

Predicting walleye recruitment as a tool for prioritizing management actions

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Abstract: We classified walleye (*Sander vitreus*) recruitment with 81% accuracy (recruitment success and failure predicted correctly in 84% and 78% of lake-years, respectively) using a random forest model. Models were constructed using 2779 surveys collected from 541 Wisconsin lakes between 1989 and 2013 and predictor variables related to lake morphology, thermal habitat, land use, and fishing pressure. We selected predictors to minimize collinearity while maximizing classification accuracy and data availability. The final model classified recruitment success based on lake surface area, water temperature degree-days, shoreline development factor, and conductivity. On average, recruitment was most likely in lakes larger than 225 ha. Low degree-days also increased the probability of successful recruitment, but primarily in lakes smaller than 150 ha. We forecasted the probability of walleye recruitment in 343 lakes considered for walleye stocking; lakes with high probability of natural reproduction but recent history of recruitment failure were prioritized for restoration stocking. Our results highlight the utility of models designed to predict recruitment for guiding management decisions, provided models are validated appropriately.

Résumé : Un modèle de forêt aléatoire pour la catégorisation du recrutement de dorés jaunes (*Sander vitreus*) s'est avéré exact dans 81 % des cas (prédiction correcte du succès ou de l'échec du recrutement pour 84 % et 78 % des années-lac, respectivement). Des modèles ont été élaborés à partir de 2779 évaluations obtenues pour 541 lacs du Wisconsin de 1989 à 2013, et de variables prédictives reliées à la morphométrie des lacs, à l'habitat thermique, à l'utilisation du sol et à la pression de pêche. Nous avons sélectionné les variables prédictives de manière à minimiser la colinéarité tout en maximisant l'exactitude de la catégorisation et la disponibilité des données. Le modèle final catégorisait le succès de recrutement en fonction de la superficie du lac, des degrés-jours de température du lac, d'un facteur d'aménagement des berges et de la conductivité. En moyenne, le recrutement était plus probable dans les lacs de plus de 225 ha. De faibles degrés-jours se traduisaient également par une probabilité accrue de succès du recrutement, mais principalement dans les lacs de moins de 150 ha. Nous avons prédit la probabilité de recrutement de dorés jaunes dans 343 lacs considérés comme candidats pour l'ensemencement de dorés; la priorité en ce qui concerne l'ensemencement aux fins de rétablissement a été donnée aux lacs présentant une forte probabilité de reproduction naturelle, mais un historique récent d'échec du recrutement. Nos résultats soulignent l'utilité de modèles conçus pour prédire le recrutement pour ce qui est d'orienter les décisions de gestion, pourvu que ces modèles soient validés adéquatement. [Traduit par la Rédaction]

Introduction

Recruitment is the most variable and most influential vital rate for many fish populations (Ricker 1975). Understanding the causes of recruitment variability is a major goal of fisheries ecology and management (Gulland 1982; Hilborn and Walters 1992), with successful prediction of recruitment dubbed by some as the “holy grail” of fisheries (Houde 2008; Ludsins et al. 2014). Although most recruitment analyses have considered variability over time within a single population, management of inland recreational fisheries requires that spatial variability in recruitment also be considered. Many recreational fisheries consist of a landscape of relatively isolated stocks linked by mobile anglers, and these fisheries are managed using a small set of regulations to limit harvest on a large number of systems (Cox et al. 2002; Carpenter and Brock 2004; Parkinson et al. 2004). Failure to account for heterogeneity among systems — including recruitment heterogeneity — may

contribute to collapse of important recreational fisheries (Cox and Walters 2002; Parkinson et al. 2004). Recruitment variability can also obscure population trends (e.g., Peterman and Bradford 1987) and responses to management actions (e.g., Allen and Pine 2000). At the same time, measuring recruitment of hundreds to thousands of individual populations to set lake-specific management targets is impossible (Hayes et al. 2003; Lester et al. 2003; Fayram et al. 2009). The capacity to predict recruitment accurately from widely available lake characteristics across a landscape can improve fisheries management by targeting management actions to locations where they are most likely to succeed.

Walleye (*Sander vitreus*) are a recreationally and economically important sport fish throughout North America (Schmalz et al. 2011) with highly variable recruitment (e.g., Hansen et al. 1998; Bozek et al. 2011). Walleye recruitment from natural reproduction in Wisconsin, USA, has declined in recent years, leaving managers and anglers eager to identify the cause of these declines and de-

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velop management actions to reverse them (Hansen et al. 2015). In 2013 the Wisconsin Walleye Stocking Initiative (WWSI) was initiated, under which millions of dollars have been dedicated to hatchery production and stocking of large walleye fingerlings (at least 15.2 cm total length at time of stocking), which are known to survive at higher rates than walleye stocked at smaller sizes (Kampa and Hatzenbeler 2009). Based on stakeholder input, Wisconsin managers have prioritized stocking walleye in waters that are currently experiencing recruitment failures but have the potential to support natural reproduction, with the goal of restoring natural reproduction and eliminating the need to stock in the future. Thus, a method for forecasting the likelihood of successful recruitment in candidate lakes is needed to use objective, scientific criteria to prioritize lakes for stocking under this multi-million dollar program.

Recruitment of walleye is affected by a large number of biotic and abiotic factors (Baccante and Colby 1996). Previous analyses have identified biotic predictors of walleye recruitment, including adult stock size (Chevalier 1977; Hansen et al. 1998; Beard et al. 2003) as well as predation and competition by other species (e.g., Forney 1977; Madenjian et al. 1996; Fielder et al. 2007). Abiotic factors affecting walleye recruitment have also been identified; these include lake size (Nate et al. 2000), spring water temperatures (e.g., Serns 1982; Hansen et al. 1998; Quist et al. 2003), a surrogate for regional climate variability (Beard et al. 2003), and (or) water levels (Chevalier 1977; Quist et al. 2004). However, the utility of these prior analyses for forecasting recruitment has not been evaluated in most cases.

To be useful for forecasting recruitment and guiding management decisions, models of recruitment variability must be robust to the addition of independent data not used in model construction (Sissenwine 1984; Walters and Collie 1988; Fernandes et al. 2010). Despite widespread recognition for several decades of the need for validation using independent data, such validation is not commonplace in ecology (Power 1993; Fielding 1999; Guthery et al. 2005). When the predictive capacity of published environment-recruitment correlations have been formally tested using new data, these correlations break down with “disturbing regularity” (Walters and Collie 1988; Myers 1998). Of the myriad studies examining correlates of walleye recruitment across space and (or) time, only one (Hansen et al. 1998) tested the predictive capacity of their model by validating with independent data. The results were equivocal at best, with model residuals from 3 of 5 validation years exceeding residuals from any of the 34 model construction years. We are aware of no other walleye recruitment models that have been validated using independent data. Finally, if a model is to be effective in forecasting recruitment in a large number of lakes, variables used for prediction must themselves be either predictable or measurable on a large scale (Walters and Collie 1988). For example, models that rely upon adult stock size to predict recruitment would have limited utility in forecasting recruitment in a large number of lakes, because estimating adult populations is costly and doing so in all lakes in a single year would be impossible.

