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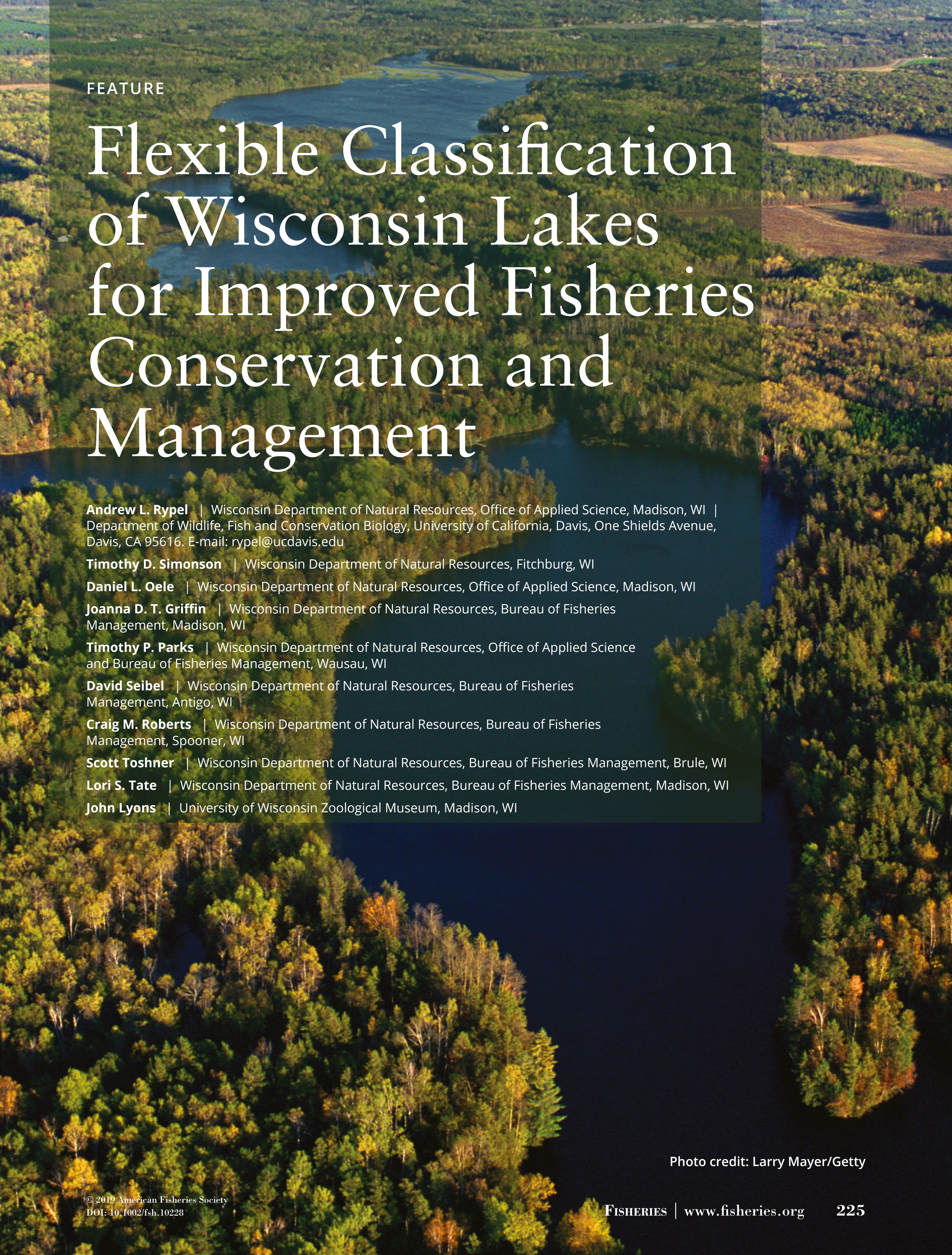

Flexible Classification of Wisconsin Lakes for Improved Fisheries Conservation and Management

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Successful fisheries management practices developed for one ecosystem can often be used in similar ecosystems. We developed a flexible lake classification framework in collaboration with ~100 fisheries biologists for improved fisheries conservation management in Wisconsin, USA. In total, 5,950 lakes were classified into 15 lake classes using a two-tiered approach. In tier-one, lakes were clustered into "simple" and "complex" sportfish assemblages. In tier-two, lakes were further clustered using accumulated degree days, water clarity, and special cases. We focus on temperature and clarity because these factors often drive fisheries change over time—thus a lake's class can change over time. Lake class assignments were refined through a vetting process where fisheries biologists with expert knowledge provided feedback. Relative abundance, size-structure, and growth rates of fishes varied significantly across classes. Biologists are encouraged to utilize class interquartile ranges in fisheries metrics to make improved fisheries assessments. We highlight hard-won lessons from our effort including: (1) the importance of co-developing classification frameworks alongside fisheries biologists; and (2) encouraging frameworks where lakes can shift classes and fisheries expectations over time due to factors like climate change and eutrophication.

INTRODUCTION

Ecosystem classification frameworks often represent a key step towards stronger fisheries management (Moyle 1949; Moyle and Ellison 1991; Schupp 1992; Wehrly et al. 2012). For lakes in particular, there is dramatic diversity in the physical, chemical, and biological attributes of these ecosystems over landscapes (Mcdonald et al. 2012; Verpoorter et al. 2014; Oliver et al. 2016). Correspondingly, lake fisheries also express wide spatial heterogeneity in virtually all fisheries metrics (Eadie and Keast 1984; Lester et al. 2003; Rypel and David 2017). Lake classification frameworks are foundational for lake fisheries management because they simplify this high degree of landscape complexity, allow better "apples-to-apples" comparisons, and thus encourage more direct evaluations of fisheries data (Austen and Bayley 1993; Kelly et al. 2012; Olin et al. 2013). Lake classification also fosters communication among stakeholders and policy makers by forming a common ecological language that can be used to focus resource management dialogue (Howard and Larson 1985; Mumby and Harborne 1999).

While lake classification has been foundational for fisheries management, some frameworks have fallen short by being based exclusively on static variables that do not change over time (e.g., lake size, depth, and landscape position). Temporal environmental change is an essential element that has been not been integrated into many lake classification frameworks (but see Wehrly et al. 2012). The vast majority of lake classification systems rely on static landscape variables that cannot change over time such as lake area, lake depth, and landscape position. Thus as lakes change over time (e.g., due to human domination of ecosystems; Vitousek et al. 1997; Carpenter et al. 2017), lake classes cannot change. Wehrly et al. (2012) recently recognized that fish assemblages in lakes are largely governed by lake thermal regime, and that a modern lake classification system should incorporate temperature and potential consequences of climate change in particular. Parallel work in stream fisheries has also recognized and integrated this need (Lyons et al. 2010; Myers et al. 2018). In this study, we build on these conceptual advances by forging a flexible lake classification system for Wisconsin lakes (i.e., one that allows lakes to change classes over time) for use in conservation management of inland Wisconsin fisheries. We stress several key lessons from our work including: (1) statistical classification based on ecological variables that can change over time, thereby allowing a lake's class to change over time; (2) the importance of collaborating with fisheries biologists (i.e., the end users of the system) to better refine the product and build internal support for its use; and (3) having the end goal of developing a model that will be immediately useable by managers.

