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ARTICLE

Walleye recruitment success is less resilient to warming water temperatures in lakes with abundant largemouth bass populations

Gretchen J.A. Hansen, Stephen R. Midway, and Tyler Wagner

Abstract: Lakes respond heterogeneously to climate, with implications for fisheries management. We analyzed walleye (*Sander vitreus*) recruitment to age-0 in 359 lakes in Wisconsin, USA, to (*i*) quantify the relationship between annual water temperature degree days (DD) and walleye recruitment success and (*ii*) identify the influence of lake characteristics — area, conductivity, largemouth bass (*Micropterus salmoides*) catch rates, and mean DD — on this relationship. The relationship between walleye recruitment and annual DD varied among lakes and was not distinguishable from zero overall (posterior mean = –0.11, 90% CI = –0.34, 0.15). DD effects on recruitment were negative in 198 lakes (55%) and positive in 161 (45%). The effect of annual DD was most negative in lakes with high largemouth bass densities, and, on average, the probability of recruitment was highest in large lakes with low largemouth bass densities. Conductivity and mean DD influenced neither recruitment nor the effect of annual DD. Walleye recruitment was most resilient to warming in lakes with few largemouth bass, suggesting that the effects of climate change depend on lake-specific food-web and habitat contexts.

Résumé : Les lacs ne réagissent pas au climat de manière uniforme, ce qui a des conséquences sur la gestion des pêches. Nous avons analysé le recrutement de dorés jaunes (*Sander vitreus*) de moins de 1 an dans 359 lacs du Wisconsin (États-Unis) pour (*i*) quantifier la relation entre les degrés-jours (DJ) annuels de température de l'eau et le succès du recrutement de dorés jaunes et (*ii*) cerner l'influence des caractéristiques du lac — superficie, conductivité, taux de prise d'achigans à grande bouche (*Micropterus salmoides*) et DJ moyens — sur cette relation. La relation entre le recrutement de dorés jaunes et les DJ annuels varie selon le lac et, en général, s'assimile à zéro (moyenne postérieure = –0,11, IC 90 % = –0,34, 0,15). Les effets des DJ sur le recrutement étaient négatifs dans 198 lacs (55 %) et positifs dans 161 lacs (45 %). L'effet des DJ annuels était le plus négatif dans les lacs à forte densité d'achigans à grande bouche et, en moyenne, la probabilité de recrutement était la plus élevée dans les lacs à faible densité d'achigans à grande bouche. La conductivité et les DJ moyens n'exerçaient pas d'influence sur le recrutement ni sur l'effet des DJ annuels. Le recrutement de dorés jaunes présentait la plus forte résilience au réchauffement dans les lacs avec peu d'achigans à grande bouche, ce qui semble indiquer que les effets des changements climatiques dépendent des contextes trophiques et d'habitats propres au lac. [Traduit par la Rédaction]

Introduction

Understanding how lakes respond to natural and anthropogenic environmental change is critical to the ecological and economic management of lacustrine resources. (Woodward et al. 2010; Carpenter et al. 2011). Both lakes and fish integrate environmental conditions across multiple spatial and temporal scales (e.g., Adrian et al. 2009; Schindler 2009; Williamson et al. 2009), and fish, in particular, can serve as indicators of ecological stressors on aquatic systems (Fausch et al. 1990; Minns et al. 1994; Drake and Pereira 2002). Long-term temporal trends have recently been documented in the relative abundance of lake fishes throughout the American upper Midwest (Bethke and Staples 2015; Hansen et al. 2015*b*). These studies have demonstrated large-scale regional declines in several economically and ecologically important species, while also identifying variability in trends even among neighboring lakes subject to similar environmental conditions. Although hypotheses abound, the drivers of temporal trends in fish abundance in these lakes have not been identified.

Temperature is a critical environmental driver for poikilotherms such as fish, and is correlated with the presence of numerous fish species at broad spatial scales (e.g., Tonn 1990; Wehrly et al. 2012). Projected warming air temperatures associated with climate change are predicted to influence cool- and cold-water fish species negatively, while affecting warmwater species positively (e.g., Chu et al. 2005; Sharma et al. 2007; Hein et al. 2012; Van Zuiden et al. 2016). However, documented effects of contemporary climate change on inland fish populations are relatively scarce (Lynch et al. 2016). Furthermore, lake temperatures respond heterogeneously to climate depending on lake size, depth, clarity, and sheltering from wind (Read et al. 2014; O'Reilly et al. 2015; Rose et al. 2016). Thus, certain lakes may be resilient to increased air temperatures associated with climate change, and may provide refugia for cool- and cold-water species even as regional air temperatures increase.

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Walleye (*Sander vitreus*) is an economically and ecologically important coolwater fish species throughout North America, the abundance of which has declined in inland lakes across Wisconsin (Hansen et al. 2015*b*). Population declines have been linked to widespread failures in walleye recruitment, as measured by the relative abundance of walleye in the fall of their first year (Hansen et al. 2015*b*). In response to walleye declines, the state of Wisconsin invested over US$12M in 2013 to expand the production capacity of extended-growth walleye fingerlings in state hatcheries and to increase walleye stocking in hundreds of its lakes (Wisconsin State Legislature 2013).

Climate change may play a role in declining walleye recruitment in Wisconsin lakes, although previous studies have shown contrasting effects of temperature on lacustrine walleye populations. The likelihood of walleye recruitment success in Wisconsin lakes is lower in warm lakes than in cool ones (as indexed by water temperature degree days, or DD); Hansen et al. 2015*a*, 2017). Furthermore, high variability in spring water temperatures is associated with walleye recruitment failure in Escanaba Lake, Wisconsin (Serns 1982*a*, 1982*b*; Hansen et al. 1998) and elsewhere (Kallemeyn 1987). However, lake-averaged variability in spring water temperatures was not an important predictor of walleye recruitment success in hundreds of other Wisconsin lakes at a broader spatial scale (Hansen et al. 2015*a*). In other studies, walleye populations were positively correlated with temperature. For example, walleye year-class strength in Minnesota's nine largest walleye lakes was highest in years with warm June air temperatures from 1979 to 1997 (Shupp 2002), and recruitment in 162 Wisconsin lakes varied synchronously, suggesting that warmer years led to higher year-class strength (Beard et al. 2003).

