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Predicted effects of future climate warming on thermal habitat suitability for Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in rivers in Wisconsin, USA

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Summary

The Lake Sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) may be threatened by future climate warming. The purpose of this study was to identify river reaches in Wisconsin, USA, where they might be vulnerable to warming water temperatures. In Wisconsin, *A. fulvescens* is known from 2291 km of large-river habitat that has been fragmented into 48 discrete river-lake networks isolated by impassable dams. Although the exact temperature tolerances are uncertain, water temperatures above 28–30°C are potentially less suitable for this coolwater species. Predictions from 13 downscaled global climate models were input to a lotic water temperature model to estimate amounts of potential thermally less-suitable habitat at present and for 2046–2065. Currently, 341 km (14.9%) of the known habitat are estimated to regularly exceed 28°C for an entire day, but only 6 km (0.3%) to exceed 30°C. In 2046–2065, 685–2164 km (29.9–94.5%) are projected to exceed 28°C and 33–1056 km (1.4–46.1%) to exceed 30°C. Most river-lake networks have cooler segments, large tributaries, or lakes that might provide temporary escape from potentially less suitable temperatures, but 12 short networks in the Lower Fox and Middle Wisconsin rivers totaling 93.6 km are projected to have no potential thermal refugia. One possible adaptation to climate change could be to provide fish passage or translocation so that riverine Lake Sturgeon might have access to more thermally suitable habitats.

Introduction

The Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817) was once common in many large rivers and lakes across a wide area of eastern North America in the Mississippi River, Laurentian Great Lakes/St. Lawrence River, and Hudson Bay/James Bay basins (Scott and Crossman, 1973; Gruchy and Parker, 1980). Current abundance has been much reduced from historical levels, and the species is considered imperiled in many areas and vulnerable overall (Jelks et al., 2008). Population declines have been caused primarily by overfishing, pollution, and dams that modified habitats and blocked migrations (Scott and Crossman, 1973; Becker, 1983; Ferguson and Duckworth, 1997; Haxton and Findlay, 2008). Over the past 50 years there have been major efforts to restore Lake Sturgeon populations, involving strict fishery regulations and closures, stocking of juveniles, pollution abatement, habitat restoration, modification of hydroelectric dam operation, and provision of fish passage through barrier dams (Auer, 1996a; Schram et al., 1999; Lyons et al., 2000; Johnson et al., 2006; Drauch and Rhodes, 2007). In some areas, Lake Sturgeon populations have stabilized and have begun to rebound (e.g. Bruch, 1999; Chalupnicki and Dittman, 2011). However, the relatively new environmental threat of climate change has the potential to reverse some of these gains and make portions of the Lake Sturgeon native range thermally less suitable in the future.

The exact thermal preferences and tolerances of the Lake Sturgeon are poorly known, but field observations and laboratory tests with juveniles indicate that, in general, the species survives and grows best at 'cool' summer water temperatures intermediate between the colder temperatures favored by salmonids and cottids and the warmer temperatures preferred by centrarchids, ictalurids, and most cyprinids, catostomids, and percids (Scott and Crossman, 1973; Wang et al., 1985; Wehrly, 1995; Holm et al., 2009). As a 'coolwater' species, the upper thermal limits of the Lake Sturgeon can be inferred from those of other coolwater species such as the white sucker *Catostomus commersonii* (Catostomidae), northern pike *Esox lucius* (Esocidae), threespine stickleback *Gasterosteus aculeatus* (*Gasterosteidae*), and yellow perch *Perca flavescens* (Percidae). Coolwater species generally have preferred water temperatures at or near 20–22°C and lethal temperatures at or near 31–33°C (Lyons et al., 2009). Water temperatures above 28°C may be metabolically challenging for coolwater species and could cause reduced growth or movement towards cooler areas (Mohseni et al., 2003). Such temperatures could also affect spawning, juvenile survival, and recruitment.