METHODS

Data

The Wisconsin Lakes dataset (Supplementary Dataset 1) describes presence–absence of nine groups of sportfish species in all Wisconsin lakes > 8 ha (Wisconsin Department of Natural Resources 2009). The dataset included information on Muskellunge *Esox masquinongy*, Northern Pike *E. lucius*, Walleye *Sander vitreus*, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *M. dolomieu*, catfish—inclusive of primarily Channel Catfish *Ictalurus punctatus* but occasionally Flathead Catfish *Pylodictis olivaris*—trout—inclusive of Brook Trout *Salvelinus fontinalis*, Rainbow Trout *Oncorhynchus mykiss*, and Brown Trout *Salmo trutta*—Lake Sturgeon *Acipenser fulvescens*, and panfish—Inclusive of primarily Bluegill *Lepomis macrochirus*, Black Crappie *Pomoxis nigromaculatus* and Yellow Perch *Perca flavescens*, but potentially other species like bullheads *Ameiurus* spp., Green Sunfish *L. cyanellus*, Pumpkinseed *L. gibbosus* and Rock Bass *Ambloplites rupestris*. Data were originally assembled by biologists in the 1950s and 1960s, but these data were updated for this project using direct input from current local fisheries biologists.

Primary physical characteristics for each lake were based on data in the Wisconsin Register of Waterbodies (ROW) database (Supplemental Dataset 2). The ROW database included estimates of lake area (ha), maximum depth (m), watershed area, and latitude-longitude for almost every lake of interest. Hydrologic residence time data for 2,052 lakes (Supplementary Dataset 3) were derived from another Wisconsin Department of Natural Resources (WDNR) project on total maximum daily load standards for phosphorus in Wisconsin lakes (http://dnr.wi.gov/topic/surfacewater/models.html).

Lake temperature estimates were based on recent modeling efforts for Wisconsin lakes (Winslow et al. 2015, 2017; Hansen et al. 2017). Modeling focused on ~2,100 Wisconsin lakes with a history of active fish management. Daily lake temperature profiles were re-created for 1980–2014 using a general, open source lake model (Hipsey et al. 2013). Ultimately, modeled epilimnetic temperature data were converted to accumulated annual degree days (DD) using a base value of 10°C (Supplementary Dataset 4). A 10°C base value has been previously suggested as a standard base value for studies on diverse temperate fishes (Venturelli et al. 2010; Rypel 2012; Chezik et al. 2014). Mean annual temperature and DD values were averaged across available years to approximate average annual thermal conditions in each lake.

Lake clarity data were derived from remotely sensed lake Secchi depth estimates (2003–2012). These data are more thoroughly described in previous studies (Wisconsin

Department of Natural Resources 2014; Rose et al. 2017), and ultimately included water clarity estimates for 8,132 Wisconsin lakes derived from Landsat satellite data. Consistent with previous work (Olmanson et al. 2008), water clarity estimates were restricted to the months of June–September. As with temperature and DD estimates, data were averaged across years to approximate average clarity conditions for each lake (Supplementary Datasets 5, 6).

Lake classification

Philosophy and general approach

Our classification approach required quantitative analyses and a work flow that could accommodate divergent data forms and feedback loops from professional biologists. For example, fish community data were binomial whereas other fisheries and limnological data were continuous. Furthermore, from our outreach efforts with fisheries managers and biologists, we learned that there was desire for an easy-to-understand system with a reasonable number of classes (preferably <20). We developed an intuitive two-tiered classification system that used all available data, but also maximized flexibility, i.e., incorporated the ability for lakes to change classes over time. Flexibility also encompasses an ability to adjust the classification of a lake to a more appropriate class based on manager knowledge and other new information not included in initial statistical analyses. Our workflow (Figure 1) incorporated extensive interactions with the end users of our tool. This process allowed for multiple loops with users, including opportunities for feedback and flexibility in classifications based on expert judgement.

Tier-one classification

Lakes were initially clustered using a k-means cluster analysis of presence–absence data of nine primary sportfish species from the Wisconsin lakes book dataset (Figures 1, 2; Supplementary Dataset 1; Wisconsin Department of Natural Resources 2009). K-means cluster analysis seeks to partition available observations into either a predefined or an undefined number of central tendencies based on user choice (Hartigan and Wong 1979). Ultimately, all observations belong to specific clusters with nearest central tendencies. Our initial k-means analysis resulted in six preliminary clusters. Based on biologist feedback, these clusters were re-organized into two new tier-one clusters: "simple" and "complex" sportfish communities (Figure 2). Simple sportfish communities were those defined as having fewer than three sportfish species groups and no Walleye. Complex sportfish communities were those defined as having more than four sportfish species; all Walleye and most Muskellunge lakes were in this cluster.

Tier-two classification

Two new k-means cluster analyses were performed on all members of the simple and complex tier-one clusters using DD and Secchi depth data (Figure 2). All DD and Secchi depth data were normalized and centered using an $n - 1$ transformation (Bradley and Fayyad 1998). In both cluster analyses, the number of terminal clusters was pre-defined at four to systematically produce combinations of water temperature and clarity characteristics (Figure 3). Once the clusters had been defined, lakes without temperature data were added to the warm classes (the most abundant thermal class) with their clarity class membership determined by Secchi depth data (available for almost all lakes). Finally, we identified transitional members of temperature and clarity classes as those lakes having the upper or lower 5% of DD or mean Secchi values (Figure 3).

Special cases

We identified several unique lake types *a priori* through lake lists already used in existing laws or policies. In Wisconsin, "two-story lakes" receive additional protection in the form of more stringent phosphorus water quality standards. Two-story lakes are deep stratified lakes with sufficient oxythermal habitat to support both warmwater and coldwater fisheries (Lyons et al. 2017a; Parks and Rypel 2018). Two-story lakes were included in the tier-one cluster analysis, therefore, we combined results from that analysis with the existing two-story list to produce two terminal lake classes termed "simple–two-story," and "complex–two-story" lakes. We identified riverine lakes a priori as those with brief hydrologic retention times (<15 d). This value is already used to define riverine lakes for existing phosphorus water quality standards. Again, we used the tier-one classification to first identify simple and complex lakes and, subsequently, "simple–riverine" and "complex–riverine" lakes.

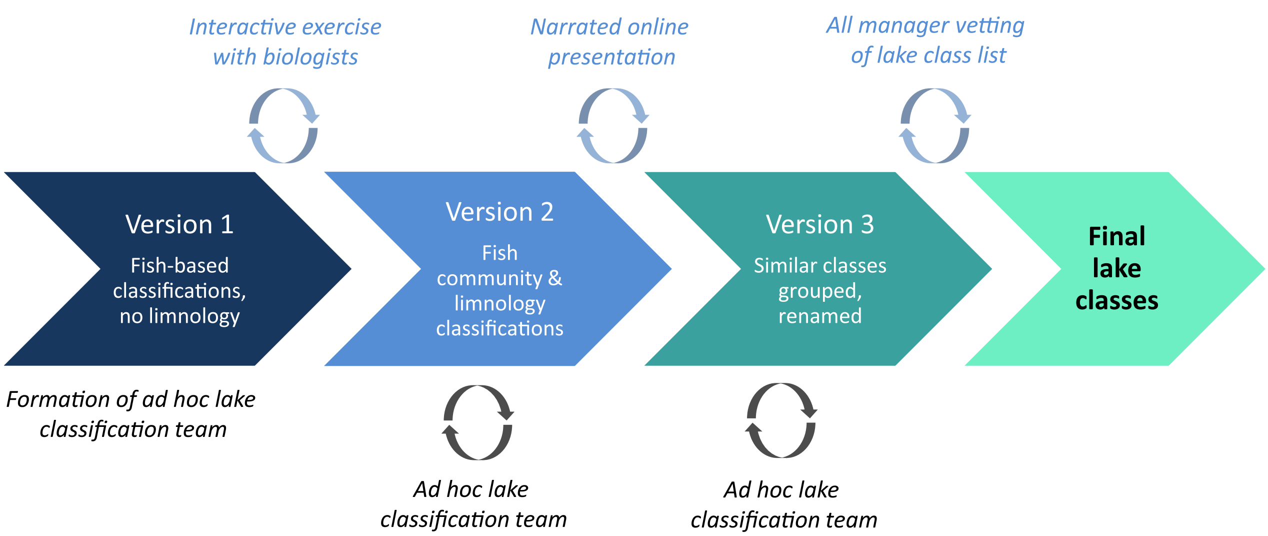

Figure 1. Workflow documenting iterative and collaborative development of lake classification system.

