 2015, 2001, 2011
Day Lake	1843500	0.483598	44.55	2019, 2015
Lone Tree Lake	1000400	0.437012	52.65	2019, 2015
Street Lake	1884200	0.404973	18.63	2019, 2015
Camp Lake	1839100	0.390038	15.39	2018, 2019, 2015
Lake of the Hills	1620500	0.385468	24.705	2018, 2019, 2015
Little Star Lake	2334300	0.331636	105.3	1999, 2004

Sparkling Lake	1881900	0.302415	63.585	1996, 2006
Dead Pike Lake	2316600	0.279634	125.145	2016, 2005
Nichols Lake	1870400	0.246555	14.985	2019, 2015
Lost Canoe Lake	2339800	0.242777	112.995	2015, 1995
Wabasso Lake	2045000	0.232163	21.06	2018, 2016
Indian Lake	2764400	0.209596	32.4	2019, 2015
Whitney Lake	2338100	0.203369	91.53	2019, 2015
Lake Adelaide	1831700	0.199687	23.085	2019, 2015
Little Rock Lake	1862100	0.08288	15.795	2019, 2015, 2008
Averill Lake	2956700	0.075635	27.54	2012

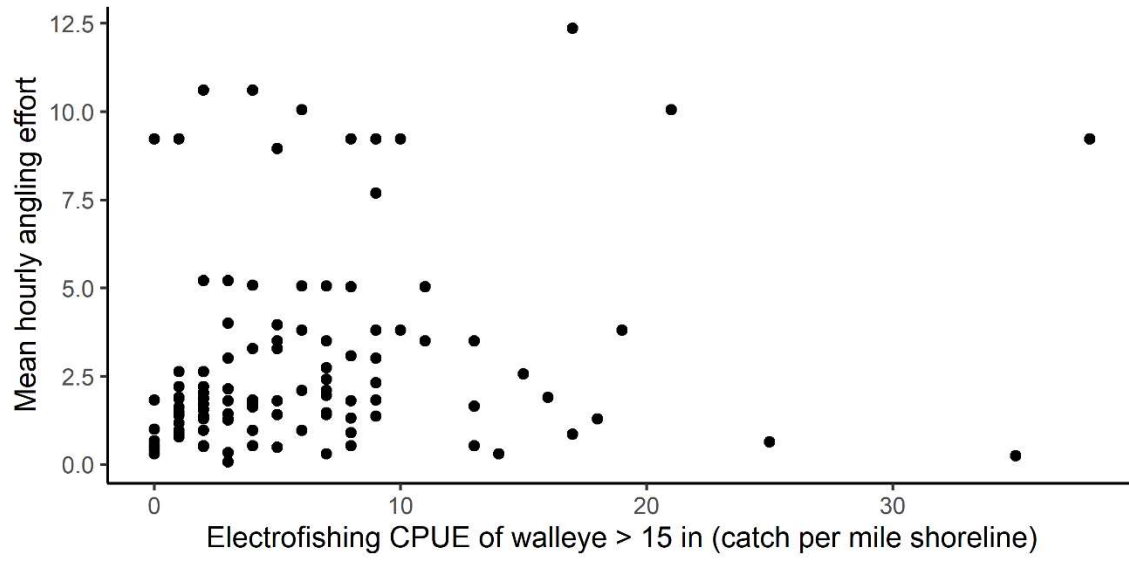


Figure S5: Lake-specific random intercepts estimated for all lakes surveyed versus electrofishing catch per unit effort of adult walleye.

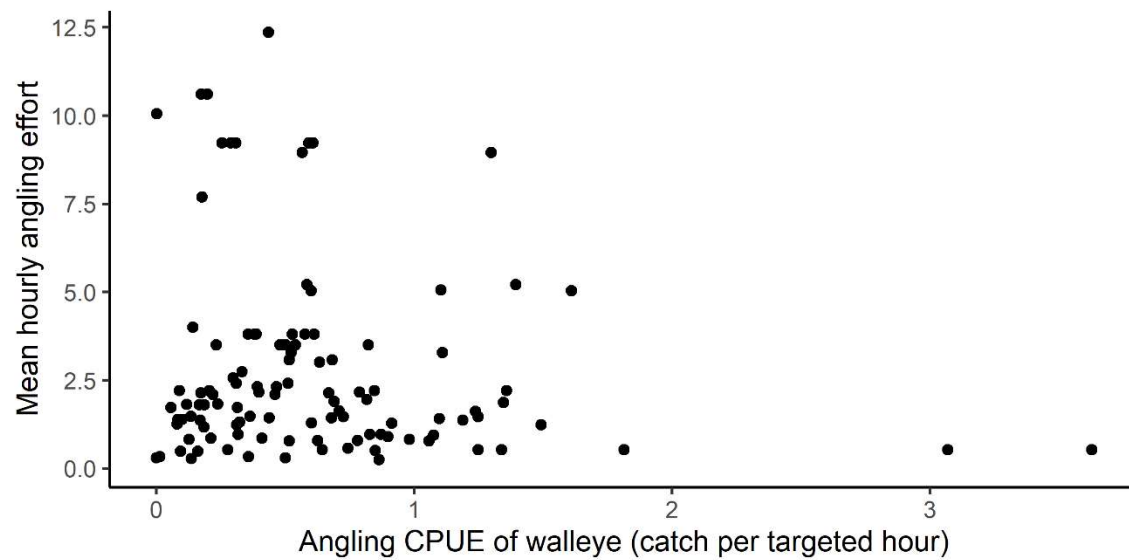


Figure S6: Lake-specific random intercepts estimated for all lakes surveyed versus angling catch per unit effort of walleye.

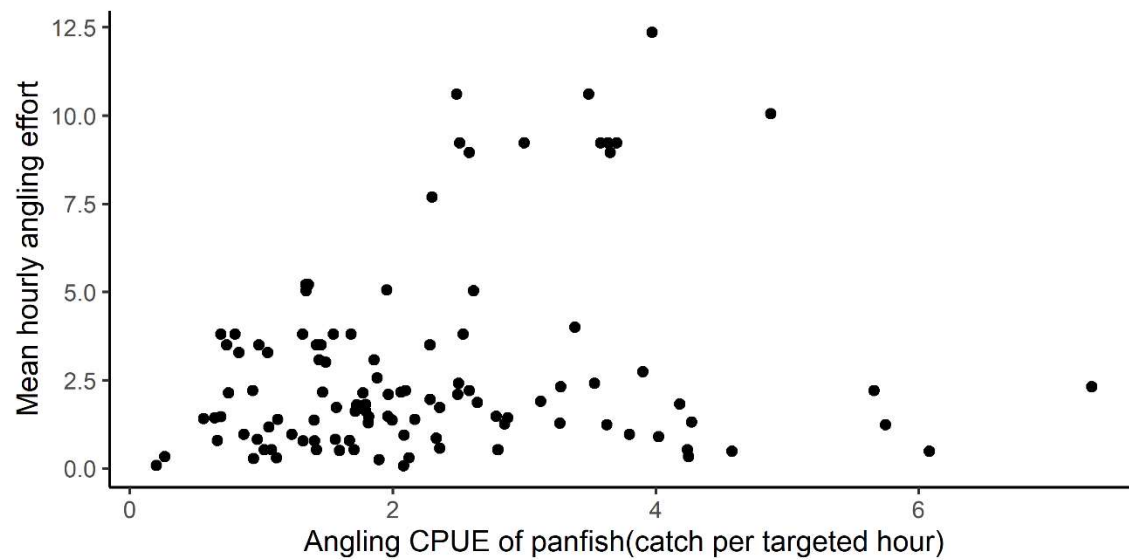


Figure S7: Lake-specific random intercepts estimated for all lakes surveyed versus angling catch per unit effort of panfish, including yellow perch, bluegill, pumpkinseed, and black crappie.

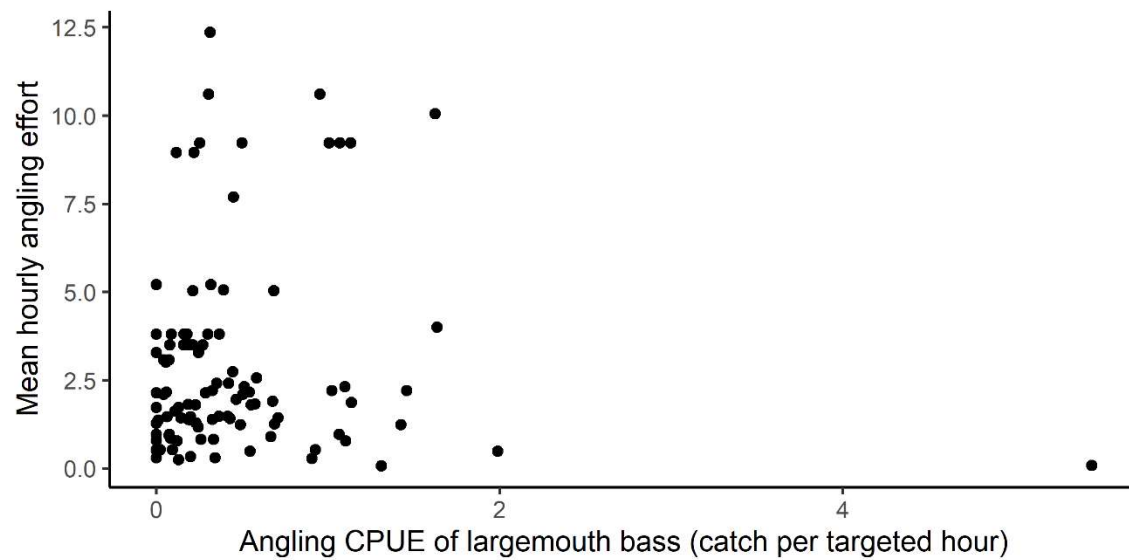


Figure S8: Lake-specific random intercepts estimated for all lakes surveyed versus angling catch per unit effort of largemouth bass.

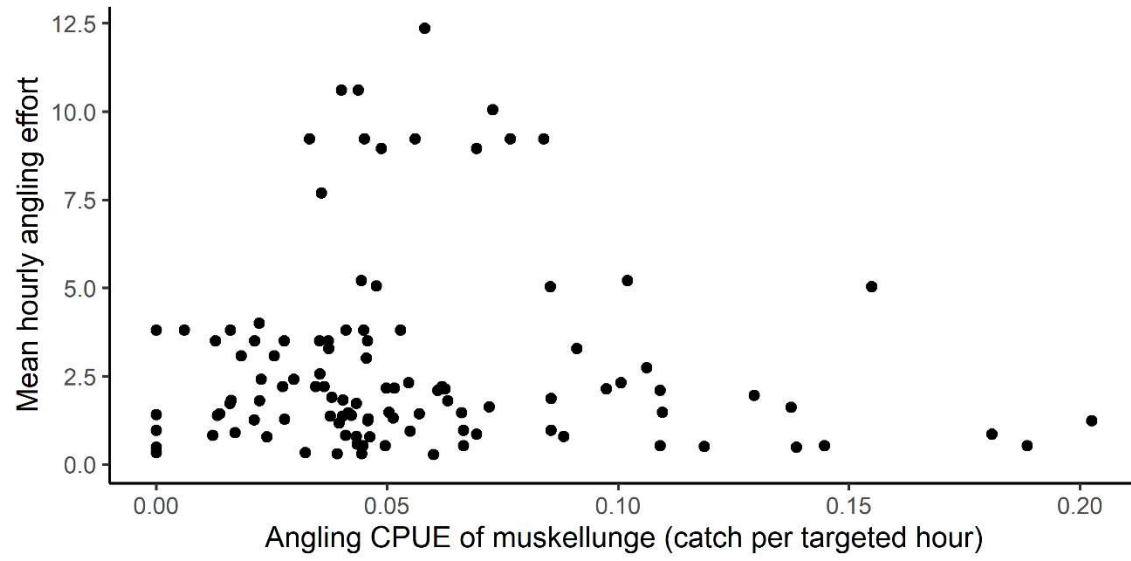


Figure S9: Lake-specific random intercepts estimated for all lakes surveyed versus angling catch per unit effort of muskellunge.

Chapter 2: Social fish-tancing in Wisconsin: The effects of the COVID-19 pandemic on statewide license sales and fishing effort in northern inland lakes

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Abstract

The first year of the COVID-19 pandemic in 2020 was associated with an “anthropause” in many industries, initially reducing greenhouse gas emissions and other negative anthropogenic influences. Outdoor recreation, however, has exploded in popularity in response to closures of indoor recreation options, increased free time, and/or increased levels of stress. We tested for the effects of the COVID-19 pandemic on the sale of fishing licenses in Wisconsin and on vehicle counts observed at public lake access points in Vilas County, Wisconsin in 2020. In the summer of 2020, fishing license sales in Wisconsin, USA increased, particularly among first-time license purchasers for whom cumulative sales in 2020 increased by 71% and 35% compared to the previous five-year average for WI residents and nonresidents, respectively. Changes in vehicle counts at lake access points in the summer of 2020 varied considerably by lake. However, lakes with greater proportions of public shoreline experienced increases in lake visitors associated with the pandemic. Our results suggest that the distribution of recreational fishing effort in Wisconsin changed during the pandemic, potentially placing additional harvest pressures on “hotspot” inland lakes.

Introduction

One of the early side effects of the COVID-19 pandemic has been the “anthropause” in the summer of 2020 (Rutz et al., 2020). Reduced movement and activity of humans within many industries has resulted in varied social, ecological, and economic responses globally (Searle et al., 2021). Given the vulnerability of inland waters to human influences (e.g. Dudgeon et al., 2006), the effects of the pandemic on inland fisheries have been of particular research interest (Cooke et al., 2020; Stokes et al., 2020). Pandemic-related reductions in polluting industries and commercial fishing effort may have temporarily released many fish stocks from a variety of anthropogenic pressures in mid/late 2020. However, the direction of global changes in these pressures are most likely mixed (Cooke et al., 2020). Economic hardship and food insecurity, for example, have also resulted in increased subsistence harvest of some fishes (Stokes et al., 2020). In addition, commercial fishers have implemented a variety of adaptation strategies (e.g. switching species or direct sales to customers) in response to the first year of the pandemic, often maintaining their overall landings in spite of decreased market prices and supply chain disruptions (Smith et al., 2020). Globally, the effects of the early pandemic on inland stocks in mid/late 2020 have varied depending in part on a country’s economic development (Stokes et al., 2020). Within countries classified as “developed,” the primary or sole consumptive use of inland waters is recreational fishing (FAO, 2012).

As lockdown orders have reduced travel opportunities and limited indoor recreation options, demand for fishing and many other outdoor activities has increased (Derks et al., 2020; Landry et al., 2020; Morse et al., 2020). Closures of public parks, travel restrictions, and fear of contracting or spreading disease resulted in decreases in outdoor recreation towards the beginning of the pandemic in March 2020, particularly among urban residents (O’Connell et al.,

2020, p. 19; Rice et al., 2020). As the relative safety of outdoor activities became apparent, however, increases in free time associated with stay-at-home orders, unemployment, and the lack of indoor recreational activities resulted in an influx of new participants into outdoor recreation in the US and Europe (Derks et al., 2020; Leeuwen et al., 2020). New participants also tended to choose outdoor recreational sites close to home, particularly urban residents (Landry et al., 2020; Rice et al., 2020). Recreational fisheries have largely remained open within the United States during the pandemic (Paradis et al., 2021). Anglers were therefore limited more by their willingness or ability to travel to fishing sites than by any top-down restrictions on fishing.

To test whether these broader trends in outdoor recreation during the first summer of the pandemic manifested at a local scale in Wisconsin, we compared fishing license sales, vehicle counts at lake access points, and proportions of boats observed fishing in summer, 2020 to previous years (2018 and 2019). Given the observed reductions in travel distance by outdoor recreationists (Rice et al., 2020), we hypothesized that reduced numbers of out-of-state anglers would be associated with changes in vehicle numbers at lake access points, a proxy for fishing effort. Because lakes vary widely in their accessibility, size, and other characteristics, we anticipated that the effects of the pandemic on fishing effort may vary by lake. We hypothesized that larger lakes or lakes with lower building densities would be attractive to anglers wishing to avoid crowds. Due to the popularity of lakeside camping, we also expected lakes associated with public campgrounds to attract more visitors during the pandemic. Finally, lakes surrounded by more public lands were expected to have a more pristine appearance and potentially attract more visitors wishing to experience nature. Although numerous survey-based studies have evaluated the effects of the pandemic on recreational anglers (Howarth et al., 2021; Midway et al., 2021; Pita et al., 2021), pandemic-related restrictions precluded collecting many empirical observations

(Bunt and Jacobson, 2022; Gundelund and Skov, 2021; but see Ryan et al., 2021). A reduction in fishing effort associated with pandemic-related reductions in out-of-state tourism would result in reduced revenue from license sales and reduced spending in counties that rely on recreational fishing tourism. Conversely, increased fishing effort during the pandemic could increase revenue and potentially the exploitation rates of fish populations. By 1) understanding the overall effect of the pandemic on fishing effort and 2) identifying potential “hotspots” of additional fishing effort, fisheries managers can account for the numbers and preferences of new anglers to the fishery in their decision-making and lake monitoring.

Methods

Study site

Wisconsin contains about 15,000 lakes, most of which are concentrated in the northern and eastern glaciated regions (Wisconsin Department of Natural Resources, 2009). These lakes vary greatly in surface area, ranging from 0.5 to 53,394 hectares, and support a variety of coolwater and warmwater species that are popular with anglers, including Walleye (*Sander vitreus*), Bluegill (*Lepomis macrochirus*) and other sunfishes (*Lepomis spp.*), Black Crappie (*Pomoxis nigromaculatus*), Largemouth (*Micropterus salmoides*) and Smallmouth Bass (*M. dolomieu*), Yellow Perch (*Perca flavescens*), Northern Pike (*Esox lucius*), and Muskellunge (*Esox masquinongy*). The Ceded Territory (the northern third of the state), was ceded to the United States by the Lake Superior Chippewa (Ojibwe) Tribes in the treaties of 1837 and 1842. Fisheries in the Ceded Territory are co-managed by state and Tribal governments. Vilas County lies within the Ceded Territory and the glaciated Northern Highlands Lake District (NHLD). Although the county is less densely populated than much of the state, it is an economically important destination for fishing tourism (Peterson et al., 2003; Shapiro, 2006). Over 40% of

Vilas County is comprised of public lands, which are largely undeveloped and open to recreation, including the Northern Highland American Legion State Forest, the Chequamegon-Nicolet National Forest, and the Vilas County Forest. Of the 1318 natural lakes in the county, 175 have public access. These lake vary widely in surface area, accessibility, and fish species composition (Wisconsin Department of Natural Resources, 2009) as well as in the fishing effort that these characteristics attract (Trudeau et al., 2021). It is therefore essential to account for lake-specific differences in mean fishing effort as well as potential variation in the response of fishing effort to the COVID-19 pandemic in summer, 2020.

License sales

The Wisconsin Department of Natural Resources (WDNR) collects data on fishing license sales to WI residents, nonresidents, and first-time buyers in both of these groups. Fishing licenses are required for anglers 16 years and older. For WI residents, an annual general fishing license is \$20, and a nonresident annual fishing license costs \$50. Reduced price first-time buyer licenses are available for those who have never fished in WI and those who have not held a WI fishing license for 10 years or more. First time buyer annual licenses cost \$5 for WI residents and \$25.75 for nonresidents. Daily cumulative license sales between March 1 and September 24, 2020 were compared to the same date range in 2018, 2019, and to the average of cumulative sales in the past five years (2015-2019). License sales for resident and nonresident regular and first-time buyer licenses were compared to test for changes associated with the COVID-19 pandemic.

Boat landing vehicle counts

Instantaneous counts of vehicles at 38 lake access points in Vilas County, WI were collected in the summers of 2018, 2019, and 2020. Counts in the summers of 2018 and 2019 took

place hourly during 8-hour access point angler-intercept creel survey shifts as part of another study (Trudeau et al., 2021). Creel survey shifts were randomly distributed among lakes and stratified by weekends/weekdays and mornings/evenings. Thirty-eight lakes were selected as part of a multi-objective study of the NHLD region. Selection criteria included a requirement that lakes did not cross county or state borders, spanned a gradient of Largemouth Bass populations, had conductivity values that allowed electrofishing, and had a maximum size of 250 hectares. In 2018, 16 of the selected lakes were surveyed. In 2019, the 22 remaining lakes were surveyed as well as five that had also been surveyed in 2018.

To maintain social distancing in the summer of 2020, a bus-route survey design was used to collect vehicle counts. An efficient route was planned between all 38 previously surveyed lakes. During a survey shift, a random starting lake was selected. Instantaneous counts of vehicles at lake access points were then collected at each stop on the route until the end of the shift. Bus route surveys took place as schedules allowed, and each lake on the route was observed between 9 and 20 times between June 7 and August 14, 2020. No COVID-related restrictions on outdoor activities were in place during this time in Wisconsin. Two sets of outlier counts were removed prior to our analysis: on July 4, 2020, an unusually high number of vehicles (23) was observed at Black Oak Lake. Black Oak Lake is a popular swimming and recreational boating lake with a public beach, and it is located close to the town of Land O'Lakes, WI. July 4 is a highly popular day for recreational boating and swimming at this lake. To avoid an outsized effect on mean vehicle counts in 2020, and because ten July 4, 2018 observations at the same lake were completed improperly (only fishing boats were counted, not recreational boaters or swimmers), all July 4 observations (11 in total, 10 hourly counts and 1 bus-route count) were removed from the analysis.

Observations of fishing boats

Vehicle counts did not differentiate between anglers, other recreational boat users, or other non-boating lake visitors, so it would be unclear whether any observed changes in vehicle counts reflected a change in fishing effort. We therefore compared the proportion of boats observed fishing during boat-based counts of fishing effort in 2018 and 2019 with dock-based observations of the proportions of boats observed fishing in 2020. In 2018 and 2019, boat-based counts of fishing effort took place at two randomly-selected times during eight hour creel shifts randomly assigned to the morning (5:30 AM-1:30 PM) or evening (1:30 PM-9:30 PM). During these counts, the number of boats on the lake was recorded and each boat was described as fishing or not fishing. In the summer of 2020, these boat-based counts were not possible. Instead, to estimate the proportion of boats on the lake that were fishing, a count of fishing (defined as boats with fishing equipment, such as rods, visible) and non-fishing boats was taken at the boat launch dock. Only boats visible from the boat launch dock were therefore included in this count. Although the shore-based counts potentially observed only a fraction of the boats on the lake, the visible proportion of boats fishing should be comparable to the proportions observed during the full-lake counts.

Lake characteristics

We obtained lake surface areas from the WDNR lake database (Wisconsin Department of Natural Resources, 2009). We calculated building density (buildings per km shoreline) within 200 m of each lake's shoreline using GIS data obtained from the WDNR and Vilas County. Campgrounds located on lakes were identified using the WDNR website describing camping opportunities in the Northern Highland American Legion State Forest ("Camping | Wisconsin DNR," n.d.). We used the Vilas County Owner Listings MapApp

(<https://maps.vilascountywi.gov/>) to estimate the proportion of lake shorelines made up of public lands. Public lands were defined as lands owned by federal, state, county, or municipal governments or agencies.

Data analysis

We used a hypothesis-driven model selection approach to test for the effects of the first summer of the COVID-19 pandemic on instantaneous vehicle counts. We fit negative binomial generalized linear mixed models (GLMM) with a log link to the vehicle counts using the lme4 package in R version 4.1.0 (Bates et al., 2015, p. 4; R Core Team, 2021). Each model included the quadratic effect of hour of day as a fixed effect. Hour of day was centered and scaled to aid convergence. In addition, indicator variables describing month, weekends or holidays, and the occurrence of adverse weather (i.e. heavy rain, storm clouds, or heavy wind) were included as fixed effects in all models. All models also included lake-specific random intercepts. A null candidate model representing the hypothesis that no changes in vehicle counts occurred in the summer of 2020 contained no additional predictors. Two additional candidate models tested for the influence of the COVID-19 pandemic. The first of these two models included a COVID-19 indicator variable as a fixed effect, which would predict a consistent mean effect of summer 2020 on vehicle counts across all lakes. The second model included COVID year observations as a random slope, meaning that the value of the lake-specific random intercept was allowed to vary between COVID and non-COVID years. With this random effect structure, the pandemic was allowed to have different effects on vehicle counts at different lakes. Because vehicle counts were collected using different methods in different years, direct comparisons of counts between years would be misleading. Mean changes in vehicle numbers between COVID and non-COVID

years by lake were therefore produced through GLMM predictions for weekday counts in May at 13:37 (the mean time of day in our observations) under normal weather conditions.

Model assumptions were tested with the DHARMA package (Hartig, 2019). Two outlier values from 2020 with an excess effect on model estimates were detected with the package's testOutliers function. Because these observations were both from 2020 and would therefore positively bias the estimated COVID year effect, they were removed from the analysis. We compared candidate models using corrected Akaike Information Criterion scores and weights, with a cutoff of $\Delta AICc > 2$ indicating a worse model fit than the model with the minimum AICc value (Burnham and Anderson, 2002). We estimated P values for parameter estimates using log likelihood ratio (LLR) testing of nested models. Marginal and conditional pseudo r^2 values were calculated using the trigamma method (Bartoń, 2020).

Further explaining the effects of a COVID year on fishing effort on different lakes is relevant to fisheries managers. We therefore fit an additional GLMM with the same random effects structure and additional fixed effects describing lake characteristics: lake surface area (ha), the presence of public campgrounds, building density within 200 m of the lake shore, and the proportion of public lands making up the shoreline. Interactions of these predictors with the COVID year indicator variable tested whether these characteristics influenced the changes in vehicle traffic associated with the COVID-19 pandemic in summer, 2020 (i.e. whether larger lakes, for example, experienced higher vehicle traffic in 2020 than in previous years).

COVID year effects on probability of fishing

We used a binomial generalized linear mixed effects model to test for any change in the log odds that an observed boat was engaged in fishing in the summer of 2020. Similar to the models fit to observations of vehicle counts, fixed effects accounted for differences in fishing

probability associated with time of day and seasonality. Monthly indicator variables and a quadratic time of day effect were included as fixed effects. A COVID year indicator was included as a fixed effect to test the overall effect of summer, 2020 on fishing probability across lakes. Random intercepts by lake accounted for mean differences in fishing probability between lakes, and a random slope by COVID year allowed the change in fishing probability associated with 2020 to vary by year. This maximal random effects structure was verified by comparing AICc scores of the random slopes model with an otherwise-identical random intercept model. Pseudo r^2 values were estimated using the delta method (Bartoń, 2020).

Results

Fishing license sales

Beginning in April 2020, fishing license sales to WI residents were higher than in previous years (Fig. 1A). By September 30, 2020, cumulative resident license sales had increased by 8% in comparison to the average cumulative sales of the previous five years (2015-2019). Contrary to expectations, nonresident annual fishing license sales also increased by a similar margin of 7.5%. Both sales of resident and nonresident licenses, however, were within the 95% confidence interval of the past five years' average sales.

Although total annual license sales showed modest growth, sales of first-time buyer (FTB) fishing licenses boomed in 2020. The WDNR offers a reduced-price license to purchasers who have not held a WI fishing license for at least ten years. Cumulative sales of this license to WI residents in 2020 increased by 71% compared to the previous five-year average (Fig. 1C), well outside the bounds of sales in the previous five years. Among nonresidents, FTB license sales rose by 35%. Notably, 87% of the increase in annual nonresident sales illustrated in Fig 1B

came from this increase in FTB licenses. For resident license sales, 47% of the increase in sales came from FTB licenses.

Boat landing vehicle counts

The change in raw vehicle counts associated with the summer of 2020 varied considerably by lake (Fig. 2). Notable increases in mean vehicle counts occurred at Allequash (AQ), Black Oak (BK), Day (DY), Irving (IV), and Little Arbor Vitae (LV) lakes. Estimating the effects of the COVID-19 year, however, required accounting for differences in time of day and seasonality among lake-specific observations. The best fitting candidate model that did not include lake characteristics as predictors included a fixed effect indicating the COVID year (2020), a lake-specific random intercept accounting for mean differences in visitor counts among lakes, and a random slope allowing lake intercepts to vary by the COVID year (Table 1). This result confirms that the effect of the COVID year on the number of lake visitors varied by lake. No significant effect of the COVID year on mean vehicle counts was detected ($P = 0.06$, Table 2). Mean vehicle counts were highest in June, where they were 60% higher than mean vehicle counts in May ($P < 0.0001$, Table 2). Vehicle counts peaked mid-day, and counts were 39% higher on weekends and holidays ($P < 0.0001$, Table 2). During poor weather conditions, 51% fewer vehicles were observed ($P < 0.0001$, Table 2).

