North American Journal of Fisheries Management 42:630–641, 2022

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10729

SPECIAL SECTION: EFFECTS OF ECOSYSTEM CHANGE ON NORTH AMERICAN PERCID POPULATIONS

Similar Environmental Conditions are Associated with Walleye and Yellow Perch Recruitment Success in Wisconsin Lakes

Ethan J. Brandt[1]
Wisconsin Cooperative Fishery Research Unit, Fisheries Analysis Center, College of Natural Resources, University of Wisconsin–Stevens Point, 800 Reserve Street, Stevens Point, Wisconsin 54481, USA

Zachary S. Feiner*
Wisconsin Department of Natural Resources, Office of Applied Science, Science Operations Center, 2801 Progress Road, Madison, Wisconsin 53716, USA; and Center for Limnology, University of Wisconsin–Madison, 680 North Park Street, Madison, Wisconsin 53706, USA

Alexander W. Latzka
Wisconsin Department of Natural Resources, Bureau of Fisheries Management, GEF II, 101 South Webster Street, Madison, Wisconsin 53703, USA

Daniel A. Isermann
U.S. Geological Survey, Wisconsin Cooperative Fishery Research Unit, Fisheries Analysis Center, College of Natural Resources, University of Wisconsin–Stevens Point, 800 Reserve Street, Stevens Point, Wisconsin 54481, USA

Abstract

Since the mid-2000s, recruitment of Walleye *Sander vitreus* in some northern Wisconsin lakes has declined, potentially because of climate-induced changes in lake environments. Yellow Perch *Perca flavescens* is also an ecologically and culturally important fish species in this region, but mechanisms driving Yellow Perch recruitment are unclear because of a lack of targeted sampling. Previous studies have suggested that recruitment of these two species may be regulated by similar factors, and observed declines in Walleye recruitment may be cause for concern about Yellow Perch recruitment. Our objectives were to determine if abiotic factors related to recruitment success were similar between Walleye and Yellow Perch populations in northern Wisconsin lakes and if the probability of successful Walleye recruitment was related to estimates of juvenile Yellow Perch abundance before Walleye recruitment declines were observed. We addressed these objectives using historical data from Wisconsin lakes. Random forest analysis incorporating lake-specific averages of predictor variables indicated that winter conditions (duration or severity), growing degree days, variation in spring temperatures, peak summer temperature, and Secchi depth were important predictors of recruitment success for both species. Logistic regression indicated that before Walleye recruitment declines were observed on some lakes (2000–2006), Walleye recruitment success was related to relative abundance of juvenile Yellow Perch in mini-fyke-net sampling. Our results indicate that landscape-level patterns in recruitment success for the two species are likely similar and additional research to understand Yellow Perch recruitment trends is warranted. Better information on Yellow Perch recruitment could contribute to a better understanding of Walleye recruitment trends as declines in Yellow Perch could influence prey availability and survival of age-0 Walleye. Furthermore,

*Corresponding author: zachary.feiner@wisconsin.gov
[1]Present address: Oregon Department of Fish and Wildlife, Eastern Oregon University, One University Boulevard, 203 Badgley Hall, La Grande, Oregon 97850, USA.
Received March 8, 2021; accepted October 20, 2021

potential declines in Yellow Perch could lead to changes in the numbers and size of Yellow Perch caught by anglers, which may have implications for harvest management.

Sustainability of recreational fisheries relies upon successful recruitment of young fish to adult populations (Beverton and Holt 1957; Maceina and Pereira 2007). Recruitment is notoriously variable (Sissenwine 1984; Houde 2009) as small fluctuations in juvenile survival rates can lead to large changes in year-class strength (Houde 1987, 1989). Factors influencing survival early in life can be complex and difficult to understand as they are regulated by direct and indirect processes that are influenced by multiple abiotic and biotic factors (Ludsin et al. 2014) that may vary within and among lakes within a relatively small geographic region (Hansen et al. 2015a). Nevertheless, understanding the mechanisms driving variation in recruitment is crucial for managing exploited populations (Ricker 1975; Sissenwine 1984). In particular, understanding how among-lake variation in prevailing environmental conditions relate to higher average recruitment success for individual species can be valuable at a landscape scale for identifying where management actions, such as stocking or more restrictive harvest regulations, are warranted (Noble 1986; Isermann and Paukert 2010; Trushenski et al. 2010). Understanding these relationships may prove even more valuable if factors related to average recruitment success are similar among multiple species that support important fisheries.

In north temperate lakes, poor recruitment and apparent population declines observed for two important members of the Percidae family, Walleye *Sander vitreus* and Yellow Perch *Perca flavescens*, are cause for concern among fishery managers (Bethke and Staples 2015; Raabe et al. 2020). Both species support important fisheries and play ecologically significant roles in lakes as predators and prey (Forney 1974; Feiner and Höök 2015; Embke et al. 2020). Since the early to mid-1990s, the number of Walleye populations in Wisconsin that are supported by natural recruitment has declined, while the number that are supported either in part or totally by stocking has increased (Raabe et al. 2020). Similarly, Yellow Perch relative abundance has decreased markedly from 1970 to 2013 among Minnesota lakes (Bethke and Staples 2015), and in Wisconsin, angler catch and harvest rates for Yellow Perch have decreased over time (Feiner et al. 2020).

Both Walleye and Yellow Perch can exhibit highly variable recruitment, which is often related to environmental factors (Kallemeyn 1987; Bozek et al. 2011; Kaemingk et al. 2014). Walleye recruitment has been intensely studied in north temperate systems, and it appears that observed declines in some northern Wisconsin lakes are due to recruitment bottlenecks occurring in the first year of life (Hansen et al. 2015b; Gostiaux et al. 2022, this special section). Although the exact mechanisms resulting in recruitment declines are currently unknown and likely complex (Peters et al. 2007; Soranno et al. 2014), these declines are potentially related to climate-induced changes in lake environments (Hansen et al. 2015b). Walleye recruitment has been related to temperature (Hansen et al. 1998, 2015a; Honsey et al. 2020), which may influence similar recruitment patterns across Walleye populations (Koonce et al. 1977; Schupp 2002; Beard et al. 2003). Moreover, Walleye recruitment declines have coincided with increases in warmwater species, such as Largemouth Bass *Micropterus salmoides* in Wisconsin (Hansen et al. 2015b, 2015c) and Ontario, Canada (Robillard and Fox 2006), but whether this is an environment-induced correlation or cause and effect remains unknown.

Factors influencing Yellow Perch recruitment in inland Wisconsin lakes have not been specifically examined largely because sampling designed to index Yellow Perch recruitment early in life (age 0 or age 1) is rarely conducted on these lakes. Evidence from other temperate systems suggests that factors regulating recruitment dynamics may be similar for Walleye and Yellow Perch. Therefore, observed trends in Walleye recruitment may provide insights regarding trends in Yellow Perch recruitment. Specifically, winter and spring temperatures can also influence Yellow Perch recruitment (Clady 1976; Kallemeyn 1987; Farmer et al. 2015). When comparing species, age-0 Yellow Perch and Walleye share similar thermal niches, exhibit optimum growth at 22°C, and their recruitment is similarly correlated with temperature (Huh et al. 1976; Koenst and Smith 1976; Koonce et al. 1977).

Evidence of similar population declines for Walleye and Yellow Perch across north temperate systems suggests the potential for fish community shifts away from coolwater, percid-abundant systems toward warmwater, centrarchid-dominated communities (Hansen et al. 2017). However, to date there have been few concurrent analyses of recruitment trends or associations between Walleye and Yellow Perch in the Midwestern USA, particularly in small inland systems (Koonce et al. 1977; Kallemeyn 1987; Rose et al. 1999). We aimed to address this crucial knowledge gap using historical data from Wisconsin lakes. Our first objective was to determine if abiotic factors related to recruitment success were similar between Walleye and Yellow Perch populations in northern Wisconsin lakes. In addressing this objective, we did not attempt to directly assess whether Walleye and Yellow Perch year-class strengths were synchronous; rather, we examined whether probability of recruitment success for each species was related to average environmental conditions associated with individual lakes. Our second objective was to determine if the probability of successful Walleye recruitment was related to estimates of juvenile Yellow Perch abundance before Walleye recruitment declines were observed in some lakes. Our goal related to our second objective was to assess whether variation in juvenile Yellow Perch abundance among lakes might help in understanding among-lake variation in Walleye recruitment success, which could provide additional justification for standardized sampling that specifically targets Yellow Perch. Identifying correlations and common environmental associations with recruitment success between species could indicate whether declines in Walleye reflect similar declines for Yellow Perch and help to determine the extent to which local management actions might be used to offset the effects of a changing climate (Paukert et al. 2016).

