Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*)

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Abstract

Redd (nest) surveys for resident brook trout (*Salvelinus fontinalis*) were conducted annually in a mountain lake in northern New York for 11 years with multiple surveys conducted during the spawning season in eight of those years. Repeated surveys throughout the spawning season allowed us to fit an individually based parametric model and estimate the day of year on which spawning was initiated, reached its midpoint, and ended during each year. Spawning phenology was then assessed relative to (1) mean of maximum daily air temperature and (2) mean of maximum daily water temperature at the lake bottom during summer in each year using a linear model. Elevated temperatures in summer were correlated with a delay in spawning and a reduction in the total number of redds constructed. Increasing the summer mean of maximum daily air temperatures by 1 °C delayed spawning by approximately 1 week and decreased the total number of redds constructed by nearly 65. Lake spawning brook trout select redd sites based on the presence of discharging groundwater that is relatively constant in temperature within and across years, leading to relatively consistent egg incubation times. Therefore, delayed spawning is likely to delay fry emergence, which could influence emergence synchrony with prey items. This work highlights non-lethal and sub-lethal effects of elevated summer temperatures on native resident salmonids in aquatic environments with limited thermal refugia.

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Introduction

Global and regional climate models predict increases in temperature across the north temperate eco-region over the next century (Bell *et al.*, 2004; Hayhoe *et al.*, 2007; Plattner *et al.*, 2008), and these changing climate conditions are expect to lead to associated increases in stream and lake temperatures (Magnuson *et al.*, 1997; Jansen & Hesslein, 2004; Keller, 2007; Isaak *et al.*, 2010). The influence of changing climate on the timing of life-history events (phenology) has been well-established for a wide variety of species, with clear links between temperature and phenologic events such as bud-break, first flower, insect emergence, or migration timing for birds and butterflies (Parmesan & Yohe, 2003; Parmesan, 2006). Most research evaluating climate impacts on fish phenology has focused on marine or migratory freshwater species with relatively little attention paid to resident freshwater populations (Quinn & Adams, 1996; Dahl *et al.*, 2004; Bryant, 2009; Jonsson & Jonsson, 2009; Scheuerell *et al.*, 2009; Pankhurst & Munday, 2011; Rogers & Schindler, 2011). However, the effects of changing temperature conditions are likely to be particularly important for resident fish, which often have limited capacity to move away or migrate long distances in response to thermally stressful conditions. Indeed, resident freshwater fish – particularly thermally sensitive salmonid species – are expected to be increasingly exposed to sub-optimal temperature conditions through the summer. A number of studies predict a reduction in the distribution of resident salmonids across North America in response to climate change (Meisner, 1990a; Flebbe *et al.*, 2006; Wenger *et al.*, 2011), but the potential impact of changing climate conditions on the phenology of these resident fish has received little attention. In this work we use an 11-year data set to quantify relationships between

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summer climate and fall spawning activity (both timing and the abundance of redds – spawning nests) for resident brook trout (*Salvelinus fontinalis*) in a mountain lake ecosystem with limited thermal refugia.

Spawning phenology is a key life history trait in fish that has substantial implications for the survival of eggs and early life stages (Fausch *et al.*, 2001; Skoglund *et al.*, 2011). While the general timing of spawning for most salmonid species is seasonally consistent and broadly established by photoperiod [e.g. brook trout spawn in the fall and rainbow trout (*Oncorhynchus mykiss*) spawn in the spring], local factors can control the specific timing of spawning within a broader seasonal window (Holcombe *et al.*, 2000). For anadromous and potamodromous salmonids, the timing of migration is often used as a proxy for spawning phenology itself and has been tied to a number of environmental cues including river discharge and both river and ocean temperature (Trepanier *et al.*, 1996; Dahl *et al.*, 2004; Strange, 2010; Wedekind & Kung, 2010), as well as life-history trade-off decisions influenced by size and associated fecundity (Elliott & Hurley, 1998). However, migration and spawning phenology important for resident salmonids are more difficult to evaluate. Few studies have quantified spawning timing for resident salmonids and no studies have evaluated more than 2 years of field data examining the influence of climate on spawning phenology for resident salmonids (Blanchfield & Ridgway, 1997).

We expect a close association between spawning phenology and temperature across the North American continent because fish are ectothermic with physiological processes associated with reproduction strongly influenced by the temperatures to which they are exposed (Brett, 1970; Jobling, 1995; Luksiene & Svedang, 1997; Falke *et al.*, 2010). All fish have a thermal range over which they can survive and a smaller window within which growth is optimized. Fish metabolic rates are elevated in warmer water and therefore require more food consumption to grow than under cold water conditions (see review by Jonsson & Jonsson, 2009). Consequently, in addition to stress associated with survival at the edge of one's physiological capability, food limitation may be exacerbated at the upper end of a fish's thermal range. Under these conditions, gonad development, which occurs over many months, can be slowed, temporarily arrested, or in extreme cases, aborted entirely – all of which have substantial implications for the timing and amount of subsequent spawning (Hokanson *et al.*, 1977; Luksiene & Svedang, 1997; Mccarthy & Houlihan, 1997; Pankhurst & King, 2010).