The state of Wisconsin, in the upper Mississippi River and Laurentian Great Lakes basins of the north-central United States, still maintains *A. fulvescens* populations in many of its larger lakes and rivers (Becker, 1983; Lyons et al., 2000). However, some of these waters already approach or exceed 28°C during the summer and are predicted to warm further as result of the higher air temperatures expected under climate change (Lyons et al., 2009, 2010; WICCI, 2011). This suggests that climate change could affect *A. fulvescens* in some places. In this study, an existing lotic summer water temperature model coupled with future air temperature and precipitation predictions were used to assess how thermal habitat suitability for Lake Sturgeon might change in

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Wisconsin rivers. Also considered were the availability and accessibility of cooler areas that might serve as thermal refugia when particular river reaches have potentially less suitable water temperatures.

Materials and methods

Current *A. fulvescens* distribution in Wisconsin rivers was determined from published references (Priegel and Wirth, 1977; Becker, 1983; Lyons et al., 2000; Clapp et al., 2012) and an extensive online database on fish distribution and abundance (WDNR Fish Mapping Application, 2014). Their populations in each large-scale river reach were classified as either stocked or un-stocked based on whether hatchery-raised juveniles had been added to the reach within the last 20 years to restore or enhance populations (WDNR, unpublished data).

Current Lake Sturgeon distribution was mapped on the spatial hydrography framework National Hydrography DataPlus (NHDPlus: Horizon Systems Corporation, 2008) to allow for water temperature modeling. This hydrography network divided rivers into a series of discrete river segments, bounded by lakes or tributary confluences. Each segment had specific attributes that characterized location, catchment area, topography, geology, soils, land cover, and climate. The 1639 river segments where Lake Sturgeon occurred ranged in length from 0.1 to 19.6 km, with a mean of 1.3 km. Dams at the boundaries of these segments were classified as passable when they were low enough for movement of fish upstream during high flows or when they had regularly operated navigation locks or upstream fish passage facilities that were judged to be effective for the Lake Sturgeon. Otherwise, dams were considered impassable. Based on the locations of impassable dams, river segments were grouped into 48 river-lake networks within which Lake Sturgeon movements were unlikely to be restricted by dams or natural barriers. For each of these networks, the lowermost segment of each tributary with a drainage area greater than 150 km^2, large enough for *A. fulvescens* to enter during summer low-water levels, was identified; the tributary segment was then associated with the river segment into which it flowed.

An existing lotic water temperature model, described below, was used to estimate the average summer maximum daily mean water temperature – which is the average of the mean water temperature for the warmest day of each year over a long period – for each river and tributary segment. This water temperature metric is an ecologically meaningful representation of the summer thermal maximum in rivers in the north-central United States (Lyons et al., 2009). The water temperature model was developed from an artificial-neural-net statistical analysis of continuously recorded summer water temperatures from 304 sites on Wisconsin streams and rivers during the period 1990–2008 (Roehl et al., 2006; Stewart et al., 2006; Westenbroek et al., 2011). Inputs to the model included segment-specific information on climate (air temperature, precipitation) and catchment topography, geology, soils, and land cover. In independent validation tests at 67 different sites, the model explained 76% of the variation in summer daily mean water temperature. To estimate current temperatures, observed climate data from 160 weather stations were input for the period 1990–2008.

Future water temperatures anticipated for the period 2046–2065 were estimated from the water temperature model using air temperature and precipitation projections from 13 global climate models (GCM) downscaled to Wisconsin (10 km^2 grid cells; Serbin and Kucharik, 2009; Notaro et al., 2011) and the A1B greenhouse-gas emissions scenario (IPCC, 2007). Each GCM incorporates large-scale earth and atmospheric attributes and processes to predict future climate conditions over the entire globe. However, because global climate is exceedingly complex, no single GCM can fully incorporate all relevant attributes and processes, and reliance on any particular GCM to forecast future air temperature and precipitation is not recommended. Instead, standard practice for climate change projections is to use an ensemble of GCM, each optimized for specific climate attributes and processes, to estimate a range of possible future conditions. Because GCM make projections at very coarse scales (uniform conditions within 200–300 km^2 grid cells), statistical relations between modeled broad-scale conditions and observed finer-scale conditions are used to 'downscale' GCM results to better reflect local temperature and precipitation patterns. Greenhouse gases such as carbon dioxide and methane are key drivers of climate change, and several different greenhouse-gas emission scenarios have been developed to forecast future concentrations of greenhouse gases in the atmosphere. The A1B scenario is a 'middle of the road' scenario, assuming moderate increases in greenhouse-gas concentrations over the forthcoming 50 years.