Lakes showed considerable variation in mean vehicle counts (i.e., lake-specific random intercept values, $\sigma = 1.17$) and the effects of the COVID-19 year (i.e., the lakes' random slope values, $\sigma = 0.57$). Lakes that experienced increased vehicle numbers in 2020 appeared to be clustered in the north-central part of the county (Fig. 3). Percent changes in mean vehicle counts varied widely among lakes, ranging from a 257% increase in vehicles at Partridge Lake to a 66%

decrease at Oxbow Lake. The largest changes in absolute mean vehicle counts were observed at Irving Lake (+ 2.2 vehicles) and Oxbow Lake (- 1.04 vehicles).

Because the effect of the COVID year on vehicle counts varied greatly by lake, lake characteristics were introduced to the GLMM to test for explanations for these different responses. Although no significant main effect of the COVID year was detected, we found a positive interaction effect with the proportion of public shoreline. Lakes with entirely public shoreline attracted 103% more vehicles in 2020 compared to the previous two years ($P = 0.03$, Table 3). Larger lakes ($P < 0.0001$) and lakes with campgrounds ($P = 0.03$, Table 3) also experienced significantly higher vehicle traffic in all years of the survey.

Proportion of boats angling

Recreational anglers made up 48.4%, 64.2%, and 64.3% of all observed boats in 2018, 2019, and 2020, respectively (Fig. S1). We detected no significant effect of the COVID year on the probability of an observed boat engaging in fishing. However, during the COVID year, boats on larger lakes were more likely to be observed fishing than in previous years ($P = 0.01$, Table 4). In all years, boats were less likely to be fishing on lakes with greater building densities on and near their shoreline ($P = 0.03$). The log odds of fishing showed a quadratic response to time of day; boats were more likely to be fishing in the morning and evening. The probability of fishing also declined over the summer: boats in July and August were 34% and 43% less likely to be fishing than boats in May, respectively.

Discussion

During the first summer of the COVID-19 pandemic, fishing license sales in Wisconsin substantially increased, particularly among first-time buyers. Contrary to our expectations that the pandemic would decrease visits by out-of-state anglers, both resident and nonresident license

sales increased in 2020. Much of the increase in nonresident fishing license sales came from first-time buyers, suggesting that angling tourism in Wisconsin attracted new groups of anglers in 2020. According to a survey conducted by the WDNR, these first time buyers were younger, more likely identify as an underrepresented gender among anglers (i.e., women or nonbinary/other), and somewhat more racially diverse than previously existing license holders (Beardmore, 2021). Similar influxes of new anglers associated with COVID-19 have also been documented elsewhere in the US (Midway et al., 2021), Canada (Howarth et al., 2021), and Denmark (Gundelund and Skov, 2021). However, not all the new license holders in Wisconsin were new anglers. Based on the same WDNR survey, 28% of first-time license buyers were experienced anglers who were fishing in Wisconsin for the first time (Beardmore, 2021). In open ended survey responses, these out-of-state anglers stated that they previously traveled to Canada to fish. In 2020, the US-Canada border was closed due to the pandemic, which prevented these sorts of fishing trips (Paradis et al., 2021). Wisconsin may therefore have presented an alternative fishing location for anglers who would typically travel to Canada.

Not everyone who purchases a fishing license goes fishing. We therefore used previously-collected instantaneous counts of vehicles at lake access points to investigate empirical changes in vehicle counts in 2020 as a proxy for fishing effort. Different lakes showed different pandemic-related responses of lake visitors. These among-lake differences suggest that, at least in Vilas County, new anglers may have been most attracted to a subset of the lakes that we surveyed. When we incorporated several lake characteristics into our analysis, we found that vehicle counts tended to increase in 2020 primarily among lakes surrounded by more public lands. Public lands on lake shorelines in Vilas County tend to be forested, which may influence water quality or the availability of littoral habitat for fish populations (Christensen et al., 1996).

However, no effect of shoreline building density was detected, suggesting that the inverse proportion of natural shoreline did not influence the lake-specific changes in fishing effort. Instead, anglers may enjoy easier access to lakes that are not surrounded by private properties. Maintaining public ownership of these shorelines and/or public access to lakes may therefore be an important step towards retaining this new group of anglers. As potential new “hotspots” of fishing effort, lakes surrounded by more public lands should also be monitored for the potential effects of increased fishing effort on fish populations.

Although we could not distinguish between vehicles that had traveled to the lake to fish from vehicles carrying recreational boaters and other lake visitors, the similarity in proportions of boats that were observed fishing among years suggests that a similar proportion of vehicles were associated with fishing in 2020 compared to the previous two years. For lakes surrounded by a greater proportion of public lands, an increase in vehicles would then most likely correspond to an increase in fishing boats, assuming that the proportions of boats observed fishing were not influenced by our shore-based counts in 2020. In addition, although larger lakes did not experience any significant change in vehicle counts among years, the higher proportion of boats observed fishing in 2020 may also suggest increased fishing effort at larger lakes. Therefore, the increase in vehicle counts may have reflected a corresponding increase in fishing effort, particularly at larger lakes and lakes with more natural shoreline. This potential increase in fishing effort that we observed in Vilas County, WI corresponded with similar increases in fishing effort that have been detected through surveys (Midway et al., 2021) and, where available, empirical observations (Bunt and Jacobson, 2022; Ryan et al., 2021).

Although our results corresponded to a potential pulse in fishing effort on lakes surrounded by public lands in Vilas County during the first summer of the pandemic, several

caveats remain. Vehicle count surveys took place for only two summers prior to the pandemic and one summer during the pandemic. Differences in vehicle traffic that were attributed to the COVID year could instead be attributed to inter-annual variation in vehicle traffic to these lakes. We also excluded lakes from our sampling framework that were too large for a previous project's survey methodology (i.e. larger than 250 hectares). Several larger lakes are located near population centers outside of public lands and were likely popular angling destinations. The omission of these lakes may therefore have overemphasized the importance of public lands in predicting the distribution of fishing effort across the landscape and underemphasized the importance of lake size and accessibility.

The agreement between fishing license sales data at the state level and our vehicle count data within Vilas County suggests that the first summer of the pandemic was associated with increased fishing activity on northern Wisconsin inland lakes. Vilas County, however, represents only a subset of Wisconsin's inland lake fishing opportunities. Among respondents to the WDNR's survey of first-time license buyers, notable differences in destination counties were present among new anglers, reactivated anglers, and active anglers who were fishing in Wisconsin for the first time (Beardmore, 2021). When asked about their favorite fishing experiences in 2020, new anglers more frequently described trips to Dane and Door Counties than Vilas County. Dane County is largely urban, featuring the state capital as well as the Yahara Chain of lakes. Door County is a sparsely populated peninsula surrounded by Lake Michigan and a popular destination for Great Lakes fishing and other forms of outdoor recreation. Reactivated and active anglers, in contrast, more frequently described Vilas County as a location of their best fishing trips. Our observations of lake visitors therefore represents a limited snapshot of the pulse

of anglers that entered the WI inland lake fishery during the first year of the COVID-19 pandemic.

We found that the COVID-19 pandemic was associated with increased purchases of fishing licenses in Wisconsin, and in Vilas County, potentially increased fishing effort. In addition, a considerable number of first-time anglers purchased fishing licenses in the summer of 2020. This increase in first-time license buyers represents an opportunity for Wisconsin's Recruitment, Reactivation, and Retention (RRR) program. First-time license buyers were more likely to be women and under 30 years old compared to return license buyers (Beardmore, 2021). If these anglers are retained, a "silver lining" of the COVID-19 pandemic may be a diversification of fisheries stakeholders and their values. Increased investment in the state's fisheries resources by a greater diversity of stakeholders could present an opportunity for increased public engagement in ecosystem-based management of inland lakes.

Conclusion

Continued monitoring of fishing effort will reveal whether this pulse of participation related to the pandemic will continue and how the entrance of new anglers to the fishery could change the distribution of fishing effort across inland lakes. Collecting observations of fishing effort from remote sensing data (e.g. Provost et al., 2021) using machine learning techniques (e.g. Sasamal and Mallenahalli, 2019) is one promising approach to increasing the spatial and temporal resolution of lake monitoring. In particular, expanding this monitoring across more counties and a greater size distribution of lakes could aid managers in detecting and responding to similar pulses of recreational fishing effort associated with future crises, such as an economic recession. Of the new anglers surveyed by the WDNR, 44% reported spending less than \$25 to begin fishing. In addition to their economic importance for fishing destinations, recreational

fisheries can also be important sources of food (Embke et al., 2020; Nyboer et al., 2022). In a potential future recession, where unemployment rises and income inequality accelerates, fisheries with a lower barrier to entry such as Wisconsin Bluegill fishing may constitute an important supplemental food source. Social and economic incentives therefore exist for maintaining public ownership of shorelines around hotspots of recreational fishing effort for maintaining fishing effort and supporting robust fish populations.

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Tables

Table 1: Model selection results for GLMMs testing for the effect of the COVID year on vehicle counts at 38 Vilas County, WI lake access points. Bold font indicates the best fit model.

Model random effects structure	Degrees of freedom	AICc	Δ AICc	Weight
Random lake intercept only	10	5860.7		0
COVID year + random lake intercept	11	5845.1		0
COVID year + random lake intercept and slope	13	5797.1	0	1

Table 2: Parameter estimates for the best-fit negative binomial GLMM estimating the effect of the COVID year on vehicle counts at lake access points. Bold font indicates significant parameters at $p < 0.05$.

Parameter	Estimate (SE)	Chi squ	<i>P</i> value
Intercept	-0.862 (0.216)		
June	0.472 (0.104)***	21.279	<0.0001
July	0.269 (0.103)**	6.887	0.009
August	0.265 (0.115)*	5.333	0.021
Hour of day	2.357 (0.169)***	212.529	<0.0001
Hour of day²	-2.369 (0.170)***	213.480	<0.0001
Weekend or holiday	0.331 (0.053)***	38.448	<0.0001
Adverse weather	-0.722 (0.134)***	31.825	<0.0001
COVID-19 year	0.235 (0.121)	3.620	0.057
Log likelihood	-2885.4		
σ Lake random intercept	1.169		
σ COVID year:Lake random slope	0.565		
Correlation of Lake intercept and COVID year	-0.31		
Marginal r^2	0.079		
Conditional r^2	0.497		

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

Table 3: Parameter estimates for the best-fit negative binomial GLMM estimating the effects of lake characteristics and the COVID year on vehicle counts at lake access points. Bold font indicates statistically significant parameters at $P < 0.05$.

Parameter	Estimate (SE)	Chi squ	<i>P</i> value
Intercept	-0.813 (0.222)		
June	0.480 (0.104)***	22.096	<0.0001
July	0.270 (0.103)**	6.987	0.008
August	0.266 (0.115)*	5.427	0.020
Hour of day (scaled)	2.354 (0.169)***	212.185	<0.0001
Hour of day² (scaled)	-2.365 (0.170)***	212.887	<0.0001
Weekend or holiday	0.332 (0.053)***	38.659	<0.0001
Adverse weather	-0.723 (0.134)***	31.982	<0.0001
COVID year	-0.055 (0.158)	0.122	0.727
Lake surface area (ha) (scaled)	0.711 (0.141)***	19.493	<0.0001
Proportion shoreline public lands	-0.531 (0.555)	0.904	0.342
Building density within 200 m (scaled)	-0.056 (0.184)	0.093	0.761
Campground presence	1.088 (0.509)*	4.358	0.037
COVID year * Lake surface area (scaled)	-0.002 (0.103)	0.000	0.987
COVID year * Proportion shoreline public	0.941 (0.423)*	4.835	0.028
COVID year * Building density (scaled)	0.157 (0.134)	1.381	0.240
COVID year * Campground presence	0.229 (0.364)	0.390	0.532
Log likelihood	-2867.9		
σ Lake random intercept	0.820		
σ COVID year:Lake random slope	0.485		
Correlation of Lake intercept and COVID year	-0.42		
Marginal r^2	0.215		
Conditional r^2	0.378		

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

Table 4: Binomial GLMM predicting the effects of seasonality, time of day, lake characteristics, and the COVID year on the probability of an observed boat engaging in fishing activities. Adverse weather is not included as a predictor because the occurrence of adverse weather precluded boat-based counts and bus route surveys. Bold font indicates statistically significant parameters at $P < 0.05$.

Parameter	Estimate (SE)	Chi Sq	<i>P</i> value
Intercept	1.469 (0.367)		
June	-0.536 (0.347)	2.486	0.115
July	-1.376 (0.334)***	18.575	<0.0001
August	-1.196 (0.354)***	12.168	0.0005
Hour of day	-3.614 (0.478)***	62.551	<0.0001
Hour of day²	3.543 (0.475)***	59.851	<0.0001
Weekend or holiday	-0.125 (0.128)	0.914	0.339
COVID-19 year	0.194 (0.300)	0.404	0.525
Lake surface area (ha) (scaled)	-0.125 (0.143)	0.753	0.385
Proportion shoreline public lands	-0.046 (0.621)	0.005	0.942
Building density within 200 m (scaled)	-0.423 (0.194)*	4.546	0.033
Campground presence	0.321 (0.535)	0.353	0.553
COVID year * Lake surface area (scaled)	0.447 (0.183)*	4.546	0.012
COVID year * Proportion shoreline public	0.883 (0.826)	1.169	0.280
COVID year * Building density (scaled)	0.366 (0.252)	2.141	0.143
COVID year * Campground presence	-1.077 (0.669)	2.587	0.108
Log likelihood	-976.6		
σ Lake random intercept	0.624		
σ COVID year:Lake random slope	0.607		
Correlation of Lake intercept and COVID year	-0.08		
Marginal r^2	0.13		
Conditional r^2	0.23		

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

Figures

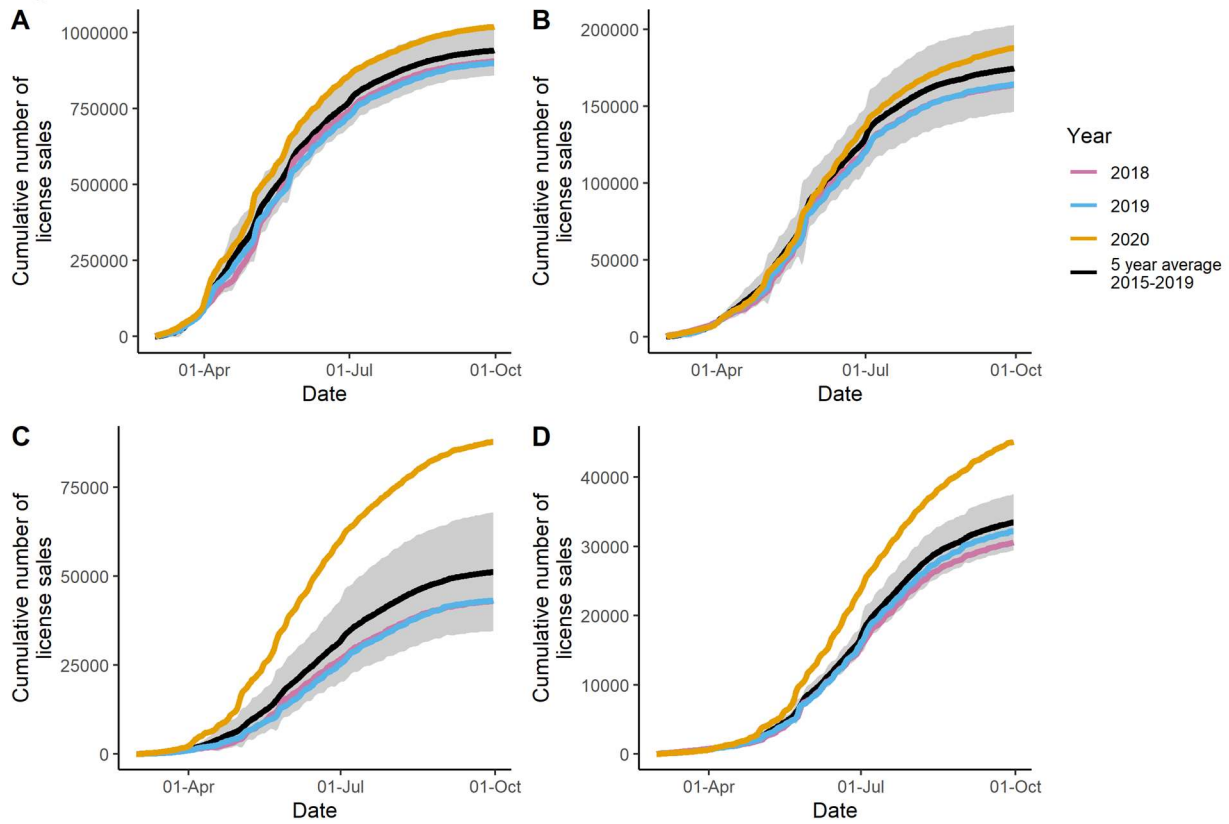


Figure 1: Cumulative sales of A) all Wisconsin resident licenses, B) All nonresident licenses, C) Wisconsin resident first-time buyer licenses, and D) nonresident first-time buyer licenses in 2020 compared to 2018, 2019, and the previous five year average. Gray ribbons indicate 95% confidence intervals around the five year average of license sales between 2015 and 2019. Note the differences in scale of the y axis between plots.

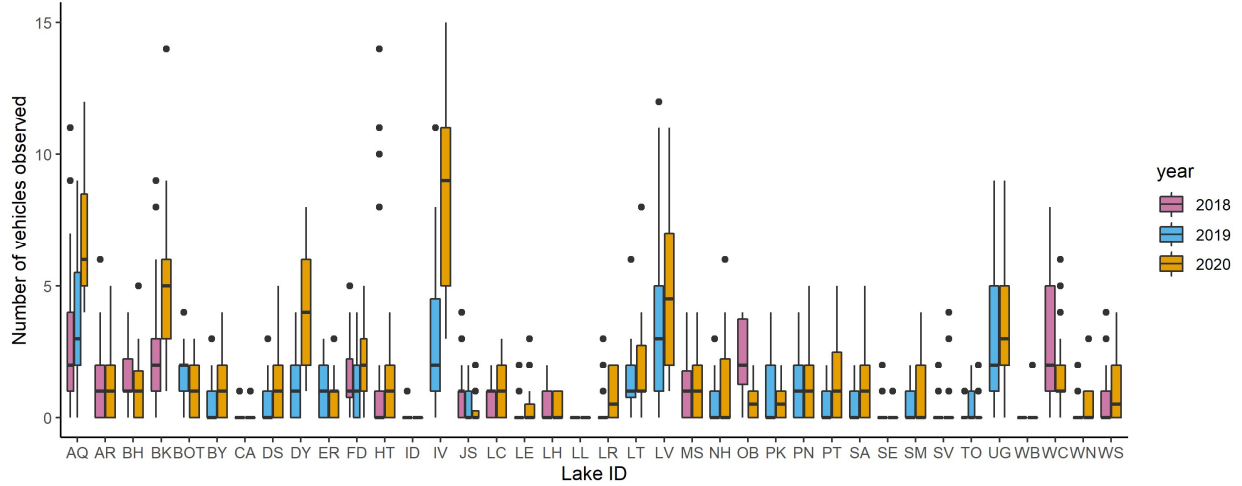


Figure 2: Distribution of vehicle count values in 2018, 2019, and 2020 at 38 Vilas County, WI lakes. Note that 13 outlier values at Black Oak (BK) and Silver (SV) Lakes have been removed from this visualization.

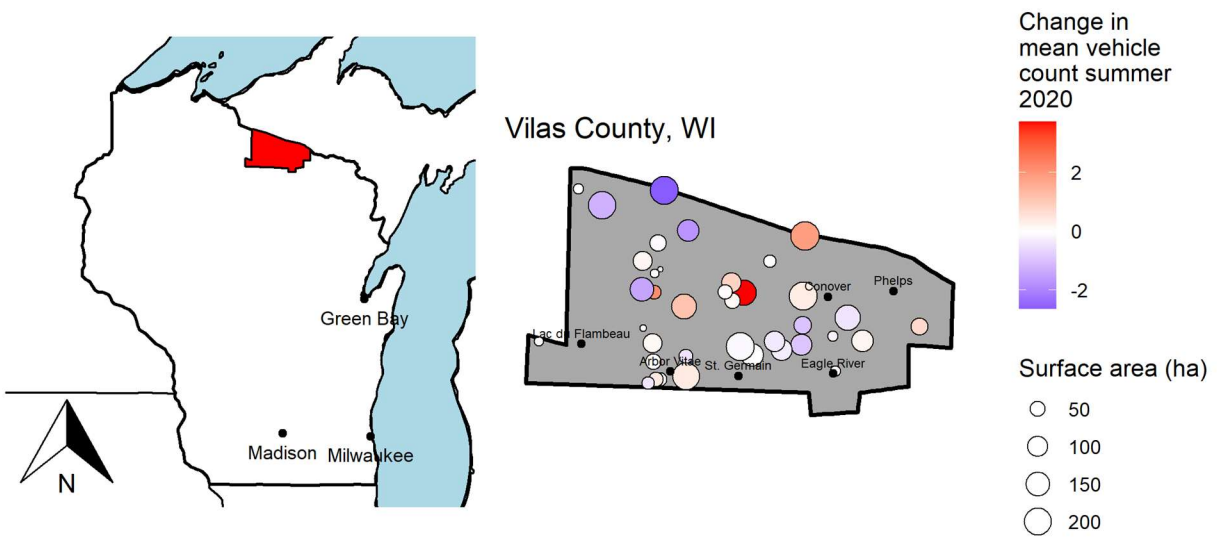


Figure 3: Changes in mean vehicle counts in the COVID year for each lake surveyed in Vilas County, WI. These mean counts are derived from GLMM predictions for an average weekday in May assuming mean time of day.

Supplementary materials

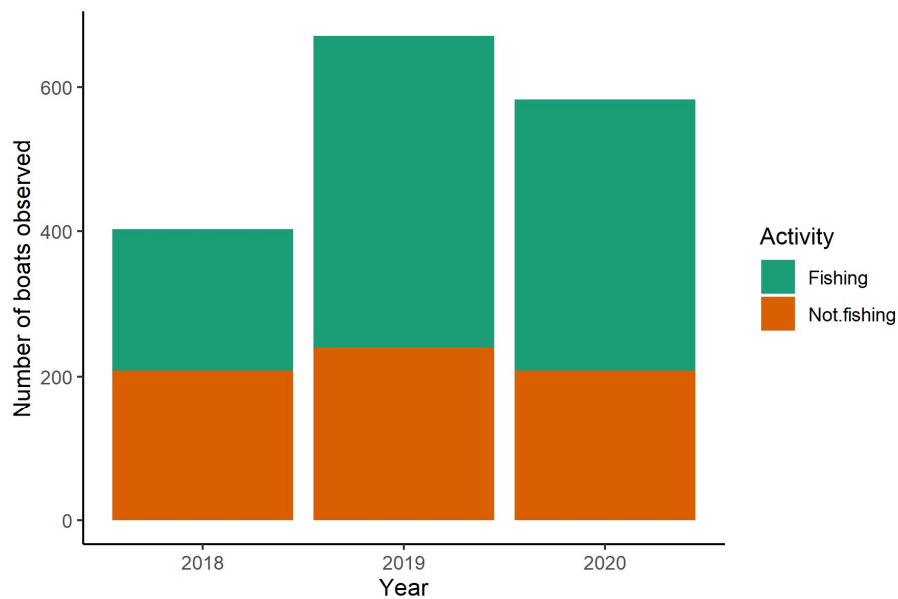


Figure S1: Stacked bar chart of all boats observed fishing (top) and not fishing (bottom) in each year of the survey. Boats were observed during boat-based counts of fishing effort in 2018 and 2019, and boats were observed from shore in 2020. A smaller proportion of boats were observed fishing in 2018, but no change in observed boats' probability of fishing was observed in 2020.

Chapter 3: Lower possession limits and shorter seasons directly reduce for-hire fishing effort in a multispecies marine recreational fishery

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Abstract

Managers of recreational fisheries often rely on implicit and rarely-tested assumptions regarding how fishing effort will change in response to regulations. For instance, they assume that reduced seasons will directly reduce fishing effort without producing angler behavioral adaptations to maintain fishing opportunities and harvest. Vessel trip reports from a multispecies for-hire fishery in New Jersey, USA allowed us to empirically evaluate changes in fishing effort as overlapping seasons for four species became shorter and as possession limits decreased. We conducted focus groups with fishery stakeholders and then developed statistical models to evaluate hypotheses describing how anglers aboard for-hire vessels adapted to regulations. Fishing effort aboard charter boats remained consistent and primarily responded to the availability of “something” to harvest, suggesting that their customers are willing to substitute target species. Party boat anglers, in contrast, responded to the possession limits of black sea bass (*Centropristis striata*), and summer flounder (*Paralichthys dentatus*). Because party anglers were

less willing to substitute target species, party vessel operators are likely particularly vulnerable to reductions in fishing opportunity and harvest potential.

Introduction

Recreational fisheries management worldwide struggles to limit harvest while concurrently meeting biological and socioeconomic objectives (Cox et al. 2002; Post et al. 2002; Abbott et al. 2018). Fisheries managers set and tune regulations such as season length, possession limits, and size limits to meet recreational harvest quotas, but angler response to these management changes is poorly understood. Anglers may adjust their behavior to compensate for new restrictions (e.g. Beaudreau et al. 2018; Gentner 2004; Powers and Anson 2018), or they may choose to leave the fishery (e.g. Holzer and McConnell 2017; Mackay et al. 2020; Whitehead et al. 2015). Restrictive regulations may not result in the expected reduction in harvest in the presence of compensatory behavior. Conversely, declining participation in the fishery can harm coastal communities that rely on income from the recreational fishing industry (Chan et al. 2018; Murray et al. 2010; NMFS 2018). Further complicating this calculation, in multispecies fisheries, anglers may switch targets when regulations are no longer acceptable to them (Beaudreau et al. 2018). This may be a desirable outcome if it relieves pressure on threatened stocks, but these alternative targets may then be subject to enough harvest pressure to become depleted (Abbott et al. 2018). Whereas fisheries managers can frequently monitor commercial harvest throughout the season (e.g. Gerritsen and Lordan 2011; Lee et al. 2010), recreational fisheries managers generally have few options for monitoring harvest or making changes mid-season (Pereira and Hansen 2003). An empirical understanding of the link between

fishing regulations and resulting fishing effort is therefore needed to better inform fisheries management choices.

Regulations have the potential to reduce the utility that anglers receive from fishing, but their effects depend on individual preferences. Recreational anglers place value on catch (i.e. the number of fish kept and released), harvest (i.e. the number of fish kept), and the overall fishing experience (Hunt et al. 2019). Throughout this paper, we will use “catch” to indicate all fish caught, including those kept and released, while “harvest” refers only to fish that are caught and kept. In a utility-maximizing approach to understanding angler decisions, the choice of whether or not to fish will depend on whether the expected fishing experience, catch, and harvest provide enough utility to outweigh the cost in time and money incurred by taking the trip (e.g. McFadden 1974). Reductions in season length do not necessarily reduce the value of fishing trips, but they narrow the window of opportunity for anglers to schedule their fishing trips. This loss of opportunity potentially results in the loss of benefits related to the overall fishing experience if, for instance, inclement weather cancellations are proportionally more common. Reduced possession limits, in contrast, may reduce the benefits anglers receive from harvest itself. Anglers may still catch a lot of fish, which may still be satisfying to individuals who are highly catch-oriented (e.g. Schroeder and Fulton 2013). However, the lower possession limit places a ceiling on the harvest that anglers can take home, meaning that anglers who primarily fish for food may no longer decide to take the trip. Since the experience of the fishing trip is still valued by many anglers regardless of catch, however, fishing effort can remain highly elastic to regulations, depending on angler preferences (e.g. Beardmore et al. 2011a). When anglers do leave the fishery as a result of benefit loss associated with restrictive regulations, coastal communities experience negative economic effects as vessel operators and other businesses

associated with the recreational fishery lose revenue (NMFS 2018). Understanding these potential angler responses therefore allows fisheries managers to weigh tradeoffs in the biological, social, and economic outcomes of their decisions.