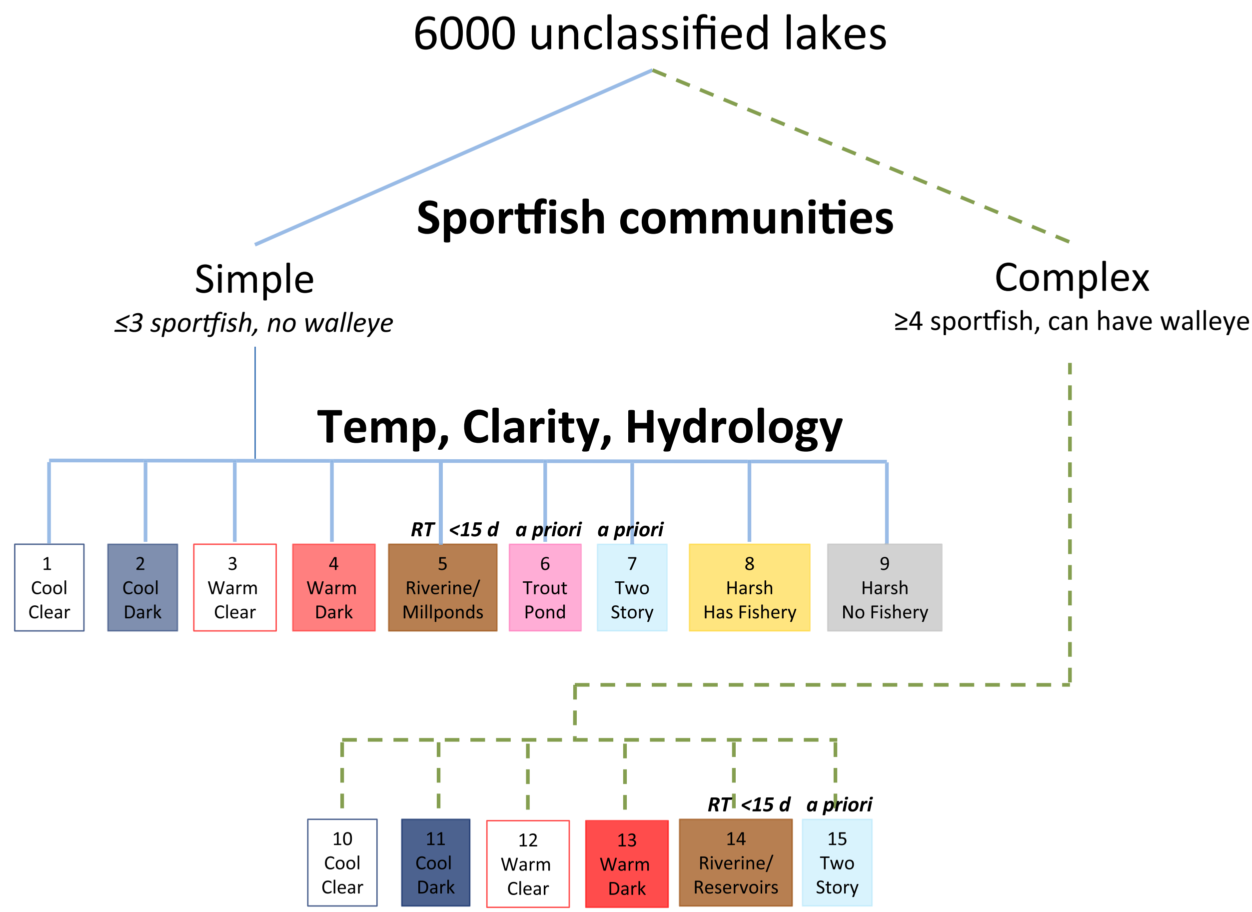

Figure 2. Two-tiered approach leading to 15 terminal lake classes for 5,951 Wisconsin lakes. RT = "hydrologic retention time".

Figure 3. Example lakes for each of the 15 lakes classes. All photos by the first author with the exception of 1, 5, 6, 7, 11, 12, 13; source: Wikimedia Commons: https://commons.wikimedia.org/wiki/Main_Page

Wisconsin also has a unique set of shallow coldwater lakes locally referred to as "spring ponds" (Carline 1980). These lakes are very small (typically <5 ha), and sourced by groundwater within and outside the catchment (Carline 1977). Spring ponds support naturally reproducing and stocked Brook Trout, Brown Trout, and Rainbow Trout populations. An updated list of spring ponds was developed by way of this study; however, this list remains a work in progress because of the large number of small and private ponds with limited to no access. It was also evident from our initial tier-one cluster analysis that one cluster incorporated most of the spring ponds. However, this same cluster also included small impoundments on trout streams that supported simple fish communities dominated by trout. Therefore, we retained Cluster 3 as a terminal lake class that incorporated both spring ponds and small impoundments on trout streams. This lake class was renamed "simple–trout ponds," which we now define as small, shallow lakes with sufficient coldwater habitats to support trout fisheries. Example photos of all lake classes are presented in Figure 4.

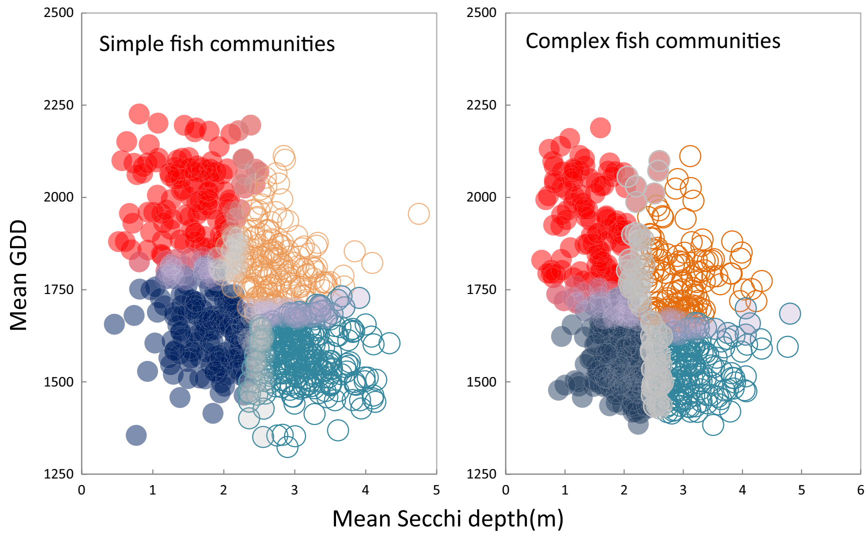

Figure 4. K-means cluster analysis of accumulated degree days (DD) and Secchi depth data from simple and complex sportfish communities. Transitional lakes were identified as those with the highest or lowest 5% of DD or Secchi values. Red filled circles = warm dark lakes, blue filled circles = cool dark lakes, orange open circles = warm clear lakes, blue open circles = cool clear lakes, gray filled circles = clarity transitional lakes, purple filled circles = temperature transitional lakes.