Contrasting effects of temperature on walleye suggest that lake-specific factors may influence walleye populations and their response to warming. For instance, lake size is strongly related to walleye recruitment success (Nate et al. 2000), and the negative effect of water temperature DD on walleye recruitment success in Wisconsin does not appear to operate in large lakes (Hansen et al. 2015*a*). Lake productivity also plays a role in walleye habitat suitability. (Ryder 1977; Lester et al. 2004), and could influence the effects of temperature. Temperature may also affect walleye indirectly through biotic interactions. For example, largemouth bass (*Micropterus salmoides*) population densities have increased concurrently with walleye recruitment declines (Hansen et al. 2015*c*), leading some to hypothesize that largemouth bass predation is directly impeding walleye recruitment. Empirical diet studies, however, have provided only mixed support for this hypothesis. In a recent diet study, only one walleye was observed in nearly 1000 largemouth bass diets from four lakes over 2 years (Kelling et al. 2016), while other studies have found low but potentially biologically important predation of largemouth bass on walleye (Fayram et al. 2005; Freedman et al. 2012). Context-dependent effects, such as those of temperature on walleye, are indicative of cross-scale interactions, where the effects of an environmental driver operating on one spatial or temporal scale depend on other drivers operating at different scales (Soranno et al. 2014). Such interactions can be understood using hierarchical models (Wagner et al. 2016).

Here, we evaluate the influence of water temperature on annual walleye recruitment success in Wisconsin lakes. Our objectives were to (*i*) quantify lake-specific effects of annual water temperature on walleye recruitment success; (*ii*) identify how lake characteristics — specifically largemouth bass relative abundance, lake area, conductivity, and average water temperature — influence the relationship between annual water temperature and recruitment; (*iii*) quantify the expected change in lake-specific recruitment probability, given increases in water temperature from the early 1980s to the 2010s.

Methods

Walleye data

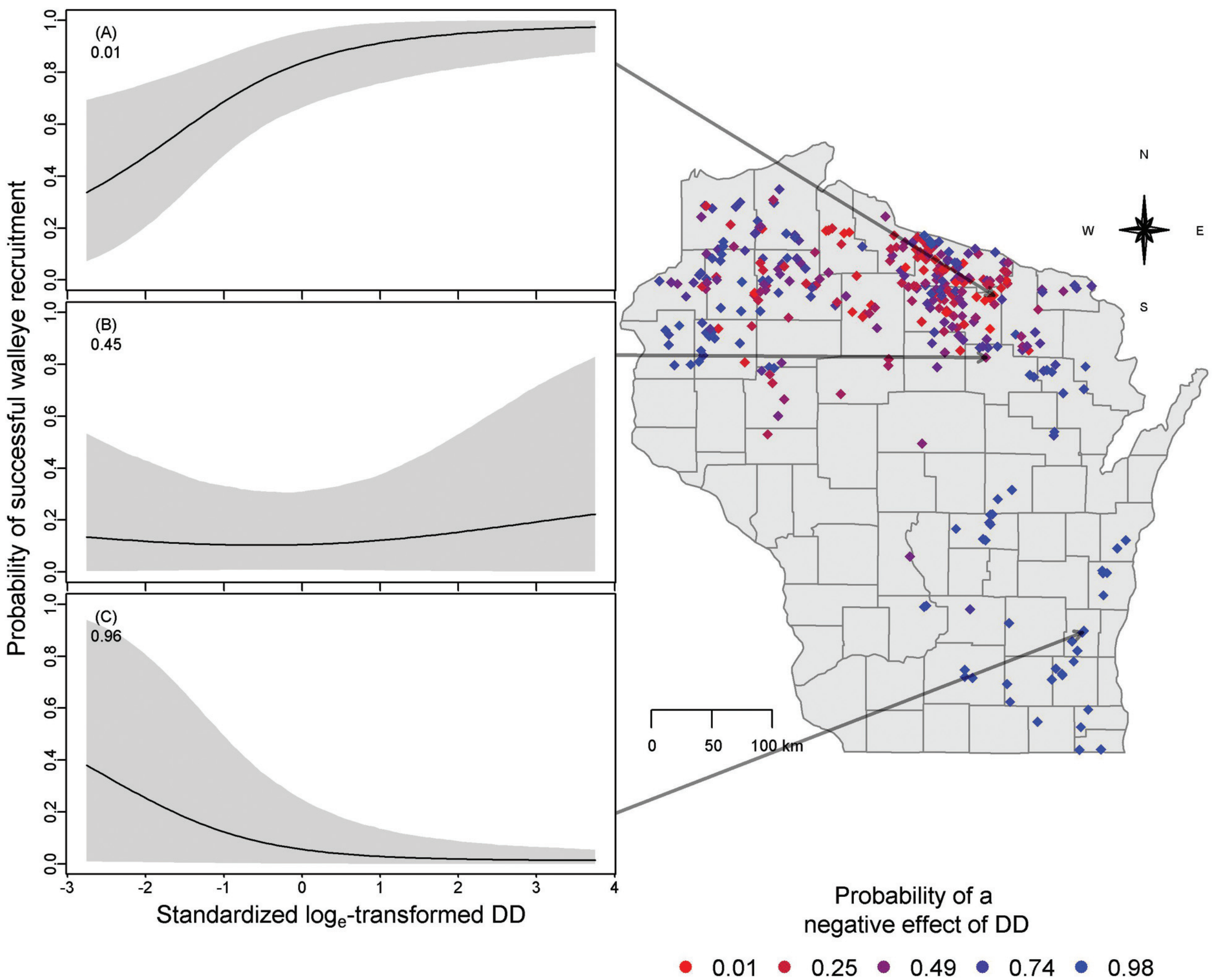
Fish data were collected by the Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) as a part of their standardized monitoring protocols (Serns 1982*a*; Hansen et al. 2004). Age-0 walleyes were collected annually each fall when water temperatures were between 10 and 21 °C using nighttime boat electrofishing (230 V AC). Recruitment was indexed as the number of naturally reproduced (i.e., not stocked) age-0 walleye collected per kilometre (km) of shoreline sampled. Age-0 walleye were identified either by length-frequency analysis or verified from scale annuli following WDNR protocols (Serns 1982*a*; Hansen et al. 2004). We used surveys conducted between 1980 and 2014 but excluded those from lake-years where age-0 walleye were stocked prior to that year's survey. To ensure that effort was sufficient for indexing whole-lake relative abundances of age-0 walleye, we restricted our analysis to surveys where at least 70% or 16.1 km of shoreline was sampled per WDNR protocols. We excluded surveys in which water temperatures were <10 °C or >21 °C (following WDNR protocols) and those in which survey reliability was low owing to adverse conditions identified by the survey operator. Our final analysis was based on 2061 records of walleye recruitment from 359 lakes (Fig. 1).

