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ARTICLE

Trends in the Reproductive Phenology of two Great Lakes Fishes

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Abstract

To assess potential effects of climate change on Great Lakes fish populations, we evaluated trends in the reproductive phenology of Yellow Perch *Perca flavescens* (spring spawner) and Lake Trout *Salvelinus namaycush* (autumn spawner). For Yellow Perch in Lake Michigan, the estimated reproductive midpoint date (50% of mature females ripe or spent, 50% not yet spawned) took place 6.2 d/decade earlier in the spring near Milwaukee from 1988 to 2012 and 1.8 d/decade earlier in Green Bay from 1980 to 2012. At both locations water temperatures at the spawning sites on the midpoint date showed no trends, but mean water temperatures during the spring at the spawning site and midlake increased over the study period. This suggests that Yellow Perch spawning areas were warming sooner in the spring and that Yellow Perch were spawning earlier to maintain a consistent spawning temperature. Lake Trout phenological patterns were more complex. For Lake Trout in Lake Michigan near Milwaukee, there was a marginally significant trend for spawning to take place 2.1 d/decade later in the autumn from 1983 to 2006. However, water temperatures at the spawning site at the midpoint date did not change and autumn temperatures at the site and at midlake did not show a warming trend. For Lake Trout in Lake Superior near the Apostle Islands, the midpoint date did not change from 1988 to 2012. Water temperatures at the spawning site on the midpoint date and during the autumn also showed no trends, but midlake summer and autumn water temperatures increased significantly. Overall, Yellow Perch in Lake Michigan have shifted reproductive timing in a manner consistent with a warming climate, but the relationship of climate change to reproductive phenology remains unclear for Lake Trout in Lake Michigan and Lake Superior.

The earth's climate is warming, resulting in major changes in the thermal conditions of many lakes (Magnuson et al. 2000; Schneider and Hook 2010). Over the last century, the

Laurentian Great Lakes have experienced well-documented trends towards less ice and shorter winters (Assel and Robertson 1995; Assel et al. 2003), warmer summer temperatures

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(Austin and Colman 2007, 2008), higher surface wind speeds (Desai et al. 2009), earlier spring warming and later autumn cooling (McCormick and Fahnenstiel 1999; Austin and Colman 2008), and longer periods of lake stratification (Bennington et al. 2010). Of particular note, since the 1970s water temperatures in Lake Superior have been increasing more rapidly than air temperatures because of reductions in the extent and duration of winter ice cover and increases in the length of summer stratification (Austin and Colman 2007). Rises in water temperature, shifts in the availability of different thermal habitats, and variation in the onset and duration of the seasons could have profound effects on Great Lakes fish populations and the fisheries they support (Magnuson et al. 1990, 1997; Lynch et al. 2010; Cline et al. 2013).

Long-term studies from fish populations have documented that climate change is often associated with shifts in the phenology of reproduction. In some populations, warming water temperatures and shorter winters have led to earlier migrations, spawning, and egg hatching in the spring and later migrations and spawning in the autumn (Ahas and Aasa 2006; Crozier and Hutchings 2014; Peer and Miller 2014). More broadly, climate change has caused significant phenological shifts for many taxa across a wide range of aquatic and terrestrial environments (Parmesan and Yohe 2003; Ahas and Aasa 2006; Thackeray et al. 2010). These shifts are expected to have major consequences for myriad species and ecosystems, including those used and managed by humans (Post 2013). Differential phenological shifts in the patterns of abundance and availability of lower (i.e., phytoplankton, zooplankton, benthic invertebrates) versus upper (i.e., fish) trophic levels could lead to mismatches in the availability of suitable prey for larval and juvenile fish (Winder and Schindler 2004; Visser and Both 2005; Peeters et al. 2007), potentially leading to declines in larval and juvenile fish growth and recruitment and ultimately reduced adult abundance (Thackeray et al. 2010, 2013; Jonsson and Setzer 2015).

To explore the possible effects of a warming climate on the phenology of Great Lakes fishes, we examined long-term

annual records of the timing of reproduction by Yellow Perch *Perca flavescens*, a spring spawner, in Lake Michigan and the “lean” (Moore and Bronte 2001) morphotype of Lake Trout *Salvelinus namaycush*, an autumn spawner, in Lake Michigan and Lake Superior. Our hypotheses were that earlier spring warming would cause a trend towards earlier spawning by Yellow Perch and later autumn cooling would cause a trend towards later spawning by Lake Trout.

METHODS

The Wisconsin Department of Natural Resources has tracked the spawning of two Yellow Perch populations in Lake Michigan, one lean Lake Trout population in Lake Michigan, and one lean Lake Trout population in Lake Superior annually for many years (Table 1). Yellow Perch reproduction in Lake Michigan was monitored on shoals (<10 m deep) near Little Tail Point in Green Bay (44.58°N, 87.99°W) with trap nets (25-mm stretch mesh) from 1980 to 2012 and on shoals southeast of Milwaukee (42.55°N, 87.45°W) with graded multimesh (51–83-mm stretch by 6.3-mm increments) gill nets from 1988 to 2012. Lake Trout were monitored on these same Milwaukee shoals with graded multimesh (76–203-mm stretch by 19.1-mm increments) gill nets from 1983 to 2006. In Lake Superior, Lake Trout were sampled with similar graded multimesh gill nets from 1988 to 2012 on shoals near Gull and Michigan islands in the Apostle Islands region (46.90°N, 90.44°W).

For all four populations, standardized monitoring in known spawning areas occurred for 1–19 d within a 1–25-d period each year. The breakdown of sampling effort per site was as follows: Green Bay Yellow Perch—199 total sampling dates, 1–11 d each year, mean = 7.1 d, median = 6.5 d; Milwaukee Yellow Perch—166 total sampling dates, 2–19 d each year, mean = 4.8 d, median = 4 d; Milwaukee Lake Trout—81 total sampling dates, 1–8 d each year, mean = 3.3 d, median = 4 d; and Apostle Islands Lake Trout—97 total sampling dates, 4–6 d each year, mean = 5.8 d, median = 6 d. The actual sampling

TABLE 1. Type of data used in the analyses and the range of years for which that data was recorded for Yellow Perch and Lake Trout in the Great Lakes. Data includes fish catches, measured water temperature, and information from the Great Lakes Environmental Assessment and Mapping (GLEAM) Program.

Type of data	Years with data			
	Yellow Perch		Lake Trout	
	Milwaukee	Green Bay	Milwaukee	Apostle Islands
Daily fish catches at sampling site during spawning	1988–2012	1980–2012	1983–2006	1988–2012
Measured water temperature at sampling site on midpoint date	1988–2012	1980–2012	No data	1988–2012
Remotely sensed GLEAM water temperature at sampling site on midpoint date	1995–2012	No data	1994–2006	1994–2012
Seasonal water temperature at sampling site from GLEAM	1995–2012	1980–2012	1994–2006	1994–2012
Measured seasonal water temperature at midlake buoy	1988–2012	1980–2012	1983–2006	1988–2012

dates and catches for each site are provided in Supplementary Tables S.1, S.2, S.3, and S.4 available in the online version of this article. Sampling was timed in an attempt to coincide with the approximate peak of reproductive activity based on air and water temperatures during the year of sampling. Thus, actual sampling period and duration varied from year to year. The sampling period was rarely long enough to encompass the entire duration of the spawning period. Typically 25–250 mature females were captured each sampling day once spawning had begun, and the reproductive status of each was recorded. Female status was coded as green (abdomen robust but no eggs expressed when gently squeezed), ripe (eggs expressed), or spent (abdomen shrunken or flaccid and no eggs expressed). For purposes of analysis, all mature females were then classified as either not-yet-spawned (green) or spawned (ripe or spent) fish.