Here, we combine a novel analytical approach and a dataset spanning 25 years and 508 lakes across Wisconsin to predict walleye recruitment as a function of environmental variables. Our objectives were to (i) identify environmental variables correlated with recruitment success of Wisconsin walleye, and (ii) use relationships between environmental variables and recruitment to forecast walleye recruitment success in lakes considered for stocking under the WWSI. Because our second objective was forecasting, we used an analytical approach (random forest modeling; Breiman 2001; Cutler et al. 2007) in which model accuracy is based on the ability to predict independent validation data. To further increase the applicability of our results to management decision making, we restricted our set of potential predictor variables to those that were widely available for a large number of lakes. We

highlight the application of our results to stocking prioritization under the WWSI as a case study demonstrating how models designed to understand and predict recruitment can be used to direct management decisions.

Methods

Study system

We analyzed walleye recruitment from 1989 to 2013 in lakes throughout Wisconsin (Fig. 1). Sampling was more frequent in the northern third of Wisconsin, known as the Ceded Territory. This area was ceded by the Lake Superior Chippewa Tribes to the United States through treaties in 1837 and 1842, and tribal rights to spear walleye in the Ceded Territory were reinstated in 1983 (USBIA 1991). The Ceded Territory contains 77% of Wisconsin's lakes, including the majority of walleye lakes (Staggs et al. 1990), and these lakes support a joint fishery composed of tribal spearfishing and recreational angling (USBIA 1991).

Walleye recruitment

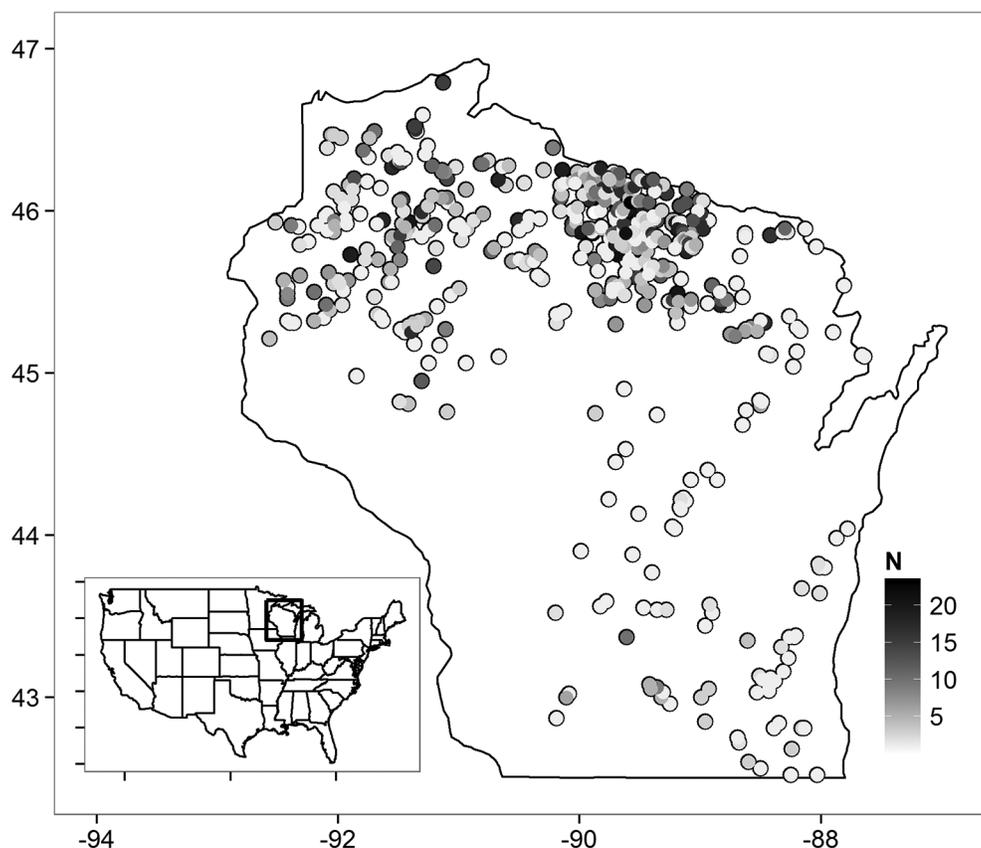
Walleye recruitment was indexed by electrofishing catch of age-0 fish per surveyed kilometre collected in nighttime fall surveys using a 230 V AC electrofishing boat. Walleye recruitment to age 0 is measured on dozens of lakes annually to support management of Wisconsin's walleye fishery, and we used surveys collected from 1989 to 2013. Each walleye collected was assigned an age based on length frequency distributions or analysis of scale annuli. We analyzed all surveys from lakes with past evidence of natural reproduction, although surveys from lake-years in which fry or fingerling stocking occurred were excluded. To ensure that survey effort was sufficient to index whole lake densities of age-0 walleye, we only included surveys in which at least 70% of the lake shoreline was sampled for lakes under 25.75 km circumference. For lakes larger than 25.75 km circumference, we restricted analysis to surveys in which at least 16.1 km of shoreline were sampled (following Ceded Territory age-0 walleye sampling protocols). We excluded surveys conducted in water temperatures less than 10 °C and greater than 21 °C (Hansen et al. 2004) and those in which survey reliability was classified as low because of suboptimal conditions known to influence catchability (e.g., low water clarity) to ensure consistency in vulnerability to sampling. When multiple surveys meeting these criteria in a given lake-year were available, catch rates were averaged for that lake-year.

Although recruitment is measured as a continuous variable, high variability makes the absolute value of recruitment difficult to predict. Knowledge of whether recruitment was successful is often sufficient for prioritizing management; one method of translating continuous recruitment data into discrete classifications is to use classification of fisheries experts (Fernandes et al. 2010). We classified walleye recruitment in each survey as successful or unsuccessful based on a cutoff of 6.2 age-0 walleye-km⁻¹ (10 age-0 walleye-mile⁻¹), identified by Wisconsin Department of Natural Resources (WDNR) biologists as the threshold above which recruitment to the fishery is likely. Our initial dataset contained 2779 observations of recruitment from 541 Wisconsin lakes; final sample size was determined after model selection because data for some predictor variables were not available for all lakes.