METHODS

Landscape-level comparison of Yellow Perch and Walleye recruitment.— To evaluate conditions associated with Yellow Perch and Walleye recruitment success across many individual lakes, age-specific relative abundance of Yellow Perch and Walleye was determined from annual spring (Yellow Perch) and fall (Walleye) sampling performed by the Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission from 1990 to 2020. Data were obtained from databases maintained by each agency. Yellow Perch abundance was assessed using spring (March–May) fyke-netting surveys targeting adult Walleye (see Rogers et al. 2003 for detailed description) that also occurred during Yellow Perch spawning when water temperatures were between 10°C and 21°C. Number of nets set per lake varied with lake size, and following criteria defined in Feiner et al. (2020), we only included surveys where (1) Yellow Perch were a target species (e.g., lengths, counts, and age estimates were obtained), (2) the minimum number of net-nights met defined requirements based on surface area, and (3) no adverse conditions that could reduce sampling efficiency were noted. Fyke nets were checked daily, Yellow Perch were counted and measured (nearest 2.5 mm, total length [TL]), and ages were estimated for a subsample (sampling target of at least five fish per 12.7-mm length-group) using calcified structures (scales, dorsal spines, or otoliths).

To develop age-specific relative abundances of Yellow Perch as an indicator of recruitment, we constructed age–length keys (12.7-mm TL bins) for individual lake-years using length-at-age data obtained from sampling conducted in spring (March–May). In addition to fish captured in fyke nets, we also used length-at-age data from electrofishing surveys performed in the same lake and year to maximize the number of ages available in individual length bins for constructing age–length keys. Electrofishing surveys were also conducted during spring (March–May). We did not use electrofishing data to estimate relative abundance or to index recruitment. We included all lake-years that had at least three fish with estimated ages in at least 50% of the survey's observed length bins. We assigned ages to unaged fish from fyke nets using semirandom assignment (R package FSA, Ogle et al. 2020; Isermann and Knight 2005). Once ages were assigned, we calculated age-specific relative abundances (fish caught per net-night = CPE) from spring fyke-net catches. The CPE of age-3 Yellow Perch was used as an indicator of recruitment because it was the youngest age at which Yellow Perch exhibited full catchability to the gear and represented an age at which fish reached large enough sizes to enter the recreational fishery (Feiner et al. 2020). In other studies, Yellow Perch year-class strength is usually set by age 0 or age 1, with high correlations in age-specific abundances of cohorts through the first few years of life (e.g., Ivan et al. 2011; Bogner et al. 2016), suggesting that the relative abundance at age 3 is not only an index of recruitment to the fishery, but also likely reflects relative differences in year-class strength at younger ages.

Age-0 Walleye abundance was quantified using nighttime electrofishing performed in the fall (September and October) when water temperatures were between 10°C and 21°C (see Hansen et al. 2015a for details). We required that at least 70% of the shoreline was electrofished in lakes with ≤23 km of shoreline and at least 16.1 km of shoreline was electrofished in lakes with >23 km of shoreline. We removed surveys with unreliable abundance estimates for age-0 Walleye based on sampling conditions (e.g., poor conductivity reducing sampling efficiency; see also Hansen et al. 2015a) and only included lakes with a previous history of at least some Walleye natural recruitment. Lastly, we removed surveys that coincided with Walleye stocking events (Hansen et al. 2015a). Age-0 Walleye were identified using length frequency distributions and verified by estimating age for a subsample of fish using scales. Walleye recruitment, indexed as CPE of age-0 Walleye, was quantified as fish per kilometer.

Attempts to predict recruitment tend to be highly uncertain and often yield irreplicable relationships (Myers 1998; Zhao et al. 2013). Moreover, managers may be more interested in whether recruitment is sufficient to support a fishery or surpasses some baseline threshold (Hansen et al. 2015a). Therefore, we classified Yellow Perch and Walleye recruitment into "successful" or "unsuccessful" recruitment years using estimates of relative abundance. Based on previous work, age-0 Walleye CPE > 6.2

fish/km in fall electrofishing was used to designate a Walleye year-class as successful (as in Hansen et al. 2015a, 2018; Gostiaux et al. 2022). However, no benchmark currently exists for Yellow Perch. Therefore, we classified "successful" Yellow Perch year-classes as having age-3 CPE ≥0.39 fish/net-night, which represented the overall median value for our data. Year-classes with CPE below the median were considered "unsuccessful." It is important to note that this was a statewide index, meaning some lakes could consistently produce successful (>50th percentile) year-classes, while others may never produce one. Classifying recruitment in this way allowed us to make inferences about average environmental conditions associated with lakes that consistently produce successful year-classes compared with those unable to do so, which may be more useful for managers seeking to generally categorize probability of recruitment success at a landscape scale.

We developed a set of predictor variables based on their likelihood to influence percid recruitment in previous research (see Feiner and Höök 2015; Hansen et al. 2015a; Honsey et al. 2020). Conductivity (μS/cm) and in situ and satellite-derived measures of Secchi depth (m), indicators of primary productivity and water clarity that can influence juvenile Walleye growth (Lester et al. 2004), were obtained from the WDNR Surface Water Integrated Monitoring System database (SWIMS: https://dnr.wisconsin.gov/topic/SurfaceWater/SWIMS), a database of historical lake limnological parameters developed by the North Temperate Lakes Long-Term Ecological Research project (Papes and Vander Zanden 2013), and from Hansen et al. (2015a); in situ observations were always used when available. Conductivity and Secchi depth data were typically collected from May to September, and we used all available data in calculating average values for a lake. While seasonal variation in conductivity and Secchi depth can occur, our assumption was that interlake differences in these metrics would be larger than intralake variations over time, and averaging all available observations would reduce temporal variation within and among years. Lake morphology data, including lake area (ha), maximum depth (m), and shoreline development index, which can influence thermal–optical habitat availability (Lester et al. 2004; Hansen et al. 2019), were acquired from various WDNR databases and the R package "lakeattributes" (Winslow 2015). Lastly, we indexed thermal conditions in lakes using updated daily water temperature and ice phenology predictions from a process-guided deep learning model of lake water temperatures (Read et al. 2021). Thermal metrics were summarized into hypothesized important predictors of percid recruitment based on the importance of winter, spring, and summer temperatures for adult reproduction (Schneider et al. 2010; Farmer et al. 2015; Feiner et al. 2016a, 2016b) and juvenile growth (Kitchell et al. 1977). We specifically included annual growing degree days (base 0°C; GDD_0), annual peak epilimnetic water temperature (peak temperature; °C), winter severity (number of days with water temperatures between 0°C and 4°C), duration of ice cover (d), and variation in spring temperatures (coefficient of variation [CV] in water temperatures 0–30 and 30–60 d after ice-off), which reflects variability in spring warming rates and has been important for Walleye recruitment in Escanaba Lake, Wisconsin (Serns 1982; Hansen et al. 1998). While several of these thermal variables are likely associated with latitude (i.e., more northerly lakes are cooler and have more ice cover), we did not include latitude as an explanatory variable because it has previously been shown to be a poor predictor of Walleye recruitment in Wisconsin (Hansen et al. 2015a) and because we were interested in directly testing for more clearly interpretable, mechanistic environmental associations with successful percid recruitment.