Iteration and vetting

Our approach to lake classification was collaborative with fisheries biologists and managers, and involved multiple iterations based on feedback from more than 100 professional fisheries biologists (Figure 1). Feedback was solicited using presentations at internal staff meetings, active forums on the topic, an ad hoc working group, online presentations, and email. Biologist recommendations were recorded, and recommendations evaluated for a final determination by an ad hoc team (Supplementary Datasets 7, 8).

Class predictions

For the eight temperature and water clarity classes, we conducted discriminate function analyses (DFA) to estimate classification success and generate model coefficients for future lake class assignments (Supplementary Table S1; Supplementary Datasets 4, 6). In all DFAs, data were not standardized and centered to simplify future classification predictions; however, data were $\log_{10}$-transformed to meet traditional DFA assumptions of normality. Significance of models were assessed using Wilks' Lambda test (Rao's approximation). Classification success was evaluated using crossvalidation where observations were reclassified according to model coefficients and probabilities determined through Bayes formula.

Fisheries standards for each lake class

Standards for each of three major fisheries statistics (relative abundance, size-structure, and growth) were calculated from data archived in our statewide fisheries management database (Rypel et al. 2016). To account for catch biases, we only examined data collected using pre-defined gear types used in specific seasons (Table 1).

For relative abundance, catch per unit effort (CPUE) for each species in each lake and lake-year combination was calculated. Zero catches of a species in a survey year were not included in our calculations because zero catches were not noted for most species and there is no known way to extract zero catches. However, CPUE calculations were integrated across all gear types in a single survey year combination. Median and interquartile ranges of CPUE values were calculated across lake averages for a class.

Lake-class standards for fish sizestructure were calculated using a combination of mean and mean maximum size (Rypel 2015; Rypel et al. 2016). For each lake and survey year combination, mean total length was calculated by species. Subsequently, a mean of means was calculated across all available years for a single lake (Beard and Kampa 1999; Rypel et al. 2016). Finally, a median and interquartile range of mean total length was calculated for each species across all lakes in a given class. An analogous procedure was conducted for mean maximum size (i.e., mean of the five largest fish in a survey year) (Rypel 2015; Rypel et al. 2016). We tested for significant lake class differences in abundance and size metrics using mixed effects models. In each model, the fishery metric of interest was the response variable, lake class was a categorical variable, and individual lakes (because of pseudo replication) were random effects (Supplementary Datasets 14–16).

Growth data were composed of length-at-age estimates from calcified structures removed and processed from target species. In general, sectioned spines or fin rays were used to estimate ages from larger Walleye and Muskellunge while scales were used to estimate ages from small individuals. Scales were used to generate age estimates for most other species. We recognize that for most species age data from scales are often inferior to that from otoliths or spines (Isermann et al. 2003; Maceina et al. 2007; Oele et al. 2015). Therefore, we do not intend to imply these data represent absolute age and growth estimates rather patterns from available data. Length-at-age data were processed in the following way: A total of 10 fish age estimates per species needed to be available in a lake-year combination. Further, at least five age classes needed to be present across all age estimations for the same lake-year combination. A mean length-at-age was calculated for each species in each lake-year combination. Using these data, growth rates standards for each lake class were estimated using the von Bertalanffy growth function:

Table 1. Standardized sampling protocol for fisheries data standards by lake class.

Common Name	Scientific Name	Gear	Time of Collection
Black Bullhead	*Ameiurus melas*	Fyke Nets	April–May
Black Crappie	*Pomoxis nigromaculatus*	Fyke Nets	April–May
Bluegill	*Lepomis macrochirus*	Shoreline Boat Electrofishing	May–June
Common Carp	*Cyprinus carpio*	Shoreline Boat Electrofishing	May–June
Largemouth Bass	*Micropterus salmoides*	Shoreline Boat Electrofishing	May–June
Muskellunge	*Esox masquinongy*	Fyke Nets	April–May
Northern Pike	*E. lucius*	Fyke Nets	April–May
Pumpkinseed	*L. gibbosus*	Shoreline Boat Electrofishing	May–June
Rock Bass	*Ambloplites rupestris*	Shoreline Boat Electrofishing	May–June
Smallmouth Bass	*M. dolomieu*	Shoreline Boat Electrofishing	May–June
Walleye	*Sander vitreus*	Fyke Nets	April–May
White Sucker	*Catostomus commersonii*	Fyke Nets	April–May
Yellow Bullhead	*A. natalis*	Fyke Nets	April–May
Yellow Perch	*Perca flavescens*	Fyke Nets	April–May

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right] \qquad (1)$$

where L_t is the total length at time t, L_∞ is the average maximum or asymptotic length, k is a growth rate constant, and t_0 is the theoretical age-at-length zero. To account for low sample sizes in some lake classes, a re-sampling procedure was conducted that produced 1,000 new length-at-age datasets for each lake class, followed by 1,000 estimates of each von Bertalanffy growth parameter (Mooij et al. 1999; Welsford and Lyle 2005). Class medians and interquartile ranges for von Bertalanffy growth curve parameters were based on bootstrapped von Bertalanffy growth function data (Supplementary Datasets 9, 10). Because of potential uncertainty in age estimation precision, we do not present significant differences in growth rates across size classes, but still present lake class medians and interquartile ranges for illustration of general patterns using available data. All classification analyses were conducted using SAS statistical software (Version 9.4, SAS Institute Inc., Cary, North Carolina, USA); growth (including bootstrapping), size, and CPUE lake class standards for fisheries data were computed in R (R Core Team 2015).

RESULTS

A total of 5,950 Wisconsin lakes were placed into the 15 lake classes (Figures 2, 3). We received suggestions from biologists on ~10% of the 5,950 lakes. Comments were wide-ranging, but were mostly of the following types: (1) the lake should be riverine—usually because the lake was either a millpond or a floodplain lake and not included in our retention time dataset; (2) the lake should be simple when it was classified as complex or vice versa; (3) the biologist had a strong inclination or data suggesting the lake should be cool when classified as warm or vice versa, or classified as clear when dark or vice versa; (4) observations on the periodicity of winterkill.

The three most common lake types, by number, were simple–warm–dark, simple–harsh–no fishery, and simple–harsh has fishery (Tables 2, 3; Figure 5). By total lake area, the top three lake classes were complex–warm–dark, complex–two-story, and complex–cool–dark (Table 2). Classification success in DFA was 90% for simple lakes and 94% for complex lakes. There were geographic patterns in the distribution of certain lake classes. Cool lakes were located primarily in northern Wisconsin, and simple trout ponds were concentrated in east–central and northwestern Wisconsin (Figure 5). Lake classes expressed critical differences in physical and chemical characteristics. Two-story lakes were deep; complex riverine lakes had large watershed areas and fast retention times; warm lakes had high DD; clear lakes (whether simple, complex, warm, or cool) showed increased water clarity (Figure 6).