Predictor data

We evaluated 46 potential predictor variables selected to represent variability in lake morphometry, productivity, land use, fishing pressure, habitat, and thermal conditions, all of which may affect various walleye life stages (Table 1). Because our goal was prediction of walleye recruitment, we primarily used single measures of variables that change on relatively slow timescales (i.e., decades to centuries) that were available for most or all lakes with walleye recruitment data. However, we did include some predictors that vary over months to year timescales, and in those cases

Fig. 1. Wisconsin lakes with surveys used to generate predictive model of walleye recruitment. Dot shading represents number of years (N) of walleye recruitment survey data collected between 1989 and 2013.



we used the mean value of the predictor for a given lake across the entire time series (see below and Table 1 for details).

Lake surface area, shoreline development factor (SDF; a measure of shoreline complexity; Wetzel 2001), land use data, and surrogates for angling pressure were calculated using ArcGIS (ESRI, Redlands, California). Land use values are included both for the riparian zone and the entire watershed, calculated as the percent land covers for a 100 m buffer surrounding the perimeter of the lake and for the HUC10 (hydrologic unit code, region 10) watershed, respectively. Percent cover is the area of each land cover type (from the 2006 National Land Cover Dataset) divided by the total non-open water area. “Developed” is the sum of low-, moderate-, and high-density developed land cover classes, “Forest” is the sum of deciduous, evergreen, and mixed forest classes, and “Wetlands” is the sum of emergent herbaceous and woody wetlands. Lake depth, alkalinity, and conductivity were compiled from many sources available online at <https://lter.limnology.wisc.edu/dataset/wisconsin-lake-historical-limnological-parameters-1925-2009>; only values since 1970 were used and multiple observations were averaged. Secchi depth was estimated both in situ and via satellite (see Torbick et al. 2013 for satellite methodology) from the WDNR monitoring database (<http://dnr.wi.gov/topic/surfacewater/swims/>) and lakesat.org. When available we used Secchi depth measured in situ between July and September; when applicable, multiple observations were averaged within a year and then across years. If in situ measurements were unavailable, we used satellite-derived Secchi depth averaged first within a year and then across years for a given lake.

We incorporated a number of different variables related to lake thermal characteristics, including water temperature degree-days (DD_5 ; base temperature 5 °C, a measure of cumulative annual thermal energy; Chezick et al. 2014), various measures of optimal

thermal habitat for different life stages, and measures of suboptimal or lethal temperature conditions (Table 1). All thermal habitat characteristics were calculated from daily water temperature profiles generated for each lake using a mechanistic simulation model as described in Read et al. (2014). Briefly, this model uses downscaled climate drivers, including air temperature, wind speed and direction, and solar radiation, combined with lake size, depth, and clarity to hindcast daily, midlake thermal profiles for each lake during the ice-free season. We calculated thermal habitat metrics for each lake and each year from 1989 to 2011 and used the mean value as model inputs. Duration of ice cover was estimated empirically following methods of Shuter et al. (2013) as described in Read et al. (2014). We did not include walleye adult stock size or abundance of other fish species as predictors because they could not be forecasted, and because of lack of data representing the entire spatial (restricting number of lake-years in analysis) and temporal range of study (limiting relevance of mean values).

Prior to analysis, we identified pairs of predictors with Pearson correlations >0.8 . For correlated predictors, we removed one variable; we retained measured variables over modeled variables and otherwise retained the variable that was available for more lakes or most commonly cited as important for walleye recruitment in scientific literature. Table 1 has final list of 38 candidate predictors.

Random forest model

We used a random forest model (Breiman 2001; Cutler et al. 2007) to identify relationships between environmental predictors and walleye recruitment. Random forest models are a machine learning method based on a large number of classification trees, which use recursive partitioning of data to group observations into predefined classes (i.e., recruitment success or failure) based on binary split points in predictor variables. Predictions from all

Table 1. Environmental variables used to predict walleye recruitment success in the global model, with key references where appropriate.