This study addresses sub-lethal effects of climate change and specifically asks whether changing summer temperatures are likely to influence spawning phenology and overall spawning activity of resident salmonids in a lake ecosystem with limited thermal refugia. We were particularly interested in determining whether or not there was a significant relationship between spawning activity and air temperature in this study. The vast majority of climate models include air temperature as a key response variable, so a significant relationship between summer air temperatures and spawning activity of resident fish may allow for broader interpretation of these model results with regard to anticipated non-lethal effects of climate change on aquatic communities.

Methods

Study site

This study was conducted in Rock Lake, an unstratified lake in the central Adirondack Mountains of New York State. Rock Lake is located within the Adirondack Park of New York (43° 57′N, 74°52′W) near the southern boundary of the range of lentic brook trout populations. Rock Lake has a surface area of 78.9 ha and a maximum depth of 5.5 m. Brook trout are the only fish species inhabiting the lake. Since the cessation of stocking in 2002, the brook trout population has been sustained solely by natural reproduction of fish spawning on in-lake shoals and one small tributary. Rock Lake is relatively well buffered (pH > 5.7 in spring and >5.9 in summer) and has high water clarity (>3 m). Additional details regarding the characteristics of Rock Lake are presented in Robinson *et al.* (2010) and Robinson (2008).

Due to the absence of a thermocline during summer months, water temperatures in an unstratified lake are likely to correlate with summer air temperature. In Rock Lake, the temperatures that adult fish experience during the summer are not significantly different from water temperatures measured on the lake bottom, indicating limited summer thermal refuge for adult brook trout (Robinson, 2008). With no deep-water thermal refuge, the conditions that fish in Rock Lake experience during summer – an important period for gonad development in brook trout – are closely associated with both air and water temperatures. The Rock Lake brook trout population is closed (i.e. self-contained) due to the absence of substantial tributaries and the presence of a barrier that prevents the return of emigrating fish via an outlet stream. Given its relatively uniform benthic temperatures in summer and a closed brook trout population, Rock Lake is well-suited to evaluate the influence of climate on the spawning phenology of a wild resident salmonid fish population.

Redd counts and temperature data

Reproductive effort (spawning) was quantified by conducting whole-lake redd (nest) surveys from 1998 to 2010. The number of redd surveys in a year varied from a single survey in early November (years 1998, 1999, 2001, 2002, 2003) to as many as

6 weekly surveys from mid-October to mid-November (2007). A minimum of three surveys were conducted annually from 2004 to 2010. During years in which only one survey was conducted, redds were counted during the second week of November (after Day 310). All visible redds were counted by two individuals from a small boat navigating the entire lake shoreline along the 2-m depth contour. Brook trout redds on the spawning shoals accumulate over the course of the fall as spawning activity increases. Although no specific repeated measure of redd counts was conducted to assess error in the counts themselves, redd count surveys were conducted by the same individuals over multiple years, thereby reducing observer bias and providing a high degree of internal consistency (D. Josephson participated in all redd counts for all 11 years and J. Robinson participated in all redd counts in 8 of the 11 years). In addition, redd counts increased regularly in years with multiple surveys, and estimates were more comparable toward the end of spawning when new redds are uncommon, which also suggests internal consistency in the counts.

The use of redd surveys as a proxy for spawning has been criticized in some cases because female trout can construct multiple test pits before depositing their eggs (false redds) and other females dig redds on top of existing redds (redd superimposition) (Maxell, 1999; Dunham *et al.*, 2001; Muhlfeld *et al.*, 2006). For the purposes of this study, the construction of false redds does not compromise the analysis. We are not estimating the spawning population from these redd counts; rather, we are using redd counts as a measure of spawning activity and both false and real redds represent active spawning. The total number of redds is a relative measure to which a parametric model was fit (see next). Although redd superimposition could potentially lead to an underestimate of total redds (Essington *et al.*, 1998), superimposition is likely to be limited early in the spawning season in our study lake when redd densities are low. This process is therefore unlikely to influence our estimate for the onset and mid-point of spawning, though it may affect the final redd count estimate in years with a large amount of spawning activity.