We converted age-0 walleye catch rates into a qualitative measure representing successful or failed recruitment for that lake-year. Based on Hansen et al. (2015*a*), walleye recruitment was classified as successful if age-0 catch rates in fall electrofishing surveys were greater than 6.2 fish·km^{-1} (10·mile^{-1}). This threshold is used by WDNR managers to distinguish between successful and failed walleye year classes. Recruitment was modeled as a binary response variable using hierarchical logistic regression as described below.

Predictor data

We quantified the response of annual walleye recruitment success to two annually varying water temperature variables previously found to correlate with walleye recruitment success in Wisconsin lakes: DD (Hansen et al. 2015*a*, 2017) and variability of spring water temperatures (Serns 1982*a*, 1982*b*; Kallemeyn 1987; Hansen et al. 1998). Daily water temperature profiles for calculating both temperature metrics were obtained from a thermodynamic simulation model of ~5200 Wisconsin lakes (Read et al. 2014; Winslow et al. 2017). This model uses daily, dynamically downscaled historical weather data and lake characteristics including riparian tree height, average water clarity, and maximum lake depth to simulate daily water temperature profiles from 1980 to 2015. Water temperature DD were quantified using surface water temperature DD with a 5 °C base (Chezik et al. 2014). DD, a measure of cumulative heat for the entire growing season, have been used to explain variability in growth and life history for a variety of fishes, including walleye (e.g., Venturelli et al. 2010; Chezik et al. 2014; Lester et al. 2014). We used DD to index water temperature on the basis of a recent analysis identifying DD as the best thermal predictor of walleye recruitment out of 15 possible temperature metrics (Hansen et al. 2015*a*). Annual, lake-specific estimates of water temperature DD were calculated from modeled surface water temperatures, and these year-specific DD estimates were related to annual measures of walleye recruitment success as described below. Annual variability in springtime water temperatures was calculated as the coefficient of variation in modeled surface-water temperatures from 30–60 days post-ice-off for each lake-year. We used variability tied to ice-off date rather than a set calendar period, as walleye spawning is triggered by ice off (Becker 1983; Schneider et al. 2010), and variable temperatures are thought to influence the survival of posthatch larval walleye rather than eggs (Hansen et al. 1998).

Fig. 1. Map of Wisconsin showing the locations of the 359 lakes with walleye recruitment data for which we developed a hierarchical logistic regression model to predict the probability of successful walleye recruitment as a function of annual water temperature degree days (DD). Points are coloured by the probability that the effect of DD on walleye recruitment is negative. The three panels show example lakes exemplifying positive (A), uncertain (B), and negative (C) relationships observed between walleye recruitment success and DD. The 90% credible region for the relationship between DD and the probability of a negative effect of DD on recruitment is also shown for each panel. The Wisconsin map was created using the "maps" package in R (Brownrigg 2016).



We evaluated the influence of four lake-level covariates on the relationship between annual water temperature and walleye recruitment success. Mean water temperature DD for each lake from 1980–2014 were used as a measure of average lake temperature. Therefore, DD entered the model at two levels (Table 1): annual DD (calculated for each lake-year and used to model lake-specific effects on annual recruitment success), and mean DD (calculated for each lake and used to model variability in lake-specific slopes and intercepts as described below).

Largemouth bass relative abundance was indexed from 1995 to 2014 using catch per kilometre of largemouth bass over 20.3 cm (8 inches) collected in fall surveys using a 230 V AC electrofishing boat. In some historical surveys, time was recorded as the measure of survey effort instead of distance shocked. In these cases, hours were converted to km based on the empirical relationship observed in historical data ($\text{Effort}_{\text{km}} = 3.274 \cdot \text{Effort}_{\text{hours}} + 0.071$, $R^2 = 0.84$, $p < 0.0001$, $N = 9043$; J.F. Hansen, WDNR, personal communication). We excluded surveys in which water temperatures were <10 °C or >21 °C (following WDNR protocols), or in which survey reliability was low because of adverse conditions identified by the survey operator. Lake-specific mean largemouth bass catch per effort was used because annual estimates of largemouth bass catch per effort were not available for most lakes (median years sampled for largemouth bass = 2, range = 1–14).