Variable	Explanation	Mean (range)	Mean variable importance (SD)
Surface area	Lake surface area (ha)	386.00 (11.80–5377.00)	74.7 (2.04)
Degree-days (5)	Mean water temperature degree-days (°C·days; base temp. = 5 °C) (Chezik et al. 2014) as calculated from daily simulated surface water temperatures (Read et al. 2014)	2513.85 (2305.95–3284.68)	33.34 (0.84)
Shoreline development factor	Ratio of shoreline length to that expected if lake were a perfect circle (shoreline length/2 × (π × area) ^{0.5}) (Wetzel 2001)	2.32 (1.04–14.95)	32.59 (0.98)
Conductivity	Mean conductivity (μS·cm ⁻¹); a proxy for lake productivity or trophic status (Ryder 1965; Lester et al. 2004)	97.82 (13.4–679)	32.25 (0.77)
Major road distance	Distance (m) from nearest major road, surrogate for angling pressure (Post et al. 2008; Hunt et al. 2011); major roads were defined by ESRI (Redlands, California): http://www.arcgis.com/home/item.html?id=06e71cbbefab401fb99b6c2bb5139487	0.76 (0–10.72)	31.68 (0.79)
Height 10.6–11.2	Mean proportion of water column height between 10.6 and 11.2 °C (optimal larval walleye thermal habitat; Wismer and Christie 1987)	0.03 (0–0.09)	31.57 (0.76)
Ice-free season	Mean duration of ice-free season (days)	229.96 (214.91–293.68)	31.27 (0.72)
Peak temp.	Mean of maximum surface water temperature in each year (°C)	26.24 (23.51–31.49)	31.09 (0.81)
Post-ice-off warming rate	Mean change in surface water temperature, 30 days post-ice-off (°C·day ⁻¹) (Busch et al. 1975; Madenjian et al. 1996)	0.27 (0.11–0.35)	30.72 (0.79)
Forest	Proportion of land within 100 m buffer that is forested	0.6 (0.08–0.97)	27.35 (0.77)
Wetlands	Proportion of land within 100 m buffer that is wetlands	0.24 (0–0.84)	26.61 (0.66)
Date over 8.9	Mean Julian date at which surface temperatures ≥8.9 °C, the median temperature at which walleye spawn in northern Wisconsin (Wismer and Christie 1987)	117.62 (86.2–134.91)	26.32 (0.58)
Distance to road	Distance (m) from nearest road, surrogate for angling pressure (Post et al. 2008; Hunt et al. 2011); major roads were defined by ESRI (Redlands, California): http://www.arcgis.com/home/item.html?id=f38b87cc295541fb88513d1ed7cec9fd	9.2 (0–405.02)	26.29 (0.73)
Developed	Proportion of land within 100 m buffer that is developed	0.13 (0–0.83)	25.48 (0.85)
CV 30–60 days	Mean coefficient of variation in surface water temperature, 30–60 days post-ice-off (Serns 1982; Hansen et al. 1998)	0.15 (0.12–0.21)	24.8 (0.75)
Max. depth	Maximum depth (m)	12.96 (2.4–40.5)	23.84 (0.65)
Winter duration	Mean duration of consecutive days between 0 and 4 °C from fall of the previous year through spring (Hokanson 1977; Jones et al. 2006)	152.32 (91.05–250.22)	23.52 (0.53)
Days 10.6–11.2	Mean number of days where the temperature at any point in the water column falls between 10.6 and 11.2 °C (optimal larval walleye thermal habitat; Wismer and Christie 1987)	74.04 (3.7–193.27)	23.11 (0.73)
Longitude	Longitude (geographic coordinate system 2006 decimal degrees at centroid of waterbody)	–90.13 (–92.45–87.66)	23.11 (0.77)
CV 0–30 days	Mean coefficient of variation in surface water temperature, 30–60 days post-ice-off (Koonce et al. 1977)	0.28 (0.21–0.35)	21.7 (0.67)
Height 19–23	Mean proportion of water column height between 19 and 23 °C (walleye optimal thermal habitat of 21 ± 2 °C; Lester et al. 2004; Cline et al. 2013)	0.18 (0.01–0.29)	21.69 (0.6)
Spring days 10.5–15.5	Mean number of days in spring where surface water temperatures are between 10.5 and 15.5 °C (larval walleye incubation period; Wismer and Christie 1987)	25.71 (11–45.96)	21.68 (0.61)
Landscape position	Lake orders (Riera et al. 2000): drainage lakes are positive, headwater lakes are 0, and seepage lakes are negative	0.85 (–3–6)	21.05 (0.55)
Latitude	Latitude (geographic coordinate system 2006 decimal degrees at centroid of waterbody)	45.83 (42.52–46.79)	20.96 (0.68)
Watershed wetlands	Proportion of watershed that is wetlands	0.28 (0.01–0.52)	20.49 (0.47)
Epi-hypo ratio	Mean ratio of epilimnion to hypolimnion volume during stratified period	5.94 (0.41–49.09)	20.48 (0.54)
Secchi	Mean Secchi depth (m)	3.07 (0.31–8.21)	20.19 (0.6)
Days 19–23	Mean number of days in which the water temperature at any point in the water column falls between 19 and 23 °C (walleye optimal thermal habitat of 21 ± 2 °C; Lester et al. 2004; Cline et al. 2013)	91.18 (34.91–119.91)	19.63 (0.7)
Watershed cultivated	Proportion of HUC10 (hydrologic unit code, region 10) watershed that is cultivated crops	0.04 (0–0.69)	19.18 (0.67)
Watershed shrub–scrub	Proportion of HUC10 watershed that is shrubland	0.02 (0–0.16)	18.96 (0.64)
Watershed forest	Proportion of HUC10 watershed that is forest	0.55 (0.04–0.79)	18.26 (0.67)
Watershed pasture–hay	Proportion of watershed that is pasture or hay	0.03 (0–0.36)	17.78 (0.46)
Watershed grassland	Proportion of HUC10 watershed that is grassland	0.01 (0–0.05)	17.7 (0.69)

Table 1 (continued).

Variable	Explanation	Mean (range)	Variable importance (SD)
Watershed area	HUC10 watershed area (ha)	59 364 (1–100 783)	17.17 (0.84)
Watershed developed Days over 29	Proportion of HUC10 watershed that is developed Mean number of days where any portion of the water column temperature is greater than 29 °C (lethal temperature for walleye; Wismer and Christie 1987; Fang et al. 2004)	0.06 (0.02–0.54) 0.24 (0–14.3)	17.17 (0.69) 12.98 (0.62)
Hydrology type	Classification of water source (Nate et al. 2001)	Drainage (68%); seepage (22%); spring (6.6%); drained (2.4%)	9.27 (0.65)
Public access	Whether lake has public access (binary); surrogate for fishing pressure	No (4%); Yes (96%)	5.7 (0.64)
Depth of thermocline	Mean depth of thermocline during stratified period (m) (Schindler et al. 1996)	6.56 (0.79–14.65)	NA
Duration of stratified period	Mean duration of stratification (days) (Schindler et al. 1996)	132.74 (0.96–229.18)	NA
Date over 5	Mean Julian date at which surface temperatures > 5 °C (lowest temperature at which walleye spawning occurs in northern Wisconsin; Wismer and Christie 1987)	106.7 (75.03–114.25)	NA
Height over 29	Mean proportion of the water column where temperature is greater than 29 °C (lethal temperature for walleye; Wismer and Christie 1987; Fang et al. 2004)	0 (0–0.05)	NA
Alkalinity	Mean alkalinity (mg·L ⁻¹)	42 (2–236)	NA
Ice-off date	Mean Julian date of ice breakup (estimated empirically as described in Read et al. 2014)	105.24 (74.78–110.78)	NA
Mean July surface	Mean of mean surface water temperature in July (°C)	23.37 (21.46–27.3)	NA
Mean July–Aug.–Sept. surface	Mean of mean surface water temperature in July, August, and September (°C)	21.6 (20.29–24.48)	NA

Note: Variables are presented in order of decreasing variable importance as measured by the mean of the decrease in accuracy across 50 model runs of the global model (see text and Table 2). The first four variables were included in the final model, and the last eight variables for which variable importance = NA were excluded due to collinearity ($r \geq 0.8$) with other predictors. All variables derived from water temperature were calculated from simulated daily thermal profiles (Read et al. 2014).