Shoreline air temperature and lake water temperature at 5.5 m depth were measured with temperature data loggers from June through September at 1-hour intervals. We used two temperature metrics to evaluate the relationship between summer temperature and brook trout spawning: (1) the mean of the maximum daily water temperature at the lake bottom (5.5 m) in summer (from June 10 to September 10), and (2) the mean of maximum daily air temperature along the lake shoreline in summer (from June 10 to September 10); hereafter 'water temperature' and 'air temperature', respectively.

Analysis

In the years with multiple redd count surveys (2000, 2004–2010) we estimated the onset, mid-point, and end of spawning activity by fitting an individually based parametric model for the timing of redd construction (henceforth: *redd timing model*) to the survey data (see Appendix S1 for the Matlab code and Appendix S2 for example input data with associated example output from the model). The model assumes that an unknown number of redds (N) are constructed in a given year, with each date chosen independently from a normal distribution with mean date μ and variance σ^2. The counts of the number of redds constructed in the time intervals between successive surveys were analogous to what are referred to as 'grouped lifetime data' in survival analysis (Lawless, 2003; Section 4.3). For each year, we fit the parameters N, μ, and σ^2 by maximum likelihood, using general-purpose numerical optimization for the maximization with respect to μ, and σ^2, and closed form estimates for N (Sanathan, 1972). In 2005, no redds were observed in any of the three surveys so no model could be fit for that year. Based on the fitted model parameters we estimated the day of year on which a given proportion of the total redds were constructed for each year. We used the day of year on which 5% of redds were constructed as an estimate for onset of spawning. The day of year on which 50% of redds were constructed (fitted μ) represents the mid-point of the spawning season (and likely reflects the general period of peak spawning). Finally, the day of year on which 95% of redd construction was completed was used as an estimate of the date on which spawning ended in a given year. We obtained 95% confidence intervals around the estimated mean date μ (mid-point of spawning) using the observed Fisher information matrix (Lawless, 2003, p. 548), which was computed by the same numerical optimization routine used to find the maximum likelihood estimates. We also assessed the fit graphically for all 7 years.

A linear model was used to evaluate the relationships between summer temperatures (air or water) and point-estimates for the day of year on which spawning was initiated, on which spawning peaked (mid-point of spawning assuming a normal distributions), and the end of spawning over the course of the study. The total number of redds counted in each year (including single survey years) was also evaluated as a function of summer air temperatures and summer water temperatures.

Results

For years with three or more redd surveys per spawning season (2004–2010), the redd timing model fit our data well. Given the data available and the nature of the model, we have the greatest confidence in the timing for the mid-point of spawning each year (relative to the onset or end of spawning). In years when three or more surveys were conducted, the 95% confidence intervals for the mid-point (peak) of spawning ranged from plus or minus 2.6 days to plus or minus 6.9 days (Table 1). However, in 2000, when only two survey data points were available, model fit was poor with a 95% confidence interval of plus or minus 178.6 days around the estimated day of year for the mid-point of spawning. A primary source of uncertainty in this year resulted from the unknown total number of redds. We repeated the analysis for the year 2000 while constraining the total number of redds to two specific values

Table 1 Estimated day of year for the onset, midpoint, and end of spawning as well as total estimated number of redds as calculated by the redd timing model for each of the years with multiple annual surveys and redds present (no redds were observed in 2005). The 95% confidence interval around the 50th percentile value (fitted μ) is equivalent to the 95% confidence around the mean in this analysis. Sigma represents an estimate of variability around the mean for the fitted model

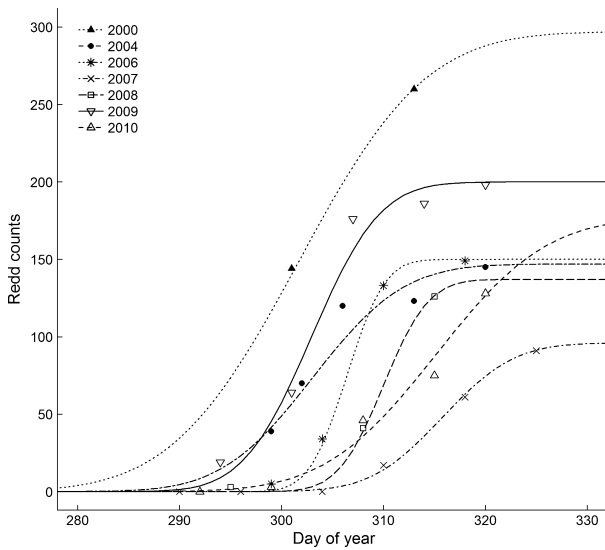| Year	5th% (onset)	50th% (midpoint)	95th% (end)	Total number of redds	± 95% CI the 50th% (mid-point)	Sigma	± 95% CI around sigma
2000	285.5	301.7	317.8	297	178.6	9.8	286.0
2004	291.5	303.0	314.6	147	2.6	7.0	3.5
2006	301.7	306.4	311.2	150	6.8	2.9	8.4
2007	306.7	315.8	324.9	96	3.1	5.5	4.2
2008	304.2	310.0	315.7	137	5.6	3.5	6.1
2009	294.3	303.0	311.6	200	4.4	5.3	5.2
2010	301.1	315.1	329.2	177	2.8	8.6	3.0

Fig. 1 Model estimates and observed redd counts for years with multiple surveys: 2000, 2003, 2004, 2006, 2007, 2008, 2009, 2010. Lines represent the fitted models for each year.