Lake area (ha) and conductivity ($\mu S \cdot cm^{-1}$) influence walleye recruitment success (Hansen et al. 2015*a*), and were included as lake-level predictors to evaluate whether they influenced temperature effects on walleye recruitment. Multiple studies have documented the positive correlation between lake area and walleye production or recruitment, although the mechanism of this effect is unknown (Ryder 1965; Nate et al. 2000; Hansen et al. 2015*a*). Conductivity served as a surrogate for water quality (USEPA 2003) or lake productivity, also known to influence walleye populations (with intermediate productivity values associated with the highest levels of walleye production; Ryder 1965; Lester et al. 2004). Conductivity data were more widely available than other surrogate metrics of lake productivity. Mean conductivity for each lake was calculated using data from WDNR water quality surveys conducted between 1970 and 2014 (archived in the surface water integrated monitoring system SWIMS; http://dnr.wi.gov/topic/surfacewater/swims/). Information on distributions of predictor variables can be found in Table 1. All covariates were log$_e$-transformed and standardized (mean = 0, SD = 1) prior to analysis.

Table 1. Predictor variables used in Bayesian hierarchical logistic regression model of walleye recruitment success.

Variable	Level	Mean	Median	Range
Annual DD (°C·days^{-1})	1 (lake-year)	2400	2391	1817–3462
Annual CV 30–60 days post-ice-off	1 (lake-year)	0.17	0.15	0.04–0.39
Surface area (ha)	2 (lake)	282	108	12–5377
Conductivity (μS·cm^{-1})	2 (lake)	11	81	13–679
Largemouth bass catch (fish·km^{-1})	2 (lake)	4	2	0–55
Mean DD (°C·days^{-1})	2 (lake)	2449	2393	2085–3175

Note: Predictor variables enter the model either at level 1 (lake-years, N = 2061) or at level 2 (lake, N = 359).

Hierarchical logistic regression

We used a Bayesian hierarchical logistic regression model to evaluate the effects of annually varying water temperature DD and spring water temperature variability on successful walleye recruitment. As part of the model-building process, we first fitted Bayesian hierarchical logistic regression models (using methods outlined below) solely with annual DD or annual variability in spring water temperatures as a predictor of walleye recruitment success, with no lake-level covariates included. We then selected the annually varying water temperature metric(s) pertinent to predicting annual walleye recruitment success for use in building more complex models. Important predictors were defined as those for which 90% credible intervals (CI) did not overlap zero. Once the annually varying water temperature metric(s) was selected, we evaluated the effects of other lake-level covariates (lake area, conductance, largemouth bass relative abundance, and lake-average DD) on (*i*) the mean probability of recruitment success for each lake (i.e., the lake-specific modeled intercept) and (*ii*) the lake-specific effect of annual water temperatures on annual recruitment success (i.e., the lake-specific modeled slope).

The full varying intercept, varying slope model was as follows (the notation $j[i]$ indexes observation i for lake j):

Level 1 of the hierarchical model:

$$\Pr(y_i = 1) = \text{logit}^{-1}(\alpha_{j[i]} + \beta_{j[i]} \times \text{temperature}_i) \quad \text{for } i = 1 \ldots n$$

Level 2 of the hierarchical model:

$$\begin{pmatrix}\alpha_j \\ \beta_j\end{pmatrix} \sim \text{MVN}\left[\begin{pmatrix}\gamma_0^\alpha + \gamma_1^\alpha \times \text{area}_j + \gamma_2^\alpha \times \text{cond}_j + \gamma_3^\alpha \times \text{bass}_j + \gamma_4^\alpha \times \overline{\text{degree days}_j} \\ \gamma_0^\beta + \gamma_1^\beta \times \text{area}_j + \gamma_2^\beta \times \text{cond}_j + \gamma_3^\beta \times \text{bass}_j + \gamma_4^\beta \times \overline{\text{degree days}_j}\end{pmatrix}, \begin{pmatrix}\sigma_\alpha^2 & \rho\sigma_\alpha\sigma_\beta \\ \rho\sigma_\alpha\sigma_\beta & \sigma_\beta^2\end{pmatrix}\right] \quad \text{for } j = 1 \ldots J$$

where y_i = 1 if recruitment was successful, 0 otherwise, α_j is the intercept for lake j, β_j is the slope for the jth lake of the effect of annually varying water temperature (DD or spring variability) on recruitment success. Mean probability of recruitment success for each lake (on the logit scale; α_j), and the lake-specific effect of annual water temperature on recruitment success (β_j) were assumed to come from a multivariate normal (MVN) distribution. The parameters γ_0^x and γ_z^x describe the effects of lake-specific covariates on α_j and β_j (z = 1–4 for each covariate: area = lake area, cond = conductivity, bass = largemouth bass catch per kilometre, and $\overline{\text{degree days}}$ = lake-specific mean DD). The variances σ_α^2 and σ_β^2 are the conditional variances of the intercepts and slopes, respectively, and $\rho\sigma_\alpha\sigma_\beta$ describes the covariance between α_j and β_j, with ρ describing the correlation between α_j and β_j. Diffuse normal priors were used for γ_0^x and γ_z^x, and we modeled the variance-covariance matrix using the scaled inverse-Wishart distribution (Gelman and Hill 2007).