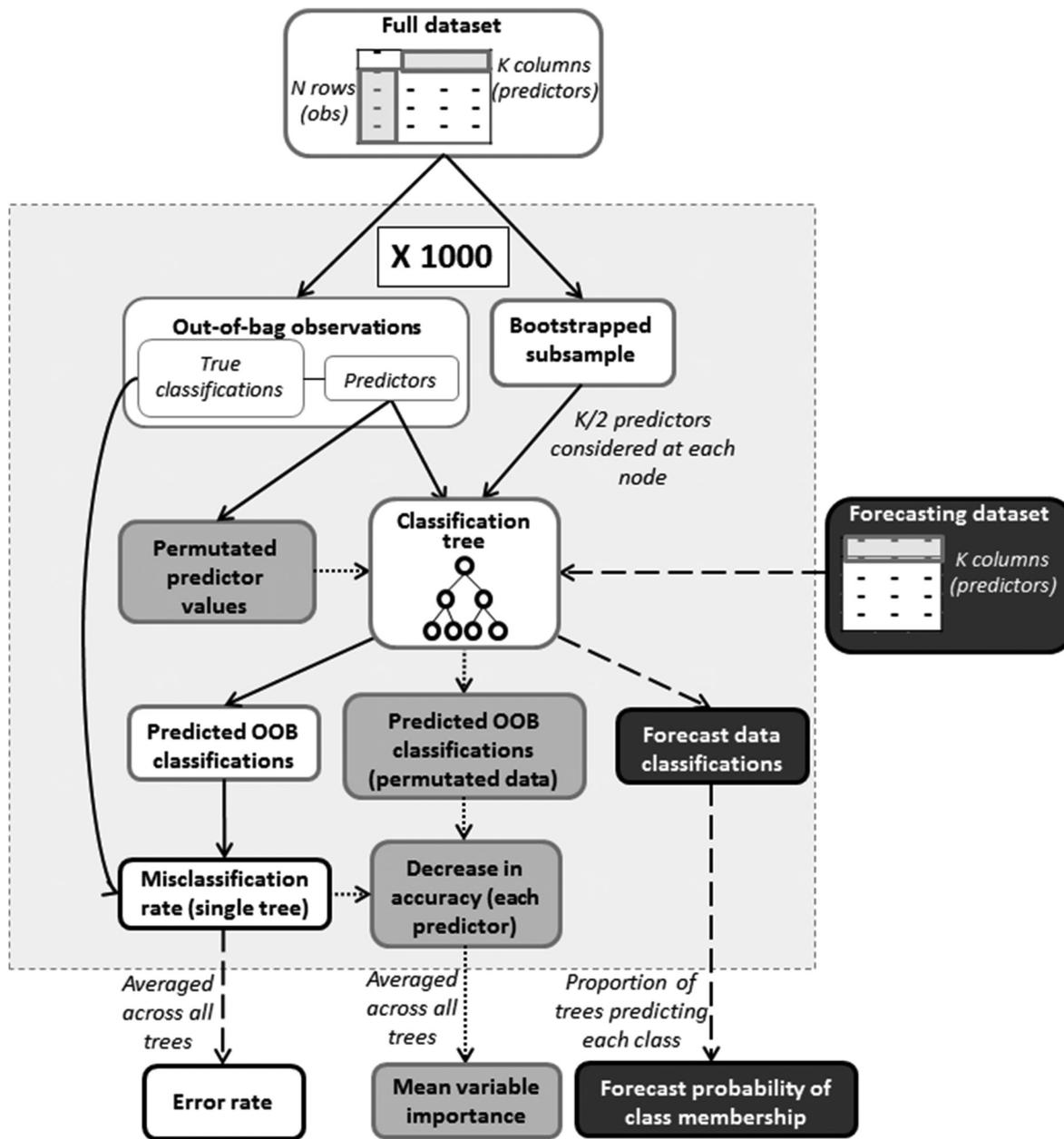
trees are combined to improve predictive accuracy and reduce the potential for overfitting. This method is well suited to our objectives because random forest models identify nonlinear relationships and interactions and are internally validated based on capacity to predict independent data and thus are accurate tools for forecasting outside the realm of data used to build the model (Breiman 2001; Cutler et al. 2007). We used the randomForest package (Liaw and Wiener 2002) in R version 3.0 (R Development Core Team 2012).

Random forest models produce several outputs relevant to our objectives, including overall model accuracy, the importance of individual predictor variables, and forecasted outcomes for independent data (Fig. 2). Models are built from a dataset in which the class of each observation is known. For each classification tree in the random forest, the tree is built using a bootstrapped subsample of the full dataset, and error rates are assessed using all data points not appearing in the bootstrapped (known as the out-of-bag (OOB) observations). The bootstrapped subsample contains the same number of observations as the original dataset, with approximately 2/3 of the unique observations appearing in each bootstrapped subsample (Cutler et al. 2007). The bootstrapped subsample is used to generate a classification tree in which only a small number of predictor variables are considered for inclusion at each split point (node) in the tree. This parameter is set by the user; we used half of the available predictors. Once the classification tree is built, predictor data from the OOB observations are passed through the tree, generating predicted classifications for each observation in the OOB dataset. These predictions are compared with the true classification of the OOB data to generate a misclassification rate for the tree, and this process is repeated to generate a large number of trees (we used 1000). Misclassification rates of individual trees are averaged across all trees to produce an overall model error rate. Random forest models also measure variable importance directly in terms of predictive accuracy. For each tree, each predictor value is randomly permuted and then passed through the tree to generate predictions based on permuted data. The mean difference between the misclassification rate of the data with the scrambled variable and that of the true data, divided by the standard error, is the mean percent decrease in accuracy for each variable (Cutler et al. 2007). When forecasting outcomes for independent data, random forest models predict class membership for each observation in the independent dataset for each of the 1000 trees. The proportion of all trees classifying each observation in a given class (e.g., successful recruitment) represents the probability of each observation belonging to that class.

We used the stratification feature of the randomForest package (Liaw and Wiener 2002) to avoid pseudoreplication (Pecl et al. 2011). Because we had multiple years of data for our response variable (recruitment success) in many lakes but our predictors were constant for each lake, we stratified bootstrapped samples by lake. This stratification means that for each tree a maximum of one observation from each lake in the dataset was used for tree construction. Users can also specify the size of the “terminal nodes”: the minimum number of observations that must be present in the final endpoints of each classification tree after which no further split points are investigated. We set this value to five, which in combination with the stratified data selection ensured that observations from at least five unique lakes were included in each terminal node, thereby reducing the possibility of overfitting and increasing the predictive capacity of our model when applied to new data.

We used a model selection procedure to achieve a balance between predictive accuracy and model interpretability and to minimize the inclusion of spurious variables (Diaz-Uriarte and De Andres 2006). We first generated a set of 50 random forest models using all noncorrelated predictor variables — we refer to models including all predictors as the global model. Multiple random forest models were used to increase stability of results. We ranked predictors

Fig. 2. Conceptual model illustrating how random forest models assess model error rate (white boxes, solid lines), assess variable importance of individual predictors (medium grey boxes, dotted lines), and forecast outcomes for independent datasets (dark grey boxes, dashed lines). Compartments outside light grey box are inputs to and outputs of the model. See text for full description of the modeling process.



from this global model in order of decreasing variable importance based on the mean of the mean decrease in accuracy value across the 50 models (Table 1). We then built subsequent sets of random forests ($N = 50$ for each model), dropping the least important 20% of predictors for each subsequent model. We did not recalculate variable importance each time, because this can lead to overfitting (Díaz-Uriarte and De Andres 2006). For each reduced model, we calculated the mean model misclassification rate (proportion of the OOB samples that were misclassified, p) across the 50 random forests. We calculated the standard error of this misclassification rate (SE_p) as $SE_p = \sqrt{p \times (1 - p) \times \left(\frac{1}{N}\right)}$, where N = the number of recruitment observations. Models with overall misclassification rates within 1 SE_p of the minimum misclassification rate of all candidate models were considered comparable (Díaz-Uriarte and

De Andres 2006). We used the simplest model (that with the lowest number of predictors) meeting these criteria as our final model.