We were interested in whether percid recruitment success was associated with average environmental conditions observed among individual lakes. Moreover, environmental data were generally not available for every lake and year in which we had measures of percid recruitment. Therefore, we averaged all available observations of predictors first within years and then across years to generate mean indices of environmental conditions for each lake. This approach has been previously used to assess environmental conditions associated with high probabilities of Walleye recruitment success in previous studies and thus also allowed for more direct comparisons of results between studies (Hansen et al. 2015a; Feiner et al. 2019b).

We evaluated and compared the importance of average environmental conditions to Yellow Perch and Walleye recruitment success using random forest modeling. In brief, random forests are a machine learning technique that identifies relationships between variables by constructing many classification trees based on partitions of the data; i.e., many bootstrapped subsamples of the data are taken for development of many distinct classification trees that predict recruitment success (or failure) by splitting the subsamples along predictor variables (Cutler et al. 2007). Predictions and variable importance measures from all trees are then combined to assess predictive accuracy and the effect of explanatory variables. By maintaining all recruitment observations in our data instead of averaging them within lakes, we were able to propagate variability in recruitment success across classification trees and assess which average environmental conditions were most often associated with "successful" recruitment years. To clarify, while abiotic predictor variables were averaged for a lake, recruitment data for Walleye and Yellow Perch were not. This allowed the random forest algorithm to select different recruitment years when subsetting the data across many trees.

We specifically used conditional random forests, using "cforest" in R package "partykit" (Hothorn and Zeileis 2015), because of their ability to robustly handle correlated or skewed predictor variables (Strobl et al. 2008). Random forests were constructed by increasing the number of trees until model results stabilized (1,000 for Yellow Perch and 400 for Walleye). Predictive power of the model was determined by calculating classification error rates (R package "DescTools"; Signorelli et al. 2020) and performing a one-sided exact binomial test to determine whether model predictions were more accurate than a "no information" model. Relative importance of predictors was determined by calculating the mean decrease in "out-of-bag" classification accuracy among trees when permuting the predictor of interest (function "varimp" in the "partykit" package). The effects of important predictors were evaluated using partial dependence plots (package "pdp"; Greenwell 2017), developing predictions across 100 levels spanning the range of each predictor variable while holding other predictors at their observed levels and calculating the mean, 25th, and 75th quantiles of the predicted probability of recruitment success.

Historic mini-fyke-net data.— We used Yellow Perch catch data from mini-fyke-net surveys conducted during 2000–2006 to test whether the probability of Walleye recruitment success may have been related to relative abundance of juvenile (age-0 and age-1) Yellow Perch abundance before Walleye recruitment declines became evident in some lakes. We used this approach because Yellow Perch data from mini-fyke-net sampling were only available from 2000 to 2006 as this gear is not routinely used by the WDNR as a panfish and community assessment tool (Treaty Fisheries Assessment Team 2005; Simonson 2006) and prevalence of this sampling was higher in 2000–2006. However, only 24 of the 174 lakes used in analyses were sampled with mini-fyke-net surveys in more than 1 year during 2000–2006. Mini-fyke-net surveys were conducted from July through early September with nets that had either 0.92-m × 0.61-m or 0.92-m × 0.92-m frames, 4.76-mm mesh, 0.61-m-diameter hoops, and sometimes 25.4-mm mesh exclusion netting (Treaty Fisheries Assessment Team 2005; Simonson 2006). On lakes ≤202 ha, at least six nets were fished, and on lakes >202 ha, at least eight nets were fished (Treaty Fisheries Assessment Team 2005; Simonson 2006). Nets were fished for 1–2 nights such that the number of net-nights per lake ranged from 6 to 16. Yellow Perch relative abundance was calculated as fish per net-night (CPE), and mean CPE was used for the 25 lakes where more than 1 year of mini-fyke-net sampling was conducted. Mini-fyke-net sampling primarily captured Yellow Perch less than 100 mm (89% of all fish collected) that were largely age 0 and age 1. We note that while most lakes were sampled with mini-fyke nets in only 1 year, these nets provide a composite index of abundance for two subsequent year-classes of Yellow Perch.

Lakes where mini-fyke netting occurred were classified as having "successful" or "unsuccessful" Walleye recruitment based on mean CPE of age-0 Walleye in fall electrofishing, also conducted from 2000 to 2006, but not necessarily in the same year mini-fyke-net data were collected. We only included lakes with more than one annual estimate of age-0 Walleye CPE from 2000 to 2006, and 78% (135 of 174) of the lakes were sampled for age-0 Walleye at least three times in this period. Lakes with mean age-0 Walleye CPE >6.2 age-0 Walleye/km were classified as supporting successful recruitment (Hansen et al. 2015a, 2018). Using logistic regression, we tested whether the probability that a lake supported successful Walleye recruitment was related to juvenile Yellow Perch CPE in mini-fyke nets. We used mean values of age-0 Walleye CPE in fall electrofishing for this analysis rather than year-specific estimates used in our landscape-level analysis because mini-fyke-net surveys were typically conducted in only 1 year on each lake during 2000–2006, limiting the availability of paired observations of within-year estimates of year-class strength for both species. Consequently, our analyses were focused on the generalized relationship between Walleye recruitment success and juvenile Yellow Perch abundance at a relatively coarse scale (e.g., is the probability of Walleye recruitment success generally higher in lakes with higher Yellow Perch abundance).

RESULTS

Landscape-Level Comparison of Yellow Perch and Walleye Recruitment

Yellow Perch recruitment to age 3 was quantified in 55 surveys across 43 lakes, whereas age-0 Walleye recruitment was quantified in 3,440 surveys across 460 lakes from 1990 to 2020 (Figure 1). Similar sets of environmental variables, particularly thermal variables, were identified as important for explaining the probability of successful year-classes for both Yellow Perch and Walleye, although the order of variable importance was not the same (Table 1). For Yellow Perch, the duration of ice cover was most important, followed by conductivity, GDD_0, Secchi depth, and peak temperature, with spring water temperature CV being secondarily important. The model predicted successful year-classes with 67.3% accuracy (95% CI = 54.1–78.2%) and performed significantly better than a null model ($P = 0.01$). The most important predictors of Walleye recruitment success were water temperature CV 30–60 d after ice-off, lake area, and peak temperature, with GDD_0, winter severity, and Secchi depth being