To determine trends in spawning phenology, we fit mixed-effects logistic regression models to the binomial response variable of not-yet-spawned versus spawned fish with the fixed-effects predictor variables of Julian day (day of year) and year and with a random effect for sampling dates. The models gave estimates of the proportion of fish that had spawned for each day in each year. Because fish spawned over several days, we summarized model results by estimating for each year the date of the midpoint of reproduction, which we defined as the day of the year on which 50% of females were estimated to have spawned and 50% had not yet spawned. To run the models, observations from individual fish were summarized for each sample day as the number of fish not yet spawned and the number spawned. Models were fit separately for each of the four populations and included data for all years sampled. Some years had few sampling dates and did not include the midpoint of reproduction, but if there were consistent annual patterns in the data, observations from adjacent years should provide coverage of the spawning season and allow quantification of trends with respect to year. The fixed-effect coefficients from the models permitted estimation of the proportion of fish that had spawned for each Julian day in each year. The random effect for sampling date allowed the estimated proportion spawned for each sample date to deviate from the value determined by the fixed effects of Julian day and year. Incorporating random effects for sampling date made it impossible to fit models with an interaction between Julian day and year and prevented us from estimating nonlinear trends. Logistic regression coefficients for Julian day were always positive because the estimated proportion of females that had spawned increased with Julian day; a larger coefficient indicated a greater rate of increase. A positive coefficient for year indicated that the proportion of fish that had spawned on any particular Julian day increased with year, i.e., that reproduction tended to occur earlier in the year. Our hypotheses that a warming climate would lead to Yellow Perch spawning earlier in the spring and to Lake Trout spawning later in the autumn would be supported if Yellow Perch populations

had a positive coefficient for year and Lake Trout populations had a negative coefficient. The models also provided an estimate of variance associated with the random effect of sampling date. This variance may include extra heterogeneity not accounted for by the fixed effects of Julian day and year or by the binomial variance associated with the binomial response variable. All computing was done in R (R Development Core Team 2014).

The computation of degrees of freedom, *P*-values, and goodness-of-fit tests are difficult in mixed-effects logistic regression models, and there is no general agreement on an appropriate computational approach. We followed the procedures outlined in Bolker et al. (2009) and used Wald tests (parameter estimate divided by its standard error) for hypothesis tests of parameters, assessed goodness of fit with residual plots, and computed the sum of squared Pearson residuals to evaluate overdispersion. The inclusion of random effects in the model can reduce overdispersion (Harrison 2014). Residual plots suggested some minor non-linearity in the relationship of residuals to fitted values; at the smallest fitted values (i.e., earliest years and Julian days) the residuals tended to be more negative (i.e., midpoint of reproduction was earlier than predicted by the model), and at the largest fitted values (i.e., latest years and Julian days) they tended to be more positive (i.e., midpoint of reproduction was later). Transformations of the predictor variables (Julian day and year) did not eliminate these patterns and made interpretation of parameters more difficult. No other unusual residual patterns or evidence of bias were evident in plots of the residuals versus the predictors. Computation of the sum of squared Pearson residuals gave no indication of overdispersion for models for any of the four data sets (Bolker et al. 2009). Estimates of among-sampling-date standard deviations (square root of estimated variance of random effects) were large relative to the fixed-effect parameter estimates (~5–85 times greater; see Results), suggesting that there was considerable variability among sampling dates in the percentage of fish that had spawned even after the fixed effects of Julian day and year were taken into account. Thus, including the random effect substantially improved model fit, and we concluded that it was best to retain sampling date as a random effect in the models despite the possibility of some nonlinearity in the trends for the midpoint of reproduction.

To make our results more easily interpretable and comparable with other studies, we computed the rate of change per decade in the midpoint of reproduction. This rate can be computed from model estimates or as a function of estimated model parameters, and the variance of the rate can be estimated using the delta method (Rao 1973:385–389). To estimate the median day of spawning as a function of year with a 95% confidence interval is more complicated as it requires estimating the median day and its variance for each year. For this purpose we used the parametric bootstrap method, which

has been implemented in the R package lme4 (function bootMer; R Development Core Team 2014; Bates et al. 2015).

We also examined time trends in water temperature at each site. We had three sources and four types of data (Table 1). First, we used water temperature measured during fish sampling to estimate the water temperature at the midpoint of reproduction for each population, except for Lake Trout at Milwaukee for which no data were available. In some years water temperature measurements were made on the actual midpoint and in others the temperature could be interpolated from measurements made before and after the date. However, in some years the sampling did not encompass the estimated midpoint of reproduction and no determination of water temperature at the midpoint date could be made. Second, we compiled satellite-estimated mean nighttime surface water temperatures from the Great Lakes Environmental Assessment and Mapping (GLEAM) Program accessed through the National Oceanic and Atmospheric Administration (NOAA) CoastWatch Great Lakes node (<http://coastwatch.glerl.noaa.gov/>). The GLEAM remotely sensed water temperatures were averaged daily for a 3-km \times 3-km area surrounding each study site during the spring and fall for September 1994 through December 2012 (following Allan et al. 2013). Using the GLEAM data, we determined the water temperature at the midpoint date (unavailable for Yellow Perch in Green Bay because of gaps in the dataset) and also the monthly and seasonal (spring: April–late June; summer: late June–late September; autumn: late September–late December) mean temperatures during the open-water period (April–early December) for each year. Finally, we used measured water temperatures from two continuous-monitoring offshore weather buoys in midlake Lake Michigan and one in midlake Lake Superior obtained from the NOAA National Data Buoy Center (http://www.ndbc.noaa.gov/station_page). The southern Lake Michigan buoy (number 45007; 42.674°N, 87.026°W) was located about 80 km east-southeast of the Milwaukee sampling site, the northern Lake Michigan buoy (number 45002; 45.344°N, 86.411°W) was located about 150 km northeast of the Green Bay sampling site, and the western Lake Superior buoy (number 45006; 47.335°N, 89.793°W) was located about 65 km northeast of the Apostle Islands sampling site. We calculated mean monthly and seasonal water temperatures from each buoy. For all three sources and types of data, we used general linear regressions to assess trends over time.

RESULTS

Large numbers of the target species were observed at each location. Over the course of the study the total numbers of mature females collected were 26,518 Yellow Perch from 199 sampling dates in Green Bay, 6,814 Yellow Perch from 116 dates near Milwaukee, 5,373 Lake Trout from 81 dates near Milwaukee, and 9,681 Lake Trout from 97 dates in the Apostle Islands.

Both Yellow Perch populations displayed a trend towards earlier reproduction in the spring. For Milwaukee, there was a significant relationship between the reproductive midpoint date and year (Julian day parameter = 0.121, SE = 0.018, $P < 0.0001$; year parameter = 0.075, SE = 0.020, $P = 0.0003$; among-sampling-dates SD = 1.466) that indicated a tendency for spawning to take place increasingly earlier in the year over the study period (Figure 1). In 1988 the estimated reproductive midpoint occurred on June 12, but by 2012 it had advanced about 15 d to May 28 for an estimated rate of change of 6.2 d/decade (95% CI = 3.0–9.3 d/decade). The width of the 95% CI for the reproductive midpoint increased over the course of study from about 5 d in 1988 to 9–10 d in 2012, showing that the estimates of the reproductive midpoint were more uncertain in more recent years. In Green Bay there was also a significant relationship between the reproductive midpoint date and the year (Julian day parameter = 0.186, SE = 0.013, $P < 0.0001$; year parameter = 0.034, SE = 0.010, $P = 0.0006$; among-sampling-dates SD = 1.321) that signified earlier spawning (Figure 2). However, the shift in reproductive midpoint was not as dramatic as at Milwaukee. In 1980 the estimated reproductive midpoint was May 1, and by 2012 it had advanced about 5 d to April 26 for a rate of change of 1.8 d/decade (95% CI = 0.8–2.9 d/decade). The width of the 95% CI for the reproductive midpoint remained fairly steady at about 4 d, indicating that the reproductive midpoint was estimated with similar precision throughout the study period.

Limited trends were evident for the reproductive phenology of the two Lake Trout populations. In Lake Michigan near Milwaukee, there was a marginally significant relationship between the reproductive midpoint date and the year (Julian day parameter = 0.101, SE = 0.013, $P < 0.0001$; year parameter = -0.022 , SE = 0.012, $P = 0.07$; among-sampling-dates SD = 0.750) that indicated a possible tendency for spawning to take place later in the autumn over the study period (Figure 3). In 1983, the estimated midpoint date was October 30, but by 2006 it may have moved back 5 d to November 4 for a rate of change of 2.1 d/decade (95% CI = -0.5 to $+4.7$ d/decade). The width of the 95% CI varied from 5 to 8 d but showed no trend over the study period. In Lake Superior near the Apostle Islands, there was not a significant relationship between reproductive midpoint date and year (Julian day parameter = 0.154, SE = 0.019, $P < 0.0001$; year parameter = 0.010, SE = 0.010, $P = 0.35$; among-sampling-dates SD = 0.850) indicating no clear trend in the timing of spawning. Over the course of the study, the midpoint of reproduction usually occurred October 18–20, with a 95% CI of about 4 d (Figure 4).