The relationship between predictor and response variables in random forest models can take any form. Partial dependence plots are frequently used to visualize these relationships (Hastie et al. 2001; Cutler et al. 2007). Partial dependence plots isolate the influence of individual predictor variables by fixing the variable of interest to a set value, predicting outcomes for all possible combinations of the other variables in the model, and averaging the predicted response. This process is repeated across the entire range of values for the predictor variable of interest. In addition, we visualized the interactive effects of combinations of two variables using a similar process whereby we generated model predictions for the entire range of values of one variable while setting a

Table 2. Candidate models generated by sequentially dropping the least important 20% of predictor variables from the global model (Model 1) at each step.

Model	No. of predictors	Overall misclassification rate	“Success” misclassification rate	“Failure” misclassification rate
1	38	0.200	0.176	0.226
2	30	0.200	0.176	0.225
3	24	0.200	0.173	0.228
4	19	0.200	0.173	0.229
5	16	0.200	0.174	0.226
6	12	0.198	0.174	0.224
7	10	0.199	0.173	0.225
8	8	0.204	0.176	0.233
9	6	0.198	0.170	0.226
10	5	0.194	0.168	0.221
11	4	0.192	0.164	0.222
12	3	0.209	0.211	0.207
13	2	0.207	0.208	0.207

Note: Overall misclassification rates were used for model selection, and class-specific misclassification rates in predicting recruitment success and failure rates are also shown. The final selected model (Model 11, shown in bold) is the simplest model with an overall misclassification rate within 1 standard error (0.008) of the minimum observed misclassification rate. The four variables included in the selected model are lake area, water temperature degree-days, shoreline development factor, and conductivity.

second variable of interest to a small number of fixed values and fixing the other variables in the model.

Case study application: forecasting probability of recruitment success for stocking prioritization

Under the WWSI, WDNR fisheries managers requested walleye stocking in 343 inland lakes in which natural reproduction was insufficient to support a walleye fishery. These requests were classified as either “restoration”, meaning stocking was intended to restore populations that had previously supported natural reproduction but experienced recent declines in recruitment success, or “maintenance”, meaning no natural reproduction was expected and any walleye fishery would be solely supported by stocking. These nominations occurred independently from this analysis and were based on the subjective judgment of WDNR biologists. We used the final predictive model of walleye recruitment success to forecast the probability of successful natural recruitment in locations nominated for stocking, with a specific focus on systems in which the stated objective was restoration. We assumed that restoration would be most valuable in locations where the predicted probability of recruitment success was high but the actual current recruitment success was low. The output of the predictive model was the probability of successful recruitment in each lake, where the probability represents the proportion of the 1000 classification trees that classified a lake as having successful recruitment.

Results

The global model of walleye recruitment using all 38 potential predictor variables classified recruitment with a misclassification rate of 20.0% (Table 2). The most accurate model misclassified recruitment in 19.2% of cases ($SE_p = 0.008$) and was more accurate in predicting successful recruitment (16.4% misclassification rate) than in predicting failed recruitment (22.2% misclassification rate). Models containing 4–38 predictors were comparable in their predictive accuracy (overall misclassification rate within 1 SE_p of the minimum error rate). The final selected model (the simplest model with an overall misclassification rate within 1 SE_p of the minimum error rate of all candidate models) was also the most accurate model (Table 2). The final model included four predictor

variables: lake area, water temperature degree-days, shoreline development factor, and conductivity (Table 2). Final sample size after removing observations with missing data was 2710 from 508 lakes.

Lake surface area was the most important predictor of walleye recruitment in the final model (Table 1). On average, the probability of successful walleye recruitment increased with increasing lake size and plateaued around 50% for lakes greater than approximately 225 ha (Fig. 3). Walleye recruitment was also influenced by DD_5 ; on average, recruitment was more likely in lakes with lower DD_5 than in lakes with higher DD_5 . The relationship between conductivity (a proxy for productivity) and recruitment was hump-shaped, with the highest probability of recruitment in lakes where conductivity was approximately $50 \mu\text{S}\cdot\text{cm}^{-1}$ and declining probability of recruitment either above or below this value. Walleye recruitment was predicted more accurately when SDF was included in the model, although the effect of SDF on recruitment was relatively flat when averaged across all values of other variables (Fig. 3), indicating that the effect of SDF on recruitment success depends on the value of other predictors.

The four predictor variables interact to predict walleye recruitment in ways that are not immediately obvious based on single variable partial plots shown in Fig. 3. For example, the effect of DD_5 varied with lake size; in fact, the effect of DD_5 was only evident in small lakes (e.g., 100 ha) where recruitment was most likely when DD_5 were low (Fig. 4). In larger lakes (e.g., 1000 ha), the effect of DD_5 was negligible, with the probability of recruitment predicted to be approximately equal in lakes spanning the range of observed DD_5 .

Probability of recruitment was predicted to be low (<0.25) in the majority of systems nominated for stocking under the WWSI (Fig. 5). Lakes proposed for restoration stocking were twice as likely to be predicted by our model to produce successful walleye recruitment as those proposed for maintenance stocking (mean \pm SD probability success of $.20 \pm .20$ and $.10 \pm .16$, respectively).

Discussion

Predictive model of walleye recruitment

We predicted the presence or absence of walleye recruitment in over 500 Wisconsin lakes over the course of three decades with greater than 80% accuracy using lake-specific, constant predictors related to morphometry, productivity, and thermal habitat. Statistical models of recruitment have historically performed poorly when confronted with new, independent datasets (Myers 1998). Because we eliminated collinear predictors and used random forest modeling to validate model predictions, our model was able to predict recruitment accurately on independent datasets, and the model was used by managers to forecast recruitment probability and prioritize stocking efforts in hundreds of Wisconsin lakes.

Although our model performed well and was useful for management decisions, our focus was on successful recruitment to age 0 rather than recruitment to the walleye fishery. In Ceded Territory lakes, age-0 walleye density explains ~40% of variability in the density of age-4 walleye (Hansen et al. 2012). Although our model accuracies are not directly comparable because we used different measures of recruitment success, the accuracy of our model will certainly be less than 80% in predicting recruitment to the walleye fishery. Our approach also ignores variability in recruitment above or below our threshold of success; successful recruitment ranged from our threshold of 6.2 age-0 walleye-km⁻¹ to a maximum of 326.5 age-0 walleye-km⁻¹. This variation is certainly affected by time-varying and (or) biotic factors that were not included in this analysis, such as the abundance of other fish species or age groups of walleye. We did not consider walleye spawning stock or adult walleye population estimate as a predictor in our model because our goal was to forecast recruitment for a large number of lakes, most of which lack an adult population

Fig. 3. Partial dependence plots showing predicted probability of walleye recruitment success across the entire range of each of the four predictor variables included in the final model: (A) lake surface area; (B) degree-days; (C) shoreline development factor; (D) conductivity. Partial dependence plots isolate the influence of individual predictor variables by fixing the variable of interest to a set value, predicting outcomes for all possible combinations of the other variables in the model, and averaging the predicted response. This process is repeated across the entire range of values for the predictor variable of interest.