Much uncertainty therefore exists when predicting how recreational fishing effort, and therefore harvest, will respond to changes in regulations. This uncertainty arises in part from unknowns associated with angler behavior, motivations, and preferences (e.g. Brinson and Wallmo 2017; Johnston et al. 2010). While anglers tend to express preferences for longer open seasons (Holzer and McConnell 2017; Young et al. 2019; Melnychuk et al. 2021), shorter seasons do not necessarily cause anglers to reduce their fishing effort. For example, during extreme reductions in season length for the red snapper (*Lutjanus campechanus*) fishery in the Gulf of Mexico, daily angler effort substantially increased, leading to a “derby style” fishery where private anglers, who own or rent their own boats, attempted to fish as much possible during their allotted time (Powers and Anson 2018, 2016). Shorter seasons therefore still corresponded to lower harvest across the season, but not in proportion to the change in season length. Because the functional response of fishing effort to shorter seasons is not often quantified and likely varies widely by fishery, this “effort compression” effect complicates managers’ predictions of the response of harvest to changes in regulations. Further, reductions in possession limits can reduce the attractiveness of fishing opportunities to anglers (Whitehead et al. 2015), but angling effort in different fisheries may show different degrees of elasticity to changes in these regulations (Beard et al. 2003; Beardmore et al. 2011a) and may therefore not substantially affect overall harvest (van Poorten et al. 2013). In fisheries where open seasons overlap for multiple species, predicting angler response is further complicated. For example, in the multispecies for-hire recreational fisheries in Alaska, increased restrictions on harvest of Pacific

halibut (*Hippoglossus stenolepis*) has been associated with increased harvest of less restricted species (Beaudreau et al. 2018). This substitution behavior can lead to a continuous “spiraling” effect of regulations where managers implement increasingly strict limits on an increasing variety of species, and anglers continue to adapt by diversifying their targets in order to maintain their harvest (Abbott et al. 2018; Beaudreau et al. 2018). The effects of regulations on fishing effort may therefore depend on how anglers and operators of for-hire vessels respond to fishing opportunity (i.e. season length), harvest potential per trip (i.e. possession limit or variety of species available), and preferences for specific species (e.g. the popularity of species among harvest- or trophy-oriented anglers).

Because of this uncertainty in angler response to regulation, managers of open-access fisheries have not always successfully kept removals below sustainable harvest limits (Coleman et al. 2004; Cooke and Cowx 2004; Cox et al. 2002; Post et al. 2002; NEFSC 2019). This inconsistency in constraining recreational harvest points to a need for empirically understanding the effects of regulations on fishing effort in a multispecies context. Forecasting and “nowcasting” techniques have already been successfully used to predict landings in the Gulf of Mexico recreational fishery for individual species (Carter et al. 2015; Farmer and Froeschke 2015), but not to infer the effects of multiple species’ regulations on fishing effort. By understanding the dynamics of both catch and effort in response to regulations, managers can reduce the uncertainty around how changes in season length of multiple (or individual) seasons in multi-species fisheries will affect fishing effort.

The Marine Recreational Information Program (MRIP) produces estimates of recreational catch and effort for most coastal states. Estimates are aggregated by two-month “waves” or by year. More granular estimates of fishing effort, however can be difficult and expensive to obtain

in recreational fisheries (McCluskey and Lewison 2008), but Vessel Trip Report (VTR) data provide a daily census count of recreational fishing effort aboard federally-permitted for-hire vessels in the Greater Atlantic Region. We then empirically evaluated the response of weekly fishing effort to changes in possession limits, season length, and season overlap in the New Jersey (NJ), USA, for-hire sector of the bottom fishery using this VTR data. To do this, we fit statistical models incorporating effects of four species' overlapping open seasons, their season lengths, and the number of "blackout" days during which none of the four species are available to harvest to a time series of weekly fishing effort. Guided by hypotheses formulated through focus-group interviews with stakeholders, a model selection process allowed us to infer the dominant mechanisms by which changes in possession limits, season length, and species availability could have influenced overall fishing effort in the NJ for-hire bottom fishery. Differences in overall preferences between anglers participating in the charter and party boat fisheries were inferred by fitting these models to time series separately for each sector.

The New Jersey bottom fishery is primarily harvest-motivated (e.g. Bochenek et al. 2012), so we hypothesized that lower possession limits for popular species would be associated with a reduction in angler trips in a given week. While lower possession limits reduce the harvest potential of single fishing trips, shorter and more fragmented fishing seasons instead limit angler access to the fishery. During closed seasons, no targeting of any affected species is permitted, even for catch and release angling. Shorter seasons therefore leave fewer days available to fish for a given species each year, and reduced overlap of these seasons may limit the variety of fish that an angler is allowed to catch and harvest. Reductions in fishery access through shortened seasons has historically been assumed to have a direct effect on fishing effort, where angling trips that would have taken place during the now-closed season simply do not occur. We

hypothesized that reductions in fishing effort associated with shorter seasons may instead be lower or higher than expected depending on whether anglers tended to respond to benefit loss associated with regulatory change by either 1) compensating for reduced fishing opportunity or 2) reducing their participation in the fishery. Of course, angler response to these changes in regulations will be heterogeneous because their responses depend on motivations and preferences that vary among anglers (e.g. Beardmore et al. 2011b). If particular responses dominate angler effort dynamics, however, the overall effect on all angler effort will be useful in a broad-scale policymaking context. We conducted a time series analysis of weekly total angler trips from the recreational for-hire sector in NJ to test the following hypotheses derived from focus group data describing how anglers may have adapted to changes in fishing opportunity:

- 1) *Species availability hypothesis*: Anglers switch between preferred species to maintain their opportunities to go fishing.
- 2) *Season length hypothesis*: Anglers intensify their fishing effort during shorter open seasons to maintain their preferred harvest levels.
- 3) *Blackout effect hypothesis*: In response to an increasing number of “blackout” days, where neither of these four bottomfish are available for harvest, anglers will either a.) increase their fishing effort during the remaining open seasons or b.) begin to exit the fishery.

Methods

Study system

The NJ marine recreational fishery is socioeconomically important, ranking fourth in the nation in state sales revenue generated by the recreational fishing industry (NMFS 2018). NJ anglers are also responsible for substantial removals, ranking second among US states in pounds of recreational harvest and fourth in release numbers (NMFS 2020). The for-hire sector makes

up between 5 and 20% of total recreational catch, depending on the species, while the remaining catch is made up by shore-based anglers and private anglers who own or rent their own boats (ASMFC 2017; MAFMC and ASMFC 2020). The for-hire fleet is made up of party boats (also called head boats), where anglers pay between \$30 and \$90 “per head” for a 4-8 hour guided trip shared with up to 100 other anglers, and charter boats, where a smaller group of anglers (typically 6 or fewer) pays more, currently between \$400 and \$1000, for a more personalized guided fishing trip on a smaller vessel (Steinback and Brinson, 2013). For-hire fishing vessels are highly accessible. Anglers may borrow or rent fishing gear, and no additional licensing or registration is required to participate. Spending by out-of-state anglers is particularly impactful in the for-hire fishing industry, and fishing effort by these anglers in this sector is sensitive to changes in fares (Li et al. 2019; Steinback 1999). As overhead costs (e.g. fuel, bait, boat maintenance) increase among for-hire operators as a result of fuel prices and reduced season lengths, businesses and communities relying on revenue from this sector are increasingly vulnerable to volatility in angler numbers which could result from regulatory changes (Murray et al. 2010).

As fisheries managers have struggled to limit harvest in order to maintain or rebuild fish stocks, the NJ marine recreational fishery has experienced marked changes in possession limits and season lengths for summer flounder (*Paralichthys dentatus*), black sea bass (*Centropristis striata*), scup (*Stenotomus chrisops*), and tautog (*Tautoga onitis*) (Fig. 1, Tables S1-S4). In spite of these changes, black sea bass recreational harvest in recent years (2013-2017) has exceeded harvest limits by an average of 41% (MAFMC 2018), and tautog continues to be classified as overfished (ASMFC 2007; ASMFC 2017). Although summer flounder was not overfished as of the latest stock assessment (NEFSC 2019), changes in distribution, reductions in recruitment,

upward corrections of previous years' harvest estimates, and a strict fisheries management plan have led to the continuation of stringent harvest regulations (ASMFC 2018; Terceiro 2018). Summer flounder is a highly popular target species in the NJ marine recreational fishery, and the resulting short and fragmented seasons in the face of perceived improvement in the summer flounder stock have led to widespread frustration among stakeholders (Terceiro 2018). Tautog season lengths were reduced in 2008 in response to overfishing in the recreational sector (ASMFC 2007). In spite of the rebuilding plan implemented at this time, tautog spawning stock biomass remains low, and the stock is classified as overfished (ASMFC 2017). In contrast, a fisheries management plan for scup that was implemented in 1998 and amended in 2007 was successful in reducing harvest, and the stock was declared recovered in 2009 (MAFMC and NMFS 2007; Northeast Data Poor Stocks Working Group 2009).

Focus groups

Four focus groups were conducted across a north-south transect of the NJ coast in the towns of Atlantic Highlands, Toms River, Tuckerton, and Cape May in the winter and spring of 2019. Participants were identified through purposive sampling in which researchers consulted with NJ state agency staff, extension agents, and industry representatives to identify knowledgeable, experienced, and collaborative recreational fishing industry stakeholders. Two to four stakeholders from each of four industry segments (party boats, charter boats, private anglers who own their own boats or fish from shore, and associated businesses) in each of the four regions were identified, for a potential maximum of 16 participants per focus group. Of these, 44 stakeholders were successfully contacted and invited, and 37 attended. The focus groups ranged from 8 to 11 participants, plus two note takers and a moderator, and they lasted between two and two and a half hours. Focus group participants were asked open-ended questions about their

process for choosing bottomfish target species and how those decisions are influenced by management regulations and their clients' or their own personal preferences. All focus groups were audio recorded, transcribed, and coded for common themes, following the standard analysis guidelines for qualitative research in Creswell and Poth (2016) and Roller and Lavrakas (2015). The focus group procedure was approved by the Rutgers Institutional Review Board (Protocol #E18-112).

Results from the focus groups were used to develop alternative hypotheses to be tested in the analysis of VTR data. Overall, recreational industry representatives expressed strong dissatisfaction with current regulations, especially season length and timing. As one focus group participant said, "What I've observed here is just absolute, total frustration, bordering on anger. And I keep saying to myself, these regulations are going to turn a lot of local fishermen to pirates." Of particular concern to stakeholders were the partitioning of open seasons into shorter periods and the loss of overlapping seasons for different species (Table S5). A common point that stakeholders discussed was that the loss of overlap between different species' open seasons was leading anglers to intensively harvest whatever species remained open at a given time. Two possible mechanisms for this change in behavior were incorporated into the hypotheses for our model selection: 1) anglers maintain harvest potential by compressing fishing effort into shorter seasons to maintain harvest of particular species or 2) anglers switch target species in order to continue fishing on a consistent basis.

Effort, catch, and management data

Vessel Trip Report (VTR) data from for-hire vessels between 2001 and 2017 were obtained from the NOAA VTR database for the Greater Atlantic region. VTRs are a census of vessels with federal permits for black sea bass, summer flounder, or scup where operators report

the number of anglers aboard and enumerate their catch and harvest. VTR data from 2018 and 2019 were not included in the analysis because the 2018 switch to mandated electronic reporting may have resulted in a systematic change in reporting compliance. VTRs do not report target species, so data were filtered according to the vessels' port state and the species they reported catching in order to capture NJ bottom fishing effort. Reports listing capture of bottom fish (defined in Table S6) and a port of departure in NJ were retained. Many more angler trips were reported aboard party vessels, so fishing effort was evaluated separately for party and charter vessels to avoid dominance of fishing effort dynamics by party operators. We first investigated how the for-hire fleet changed during this time period. To do this, we compiled annual counts of reporting vessels, the mean number of anglers per trip, and the mean number of trips per week for party and charter vessels. Next, to build our time series for testing our hypotheses of angler response to regulations, we compiled a weekly time series of fishing effort by summing the total number of angler trips reported by all vessels for each week. This process produced two time series of weekly counts of angler trips on charter and party boats.

Fishing effort can also respond to fishing quality (e.g. Wilson et al. 2020), so we included species-specific catch rates as predictors in our models. Although catch by species is reported in VTRs, reports of catch (number of fish caught) and harvest (number of fish retained, i.e., catch minus fish caught and released) after a trip are prone to recall bias (Bochenek et al., 2012). Catch rates to be used as predictor variables were therefore obtained instead from Marine Recreational Information Program (MRIP) access point intercept survey data (NOAA Fisheries 2021). These surveys take place at ocean access points that are selected within a stratified random sampling regimen. Among other data, respondents report their total species-specific catch, which includes both kept and released fish. Using the procedure described in the MRIP Survey Design and

Statistical Methods documentation (Papacostas and Foster, 2021), we calculated the mean catch per trip for each of our four focal species for each two month survey “wave” in our time series (Fig. S1). Missing values were imputed using linear interpolation for black sea bass and tautog catch rates. Scup catch rates were not included as predictors because of the high number of missing values. Summer flounder missing values occurred in winter months when the stock has migrated off-shore. These missing values were therefore replaced with zero. Average catch rates, rather than spawning stock biomass (SSB), were used to estimate the effects of fishing quality because fish species associated with bottom structure likely exhibit catch rate hyperstability (e.g. Dassow et al. 2019; Erisman et al. 2011). In addition, these catch rates could be calculated for every two months of the time series, while SSB estimates are only available on an annual basis.

NJ fishing regulations for summer flounder, black sea bass, tautog, and scup were collected for the years between 2001 and 2017. Open seasons and possession limits were obtained from annual releases of NJ recreational fishing regulations. Mid-season closures were found by searching the Federal and NJ Registers for rule changes impacting fisheries of the Northeastern United States. State and Federal Registers document rule changes for the federal and NJ state government. The Federal Register can be accessed at <https://www.federalregister.gov/> and the NJ Register at <https://www.state.nj.us/oal/rules/accessp/>. In cases where changes to regulations occurred mid-season, we included only the final regulations in the analysis.

Statistical Analysis

Base ARMA model

We used autoregressive-moving average (ARMA) models to quantify how implementing or changing a management measure affected fishing effort while accounting for autocorrelation and seasonal trends. Fitting a time series model at this granular scale allowed us to detect

average effects of changes in regulations within and between years using external regressors. Simultaneously, additional unexplained variation (i.e. variation in angler trips attributable to weather, changes in trip price, etc) is accounted for implicitly by seasonal and ARMA components. ARMA models account for short-term temporal autocorrelation in time series data by fitting autoregressive (AR) terms to lagged observations and moving average (MA) terms to lagged residuals (Box et al. 2008; Box and Jenkins 1970). Weekly time series have a long and non-integer period (52.14 weeks/year), but seasonal models are periodic, being at the same state as one year previous and repeating. To better align these weekly data with the model's seasonal component, a dynamic harmonic regression approach (Hyndman and Athanasopoulos 2018; Young et al. 1999) was used to fit an appropriate number of Fourier sine-cosine pairs to each time series of fishing effort data. Open seasons for our focal species are highly correlated with seasonality (Fig. 1), so by fitting an identical seasonal trend to each year, we were able to examine how differences in possession limits and season length (e.g. the loss of early and late summer for the summer flounder fishing season) influenced weekly fishing effort in the weeks that did experience differences in regulations among years. Following this approach, increasing numbers of sine-cosine pairs were generated using the forecast package in R v.4.1.0 (Hyndman et al. 2020; R Core Team 2021), and for each of these model fits, the `auto.arima` function of the forecast package was used to find the best fitting ARMA components. The best fitting combination of ARMA components and Fourier sine-cosine pairs was then chosen based on its AICc score. We tested for serial autocorrelation using the Breusch-Godfrey test.

Candidate model construction

In addition to the aforementioned ARMA and seasonality components, we included as predictors the regulations and catch rate variables relevant to the candidate model's hypothesis

(Table 1, Appendix 1). Considerable variation in catch rates both within and between years were evident (Fig. S1). To indicate possession limits and closed seasons for summer flounder, black sea bass, and tautog, an integer predictor indicated the possession limit in that week. A possession limit of 0 indicated a week where targeting the species was not permitted. Scup possession limits during open season remained at 50 for the entire time series, so an indicator variable was used instead to indicate whether week was open (1) or closed (0) for scup fishing (Table 1). An additional dummy variable ('Something open') was used to indicate whether at least one of the four bottomfish species was available for harvest during the week (i.e. a 0 during a blackout period, 1 otherwise).

The models did not include year as a covariate but instead attempted to explain annual variation in fishing effort through six co-variates that described fishing opportunities in each year. Four continuous variables specified the length of each species' season in days for each year. Two additional continuous variables indicated the total number of blackout days in each year as well as the number of open species available each week. In most years, regulations are announced in late spring of their effective year (i.e. shortly before the start of peak summer season). In 2010, 2011, and 2013, however, season lengths were adjusted mid-season for summer flounder and/or black sea bass. In years when regulations were changed mid-season, the final effective season length was used as a predictor. To correspond with the approximate date of the release of new regulations, annual variables, which included season lengths and annual harvest days, were updated annually on May 1.

The *null model* incorporated the assumption that anglers do not compensate for changes in season length and overlap by changing their behavior. This model therefore included only the focal species' possession limits and their catch rates (Table 1). The other three candidate models

included additional predictor variables and interaction effects that tested three hypotheses for how anglers may compensate for regulatory changes (Tables 1 and 2). The *blackout effect model* added the ‘Something open’ predictor to test the hypothesis that open seasons for any of the four focal species would attract fishing effort, regardless of which species were open. In addition, the annual number of blackout days and its interaction with ‘Something open’ was included to test for anglers’ response to an increasing number of blackout days on the calendar (Table 2). A positive interaction effect would suggest that anglers increased their fishing effort during the remaining open days in response to a higher number of blackout days, and a negative interaction effect would indicate that anglers instead tended to stop fishing in response to these changes. To illustrate, as the number of blackout days in a year increases from 0 to 30, an intensification of fishing effort during the open season would be indicated by a positive parameter value for the two-way interaction of the number of blackout days and the ‘Something open’ indicator. A week where at least one species is open during a year with 30 blackout days would then have a higher predicted fishing effort than that of a week in a year with 0 blackout days. On a blackout week, however, the ‘Something open’ indicator is zero, negating the interaction effect.

The *season length model*, in contrast, allowed anglers to display different responses to changes in the season length of different species. The model incorporated this behavior by including season length as a predictor conditional on the corresponding species’ open season (i.e. the possession limit is greater than 0). Our hypothesis that anglers would compensate by increasing their fishing effort during the remaining open season would be supported by a negative interaction effect between species-specific season length and the corresponding open season indicator. The *species availability model* accounted for specific substitution patterns used by anglers to maintain their fishing opportunities as the overlap between different species’ open

seasons was reduced. A negative interaction effect between species-specific open seasons and the number of species that were available would indicate a non-additive response of fishing effort to new open seasons. In other words, adding an additional open species to a given week would result in a lower increase in fishing effort than expected because many of those anglers were already fishing.

Model selection

We evaluated the ability of our four candidate models to explain weekly natural log-transformed total fishing effort for party boats and charter boats. Angler trip counts were log-transformed to account for the greater variance in fishing effort during peak fishing season. The fit of the competing models was compared using the corrected Akaike Information Criterion (AICc) and their associated Akaike weights calculated using the MuMIn package (Bartoń 2020).

To evaluate the relative effects of changes in black sea bass and summer flounder possession limits and season length, we produced annual predictions of angler trips for hypothetical years under different regulations. Tautog regulations were not evaluated in this way because possession limits primarily changed within rather than between years in order to protect tautog from excessive harvest during their summer spawning season (Table S3). For each of these predictions, the fishing effort associated with each week of an average year (i.e. the average value of each week's sine-cosine coefficient pairs across all years of the time series) at average catch rates (i.e. the average value of each week's CPUE for summer flounder, black sea bass, and tautog) were forecast using the best fitting ARMA model with the predict.Arima function (R Core Team, 2021). Only the species of interest was "opened" for the hypothetical forecasted year. A year of weekly predictions were forecasted for each combination of possession limits and season lengths. We then applied a bias correction to these predictions

based on a non-parametric smearing adjustment (Duan, 1983), and annual fishing effort was summed for each forecasted year. These predictions produced estimates of the annual fishing effort associated with different combinations of season length and possession limits for specific species. These forecasts are intended to illustrate the relative effects of possession limit and season length changes for different species on angler trips in past years. They are not intended to forecast out-of-sample future changes in fishing effort.

Results

Fleet changes

The NJ for-hire bottom fishing fleet has experienced a number of changes since 2001. The decline in charter vessels reporting each year since 2010 is particularly distinctive, declining from 119 to 57 reporting vessels (Fig. 2A). In spite of the decline in charter vessels, the number of charter boat anglers and the mean number of anglers per charter trip have remained largely constant (Fig. 2B and 2C). This consistency in angler numbers is explained by a near-doubling in the average number of trips taken per charter vessel between 2010 and 2015, from 17.6 to 28.6 charter trips per year. In contrast, the number of party boats has shown a less extreme overall decline, with the exception of a period between 2001 and 2005, where the number of reporting party boats dropped by nearly half (Fig. 2A). This change in party boat numbers corresponds with simultaneous decline in party boat angler trips (Fig. 2B) and a reduction in the average number of trips taken by each vessel (Fig. 2D). Both party boat numbers and angler numbers largely recovered by 2010, but they remained lower than in the early 2000s.

Model selection

Charter boat fishing effort

The time series of charter boat and party boat fishing effort differed in their best fitting models (Tables 3 and 5), indicating that charter and party boat anglers responded differently to changes in regulations. The *blackout effect model* was unambiguously the best fit to charter boat fishing effort, receiving 100% of the Akaike weight (Table 3). The ARMA and seasonal components of the model effectively removed serial autocorrelation of the residuals according to the Breusch-Godfrey test (Table S7). Total fishing effort on charter boats was relatively consistent between years (Fig. 2B), and variation in weekly effort was driven mainly by seasonality rather than by open seasons of specific species (Tables 4 and S8). In spite of these species' popularity, neither black sea bass, summer flounder, or tautog possession limits, nor scup open seasons were associated with significant changes in fishing effort on their own (Table 4). All else being equal, the opening of at least one of the four species was associated with an over 6-fold increase in angler trips (i.e. $\exp(1.954)=7.06$), suggesting that charter anglers are flexible in their species preferences ($p=0.008$, Table 4). All else being equal, the availability of at least one of the four focal species was associated with an over 600% increase in fishing effort compared to a "blackout" day. The interaction of the 'Something open' indicator with the annual number of blackout days, however, was not significant ($p=0.143$, Table 4). Charter boat anglers therefore did not appear to leave the fishery in response to increasing numbers of blackout days, which would have been evident by a negative interaction. Nor did they appear to compensate for blackout days by increasing fishing effort, which would have been evident by a positive interaction. Fishing effort of charter angler trips also did not appear to respond to summer flounder, black sea bass, or tautog catch rates when aggregated at the two-month level.

Party boat fishing effort

The species availability model was unambiguously the best fit to the time series of party boat angler trips (Table 5). Summer flounder, tautog, and black sea bass possession limits were significant predictors of fishing effort, where an increase in limit of 1 fish was respectively associated with a 26%, 15%, and 5% increase in angler trips. The opening of multiple species simultaneously, however, did not have an additive effect on fishing trips. The negative interaction between summer flounder, tautog, and black sea bass open seasons and the number of open species suggests that a subset of the anglers fishing for summer flounder, for example, were already previously fishing for black sea bass or tautog before the flounder season opened. Weeks where all three species are open for harvest therefore experienced fewer angler trips than would be predicted by only the species-specific possession limits. Scup open seasons, in contrast, were associated with increased angler trips in combination with the availability of additional target species. In our dataset, scup only occurred in combination with at least one other species ($N_{\text{species}}=2$). During these combined seasons of two species (usually tautog and scup), scup is associated with only a small decrease in mean angler trips (i.e. $\exp(-0.944+1*0.99)=0.996$, or a 0.4% decrease in angler trips). In combination with two or three other species, however, scup season is respectively associated with a 63% or 268% increase in fishing trips. These overlaps typically occurred in the peak summer season, when scup is available inshore. During the rest of its winter open season, scup has migrated offshore to deeper water, where it is more difficult to target (NMFS 1999). Fishing effort did not obviously respond to black sea bass or summer flounder catch rates, but angler trips did increase by 3% in correspondence with an increase in tautog catch rates of 1 fish per trip ($p = 0.015$, Table 6).

Multicollinearity was detected between certain predictor variables for the species availability model, with variance inflation factors (VIF) as high as 9.9 (Table S11). To test the

sensitivity of the parameter estimates to this collinearity, we completed a supplemental analysis by re-fitting the model without the most highly correlated predictors (i.e. summer flounder possession limits and catch rates). Coefficient estimates were effectively the same, except for the interaction effect of tautog possession limits with the number of open species (Tables S12 and S13). When summer flounder-associated predictors were removed from the model, this interaction was no longer significant.

Black sea bass seasons experienced substantial variation in both possession limits and season lengths among years (Fig. 3). Only modest increases in annual angler trips relative to closed season were associated with the possession limits of two or three fish that were implemented in peak summer fishing seasons starting in 2014 (Fig. 1). Higher possession limits, in contrast, were associated with tens of thousands more angler trips per year. Summer flounder season lengths experienced less change among years in our analysis (Fig. 4A). In spite of this limited variation of season lengths, distinct changes in annual fishing effort were detected. As possession limits were lowered, however, the response of annual fishing effort to season length became less distinct (Fig 4B).

Discussion

Previous survey-based studies of recreational anglers' stated preferences have highlighted the importance of preserving fishing opportunities in the form of open fishing seasons in order to maintain angler satisfaction (Brinson and Wallmo 2017; Young et al. 2019). The use of VTR data allowed us to investigate the empirical response of anglers aboard for-hire vessels to reduced fishing opportunity. We found evidence of substantial reductions in annual fishing effort within the party and charter boat fisheries as a result of reduced possession limits and, to a lesser extent, contracting season lengths. These results support the concerns expressed by focus group

participants regarding reduced profitability of for-hire fishing vessels in the face of these increased restrictions. Fishing effort dynamics within the charter boat fishery were best explained by the *blackout effect model*, where the ability to harvest any one of the four species was a more important predictor of fishing effort than the availability of any specific species. Fishing effort in the party boat fishery, in contrast, was best explained by the *species availability model*, and angler trips specifically responded positively to summer flounder and black sea bass open seasons. The non-additive effects of additional open seasons suggested a significant degree of substitution behavior occurring among party boat angler trips as species open and close throughout the season. The interaction effect of tautog open season with species availability was non-significant in the sensitivity model fit that eliminated summer flounder predictors. Substitution behavior may therefore be less common among tautog anglers. Among charter boat anglers, however, substitution behavior appears to be even more prevalent, as indicated by the strong positive effect of the “Something open” predictor.

Although substitution behavior appears to vary between charter and party boat anglers, our ability to infer specific angler behaviors is limited because the number of angler trips in a week also depends on the availability of trips for hire. Responses of angler trips to regulations may therefore indicate differences in operator behavior rather than angler preferences. The corresponding decline in federally permitted charter vessels and increase in annual trips per vessel, for example, suggest that the demand for charter trips may exceed the supply. If the remaining operators are allowed to target bottom fish on a given day, they will most likely be able to reserve enough customers to fill their vessel. The response of charter angler trips to the availability of “something” may therefore be an indication of operator behaviors. Angler trips aboard party vessels, however, appeared to show more room for variation. Similar to charter

trips, the number of weekly party angler trips can be limited by the availability of spots aboard party vessels. Conversely, at very low demand, party vessels will cancel trips if the number of spots sold do not recoup costs. However, considerably more variation is possible in the number of anglers aboard large party boats once this threshold of profitability is reached, suggesting to us that party boat fishing effort dynamics primarily reflect angler preferences. In particular, the large negative effects of reduced possession limits on the number of weekly angler trips suggest that many anglers have quit bottom fishing on party vessels in response to these changes.

Because substitution behaviors do not appear to be as strong in the party fishery as in the charter sector, party vessel operators probably could not rely on angler substitution of less popular bottom species to maintain their profits. Party vessel operators may therefore be particularly vulnerable to the negative economic effects of increased restrictions on bottomfish harvest.