Fisheries statistics varied significantly and in interesting ways across classes (Figure 7; Supplementary Datasets 11–16; all mixed effect models P < 0.0001). We extracted a small subset of our results from key sportfish species to demonstrate some of the interesting patterns observed. For example, Walleye had the highest CPUEs in cool lakes

Table 2. Summary of numerical and area contributions across classes for 5,950 Wisconsin lakes.

	Number		Area (ha)	
Lake Class	Total	%	Total	%
Complex–Cool–Clear	232	4	19,363	5
Complex–Cool–Dark	240	4	48,961	13
Complex–Riverine	183	3	43,244	11
Complex–Two-Story	146	2	55,323	14
Complex–Warm–Clear	199	3	13,271	3
Complex–Warm–Dark	198	3	119,665	31
Simple–Cool–Clear	419	7	8,244	2
Simple–Cool–Dark	209	3	8,088	2
Simple–Harsh–Has Fishery	613	10	10,462	3
Simple–Harsh–No Fishery	1,059	18	11,676	3
Simple–Riverine	175	3	7,129	2
Simple–Trout Pond	308	5	935	0
Simple–Two-Story	58	1	1,865	0
Simple–Warm–Clear	261	4	8,785	2
Simple–Warm–Dark	1,650	28	24,661	6
Total	5,950	100	381,672	100

Table 3. Brief description of the 15 lake classes.

Lake Class		
No.	Name	Description
1	Complex–Cool–Clear	≥4 sportfish species, low DD, high secchi, low in landscape, these lakes are found primarily in the north, Walleye are an indicator species, Smallmouth Bass can be in high abundance.
2	Complex–Cool–Dark	≥4 sportfish species, low DDs, low secchi, low in landscape, these lakes are found primarily in the north, Walleye are an indicator species, Yellow Perch can be in abundance, can develop quality Northern Pike and/or Muskellunge size structure.
3	Complex–Riverine	≥4 sportfish species, <15 d hydrologic retention time, large watershed areas, often a low secchi, Walleye and other riverine taxa are indicator species, common carp often present.
4	Complex–Two-Story	≥4 sportfish species, large lake area, deep, cold and oxygenated hypolimnetic habitats support coldwater fishes - primarily Cisco, managed differently for phosphorus water quality standards, low in landscape, can develop quality Walleye size structure.
5	Complex–Warm–Clear	≥4 sportfish species, high DD, high secchi, low in landscape, Walleye are an indicator species, Largemouth Bass and Bluegill are in high abundance.
6	Complex–Warm–Dark	≥4 sportfish species, high DD, low secchi, low in landscape, Walleye are an indicator species, Black Crappie can be in abundance, can develop quality Northern Pike and/or Muskellunge size structure.
7	Simple–Cool–Clear	≤3 sportfish species, small lake area, high DD, high secchi, high in landscape, these lakes are found primarily in the north, no Walleye, can develop high numbers of Smallmouth Bass.
8	Simple–Cool–Dark	≤3 sportfish species, small lake area, high DD, low secchi, high in landscape, these lakes are found primarily in the north, no Walleye, can develop high numbers of Black Crappie.
9	Simple–Harsh–Has Fishery	Usually only 1–2 sportfish species, very small lake areas, high in landscape, relatively frequent winterkill, can be dominated by bullheads.
10	Simple–Harsh–No Fishery	Usually no sportfish species present, very small lake areas, high in landscape, frequent winterkills or extremely low pH that prevents most fish populations from persisting. When fishes are present, Central Mudminnow *Umbra limi* and potentially other small-bodied Cyprinidae species dominate.
11	Simple–Riverine	≤3 sportfish species, <15 d hydrologic retention time, small lake area, high DD, small millponds on warmwater streams typify class.
12	Simple–Trout Pond	Shallow, small lake area, groundwater flows reduce water temperatures to support trout fisheries, “spring ponds,” these lakes are common in Langlade (epicenter), Menominee, Forest, Shawano, Oconto and Lincoln Counties.
13	Simple–Two-Story	≤3 sportfish species, small lake area, deep, cold and oxygenated hypolimnetic habitats support coldwater fishes, managed differently for phosphorus water quality standards, high in landscape.
14	Simple–Warm–Clear	≤3 sportfish species, small lake area, high DD, high secchi, high in landscape, no Walleye, Largemouth Bass and Bluegill frequently in high abundance.
15	Simple–Warm–Dark	≤3 sportfish species, small lake area, high DD, low secchi, high in landscape, no Walleye, can develop high numbers of Black Crappie.

and lowest CPUEs in warm lakes (Figure 7). In contrast, Largemouth Bass CPUEs were highest in warm clear lakes (Figure 7); lower in warm–dark lakes and lowest in cool lakes and riverine lakes. Yellow Perch had high CPUEs in cool–dark lakes. Both Northern Pike and Muskellunge had the greatest mean and maximum lengths in complex–cool–dark lakes (Supplementary Datasets 12, 13). And while CPUE of Largemouth Bass and Bluegill was usually higher in warm lake classes, mean and mean maximum size was higher in cool lakes.

DISCUSSION

Successful fisheries management approaches in one lake are often transferable to similar lakes (Moyle 1949; Tonn et al. 1983; Schupp 1992; Shuter et al. 1998). Yet identifying lakes sufficiently similar in terms of factors relevant to fisheries, is often a difficult step. We developed a lake classification system that placed 5,950 Wisconsin lakes into 15 lake classes with the goal of improving fisheries management. Below, we discuss potential uses, general patterns, and heuristic themes from our work that might aid others interested in a similar approach.

Key patterns were uncovered in the relative abundance, sizestructure and growth rates of focal fish species. For example, Walleye were uniformly more abundant in cool lakes (and were most abundant in two-story lakes), a pattern consistent with other research on the species (Jobling 1981; Van Zuiden and Sharma 2016; Hansen et al. 2017; Rypel et al. 2018). Unlike previous research (Ryder 1977; Lester et al. 2004), water clarity was not a major driver of Walleye abundance patterns within cool lakes. In contrast, Largemouth Bass showed the highest abundances in warm lakes, especially warm–clear lakes. These results also align with previous research characterizing the species as best suited for warm, clear-water habitats (Rypel 2009; Hansen et al. 2017).

Panfish populations have historically been passively managed in Wisconsin (Beard and Kampa 1999; Rypel 2015; Rypel et al. 2016). However, there is increasing interest in novel ways to manage panfish species for sustainability and yield (Lyons et al. 2017b). Our lake classification system provides a tool that could be used for panfish management. Black Crappie were most abundant in dark lakes whether cool or warm; Bluegill, were more abundant in warm and clear lakes; Yellow Perch abundance was highest in complex–cool–dark lakes. Yet maximum size for Black Crappie and Bluegill was highest in complex–cool–clear lakes. Yellow Perch had highest maximum size in riverine ecosystems. These results may point to lake types more or less amenable to special regulations aimed