Water temperatures at the midpoint of reproduction remained generally stable for all four populations over the study period. For Yellow Perch at Milwaukee, neither measured nor GLEAM water temperatures at the reproductive midpoint date showed a trend with year. Measured temperatures had a mean of 11.6°C from 1988 to 2012 ($N = 11$; SD =

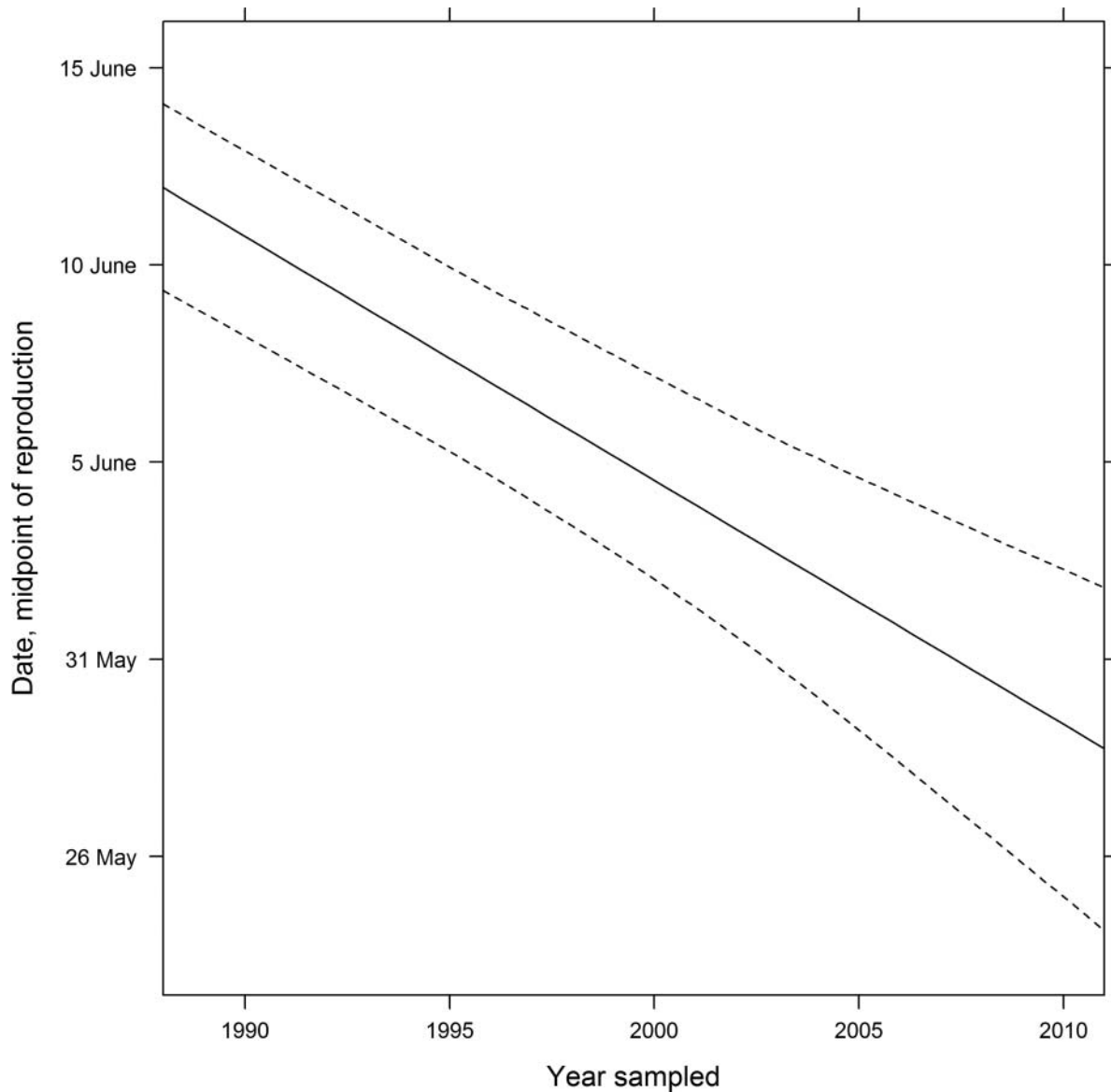


FIGURE 1. Plot of the estimated date of the midpoint of reproduction versus the sampling year (the dashed lines indicate the 95% CI) for Yellow Perch from Lake Michigan near Milwaukee (42.99°N, 87.85°W). The trend line is highly significant ($P = 0.0003$).

2.5°C; range = 6.7–14.5°C), and GLEAM temperatures had a mean of 10.7°C from 1995 to 2012 ($N = 18$; SD = 3.5°C; range = 3.3–16.9°C). For Yellow Perch in Green Bay, measured water temperatures at the reproductive midpoint date also showed no trends with year, averaging 10.7°C from 1980 to 2012 ($N = 14$; SD = 1.3°C, range = 7.9–12.6°C); GLEAM water temperatures were unavailable. Similarly, for Late Trout at Milwaukee, GLEAM water temperatures at the reproductive midpoint date had no trend with year from 1994 to 2006 and had a mean of 11.0°C ($N = 13$; SD = 1.7°C; range = 8.5–13.6°C); measured water temperatures were unavailable. For Lake Trout at the Apostle Islands, neither measured nor GLEAM water temperatures displayed a trend and measured

temperatures had a mean of 9.4°C from 1988 to 2012 ($N = 23$; SD = 1.3°C; range = 7.2–11.4°C) and GLEAM water temperatures had a mean of 9.3°C from 1994 to 2012 ($N = 19$; SD = 1.5°C; range = 4.5–11.2°C).

For the two Yellow Perch populations, the trend toward earlier spring spawning was associated with warmer spring water temperatures (Figure 5). Near Milwaukee, GLEAM water temperature means from 1995 to 2012 for the months of April ($F = 12.14$, $P = 0.0031$; $r^2 = 0.40$), May ($F = 5.86$, $P = 0.027$; $r^2 = 0.21$), and June ($F = 4.37$, $P = 0.0519$; $r^2 = 0.16$) and for the entire spring ($F = 5.48$, $P = 0.0317$; $r^2 = 0.20$) and also southern Lake Michigan buoy water temperature means from 1988 to 2012 for the month of April ($F = 14.18$,