Considerable additional variation existed in angler trips that was not explained by changes in regulations. For example, a nearly 50% drop in angler trips occurred between 2005 and 2010 (Fig. 5), which did not correspond to any specific changes in regulations. This time period does, however, roughly correspond with a period of conflict over reductions in the acceptable biological catch (ABC) for summer flounder, the implementation of conservation equivalency among states, and the stock assessment methods used by fisheries scientists (Terceiro 2011). The rebound in party boat angler numbers in 2010 is also coincident with a new stock assessment indicating that the summer flounder stock was not overfished and did not experience overfishing between 2008 and 2010 (Terceiro 2018). As a new control rule was implemented after the 2011 season, however, the ABC was reduced, leading to another round of conflict between scientists, managers, and stakeholders (Terceiro 2018). At the seasonal level, these changes in annual fishing effort stem from a reduction in “peak” fishing effort for summer

flounder during the summer months of May through August (Fig. 5A). Although black sea bass availability is also associated with higher fishing effort aboard party boats, similar patterns in monthly fishing effort are evident during years with and without year-round black sea bass seasons (Fig. 5B). Therefore, although fishing regulations influenced the number of angler trips each week, we speculate that trust in management and public perceptions of summer flounder stock health are potentially important predictors of fishing effort.

Vessel Trip Report data represent a large and mostly untapped resource for studying marine recreational fishing effort dynamics. However, they also present several challenges. First, only vessels with federal permits are required to submit VTRs. Federal permits are required for summer flounder, black sea bass, and scup fishers, but not for tautog. Charter vessels in particular may be underreported in the VTR data if they do not target either of these three species. In addition, VTRs report catch but not target species. We therefore defined bottomfishing trips based on the reported capture of at least one of nine bottom-associated species, which may have excluded some bottomfishing trips where nothing was caught. However, fishing trips with no reported catch made up only 1.5% of all fishing reports, so we believe that any effects of their elimination should be minimal. By filtering data by catch, we may also have included some trips targeting non-bottomfish species, such as striped bass (*Morone saxatilis*) or bluefish (*Pomatomus saltatrix*), during which bottomfish were caught incidentally. Both of these species remained open during the “blackout” periods recorded in our time series. The distinctively reduced weekly effort aboard charter vessels evident during these blackout periods suggests, however, that our filtering was largely successful at removing these trips. In addition, minimum length limits are important issues for fishery stakeholders (Table S5), but they were not included as predictor variables because of excessive collinearity with

possession limits. Minimum length limits tended to increase as possession limits decreased, so some of the effects of minimum length limits on fishing effort were explained in our model fits by changes in possession limits. Lastly, although VTRs provide a census count of anglers aboard federally permitted for-hire vessels, operators targeting tautog are not required to acquire a federal permit. We expected that operators targeting tautog would also target other highly popular bottomfish that do require federal permits, but we may have missed vessels specializing in tautog fishing, particularly among charter vessels.

The apparent willingness of anglers to substitute target species aboard charter boats, and to a lesser extent aboard party boats, has a number of implications for management of marine recreational fisheries. In particular, the relatively stable fishing effort in the charter sector regardless of individual species' closures suggests that discards may be high for closed species that are caught incidentally when anglers target other bottom fish. In other fisheries where anglers show high willingness to substitute target species, discard mortality has been demonstrated to reduce the effectiveness of seasonal closures (Chagaris et al., 2019). This phenomenon highlights the importance of understanding angler motivations for maintaining fishing opportunities and/or harvest. The relative importance of preserving fishing opportunity versus harvest capacity has been investigated in a variety of systems (e.g. Melnychuk et al., 2021; Young et al., 2019) and angler response to these changes appears to depend in part on anglers' willingness to re-allocate fishing effort to other time periods or alternative species. In other harvest-oriented fisheries, anglers express strong preferences for higher possession limits (e.g. Mackay et al. 2020). Reductions in possession limits and complete closures reduce anglers' harvest capacity and therefore their expected satisfaction, resulting in reduced fishing effort overall if anglers are unwilling to substitute less-restricted species (Powell et al., 2010).

Redirected fishing effort can lead to increased harvest of substitute species (Beaudreau et al., 2018) or increased discard mortality when closed or restricted species are caught and released (Chagaris et al., 2019). Although we investigated only the response of for-hire recreational fishing effort, the effect of regulation change on total recreational fishing effort also depends on the response of private boat anglers. These anglers do not rely on the availability of spots aboard for-hire vessels, suggesting that they have more ability to respond to closures by re-allocating fishing effort to different times of year. This response was observed in the Gulf of Mexico red snapper fishery when season length was drastically reduced (Chagaris et al., 2019; Powers and Anson, 2018, 2016). In less extreme instances of season reductions, however, private anglers may instead target alternative species to maintain their level of harvest or opportunities to fish, leading to a more stable pattern of fishing effort similar to our observations of charter vessels. Alternatively, the costs of maintaining a private vessel may drive some private anglers to leave the fishery when regulations become more stringent. If this choice is widespread, fishing effort, harvest, and discards would decline, but coastal communities would also experience the negative economic impacts associated with reduced angler participation. Responses to regulations among both private and for-hire anglers are therefore important to understand when evaluating the effects of new regulations on fishing effort, harvest, and discard mortality. An ongoing project by this team is using stated preference methods to investigate these potential responses among private and for-hire anglers.

Fisheries managers constantly consider tradeoffs in ecological, social, and economic objectives with the goal of maintaining stocks above safe harvest limits, maintaining public access to the fishery, and supporting the economies of coastal communities (e.g. Punt 2017). In addition to wrestling with uncertainties in population dynamics of important stocks, considerable

uncertainty surrounds the response of fishers to changes in regulations and ecological conditions (Fulton et al. 2011). Accounting for the responses of human stakeholders with heterogeneous and often competing preferences is vital for enacting proactive management decisions (Johnston et al. 2010). For-hire vessels make up one of these heterogeneous stakeholder groups and provide relatively low-cost access to fish stocks for recreational anglers globally. Recreational fisheries are also a major source of fishing mortality (Coleman et al. 2004; Cooke and Cowx 2004), and many of the costs of reduced harvest are borne by for-hire vessels, their customers, and the coastal communities relying on their economic contributions. In recent years, for example, fleet diversity of the recreational fishery in the Mid-Atlantic has declined as more anglers switch to shore-based modes of fishing and away from for-hire vessels (NEFSC 2021). Between uncertainty surrounding new regulations each year and reduced participation of anglers in the for-hire sector, for-hire operators are left in a precarious economic position. Illustrating this concern, one focus group participant stated, “Name me one industry besides fishing [...] where we can’t go year to year and we can’t budget, we can’t forecast, we can’t predict. And you show me one industry where you have that every year, year after year, and still stay in business.” Fisheries managers are therefore left in the difficult position of being accountable for keeping recreational harvest within imposed limits while also balancing the biological, social, and economic objectives of stakeholders, including these for-hire operators. Uncertainty associated with angler responses to changes in fishing regulations is an important limitation in managers’ ability to constrain recreational harvest. Further investigations of angler behavioral responses to regulation should continue to help managers to enact regulations that prevent overharvest while meeting the economic needs of coastal communities.

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Tables

Table 1: Predictor variable descriptions for each of the four models. Checks mark the predictors that were included in each model, and asterisks indicate the predictors that were included as predictors conditional on the corresponding open season. Obelisks indicate predictors with two-way interactions with corresponding species' possession limits. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP).

Predictors	Description	Variable type	Update frequency	Null model	Blackout effect model	Season length model	Species availability model
'BSB PL'	Possession limits of each focal species, with 0 indicating closed season.	Integer	Weekly				
'SMF PL'							
'TOG PL'							
'SCP open'							
	Scup possession limits did not change, so scup open season is a binary variable, with 1 indicating open season and 0 closed.			✓	✓	✓	✓
'CPUE BSB'	Mean catch per trip of each focal species	Continuous	Bimonthly				
'CPUE SMF'							
'CPUE TOG'				✓	✓	✓	✓
'Something open'	Indicator that at least one of the focal species' seasons is open (i.e. $PL > 0$)	Binary	Weekly		✓		
'N blackout days'	Annual number of blackout days, where none of the focal species are open	Integer	Annual		✓		

'Season length BSB'	Number of days of open season	Integer	Annual	
'Season length SMF'	per year for each focal species			✓*
'Season length TOG'				
'Season length SCP'				
'N species open'	Number of focal species open each week	Integer	Weekly	✓+

Table 2: Hypotheses about angler behavioral responses to changes in regulations for flounder (SMF), black sea bass (BSB), tautog (TOG), and scup (SCP). Hypotheses are illustrated with representative quotations from stakeholder focus groups and operationalized in candidate models with different interaction effects. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP). Bolding indicates the interaction sign that supports the hypothesis represented by the selected quotation. Further detail on model parameterization can be found in Appendix 1 of the Supplementary materials.

Model	Representative quotation	Interaction effects	Interpretation
0. Null	N/A	N/A	N/A
1. Blackout effects	<i>“We do see a tremendous setback that occurs because of the eight or ten-day closure during the end of June. The people just kind of stop coming when that happens and you go [snaps fingers] it’s over.”</i>	Something open * number of blackout days	Positive: Anglers compensate for fewer harvest days (or more blackout days) with higher weekly fishing effort
2. Season length	<i>“We used to fish through March. When you could do that, you didn’t need to all press in to whatever the next fishery was...Now everybody’s just trying to get every last day in that they can because there’s so few of them available.”</i>	Season length BSB : BSB open Season length SMF : SMF open Season length TOG : TOG open Season length SCP : SCP open	Negative: Anglers leave the fishery on year with fewer harvest days/more blackout days. Negative: Effort compression. Anglers compensate for shorter seasons of particular species by increasing weekly fishing effort while that species is open.

1. Species availability	<p><i>“[Black] sea bass is the only thing open. [Tau]tog’s closed, fluke’s closed. All of the angler pressure is now on sea bass. Where it used to spread out and diversify and the anglers would do other things, no matter what it was. You have a very severe angler impact on a single species due to the way regulations are set up, leaving no other choice but to target specific species.”</i></p>	<p>BSB PL * N species open SMF PL * N species open TOG PL * N species open SCP Open * N species open</p>	<p>Negative: Anglers switch target species when the season for their initial target species closes.</p>
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Table 3: Model fit and Akaike weights of all candidate models for the time series of charter boat fishing effort. Bolded values indicate the lowest AICc and highest weight.

Model	AICc	AICc weight	Log Likelihood	# Parameters
Null model	2192.76	0	-1052.24	42
Blackout effect model	2173.31	1	-1063.02	23
Season length model	2189.84	0	-1044.11	48
Species availability model	2193.47	0	-1048.16	46

Table 4: Coefficients of blackout effect model fit to charter boat fishing effort time series. Coefficients of the autoregressive, moving average, and seasonal component can be found in Table S8. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP). Bolded values are significant at the $p < 0.05$ level. DF=870

Coefficient	Estimate	Standard error	T value	P value
Intercept	2.203	0.760	2.897	0.004
BSB PL	0.004	0.005	0.733	0.464
SMF PL	0.018	0.022	0.852	0.394
TOG PL	0.032	0.025	1.307	0.192
SCP Open	0.229	0.152	1.507	0.132
Something open	1.954	0.740	2.641	0.008
N blackout days	0.024	0.017	1.465	0.143
Something open * N blackout days	-0.019	0.017	-1.170	0.242
SMF CPUE	0.010	0.029	0.350	0.727
BSB CPUE	0.007	0.006	1.069	0.285
TOG CPUE	-0.017	0.019	-0.902	0.367

Table 5: Model fit and Akaike weights of all candidate models for the time series of party boat fishing effort. Bolded values indicate the lowest AICc and highest weight.

Model	AICc	AICc weight	Log Likelihood	# Parameters
Null model	1517.43	0	-726.55	31
Blackout effect model	1502.68	0	-715.94	34
Season length model	1510.27	0	-710.29	39
Species availability model	1482.59	1	-704.82	35

Table 6: Coefficients of species availability model fit to party boat fishing effort time series. Coefficients of the autoregressive, moving average, and seasonal component can be found in Table S10. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP). Bolded values are significant at the $p < 0.05$ level. DF=855

Coefficient	Estimate	Standard error	T value	P value
Intercept	5.745	0.168	34.228	<0.0001
BSB PL	0.050	0.010	5.050	<0.0001
SMF PL	0.227	0.045	5.089	<0.0001
TOG PL	0.141	0.033	4.283	<0.0001
SCP Open	-0.994	0.268	-3.712	0.0002
BSB PL x N species available	-0.014	0.004	-3.880	0.0001
SMF PL x N species available	-0.047	0.014	-3.474	0.001
TOG PL x N species available	-0.034	0.013	-2.506	0.012
SCP Open x N species available	0.495	0.095	5.185	<0.0001
SMF CPUE	0.005	0.023	0.219	0.827
BSB CPUE	0.004	0.004	0.923	0.356
TOG CPUE	0.030	0.012	2.444	0.015

Figures

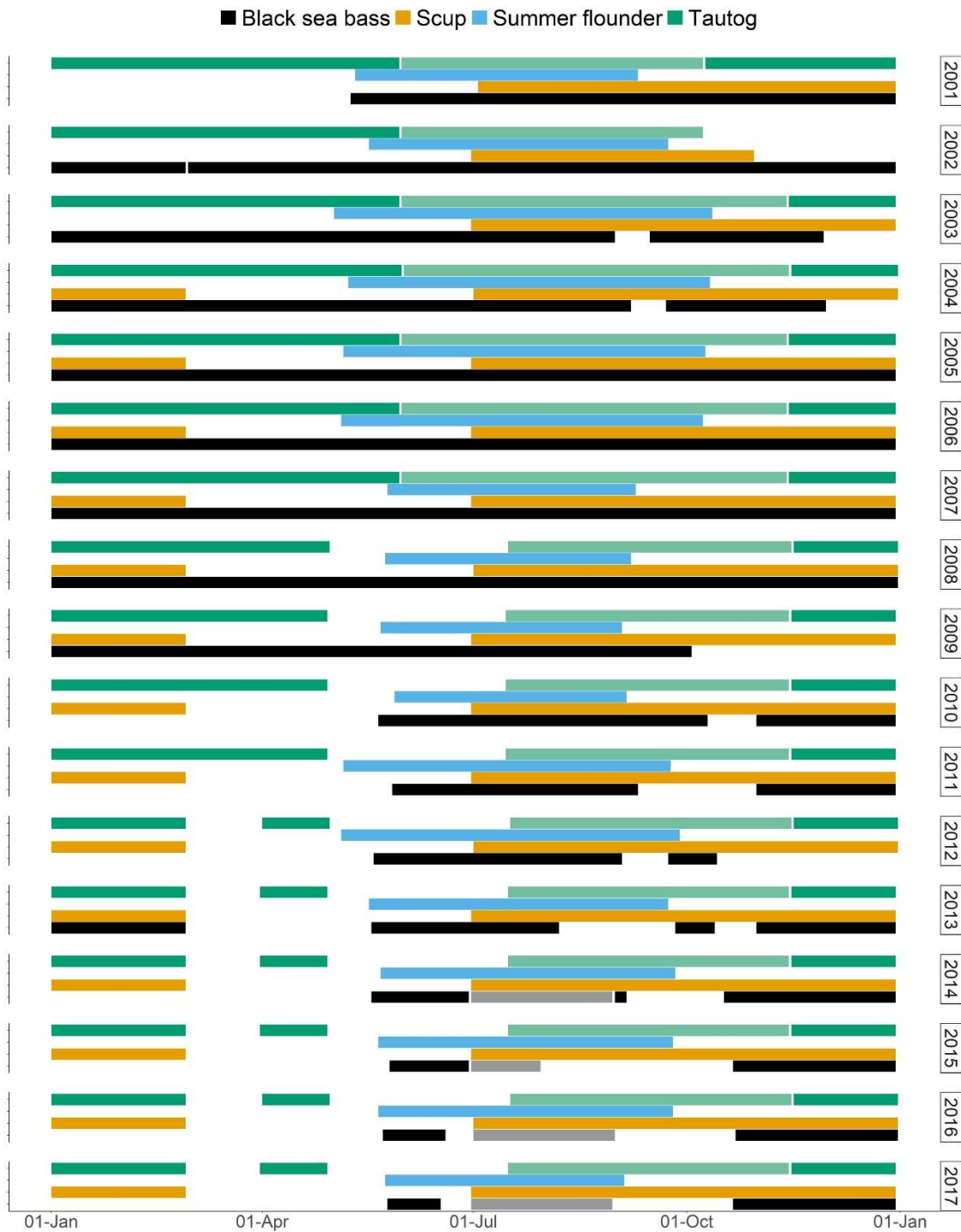


Figure 1: Changes in New Jersey season length and overlap for tautog (top, green), summer flounder(blue), scup (yellow), and black sea bass (bottom, black) between 2001 and 2017. Colored bars delineate open seasons for each of the four species. Light green bars for tautog

indicate 1 fish possession limits during the summer and fall months. Gray bars starting in 2014 illustrate black sea bass summer seasons with 2 or 3 fish possession limits.

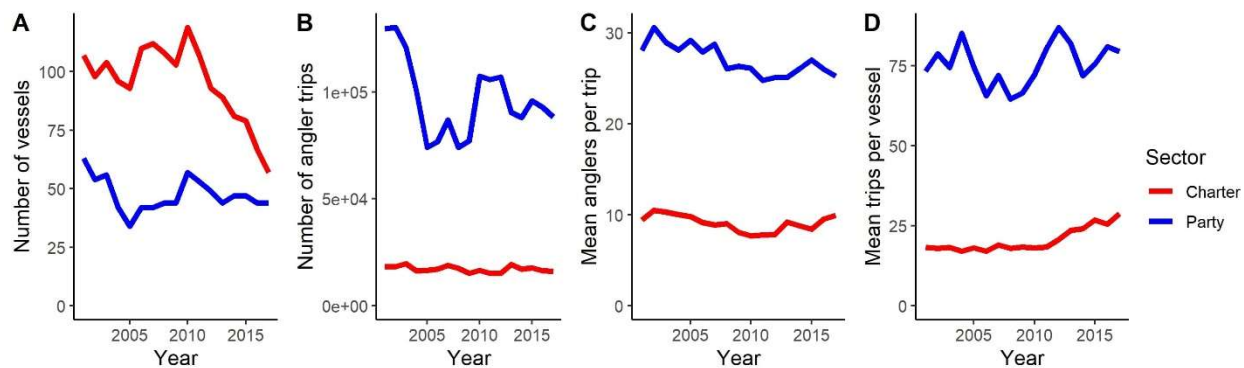


Figure 2: Changes in the annual number of vessels reporting from the for-hire bottom-fishing fleet (A), the number of angler trips reported (B), the mean number of anglers per trip reported (C), and the mean number of trips per vessel reported (D) between 2001 and 2017 in the NJ charter and party boat fleets.

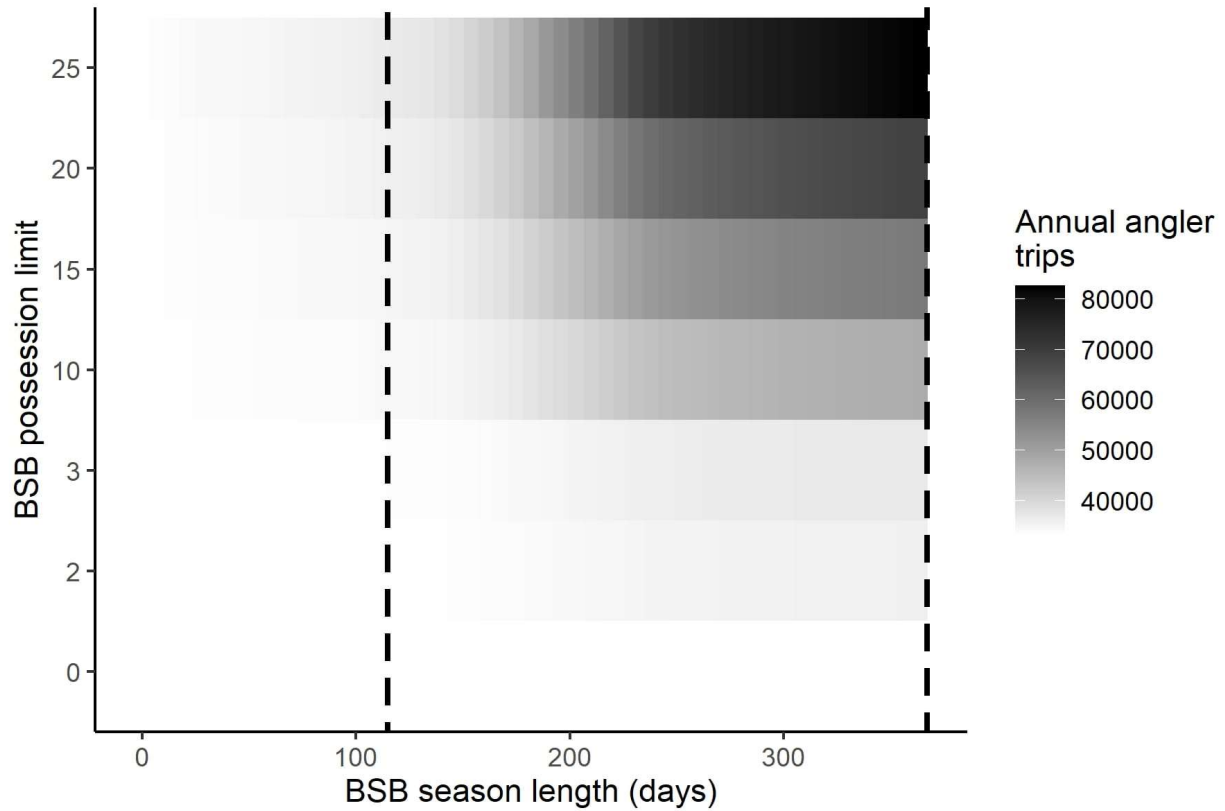


Figure 3: Annual party boat angler trips predicted across a range of season lengths and possession limits for black sea bass. In these model predictions forecasting effort from hypothetical regulations, only black sea bass season is open. The area between the two dashed lines indicates season lengths that are represented in the data.

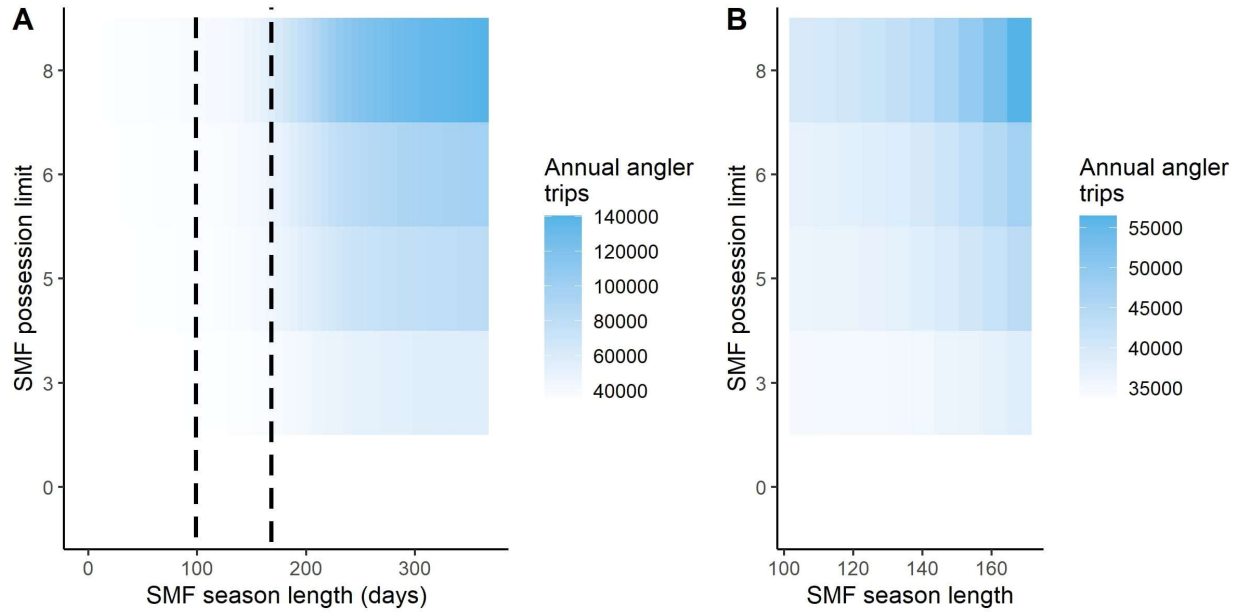


Figure 4: Annual party boat angler trips predicted across a full range of possession limits, hypothetical season lengths (A), and the season lengths represented in the data (B) for summer flounder (i.e. B is a subset of A). The area between the two dashed lines indicates season lengths that are represented in the data. In these model predictions forecasting effort from hypothetical regulations, only summer flounder season is open.

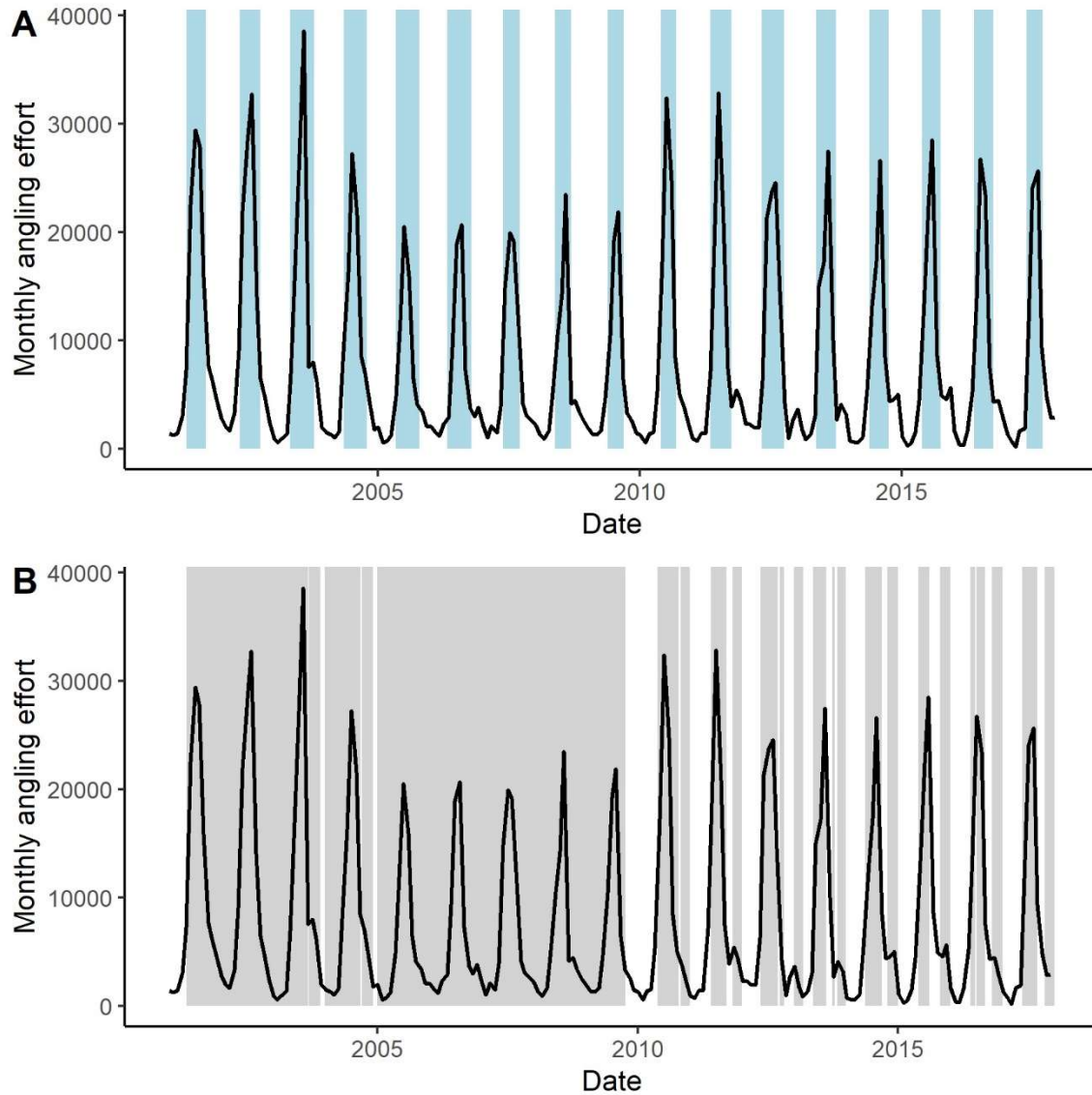


Figure 5: Monthly fishing effort in the party boat sector of the NJ for-hire recreational fishery. Summer flounder open seasons are highlighted in blue on plot A, and black sea bass seasons are in gray on plot B.