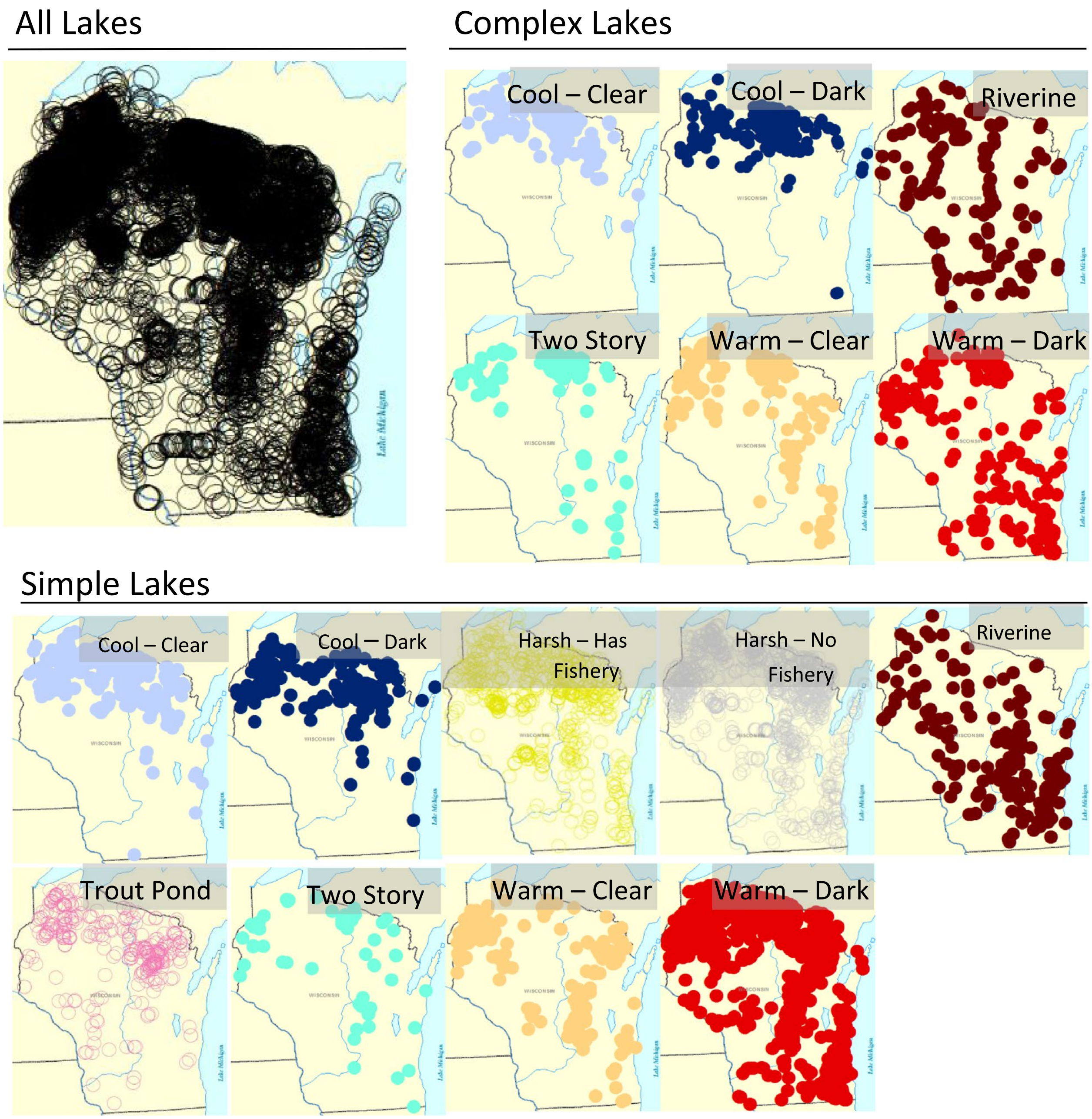

Figure 5. Distribution of 15 terminal lake classes in Wisconsin.

at improving size (Hansen et al. 2015; Rypel 2015; Lyons et al. 2017b) or other efforts like in-lake habitat improvement (Sass et al. 2017).

There were intriguing patterns for several non-game species. For example, White Sucker *Catostomus commersonii* were most abundant in cool–clear lakes (Figure 7A). Even though White Sucker are cosmopolitan in Wisconsin lakes (Becker 1983), little research has been conducted on their ecology, role in food webs, and importance to consumption fish production. Because they are apparently a cool water fish with higher abundance in cool lakes, White Suckers could be vulnerable to climate change effects (Eaton and Scheller 1996; Lyons et al. 2010). In an analysis of fish vulnerabilities to climate change, Lyons et al. (2010) projected a 20–80% decline in stream and river distributions of White Sucker in Wisconsin depending on warming magnitude. White Sucker may also be sensitive to other human impacts like reductions in water quality (Jobling 1981; Munkittrick and Dixon 1989). This classification system could be used as an organizing framework for investigating the distribution and ecology of sentinel fishes like White Sucker in lakes.

Fisheries managers can use this lake classification information to make improved fisheries assessments. As just one example, an early summer electrofishing survey for bass and panfish was recently conducted in Ennis Lake, Marquette County. Ennis Lake (pictured in Figure 4) is an 11.7 ha lake, and the childhood lake of famous naturalist John Muir, although the lake and its name trace back to Native American culture. This lake was classified as simple–warm–dark (Supplementary Dataset 8). Median CPUE for Bluegill in this class is 98 fish/h with an interquartile range of 38–184 fish/h