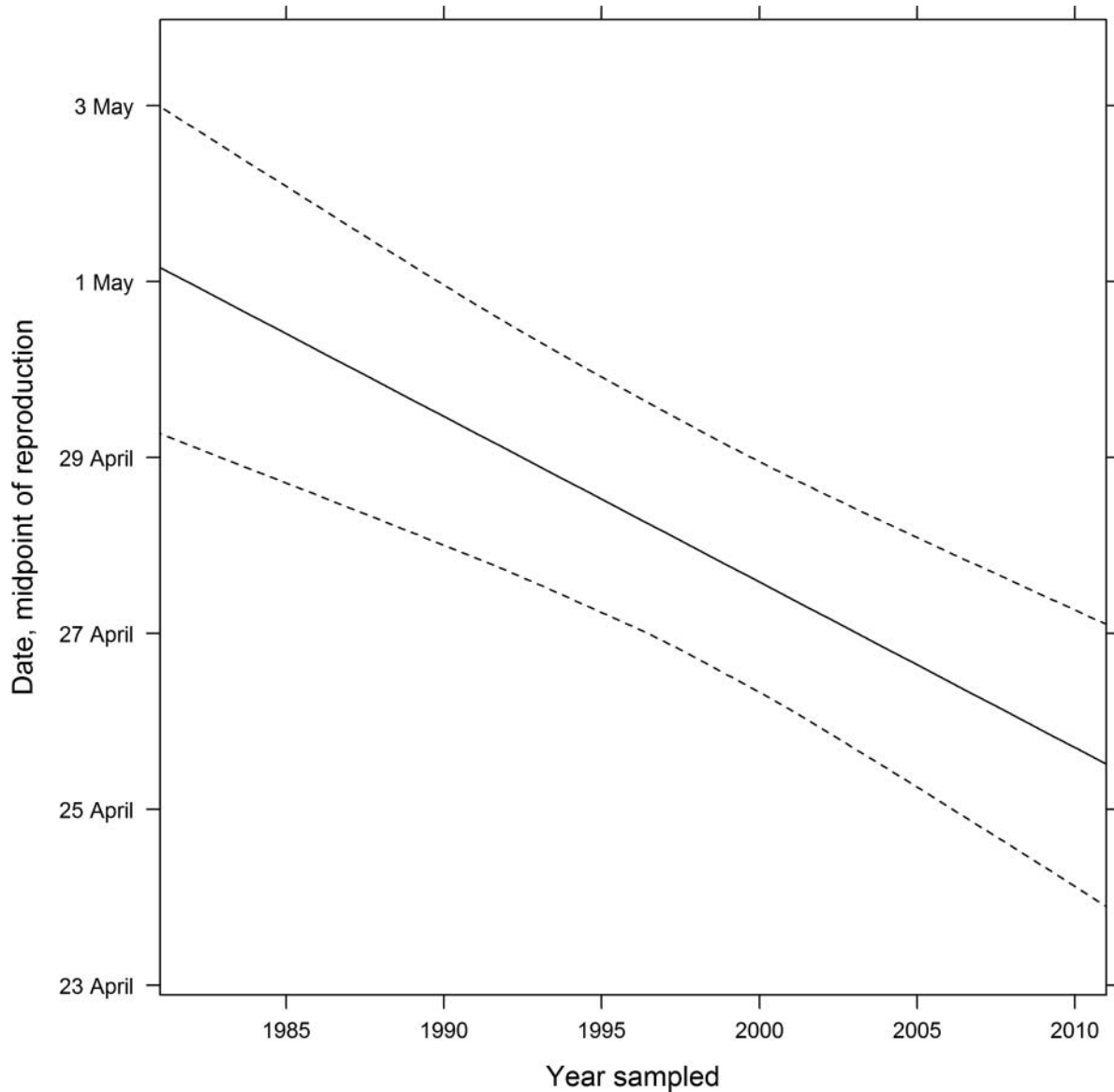


FIGURE 2. Plot of the estimated date of the midpoint of reproduction versus the sampling year (the dashed lines indicate the 95% CI) for Yellow Perch from Lake Michigan in Green Bay (44.58°N, 87.99°W). The trend line is highly significant ($P = 0.0006$).

$P = 0.001$; $r^2 = 0.35$) and for the entire spring ($F = 6.24$, $P = 0.0201$; $r^2 = 0.18$) were positively related to year, indicating a warming trend. Near Green Bay, GLEAM water temperature means from 1995 to 2012 for the months of April ($F = 4.92$, $P = 0.0414$; $r^2 = 0.19$) and May ($F = 6.51$, $P = 0.0207$; $r^2 = 0.23$) and for the entire spring ($F = 8.86$, $P = 0.0089$; $r^2 = 0.32$) and northern Lake Michigan buoy temperature means from 1980 to 2012 for the months of April ($F = 11.33$, $P = 0.0026$; $r^2 = 0.29$), May ($F = 6.32$, $P = 0.0179$; $r^2 = 0.16$), and June ($F = 9.80$, $P = 0.004$; $r^2 = 0.23$) and for the entire spring ($F = 8.16$, $P = 0.0076$; $r^2 = 0.18$) were positively related to year, also indicating a warming trend.

For the two Lake Trout populations, trends in the date of the reproductive midpoint were not clearly related to trends in

autumn water temperatures (Figure 5). Near Milwaukee, where Lake Trout may have tended to spawn later in the autumn, neither the GLEAM mean water temperature data for 1994–2006 nor the southern Lake Michigan buoy mean water temperature data for 1983–2006 showed any significant relationships with year for the months of July, August, September, October, or November or for the entire summer or entire autumn, indicating no trend towards autumn warming. For the Apostle Islands, where Lake Trout showed no trend in reproductive midpoint, the GLEAM mean water temperature data for 1994–2012 did not correlate with year for the months of July, August, September, October, or November or for the entire summer or the entire autumn, indicating no warming trend for the spawning area. However, western Lake Superior

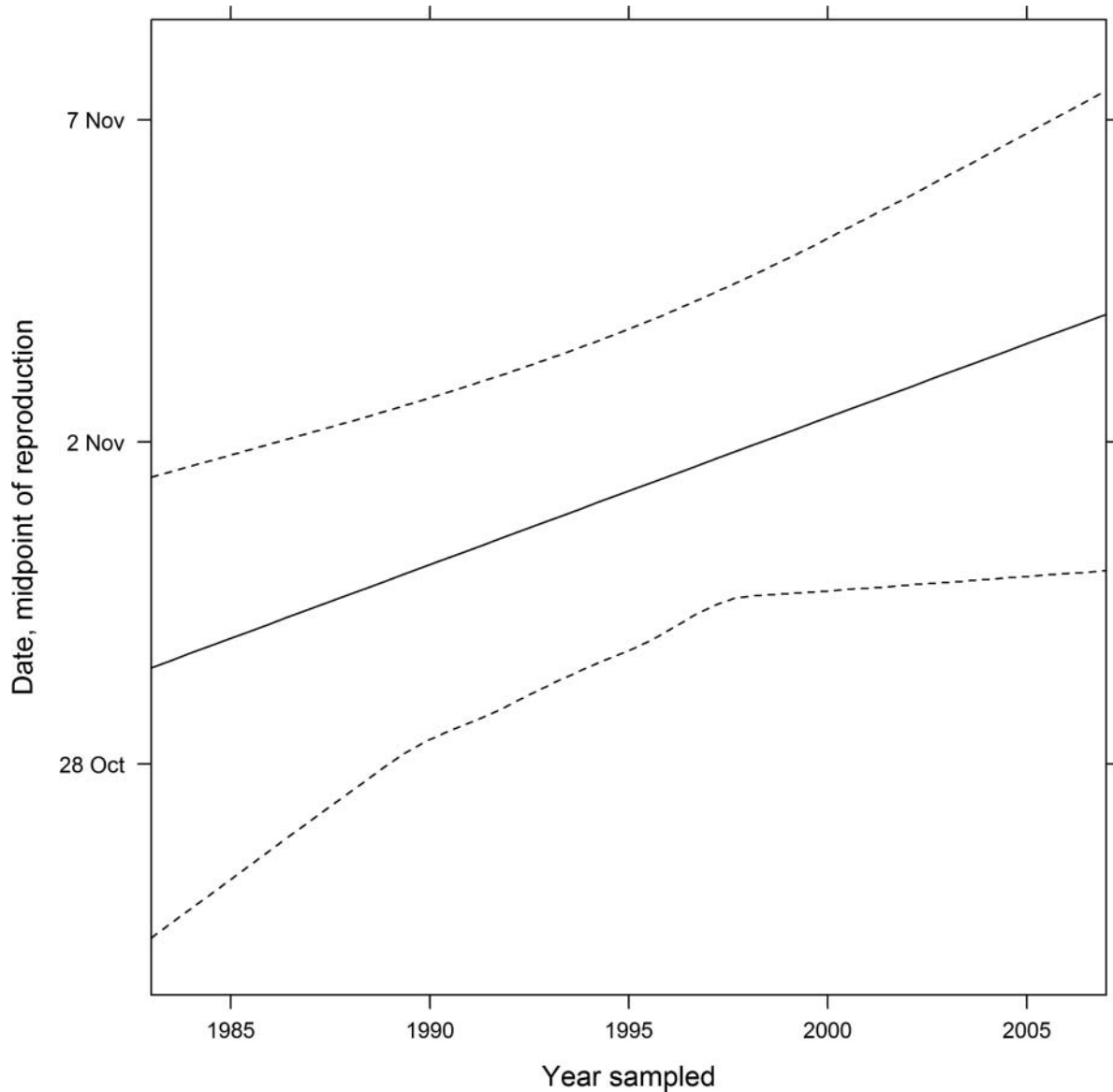


FIGURE 3. Plot of the estimated date of the midpoint of reproduction versus the sampling year (the dashed lines indicate the 95% CI) for Lake Trout in Lake Michigan near Milwaukee (42.99°N, 87.85°W). The trend line is marginally significant ($P = 0.07$).

buoy mean water temperature data for 1988–2012 had highly significant positive correlations with year for the months of July ($F = 33.83$, $P < 0.0001$; $r^2 = 0.61$), August ($F = 19.65$, $P = 0.0003$; $r^2 = 0.47$), September ($F = 23.23$, $P < 0.0001$; $r^2 = 0.51$), October ($F = 20.27$, $P = 0.0002$; $r^2 = 0.48$), and November ($F = 25.92$, $P < 0.0001$; $r^2 = 0.59$) and for the entire summer ($F = 36.86$, $P < 0.0001$; $r^2 = 0.63$) and the entire autumn ($F = 19.23$, $P = 0.0003$; $r^2 = 0.46$), indicating a clear warming trend for the middle of the lake.