Fig. 2 Influence of (a) summer maximum daily air temperature and (b) maximum daily lake-bottom (5.5 m) temperature on brook trout spawning phenology in years with multiple surveys. Summer temperature metrics are evaluated relative to the day of year on which (1) spawning was initiated (5% of redds constructed; triangles), (2) the mid-point of spawning (50% of redds constructed; circles) and (3) the end of spawning (95% of redds constructed; X's) as estimated from the redd timing model fit to repeated redd survey observations. Solid lines represent a significant relationship.

within a wide range of potential total redds, 260 (the count on day 313) and 400 (twice the largest count from any other year). With these constraints the confidence intervals were always smaller than plus or minus 4 days, and the mid-point estimate shifted by fewer than 7 days. Overall, graphical assessment of the data also indicated a good model fit for all years (Fig. 1).

Brook trout spawning phenology was positively related to summer air and water temperatures in Rock Lake. The mid-point of the spawning period (50% of redd construction) occurred 8.6 days later for every additional degree of mean maximum daily shoreline air temperature in summer ($r^2 = 0.68$, F = 10.94, $P = 0.02$; Fig. 2a) and 7.0 days later for each additional degree of mean maximum daily lake-bottom water temperature in summer ($r^2 = 0.76$, F = 16.27, $P = 0.01$; Fig. 2b). The date for the onset of spawning (5% of redd
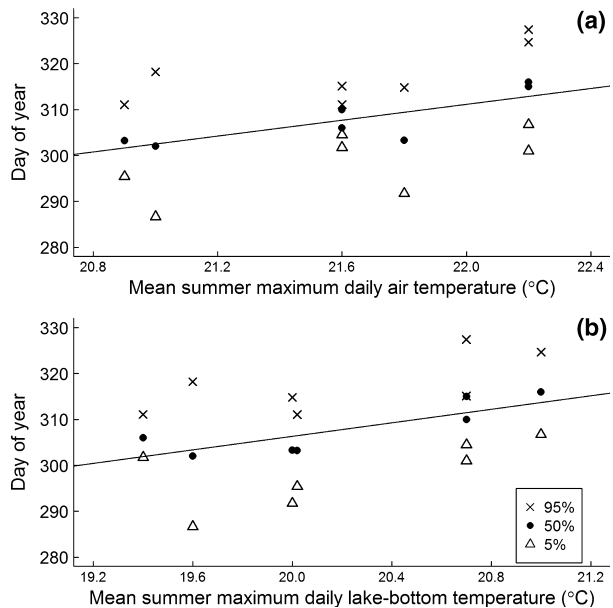
construction) was similarly related to summer air temperatures with the onset of spawning occurring later in warmer years, but the relationships were not significant (slope = 9.0, $r^2 = 0.42$, F = 3.66, $P = 0.11$, and slope = 7.0, $r^2 = 0.44$, F = 3.97 $P = 0.10$ for shoreline air and lake-bottom water temperature relationships, respectively; Fig. 2). The day of year on which 95% of redds were constructed was also positively related to both summer air temperatures and summer water temperatures,

but these relationships also were not significant at $\alpha = 0.05$ (slope = 8.3, $r^2 = 0.46$, F = 4.33, $P = 0.09$, and slope = 7.0, $r^2 = 0.55$, F = 6.14, $P = 0.06$ for summer air temperatures and summer water temperatures, respectively; Fig. 2).

Both summer air temperatures and summer water temperatures were significantly negatively related to the annual total number of redds constructed over the 11 years of this study. Summer air temperatures accounted for 79% of the variability in total redd construction annually ($r^2 = 0.79$, F = 33.61, $P < 0.001$; Fig. 3a), and summer water temperatures accounted for 83% of the variability in total redd construction annually ($r^2 = 0.83$, F = 43.22, $P < 0.001$; Fig. 3b). The projected total number of redds based on the redd timing model for the 7 years that the model could be fit was also significantly related to the summer air temperatures ($r^2 = 0.56$, F = 7.13, $P = 0.04$). Overall, our analyses indicated that each one-degree (C) increase in the mean of maximum daily air temperatures from June to September yielded approximately a 1-week delay in the onset of spawning and approximately 65 fewer total redds constructed in a given year (22–65% of the total redd count in a given year).