We ran three parallel Markov chains, beginning each with different values and running them for 60 000 samples, from which the first 30 000 were discarded. The remaining 30 000 were thinned to every other sample, resulting in 15 000 per chain and 45 000 total samples used to characterize the posterior distributions (Gelman et al. 2004). We assessed convergence for all parameters both visually (trace and posterior-distribution plots), as well as with the Brooks–Gelman–Rubin statistic, $\hat{R}$, with values <1.1 indicating convergence. Analyses were run using JAGS in the R2jags package (Su and Yajima 2015) run from within R version 3.2.4 (R Core Team 2015). We examined 90% CI for all parameter estimates to determine the importance of predictor variables (i.e., examined if 90% CI overlapped zero). To represent more fully the uncertainty in the posterior distributions of parameter estimates, we also calculated the probability that the direction of the relationship (i.e., positive or negative) between predictors and response variables was in the direction of the estimated posterior mean (Filstrup et al. 2014). Model fit was assessed by the conditional R^2 (Nakagawa and Schielzeth 2013) calculated using the MuMIn package (Barton 2015). The R^2 value was based on refitting the model described above using the glmer function in the lme4 package (Bates et al. 2015).

Lakes were sampled for walleye recruitment from 1–22 times between 1980 and 2014 (mean = 6, median = 3). Inferences from our analysis were not sensitive to the lakes included, owing largely to the partial pooling of the hierarchical model. For example, when restricted to include only lakes sampled a minimum of five times from 1980 to 2014, the same predictor variables were deemed important (based on whether 90% CI overlapped zero), and the effect sizes were similar. However, by including all lakes, we were able to use all available data to characterize the effect of water temperature on walleye recruitment success.

To establish how lake-specific probabilities of successful walleye recruitment have changed over time, we estimated the predicted probabilities in each lake for each year from 1980 to 2014. We used lake-specific estimated annual water temperature DD as level 1 model inputs, and all other predictor variables (i.e., level 2) were held constant at their lake-specific values. Lake-specific posterior distributions of the parameter estimates were used to simulate lake-specific probabilities of recruitment for each observed DD value, and mean predicted probabilities across all parameter estimates were calculated for each lake-year.

Results

Initial models quantifying the influence of annual DD and annual variability in spring water temperatures on the annual probability of successful recruitment suggested that annual DD were

Table 2. Parameter estimates from the Bayesian hierarchical logistic model evaluating the effects of annually varying water temperature DD on the probability of walleye recruitment success, and the effects of lake-level covariates on the lake-specific mean probability of recruitment success (intercepts) and effect of annual DD on recruitment success (slopes).

Description	Symbol	Estimate (90% CI)	Pr (direction of posterior mean)
Population-average intercept	γ_0^α	**−1.56 (−1.90, −1.23)**	1.0
Effect of lake area on intercept	γ_1^α	**0.77 (0.53, 1.02)**	1.0
Effect of conductivity on intercept	γ_2^α	0.17 (−0.14, 0.49)	0.81
Effect of largemouth bass relative abundance on intercept	γ_3^α	**−1.31 (−1.64, −1.01)**	1.0
Effect of mean DD on intercept	γ_4^α	−0.39 (−0.81, 0.03)	0.93
Population-average slope	γ_0^β	−0.11 (−0.34, 0.15)	0.74
Effect of lake area on slope	γ_1^β	−0.05 (−0.21, 0.12)	0.68
Effect of conductivity on slope	γ_2^β	−0.20 (−0.40, 0.06)	0.94
Effect of largemouth bass relative abundance on slope	γ_3^β	**−0.22 (−0.43, −0.02)**	0.97
Effect of mean DD on slope	γ_4^β	−0.15 (−0.41, 0.11)	0.82

Note: Posterior means are provided followed by 90% CI in parentheses (90% CI that do not overlap zero are shown in bold), and the probability that the effect is the direction of the estimated posterior mean (positive or negative).

an important predictor of recruitment success (posterior mean of the effect of DD = −0.32 (90% CI = −0.50, −0.14)). Spring variability in water temperature had little effect on walleye recruitment success in our data set (posterior mean for the effect of variability in spring water temperature = 0.01 (−0.17, 0.18)). All subsequent modeling therefore included annual DD as the only level 1 predictor of the probability of successful walleye recruitment.

The hierarchical logistic regression model explained a substantial proportion of variation in walleye recruitment success (conditional R^2 = 0.64). Across all lakes (i.e., the population-average effect), the effect of annual water temperature DD was not important based on the population-average slope γ_0^β 90% CI including zero (Table 2). However, the population-average effect of annual water temperature DD on the probability of successful walleye recruitment had a 74% probability of being negative (Table 2). The direction, magnitude, and uncertainty of the relationship between annual DD and walleye recruitment success varied substantially among lakes (Fig. 1; also see online Supplementary material Figs. S1–S4[1]). Of the 359 lakes analyzed, the most likely relationship between annual water temperature DD and the probability of successful walleye recruitment was negative for 198 lakes (55%) and positive for 161 lakes (45%; Figs. S1–S4[1]). When restricted to include only lakes for which the probability was at least 90% that the estimated effect of annual water temperature DD was in the direction (i.e., negative or positive) of the estimated posterior mean, the relationship was negative for 40 lakes (11%) and positive for 15 lakes (4%); (Figs. S1–S4[1]). The cut-off probability of 90% used here is arbitrary and is for illustrative purposes; similar summaries based on any biologically or socially relevant criteria are possible. Lakes also differed in their average probability of successful walleye recruitment (as measured by the lake-specific intercept; Figs. S1–S4[1]).

Lake characteristics influenced both the lake-specific average probability of successful walleye recruitment and the lake-specific effect of annual DD on annual walleye recruitment success (Table 2). The average probability of successful walleye recruitment (i.e., lake-specific intercept) increased with increasing lake surface area and with decreasing largemouth bass relative abundance (Figs. 2A and 2C). Average recruitment success also increased somewhat with increasing conductivity (probability of a positive effect of conductivity on average recruitment success = 0.81) and decreasing mean water temperature (probability of a negative effect of mean DD on average recruitment success = 0.93; Figs. 2B and 2D), but these effects were not distinguishable from zero based on 90% CI overlapping zero (Table 2).