DISCUSSION

Yellow Perch and Lake Trout spawning phenologies in the Great Lakes have responded differently to a changing climate. As we hypothesized would occur, a trend towards warmer

spring temperatures has been associated with earlier spring spawning by Yellow Perch. The temporal patterns of Yellow Perch spawning illustrate the importance of water temperature in interpreting climate change effects. At both Milwaukee and Green Bay, Yellow Perch had no trends in the water temperature at which spawning took place and the reproductive midpoint occurred at a mean of 10.7–11.6°C, which is within the published thermal range of 6.7–12.2°C for spawning by the species (Scott and Crossman 1973; Thorpe 1977). Water temperatures in Lake Michigan, both near the spawning sites in Milwaukee and Green Bay and at midlake sites, clearly indicated that spring water temperatures were warming. Thus shifts towards earlier reproduction were associated with a trend toward greater spring warming, suggesting that water

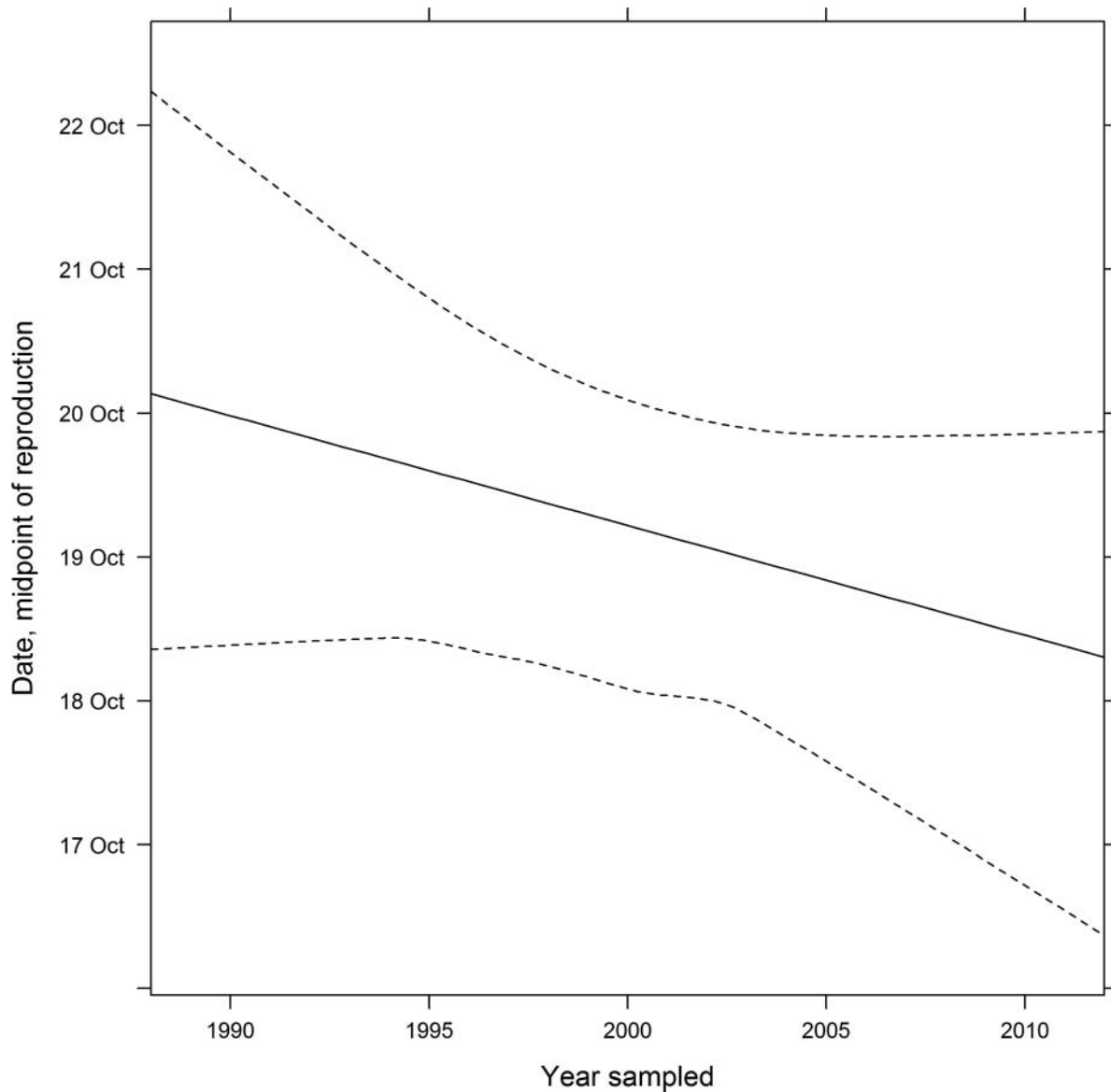


FIGURE 4. Plot of the estimated date of the midpoint of reproduction versus the sampling year (the dashed lines indicate the 95% CI) for Lake Trout in Lake Superior near the Apostle Islands (46.90°N, 90.44°W). The trend line is not significant ($P = 0.35$).

temperature was likely a spawning cue and Yellow Perch populations in Lake Michigan had apparently adjusted the timing of their reproduction in order to maintain a consistent spawning temperature. Field and laboratory studies have shown that the initiation of reproduction in Yellow Perch and in the closely related Eurasian Perch *Perca fluviatilis* is influenced by both the rate of water temperature warming and photoperiod change, with temperature being important in determining the initiation and duration of spawning (Thorpe 1977; Kayes and Calbert 1979; Dabrowski et al. 1996; Ciereszko et al. 1997; Thackeray et al. 2013), so shifts in timing to ensure suitable water temperatures (e.g., for egg hatching and fry survival) are not surprising. Interestingly, ovarian development appears to be tuned to photoperiod more than water

temperature (Ciereszko et al. 1997; Abdulfatah et al. 2011, 2013), suggesting potential constraints on plasticity in spawning responses to earlier warming.

Lake Trout reproductive phenology in the Great Lakes has not shifted to the same extent as has that of Yellow Perch, and the influence of climate change on the reproductive phenology of Lake Trout in the Great Lakes remains unclear. In Lake Michigan near Milwaukee, Lake Trout displayed a possible trend towards spawning later in the autumn over the study period, as would be expected under a warming climate. The temperature of the midpoint of reproduction has remained generally stable at a mean of 11°C, within the published range of 8.9–13.9°C for spawning by the species (Martin 1957; Scott and Crossman 1973). However, there has been no apparent trend in mean water