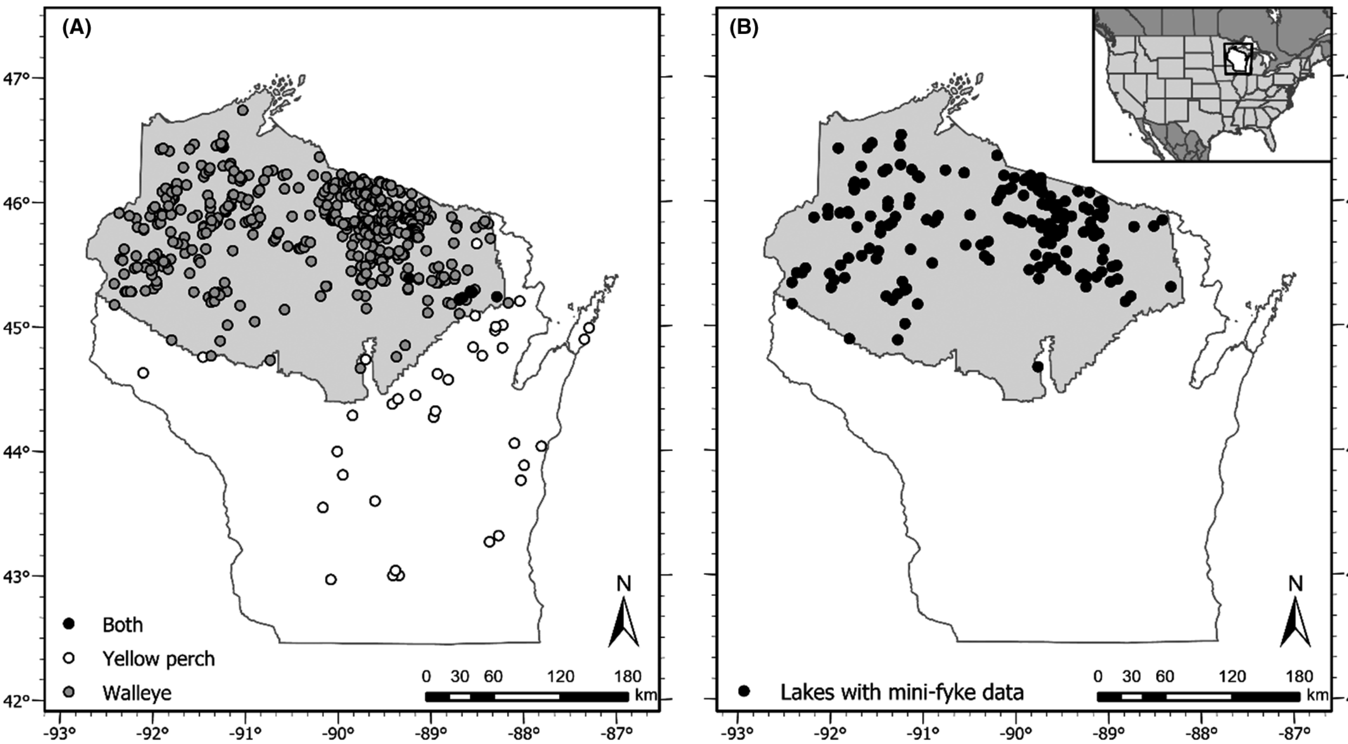

FIGURE 1. Maps of Wisconsin showing the locations of lakes used for **(A)** the landscape-level comparison of environmental characteristics associated with Yellow Perch (43 lakes) and Walleye (460 lakes) recruitment success and **(B)** determining if the probability of Walleye recruitment success during 2000–2006 was related to juvenile Yellow Perch catch per effort in mini-fyke-net sampling (174 lakes). Shaded areas indicate the Ceded Territory of Wisconsin.

secondarily important. Walleye recruitment success was predicted with 79.5% accuracy (95% CI = 78.2–80.8%) by the model, which performed significantly better than a null model ($P < 0.001$).

Negative associations were apparent between lakes with warm and variable water temperatures and the probability of recruitment success for both species. Longer, colder winters were positively associated with recruitment success in both species (Figure 2A), whereas higher annual GDD_0 (Figure 2C), higher peak temperatures (Figure 2E), and more variable late spring temperatures (Figure 2F) were negatively associated with recruitment success. Recruitment success was negatively associated with Secchi depth for both species (Figure 2D), whereas conductivity was positively associated with Yellow Perch recruitment success but negatively associated with Walleye recruitment success (Figure 2B).

Historic Mini-Fyke Data

Yellow Perch CPE in mini-fyke nets ranged from 0.06 to 2,312 fish/net-night, with a median value of 2.6. Mean Yellow Perch CPE in mini-fyke nets for 72 lakes classified as supporting successful Walleye recruitment during 2000–2006 was 167 fish/net-night (SE = 51), and CPE in the 102 lakes not supporting successful Walleye recruitment was 15 fish/net-night (SE = 6). Probability of Walleye recruitment success from 2000 to 2006 was significantly related to Yellow Perch CPE ($Z = 2.8$, $P < 0.01$; Figure 3), with a CPE increase of one Yellow Perch resulting in a 1.008 (i.e., $e^{0.007544}$) times increase in the odds that a lake supported successful recruitment from 2000 to 2006. Removal of seven extreme observations where Yellow Perch CPE in mini-fyke nets was >500 fish/net-night (>95% percentile for all observations) resulted in only a slight change in the odds that a lake supported successful Walleye recruitment (odds ratio = 1.013; $Z = 3.1$; $P < 0.01$). Of the 87 lakes with a Yellow Perch CPE ≥2.6 fish/net-night (median value for all lakes), 51 (59%) were classified as supporting successful Walleye recruitment. Conversely, only 21 of the 87 lakes (24%) with Yellow Perch CPE ≤ 2.6 fish/net-night were classified as supporting successful Walleye recruitment.

DISCUSSION

This study provides important information regarding conditions associated with Yellow Perch and Walleye recruitment in the upper Midwestern USA that can help explain and predict spatial patterns in recruitment success

TABLE 1. Mean (SD in parentheses) of lake-specific average environmental conditions and variable importance (measured as the percent increase in mean squared error when a given variable is permuted) of environmental predictors of Yellow Perch and Walleye recruitment success used in random forest modeling. The six most important predictors are bolded for Yellow Perch and italicized for Walleye (four are shared between species).

	Yellow Perch		Walleye	
Variable	Mean (SD)	Importance	Mean (SD)	Importance
Ice cover duration	130.99 (12.38)	0.112	152.16 (7.34)	0.029
Conductivity (μS/cm)	283.94 (130.96)	0.073	94.56 (54.52)	0.034
GDD$_0$	3,873.4 (242.92)	0.063	3,405.93 (183.83)	0.038
Secchi depth (m)	2.62 (1.18)	0.061	2.9 (1.43)	0.035
Peak summer temperature	29.45 (1.65)	0.057	27.45 (1.42)	0.058
Temperature CV 30–60 d post ice-off	0.17 (0.02)	0.043	0.15 (0.01)	0.09
Temperature CV 0–30 d post ice-off	0.35 (0.04)	0.023	0.33 (0.04)	0.033
Lake area (ha)	614.75 (1,708.5)	–0.006	244.16 (491.23)	0.083
Shoreline development index	2.25 (1.31)	–0.022	2 (1)	0.029
Maximum depth (m)	9.87 (5.16)	–0.033	10.78 (6.28)	0.028
Winter severity (days at 0–4°C)	126.65 (26.36)	–0.034	149.63 (20.62)	0.034

for both species. Although our work was focused on Wisconsin, we analyzed data from a broad spectrum of lakes that would encompass environmental conditions and fish communities observed for many lakes in Minnesota, Michigan, and other lakes within the Midwestern USA. Across individual lakes, average thermal conditions early in life appear to be related to production of successful year-classes for both species, which is consistent with other studies that have focused on Walleye (Hansen et al. 1998, 2015a; Honsey et al. 2020) and Yellow Perch (Clady 1976; Ward et al. 2004; Farmer et al. 2015). The general similarity in the suite of variables associated with high probability of recruitment success between the two species suggests that Walleye recruitment patterns previously reported for Wisconsin lakes (e.g., Hansen et al. 2018; Rypel et al. 2018) may also reflect patterns in Yellow Perch recruitment across Wisconsin. Moreover, before Walleye recruitment declines were observed the probability of Walleye recruitment success appeared to be positively related to relative abundance of juvenile Yellow Perch. Similarities in environmental conditions associated with recruitment success and in general abundance patterns among lakes suggest that Walleye and Yellow Perch may respond similarly to climatic changes across northern Wisconsin and may be indicative of overall changes in fish community structure in temperate lakes (Hansen et al. 2017).

Our results were consistent with previous work indicating that changes in annual water temperature regimes, including shorter, less severe winters, higher annual GDD$_0$, and more variable late spring temperatures, were associated with lower recruitment for both age-0 Walleye (Hansen et al. 2015a, 2017, 2018) and age-3 Yellow Perch (Farmer et al. 2015; Feiner et al. 2016a). The generally negative association of warm water temperatures with Walleye and Yellow Perch recruitment could be moderated by lake size and water clarity—recruitment success in both species was positively associated with lake size while negatively associated with Secchi depth and differentially associated by conductivity. Hansen et al. (2015a) showed that the effect of water temperature GDD$_5$ (base temperature 5°C) on probability of Walleye recruitment success in Wisconsin lakes was negligible in lakes ≥1,000 ha and that the relationship between recruitment probability and conductivity was dome-shaped. Thermal–optical habitat availability has also been related to Walleye recruitment (Honsey et al. 2020) and fishery yields (Lester et al. 2004). Understanding how water clarity, lake morphology, and climate change will interact to affect recruitment could allow managers to identify resilient populations or potential candidates for rehabilitation.