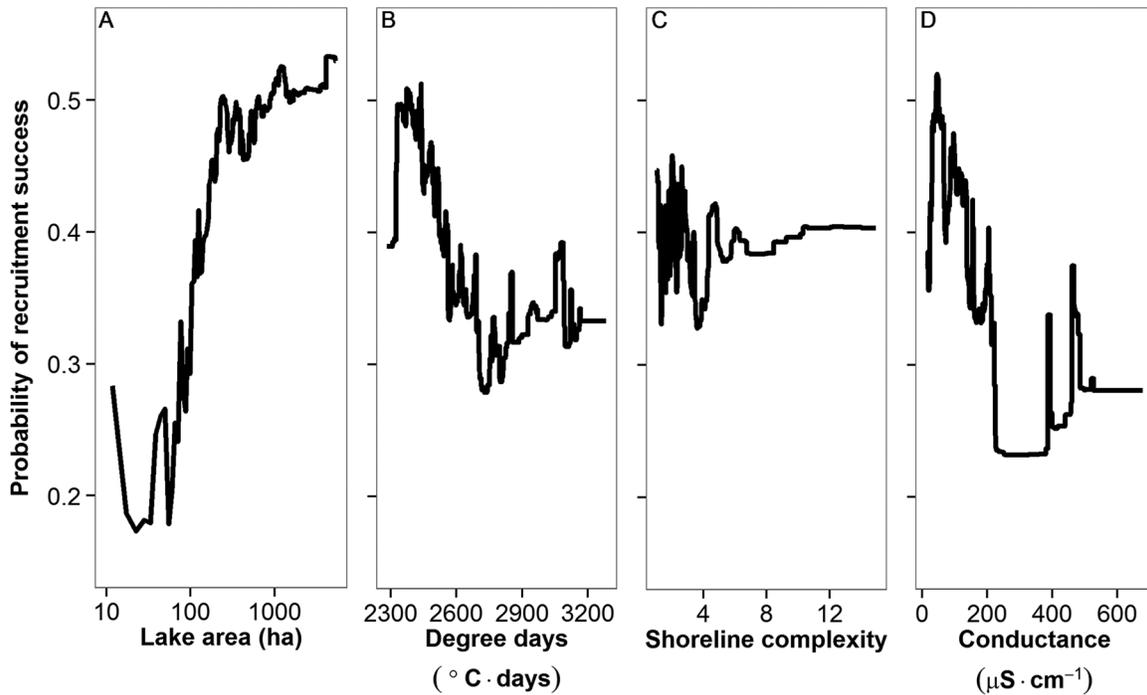


Fig. 4. Predicted probability of walleye recruitment success as a function of degree-days (DD_5) in large (1000 ha; grey line) and small (100 ha; black line) lakes, illustrating that the effect of DD_5 shown in Fig. 3 operates primarily on small lakes. Predictions are contingent upon values of other predictors, which were set to values expected to maximize the probability of recruitment success (conductivity = $59 \mu\text{S}\cdot\text{cm}^{-1}$, shoreline development factor (SDF) = 1.9).

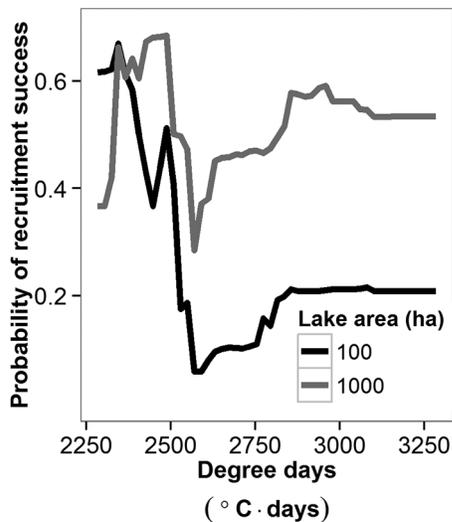
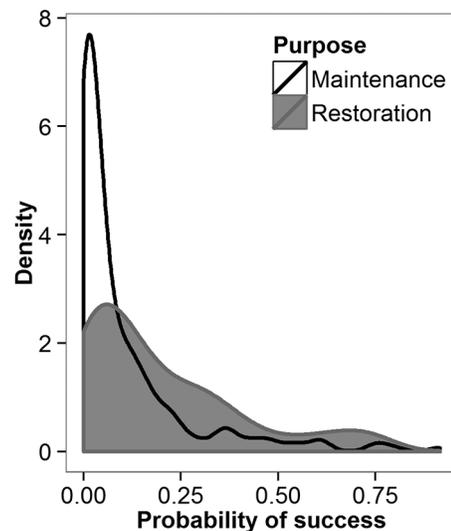


Fig. 5. Probability density of recruitment success in lakes nominated for stocking under the Wisconsin Walleye Stocking Initiative. Shading corresponds to stated stocking objective when lakes were nominated (independent of this analysis), where “Maintenance” stocking (black outline, no fill) is intended for lakes in which managers expect no natural reproduction, and “Restoration” stocking (grey outline and fill) is intended for lakes where natural reproduction is likely.



estimate. Furthermore, environmental factors have greater explanatory power than stock size for recruitment of many fish species (Szuwalski et al. 2014), including walleye (e.g., Koonce et al. 1977; Beard et al. 2003). Forecasting temporal variability is likely to continue to be a challenge because factors influencing year to year variability in recruitment are themselves highly vari-

able and difficult to forecast (Walters and Collie 1988). Our accuracy in predicting recruitment in the absence of time-varying predictors suggests that walleye recruitment to age 0 in Wisconsin lakes is regulated in large part by density-independent, abiotic factors as is the case for fish communities in general when exam-

ined on broad spatial scales (Barbour and Brown 1974; Johnson et al. 1977; Jackson et al. 2001).

Random forest models are excellent for forecasting recruitment from environmental data because of their ability to deal with large datasets with high numbers of potential predictors, identify nonlinear relationships and interactions, and predict accurately when validated using independent data (Cutler et al. 2007; Crisci et al. 2012). Random forest models have been used in a variety of contexts in aquatic ecology, including predicting lake trophic status from landscape variables (Catherine et al. 2010; Cross and Jacobson 2013), identifying habitat requirements of aquatic species (e.g., Hegeman et al. 2014), and projecting the impacts of climate change on fish communities (e.g., Comte et al. 2013). However, we are unaware of any other study using random forest to forecast recruitment of sport fishes. Given the high value placed on prediction of recruitment for managed fisheries (Houde 2008; Ludsins et al. 2014), random forest modeling may prove to be a useful method for predicting recruitment and identifying relationships between recruitment and environmental variables while avoiding some of the pitfalls of previous environment–recruitment relationships (Walters and Collie 1988; Myers 1998).