Appendix

Candidate models take the following form for the best fit number of sine-cosine pairs, k , autoregressive coefficients p , and moving average coefficients q at time t . Sine-cosine pairs are fit to observations at time t through the ω coefficients. Error terms are indicated by ε . Catch per unit effort (CPUE) and regulation covariates are included for black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP).

Null model

$$\ln(1 + N \text{ angler trips}_t)$$

$$= \sum_{k=1}^K [\alpha_{1,k} \cos(\omega_{1k}t) + \alpha_{2,k} \sin(\omega_{2k}t)]$$

$$+ \sum_{p=1}^P \phi_p \ln(N \text{ anglers})_{t-p}$$

$$+ \sum_{q=1}^Q \theta_q \varepsilon_{t-q}$$

$$+ \beta_0 + \beta_1 \text{ Possession limit SMF}_t + \beta_2 \text{ Possession limit BSB}_t$$

$$+ \beta_3 \text{ TOG Possession limit}_t + \beta_4 \text{ Open season SCP}_t + \beta_5 \text{ CPUE SMF}_t$$

$$+ \beta_6 \text{ CPUE BSB}_t + \beta_7 \text{ CPUE TOG}_t + \varepsilon_t$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

Blackout effect model

$$\ln(1 + N \text{ angler trips}_t)$$

$$= \sum_{k=1}^K [\alpha_{1,k} \cos(\omega_k t) + \alpha_{2,k} \sin(\omega_k t)]$$

$$+ \sum_{p=1}^P \phi_p \ln(N \text{ anglers})_{t-p}$$

$$+ \sum_{q=1}^Q \theta_q \varepsilon_{t-q}$$

$$+ \beta_0 + \beta_1 \text{ Possession limit SMF}_t + \beta_2 \text{ Possession limit BSB}_t$$

$$+ \beta_3 \text{ Possession limit TOG}_t + \beta_4 \text{ Open season SCP}_t + \beta_5 \text{ CPUE SMF}_t$$

$$+ \beta_6 \text{ CPUE BSB}_t + \beta_7 \text{ CPUE TOG}_t + \beta_8 \text{ Something open}_t$$

$$+ \beta_9 N \text{ blackout days}_t + \beta_{10} \text{ Something open}_t * N \text{ blackout days}_t + \varepsilon_t$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

Season length model

$$\ln(1 + N \text{ angler trips}_t)$$

$$= \sum_{k=1}^K [\alpha_{1,k} \cos(\omega_k t) + \alpha_{2,k} \sin(\omega_k t)]$$

$$+ \sum_{p=1}^P \phi_p \ln(N \text{ anglers})_{t-p}$$

$$+ \sum_{q=1}^Q \theta_q \varepsilon_{t-q}$$

$$+ \beta_0 + \beta_1 \text{ Possession limit SMF}_t + \beta_2 \text{ Possession limit BSB}_t$$

$$+ \beta_3 \text{ Possession limit TOG}_t + \beta_4 \text{ Open season SCP}_t + \beta_5 \text{ CPUE SMF}_t$$

$$+ \beta_6 \text{ CPUE BSB}_t + \beta_7 \text{ CPUE TOG}_t + \beta_8 \text{ Season length SMF}_t$$

$$+ \beta_9 \text{ Season length BSB}_t + \beta_{10} \text{ Season length TOG}_t$$

$$+ \beta_{11} \text{ Season length SCP}_t + \beta_{12} \text{ Open season SMF}_t * \text{ Season length SMF}_t$$

$$+ \beta_{13} \text{ Open season BSB}_t * \text{ Season length BSB}_t$$

$$+ \beta_{14} \text{ Open season TOG}_t * \text{ Season length TOG}_t$$

$$+ \beta_{15} \text{ Open season SCP}_t * \text{ Season length SCP}_t + \varepsilon_t$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

Species availability model

$$\ln(1 + N \text{ angler trips}_t)$$

$$\begin{aligned}
&= \sum_{k=1}^K [\alpha_{1,k} \cos(\omega_k t) + \alpha_{2,k} \sin(\omega_k t)] \\
&+ \sum_{p=1}^P \phi_p \ln(N \text{ anglers})_{t-p} \\
&+ \sum_{q=1}^Q \theta_q \varepsilon_{t-q} \\
&+ \beta_0 + \beta_1 \text{ Possession limit SMF}_t + \beta_2 \text{ Possession limit BSB}_t \\
&+ \beta_3 \text{ Possession limit TOG}_t + \beta_4 \text{ Open season SCP}_t + \beta_5 \text{ CPUE SMF}_t \\
&+ \beta_6 \text{ CPUE BSB}_t + \beta_7 \text{ CPUE TOG}_t \\
&+ \beta_8 \text{ Possession limit SMF}_t * N \text{ species open}_t \\
&+ \beta_9 \text{ Possession limit BSB}_t * N \text{ species open}_t \\
&+ \beta_{10} \text{ Possession limit TOG}_t * N \text{ species open}_t \\
&+ \beta_{11} \text{ Open season SCP}_t * N \text{ species open}_t + \varepsilon_t
\end{aligned}$$

$$\varepsilon_t \sim N(0, \sigma^2)$$

Supplementary materials

Table S1: Black sea bass seasons, possession limits, and minimum length limits from 2001 to 2017.

Season open	Season close	Possession limit	Minimum length limit (inches)
5/10/2001	12/31/2001	25	11
1/1/2002	2/28/2002	25	11
3/1/2002	12/31/2002	25	11.5
1/1/2003	9/1/2003	25	12
9/16/2003	11/30/2003	25	12
1/1/2004	9/7/2004	25	12
9/22/2004	11/30/2004	25	12
1/1/2005	12/31/2005	25	12
1/1/2006	12/31/2006	25	12
1/1/2007	12/31/2007	25	12
1/1/2008	12/31/2008	25	12
1/1/2009	10/4/2009	25	12.5
5/22/2010	10/11/2010	25	12.5
11/1/2010	12/31/2010	25	12.5
5/28/2011	9/11/2011	25	12.5
11/1/2011	12/31/2011	25	12.5
5/19/2012	9/3/2012	25	12.5
9/23/2012	10/14/2012	25	12.5
1/1/2013	2/28/2013	15	12.5
5/19/2013	8/8/2013	20	12.5
9/27/2013	10/14/2013	20	12.5
11/1/2013	12/31/2013	20	12.5
5/19/2014	6/30/2014	15	12.5
7/1/2014	8/31/2014	3	12.5
9/1/2014	9/6/2014	15	12.5
10/18/2014	12/31/2014	15	12.5
5/27/2015	6/30/2015	15	12.5
7/1/2015	7/31/2015	2	12.5
10/22/2015	12/31/2015	15	12.5
5/23/2016	6/19/2016	10	12.5
7/1/2016	8/31/2016	2	12.5
10/22/2016	12/31/2016	15	13
5/26/2017	6/18/2017	10	12.5
7/1/2017	8/31/2017	2	12.5
10/22/2017	12/31/2017	15	12.5

Table S2: Season lengths, possession limits, and minimum length limits for summer flounder between 2001 and 2017. Differences in regulations between marine and Delaware Bay regulations were implemented starting in 2016.

Season open	Season close	Possession limit marine	Possession limit Del. Bay and tributaries	Minimum length limit marine (inches)	Minimum length limit Del. Bay and tributaries (inches)
5/15/1999	10/11/1999	8	8	15.5	15.5
5/6/2000	10/20/2000	8	8	15.5	15.5
5/12/2001	9/11/2001	8	8	16	16
5/18/2002	9/24/2002	8	8	16.5	16.5
5/3/2003	10/13/2003	8	8	16.5	16.5
5/8/2004	10/11/2004	8	8	16.5	16.5
5/7/2005	10/10/2005	8	8	16.5	16.5
5/6/2006	10/9/2006	8	8	16.5	16.5
5/26/2007	9/10/2007	8	8	17	17
5/24/2008	9/7/2008	8	8	18	18
5/23/2009	9/4/2009	6	6	18	18
5/29/2010	9/6/2010	6	6	18	18
5/7/2011	9/25/2011	8	8	18	18
5/5/2012	9/28/2012	5	5	17.5	17.5
5/18/2013	9/24/2013	5	5	17.5	17.5
5/23/2014	9/27/2014	5	5	18	18
5/22/2015	9/26/2015	5	5	18	18
5/21/2016	9/25/2016	5	4	18	17
5/25/2017	9/5/2017	3	3	18	17

Table S3: Season lengths, possession limits, and minimum length limits for tautog between 2001 and 2017.

Season open	Season close	Possession limit	Minimum length limit (inches)
1/1/2001	5/31/2001	10	14
6/1/2001	10/9/2001	1	14
10/10/2001	12/31/2001	10	14
1/1/2002	5/31/2002	10	14
6/1/2002	10/9/2002	1	14
1/1/2003	5/31/2003	4	14
6/1/2003	11/14/2003	1	14
11/15/2003	12/31/2003	8	14
1/1/2004	5/31/2004	4	14
6/1/2004	11/14/2004	1	14
11/15/2004	12/31/2004	8	14
1/1/2005	5/31/2005	4	14
6/1/2005	11/14/2005	1	14
11/15/2005	12/31/2005	6	14
1/1/2006	5/31/2006	4	14
6/1/2006	11/14/2006	1	14
11/15/2006	12/31/2006	8	14
1/1/2007	5/31/2007	4	14
6/1/2007	11/14/2007	1	14
11/15/2007	12/31/2007	8	14
1/1/2008	4/30/2008	4	14
7/16/2008	11/15/2008	1	14
11/16/2008	12/31/2008	6	14
1/1/2009	4/30/2009	4	14
7/16/2009	11/15/2009	1	14
11/16/2009	12/31/2009	6	14
1/1/2010	4/30/2010	4	14
7/16/2010	11/15/2010	1	14
11/16/2010	12/31/2010	6	13
1/1/2011	4/30/2011	4	14
7/16/2011	11/15/2011	1	14
11/16/2011	12/31/2011	6	14
1/1/2012	2/28/2012	4	15
4/1/2012	4/30/2012	4	15
7/17/2012	11/15/2012	1	15
11/16/2012	12/31/2012	6	15
1/1/2013	2/28/2013	4	15
4/1/2013	4/30/2013	4	15
7/17/2013	11/15/2013	1	15

11/16/2013	12/31/2013	6	15
1/1/2014	2/28/2014	4	15
4/1/2014	4/30/2014	4	15
7/17/2014	11/15/2014	1	15
11/16/2014	12/31/2014	6	15
1/1/2015	2/28/2015	4	15
4/1/2015	4/30/2015	4	15
7/17/2015	11/15/2015	1	15
11/16/2015	12/31/2015	6	15
1/1/2016	2/28/2016	4	15
4/1/2016	4/30/2016	4	15
7/17/2016	11/15/2016	1	15
11/16/2016	12/31/2016	6	15
1/1/2017	2/28/2017	4	15
4/1/2017	4/30/2017	4	15
7/17/2017	11/15/2017	1	15
11/16/2017	12/31/2017	6	15

Table S4: Season lengths, minimum length limits, and possession limits for scup between 2001 and 2017.

Season open	Season close	Possession limit	Minimum length limit (inches)
7/4/2001	12/31/2001	50	9
7/1/2002	10/31/2002	50	10
7/1/2003	12/31/2003	50	10
1/1/2004	2/28/2004	50	10
7/1/2004	12/31/2004	50	10
1/1/2005	2/28/2005	50	9
7/1/2005	12/31/2005	50	9
1/1/2006	2/28/2006	50	9
7/1/2006	12/31/2006	50	9
1/1/2007	2/28/2007	50	9
7/1/2007	12/31/2007	50	9
1/1/2008	2/28/2008	50	9
7/1/2008	12/31/2008	50	9
1/1/2009	2/28/2009	50	9
7/1/2009	12/31/2009	50	9
1/1/2010	2/28/2010	50	9
7/1/2010	12/31/2010	50	9
1/1/2011	2/28/2011	50	9
7/1/2011	12/31/2011	50	9
1/1/2012	2/28/2012	50	9
7/1/2012	12/31/2012	50	9
1/1/2013	2/28/2013	50	9
7/1/2013	12/31/2013	50	9
1/1/2014	2/28/2014	50	9
7/1/2014	12/31/2014	50	9
1/1/2015	2/28/2015	50	9
7/1/2015	12/31/2015	50	9
1/1/2016	2/28/2016	50	9
7/1/2016	12/31/2016	50	9
1/1/2017	2/28/2017	50	9
7/1/2017	12/31/2017	50	9

Table S5. Frequency table showing the number of focus group participants in each of four stakeholder groups who referred to five aspects of New Jersey recreational fishing regulations: bag limits, minimum length limits, gaps between seasons or “blackout periods,” season length, season timing, and slot limits. The “associated businesses” stakeholder group includes tackle shops and marinas, members of the fishing media, and other industry representatives.

Stakeholder group	Bag limits	Minimum length limits	Season gaps	Season length	Season timing	Slot limit*
Associated businesses	5	4	5	4	5	2
Charter boat sector	5	4	2	5	6	3
Party boat sector	2	6	4	3	4	1
Private angler	3	3	2	1	3	0
Total	18	24	18	17	23	7

* Slot limits define an intermediate size range allowable for harvest. A slot limit for summer flounder is a popular management proposal that was spontaneously brought up during several of the focus groups. Slots limits are not, however, part of the current slate of regulatory options.

Table S6: Species used to define bottomfish trips in the VTR data. Reports listing capture of at least one of these species were retained for analysis.

Bottom fish common name	Scientific name
Atlantic cod	<i>Gadus morhua</i>
Black sea bass	<i>Centropristis striata</i>
Conger eel	<i>Conger oceanicus</i>
Oyster toadfish	<i>Opsanus tau</i>
Red hake	<i>Urophycis chuss</i>
Scup	<i>Stenotomus chrysops</i>
Sea robin	<i>Prionotus carolinus</i>
Summer flounder	<i>Paralichthys dentatus</i>
Tautog	<i>Tautoga onitis</i>
Triggerfish	<i>Balistes capriscus</i>

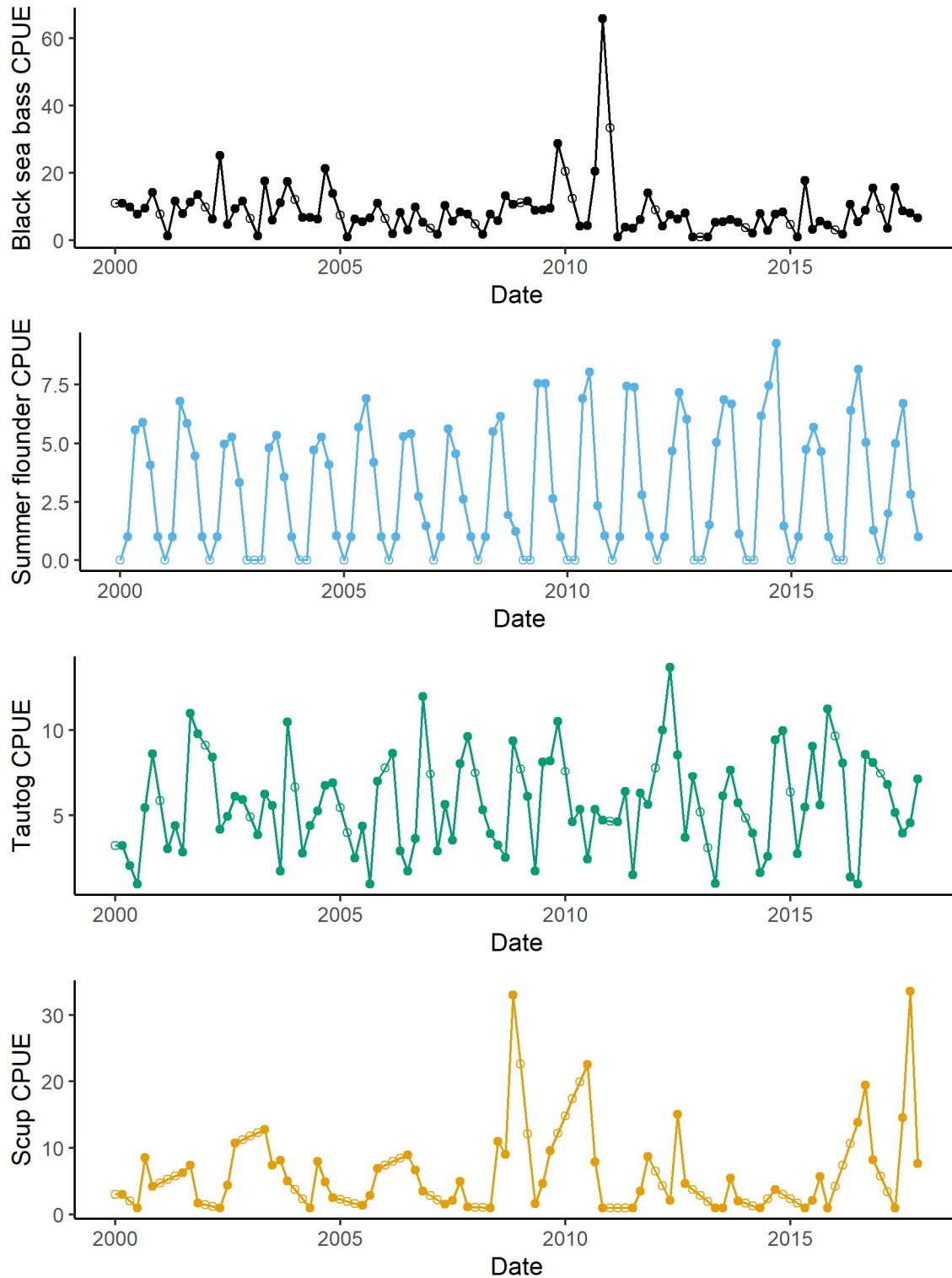


Figure S1: Mean catch per trip for each of the four focal species based on MRIP access point intercept data. Catch rates are estimated by two-month wave of sampling. Empty circles indicate imputed values. Because the scup catch rates contained so many imputed values, they were not included as predictors in the ARMA models.

Table S7: Breusch-Godfrey test results for serial autocorrelation of residuals up to lag 105 for all best-fitting models.

Model	Chi Squared value	P value
Blackout effect--charter anglers	95.265	0.7413
Species availability--party anglers	109.25	0.3687

Table S8: Coefficients of best-fitting model (blackout effect) to charter boat fishing effort time series, including the model's seasonal component. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP). DF=870

Coefficient	Estimate	Standard error	T value	P value
AR1	0.834	0.182	4.590	<0.0001
AR2	-0.021	0.071	-0.297	0.766
AR3	-0.157	0.050	-3.126	0.002
AR4	0.132	0.035	3.794	0.0002
MA1	-0.508	0.182	-2.797	0.005
Intercept	2.203	0.760	2.897	0.004
BSB PL	0.004	0.005	0.733	0.464
SMF PL	0.018	0.022	0.852	0.394
TOG PL	0.032	0.025	1.307	0.192
SCP Open	0.229	0.152	1.507	0.132
Something open	1.954	0.740	2.641	0.008
N blackout days	0.024	0.017	1.465	0.143
Something open * N blackout days	-0.019	0.017	-1.170	0.242
SMF CPUE	0.010	0.029	0.350	0.727
BSB CPUE	0.007	0.006	1.069	0.285
TOG CPUE	-0.017	0.019	-0.902	0.367
Sine 1	-1.733	0.125	-13.880	<0.0001
Cosine 1	-1.783	0.152	-11.723	<0.0001
Sine 2	-0.832	0.079	-10.495	<0.0001
Cosine 2	0.662	0.070	9.406	<0.0001
Sine 3	-0.155	0.059	-2.612	0.009
Cosine 3	0.469	0.057	8.297	<0.0001

Table S9: Variance inflation factors for the main effect predictors of the blackout effect model for the charter boat time series. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP).

Predictor main effects	VIF
Sine 1	4.45
Cosine 1	7.94
Sine 2	1.75
Cosine 2	1.42
Sine 3	1.24
Cosine 3	1.11
BSB PL	1.91
SMF PL	4.20
TOG PL	2.56
SCP Open	3.99
Something Open	1.39
N blackout days	2.01
SMF CPUE	5.13
BSB CPUE	1.23
TOG CPUE	1.35

Table S10: Coefficients of best-fitting model (species availability) to party boat fishing effort time series, including the model's ARMA and seasonal components. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP). DF=870

Coefficient	Estimate	Standard error	T value	P value
AR1	0.772	0.060	12.794	<0.0001
MA1	-0.537	0.079	-6.761	<0.0001
Intercept	5.745	0.168	34.228	<0.0001
BSB PL	0.050	0.010	5.050	<0.0001
SMF PL	0.227	0.045	5.089	<0.0001
TOG PL	0.141	0.033	4.283	<0.0001
SCP Open	-0.994	0.268	-3.712	0.0002
BSB PL x N species available	-0.014	0.004	-3.880	0.0001
SMF PL x N species available	-0.047	0.014	-3.474	0.001
TOG PL x N species available	-0.034	0.013	-2.506	0.012
SCP PL x N species available	0.495	0.095	5.185	<0.0001
SMF CPUE	0.005	0.023	0.219	0.827
BSB CPUE	0.004	0.004	0.923	0.356
TOG CPUE	0.030	0.012	2.444	0.015
Sine 1	-0.899	0.087	-10.334	<0.0001
Cosine 1	-1.003	0.110	-9.141	<0.0001
Sine 2	0.080	0.058	1.370	0.171
Cosine 2	0.370	0.048	7.630	<0.0001
Sine 3	-0.087	0.044	-1.987	0.047
Cosine 3	0.006	0.040	0.153	0.878
Sine 4	-0.006	0.037	-0.158	0.875
Cosine 4	0.019	0.033	0.585	0.559
Sine 5	0.074	0.033	2.255	0.024
Cosine 5	0.050	0.033	1.479	0.140
Sine 6	-0.065	0.028	-2.360	0.018
Cosine 6	0.065	0.028	2.327	0.020
Sine 7	0.062	0.027	2.295	0.022
Cosine 7	-0.003	0.028	-0.094	0.925
Sine 8	0.078	0.026	2.977	0.003
Cosine 8	-0.037	0.025	-1.449	0.148
Sine 9	-0.049	0.025	-1.985	0.047
Cosine 9	0.009	0.025	0.363	0.717
Sine 10	0.038	0.024	1.562	0.119
Cosine 10	0.042	0.024	1.724	0.085

Table S11: Variance inflation factors for the main effect predictors of the species availability model for the party boat time series. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), summer flounder (SMF), tautog (TOG), and scup (SCP).

Predictor main effects	VIF
Sine 1	5.03
Cosine 1	9.91
Sine 2	1.83
Cosine 2	1.46
Sine 3	1.24
Cosine 3	1.11
Sine 4	1.23
Cosine 4	1.07
Sine 5	1.20
Cosine 5	1.24
Sine 6	1.01
Cosine 6	1.03
Sine 7	1.06
Cosine 7	1.07
Sine 8	1.06
Cosine 8	1.01
Sine 9	1.01
Cosine 9	1.01
Sine 10	1.01
Cosine 10	1.01
BSB PL	1.23
SMF PL	4.73
TOG PL	2.28
SCP Open	5.27
SMF CPUE	6.46
BSB CPUE	1.24
TOG CPUE	1.37

Table S12: Coefficients of the species availability model fit to the party boat fishing effort time series. The summer flounder-associated regulations were removed as predictors to detect bias in coefficient values associated with multicollinearity. Most coefficients were unchanged, but no significant effect between tautog possession limit and the number of species open was found in this model fit. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), tautog (TOG), and scup (SCP).

Coefficient	Estimate	Standard error	T value	P value
AR1	0.722	0.074	9.722	<0.0001
MA1	-0.474	0.096	-4.935	<0.0001
Intercept	6.092	0.141	43.330	<0.0001
BSB PL	0.038	0.009	4.463	<0.0001
TOG PL	0.096	0.032	2.965	0.003
SCP Open	-0.973	0.264	-3.692	0.000
BSB PL x N species available	-0.010	0.003	-3.366	0.001
TOG PL x N species available	-0.013	0.013	-0.991	0.322
SCP PL x N species available	0.405	0.093	4.333	<0.0001
BSB CPUE	0.003	0.004	0.705	0.481
TOG CPUE	0.034	0.012	2.750	0.006
Sine 1	-1.001	0.078	-12.851	<0.0001
Cosine 1	-1.266	0.070	-18.121	<0.0001
Sine 2	0.098	0.057	1.731	0.084
Cosine 2	0.477	0.045	10.519	<0.0001
Sine 3	0.004	0.042	0.089	0.929
Cosine 3	-0.022	0.041	-0.531	0.596
Sine 4	-0.076	0.037	-2.051	0.041
Cosine 4	0.026	0.034	0.776	0.438
Sine 5	0.098	0.034	2.883	0.004
Cosine 5	0.043	0.031	1.373	0.170
Sine 6	-0.063	0.029	-2.185	0.029
Cosine 6	0.057	0.029	1.952	0.051
Sine 7	0.056	0.027	2.039	0.042
Cosine 7	0.017	0.027	0.633	0.527
Sine 8	0.082	0.027	3.041	0.002
Cosine 8	-0.032	0.026	-1.217	0.224
Sine 9	-0.056	0.025	-2.220	0.027
Cosine 9	-0.006	0.025	-0.217	0.828
Sine 10	0.043	0.025	1.734	0.083
Cosine 10	0.035	0.025	1.400	0.162

Table S13: Variance inflation factors for the main effect predictors of the species availability model for the party boat time series with summer flounder season predictors removed from the analysis. Species-specific regulations and catch rates are indicated by the following abbreviations: black sea bass (BSB), tautog (TOG), and scup (SCP).

Predictor main effects	VIF
Sine 1	3.75
Cosine 1	2.49
Sine 2	1.68
Cosine 2	1.20
Sine 3	1.09
Cosine 3	1.11
Sine 4	1.10
Cosine 4	1.04
Sine 5	1.19
Cosine 5	1.03
Sine 6	1.01
Cosine 6	1.02
Sine 7	1.02
Cosine 7	1.02
Sine 8	1.06
Cosine 8	1.01
Sine 9	1.01
Cosine 9	1.01
Sine 10	1.01
Cosine 10	1.01
BSB PL	1.13
TOG PL	2.23
SCP Open	5.23
BSB CPUE	1.23
TOG CPUE	1.35

Chapter 4: Predicting Angler Decisions When Facing Walleye Declines in Wisconsin

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Abstract

Populations of walleye (*Sander vitreus*), a popular target species and cornerstone of the recreational fishing economy, are losing their ability to naturally reproduce in most Wisconsin lakes. At the same time centrarchids such as largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) have flourished. As fewer lakes support naturally recruiting walleye populations in the future, managers will face the choice of whether to invest in maintaining more walleye lakes through stocking of extended-growth fingerlings. The success of these interventions would depend in part on angler response to changes in walleye availability, including their willingness to travel greater distances and/or substitute alternative target species. As the number of quality walleye lakes continues to decline, anglers targeting this species may leave the fishery, switch target species, or concentrate their fishing effort on the remaining walleye lakes. Stated preference methods such as choice experiments allow respondents with different preferences to weigh hypothetical fishing trips that vary systematically in their properties, including travel time and catch rates. We distributed an online discrete choice experiment and survey to holders of WI resident fishing licenses. Three latent classes of anglers varied in their willingness to travel to achieve increased walleye and largemouth bass catch rates, but we found no evidence that anglers would concentrate their fishing effort on distant lakes as walleye populations declined. Neither did we find evidence that largemouth bass and bluegill

were “second choice” species to walleye. Rather, most respondents were motivated by quality fishing sites for multiple species that were listed. The most committed class of anglers was also motivated to fish for species that were not included in the choice experiment, including black crappie (*Pomoxis nigromaculatus*), yellow perch (*Perca flavescens*), and trout (*Salvelinus namaycush* and *Oncorhynchus mykiss*). These results suggest that many Wisconsin anglers may be satisfied by quality fishing for other species in the future in spite of ongoing walleye declines.