Discussion

This study demonstrates a clear relationship between summer temperatures and brook trout spawning activ-
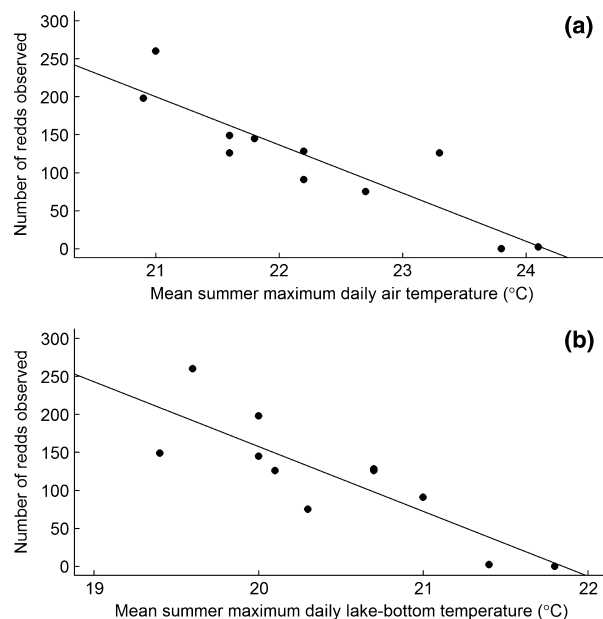

Fig. 3 Relationships between maximum number of redds counted each year and (a) mean of the maximum daily air temperature or (b) mean of the maximum daily lake bottom temperature during summer.

ity. Increased summer water temperatures in the study lake and increased air temperatures along the lake shoreline were correlated with a delay in spawning and a decrease in the total number of redds in Rock Lake. Fish populations and thermal regimes in Rock Lake are tightly constrained, thereby facilitating our ability to evaluate *in situ* the impacts of elevated summer temperature on resident brook trout spawning activity; however, thermal conditions in Rock Lake are not unique. Many wild brook trout populations inhabit mountain lakes throughout North America where changing climate conditions are expected to substantially reduce the availability of summer thermal refugia for salmonids (Jansen & Hesslein, 2004; Keller, 2007).

While deep lakes provide salmonid fishes with a thermal refuge from warm summer temperatures within the hypolimnion, a warming summer climate may reduce or eliminate stratification within shallow lakes (Magnuson *et al.*, 1997; Elliott & Elliott, 2010). The thermal conditions observed in Rock Lake over the past 11 years – with lake bottom temperatures that correlate well with air temperatures and which often reach stressful levels for a period of time during mid-summer – are likely to reflect an increasingly common scenario for future populations of brook trout and other coldwater species across the southern end of their lentic range (Jansen & Hesslein, 2004; Keller, 2007). Therefore, in addition to anticipated range contractions and the loss of thermal refuge for salmonids in response to future climate conditions (Meisner, 1990a,b; Schindler *et al.*, 1996; Magnuson *et al.*, 1997; Flebbe *et al.*, 2006), our work suggests that we can also expect changes in the timing and amount of spawning.

Delayed spawning is likely to translate directly to delayed fry emergence for lentic brook trout. Egg incubation and subsequent fry emergence is dependent on degree-day accumulation at specific redd locations (Baird *et al.*, 2002). Elevated incubation temperatures increase the rate of egg development and thereby promote earlier fry emergence, while decreased incubation temperatures decrease the rate of development and delay emergence. A constant incubation temperature from year to year will therefore yield consistent incubation rates with fry emergence times dependent upon spawning dates (Curry *et al.*, 1995). Lake-spawning brook trout build their redds almost exclusively on discharging groundwater that is constant in temperature within and across years (Webster & Eiriksdottir, 1976; Curry & Noakes, 1995; Blanchfield & Ridgway, 1997). In Rock Lake and other lakes with shoal-spawning brook trout, spawning occurs year after year at the same areas of groundwater discharge. Therefore, egg incubation times are likely to remain consistent, leading to a close association between the date of spring fry

emergence and the timing of brook trout spawning during the previous fall.

For many species emergence is timed to coincide with periods of elevated food availability and large deviations in the time of emergence can impact the success of juveniles (Einum & Fleming, 2000). As demonstrated in stocking experiments by Letcher *et al.* (2004), the date at which fry arrive in a system can have substantial implications for individual growth and cohort survival. The synchrony of prey population dynamics with brook trout fry emergence has not been assessed for the Rock Lake population or any other lentic brook trout population. Broadly, warmer temperatures in spring will likely lead to earlier phytoplankton blooms and associated successional dynamics in zooplankton populations (Sommer *et al.*, 2007; Berger *et al.*, 2010; Shimoda *et al.*, 2011), and warmer temperatures in summer will likely delay fry emergence in lake-spawning brook trout populations (this study). With anticipated increases in both spring and summer temperatures (Hayhoe *et al.*, 2007), we can expect a trend toward earlier peaks in prey availability and later fry emergence thereby increasing the potential for asynchrony between brook trout fry and their prey.