The effect of annual DD on walleye recruitment success (i.e., lake-specific slopes) was also influenced by lake characteristics. Largemouth bass catch rates influenced lake-specific slopes negatively, with the strongest negative effects of annual water temperature DD in lakes with the highest largemouth bass abundance (Fig. 3C). The influence of water temperature DD on walleye recruitment was also most likely to be negative in smaller lakes, lakes with high conductivity, and lakes with higher mean DD, with probabilities of negative effects of 0.68, 0.94, and 0.82, respectively (Figs. 3A, 3B, 3D), though these effects were not distinguishable from zero based on 90% CI overlapping zero (Table 2).

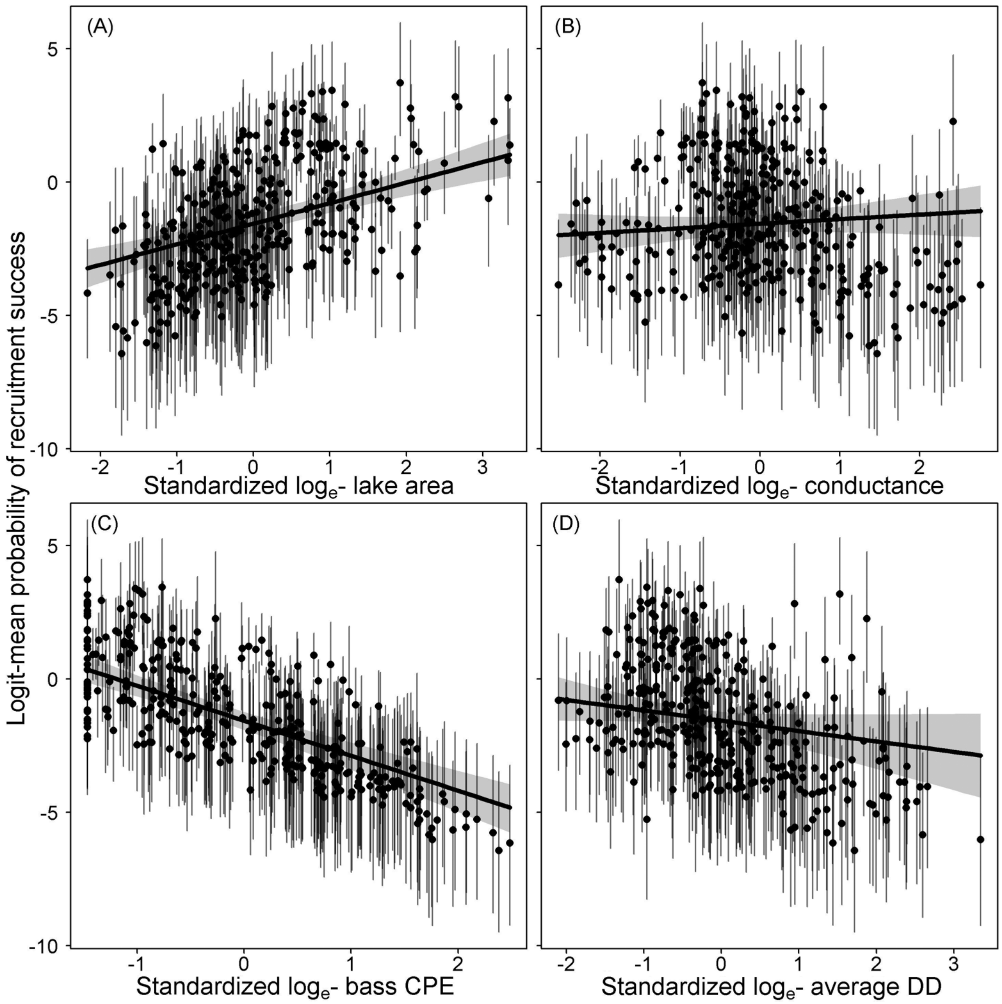
Temporal trajectories of water temperature DD from the 1980s to the 2010s affected recruitment success differently among lakes. In some lakes, the probability of walleye recruitment was predicted to have increased, while in others it was predicted to have decreased as lakes warmed (Fig. 4). Effects of increasing annual water temperature DD on walleye recruitment varied considerably for cooler lakes with fewer mean DD, but were generally negative in lakes where mean DD were 2800 or greater (Fig. 4).

Discussion

Documentation of the complex responses of fish populations to contemporary climate change is imperative for successful resource management (Lynch et al. 2016). The capacity of fish to reproduce naturally and for the young to survive their first summer (i.e., recruitment) is a particularly relevant metric for fish populations, as recruitment variation typically underlies variation in population abundance as a whole (Hilborn and Walters 1992). Here, we quantified the relationship between water temperature (in the form of annual DD) and the probability of successful walleye recruitment in Wisconsin lakes and observed varying temperature effects among diverse lakes. We found that the effect of water temperature on the probability of successful walleye recruitment varied among lakes and that lake-specific effects were not distinguishable from zero for the majority of lakes. In lakes where the effect of DD on recruitment success was important, the effect was negative in most cases — that is, walleye recruitment was less likely to be successful in warm years compared with cool years. However, walleye in other lakes were more resilient to warming temperatures, and, in some cases, walleye recruitment success was predicted to increase with increasing DD.

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0249.

Fig. 2. Relationship between lake-specific logit-scaled mean probability of recruitment success (intercepts) and lake area (A), conductivity (B), largemouth bass index of relative abundance (CPE = catch per unit effort) (C), and mean DD (D). Points are estimated posterior means and vertical lines are 90% CI. Solid line is estimated hierarchical regression line, and shaded regions are 90% credible regions.