Introduction

The recreational fishery of northern Wisconsin is approaching a tipping point. Populations of walleye (*Sander vitreus*), a popular target species and cornerstone of the recreational fishing economy (Tingley et al. 2019; Holsman and Scott 2021), are losing their ability to naturally reproduce in most Wisconsin lakes (Rypel et al. 2018). The contribution of different possible mechanisms driving this change remain unclear, but direct effects of water temperature and precipitation (Fayram et al. 2014; Hansen et al. 2015a, 2017), food web changes (Fayram et al. 2005; Kelling et al. 2016), and increased residential development (Scheuerell and Schindler 2004; Anthony and Jorgensen 2011) are all possible explanations for loss of walleye recruitment. Because harvest of walleye has remained steady as their production has declined, walleye in Wisconsin are overharvested (Embke et al. 2019). Simultaneously, warmwater fish populations such as largemouth bass (*Micropterus salmoides*) have flourished (Hansen et al. 2015b). Fisheries managers have resisted this shift in species composition by increasingly relying on stocking to supplement natural walleye recruitment (WDNR 2020; Lawson et al. 2022). However, in the face of a continuing trend of walleye losses, maintaining sustainable walleye fisheries will only become more difficult (Hansen et al. 2017).

The state of Wisconsin has invested heavily in stocking walleye fingerlings between 175 and 200 mm in length into lakes that are most likely to support self-sustaining walleye populations (Hansen et al. 2015a). Although stocking these larger individuals does improve survival by reducing predation (Grausgruber and Weber 2020), stocking failures remain relatively common, and average rates of survival for stocked walleye are declining over time as lake habitats become less suitable (Lawson et al. 2022). In addition, stocked walleye are skewed female, which may be leading to sex imbalances in walleye population and further limiting

natural reproduction (Sass et al. 2022). Stocking events in low walleye density lakes may also attract increased fishing effort, further straining the walleye population (Fayram et al. 2006). These mixed results therefore raise the question: to what extent will continued stocking of walleye benefit Wisconsin anglers? The answer to this question will depend in part on whether improved walleye catch rates or size structure drive increased fishing effort as the number of quality walleye lakes decline.

Future strategies for walleye management will depend on whether dedicated walleye anglers are willing to fish for alternative species or whether they would rather travel greater distances to continue fishing for walleye. Walleye is a highly popular target species among WI anglers, but bluegill (*Lepomis macrochirus*) is actually the number one target species in terms of fishing effort (Holsman and Scott 2021). As walleye production continues to decline and warmwater species thrive, anglers may reallocate their walleye fishing effort to warmwater species such as bluegill and largemouth bass. Anglers have heterogeneous preferences and vary in their degree of specialization to particular species (Arlinghaus et al. 2019). Maintaining diverse fishing opportunities is therefore an important strategy for achieving high angler satisfaction (Beardmore et al. 2015; van Poorten and Camp 2019). Anglers in a variety of systems have demonstrated willingness to switch target species when their first choice is depleted (Ditton and Sutton 2004; Askey and Johnston 2013) or when its harvest is restricted by regulations (Beaudreau et al. 2018; Chagaris et al. 2019; Trudeau et al. 2022). If suitable target species are available nearby, these anglers are unlikely to travel great distances to target walleye.

Diversity in target species provides redundancy to a fishery system (i.e. the water bodies, fish species, and anglers within a particular region), resulting in greater resilience and reduced probability of stock collapse (Kotschy et al. 2015). For example, the species diversity of Kenyan

artisanal reef fisheries have avoided collapse in spite of high fishing pressure in part because fishers can substitute smaller bodied target species when larger fish are depleted (McClanahan et al. 2008). In addition, targeting a variety of species has been associated with shorter travel distances in marine commercial fisheries (Young et al. 2019). As Mid-Atlantic stocks shifted north, large vessels with limited harvest portfolios traveled greater distances to harvest the same species while vessels that harvested a variety of species fished closer to their home ports. As coldwater species assemblages in Wisconsin shift towards centrarchid-dominated communities, the success of stocking efforts to supplement walleye recruitment could be counteracted by intensified fishing effort if, similar to commercial vessels with limited harvest portfolios, dedicated walleye anglers are willing to travel greater distances to maintain their walleye catch. The recreational walleye fishery in Wisconsin, however, is driven by different motivations than those of artisanal or commercial fisheries. Although both recreational and commercial fishers may need to change gears and fishing strategies to switch target species, the costs to recreational anglers are lower, no change in fish processing is required, and there is no requirement among recreational anglers to maintain or reduce profits in order to justify these investments of time and/or money. Angler populations have therefore shown that they are generally willing to substitute target species, as long as the costs of access are not substantially higher for the alternative species (Fisher and Ditton 1993) and the alternative species provides a similar type of experience to the angler, e.g. the opportunity to catch a trophy fish (Sutton and Ditton 2005).

Travel time is a common metric of costs when evaluating site choice behavior among recreational anglers (Hunt et al. 2019). Participants weigh sites' distances versus their expected benefits, choosing the site providing the greatest net utility (e.g. McConnell and Strand 1981). As preferred sites become unavailable or less beneficial, participants are expected to substitute less

preferred sites that may be further away (Carpenter and Brock 2004). In the case of the Wisconsin walleye fishery, for anglers who are unwilling to substitute nearby sites that do not support quality walleye populations, their only remaining choice would be to substitute greater travel distances. If fishing effort follows an ideal free distribution (IFD) (Fretwell and Lucas 1969), fish population densities and catch rates are expected to decline and homogenize as fishing effort and population densities approach equilibrium. The IFD hypothesizes, however, that fishing quality will decline and homogenize only among sites with similar access costs (Parkinson et al. 2004). The limits of anglers' willingness to travel when anglers are centrally located have been demonstrated as a "halo of depletion" of fishing quality around population centers in simulation models (Post et al. 2008; Carruthers et al. 2018) and empirically (Wilson et al. 2020). Among more dispersed angler populations, spatial fishing effort dynamics are more difficult to predict, as they depend on emergent effects of complex interactions between fish population dynamics, angler behavior, and management interventions such as stocking (Carruthers et al. 2018), where ecological and social heterogeneity significantly alter outcomes (Matsumura et al. 2019). Among WI walleye anglers, changes in the distribution of fishing effort across the state as walleye populations decline will likely depend on individual tradeoffs between travel times and catch rates. If the utility of quality walleye fishing is high enough to outweigh greater travel times, a pattern of sequential collapse of walleye populations could arise as fewer naturally reproducing walleye populations persist. The success of stocking interventions to prevent these collapses will also depend on efficient allocation of limited hatchery-raised walleye to achieve equitable benefits among anglers (Askey et al. 2013). This optimization relies on understanding heterogeneity in angler willingness to travel across the state.

In this study we use a stated preference method to evaluate how heterogeneous Wisconsin recreational anglers trade off travel time and species availability in their site choice behavior. By accounting for preference heterogeneity in our choice model, we inferred potential compensation behaviors for different groups of anglers as they weighed hypothetical tradeoffs between travel time, catch rates, and maximum sizes for walleye, largemouth bass, and bluegill. We hypothesized that walleye specialists would be willing to travel greater distances to achieve greater walleye catch rates, which would emerge as a positive interaction effect between travel time and walleye catch rates. In contrast, we predicted that non-walleye specialist anglers would be willing to substitute centrarchid species rather than travel greater distances to target walleye.

Methods

Statistical framework

We evaluated the choice behavior of anglers with heterogeneous preferences using the framework of random utility theory. Within this framework, anglers are assumed to make choices that maximize their expected utility, or benefit, based on an unobserved internal utility function (McFadden 1974). Utility is expressed as a linear function of observable characteristics (A) of potential fishing sites (x_{aj}), their estimated coefficients (β_a), and unobserved factors that are characterized by the error term ε . A utility function of site j for individual i is therefore written:

$$U_{ij} = \sum_{a=1}^A \beta_a x_{aj} + \varepsilon_{ij}$$

for a number of site attributes A , where the error term ε is independently and identically distributed following a Gumbel distribution (Train 2009). The probability of individual i

choosing site j out of all available sites J (P_{ij}) can then be modeled as the multinomial logit model:

$$P_{ij} = \frac{e^{\beta_0 + \sum_{a=1}^A \beta_a x_{aj}}}{\sum_{j=1}^J e^{\beta_0 + \sum_{a=1}^A \beta_a x_{aj}}}$$

Where the vector β_0 indicate alternative specific constants representing the choice to go fishing at one of the three sites (fixed to zero), to fish elsewhere for another species, and to not go fishing. Coefficients of site characteristics are represented as the vector β_a , which are all set to 0 for the opt-out choices.

Individual heterogeneity can be accommodated by specifying beta coefficients as random parameters and allowing differences among preferences by individual, such as in a mixed multinomial logit model (MMNL or MXL) (McFadden and Train 2000). Groups can also be defined *a priori* by individual characteristics in order to estimate different choice parameters for each group (e.g. Gensch and Javalgi 1987). Alternatively, latent class membership probabilities can be estimated for individuals based on their preferences and individual characteristics, such as in a latent class multinomial logit model (LC-MNL) (Kamakura and Russell 1989). A strength of the latent class approach is the ability to associate membership in maximally different groups, and therefore differences in preferences, with respondent characteristics such as avidity and specialization (e.g. Beardmore et al. 2013). Latent class membership and preferences for site attributes are estimated jointly, where individual characteristics C (represented by the vector x_{ic} for individual i) and their coefficients γ_s predict the probability of individual i belonging to latent class S with intercept constant δ_{is} .

$$\pi_{is} = \frac{e^{\delta_{is} + \sum_{c=1}^C \gamma_{sc} x_{ic}}}{\sum_{s=1}^S e^{\delta_{is} + \sum_{c=1}^C \gamma_{sc} x_{ic}}}$$

Each latent class then has its own set of parameter values (β_s) predicting the choice probability of individuals within its class. The probability of individual i choosing site j for a given choice scenario is therefore the product of their class membership multiplied by their choice probability for that class, summed over all classes.

$$P_{ij} = \sum_{s=1}^S \frac{e^{\delta_{is} + \sum_{c=1}^C \gamma_{sc} x_{ic}}}{\sum_{s=1}^S e^{\delta_{is} + \sum_{c=1}^C \gamma_{sc} x_{ic}}} * \frac{e^{\beta_0 + \sum_{a=1}^A \beta_{sa} x_{aj}}}{\sum_{j=1}^J e^{\beta_0 + \sum_{a=1}^A \beta_{sa} x_{aj}}}$$

To maximize the information gathered from each respondent, and to more closely resemble the reality of how anglers choose fishing sites, we asked respondents to allocate 10 days of fishing across five options: three hypothetical fishing sites, the option to go fishing elsewhere for an unlisted species, and the option to not go fishing at all. This allocation approach required the use of a model that could accommodate a response between 0 and 1 (i.e. between 0 and 100% of the 10 days) rather than a discrete response.

A latent class fractional multinomial logit model (LC-FMNL) extends on the LC-MNL framework to allow choices made by allocation (i.e. non-discrete choices) and accounts for repeated choices by individual respondents (Papke and Wooldridge 1996; Hess and Palma 2022). The probability of individual i choosing site j in choice scenario t dependent on a vector of utility parameters β is represented by $P_{ijt}(\beta)$.

The likelihood of a series of repeated choices made by individual i in latent class s across T tasks (s_{ijt}) with fishing sites J is then:

$$L_i(\beta) = \prod_{t=1}^{T_i} \prod_{j=1}^J P_{isjt}^{s_{ijt}}(\beta)$$

Where $0 \leq s_{ijt} \leq 1$ and $\sum s_{ijt} = 1$. In our case s_{ijt} is the proportion of days allocated to each fishing site. By substituting the multinomial logit choice probability for P_{ijt} , we have the likelihood function for latent class S :

$$L_i(\beta_s) = \prod_{t=1}^{T_i} \frac{e^{\beta_0 + \sum_{a=1}^A s_{ijt} \beta_{sa} x_{aj}}}{\sum_{j=1}^J e^{\beta_0 + \sum_{a=1}^A \beta_{sa} x_{aj}}}$$

Choice experiment design

The choice experiment was designed to elicit tradeoffs between travel time, catch rates, and maximum sizes for walleye, bluegill, and largemouth bass (Fig. 1). Rather than a single discrete choice, respondents were asked to allocate ten hypothetical fishing days between three potential fishing sites, the choice to fish elsewhere for a different species, and a choice to not go fishing at all. A preliminary design of the discrete choice experiment was pre-tested at five focus groups of Wisconsin walleye anglers. Participants were recruited from a list of anglers who had participated in public meetings for the Wisconsin Walleye Management Plan and had provided their contact information for future involvement in WI fisheries management. Focus groups took place between October 4 and 11, 2021. A total of 21 participants were shown the

discrete choice experiment and asked to provide feedback on the prompt, the importance of the attributes in their decision-making, and the attribute levels. We finalized the choice attributes and their levels based on focus group feedback (Table 1).

Attribute levels were based on two sets of creel survey data. To choose levels for catch rates and maximum fish sizes, we referenced creel data collected by the WDNR between 1990 and 2020. We chose travel time levels based on anglers' reported travel times to their fishing site from a creel survey conducted in 2018 and 2019 in Vilas County (Trudeau et al. 2021). Attribute levels initially corresponded to 5, 25, 50, 75, and 95% quantiles of creel survey responses. We pooled all data across lakes to estimate catch rate quantiles. For maximum fish sizes, we instead found maximum sizes reported within lakes before calculating their quantiles across all lakes. These preliminary levels were then adjusted to account for biases associated with the survey method (i.e. that size data represented only fish that were harvested) and feedback from focus group participants. We therefore included lower maximum sizes and higher travel times than those represented strictly within the 95% quantiles of the creel survey data. In addition, because we expected that avid, experienced anglers would respond to our survey in higher numbers than casual anglers, we included higher levels of catch rates and maximum sizes to ensure that skilled anglers would be presented with acceptable options in the choice experiment (Hilborn 1985) (Table S1). Lastly, the large number of choice attributes and the lack of any regulatory attributes were critiqued by focus group participants. To accommodate this feedback, we first removed a preliminary attribute that described typical (median) sizes for the species of interest to reduce the cognitive load on respondents (Hoyos 2010). Second, rather than introducing an additional choice attribute for fishing regulations, we changed our walleye maximum sizes to include sizes that were one inch shorter and longer than the most common minimum length limit of 15 inches

for walleye in Wisconsin. The lower two maximum sizes (12 and 14 inches) were therefore likely to be perceived as unharvestable by WI anglers. Similarly, the 24 inch maximum sized walleye is unharvestable under the most common restricted slot limit of 20 to 28 inches but may be desirable to anglers wishing to catch and release large walleye.

We generated a D-efficient (Ferrini and Scarpa 2007) fractional factorial design using the modified Federov algorithm (Cook and Nachtrheim 1980) in Ngene version 1.2 (ChoiceMetrics 2018). The design consisted of 100 versions of 5 choice tasks, each of which presented three hypothetical fishing trips that varied in travel time, catch rates, and maximum fish sizes (D error = 0.0035). We used a token allocation approach, in which respondents were asked to allocate 10 hypothetical fishing days within each choice task. These fishing days could be allocated across three fishing trips and two opt-out options: to go fishing elsewhere for another species and to not go fishing that day. Participants were randomly assigned one version of the choice experiment, consisting of 5 choice tasks.

Travel time and catch rates were included as linear effects, and maximum fish sizes were included as categorical effects. Dummy coding for maximum fish sizes included a “zero” baseline level corresponding to zero expected catch rates. No zero catch rates were included for bluegill in the design, so the baseline maximum size was instead the lowest value of 6 inches. Dummy coding of maximum sizes was used to accommodate the “zero” value associated with zero catch rates and to investigate nonlinear responses of utility to maximum fish sizes. Linear catch rates were used to avoid an excessive number of parameters in the model. Constraints on the design prevented non-zero catch rates from corresponding with this “zero” maximum size, and vice versa. The design avoided repetition of alternatives within a choice task as well as dominant choices based on the sign of the specified prior values of the parameters. We did not

have prior knowledge of the number of latent classes to expect, so we chose conservative prior values for MNL (rather than LC-MNL) parameters, e.g. low negative values for travel time and low positive values for catch rates and high maximum sizes (Table S2). The signs of interaction effects were unknown, so prior values of zero were used to generate the design.

Additional survey questions

In addition to the five choice scenarios, respondents were asked a series of survey questions to characterize differences in their fishing behaviors and preferences. First, to ensure that only active anglers (and not, for example, Wisconsin residents that had purchased a license but had never gone fishing), respondents were asked to record the number of years they had fished in Wisconsin. Anyone answering “0” was then directed to the end of the survey. Similarly, a question asking if respondents planned to continue fishing in Wisconsin in the future filtered out any respondents who would no longer be active anglers after 2021. The final filtering question asked respondents to indicate how often they target a variety of fish species on a five point Likert scale (never, seldom, half the time, usually, always), including walleye, largemouth bass, and bluegill. If respondents indicated that they never targeted either of these three species, they were directed to the end of the survey. Anglers who did not ever target bluegill, largemouth bass, or walleye therefore did not complete the choice experiment.

After completing the five choice scenarios, respondents were asked to rate their agreement on a five point Likert scale with a series of statements describing their catch-related attitudes based on a subset the statements used by Anderson et al., (2007) (Table 2). We used a subset rather than the full set of statements to reduce the length of our survey. In addition, respondents were asked to respond to a series of semantic differential (i.e. slider) questions rating the centrality of fishing to their lifestyle, catch and release behavior, and self-described fishing

skill on a scale from 1 to 100 (Table 3). These responses were divided by 20 prior to analysis to rescale them to match the statements eliciting catch-related attitudes. These questions were obtained from a survey of first-time license buyers conducted by the WDNR (Beardmore 2021). Last, respondents were asked to select their household annual income bracket, while other demographic information (age and gender) were available from the sampling frame. Respondents were also asked to indicate the number of days they had fished in the past year.

Sampling

We obtained a sample of 10,000 WI resident fishing license purchasers from 2021. Of this full sample, 9,000 were selected from among all license purchasers over 18 who also provided an email address. These residents were contacted by email. Sampling of license records was initially stratified by the proportion of the state's population residing in each region (Table S3). Walleye are a particularly important fishery in Northern Wisconsin, which is primarily rural. Sampling weights were therefore decreased in Dane and Milwaukee Counties and increased in the Northern WI region. Based on census data, 17% of the WI population is over 60. Because 28% of WI resident fishing license holders are over 60 (Table S4), we allocated 25% of our samples within each region to license purchasers in this age group (Table S5).

The remaining 1,000 were selected from among all license purchasers, regardless of whether they provided an email address. This sample was stratified by region as described above, but not by age. A push-to-online version of the survey was mailed to this subsample of anglers as a postcard in order to reach anglers that cannot be contacted by email.

Survey Distribution

We hosted the online discrete choice experiment and survey through Sawtooth Studios, and we distributed the survey and choice experiment to 9000 holders of WI residential fishing

license through Qualtrics by email. Each participant was contacted three times: one initial contact and two follow-up reminders.

For the 1000 participants contacted by mail, we sent one initial postcard and one follow-up. The postcard directed respondents to follow a QR code or copy a URL in order to reach the online survey. The follow-up contact additionally included a tear-away return postcard to opt out of the survey. This postcard asked participants to indicate the number of years they have fished in Wisconsin, whether or not they plan to fish in the future, how many days of the past year they went fishing, and how often they fish for walleye. This reduced survey was used to assess nonresponse bias.

Analysis

We tested for response bias by age, gender, and urban vs rural primary residence. Participants were classified as living in an urban county based on classifications made by the Wisconsin Office of Rural Health (Office of Management and Budget 2010). We compared ages of respondents and nonrespondents using the Kruskal Wallis test (Kruskal and Wallis 1952). We compared gender and urban vs rural primary residence between respondents and nonrespondents using Pearson's Chi Squared test (Pearson 1900). In addition, we tested for differences between respondents and nonrespondents in fishing experience, avidity, and frequency of walleye fishing using the opt-out responses to the mail survey. All analyses were completed in R v.4.1.0 (R Core Team 2021).

In addition to site attributes, our choice model included individual covariates predicting membership within latent classes with similar preferences for fishing sites. We used confirmatory factor analysis (CFA) to produce scores for four factors adapted from Kyle et al., (2007) and Beardmore et al (2013) describing catch orientation, consumptive orientation, trophy

seeking behavior, self-described skill at angling, and centrality of fishing to an angler's lifestyle. Catch orientation describes the importance of catching fish to an angler in order to achieve a satisfying fishing experience, and consumptive orientation describes an anglers' tendency to harvest fish rather than release them (Kyle et al. 2007). Trophy seeking behavior describes the importance to an angler of catching larger fish. Finally, centrality to lifestyle indicates the commitment of an individual to fishing and their tendency to specialize, i.e. to target particular species rather than "whatever bites" (Beardmore et al. 2013). We completed this analysis using the lavaan R package (Rosseel 2012). Comparative Fit Index (CFI) and root mean square error of approximation (RMSEA) were calculated to assess model fit (Table 4). A CFI of greater than 0.9 and an RMSEA of less than 0.1 indicate acceptable model fits (Brown 2015). The skill and centrality to lifestyle factors were strongly correlated ($\sigma = 0.813$), so to reduce model complexity, the skill factor was not included as a covariate predicting latent class membership. Factor scores for centrality to lifestyle, trophy orientation, consumptive orientation, and catch orientation were produced for each respondent.

We fitted latent class fractional multinomial choice models using the Apollo R package v.0.2.7 (Hess and Palma 2019). To assist convergence, continuous predictor variables were normalized (i.e. centered around 0 and scaled to a standard deviation of 1). A baseline alternative specific constant was specified for the three potential fishing sites and fixed to zero as an intercept for the site choice utility functions (Fishing ASC). Two additional alternative specific constants were specified for the "fish elsewhere for another species" (Fish elsewhere ASC) and "do not go fishing" (Do not fish ASC) opt-out options. Travel time and walleye, bluegill, and largemouth bass catch rates were fit as continuous predictors of utility. Maximum sizes were included as categorical variables. For walleye and largemouth bass, the "0" maximum length

corresponding to zero catch rates was the baseline level, and for bluegill the smallest maximum length of 6 inches was the baseline. Interactions between the catch rate for each species and maximum sizes were included to account for an expected additional effect on utility of a site with both high catch rates and large maximum sizes. To aid convergence, the second-lowest maximum size was not included as an interaction effect. An interaction between walleye catch rate and travel time was included to test the hypothesis that anglers would travel greater distances to achieve higher walleye catch rates. Interactions between walleye and largemouth bass catch rates as well as walleye and bluegill catch rates were included to test the hypothesis that anglers would substitute centrarchids for walleye. Robust standard errors were estimated to account for the panel (i.e. repeated choice) nature of the data.

We compared Akaike Information Criterion (AIC) values of models containing between 1 and 5 latent classes. We accepted a $\Delta AIC > 2$ as evidence that a model had a worse fit than the model with a lower AIC value (Burnham and Anderson 2002). Individual covariates were then added to the best fitting latent class model. These covariates were CFA factor scores summarizing individuals' centrality of fishing to their lifestyle, trophy orientation, noncatch orientation, and consumptive orientation. Each combination of these four covariates were included in 14 candidate models, and we compared their AIC scores to choose the best fitting model.

Parameters of site attributes were rescaled into willingness to travel (WTT) estimates by dividing their value by the negative of the travel time cost attribute. Because travel time was centered and scaled for the model fit, WTT estimates were then converted into minutes of travel. Standard errors were obtained by the Delta method (Daly et al. 2012). Interactions of catch rates and travel time could not produce WTT estimates, so the effect sizes of these interactions were

evaluated by predicting choice probabilities given different combinations of travel time and catch rates. Walleye catch rates and travel times were varied across all levels included in the choice experiment, and the rest of the attributes were held at their median value. Choice probability was predicted relative to a baseline option where all attributes were held at their median value as well as the two opt-out options. These choice probability predictions were produced for both median walleye maximum size (16 inches) and the largest maximum size value (24 inches).

Post hoc comparison of latent classes

We classified individual respondents into latent classes according to their largest conditional probability of class membership. We used the Kruskal Wallis test to evaluate differences among groups in the number and types of species they reported targeting. We then used Bonferroni corrected Mann Whitney-Wilcoxon tests to complete post-hoc comparisons of classes.

Results

Out of 10000 survey links distributed, 728 participants followed the link, and 600 participants completed the survey, resulting in a 6.0% response rate for completed surveys. Of the 9000 surveys distributed by email, 649 responses were received. In comparison, 79 responses were received out of the 1000 surveys distributed by mail. Of the 1000 of these participants contacted by mail, 59 returned the abbreviated opt-out mail survey. Responses to the full survey were then filtered for quality, removing 20 respondents who had allocated all fishing days to the same choice for each of the 5 choice scenarios regardless of attribute levels and a further 7 responses for incomplete survey questions.

Men responded to the survey at a greater rate than women with a response rate of 7.0% compared to a female response rate of 4.7% $\chi^2(1, N = 10000) = 13.81, p = 0.0002$. Responses

were also more likely from residents of urban counties, with a response rate of 6.8% compared to a rural response rate of 5.7% $\chi^2(1, N = 10000) = 13.89, p = 0.049$. Survey respondents also tended to be younger, with a median age of 57 ($\sigma=16.5$) years compared to 61 ($\sigma=16.6$) years for nonrespondents ($W = 121.09, N=10000, p<0.0001$). Anglers who completed the opt-out abbreviated survey reported more years of fishing experience in WI (median = 50 years, $\sigma = 21.69$) than respondents to the full online survey (median = 40 years, $\sigma = 18.42$) ($W = 6.55, N=657, p = 0.01$). However, these anglers who opted out of the survey also reported fewer days fishing in the past year (median = 15 days, $\sigma = 31.65$) than full survey respondents (median = 21 days, $\sigma = 45.92$) ($W = 7.51, N=657, p = 0.006$) and were less likely to target walleye (median = ‘seldom’ (ordinal level 2), $\sigma = 1.16$) compared to full survey respondents (median = ‘half the time’ (ordinal level 3), $\sigma = 1.17$) ($W = 5.81, N = 657, p = 0.02$). Respondents to the survey therefore over-represented younger and more frequent anglers. Survey results will reflect avidity bias (Lewin et al. 2021) and therefore may not represent the preferences of the more numerous casual anglers in WI.

A 3 class LC-FMNL model emerged as the best fit to the choice data (Table 5). When models testing the fit of individual covariates were compared, two sets of covariates emerged as the best fit (Table 6). Both models included centrality to lifestyle and non-consumptive orientation. The only covariate that differed was the noncatch orientation variable in the lowest-AIC model, which was replaced by the trophy orientation in the second-lowest AIC model. The parameter values of the second-best model (Tables S6-S8) had very similar values for shared coefficients. When individuals were classified according to their great latent class probability, latent classes A, B, and C made up 4%, 78%, and 18% of the sample, respectively. Respondents of different classes showed different preferences for fishing site characteristics (Tables 7-9).

Class A was the smallest latent class, containing only 20 respondents. Because of the class's limited sample size, estimated parameters had higher standard errors (Table 7). Respondents in this class placed a high positive utility value on the non-fishing opt-out choice ($p = 0.01$). The utility of travel time was the most negative for this class compared to the other two latent classes. Of the non-cost attributes, only bluegill catch rates ($p=0.04$) and the largest bluegill maximum size of 10 inches ($p = 0.01$) emerged as significant predictors of site choice. On average, these anglers were willing to travel 93 minutes to achieve a 1 SD increase in bluegill catch rate and 134 minutes to fish in lakes with 10 inch bluegill. A 1 SD increase in catch rate was equal to 7.51 fish per 4 hours in the choice survey design, meaning that individuals of this class were on average willing to travel an additional 12.4 minutes for an increase in catch rate of 1 fish per 4 hours. No individual covariates emerged as significant predictors of class A membership.

Class B respondents were motivated to choose the fishing sites that were presented rather than opt out, exhibiting a negative utility for not going fishing ($p < 0.0001$) (Table 8). Anglers of class B were on average more willing to travel than those of class A or C, but travel time still had a negative utility ($p < 0.0001$). Their choices were motivated by a broader range of the listed species, with walleye, largemouth, and bluegill catch rates as positive predictors of site choice. Respondents were willing to travel 54 minutes to increase their walleye catch rate by 1 fish per 4 hours (62.42 minutes / 1.16 walleye). They were willing to travel 24 and 9.73 minutes to increase their largemouth bass and bluegill catch rates, respectively, by 1 fish per 4 hours. Class B respondents' choice probabilities increased with increasing maximum size of walleye, reaching significant positive values once maximum walleye size reached the range that is typically harvestable in WI (>15 inches, < 20 inches). Their willingness to travel for larger walleye was

the greatest of all classes, estimated at 93 minutes for 16 inch, 90 minutes for 20 inch, and 114 minutes for 24 inch maximum sizes. Respondents also showed a high willingness to travel for 8 and 10 inch maximum bluegill (63 and 87 minutes, respectively) and 16 and 20 inch largemouth bass (73 and 77 minutes, respectively). No individual covariates were significant predictors of class membership. The only significant interaction effect found for class B was a positive interaction between walleye catch rate and the second-largest maximum size of 20 inches ($p = 0.05$).