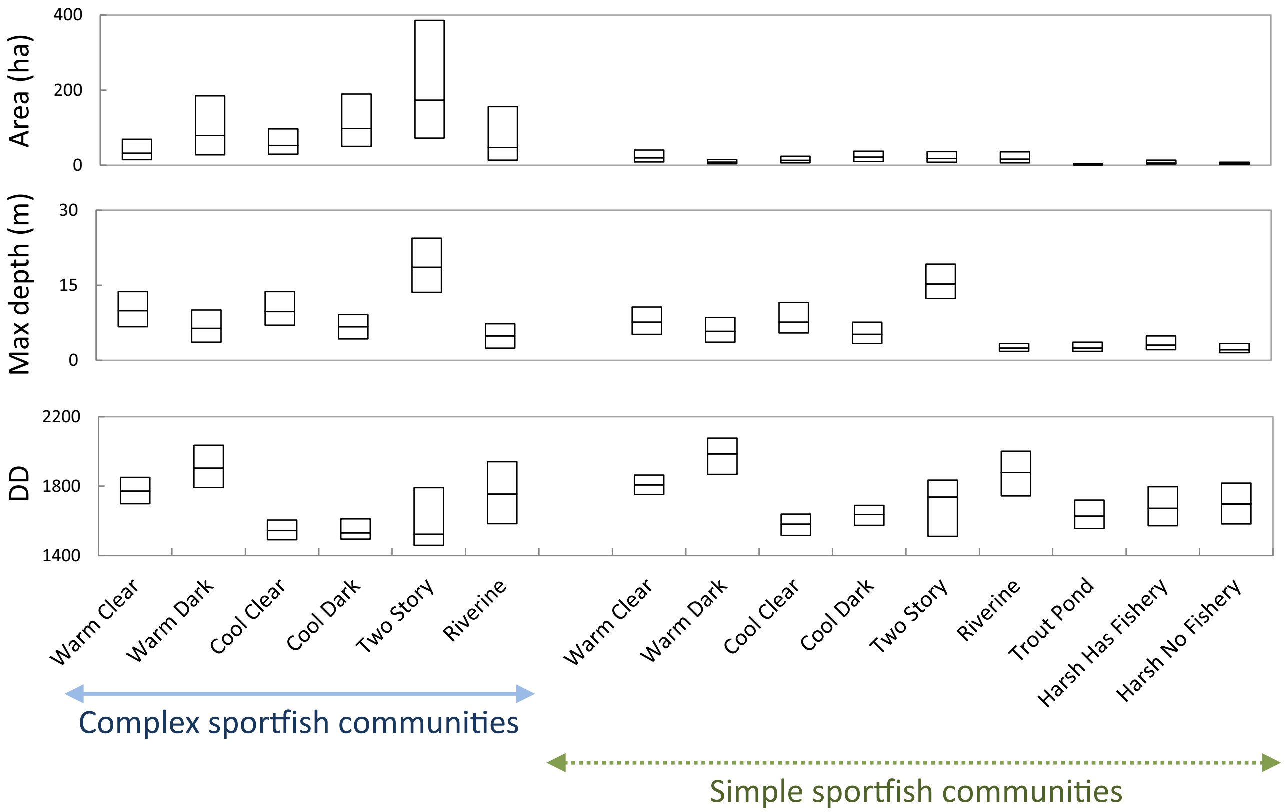

Figure 6. Box plots of lake area, maximum depth and thermal characteristics in 15 lake classes. Horizontal bar inside each box represents the median and box ends denote the interquartile range (i.e., 25th and 75th percentiles).

(Supplementary Dataset 11). Median Largemouth Bass CPUE in this class is 31 fish/h with an interquartile range of 13–52 fish/h (Supplementary Dataset 11). In the survey, observed CPUE for Bluegill was 105 fish/h, a value is well within the computed interquartile range. We strongly recommend survey data for a given lake be compared more generally to the class interquartile range standard (for CPUE or size) and not the class median. Thus, based on available data, Bluegill abundance in Ennis Lake could be considered average. However, Largemouth Bass CPUE was only 9 fish/h. This value is below the interquartile range (10th percentile). A biologist might ask themselves questions about this result. For example, why might the Largemouth Bass population be low? Do I want to do anything about it? Is there harvest pressure? Is there a habitat issue?

We designed a flexible lake classification system, meaning that lakes may move among classes as lake conditions and fisheries change with time. This is important because as the ecology of lakes changes, fisheries expectations frequently also shift (Molden et al. 2010; Sass et al. 2017; Rypel et al. 2018). Indeed, lakes can even operate under alternative stable states in that ecological change is often slow until a threshold is reached after which changes are rapid and major and reversal is slow and difficult (Carpenter et al. 2001). Common Carp *Cyprinus carpio* are an example of a fish species, that on its own, can “flip” a lake from a clear to dark water state (Weber and Brown 2009; Bajer et al. 2012). As lake clarity becomes drastically reduced, fishery expectations may change (Cahn 1929; Forester and Lawrence 1978; Wahab et al. 1995). Given that our classification accuracy from the DFA was 90–94%, we anticipate that future classification efforts would be statistically robust.

Climate change in particular is rapidly changing the fisheries ecology of lakes in Wisconsin and elsewhere (Lynch et al. 2016; Winfield et al. 2016; Hansen et al. 2017). The dynamics of fish populations and communities are strongly regulated by temperature; thus, climate change is rapidly re-organizing fisheries (Tonn 1990; Lyons et al. 2010; Magee et al. 2018; Myers et al. 2018; Rypel et al. 2018). Recruitment rates of Walleye and abundances of Largemouth Bass in Wisconsin lakes are strongly predicted by temperature but in opposite directions (Hansen et al. 2017). Body size of freshwater fishes is also strongly related to temperature (Rypel 2013), and one potential effect of climate change on fishes could be a reduction in the maximum size potential of cool and coldwater fish (Cheung et al. 2013; Rypel 2013). Because our lake classification system accounts for temperature, lakes will change classifications over time, and fisheries managers will have a tool for adapting to climate change.

Some lakes may have already crossed tipping points. Walleye data from four lakes classified as temperature transitional are presented in Figure 8. These lakes were the only lakes classified as temperature transitional lakes that also had ≥ 5 years of Walleye data. Three of these four lakes also had concurrent time series of Largemouth Bass relative abundance data. An additional bass time series representing the longest available bass abundance time series in a temperature transitional lake is also presented. We observed a general decline in the abundance of Walleye along with an increase in Largemouth Bass, which is consistent with an expectation of thermal change over time as might be predicted with past and future climate change.

Collaborative development of our lake classification tool with fisheries managers improved the model and built

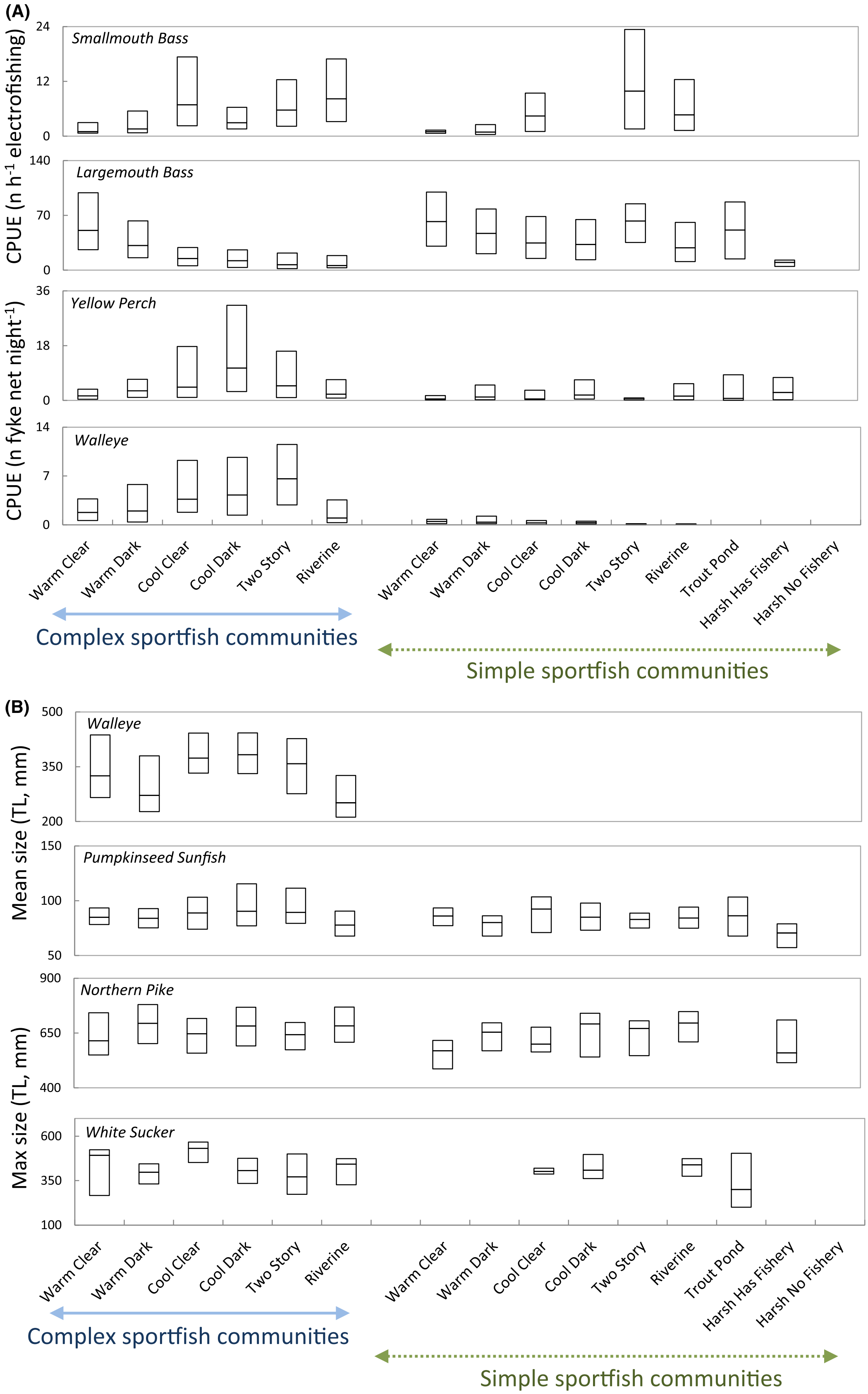

Figure 7. Box plots of **(A)** relative abundance (CPUE) and **(B)** mean and mean maximum size for four select sportfishes in 15 terminal lakes classes. Horizontal bar inside each box represents the median and box ends denote the interquartile range (i.e., 25th and 75th percentiles).