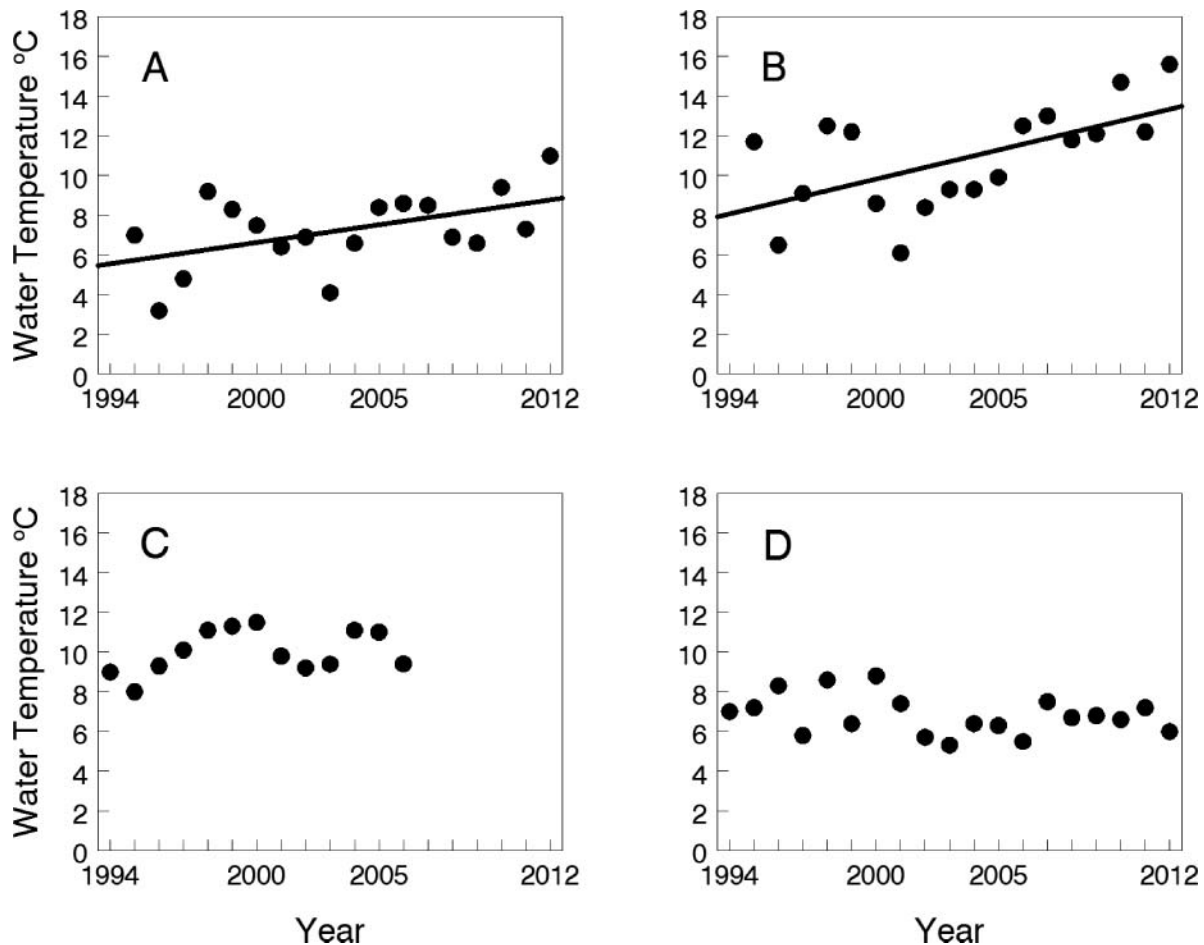


FIGURE 5. Plots of mean seasonal GLEAM water temperatures (measured by remote sensing) versus the year for the locations of the four study populations: (A) near Milwaukee in spring, (B) Green Bay in spring, (C) near Milwaukee in autumn, and (D) Apostle Islands in autumn. The trend lines are presented only if there is a significant correlation ($P < 0.05$) with year.

temperatures during the months of July, August, September, October, or November or for the summer or the autumn as a whole, either at the spawning site or in midlake waters, indicating that if a reproductive shift has actually occurred, it probably has not been driven by water temperature changes.

The possible trend toward later Lake Trout spawning at Milwaukee is difficult to explain. Casselman (2002) summarized findings from several inland lake and hatchery populations in Ontario and concluded that each population of Lake Trout reproduced at an approximately constant date each year rather than tracking variation in water temperature. Our Milwaukee results cannot address the importance of water temperature in determining spawning times, but they may contradict the notion that spawning will occur at approximately the same date each year. Eschmeyer (1955) and Martin (1957) presented data indicating that smaller and presumably younger female Lake Trout spawned earlier during the reproductive period than larger and presumably older individuals. Thus if the general spawning period had remained fairly constant but the size or age structure of the population had changed, an apparent

shift in reproductive midpoint might occur (Wright and Trippel 2009). We lack age data for many of the collection years at Milwaukee, but the mean size of spawning female Lake Trout shows no trend over the study period ($P = 0.97$), with a rather narrow range of annual means from 713 to 763 mm total length. Thus shifts in the reproductive midpoint cannot be explained by size shifts. The Lake Trout is a relatively long-lived, late-maturing species in the Great Lakes, and its reproduction is the culmination of gonadal development processes that have occurred over many months or even years (Goetz et al. 2011). Conceivably, environmental or feeding conditions occurring long before the onset of the autumn reproductive period might influence the timing of spawning, as has been found for a congener, Brook Trout *Salvelinus fontinalis* (Warren et al. 2012). Recent major changes in the food webs and fish communities of Lake Michigan (Bunnell et al. 2006; Nalepa et al. 2009) may have created conditions that altered rates of gonadal development to the extent that the reproductive period of Lake Trout has gradually shifted over time. However, this would be a difficult hypothesis to test.

In Lake Superior, Lake Trout have shown no trend in the timing of reproduction. The water temperature at the midpoint of reproduction has remained fairly constant at a mean of 9.3–9.4°C, and there has been no trend in mean water temperatures near the spawning area for July, August, September, October, or November or for the entire summer or entire autumn, which is consistent with the lack of a trend in the reproductive midpoint. However, in midlake there has been a strong warming trend in mean water temperature (see also Austin and Colman 2007, 2008). This indicates that there is significant spatial heterogeneity in thermal patterns for Lake Superior (see also Allan et al. 2013) and that midlake water temperature data should not be used to infer temperature trends or biological responses in nearshore areas.

Adjustments in the timing of spawning in response to warming spring temperatures could be either beneficial or harmful to Yellow Perch. Earlier spawning could result in a longer growing season during the first year of life. If food remained sufficient, prolonging the first growing season could yield larger sizes going into the critical first winter, which in turn could improve survival (Post and Prankevicus 1987). However, if the temporal availability and abundance of juvenile Yellow Perch food items did not shift in the same manner as Yellow Perch reproduction, mismatches between Yellow Perch and their prey might lead to reduced growth and survival. The lack of synchrony in reproductive responses to earlier spring warming could also lead to mismatches between juvenile Yellow Perch and their competitors and predators, which could have either positive or negative consequences for the Yellow Perch depending on the nature of the mismatches (Wright and Trippel 2009; Post 2013; Thackeray et al. 2013). Several studies document differential shifts in the phenology of different trophic or taxonomic groups such that aquatic predator–prey interactions are altered (Winder and Schindler 2004; Peeters et al. 2007; Krabbenhoft et al. 2014; Jonsson and Setzer 2015). Most relevantly, in Lake Windemere, England, climate warming has led to phenological shifts for many taxonomic and ecological groups but reproductive shifts for Eurasian Perch have not kept pace with the shifts for lower trophic levels, such as phytoplankton and zooplankton, with potentially major implications for the fish community (Thackeray et al. 2013).

The observed shifts in the date of the reproductive midpoint for the Lake Michigan Yellow Perch associated with climate warming, 1.8–6.2 d/decade, are similar to climate-driven shifts in reproductive phenology observed in freshwater and anadromous fishes elsewhere. For example, spring spawning by Eurasian Perch in different areas of Lake Windemere advanced by 2.5–5.0 d/decade from 1968 to 2009 (Thackeray et al. 2013). Spring reproduction by Walleye *Sander vitreus* in seven Minnesota inland lakes took place 0.5–3.0 d/decade earlier over the period of 1954–2007 (Schneider et al. 2010). In an analysis of numerous anadromous populations of Atlantic Salmon *Salmo salar* in northeastern North America, the midpoint of the adult spawning migration into freshwater occurred from