Case study application: forecasting probability of recruitment success for stocking prioritization

The predictive model of walleye recruitment developed here was immediately useful to fisheries managers in Wisconsin tasked with prioritizing hundreds of lakes for stocking under the WWSI. The predicted probability of recruitment generated from our model was used as one of several criteria for assigning scores to lakes. This scoring scheme prioritized restoration stocking in locations where the probability of natural recruitment was high, but where recruitment was declining or absent in the previous decade. Other lakes were stocked with no expectation of natural reproduction (maintenance lakes), and not surprisingly, these lakes were on average predicted to have a lower probability of natural recruitment (Fig. 5). Although these systems may support successful put-grow–take fisheries, survival of stocked fish is likely to be low (Kampa and Hatzenbeler 2009). Identifying lake characteristics associated with stocking success will be critical for allocating resources appropriately to these lakes to ensure a benefit to the fishery (Sutton et al. 2012). Work is ongoing to test the predictions of the recruitment model as applied to WWSI stocking by monitoring recruitment success and survival to fishable size (381 mm) for a large number of lakes over the next decade. Lakes with high probability of recruitment success are also targets of future research examining the mechanisms behind recruitment failures, including food web interactions and habitat alteration. By evaluating the predictions of our model and refining predictions into the future, we hope to continue to improve the allocation of limited management resources by providing tools that allow managers to prioritize stocking in locations where objectives are most likely to be achieved.

Environmental predictors of walleye recruitment success

By a large margin, the most important predictor of walleye recruitment was lake surface area (Table 1), with lakes over approximately 225 ha predicted to have the highest probability of successful recruitment (Fig. 3A). Lake area influences the availability of critical habitat (Johnson et al. 1977; Jackson et al. 2001) and influences fish production (Ryder 1965) and walleye yield (Lester et al. 2004). Lake area also affects the diversity of prey species (Barbour and Brown 1974; Tonn and Magnuson 1982; Rahel 1986). Lower availability of alternative prey in small lakes could reduce recruitment success because of increased predation on age-0 walleye by piscivores, including cannibalism by adult walleye (Forney 1976; Rudstam et al. 1996). Furthermore, larval walleye rely on

sufficient pelagic zooplankton resources when they switch from endogenous to exogenous feeding (Li and Mathias 1982; McDonnell and Roth 2014), and lower zooplankton density and richness in small lakes (Patalas 1971) as well as lower volume of pelagic habitat (Vadeboncoeur et al. 2008) could decrease the foraging success and survival of larval walleye during this critical period.

Lake surface area also influences the relationship between DD_5 and walleye recruitment. Recruitment in large lakes (e.g., 1000 ha) was relatively unaffected by DD_5 , while recruitment success in small lakes (e.g., 100 ha) was predicted to be greater than 50% only at low DD_5 values (Fig. 4). Higher DD_5 increase growth rates of walleye across broad spatial scales (Venturelli et al. 2010), which should increase survival by reducing vulnerability to predation and environmental extremes and reducing the duration of the zooplanktivorous stage (Miller et al. 1988; Sogard 1997; Galarowicz et al. 2006). Therefore, higher DD_5 would be expected to increase recruitment success, provided that temperatures do not exceed thermal tolerances (as is the case here). However, fish growth is a function of both temperature and food availability (Paloheimo and Dickie 1966; Kitchell et al. 1974; Johnston 1999), and the faster growth rates of young walleye associated with higher DD_5 will only be possible if sufficient prey resources are present. It is possible that age-0 walleye in small lakes lacking sufficient zooplankton prey are unable to meet the increased metabolic demands associated with longer growing seasons and higher temperatures and as a result suffer recruitment failures at higher values of DD_5 . As DD_5 increase throughout the range of walleye under climate change, understanding the mechanism linking lower DD_5 to higher recruitment success in small lakes should be a research priority.

The effect of SDF on walleye recruitment was not obvious when averaged across all levels of the other predictors (Fig. 3), indicating that SDF interacts with other variables to affect walleye recruitment. Examination of individual classification trees in our random forest model showed that SDF was generally positively related to recruitment success in large lakes (data not shown). Higher SDF values may be a proxy for walleye habitat; many of the large, highly complex lakes in Wisconsin are stained impoundments of river systems containing habitat characteristics known to be preferred by walleye (Kitchell et al. 1977).

Finally, conductivity in our model served as a proxy for lake productivity, and we observed a hump-shaped relationship between conductivity and walleye recruitment. Specifically, conductivity positively affected recruitment probability when conductivity was low ($<50 \mu\text{S}\cdot\text{cm}^{-1}$), but negatively affected recruitment probability at conductivity values $>50 \mu\text{S}\cdot\text{cm}^{-1}$. In contrast, both Ryder (1965) and Lester et al. (2004) reported positive relationships between lake productivity (measured using total dissolved solids) and fish production or walleye yield, respectively. However, our study encompassed a much greater range of lake productivities than either previous study, suggesting that the relationship between lake productivity and walleye production may in fact be nonlinear, with declining walleye production at very high conductivity or total dissolved solids.

Understanding the mechanisms driving recruitment success of fish populations is hindered by high variability, nonlinear interactions between recruitment and environmental drivers, and indirect or sublethal effects of both biotic and abiotic variables (Rose 2000). Mechanistic models to predict recruitment have been developed for marine and large freshwater (i.e., Great Lakes) systems (e.g., Houde 2008; Zhao et al. 2009; Ludsins et al. 2014), but the applicability of such models to predicting recruitment across a landscape of small, spatially discrete populations has not been tested. In the end, correlative statistical analyses are unlikely to elucidate mechanism in a process as highly variable and complex as recruitment, because nearly any statistically significant result

can be framed in a biological basis a posteriori (Walters and Collie 1988). However, the value of such correlative approaches is in their ability to predict future outcomes to guide management, even in the absence of an understanding of mechanism (Rigler 1982; Peters 1991). The critical test for correlative analyses is the ability to predict data not used to build the model (Power 1993; Myers 1998; Guthery et al. 2005). Our approach to predicting walleye recruitment success withstood this test, and our final model predicted recruitment with over 80% accuracy. Our model suggest relationships between walleye recruitment and environmental predictors that are robust to the addition of new data and can provide guidance for future studies explicitly designed to understand mechanisms behind recruitment variation. For example, assessing prey abundance in small lakes across the observed gradient of DD_5 may shed insight into the interactions between DD_5 and lake surface area observed in our model.

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