One explanation for the similarity in environmental conditions associated with the probability of recruitment success is that Walleye and Yellow Perch are responding similarly to these conditions (Sharma et al. 2011). Alternatively, in some lakes, Walleye recruitment declines may be caused by declines in Yellow Perch recruitment through direct interspecific interactions. Yellow Perch are both a prey item (Engel et al. 2000; Gostiaux et al. 2022) and prey buffer (Forney 1974, 1976) for juvenile Walleye. Walleye and Yellow Perch population dynamics may be strongly linked through predator–prey interactions, particularly when Yellow Perch are the main prey source for Walleye (Forney 1971; Mills et al. 1987). Specifically, previous evidence suggests that juvenile Yellow Perch are an important prey item for both age-0 and adult Walleye in northern Wisconsin lakes (Engel et al. 2000; Kelling et al. 2016; Gostiaux et al. 2022).

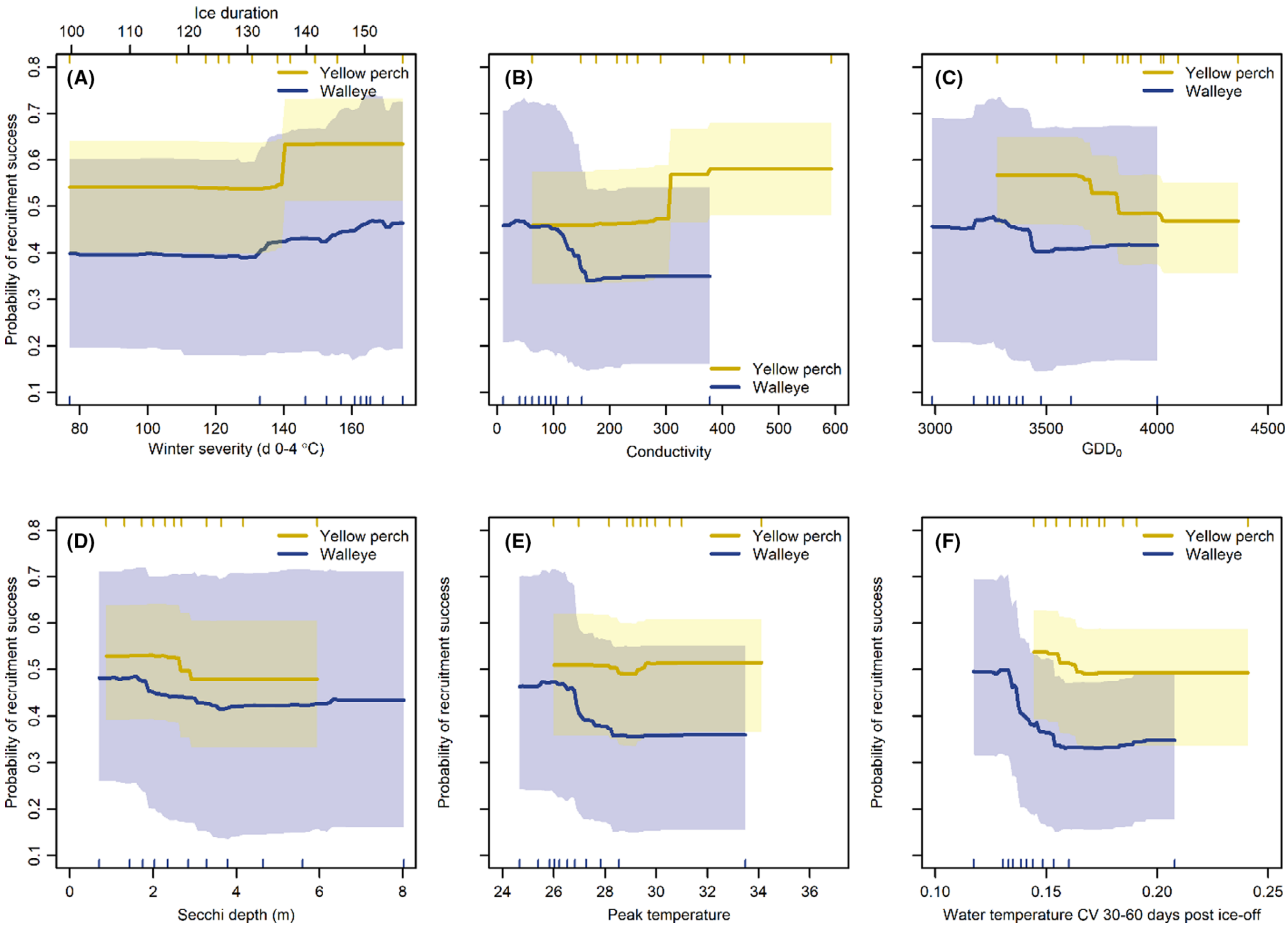

FIGURE 2. Partial dependence plots for six important variables in the random forest model for both Yellow Perch (yellow) and Walleye (blue): **(A)** indices of winter severity, including days between 0°C and 4°C (Walleye) and ice duration (Yellow Perch); **(B)** conductivity (μS/cm); **(C)** GDD_0; **(D)** Secchi depth (m); **(E)** summer peak temperature; and **(F)** water temperature CV 30–60 d after ice-off. Solid lines represent mean year-class strength predictions, shaded areas represent the region between the 25th and 75th percentiles of year-class strength predictions, and color-coded vertical dashes on the *x*-axes represent deciles of observed data.

Our analysis of the Yellow Perch CPE from mini-fyke nets offered a slightly different perspective than our analyses relying on standard fyke-net data. The mini-fyke-net data represent the only information for juvenile Yellow Perch abundance available at a relatively broad spatial scale in Wisconsin. These data did not allow us to determine if year-class strength was synchronous at annual scale between Walleye and Yellow Perch. However, results from the logistic regression and the general distribution of Walleye recruitment success relative to juvenile Yellow Perch CPE further suggest that recruitment of both species were related in some way. Recruitment for an individual species can exhibit substantial variation among systems (e.g., Janetski et al. 2013; Dembkowski et al. 2016; Honsey et al. 2016; Feiner et al. 2019a), and this likely explains some of the variation we observed between the probability of Walleye recruitment success and Yellow Perch abundance when analyzing historic fyke-net data. Additionally, introduced populations may exhibit less resilience to abiotic and biotic stressors than populations that were naturally established (Lorenzen et al. 2012). Unfortunately, the history of widespread fish stocking and translocations in northern Wisconsin means it is difficult to determine what lakes had native Walleye and Yellow Perch populations. Additional information is needed to fully understand among-lake variation in the responses of Walleye and Yellow Perch to biotic and abiotic conditions and how this may drive asynchronous or synchronous patterns in their recruitment.

Feiner et al. (2020) and Bethke and Staples (2015) suggest that some Midwestern U.S. Yellow Perch populations may be in decline. In light of similar patterns observed for Walleye in northern Wisconsin (Rypel et al. 2018), this

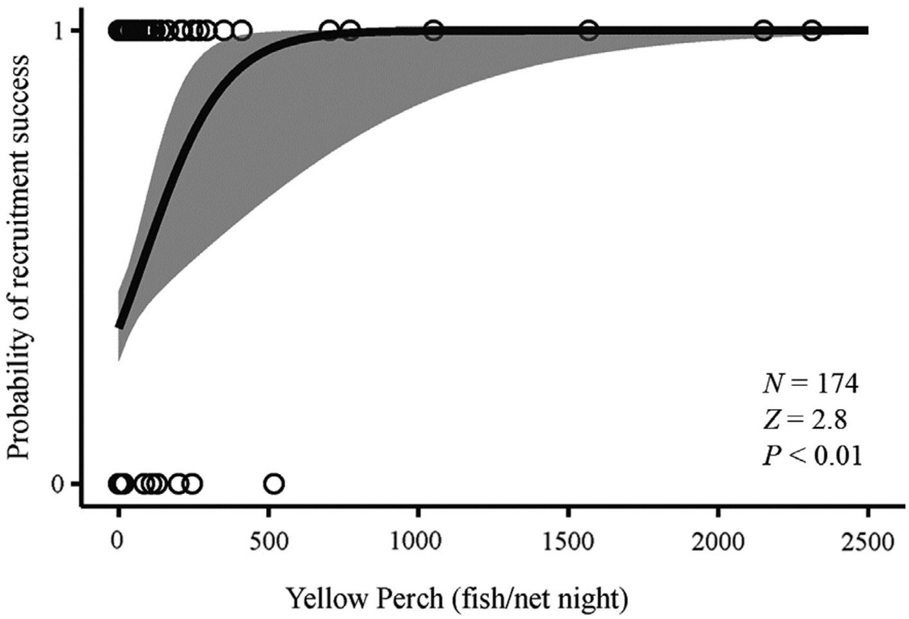

FIGURE 3. Probability (black line) of successful Walleye recruitment during 2000–2006 in relation to juvenile (age-0 and age-1) Yellow Perch catch per effort (fish/net-night) in mini-fyke-net sampling conducted on 174 lakes in Wisconsin. Results of logistic regression (*Z* and *P*) are reported. The shaded area represents 95% confidence intervals. Successful Walleye recruitment was defined as lakes with a mean catch per effort of age-0 Walleye of more than 6.2 fish/km in fall electrofishing.