4.5 to 21.0 d/decade earlier in the spring or summer from the 1950s to the 2000s, with most populations undergoing a shift of 5–7 d/decade (Juanes et al. 2004). Atlantic Salmon smolt out-migration to the ocean from these and other populations took place 2.5 d/decade earlier in the spring (Russell et al. 2012; Otero et al. 2014). In Connecticut, spring spawning migrations of anadromous Alewife *Alosa pseudoharengus* were estimated to have taken place about 4.2 d/decade earlier from 1973 to 2007 (Ellis and Vokoun 2009). Spring and summer spawning migrations by American Shad *Alosa sapidissima* occurred about 6.9 d/decade early in the Columbia River from 1938 to 1993 (Quinn and Adams 1996). Also in the Columbia River, summer spawning migrations by anadromous Sockeye Salmon *Oncorhynchus nerka* began 1.3–1.7 d/decade earlier from 1938 to 2010 (Quinn and Adams 1996; Crozier et al. 2011). In Auke Creek, Alaska, warming temperatures led to earlier spring hatching for Pink Salmon *Oncorhynchus gorbuscha* and out-migration of larvae to the ocean 2.7–5.0 d/decade earlier from 1972 to 2005 (Taylor 2008). The summer spawning migration of Pink Salmon into Auke Creek advanced by 2.6–3.5 d/decade (Kovach et al. 2012, 2013). In the Rio Grande River, New Mexico, reduced snowpack in the mountains and greater spring warming led to an earlier spring flood pulse, resulting in earlier spawning by 3.1–21.5 d/decade for eight species from 1995 to 2010 (Krabbenhoft et al. 2014). Spring reproduction by Grayling *Thymallus thymallus* in a river in Switzerland advanced 7.6 d/decade from 1962 to 2009 (Wedekind and Küng 2010). In Estonia, the start of the spring spawning migration, the initiation of spawning, or the end of spawning took place from 2.5 to 6.0 d/decade earlier for six fish species from 1948 to 1998 (Ahas 1999; Nöges and Järvet 2005; Ahas and Aasa 2006). Across the United Kingdom, spring and summer phenological metrics for 726 terrestrial and aquatic organisms occurred an average of 2.5–5.8 d/decade earlier over the period of 1976–2005, depending on the taxonomic group and type of habitat (Thackeray et al. 2010). In a meta-analysis of global phenological patterns, a large number and wide variety of terrestrial and aquatic vertebrates, invertebrates, and plants had advanced their spring activities (e.g., plant flowering, tree budding, bird and butterfly migrations, and fish and amphibian reproduction) by a mean of 2.3 d/decade with a 95% confidence interval of 1.7–3.2 d/decade (Parmesan and Yohe 2003).

Our study is the first to document phenological shifts of fish reproduction in response to climate change in the Laurentian Great Lakes and is one of only a handful for freshwater fishes anywhere. Admittedly, the possible shift for Lake Trout at Milwaukee does not appear to be directly associated with changes in fall warming and the midpoint of reproduction of Lake Trout at the Apostle Islands has not shifted, which highlights the inherent difficulty in documenting biological responses to climate change. But if we accept the trends in reproductive midpoint that we observed as valid, two salient points can be drawn from this initial analysis. First, responses

to climate change may be relatively simple in that some fish populations, such as Yellow Perch in Lake Michigan, can apparently respond to warming temperatures by simply reproducing earlier to track preferred thermal conditions. Future studies should focus on the limits of such flexibility so as to predict the degree of warming that will directly impact reproduction. Second, differences among the four populations in this study in their apparent responsiveness to regional climate warming suggest that broad generalizations may be elusive. Reproductive timing appears to shift differently among populations and only partly in accord with spatial variation in rates of water warming within Lake Michigan and Lake Superior (Allan et al. 2013). This heterogeneity highlights the need to understand variation in response to climate change at diverse spatial and temporal scales in aquatic ecosystems (see also Crozier et al. 2011). Globally, freshwater ecosystems have been warming at uneven rates (Austin and Colman 2007; Schneider and Hook 2010), and fish have likely reacted through variable shifts in phenology that have gone mostly undocumented. Further efforts to compile and analyze long-term data on reproductive timing will be essential for developing management responses to climate change that will conserve fish diversity and maintain productive fisheries.

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REFERENCES

- Abdulfatah, A., P. Fontaine, P. Kestemont, J.-N. Gardeur, and M. Marie. 2011. Effects of photothermal kinetics and amplitude of photoperiod decrease on the induction of the reproduction cycle in female Eurasian perch *Perca fluviatilis*. *Aquaculture* 322–323:169–176.
- Abdulfatah, A., P. Fontaine, P. Kestemont, S. Milla, and M. Marie. 2013. Effects of thermal threshold and the timing of temperature reduction on the initiation and course of oocyte development in cultured female of Eurasian perch *Perca fluviatilis*. *Aquaculture* 376–379:90–96.
- Ahas, R. 1999. Long-term phyto-, ornitho- and ichthyophenological time-series analyses in Estonia. *International Journal of Biometeorology* 42:119–123.
- Ahas, R., and A. Aasa. 2006. The effects of climate change on the phenology of selected Estonian plant, bird and fish populations. *International Journal of Biometeorology* 51:17–26.
- Allan, J. D., P. B. McIntyre, S. D. P. Smith, B. S. Halpern, G. L. Boyer, A. Buchsbaum, G. A. Burton Jr., L. M. Campbell, W. L. Chadderton, J. J. H. Ciborowski, P. J. Doran, T. Eder, D. M. Infante, L. B. Johnson, C. A. Joseph, A. L. Marino, A. Prusevich, J. G. Read, J. B. Rose, E. S. Rutherford, S. P. Sowa, and A. D. Steinman. 2013. Joint analysis of stressors and ecosystem services to enhance restoration effectiveness. *Proceedings of the National Academy of Sciences of the USA* 110:372–377.
- Assel, R., K. Cronk, and D. Norton. 2003. Recent trends in Laurentian Great Lakes ice cover. *Climatic Change* 57:185–204.
- Assel, R., and D. M. Robertson. 1995. Changes in winter air temperatures near Lake Michigan, 1851–1993, as determined from regional lake-ice records. *Limnology and Oceanography* 40:165–176.
- Austin, J. A., and S. M. Colman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: a positive ice-albedo feedback. *Geophysical Research Letters* [online serial] 34:L06604.
- Austin, J. A., and S. M. Colman. 2008. A century of temperature variability in Lake Superior. *Limnology and Oceanography* 53:2724–2730.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* [online serial] 67:1.
- Bennington, V., G. A. McKinley, N. Kimura, and C. H. Wu. 2010. General circulation of Lake Superior: mean, variability, and trends from 1979 to 2006. *Journal of Geophysical Research* [online serial] 115:C12015.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–135.
- Bunnell, D. B., C. P. Madenjian, and R. M. Claramunt. 2006. Long-term change of the Lake Michigan fish community following the reduction of exotic Alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:2434–2446.
- Casselman, J. M. 2002. Effects of temperature, global extremes, and climate change on year-class production of warmwater, coolwater, and coldwater fishes in the Great Lakes basin. Pages 39–59 in N. A. McGinn, editor. *Fisheries in a changing climate*. American Fisheries Society, Symposium 32, Bethesda, Maryland.
- Ciereszko, R. E., K. Dabrowski, A. Ciereszko, J. Ebeling, and J. S. Ottobre. 1997. Effects of temperature and photoperiod on reproduction of female Yellow Perch *Perca flavescens*: plasma concentrations of steroid hormones, spontaneous and induced ovulation, and quality of eggs. *Journal of the World Aquaculture Society* 28:344–356.
- Cline, T. J., V. Bennington, and J. F. Kitchell. 2013. Climate change expands the spatial extent and duration of preferred thermal habitat for Lake Superior fishes. *PLoS (Public Library of Science) One* [online serial] 8(4):e62279.
- Crozier, L. G., and J. A. Hutchings. 2014. Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications* 7:68–87.
- Crozier, L. G., M. D. Scheuerell, and R. W. Zabel. 2011. Using time series analysis to characterize evolutionary and plastic responses to environmental change: a case study of a shift toward earlier migration date in Sockeye Salmon. *American Naturalist* 178:755–773.
- Dabrowski, K., R. E. Ciereszko, A. Ciereszko, G. P. Toth, S. A. Christ, D. El-Saidy, and J. S. Ottobre. 1996. Reproductive physiology of yellow perch (*Perca flavescens*): environmental and endocrinological cues. *Journal of Applied Ichthyology* 12:139–148.
- Desai, A. R., J. A. Austin, V. Bennington, and G. A. McKinley. 2009. Stronger winds over a large lake in response to weakening air-to-lake temperature gradient. *Nature Geoscience* 2:855–858.
- Ellis, D., and J. C. Vokoun. 2009. Earlier spring warming of coastal streams and implications for Alewife migration timing. *North American Journal of Fisheries Management* 29:1584–1589.
- Eschmeyer, P. H. 1955. The reproduction of Lake Trout in southern Lake Superior. *Transactions of the American Fisheries Society* 84:47–73.
- Goetz, F., S. Sitar, D. Rosauer, P. Swanson, C. R. Bronte, J. Dickey, and C. Simchick. 2011. The reproductive biology of Siscowet and lean Lake Trout in southern Lake Superior. *Transactions of the American Fisheries Society* 140:1472–1491.
- Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* [online serial] 2:e616.