The correlation between warmer summer temperatures and both the timing and magnitude of spawning by brook trout is likely due to delayed or diminished gonad development in adult trout. Fish metabolism increases with increasing temperature, which in turn increases demand for food. Elevated summer temperatures that increase metabolism divert energy from growing season gonad development and reduce the storage of fat that is needed in the fall to complete gonad development (Luksiene & Svedang, 1997; Pankhurst & Munday, 2011). Beyond these direct effects on fish metabolism, additional stress responses associated with elevated thermal regimes (e.g. generation of heat-shock proteins) further reduce energy available for storage in fat or gonads (Luksiene & Svedang, 1997; Pankhurst & Munday, 2011). Prolonged periods of elevated summer temperature at a time when fat reserves are static or reduced are therefore likely to substantially reduce or delay subsequent reproductive capacity. In the long term, given anticipated changes in air and lake temperatures in northeastern North America, delayed and reduced spawning are likely to become increasingly common in this study lake and other lakes throughout the southern range of lentic brook trout.

The negative relationship between summer temperatures and total redd density is an additional key finding from this study. This result builds upon a previous study in Rock Lake in which we documented a negative relationship between summer water temperatures and the maximum number of redds constructed in a

given year (Robinson *et al.*, 2010). In addition to further developing the relationship between water temperature and total redd counts, our current analysis also demonstrates a clear negative relationship between air temperatures and redd density. This reduction in redd density following warmer summers can then affect population abundance in future years. In unusually warm years such as 2005, when temperatures were elevated throughout the summer, no redds were observed in the fall and the 2006 year class was lost entirely (Robinson *et al.*, 2010). In 2002, another particularly warm year in which the number of redds was diminished, Robinson *et al.* (2010) reported a substantial decline in the 2003 year class that also carried through subsequent years. A loss or reduction in year class strength is an important sub-lethal or partially lethal effect of elevated temperatures in lake systems. Here and in comparable systems, there is increasing potential for diminished abundance or even extirpation of brook trout populations following years with elevated summer temperatures. Although the brook trout population in this ecosystem is clearly resilient to occasional year class losses, it remains vulnerable to repeated years with elevated summer temperatures.

Blanchfield & Ridgway (1997) found a link between fall lake temperatures and the period of peak spawning in 2 years for lentic brook trout in a Canadian lake. In their study, the period of peak spawning was associated with declining water temperatures (below 11° C) and the presence of large rainfall events, which the authors suggested were factors promoting spawning synchrony within the breeding population. Although we found no significant relationship in our study lake between the day of year when lake temperatures fell below 11° C and the day of year at which 50% of redds were constructed (which should correspond approximately to the period of peak spawning), proximate cues near the time of spawning initiation such as changing lake temperature or an influx of water to a lake are also likely to be important local factors for synchronizing spawning in our system. While we suggest that gonad development and resource allocation throughout a stressful summer are key contributors to spawning phenology, cues that occur close to the initiation and peak of spawning are likely to account for some of the unexplained variation in our analyses.

Although fish are directly affected by water temperatures rather than air temperatures, we included air temperature in this analysis to improve the applicability of our results to a larger body of available modeled and empirical data. Air temperature changes – particularly changes in air temperature extremes – are common climate model outputs (Allen *et al.*, 2000; Plattner *et al.*, 2008; Tague *et al.*, 2009), and a greater

number of long-term data sets are available for air temperature than for lake-bottom temperatures. Evaluating brook trout phenology in response to air temperature therefore allows the greatest potential for the generalization and application of these results to the existing climate literature.

Our results demonstrate that temperature conditions in summer are closely associated with the phenology of a fall-spawning trout in ecosystems where thermal refugia are limited. The delay and reduction in spawning documented here are an important sublethal effect to consider in lakes or streams that lack thermal refugia in the face of changing climate conditions (Mccullough *et al.*, 2009). More broadly, our study lake is similar to lake ecosystems within the broad north-temperate ecoregion (including Europe, Asia and North America) that is expected to experience an increase in mean temperatures and periods of elevated temperatures in summer throughout the coming century. Although we focus on a specific lake ecosystem and one focal species, our study results are relevant to the many temperate streams and lakes globally that support resident coldwater fish, and salmonids in particular.