may be part of a larger trend for declines in percids overall. In addition to recruitment, there are strong indicators to suggest that Yellow Perch size structure has decreased in Wisconsin (Beard and Kampa 1999; Rypel et al. 2016) along with recreational harvest rates (Feiner et al. 2020). We note that observed declines in Yellow Perch size structure could explain observed declines in fyke-net CPE and angler harvest rates as both "gears" are size-selective, meaning that fewer fish may be vulnerable to fyke-net capture or acceptable for angler harvest.

Declines in Walleye recruitment in northern Wisconsin have already prompted substantial research efforts and changes to management strategies, including increased stocking of large fingerlings in lakes exhibiting recruitment declines (Hansen et al. 2015a) and implementing more restrictive harvest regulations (Raabe et al. 2020), while Yellow Perch populations have received comparatively limited attention. One potential hurdle is the lack of long-term standardized data needed to further assess the status and trends of Yellow Perch. Specifically, current sampling does not provide a means to assess Yellow Perch recruitment early in life (age 0 or age 1), whereas sampling for this purpose does occur in many other states and provinces (Irwin et al. 2009; Dembkowski et al. 2016; Zhang et al. 2017). We recognize that the Yellow Perch data from standard fyke-net sampling were not specifically collected to assess recruitment trends and for the historic mini-fyke-net sampling, there was little replication at the individual lake level. These problems emphasize the need to establish standardized Yellow Perch sampling protocols that will help biologists answer several critical questions about the status and trends of Yellow Perch populations across the region, including elucidating mechanisms driving Yellow Perch recruitment and abundance, levels of Yellow Perch recruitment necessary to sustain viable populations, and linkages between Walleye and Yellow Perch population dynamics.

Despite the lack of data on Yellow Perch recruitment, our findings have important implications for fisheries management. Our work has prompted new field-based research comparing methods to sample age-0 Yellow Perch and examining Yellow Perch recruitment trends in lakes with different Walleye histories. Our work also demonstrates that mitigating potential declines in Yellow Perch recruitment may be difficult given that environmental conditions associated with recruitment success are largely outside the control of fishery managers. However, managers may need to respond to these potential declines, which have implications for several other species. Yellow Perch have been shown to provide important prey for both adult Walleye and Largemouth Bass in northern Wisconsin lakes (Kelling et al. 2016), suggesting that declines in Yellow Perch may translate into reduced capacity to support historic densities of these predators or that predation may be shifted to other species, such as Bluegill *Lepomis macrochirus*, that also support important fisheries. Furthermore, Yellow Perch contributed to moderate to high diet overlap between Largemouth Bass and Walleye observed in four northern Wisconsin lakes in some months (Kelling et al. 2016).

Reduced availability of Yellow Perch coupled with increases in Largemouth Bass abundance (Hansen et al. 2015c) may mean that fewer Yellow Perch are available to Walleye as prey, which could translate to slower growth if alternative prey are not available. However, recent work has shown that growth of juvenile Walleye in Wisconsin lakes increased from 1990 to 2012, while growth of older fish remained relatively stable (Pedersen et al. 2018). Fewer Yellow Perch could also result in changes to growth and size structure that could result in Yellow Perch fisheries that are characterized by lower catch rates but with more fish that are of desirable size for angler harvest (Isermann et al. 2007). However, growth and size structure of Yellow Perch may be regulated by factors other than intraspecific density (Paukert and Willis 2001; Purchase et al. 2005). Lastly, larval sampling conducted on northern Wisconsin lakes (Gostiaux et al. 2022) has shown that age-0 Yellow Perch likely represent one of the dominant zooplanktivores in these lakes during May and June. Consequently, potential reductions in age-0 Yellow Perch abundance may result in greater availability of zooplankton prey for many other species that support important fisheries (e.g., centrarchids, Walleye), which could translate into improved growth and survival.

ACKNOWLEDGMENTS

Funding for this project was provided by the WDNR through the Fisheries Analysis Center at the University of Wisconsin–Stevens Point. Z. Feiner was supported by the United States Fish and Wildlife Service Federal Aid in Sportfish Restoration and the WNDR, Project F-95-P. This project was a collaborative effort of many WDNR personnel, as well as staff and students with the Wisconsin Cooperative Fishery Research Unit. We thank D. Dembkowski with the Wisconsin Cooperative Fishery Research Unit and P. Frater and Z. Driscoll of the WDNR for help with this project. This study was performed under protocol 2012.04.11 approved by the Institutional Animal Care and Use Committee at the University of Wisconsin–Stevens Point. Fish were collected under state permit SCP-NOR-355-0513. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. There is no conflict of interest declared in this article.

ORCID

Daniel A. Isermann https://orcid.org/0000-0003-1151-9097

REFERENCES

Beard, T. D., M. J. Hansen, and S. R. Carpenter. 2003. Development of a regional stock–recruitment model for understanding factors affecting Walleye recruitment in northern Wisconsin lakes. Transactions of the American Fisheries Society 132:382–391.

Beard, T. D., and J. M. Kampa. 1999. Changes in Bluegill, Black Crappie, and Yellow Perch populations in Wisconsin during 1967–1991. North American Journal of Fisheries Management 19:1037–1043.

Bethke, B. J., and D. F. Staples. 2015. Changes in relative abundance of several Minnesota fishes from 1970 to 2013. Transactions of the American Fisheries Society 144:68–80.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Chapman and Hall, London.

Bogner, D. M., M. A. Kaemingk, and M. R. Wuellner. 2016. Consequences of hatch phenology on stages of fish recruitment. PLOS ONE [online serial] 11:e0164980.

Bozek, M. A., D. A. Baccante, and N. P. Lester. 2011. Walleye and Sauger life history. Pages 233–301 *in* B. A. Barton, editor. Biology, management, and culture of Walleye and Saugeye. American Fisheries Society, Bethesda, Maryland.

Clady, M. D. 1976. Influence of temperature and wind on the survival of early stages of Yellow Perch, *Perca flavescens*. Journal of the Fisheries Research Board of Canada 33:1887–1893.

Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

Dembkowski, D. J., D. W. Willis, and M. R. Wuellner. 2016. Synchrony in larval Yellow Perch abundance: the influence of the Moran effect during early life history. Canadian Journal of Fisheries and Aquatic Sciences 73:1567–1574.

Embke, H. S., T. D. Beard, A. J. Lynch, and M. J. V. Zanden. 2020. Fishing for food: quantifying recreational fisheries harvest in Wisconsin lakes. Fisheries 45:647–655.

Engel, S., M. H. Hoff, and S. P. Newman. 2000. Walleye fry hatching, diet, growth, and abundance in Escanaba Lake, Wisconsin, 1985–1992. Wisconsin Department of Natural Resources, Research Report 184, Madison.

Farmer, T. M., E. A. Marschall, K. Dabrowski, and S. A. Ludsin. 2015. Short winters threaten temperate fish populations. Nature Communications 6:article 7724.