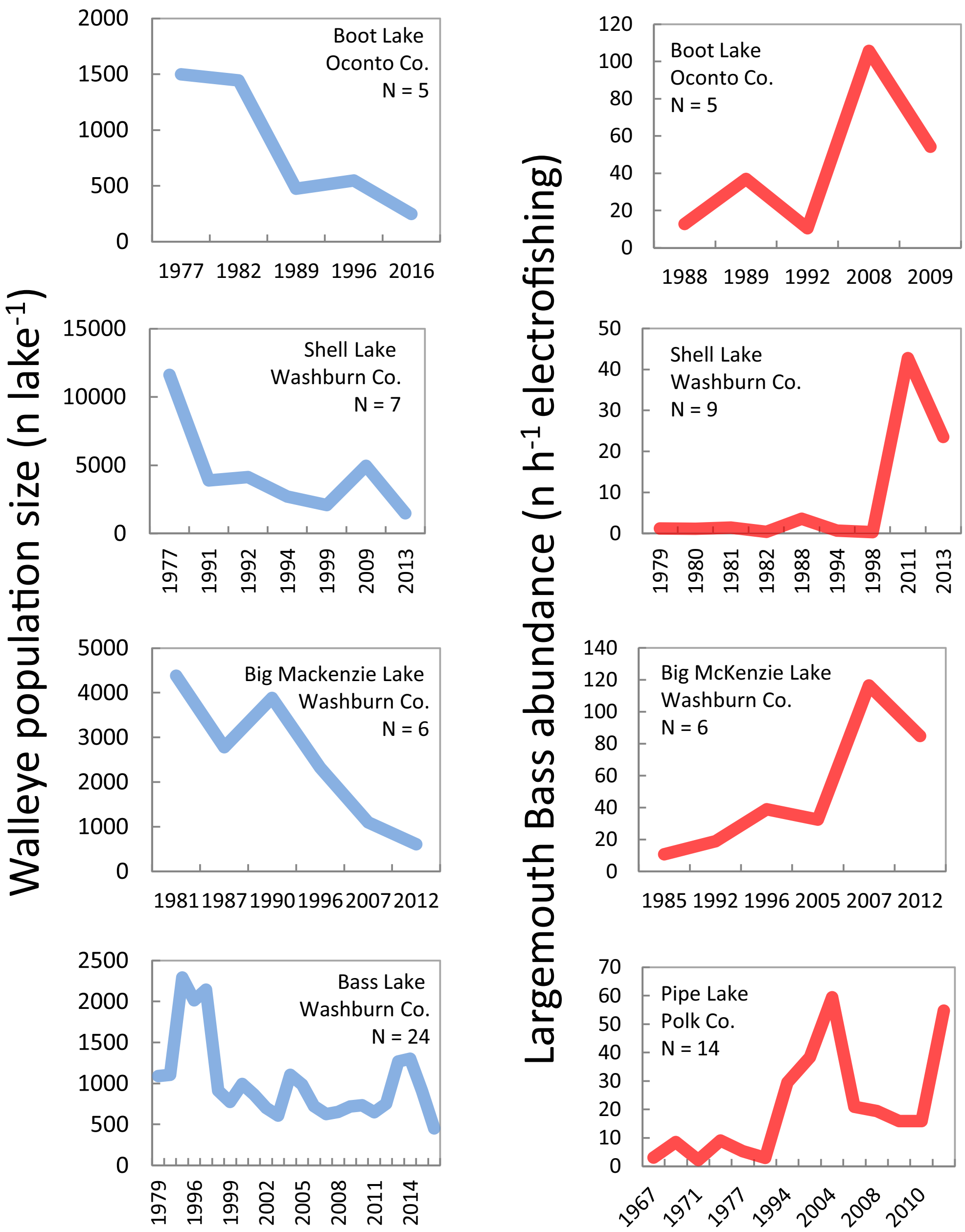

Figure 8. Temporal trends in abundance of Walleye and Largemouth Bass in lakes identified as temperature transitional.

interest in using it. Although the addition of manager feedback loops did slow our progress, it also created a vigorous internal review that improved accuracy and accessibility of the final tool. A glance at comments provided by our managers from our vetting exercise (Supplementary Dataset 7) reveals how initial classifications based only on model outputs can be grossly wrong. Our process also highlighted philosophical tension points of end users in need of resolution. For example, there was recognition that any classification system should seek to minimize the number of groups while also maximizing differences. Another common theme was the importance of maintaining flexibility for decision making (i.e., that biologists retain a capacity to deviate and make expert decisions when logical). Importantly, it was also the biologists and managers who collectively speculated lakes needed to be capable of changing classes as environments changed.

One question that has arisen is: how often should lake classes and lake class standards be updated? For any agency charged with public trust of fisheries and aquatic ecosystem management, answers to these questions become partly a workload issue and thus strategic and administrative decisions. However, a balanced approach that recognizes long-term ecological change in lakes and workload limitations seems appropriate. For these reasons, we recommend a systematic updating of lake class standards every 10 years, with a moving 25–30-year data window used to develop and curate fisheries standards.

Classification models can always be refined or redesigned over time, but resource management is better served by having a useful tool, even if the tool represents a version that might not be considered “final,” as long as there is flexibility built into the process should future refinements be developed. Perhaps the largest hindrance to progress was the temptation for continuous model improvement, analysis of alternative classification methods, and integration of new datasets. There are an increasing number of classification tools and statistical approaches that can be brought to bear on any classification effort. We encourage others to resist these temptations and establish deadlines and processes to ensure initial project completion.

CONCLUSIONS

A lack of proper evaluation in fisheries management is dangerous (Schupp 1992; Smith et al. 1999). Expensive fisheries management strategies that might otherwise be uncovered as failures can be allowed to continue and unintended socioecological consequences can result (Pikitch et al. 2004; Eby et al. 2006; Cinti et al. 2010). The approach outlined in our paper provides a method for more accurately comparing and tracking fisheries dynamics in our inland lakes. Another advantage of this approach is that it could be used by agencies to facilitate meaningful dialogue with the public, e.g., to calibrate public expectations or refute perceptions of fishery quality in different types of ecosystems. Our approach was notably unique in that it accounted for potential changes in lakes and their fisheries into the future and afforded biologists ample opportunities to provide input. Comparisons of fisheries survey data against lake class quartiles provides a simple and fast tool that will result in more informed decision making, especially in response to changing future ecological conditions.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article. AFS