Class C members placed a high positive utility value on the choice to fish elsewhere for a different species ($p < 0.0001$) (Table 9). Travel time had a significant negative utility ($p < 0.0001$). Catch rates of walleye, largemouth bass, and bluegill were not significant predictors of site choice for this class. Rather, they were willing to travel 100 minutes to fish at lakes with 24 inch walleye and 98 minutes to fish at lakes with 10 inch bluegill. Respondents with a high centrality of fishing to their lifestyle ($p = 0.01$) and a non-consumptive fishing orientation ($p = 0.03$) were more likely to be assigned to this latent class. In addition, significant additional positive effects of large maximum sizes of walleye (16, 20, and 24 inch) and largemouth bass (20 inch) were present as interaction effects with walleye and largemouth bass catch rates, suggesting that these respondents preferentially chose sites with both high catch rates and high maximum sizes. Finally, a significant positive interaction effect between walleye catch rates and travel times was detected ($p = 0.02$), suggesting that these anglers were willing to travel greater distances to achieve higher walleye catch rates.

Although the interaction effect of walleye catch and travel time for class C was positive and significant ($p = 0.02$), model predictions suggest that the interaction's effect on choice probability is limited (Fig. 2C). Even when the maximum size of walleye was raised from the

median value of 16 inches to the maximum value of 24, the probability of class C choosing to fish for walleye was still lower than 25% at all travel times and catch rates (Fig. 3C). Although class C did exhibit a preference for simultaneously high catch rates and maximum sizes of walleye, largemouth bass, and bluegill, respondents of this class were most likely to choose to fish for alternative species, especially in comparison to the much higher site choice probability of latent class B under nearly all site characteristics (Fig. 1B and 2B).

Latent class characteristics

Based on individual covariates in the latent class model, anglers belonging to class C were more avid and specialized anglers, but they did not prefer to fish for walleye, largemouth bass, or bluegill, at least at the catch rates and maximum sizes specified in the choice experiment. The question therefore remained; what species do these anglers tend to target on their actual fishing trips? When we compared the self-reported frequency of targeting a variety of species between respondents of different latent classes, the profile of target species across classes were remarkably similar (Fig. 4). We detected only one significant difference among these groups: the frequency of targeting bluegill. Latent class A was more likely than classes B or C to target bluegill ($H(2) = 8.713, p = 0.0012$) (Fig. 5). Latent class A also tended to target fewer species at least “seldom” than classes B or C ($H(2) = 9.267, N=563, p = 0.0097$) (Fig. 6A). When the threshold for targeting a species was raised to at least “occasionally,” however, both classes A and C targeted significantly fewer species than class B ($H(2) = 13.177, p = 0.0014$) (Fig. 6B).

Discussion

We detected three distinct groups of anglers in the responses to our choice experiment. Class C was composed of dedicated, skilled anglers. These respondents tended to be most selective about fish sizes, but they also demonstrated a willingness and desire to target species

other than walleye, largemouth bass, and bluegill. Although class C was the only class to demonstrate a willingness to travel greater distances to achieve the highest walleye catch rates, their lower willingness to travel for walleye catch relative to class B suggested that these respondents are unlikely to concentrate their fishing effort on the fewer remaining walleye lakes in great numbers. Class B, in contrast, was willing to travel greater distances for walleye than for the other two species, but we found no evidence that they switched from a first choice of walleye to less-preferred centrarchid fishing when walleye catch rates were low. These class B anglers may be less discerning about their target species, tending to target a greater number of species at least “occasionally” than classes A and C (Fig. 6B). In combination, these two points suggest that, on average, class B may be willing to continue fishing for a variety of warmwater species rather than travel great distance for walleye. Anglers of class C were more likely to be nonconsumptive anglers than those of class A. Class A anglers, in contrast, were more likely to both target bluegill and harvest fish, if they were going to go fishing at all. No specialized group of walleye anglers emerged from this analysis, and we did not find evidence that anglers would concentrate their fishing effort at distant walleye lakes. However, considerable unexplained heterogeneity exists within the latent classes. Of the respondents specifying that they “always” targeted walleye, 91% of them (40 out of 44) were members of class B. Based on the size of class B and the heterogeneity evident in their survey responses, within-class preference heterogeneity should be the next step for predicting behavioral responses to walleye decline.

Angler preferences for bluegill, walleye, and largemouth bass in Wisconsin were previously evaluated by Tingley et al. (2019), primarily focusing on tradeoffs between size and catch rates for each species. This study found that bluegill were the most important species predicting site choice for resident anglers, particularly sites with moderate sizes and catch rates

(i.e. “quality” fisheries rather than “action” or “trophy”). We built on this analysis by evaluating how WI resident anglers traded off travel costs and independently varying catch rates and maximum sizes for the same species. Similar to Tingley et al., we found that respondents responded most positively to optimistic scenarios, in this case simultaneously high catch rates and maximum sizes. As a result of density dependent growth, fish length tends to shrink as catch rates increase (Parkinson et al. 2004), making some of our choice options, e.g. 3 walleye in 4 hours with a maximum size of 24 inches, a potentially unrealistic expectation. In addition, even among angler reporting walleye as their primary target species, bluegill and largemouth bass attributes still contributed to site choice, corresponding to Tingley et al.’s findings. The patterns in angler preferences found in our study may also reflect broader patterns angler preferences in multispecies fisheries. In a choice experiment targeting German freshwater anglers, Arlinghaus et al., (2019) also detected three latent classes of anglers, including a group of committed anglers who benefited most from fish size, casual anglers who were more likely to harvest fish (in agreement with the specialization framework proposed by Bryan, (1977)), and an intermediate group who valued both catch and size.

Our results suggest that future management of walleye populations should combine stocking walleye as well as maintaining diverse, quality warmwater fisheries as walleye declines continue. Walleye stocking is already strategically allocated to lakes most likely to support naturally reproducing walleye populations (Hansen et al. 2015a), but success of future stocking may additionally rely on strategies prioritizing equity of angler access to quality walleye fishing. Economic models have previously been developed to maximize aggregate fishing effort for rainbow trout across a lake-rich landscape in British Columbia (Askey et al. 2013). In that fishery, however, rainbow trout were functioning in part as a substitute species for kokanee

salmon (*Oncorhynchus nerka*), which were undergoing declines (Askey and Johnston 2013). The strong willingness to substitute target species evident among Wisconsin anglers suggests that a walleye-focused management strategy would be insufficient for maintaining diverse, quality inland fisheries in the state. For example, fishing effort that is displaced from walleye onto other species could drive declines at popular fishing sites (Abbott and Fenichel 2013; Beaudreau et al. 2018; Abbott et al. 2018).

Although centrarchid populations are resilient to removals (Embke et al. 2022), centrarchid size structures can become truncated as a result of intense harvest pressure (Coble 1988), resulting in reduced benefits to anglers. Limiting harvest of highly exploited species such as bluegill through reduced bag limits, however, can restore larger sizes (Rypel 2015) and achieve the quality bluegill fisheries attractive to anglers in WI (Tingley et al. 2019). Largemouth bass in the state, in contrast, have the opposite problem. As largemouth bass populations have increased in density, average sizes have shrunk, resulting in high catch rates but less opportunity for trophy sizes (Hansen et al. 2015b). Incentivizing harvest of smaller largemouth bass may simultaneously benefit centrarchid populations by improving largemouth bass size structures and displacing fishing effort off of more popular harvest species like bluegill, but the success of these interventions would depend strongly on angler behavior and lake-specific factors (Sullivan et al. 2019). Social norms against harvesting largemouth bass, however, are deeply entrenched (Gaeta et al. 2013; Sass and Shaw 2019), suggesting that additional outreach beyond relaxed harvest regulations would be required to shift social norms. Anglers' stated willingness to travel for a variety of species could mean that there is room for this sort of shift in social norms, potentially paving the way for management actions directing inland fisheries to different but still beneficial states for Wisconsin anglers (Feiner et al. 2022).

Projections of future behavior based on these stated preferences, however, must be interpreted with caution given the hypothetical nature of the choice scenarios.

Stated preference models provide an opportunity to design choice sets that increase efficiency (reducing the number of required respondents) and orthogonality (reducing correlation between attributes) in order to produce precise parameter estimates quantifying respondent preferences (Huber and Zwerina, 1996). However, because respondents are presented with only hypothetical choices, they are subject to price discounting (e.g. Whitehead and Lew 2020). The WTT estimates presented here may therefore overstate anglers' true behavior as walleye fishing quality in their nearby lakes declines. In addition, participants that responded to this choice scenario represent a biased selection of all Wisconsin anglers. As opposed to revealed preference data collection, stated preference methods that rely on participants opting in to the survey are not collecting an exogenous, random sample of the population (Thill and Horowitz 1991). The low representation of casual anglers in our sample, for example, is most likely caused by response bias (Tarrant et al. 1993). Finally, considerable unexplained heterogeneity remains within our three latent classes of anglers, potentially obscuring committed walleye specialists. Further iterations of this analysis should include random parameters accounting for individual heterogeneity within classes. No significant differences existed between latent classes in our analysis. However, by integrating individual characteristics and individual heterogeneity into this model fit (Greene and Hensher 2013), we may also be better equipped to simulate aggregate changes in angler behavior based on demographic strata.

Given the importance of species diversity to angler satisfaction (Beardmore et al. 2015), empirical evidence of species substitution among anglers (Beaudreau et al. 2018; Trudeau et al. 2022), and the role of functional diversity in resilience of social-ecological systems (SES)

(Kotschy et al. 2015), accounting for substitution behavior among anglers and species interactions among fish are important steps towards improving SES models used to assist management decisions. The development of single species SES models of inland recreational fisheries have resulted in great strides in understanding landscape patterns of fishing effort and harvest (e.g. Parkinson et al. 2004; Post et al. 2008; Askey et al. 2013; Carruthers et al. 2018; Matsumura et al. 2019), and incorporating species interactions (e.g. Innes-Gold et al. 2021) and angler substitution behavior as landscapes undergo environmental change is an exciting next step. SES models incorporating multispecies dynamics of the Chesapeake Bay (Townsend 2014) and Australian coral reef recreational fisheries have been successfully developed (e.g. Gao and Hailu 2011, 2012, 2013), but multispecies models of inland fisheries are rare (but see Lupi et al. 2003; Carpenter and Brock 2004; Biggs et al. 2009; Fielder et al. 2016). By linking a model of angler behavior to currently existing models predicting species distribution (Hansen et al. 2017), empirical models of catch rate hyperstability (Dassow et al. 2019; Feiner et al. 2020), as well as incorporating centrarchid interspecific interactions (Seekell et al. 2013) and population dynamics under climate change, a Wisconsin-specific SES model could be developed to develop equitable and sustainable fisheries management strategies.

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Tables

Table 1: All attribute levels represented in the choice experiment distributed to WI resident anglers. Travel time and catch rates were included as linear predictors, and maximum sizes were included as categorical variables. The baseline level for walleye and largemouth bass maximum sizes was a “zero” size associated with 0 catch rates. The baseline level for bluegill was 6 inches. Attributes that were coded as continuous variables in the model fit were centered and scaled around zero. Their normalized values are reported here under ‘scaled levels.’

Attribute	Levels	Scaled levels
Daily one-way travel to fishing site	5 minutes	-0.604
	15 minutes	-0.432
	30 minutes	-0.172
	60 minutes	0.346
	120 minutes	1.38
	180 minutes	2.42
Expected walleye catch in 4 hours	0	-0.957
	1	-0.0926
	2	0.772
	3	1.64
Largest possible walleye in catch	10 inches	
	14 inches	
	16 inches	
	20 inches	
	24 inches	
Expected bluegill catch in 4 hours	5	-0.333
	10	0.332
	15	0.997
	20	1.66
Largest possible bluegill in catch	6 inches	
	7 inches	
	8 inches	
	10 inches	
Expected largemouth bass catch in 4 hours	0	-0.824
	1	-0.351
	2	0.122
	4	1.07
	6	2.01
Largest possible largemouth bass in catch	12 inches	
	16 inches	
	20 inches	

Table 2: Statements eliciting catch-related attitudes from Anderson et al., (2007). The same response scale was used for each of these statements.

Factor	Statements	Response scale
Catch big fish	I would rather catch 1 or 2 big fish than 10 smaller fish. I like to fish where I know I have a chance to catch a trophy fish. The bigger the fish I catch, the better the fishing trip.	1—Strongly disagree 2—Somewhat disagree 3—Neither agree nor disagree 4—Somewhat agree 5—Strongly agree
Keep fish	I go fishing for my personal consumption I release most of the fish that I catch. I am just as happy if I release the fish that I catch	
Catching fish	The more fish I catch the happier I am I am just as happy if I don't catch any fish A fishing trip can be successful even if no fish are caught.	

Table 3: Semantic differential questions rating centrality to lifestyle, catch and release behavior, and self-described fishing skill. For these questions, response scales varied in the meaning of the anchor values (1, 50, 100).

Factor	Question	Response scale (1-100)
Centrality	In general, how important is fishing to your quality of life? When given some leisure time, how often would you choose to go fishing rather than some other recreational activity? When you go fishing, how often do you target a particular type of fish versus targeting “whatever bites”?	1—Very unimportant 50—Neither 100—Very important 1—NEVER go fishing 50—Go fishing about half the time 100—ALWAYS go fishing 1—Always “whatever bites” 50—Both about equally 100—Always a particular type
Keep fish	In general, how often do you tend to release fish that you could otherwise legally harvest?	1—Always HARVEST them 50—Harvest or release about equally 100—Always RELEASE them
Skill	To what extent do you believe that fishing success is due to one’s skill at fishing or luck? How would you judge your fishing skills compared to the average angler?	1—Entirely LUCK 50—Equal mix of luck and skill 100—Entirely SKILL 1—My skills are much lower 50—My skills are about average 100—My skills are much higher

Table 4: Confirmatory factor analysis fit to survey questions assessing trophy orientation (catching big fish), consumptive orientation (keeping fish), noncatch orientation (valuing experience of fishing more than catch), and centrality to lifestyle.

Factor and statements	Standardized coefficient (SE)	Z value
Trophy orientation		

I would rather catch 1 or 2 big fish than 10 smaller fish.	0.694 (0.032)***	21.734
I like to fish where I know I have a chance to catch a trophy fish.	0.691 (0.032)***	21.589
The bigger the fish I catch, the better the fishing trip.	0.676 (0.032)***	20.867
Consumptive orientation		
I go fishing for my personal consumption	0.539 (0.033)***	16.565
I release most of the fish that I catch.	-0.846 (0.018)***	-46.877
I am just as happy if I release the fish that I catch	-0.754 (0.022)***	-34.136
In general, how often do you tend to release fish that you could otherwise legally harvest?	-0.817 (0.019)***	-42.537
Noncatch orientation		
I am just as happy if I don't catch any fish	0.819 (0.047)***	-6.150
A fishing trip can be successful even if no fish are caught.	0.670 (0.044)***	17.282
The more fish I catch, the happier I am.	-0.276 (0.045)***	15.323
Centrality to lifestyle		
In general, how important is fishing to your quality of life?	0.678 (0.031)***	22.235
When given some leisure time, how often would you choose to go fishing rather than some other recreational activity?	0.735 (0.029)***	25.482
When you go fishing, how often do you target a particular type of fish versus targeting "whatever bites"?	0.514 (0.037)***	14.014
Self-described skill		
To what extent do you believe that fishing success is due to one's skill at fishing or luck?	0.571 (0.035)***	16.531
How would you judge your fishing skills compared to the average angler?	0.871 (0.033)***	26.384

CFI: 0.904

TLI: 0.874

RMSEA: 0.073

Table 5: Model selection results for increasing numbers of latent classes in the latent class fractional multinomial logit (LC FMNL) model fit to choice experiment selections. The bolded model is the best fit according to Akaike Information Criterion (AIC) scores.

Model	Number of parameters	AIC	Model
1 LC	29	8190.84	1 LC
2 LC	59	7883.41	2 LC
3 LC	89	7811.83	3 LC

4 LC	119	7858.6	4 LC
5 LC	149	7876.77	5 LC

Table 6: Model selection results for 3-LC models including each combination of individual covariates predicting latent class membership.

Model	Number of parameters	AIC
Trophy + Noncatch + Consumptive + Central	97	7617.93
Trophy + Noncatch + Consumptive	95	7633.35
Noncatch + Non-consumptive + Central	95	7616.17
Trophy + Non-consumptive + Central	95	7617.04
Trophy + Noncatch + Central	95	7622.02
Trophy + Noncatch	93	7635.40

Trophy + Consumptive	93	7633.60
Trophy + Central	93	7751.31
Noncatch + Consumptive	93	7641.69
Noncatch + Central	93	7631.27
Trophy	91	7641.47
Noncatch	91	7658.43
Consumptive	91	7641.43
Central		7763.32

Table 7: Parameter estimates, robust standard errors, and willingness to travel (WTT) estimates for latent class A. The second set of WTT estimates are converted into minutes of travel from the original scaled estimates. WTT in minutes therefore describes the mean willingness to travel to achieve a 1 SD increase in catch rates or to achieve an increase from baseline maximum sizes to the maximum size described. An increase of 1 SD in catch rates is 1.16 fish per 4 hours for walleye, 2.11 fish for largemouth bass, and 7.51 fish for bluegill.

Parameter	Estimate (SE)	T statistic	P value	WTT (SE)	WTT (minutes)
Delta a	0 (fixed)				
Fishing ASC	0 (fixed)				

Fish elsewhere ASC	-1.06 (1.67)	-0.64	0.52		
Do not fish ASC	3.05 (1.21)	2.51	0.01		
Centrality to lifestyle	0 (fixed)				
Noncatch orientation	0 (fixed)				
Consumptive orientation	0 (fixed)				
Travel time	-1.35 (0.37)	-3.67	<0.0001		
Walleye catch	0.53 (1.1)	0.48	0.63	0.394 (0.47)	62.76
Largemouth bass catch	0.28 (0.37)	0.74	0.46	0.205 (0.68)	51.83
Bluegill catch	1.22 (0.58)	2.09	0.04	0.909 (2.4)	92.56
Walleye size max 10 in	-0.52 (1.18)	-0.44	0.66	-0.384 (-0.43)	17.75
Walleye size max 14 in	0.32 (0.99)	0.33	0.75	0.238 (0.34)	53.74
Walleye size max 16 in	0.39 (1.18)	0.33	0.74	0.287 (0.33)	56.57
Walleye size max 20 in	0.21 (0.87)	0.24	0.81	0.154 (0.24)	48.88
Walleye size max 24 in	-0.27 (1.14)	-0.24	0.81	-0.202 (-0.24)	28.28
Bluegill size max 7 in	2.02 (1.09)	1.86	0.06	1.501 (1.94)	126.81
Bluegill size max 8 in	1.39 (0.92)	1.51	0.13	1.036 (1.5)	99.91
Bluegill size max 10 in	2.19 (0.82)	2.67	0.01	1.626 (2.81)	134.04
Largemouth bass size max 12 in	-0.36 (1.12)	-0.33	0.75	-0.27 (-0.33)	24.35
Largemouth bass size max 16 in	-1.54 (1.31)	-1.18	0.24	-1.142 (-1.36)	-26.1
Largemouth bass size max 20 in	-0.59 (1.13)	-0.52	0.60	-0.436 (-0.54)	14.74
Walleye catch x max size 14 in	-1.27 (1.01)	-1.25	0.21	-0.944 (-1.28)	-14.65
Walleye catch x max size 16 in	-0.93 (1.02)	-0.91	0.36	-0.694 (-0.91)	-0.18
Walleye catch x max size 20 in	-0.4 (0.93)	-0.43	0.67	-0.3 (-0.43)	22.61
Walleye catch x max size 24 in	0.25 (1.62)	0.15	0.88	0.184 (0.15)	50.61
Bass catch x max size 16 in	0.45 (0.52)	0.87	0.38	0.337 (0.99)	59.46
Bass catch x max size 20 in	0.06 (0.53)	0.12	0.91	0.046 (0.12)	42.63
Bluegill catch x max size 7 in	-1.09 (0.89)	-1.23	0.22	-0.811 (-1.44)	-6.95

Bluegill catch x max size 8 in	-0.41 (0.66)	-0.62	0.53	-0.305 (-0.63)	22.32
Bluegill catch x max size 10 in	-0.74 (0.59)	-1.25	0.21	-0.55 (-1.36)	8.15
Walleye catch x travel	0.55 (0.33)	1.67	0.09		
Walleye catch x bass catch	-0.14 (0.14)	-1.01	0.31	-0.105 (-0.97)	33.89
Walleye catch x bluegill catch	-0.19 (0.35)	-0.55	0.58	-0.144 (-0.55)	31.64

Table 8: Parameter estimates, robust standard errors, and willingness to travel (WTT) estimates for latent class B. The second set of WTT estimates are converted into minutes of travel from the original scaled estimates. WTT in minutes therefore describes the mean willingness to travel to achieve a 1 SD increase in catch rates or to achieve an increase from baseline maximum sizes to the maximum size described. An increase of 1 SD in catch rates is 1.16 fish per 4 hours for walleye, 2.11 fish for largemouth bass, and 7.51 fish for bluegill.

Parameter	Estimate (SE)	T statistic	P value	WTT (SE)	WTT (minutes)
Delta b	4.04 (1.15)	3.50	<0.0001		
Fishing ASC	0 (fixed)				
Fish elsewhere ASC	-0.36 (0.2)	-0.64	0.52		

Do not fish ASC	-1.14 (0.24)	2.51	0.01		
Centrality to lifestyle	0.49 (0.43)	1.14	0.25		
Noncatch orientation	0.57 (0.54)	1.07	0.28		
Consumptive orientation	-1.17 (0.6)	-1.95	0.052		
Travel time	-0.48 (0.04)	-12.49	<0.0001		
Walleye catch	0.18 (0.08)	2.35	0.02	0.388 (2.3)	62.42
Largemouth bass catch	0.09 (0.04)	2.23	0.03	0.193 (2.16)	51.13
Bluegill catch	0.27 (0.06)	4.27	<0.0001	0.573 (4.21)	73.12
Walleye size max 10 in	-0.19 (0.15)	-1.28	0.20	-0.404 (-1.28)	16.59
Walleye size max 14 in	0.15 (0.12)	1.23	0.22	0.314 (1.21)	58.13
Walleye size max 16 in	0.44 (0.13)	3.31	0.001	0.918 (3.14)	93.08
Walleye size max 20 in	0.41 (0.13)	3.18	0.001	0.861 (3.04)	89.78
Walleye size max 24 in	0.61 (0.12)	4.88	<0.0001	1.281 (4.58)	114.08
Bluegill size max 7 in	0.09 (0.08)	1.17	0.24	0.192 (1.18)	51.08
Bluegill size max 8 in	0.19 (0.08)	2.41	0.02	0.397 (2.35)	62.94
Bluegill size max 10 in	0.38 (0.08)	4.64	<0.0001	0.809 (4.36)	86.77
Largemouth bass size max 12 in	0.02 (0.1)	0.21	0.83	0.043 (0.21)	42.46
Largemouth bass size max 16 in	0.27 (0.09)	3.07	0.002	0.57 (3)	72.95
Largemouth bass size max 20 in	0.31 (0.09)	3.43	0.001	0.645 (3.36)	77.28
Walleye catch x max size 14 in	0.13 (0.09)	1.42	0.16	0.272 (1.4)	55.7
Walleye catch x max size 16 in	-0.02 (0.09)	-0.20	0.84	-0.037 (-0.2)	37.83
Walleye catch x max size 20 in	0.19 (0.1)	1.96	0.05	0.396 (1.94)	62.88
Walleye catch x max size 24 in	0.18 (0.1)	1.81	0.07	0.387 (1.8)	62.36
Bass catch x max size 16 in	0.05 (0.06)	0.83	0.41	0.098 (0.83)	45.64
Bass catch x max size 20 in	0.1 (0.05)	1.88	0.06	0.214 (1.89)	52.35
Bluegill catch x max size 7 in	0.04 (0.08)	0.48	0.63	0.077 (0.47)	44.42
Bluegill catch x max size 8 in	-0.03 (0.08)	-0.34	0.73	-0.055 (-0.34)	36.79
Bluegill catch x max size 10 in	0.02 (0.08)	0.21	0.83	0.033 (0.21)	41.88
Walleye catch x travel	0.03 (0.03)	1.14	0.26		
Walleye catch x bass catch	-0.03 (0.03)	-1.03	0.30	-0.058 (-1.02)	36.61
Walleye catch x bluegill catch	0.01 (0.03)	0.33	0.74	0.024 (0.33)	41.36

Table 9: Parameter estimates, robust standard errors, and willingness to travel (WTT) estimates for latent class C. The second set of WTT estimates are converted into minutes of travel from the original scaled estimates. WTT in minutes therefore describes the mean willingness to travel to achieve a 1 SD increase in catch rates or to achieve an increase from baseline maximum sizes to the maximum size described. An increase of 1 SD in catch rates is 1.16 fish per 4 hours for walleye, 2.11 fish for largemouth bass, and 7.51 fish for bluegill.

Parameter	Estimate (SE)	T statistic	P value	WTT (SE)	WTT (minutes)
Delta c	2.44 (1.12)	2.17	0.03		
Fishing ASC	0 (fixed)				
Fish elsewhere ASC	3.05 (0.44)	6.99	<0.0001		
Do not fish ASC	-0.5 (0.63)	-0.80	0.43		

Centrality to lifestyle	1.33 (0.48)	2.74	0.01		
Noncatch orientation	0.52 (0.55)	0.94	0.35		
Consumptive orientation	-1.39 (0.63)	-2.21	0.03		
Travel time	-0.69 (0.1)	-6.68	<0.0001		
Walleye catch	-0.02 (0.17)	-0.12	0.90	-0.03 (-0.12)	38.23
Largemouth bass catch	-0.1 (0.1)	-1.09	0.28	-0.151 (-1.12)	31.23
Bluegill catch	0.16 (0.16)	0.98	0.33	0.23 (0.97)	53.27
Walleye size max 10 in	-0.12 (0.36)	-0.33	0.74	-0.17 (-0.32)	30.13
Walleye size max 14 in	0.08 (0.34)	0.24	0.81	0.119 (0.25)	46.85
Walleye size max 16 in	0.22 (0.35)	0.64	0.52	0.324 (0.65)	58.71
Walleye size max 20 in	0.5 (0.34)	1.48	0.14	0.726 (1.54)	81.97
Walleye size max 24 in	0.72 (0.31)	2.31	0.02	1.036 (2.37)	99.91
Bluegill size max 7 in	0.27 (0.19)	1.44	0.15	0.397 (1.39)	62.94
Bluegill size max 8 in	0.36 (0.19)	1.86	0.06	0.524 (1.78)	70.28
Bluegill size max 10 in	0.69 (0.21)	3.33	0.001	0.998 (2.86)	97.71
Largemouth bass size max 12 in	0.16 (0.26)	0.64	0.52	0.238 (0.65)	53.74
Largemouth bass size max 16 in	0.35 (0.2)	1.71	0.09	0.501 (1.73)	68.95
Largemouth bass size max 20 in	0.44 (0.24)	1.87	0.06	0.637 (1.82)	76.82
Walleye catch x max size 14 in	0.37 (0.2)	1.83	0.07	0.533 (1.79)	70.8
Walleye catch x max size 16 in	0.46 (0.22)	2.09	0.04	0.67 (2.15)	78.73
Walleye catch x max size 20 in	0.45 (0.22)	2.01	0.04	0.648 (1.99)	77.46
Walleye catch x max size 24 in	0.52 (0.2)	2.60	0.01	0.748 (2.64)	83.24
Bass catch x max size 16 in	0.19 (0.12)	1.66	0.10	0.281 (1.61)	56.22
Bass catch x max size 20 in	0.39 (0.13)	3.02	0.003	0.558 (3.02)	72.25
Bluegill catch x max size 7 in	0.05 (0.2)	0.22	0.82	0.066 (0.22)	43.79
Bluegill catch x max size 8 in	0.05 (0.19)	0.25	0.80	0.069 (0.25)	43.96
Bluegill catch x max size 10 in	0.01 (0.19)	0.03	0.98	0.008 (0.03)	40.43
Walleye catch x travel	0.18 (0.07)	2.43	0.02		
Walleye catch x bass catch	0.03 (0.05)	0.48	0.63	0.038 (0.48)	42.17
Walleye catch x bluegill catch	-0.01 (0.07)	-0.11	0.91	-0.012 (-0.11)	39.27

Figures

If these were your only options for **ten days** of fishing in Wisconsin, how many days would you spend on each of these five options?