Feiner, Z. S., D. P. Coulter, S. C. Guffey, and T. O. Höök. 2016a. Does overwinter temperature affect maternal body composition and egg traits in Yellow Perch *Perca flavescens*? Journal of Fish Biology 88:1524–1543.

Feiner, Z. S., D. P. Coulter, M. D. Linn, and T. O. Höök. 2019a. A question of scale: weak evidence for broad regional synchrony in fish year-class strength within or among species in inland lakes. Fisheries Research 214:45–55.

Feiner, Z. S., and T. O. Höök. 2015. Environmental biology of percid fishes. Pages 61–100 *in* P. Kestemont, K. Dabrowski, and R. C. Summerfelt, editors. Biology and culture of percid fishes. Springer, Dordrecht, The Netherlands.

Feiner, Z. S., S. L. Shaw, and G. G. Sass. 2019b. Influences of female body condition on recruitment success of Walleye (*Sander vitreus*) in Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Sciences 76:2131–2144.

Feiner, Z. S., H.-Y. Wang, D. W. Einhouse, J. R. Jackson, E. S. Rutherford, C. Schelb, C. S. Vandergoot, T. G. Zorn, and T. O. Höök. 2016b. Thermal environment and maternal effects shape egg size in a freshwater fish. Ecosphere [online serial] 7(5):e01304.

Feiner, Z. S., M. H. Wolter, and A. W. Latzka. 2020. "I will look for you, I will find you, and I will [harvest] you": persistent hyperstability in Wisconsin's recreational fishery. Fisheries Research 230:105679.

Forney, J. L. 1971. Development of dominant year-classes in a Yellow Perch population. Transactions of the American Fisheries Society 100:739–741.

Forney, J. L. 1974. Interactions between Yellow Perch abundance, Walleye predation, and survival of alternate prey in Oneida Lake, New York. Transactions of the American Fisheries Society 103:15–24.

Forney, J. L. 1976. Year-class formation in the Walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–1973. Journal of the Fisheries Research Board of Canada 33:783–792.

Gostiaux, J. C., H. I. A. Boehm, N. J. Jaksha, D. J. Dembkowski, J. M. Hennessy, and D. A. Isermann. 2022. Recruitment bottlenecks for Age-0 Walleye in northern Wisconsin lakes. North American Journal of Fisheries Management. DOI:10.1002/nafm.10683.

Greenwell, B. M. 2017. pdp: an R package for constructing partial dependence plots. The R Journal 9:421.

Hansen, G. J. A., S. R. Carpenter, J. W. Gaeta, J. M. Hennessy, and M. J. Vander Zanden. 2015a. Predicting Walleye recruitment as a tool for prioritizing management actions. Canadian Journal of Fisheries and Aquatic Sciences 72:661–672.

Hansen, G. J. A., J. W. Gaeta, J. F. Hansen, and S. R. Carpenter. 2015b. Learning to manage and managing to learn: sustaining freshwater recreational fisheries in a changing environment. Fisheries 40:56–64.

Hansen, G. J. A., S. R. Midway, and T. Wagner. 2018. Walleye recruitment success is less resilient to warming water temperatures in lakes with abundant Largemouth Bass populations. Canadian Journal of Fisheries and Aquatic Sciences 75:106–115.

Hansen, G. J. A., J. S. Read, J. F. Hansen, and L. A. Winslow. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biology 23:1463–1476.

Hansen, G. J. A., L. A. Winslow, J. S. Read, M. Treml, P. J. Schmalz, and S. R. Carpenter. 2019. Water clarity and temperature effects on Walleye safe harvest: an empirical test of the safe operating space concept. Ecosphere [online serial] 10(5):e02737.

Hansen, J. F., G. G. Sass, J. W. Gaeta, G. A. Hansen, D. A. Isermann, J. Lyons, and M. J. Vander Zanden. 2015c. Largemouth Bass management in Wisconsin: intraspecific and interspecific implications of abundance increases. Pages 193–206 *in* M. D. Tringall, J. M. Long, T. W. Birdsong, and M. S. Allen, editors. Black bass diversity: multidisciplinary science for conservation. American Fisheries Society, Symposium 82, Bethesda, Maryland.

Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998. Factors affecting recruitment of Walleyes in Escanaba Lake, Wisconsin, 1958–1996. North American Journal of Fisheries Management 18:764–774.

Honsey, A. E., D. B. Bunnell, C. D. Troy, D. G. Fielder, M. V. Thomas, C. T. Knight, S. C. Chong, and T. O. Höök. 2016. Recruitment synchrony of Yellow Perch (*Perca flavescens*, Percidae) in the Great Lakes region, 1966–2008. Fisheries Research 181:214–221.

Honsey, A. E., Z. S. Feiner, and G. J. A. Hansen. 2020. Drivers of Walleye recruitment in Minnesota's large lakes. Canadian Journal of Fisheries and Aquatic Sciences 77:1921–1933.

Hothorn, T., and A. Zeileis. 2015. Partykit: a modular toolkit for recursive partytioning in R. Journal of Machine Learning Research 16:3905–3909.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17–29 *in* R. D. Hoyt, editor. 10th annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.

Houde, E. D. 1989. Subtleties and episodes in the early life of fishes. Journal of Fish Biology 35:29–38.

Houde, E. D. 2009. Recruitment variability. Pages 91–171 *in* T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, editors. Fish reproductive biology. Wiley-Blackwell, Oxford, UK.

Huh, H. T., H. E. Calbert, and D. A. Stuiber. 1976. Effects of temperature and light on growth of Yellow Perch and Walleye using formulated feed. Transactions of the American Fisheries Society 105: 254–258.

Irwin, B. J., L. G. Rudstam, J. R. Jackson, A. J. VanDeValk, J. L. Forney, and D. G. Fitzgerald. 2009. Depensatory mortality, density-dependent growth, and delayed compensation: disentangling the interplay of mortality, growth, and density during early life stages of Yellow Perch. Transactions of the American Fisheries Society 138: 99–110.

Isermann, D. A., and C. T. Knight. 2005. A computer program for age–length keys incorporating age assignment to individual fish. North American Journal of Fisheries Management 25:1153–1160.

Isermann, D. A., and C. P. Paukert. 2010. Regulating harvest. Pages 185–212 *in* W. A. Hubert and M. C. Quist, editors. Inland fisheries management in North America, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Isermann, D. A., D. W. Willis, B. G. Blackwell, and D. O. Lucchesi. 2007. Yellow Perch in South Dakota: population variability and predicted effects of creel limit reductions and minimum length limits. North American Journal of Fisheries Management 27:918–931.

Ivan, L. N., T. O. Höök, M. V. Thomas, and D. G. Fielder. 2011. Long-term and interannual dynamics of Walleye and Yellow Perch in Saginaw Bay, Lake Huron. Transactions of the American Fisheries Society 140:1078–1092.

Janetski, D. J., C. R. Ruetz, Y. Bhagat, and D. F. Clapp. 2013. Recruitment dynamics of age-0 Yellow Perch in a drowned river mouth lake: assessing synchrony with nearshore Lake Michigan. Transactions of the American Fisheries Society 142:505–514.

Kaemingk, M. A., B. D. S. Graeb, and D. W. Willis. 2014. Temperature, hatch date, and prey availability influence age-0 Yellow Perch growth and survival. Transactions of the American Fisheries Society 143:845–855.

Kallemeyn, L. W. 1987. Correlations of regulated lake levels and climatic factors with abundance of young-of-the-year Walleye and Yellow Perch in four lakes in Voyageurs National Park. North American Journal of Fisheries Management 7:513–521.

Kelling, C. J., D. A. Isermann, B. L. Sloss, and K. N. Turnquist. 2016. Diet overlap and predation between Largemouth Bass and Walleye in Wisconsin lakes using DNA barcoding to improve taxonomic resolution. North American Journal of Fisheries Management 36:621–629.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34:1910–1921.