Acknowledgements

References

Allen MR, Stott PA, Mitchell JFB, Schnur R, Delworth TL (2000) Quantifying the uncertainty in forecasts of anthropogenic climate change. *Nature*, **407**, 617–620.

Baird HB, Krueger CC, Josephson DC (2002) Differences in incubation period and survival of embryos among brook trout strains. *North American Journal of Aquaculture*, **64**, 233–241.

Bell JL, Sloan LC, Snyder MA (2004) Regional changes in extreme climatic events: a future climate scenario. *Journal of Climate*, **17**, 81–87.

Berger SA, Diehl S, Stibor H, Trommer G, Ruhenstroth M (2010) Water temperature and stratification depth independently shift cardinal events during plankton spring succession. *Global Change Biology*, **16**, 1954–1965.

Blanchfield PJ, Ridgway MS (1997) Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 747–756.

Brett JR (1970) Temperature relations in physiology and freshwater ecology of sockeye salmon, *Oncorhynchus nerka*. *American Zoologist*, **10**, 314.

Bryant MD (2009) Global climate change and potential effects on Pacific salmonids in freshwater ecosystems of southeast Alaska. *Climatic Change*, **95**, 169–193.

Curry RA, Noakes DLG (1995) Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1733–1740.

Curry RA, Noakes DLG, Morgan GE (1995) Groundwater and the incubation and emergence of brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1741–1749.

Dahl J, Dannewitz J, Karlsson L, Petersson E, Lof A, Ragnarsson B (2004) The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology*, **82**, 1864–1870.

Dunham J, Rieman B, Davis K (2001) Sources and magnitude of sampling error in redd counts for bull trout. *North American Journal of Fisheries Management*, **21**, 343–352.

Einum S, Fleming IA (2000) Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, **54**, 628–639.

Elliott JM, Elliott JA (2010) Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salmo alpinus*: predicting the effects of climate change. *Journal of Fish Biology*, **77**, 1793–1817.

Elliott JM, Hurley MA (1998) An individual-based model for predicting the emergence period of sea trout fry in a Lake District stream. *Journal of Fish Biology*, **53**, 414–433.

Essington TE, Sorensen PW, Paron DG (1998) High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 2310–2316.

Falke JA, Fausch KD, Bestgen KR, Bailey LL (2010) Spawning phenology and habitat use in a Great Plains, USA, stream fish assemblage: an occupancy estimation approach. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 1942–1956.

Fausch KD, Taniguchi Y, Nakano S, Grossman GD, Townsend CR (2001) Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecological Applications*, **11**, 1438–1455.

Flebbe PA, Roghair LD, Bruggink JL (2006) Spatial modeling to project southern Appalachian trout distribution in a warmer climate. *Transactions of the American Fisheries Society*, **135**, 1371–1382.

Hayhoe K, Wake C, Huntington TG *et al.* (2007) Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynamics*, **28**, 381–407.

Hokanson KEF, Kleiner CF, Thorslund TW (1977) Effects of constant temperatures and diel temperature-fluctuations on specific growth and nortality-rates and yield of juvenile rainbow trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada*, **34**, 639–648.

Holcombe GW, Pasha MS, Jensen KM, Tietge JE, Ankley GT (2000) Effects of photoperiod manipulation on brook trout reproductive development, fecundity, and circulating sex steroid concentrations. *North American Journal of Aquaculture*, **62**, 1–11.

Isaak DJ, Luce CH, Rieman BE *et al.* (2010) Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications*, **20**, 1350–1371.

Jansen W, Hesslein RH (2004) Potential effects of climate warming on fish habitats in temperate zone lakes with special reference to Lake 239 of the experimental lakes area (ELA), north-western Ontario. *Environmental Biology of Fishes*, **70**, 1–22.

Jobling M (1995) *Environmental biology of fishes*. Springer-Verlag, New York.

Jonsson B, Jonsson N (2009) A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, **75**, 2381–2447.

Keller W (2007) Implications of climate warming for Boreal Shield lakes: a review and synthesis. *Environmental Reviews*, **15**, 99–112.

Lawless JF (2003) *Statistical Models and Methods for Lifetime Data* (2nd edn). Wiley, New Jersey.

Letcher BH, Dubreuil T, O'donnell MJ, Obedzinski M, Griswold K, Nislow KH (2004) Long-term consequences of variation in timing and manner of fry introduction on juvenile Atlantic salmon (*Salmo salar*) growth, survival, and life-history expression. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 2288–2301.

Luksiene D, Svedang H (1997) *A review on fish reproduction with special reference to temperature anomalies*. Fiskeriverket, Kustlaboratoriet, regrund, 35 pp.

Magnuson JJ, Webster KE, Assel RA *et al.* (1997) Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. *Hydrological Processes*, **11**, 825–871.