- Jonsson, T., and M. Setzer. 2015. A freshwater predator hit twice by the effects of warming across trophic levels. *Nature Communications* [online serial] 6:5992.
- Juanes, F., S. Gephard, and K. Beland. 2004. Long-term changes in migration timing of adult Atlantic Salmon (*Salmo salar*) at the southern edge of the species distribution. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2392–2400.
- Kayes, T. B., and H. E. Calbert. 1979. Effects of photoperiod and temperature on the spawning of Yellow Perch (*Perca flavescens*). *Proceedings of the World Mariculture Society* 10:306–316.
- Kovach, R., A. J. Gharrett, and D. A. Tallmon. 2012. Genetic change for earlier migration timing in a Pink Salmon populations. *Proceedings of the Royal Society B* 279:3870–3878.
- Kovach, R., J. E. Joyce, J. D. Echave, M. S. Lindberg, and D. A. Tallmon. 2013. Earlier migration timing, decreasing phenotypic variation, and bio-complexity in multiple salmonid species. *PLoS (Public Library of Science) ONE* [online serial] 8:e53807.
- Krabbenhoft, T. J., S. P. Platania, and T. F. Turner. 2014. Interannual variation in reproductive phenology in a riverine fish assemblage: implications for predicting the effects of climate change and altered flow regimes. *Freshwater Biology* 59:1744–1754.
- Lynch, A. J., W. W. Taylor, and K. D. Smith. 2010. The influence of changing climate on the ecology and management of selected Laurentian Great Lakes fisheries. *Journal of Fisheries Biology* 77:1764–1782.
- Magnuson, J. J., J. M. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. *Transactions of the American Fisheries Society* 119:254–264.
- Magnuson, J. J., D. M. Robertson, B. J. Benson, R. H. Wynne, D. M. Livingstone, T. Arai, R. A. Assel, R. G. Barry, V. Card, E. Kuusisto, N. G. Granin, T. D. Prowse, K. M. Stewart, and V. S. Vuglinski. 2000. Historical trends in lake and river ice cover in the northern hemisphere. *Science* 289:1743–1746.
- Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, D. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler, and F. H. Quinn. 1997. Potential effects of climate change on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Pages 7–53 in C. E. Cushing, editor. *Freshwater ecosystems and climate change in North America, a regional assessment*. Wiley, *Advances in Hydrological Processes*, New York.
- Martin, N. V. 1957. Reproduction of Lake Trout in Algonquin Park, Ontario. *Transactions of the American Fisheries Society* 86:231–244.
- McCormick, M. J., and G. L. Fahnenstiel. 1999. Recent climatic trends in near-shore water temperatures in the St. Lawrence Great Lakes. *Limnology and Oceanography* 44:530–540.
- Moore, S. A., and C. R. Bronte. 2001. Delineation of sympatric morphotypes of Lake Trout in Lake Superior. *Transactions of the American Fisheries Society* 130:1233–1240.
- Nalepa, T. F., D. L. Fanslow, and G. A. Lang. 2009. Transformation of the off-shore benthic community in Lake Michigan: shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. *Freshwater Biology* 54:466–479.
- Nöges, P., and A. Järvet. 2005. Climate driven changes in the spawning of roach (*Rutilus rutilus* (L.)) and bream (*Abramis brama* (L.)) in the Estonian part of the Narva River basin. *Boreal Environment Research* 1:45–55.
- Otero, J., J. H. L'Abée-Lund, T. Castro-Santos, K. Leonardsson, G. O. Storvik, B. Jonsson, B. Dempson, I. C. Russell, A. J. Jensen, J.-L. Baglinière, M. Dionne, J. D. Armstrong, A. Romakaniemi, B. H. Letcher, J. F. Kocik, J. Erkinaro, R. Poole, G. Rogan, H. Lundqvist, J. C. Maclean, E. Jokikokko, J. V. Arnekleiv, R. J. Kennedy, E. Niemela, P. Caballero, P. A. Music, T. Antonsson, S. Gudjonsson, A. E. Veselov, A. Lamberg, S. Groom, B. H. Taylor, M. Taberner, M. Dillane, F. Arnason, G. Horton, N. A. Hvidsten, I. R. Jonsson, N. Jonsson, S. McKelvey, T. F. Næsje, Ø. Skaala, G. W. Smith, H. Sægrov, N. C. Stenseth, and L. A. Vøllestad. 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic Salmon (*Salmo salar*). *Global Change Biology* 20:61–75.
- Parnesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Peer, A. C., and T. J. Miller. 2014. Climate change, migration phenology, and fisheries management interact with unanticipated consequences. *North American Journal of Fisheries Management* 34:94–110.
- Peeters, F., D. Sraile, A. Lorke, and D. M. Livingstone. 2007. Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Global Change Biology* 13:1898–1909.
- Post, E. 2013. *Ecology of climate change. The importance of biotic interactions*. Princeton University Press, Princeton, New Jersey.
- Post, J. R., and A. B. Prankevicius. 1987. Size-selective mortality in young-of-the-year Yellow Perch (*Perca flavescens*): evidence from otolith microstructure. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1840–1847.
- Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migration timing of American Shad and Sockeye Salmon. *Ecology* 77:1151–1162.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: <http://www.R-project.org/>. (June 2015).
- Rao, C. R. 1973. *Linear statistical inference and its applications*, 2nd edition. Wiley, New York.
- Russell, I. C., M. W. Aprahamian, J. Barry, I. C. Davidson, P. Fiske, A. T. Ibbotson, R. J. Kennedy, J. C. Maclean, A. Moore, J. Otero, E. C. E. Potter, and C. D. Todd. 2012. The influence of freshwater environment and the biological characteristics of Atlantic Salmon smolts in their subsequent marine survival. *ICES Journal of Marine Science* 69:1563–1573.
- 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* 139:1198–2010.
- Schneider, P., and S. J. Hook. 2010. Space observations of inland water bodies show rapid surface warming since 1985. *Geophysical Research Letters* [online serial] 37:L22405.
- Scott, W. B., and E. J. Crossman. 1973. *Freshwater fishes of Canada*. *Bulletins of the Fisheries Research Board of Canada* 184.
- Taylor, S. G. 2008. Climate warming causes phenological shift in Pink Salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Global Change Biology* 14:229–235.
- Thackeray, S. J., P. A. Henrys, H. Feuchtmayr, I. D. Jones, S. C. Maberly, and I. J. Winfield. 2013. Food web de-synchronization in England's largest lake: an assessment based on multiple phenological metrics. *Global Change Biology* 19:3568–3580.
- Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthes, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalhos, T. Clutton-Brock, A. Dawson, M. Edwards, J. M. Elliot, R. Harrington, D. Johns, I. D. Jones, J. T. Jones, D. I. Leech, D. B. Roy, W. A. Scott, M. Smith, R. J. Smithers, I. J. Winfield, and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* 16:3304–3313.
- Thorpe, J. E. 1977. Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *P. flavescens* Mitchell. *Journal of the Fisheries Research Board of Canada* 34:1504–1514.
- Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences* 272:2561–2569.
- Warren, D. R., J. M. Robinson, D. C. Josephson, D. R. Sheldon, and C. E. Kraft. 2012. Elevated summer temperatures delay spawning and reduce redd construction for resident Brook Trout (*Salvelinus fontinalis*). *Global Climate Biology* 18:1804–1811.
- Wedekind, C., and C. Küng. 2010. Shift of spawning season and effects of climate warming on developmental stages of a grayling (*Salmonidae*). *Conservation Biology* 24:1418–1423.
- Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85:2100–2106.
- Wright, P. J., and E. A. Trippel. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish and Fisheries* 10:283–304.