Koenst, W. M., and L. L. Smith Jr. 1976. Thermal requirements of the early life history stages of Walleye, *Stizostedion vitreum vitreum*, and Sauger, *Stizostedion canadense*. Journal of the Fisheries Research Board of Canada 33:1130–1138.

Koonce, J. F., T. B. Bagenal, R. F. Carline, K. E. F. Hokanson, and M. Nagięć. 1977. Factors influencing the year-class strength of percids: a summary and model of temperature effects. Journal of the Fisheries Research Board of Canada 34:1900–1909.

Lester, N. P., A. J. Dextrase, R. S. Kushneriuk, M. R. Rawson, and P. A. Ryan. 2004. Light and temperature: key factors affecting Walleye abundance and production. Transactions of the American Fisheries Society 133:588–605.

Lorenzen, K., M. C. M. Beveridge, and M. Mangel. 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. Biological Reviews 87:639–660.

Ludsin, S. A., K. M. DeVanna, and R. E. H. Smith. 2014. Physical–biological coupling and the challenge of understanding fish recruitment in freshwater lakes. Canadian Journal of Fisheries and Aquatic Sciences 71:775–794.

Maceina, M. J., and D. L. Pereira. 2007. Recruitment. Pages 887–946 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Mills, E. L., J. L. Forney, and K. J. Wagner. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. Pages 118–131 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

Myers, R. A. 1998. When do environment-recruitment correlations work? Reviews in Fish Biology and Fisheries 8:285–305.

Noble, R. L. 1986. Stocking criteria and goals for restoration and enhancement of warm-water and cool-water fisheries. Pages 139–146 *in* R. H. Stroud, editor. Fish culture in fisheries management. American Fisheries Society, Bethesda, Maryland.

Ogle, D. H., P. Wheeler, and A. Dinno. 2020. FSA: Fisheries stock analysis. R package version 0.8.31. Available: https://cran.r-project.org/package=FSA. (January 2022).

Papes, M., and J. Vander Zanden. 2013. Wisconsin lake historical limnological parameters 1925–2009 version 2. Environmental Data Initiative. Available: https://doi.org/10.6073/pasta/66320ff8063706f6b3ee83a0ef3ef439. (January 2022).

Paukert, C. P., B. A. Glazer, G. J. A. Hansen, B. J. Irwin, P. C. Jacobson, J. L. Kershner, B. J. Shuter, J. E. Whitney, and A. J. Lynch. 2016. Adapting inland fisheries management to a changing climate. Fisheries 41:374–384.

Paukert, C. P., and D. W. Willis. 2001. Comparison of exploited and unexploited Yellow Perch *Perca flavescens* (Mitchill) populations in Nebraska Sandhill lakes. Fisheries Management and Ecology 8:533–542.

Pedersen, E. J., D. Goto, J. W. Gaeta, G. J. A. Hansen, G. G. Sass, M. J. Vander Zanden, T. A. Cichosz, and A. L. Rypel. 2018. Long-term growth trends in northern Wisconsin Walleye populations under changing biotic and abiotic conditions. Canadian Journal of Fisheries and Aquatic Sciences 75:733–745.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross–scale interactions and changing pattern–process relationships: consequences for system dynamics. Ecosystems 10:790–796.

Purchase, C. F., N. C. Collins, G. E. Morgan, and B. J. Shuter. 2005. Sex-specific covariation among life-history traits of Yellow Perch (*Perca flavescens*). Evolutionary Ecology Research 7:549.

Raabe, J. K., J. A. VanDeHey, D. L. Zentner, T. K. Cross, and G. G. Sass. 2020. Walleye inland lake habitat: considerations for successful natural recruitment and stocking in North Central North America. Lake and Reservoir Management 36:335–359.

Read, J. S., A. P. Appling, S. K. Oliver, J. A. Zwart, and G. J. A. Hansen. 2021. Data release: predictions of lake water temperatures in the Midwest 1980–2019. U.S. Geological Survey, Reston, Virginia.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Robillard, M. M., and M. G. Fox. 2006. Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. Canadian Journal of Fisheries and Aquatic Sciences 63:798–809.

Rogers, M. W., M. J. Hansen, and T. D. Beard Jr. 2003. Catchability of Walleyes to fyke netting and electrofishing in northern Wisconsin lakes. North American Journal of Fisheries Management 23:1193–1206.

Rose, K. A., E. S. Rutherford, D. S. McDermot, J. L. Forney, and E. L. Mills. 1999. Individual-based model of Yellow Perch and Walleye populations in Oneida lake. Ecological Monographs 69:127–154.

Rypel, A. L., D. Goto, G. G. Sass, and M. J. Vander Zanden. 2018. Eroding productivity of Walleye populations in northern Wisconsin lakes. Canadian Journal of Fisheries and Aquatic Sciences 75:2291–2301.

Rypel, A. L., J. Lyons, J. D. T. Griffin, and T. D. Simonson. 2016. Seventy-year retrospective on size-structure changes in the recreational fisheries of Wisconsin. Fisheries 41:230–243.

Schneider, K. N., R. M. Newman, V. Card, S. Weisberg, and D. L. Pereira. 2010. Timing of Walleye spawning as an indicator of climate change. Transactions of the American Fisheries Society 139:1198–1210.

Schupp, D. H. 2002. What does Mt. Pinatubo have to do with Walleyes? North American Journal of Fisheries Management 22:1014–1020.

Serns, S. L. 1982. Influence of various factors on density and growth of age-0 Walleyes in Escanaba Lake, Wisconsin, 1958–1980. Transactions of the American Fisheries Society 111:299–306.

Sharma, S., P. Legendre, M. D. Cáceres, and D. Boisclair. 2011. The role of environmental and spatial processes in structuring native and non-native fish communities across thousands of lakes. Ecography 34:762–771.

Signorelli, A., and others. 2020. DescTools: tools for descriptive statistics. R package version 0.99.39. Available: https://cran.r-project.org/package=DescTools. (January 2022).

Simonson, T. D. 2006. Sampling procedures - baseline lakes. Wisconsin Department of Natural Resources, Madison.

Sissenwine, M. P. 1984. Why do fish populations vary? Pages 59–94 *in* R. M. May, editor. Exploitation of marine communities. Springer, Berlin.

Soranno, P. A., K. S. Cheruvelil, E. G. Bissell, M. T. Bremigan, J. A. Downing, C. E. Fergus, C. T. Filstrup, E. N. Henry, N. R. Lottig, E. H. Stanley, C. A. Stow, P.-N. Tan, T. Wagner, and K. E. Webster. 2014. Cross-scale interactions: quantifying multi-scaled cause–effect relationships in macrosystems. Frontiers in Ecology and the Environment 12:65–73.

Strobl, C., A.-L. Boulesteix, T. Kneib, T. Augustin, and A. Zeileis. 2008. Conditional variable importance for random forests. BMC Bioinformatics [online serial] 9:article 307.

Treaty Fisheries Assessment Team. 2005. Treaty fisheries assessment team fisheries survey sampling guidelines – 2005. Wisconsin Department of Natural Resources, Madison.

Trushenski, J., T. Flagg, and C. Kohler. 2010. Use of hatchery fish for conservation, restoration, and enhancement of fisheries. Pages 261–293 *in* W. A. Hubert and M. C. Quist, editors. Inland fisheries management in North America, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Ward, M. J., M. R. Anderson, S. J. Fisher, D. A. Isermann, Q. E. Phelps, and D. W. Willis. 2004. Relations between climatological variables and larval Yellow Perch abundance in eastern South Dakota glacial lakes. Journal of Freshwater Ecology 19:213–218.

Winslow, L. A. 2015. lakeattributes: a collection of lake attribute data. R package version 0.10.2.

Zhang, F., K. B. Reid, and T. D. Nudds. 2017. Relative effects of biotic and abiotic factors during early life history on recruitment dynamics: a case study. Canadian Journal of Fisheries and Aquatic Sciences 74:1125–1134.

Zhao, Y., P. M. Kocovsky, and C. P. Madenjian. 2013. Development of a stock–recruitment model and assessment of biological reference points for the Lake Erie Walleye fishery. North American Journal of Fisheries Management 33:956–964.