Daily one-way travel time to fishing site	15 minutes	120 minutes	60 minutes		
Expected walleye catch in 4 hours	1 walleye	2 walleye	1 walleye		
Largest possible walleye in catch	14 inches	16 inches	20 inches		
Expected bluegill catch in 4 hours	15 bluegill	5 bluegill	5 bluegill		
Largest possible bluegill in catch	6 inches	7 inches	10 inches		
Expected largemouth bass catch in 4 hours	2 bass	0 bass	1 bass	Go fishing elsewhere for another species	Do not go fishing
Largest possible largemouth bass in catch	16 inches		16 inches		
	3	<input type="text"/>	1	3	3

Total: 10

Figure 6: Completed sample choice scenario, where ten hypothetical fishing days have been allocated between three potential fishing sites and two opt-out options.

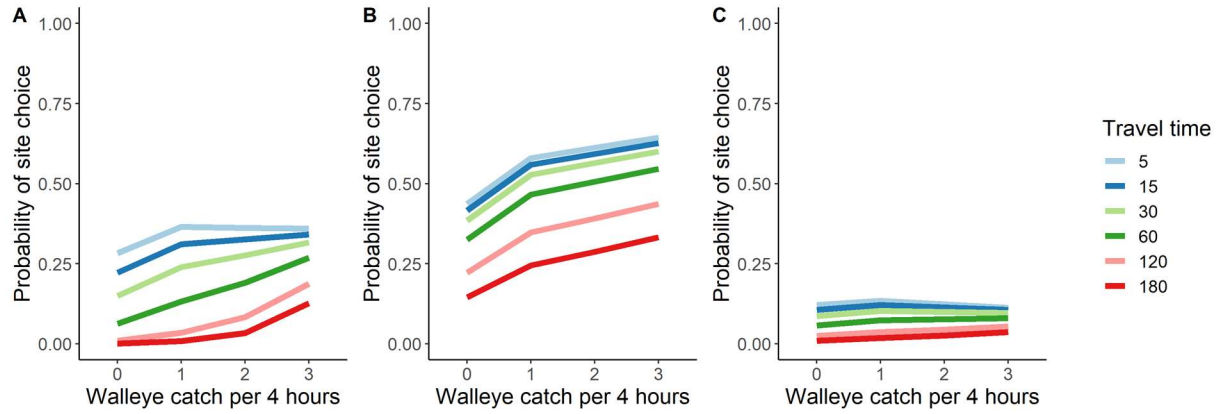


Figure 7: Site choice predictions for each latent class under identical conditions. Simulated choices took place between a site with varying travel times and walleye catch rates, two opt out options, a baseline site with an expected walleye catch rate of 0, and median values for all other site attributes.

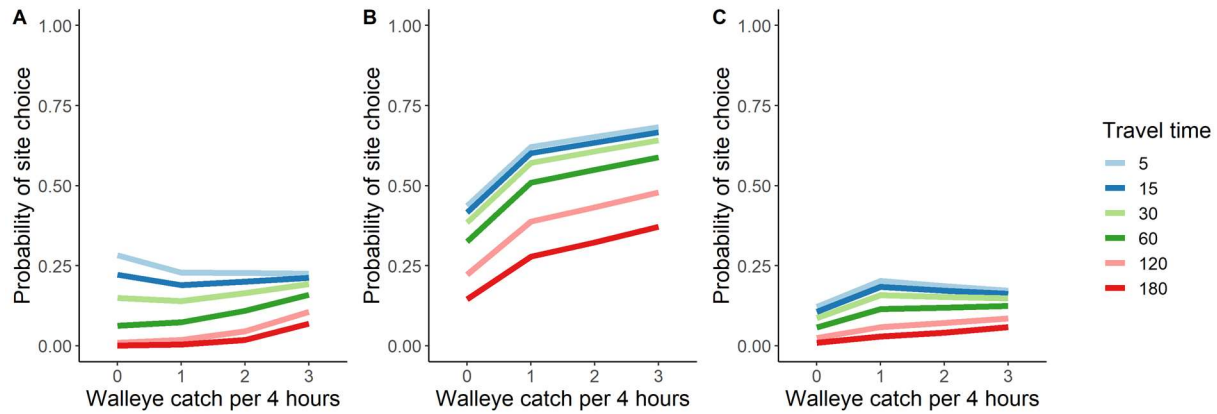


Figure 8: Site choice predictions for each latent class under identical conditions. Simulated choices took place between a site with varying travel times and walleye catch rates, two opt out options, and a baseline site with an expected catch rate of 0. Contrasting with Figure 2, the maximum walleye size for the site with a walleye catch rate > 0 is fixed at its maximum level of 24 inches. Probability of this site choice increased slightly for latent class C but remained less than 25% at all catch rates and travel times.

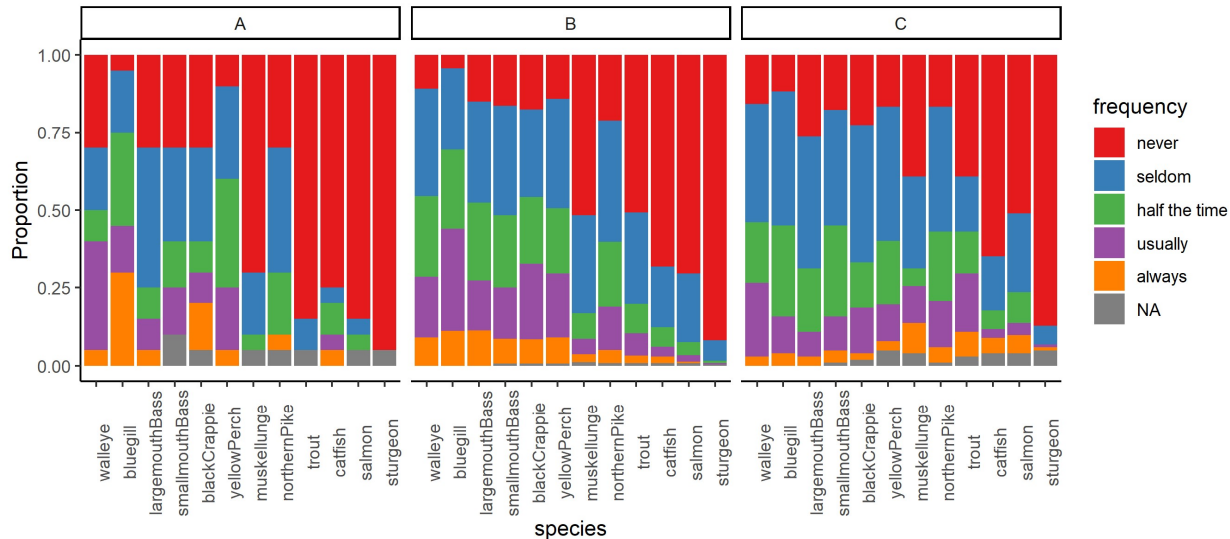


Figure 9: Proportions of self-reported frequency of fishing for each listed target species by each latent class. In spite of differences in class size (A, n=20; B, n=441; C, n=102), targeting behavior was reported as largely similar between latent classes.

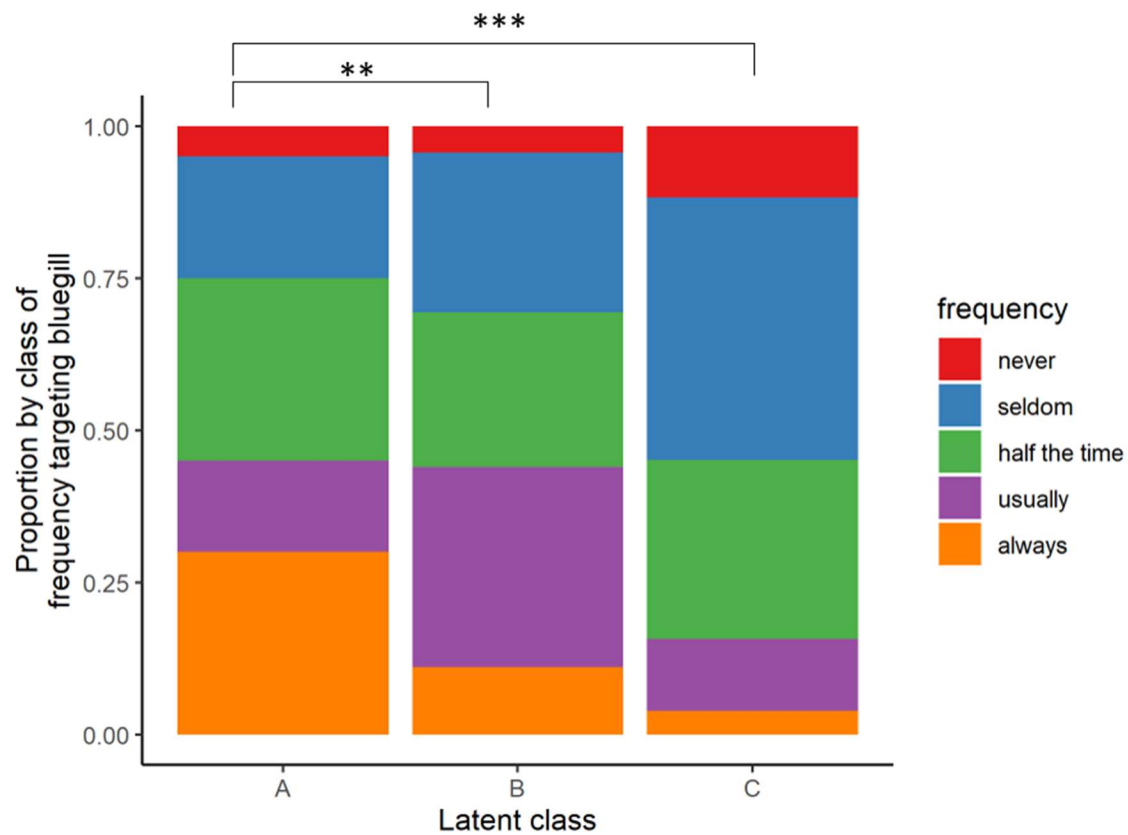


Figure 10: Out of the species listed, only targeting frequency of bluegill was significantly different among latent classes. Class A members targeted bluegill significantly more often than members of class B and C.

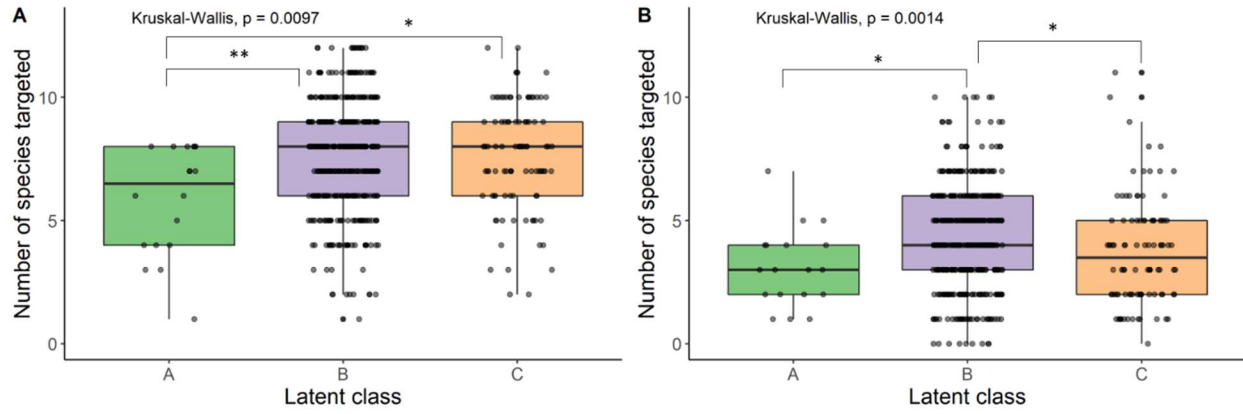


Figure 11: Comparing the number of species targeted at least “seldom” (A) and at least “occasionally” (B) on a 5 point Likert scale among the three latent classes.

Supplementary materials

Table S1: Preliminary attributes and levels for the discrete choice experiment presented to focus group participants compared to attributes and levels included in the final design. Note that typical (median) sizes were not included in the final choice experiment design, and the “panfish” attributes were changed to represent bluegill only.

Attribute	Quantiles from creel surveys	All levels (preliminary)	All levels (final)
Travel time	5%: 0	5 minutes	5 minutes
	25%: 5	15 minutes	15 minutes
	50%: 10	30 minutes	30 minutes
	75%: 20	45 minutes	60 minutes
	90%: 40	60 minutes	120 minutes
	95%: 120	75 minutes	180 minutes
Walleye catch per 4 hours	5%: 0	0	0
	25%: 0	0.5 (1 every other trip)	1
	50%: 0	1	2
	75%: 1.2	2	3
	90%: 3.69		
	95%: 6.4		
Walleye typical size	Median size by lake	8 inches	
	5%: 12.2 inches	10 inches	
	25%: 14.1 inches	12 inches	
	50%: 16.2 inches	14 inches	
	75%: 18 inches		
	95%: 21.7 inches		
Largest possible walleye size	5%: 15.6 inches	10 inches	10 inches
	25%: 20.5 inches	12 inches	14 inches
	50%: 23.5 inches	14 inches	16 inches
	75%: 26.5 inches	16 inches	20 inches
	95%: 29 inches		24 inches
	Panfish catch per 4 hours	(Based on bluegill catch rates)	5
5%: 0		10	5
25%: 0.42		15	10
50%: 4.8		20	15
75%: 14.5		25	20
90%: 30			
Panfish typical size	95%: 45.1		
	(Based on quantiles of bluegill median size by lake)	3 inches	
	5%: 6.1 inches	4 inches	
	25%: 6.95 inches	5 inches	
	50%: 7.3 inches	6 inches	
	75%: 7.6 inches		

	95%: 8.1 inches		
Largest possible panfish size	(Based on quantiles of bluegill maximum size by lake)	6 inches 8 inches 10 inches	Bluegill max size 6 inches 7 inches 8 inches 10 inches
	5%: 7.3 inches 25%: 8.5 inches 50%: 9.3 inches 75%: 9.8 inches 95%: 10.5 inches		
Largemouth bass catch per 4 hours	5%: 0 25%: 0 50%: 1 75%: 3.67 90%: 8.57 95%: 33.6	0 1 2 4	0 1 2 4 6
Largemouth bass typical size	5%: 12.4 inches 25%: 14.5 inches 50%: 15.1 inches 75%: 16 inches 95%: 16.8 inches	6 inches 8 inches 10 inches 14 inches	
Largemouth bass max size	5%: 14.7 inches 25%: 16.3 inches 50%: 18 inches 75%: 19.2 inches 95%: 21 inches	10 inches 12 inches 14 inches 16 inches 18 inches	12 inches 16 inches 20 inches

Table S2: Prior coefficient parameters used to produce the choice experiment design. The sign of these values was used to avoid dominant choices when the modified Federov algorithm produced candidate D efficient fractional factorial designs.

Parameter	Prior parameter value for survey design
Travel time	-0.02
Walleye catch per 4 hours	0.02
Walleye maximum size: 10 inches	0.02
Walleye maximum size: 14 inches	0.03
Walleye maximum size: 16 inches	0.04
Walleye maximum size: 20 inches	0.05
Walleye maximum size: 24 inches	0.06
Bluegill catch per 4 hours	0.02
Bluegill maximum size: 7 inches	0.03
Bluegill maximum size: 8 inches	0.04
Bluegill maximum size: 10 inches	0.05
Largemouth bass catch per 4 hours	0.02
Largemouth bass maximum size: 12 inches	0.02
Largemouth bass maximum size: 16 inches	0.04
Largemouth bass maximum size: 20 inches	0.06
Walleye catch * max size	0
Bluegill catch * max size	0
Largemouth bass catch * max size	0
Walleye catch * largemouth bass catch	0
Walleye catch * bluegill catch	0
Walleye catch * travel	0
Walleye size * travel	0

Table S3: Wisconsin sampling regions for fishing license sales data. Note that highly urban regions (Dane and Milwaukee counties) were down-sampled in order to up-sample Northern Wisconsin counties.

Region	Population	Proportion population	Proportion sample	Counties
Dane County	536078	0.093	0.074	Dane
Milwaukee County	951226	0.164	0.099	Milwaukee
Northeast	1130044	0.195	0.195	Brown, Calumet, Door, Fond du Lac, Green Lake, Kewaunee, Manitowoc, Marinette, Marquette, Menominee, Oconto, Outagamie, Shawano, Waupaca, Waushara, Winnebago
Northern	380839	0.066	0.150	Ashland, Barron, Bayfield, Burnett, Douglas, Florence, Forest, Iron, Langlade, Lincoln, Oneida, Polk, Price Rusk, Sawyer, Taylor, Vilas, Washburn
South Central	602044	0.104	0.104	Columbia, Dodge, Grant, Green, Iowa, Jefferson, Lafayette, Richland, Rock, Sauk
Southeast	1206375	0.208	0.208	Kenosha, Ozaukee, Racine, Sheboygan, Walworth, Washington, Waukesha
West Central	984110	0.170	0.170	Adams, Buffalo, Chippewa, Clark, Crawford, Dunn, Eau Claire, Jackson, Juneau, La Crosse, Marathon, Monroe, Pepin, Pierce, Portage, St. Croix, Trempealeau, Vernon, Wood

Table S4: Licenses held by WI residents in each WI region. License data was provided by the WDNR. Proportions of state-wide licenses held by individuals in each region were not known prior to the requested sample of fishing licenses in Tables S3 and S5. Sampling proportions by region were therefore chosen to up-sample known regions with high-density angler populations rather than based on these exact proportions.

Region	Total licenses held	Proportion licenses (18-59 years)	Proportion licenses (60+ years)	Proportion of licenses in the state
Dane County	73635	0.722	0.278	0.059
Milwaukee County	82644	0.713	0.287	0.066
Northeast	313065	0.683	0.317	0.249
Northern	160845	0.599	0.401	0.128
South Central	134982	0.696	0.304	0.108
Southeast	229204	0.689	0.311	0.183
West Central	260600	0.694	0.306	0.208

Table S5: Sample numbers stratified by age category for surveys distributed by email. Note that, due to their high population density, Dane and Milwaukee counties constituted their own regions.

Region	Age Category	Sample size (email)
Dane County	over 60	166
	under 60	500
Milwaukee County	over 60	222
	under 60	666
Northeast	over 60	439
	under 60	1317
Northern	over 60	337
	under 60	1012
South Central	over 60	234
	under 60	702
Southeast	over 60	469
	under 60	1406
West Central	over 60	382
	under 60	1148

Table S6: Parameter estimates and robust standard errors for latent class A in the second-best fitting model. Rather than non-catch orientation, trophy orientation is included as an individual covariate predicting latent class membership. In this model fit, the bluegill maximum size of 7 inches is a significant positive predictor of site choice for class A.

Parameter	Estimate (SE)	T statistic	P value
Delta a	0 (fixed)		
Fishing ASC	0 (fixed)		
Fish elsewhere ASC	-0.95 (2.2)	-0.60	0.55
Do not fish ASC	2.97 (1.85)	2.66	0.01
Centrality to lifestyle	0 (fixed)		
Trophy orientation	0 (fixed)		
Consumptive orientation	0 (fixed)		
Travel time	-1.3 (0.45)	-3.77	<0.0001
Walleye catch	0.49 (0.89)	0.54	0.59
Largemouth bass catch	0.27 (0.39)	0.81	0.42
Bluegill catch	1.15 (0.94)	2.16	0.03
Walleye size max 10 in	-0.58 (1.72)	-0.56	0.57
Walleye size max 14 in	0.21 (1.2)	0.23	0.82
Walleye size max 16 in	0.36 (1.32)	0.34	0.73
Walleye size max 20 in	0.12 (1.23)	0.15	0.88
Walleye size max 24 in	-0.21 (1.28)	-0.21	0.83
Bluegill size max 7 in	1.95 (1.42)	2.04	0.04
Bluegill size max 8 in	1.33 (1.43)	1.63	0.10
Bluegill size max 10 in	2.12 (1.39)	3.03	<0.0001
Largemouth bass size max 12 in	-0.31 (1.02)	-0.28	0.78
Largemouth bass size max 16 in	-1.29 (1.23)	-0.87	0.38
Largemouth bass size max 20 in	-0.51 (1.04)	-0.42	0.67
Walleye catch x max size 14 in	-1.15 (1.08)	-1.26	0.21
Walleye catch x max size 16 in	-0.92 (1.06)	-1.09	0.27
Walleye catch x max size 20 in	-0.37 (0.99)	-0.48	0.63
Walleye catch x max size 24 in	0.16 (1.16)	0.12	0.90
Bass catch x max size 16 in	0.4 (0.62)	0.78	0.44
Bass catch x max size 20 in	0.04 (0.59)	0.07	0.94
Bluegill catch x max size 7 in	-0.97 (1.08)	-1.19	0.24
Bluegill catch x max size 8 in	-0.36 (1.08)	-0.58	0.56
Bluegill catch x max size 10 in	-0.67 (1.04)	-1.24	0.22
Walleye catch x travel	0.51 (0.37)	1.78	0.07
Walleye catch x bass catch	-0.13 (0.26)	-0.88	0.38
Walleye catch x bluegill catch	-0.17 (0.33)	-0.60	0.55

Table S7: Parameter estimates and robust standard errors for latent class B in the second-best fitting model. Rather than non-catch orientation, trophy orientation is included as an individual covariate predicting latent class membership. In this model fit, consumptive orientation is a negative predictor of latent class B membership.

Parameter	Estimate (SE)	T statistic	P value
Delta b	3.87 (0.57)	4.31	<0.0001
Fishing ASC	0 (fixed)		
Fish elsewhere ASC	-0.35 (0.24)	-1.81	0.07
Do not fish ASC	-1.16 (0.25)	-5.45	0.000
Centrality to lifestyle	0.53 (0.31)	1.22	0.22
Trophy orientation	-0.01 (0.4)	-0.03	0.98
Consumptive orientation	-1.29 (0.41)	-2.24	0.03
Travel time	-0.47 (0.04)	-12.60	<0.0001
Walleye catch	0.18 (0.11)	2.36	0.02
Largemouth bass catch	0.09 (0.06)	2.23	0.03
Bluegill catch	0.27 (0.09)	4.29	<0.0001
Walleye size max 10 in	-0.19 (0.22)	-1.27	0.20
Walleye size max 14 in	0.15 (0.18)	1.23	0.22
Walleye size max 16 in	0.43 (0.19)	3.30	<0.0001
Walleye size max 20 in	0.41 (0.19)	3.17	<0.0001
Walleye size max 24 in	0.61 (0.18)	4.88	<0.0001
Bluegill size max 7 in	0.09 (0.12)	1.20	0.23
Bluegill size max 8 in	0.19 (0.12)	2.46	0.01
Bluegill size max 10 in	0.39 (0.12)	4.66	0.00
Largemouth bass size max 12 in	0.02 (0.14)	0.20	0.84
Largemouth bass size max 16 in	0.27 (0.13)	3.09	<0.0001
Largemouth bass size max 20 in	0.31 (0.13)	3.43	<0.0001
Walleye catch x max size 14 in	0.13 (0.14)	1.42	0.16
Walleye catch x max size 16 in	-0.02 (0.14)	-0.20	0.84
Walleye catch x max size 20 in	0.19 (0.14)	1.97	0.05
Walleye catch x max size 24 in	0.18 (0.14)	1.84	0.07
Bass catch x max size 16 in	0.04 (0.08)	0.80	0.42
Bass catch x max size 20 in	0.1 (0.08)	1.9	0.06
Bluegill catch x max size 7 in	0.03 (0.12)	0.45	0.65
Bluegill catch x max size 8 in	-0.03 (0.11)	-0.38	0.70
Bluegill catch x max size 10 in	0.01 (0.11)	0.17	0.87
Walleye catch x travel	0.03 (0.04)	1.13	0.26
Walleye catch x bass catch	-0.03 (0.04)	-1.03	0.30
Walleye catch x bluegill catch	0.01 (0.05)	0.33	0.74

Table S8: Parameter estimates and robust standard errors for latent class C in the second-best fitting model. Rather than non-catch orientation, trophy orientation is included as an individual covariate predicting latent class membership.

Parameter	Estimate (SE)	T statistic	P value
Delta c	2.26 (0.58)	2.56	0.01
Fishing ASC	0 (fixed)		
Fish elsewhere ASC	3.07 (0.7)	7.05	<0.0001
Do not fish ASC	-0.45 (0.79)	-0.76	0.45
Centrality to lifestyle	1.26 (0.36)	2.61	0.01
Trophy orientation	0.23 (0.43)	0.42	0.67
Consumptive orientation	-1.4 (0.43)	-2.30	0.02
Travel time	-0.69 (0.17)	-6.58	<0.0001
Walleye catch	-0.02 (0.36)	-0.12	0.90
Largemouth bass catch	-0.11 (0.21)	-1.13	0.26
Bluegill catch	0.15 (0.32)	0.93	0.35
Walleye size max 10 in	-0.1 (0.75)	-0.27	0.79
Walleye size max 14 in	0.09 (0.64)	0.25	0.80
Walleye size max 16 in	0.24 (0.64)	0.68	0.50
Walleye size max 20 in	0.52 (0.64)	1.51	0.13
Walleye size max 24 in	0.73 (0.62)	2.34	0.02
Bluegill size max 7 in	0.27 (0.38)	1.39	0.16
Bluegill size max 8 in	0.35 (0.37)	1.77	0.08
Bluegill size max 10 in	0.68 (0.37)	3.29	<0.0001
Largemouth bass size max 12 in	0.17 (0.46)	0.67	0.51
Largemouth bass size max 16 in	0.34 (0.42)	1.68	0.09
Largemouth bass size max 20 in	0.43 (0.42)	1.83	0.07
Walleye catch x max size 14 in	0.38 (0.44)	1.89	0.06
Walleye catch x max size 16 in	0.47 (0.46)	2.12	0.03
Walleye catch x max size 20 in	0.45 (0.42)	2.03	0.04
Walleye catch x max size 24 in	0.52 (0.42)	2.64	0.01
Bass catch x max size 16 in	0.2 (0.25)	1.70	0.09
Bass catch x max size 20 in	0.39 (0.25)	3.08	<0.0001
Bluegill catch x max size 7 in	0.06 (0.39)	0.29	0.77
Bluegill catch x max size 8 in	0.05 (0.37)	0.29	0.78
Bluegill catch x max size 10 in	0.01 (0.37)	0.07	0.94
Walleye catch x travel	0.17 (0.14)	2.35	0.02
Walleye catch x bass catch	0.02 (0.12)	0.46	0.65
Walleye catch x bluegill catch	-0.01 (0.15)	-0.12	0.90

Conclusion

Human behavior is a key source of uncertainty when managing sustainable recreational fisheries. Although predicting and controlling the behavior of recreational anglers is unlikely, effective monitoring of changes across a fishery landscape can improve biological, social, and economic outcomes of management decisions. In this dissertation, I demonstrated that landscape-scale monitoring of fishing effort is achievable by combining multiple sources of data within a statistical modeling framework. I then successfully applied this method to detect changes in vehicle traffic at lakes surrounded by public lands during the COVID-19 pandemic. Local knowledge and other underutilized data sources such as vessel trip reports emerged as promising avenues for hypothesizing and quantifying socioeconomic tradeoffs resulting from management decisions. By evaluating human response to social and ecological change using these data sources and an experimental method, I found support for the importance of understanding and anticipating substitution behavior in recreational fisheries in order to make effective management decisions. Quantitative analysis of angler populations' behavior is an effective method to understand scale and effects of these changes in behavior, but further integration of qualitative methods will continue to be important for understanding the motivations underlying these changes. Engagement in recreational fishing emerges from diverse and often conflicting personal values (e.g. Fulton et al., 1996; Jerry J. Vaske, 2001; Teisl & O'Brien, 2003). Explicitly engaging with these conflicts in values through participatory active adaptive management (e.g. Fujitani et al., 2017) and post-normal science (e.g. Funtowicz & Ravetz, 1993) essential for maintaining socioecological resilience in human-natural systems as social norms, economic incentives, and ecosystem states continue to shift over time.

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