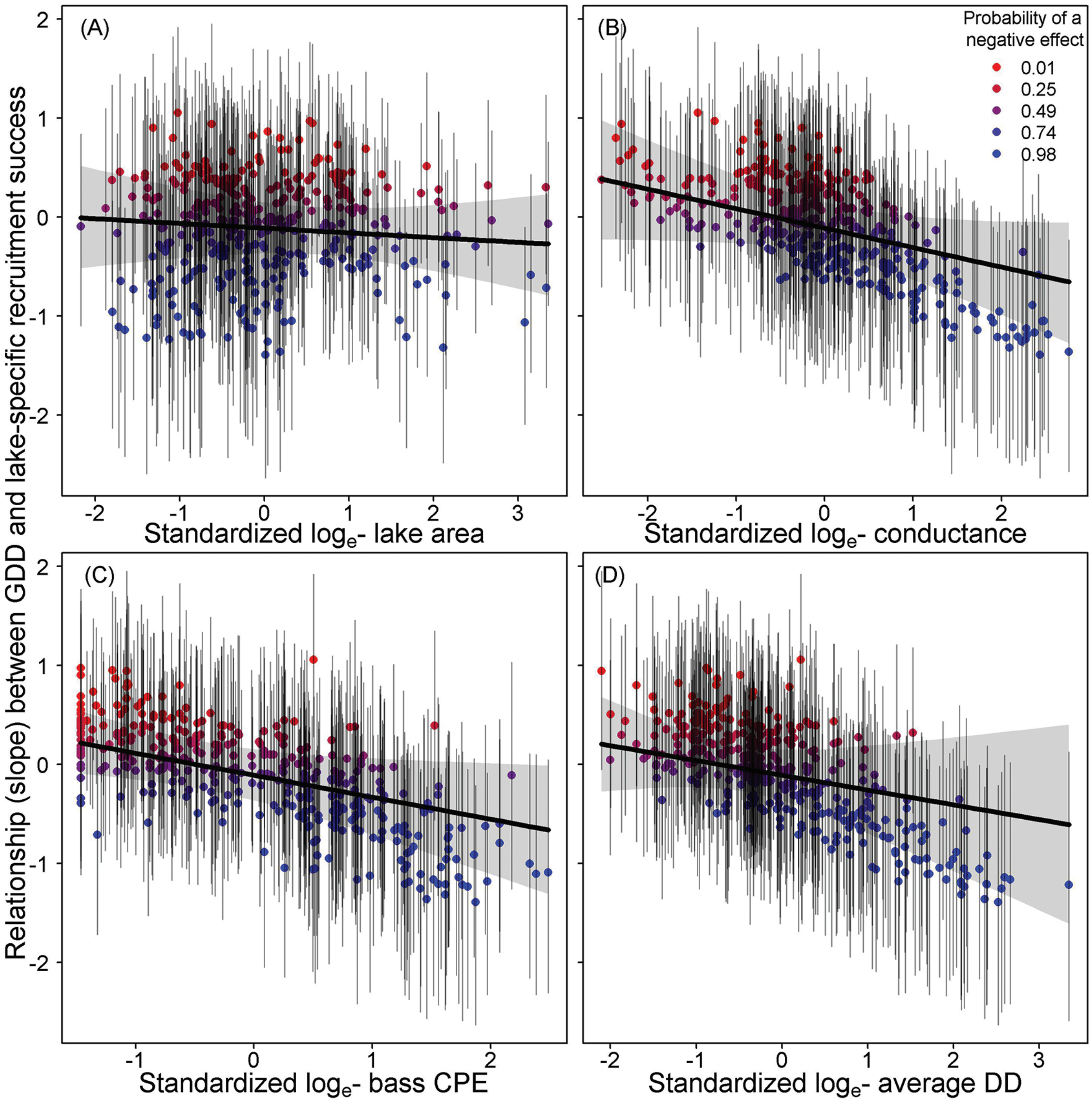


Heterogeneous responses of walleye recruitment to water temperature suggest that the effects of climate change on walleye are likely to depend on the fish community and other lake characteristics. Most notably, walleye in lakes with abundant largemouth bass appeared to respond most negatively to increasing water temperature. Average recruitment success was higher in large lakes and in those with few largemouth bass. Lake area, conductivity and mean DD did not influence the effect of annual DD on annual walleye recruitment success.

Most heterogeneity among lakes in the response of walleye recruitment to annual water temperatures was observed in lakes with average water temperatures at or below the statewide mean values (i.e., 0 on the standardized scale; Fig. 3). The probability of successful walleye recruitment was generally low in lakes with high average water temperatures, and was for the most part negatively influenced by increasing annual water temperature DD. Low probabilities of walleye recruitment at high DD values are consistent with the previously identified threshold response of walleye recruitment to DD (Hansen et al. 2015*a*, 2017). Our results suggest that parsing out differences among lakes with different responses to annual water temperatures, but similar average temperatures, could be a fruitful area of future research.