Maxell BA (1999) A prospective power analysis on the monitoring of bull trout stocks using redd counts. *North American Journal of Fisheries Management*, **19**, 860–866.

Mccarthy ID, Houlihan DF (1997) The effect of temperature on protein synthesis in fish: the possible consequences for wild Atlantic salmon (*Salmo salar L.*) stocks in Europe as a result of global warming. In: *Global Warming: Implications for Fresh- water and Marine Fish* (eds Wood CM, Mcdonald G), pp. 51–77. Cambridge University Press, Cambridge.

Mccullough DA, Bartholow JM, Jager HI *et al.* (2009) Research in thermal biology: burning questions for coldwater stream fishes. *Reviews in Fisheries Science*, **17**, 90–115.

Meisner JD (1990a) Effect of climatic warming on the southern margins of the native range of brook rrout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 1065–1070.

Meisner JD (1990b) Potential loss of thermal habitat for brook trout, due to climatic warming, in 2 southern Ontario streams. *Transactions of the American Fisheries Society*, **119**, 282–291.

Muhlfeld CC, Taper ML, Staples DF, Shepard BB (2006) Observer error structure in bull trout redd counts in Montana streams: implications for inference on true redd numbers. *Transactions of the American Fisheries Society*, **135**, 643–654.

Pankhurst NW, King HR (2010) Temperature and salmonid reproduction: implications for aquaculture. *Journal of Fish Biology*, **76**, 69–85.

Pankhurst NW, Munday PL (2011) Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research*, **62**, 1015–1026.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Plattner GK, Knutti R, Joos F *et al.* (2008) Long-term climate commitments projected with climate-carbon cycle models. *Journal of Climate*, **21**, 2721–2751.

Quinn TP, Adams DJ (1996) Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology*, **77**, 1151–1162.

Robinson JM (2008) *Effects of summer thermal conditions on brook trout (Salvelinus fontinalis) in an unstratified Adirondack Lake.* Unpublished MS thesis, Cornell University, Ithaca, NY.

Robinson JM, Josephson DC, Weidel BC, Kraft CE (2010) Influence of variable inter-annual summer water temperatures on brook trout growth, consumption, reproduction, and nortality in an unstratified Adirondack lake. *Transactions of the American Fisheries Society*, **139**, 685–699.

Rogers LA, Schindler DE (2011) Scale and the detection of climatic influences on the productivity of salmon populations. *Global Change Biology*, **17**, 2546–2558.

Sanathan L (1972) Estimating size of a multinomial population. *Annals of Mathematical Statistics*, **43**, 142.

Scheuerell MD, Zabel RW, Sandford BP (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus spp.*). *Journal of Applied Ecology*, **46**, 983–990.

Schindler DW, Curtis PJ, Parker BR, Stainton MP (1996) Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. *Nature*, **379**, 705–708.

Shimoda Y, Azim ME, Perhar G *et al.* (2011) Our current understanding of lake ecosystem response to climate change: what have we really learned from the north temperate deep lakes? *Journal of Great Lakes Research*, **37**, 173–193.

Skoglund H, Einum S, Robertsen G (2011) Competitive interactions shape offspring performance in relation to seasonal timing of emergence in Atlantic salmon. *Journal of Animal Ecology*, **80**, 365–374.

Sommer U, Aberle N, Engel A *et al.* (2007) An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. *Oecologia*, **150**, 655–667.

Strange JS (2010) Upper thermal limits to migration in adult Chinook salmon: evidence from the Klamath River basin. *Transactions of the American Fisheries Society*, **139**, 1091–1108.

Tague C, Seaby L, Hope A (2009) Modeling the eco-hydrologic response of a Mediterranean type ecosystem to the combined impacts of projected climate change and altered fire frequencies. *Climatic Change*, **93**, 137–155.

Trepanier S, Rodriguez MA, Magnan P (1996) Spawning migrations in landlocked Atlantic salmon: time series modeling of river discharge and water temperature effects. *Journal of Fish Biology*, **48**, 925–936.

Webster DA, Eiriksdottir G (1976) Upwelling water as a factor influencing choice of spawning sites by brook trout (*Salvelinus fontinalis*). *Transactions of the American Fisheries Society*, **105**, 416–421.

Wedekind C, Kung C (2010) Shift of spawning season and effects of climate warming on developmental stages of a grayling (Salmonidae). *Conservation Biology*, **24**, 1418–1423.

Wenger SJ, Isaak DJ, Luce CH *et al.* (2011) Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 14175–14180.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Matlab Code. Matlab code for the redd timing model with explanations and notes for executing the analysis.

Appendix S2: Example data. Example data input (raw data from this study) and example output for the redd timing model detailed in Appendix S1.

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