The mechanisms through which lake water temperature DD could affect walleye recruitment success are unknown, but likely complex. Our finding that increasing annual DD are likely to affect walleye recruitment success negatively in lakes containing abundant largemouth bass populations suggests that temperature may influence walleye recruitment via food-web dynamics or some other indirect pathway. For example, for walleye to survive or benefit from increased water temperatures, they must increase consumption to meet increased metabolic demands associated with warmer conditions (Kitchell et al. 1974, 1977). If high competition with other piscivores limits prey availability, or if walleye experience greater predation risk because of increased time spent foraging to obtain these resources (i.e., Walters and Juanes 1993), warmer temperatures may indirectly influence walleye survival negatively (Wuellner et al. 2010). However, direct predation of walleye by largemouth bass appears to be low to nonexistent, even in lakes experiencing walleye declines (Kelling et al. 2016). Even so, water temperature is unlikely to directly impact on age-0 walleye survival given that water temperatures in Wisconsin lakes do not exceed lethal limits in most lake-years. In fact, warming water temperatures are predicted to increase optimal walleye habitat in north temperate lakes (e.g., Fang et al. 2004; Chu et al. 2005). Similarly, the probability of successful walleye recruitment was predicted to increase with increasing water temperature in lakes containing relatively few largemouth bass. In these systems, increases in water temperature appeared to benefit walleye, perhaps by promoting growth (Venturelli et al. 2010), reproduction (Hokanson 1977), and (or) survival (Koonce et al. 1977), leading to

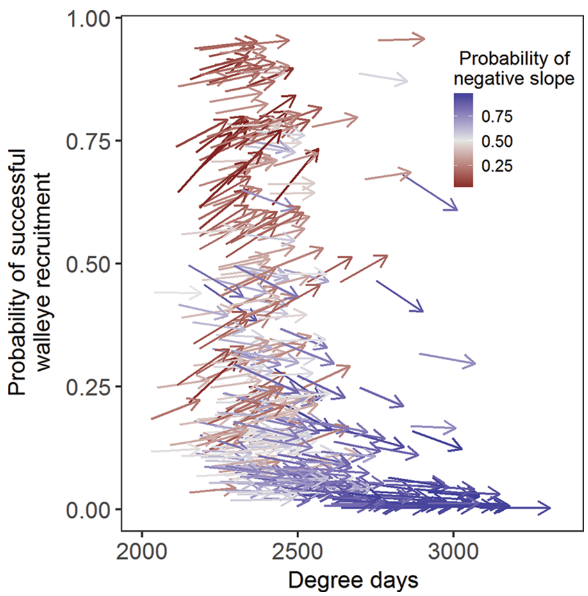
Fig. 3. Relationship between lake-specific slope parameters describing the relationship between annual water temperature DD and the probability of walleye recruitment success and lake area (A), conductivity (B), largemouth bass index of relative abundance (CPE = catch per unit effort) (C), and mean DD (D). Points are estimated posterior means, and vertical lines are 90% CI. Solid line is estimated hierarchical regression line, and shaded regions are 90% credible regions. Points are coloured by the probability that the effect of DD on walleye recruitment is negative. [Colour online.]



increased probability of successful recruitment. Interpretation of these results is further complicated by the fact that largemouth bass themselves are positively influenced by DD (Hansen et al. 2017), although largemouth bass abundance was treated as constant over the entire time period in this analysis due to data limitations. Future experimental work focused on disentangling the direct effects of temperature on walleye from indirect food-web effects could provide further insight into the mechanisms underlying the observed relationships. Regardless of the causes of variable responses of walleye recruitment success to water temperature, the observed heterogeneity across lakes supports the idea that the effects of increasing temperature operate indirectly through ecological relationships.

Even in the absence of a mechanistic understanding, the relationships observed in this analysis can be used in a management context (sensu Hilborn 2016). Small lakes and lakes with abundant largemouth bass are least likely to support successful, natural walleye recruitment. If maintaining walleye populations in these lakes is an important management goal, stocking may be the most plausible management option. Additionally, lakes with abundant largemouth bass are most vulnerable to walleye recruitment failure as water temperatures increase. Climate change is projected to increase temperatures throughout Wisconsin over the next several decades (Wisconsin Initiative on Climate Change Impacts 2009; Winslow et al. 2017). Knowing that lakes with few largemouth bass are most resilient to warming, managers may choose to devote resources to protecting walleye populations in these lakes from other stressors such as overexploitation or habitat degradation. Conversely, walleye populations in lakes with abundant largemouth bass that are most vulnerable to the effects of warming might warrant close monitoring. Because we cannot address mechanistic relationships in this study, we do not know whether walleye recruitment success is influenced directly by abundant largemouth bass or whether largemouth bass simply benefit from the same environmental conditions that reduce the resilience of walleye recruitment. We do not, therefore, know

Fig. 4. Predicted probability (posterior means) of walleye recruitment success in Wisconsin lakes based on water temperature DD in the 1980s (average from 1980 to 1989; beginning of arrows) to the 2010s (average from 2005 to 2014; end of arrows). Probability of walleye recruitment success was estimated based on lake-specific DD and predicted by a hierarchical logistic regression model quantifying lake-specific relationships between annual DD and walleye recruitment success. Water temperature DD can affect probability of successful walleye recruitment negatively in some lakes (blue arrows) and positively in others (red arrows). [Colour online.]



whether intentionally changing largemouth bass population densities would affect the probability of successful walleye recruitment in these lakes, though an adaptive management test of this idea is currently underway (Hansen et al. 2015*b*).

Inland lakes supporting recreational fisheries are interesting case studies for examining local resilience to climate change. Climate change will not affect all lakes within a region equally (Winslow et al. 2015; Hansen et al. 2017). Identifying locations that are most resilient to climatic changes can facilitate adaptation to changing conditions by focusing protection efforts on locations most likely to maintain critical habitat (Ashcroft et al. 2009; Keppel and Wardell-Johnson 2012; Keppel et al. 2015). In lake-rich landscapes, multiple stocks are managed for recreational harvest, often using a common set of regulations (Lester et al. 2003; Fayram et al. 2009). As lakes respond differently to similar climate conditions (Read et al. 2014; O'Reilly et al. 2015), angler movement and effort may adjust in response to changing fish populations (Carpenter and Brock 2004). Lake-specific relationships between temperature and walleye recruitment success can provide a framework for allocating limited resources across a landscape of many lakes to places likely to be most resilient (Midway et al. 2016). Resilient lakes may also provide sites to test hypotheses and examine more fully the complexity of freshwater lakes and their responses to large-scale change.

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