Output from the water temperature model consisted of yearly estimates of maximum daily mean water temperature for 1990–2008 (current) and predictions from each of the 13 GCM for 2046–2065 (future). From these values the mean of the yearly maximum daily means for the current period and for each GCM for the future period were calculated and used as the estimates of average maximum water temperature in each river and tributary segment.

To delineate areas that might be thermally less suitable for Lake Sturgeon, river and tributary segments with average maximum daily mean water temperatures that exceeded 28°C (which we defined as 'marginal') or 30°C ('stressful') currently or in the future for at least one of the 13 GCM were identified. Based on numerous captures of Lake Sturgeon from waters warmer than 30°C, these thermal categories are probably conservative and may overestimate their sensitivity to rising water temperatures. The distributions of segments within each of the river-lake networks were mapped and the lengths of thermally marginal and stressful river habitat, as defined herein, were quantified. For the future, the number of GCM that predicted that a segment would have marginal or stressful thermal conditions was used as an index of the likelihood of climate change impacts. If a network had marginal or stressful river segments but also had upstream or downstream river segments or tributary segments that were cooler than 28°C, it was assumed that Lake Sturgeon might be able to avoid thermally challenging areas by moving to these cooler segments. Not all of the river habitat within the network would be as thermally suitable, but access to thermal refugia could reduce climate-change impacts on *A. fulvescens* populations.

Results

Lake Sturgeon is currently widespread in the rivers of Wisconsin, occurring in 2291 km, of which 433 km (18.9%) have populations stocked with hatchery-produced juveniles within the last 20 years, and 1858 km (81.1%) that have not been stocked (Fig. 1). The 48 river-lake networks with Lake Sturgeon have from 0.5 to 551 km of riverine habitat. The longest network encompasses the Mississippi River (with 10 passable dams in Wisconsin) and the lower reaches of its three largest tributaries in Wisconsin, the St. Croix, Chippewa/Red Cedar, and Wisconsin rivers, and the second longest, at 334 km, consisting of the Upper Fox (one passable dam) and Lower Wolf rivers plus Lake Winnebago and associated smaller lakes.

At present, the water temperatures in most river segments with Lake Sturgeon are not marginal or stressful, as herein defined. Of the 2291 km of Lake Sturgeon riverine habitat, just 341 km (14.9%) have estimated long-term average maximum daily mean water temperatures that exceed 28°C, and only 6 km (0.3%) have mean water temperatures above 30°C (Fig. 2). Most of these are in the Mississippi River and its largest tributary, the Wisconsin River. The Mississippi River network has a number of river and tributary segments that could act as thermal refugia. For the 48 river-lake networks, just 12 have at least one segment above 28°C and only one (Mississippi River) has any segments above 30°C. Six short (3.6–10.0 riverine km) and contiguous networks (38.3 km total) on the Lower Fox River have all of their segments above 28°C, but no network has all of its segments above 30°C. None of the six Lower Fox River networks has tributaries that could provide a potential thermal refuge.

River habitats thermally marginal or stressful for Lake Sturgeon are predicted to increase in the future. Depending on the GCM, the length of riverine habitat with water temperatures above 28°C is expected to rise to 685–2164 km (29.9–94.5% of total river habitat), representing a factor of 1.96–6.18 increase, and the length above 30°C is expected to rise to 33–1056 km (1.4–46.1%), an increase factor of 5.50–176.00. At least half (seven or more) of the models predict that 947 km of river will exceed 28°C (41.3% of river habitat), a 2.71-fold increase, and 69 km will exceed 30°C (3.0%), an 11.5-fold increase (Fig. 3). Generally, rivers in southern Wisconsin are more likely than those in northern

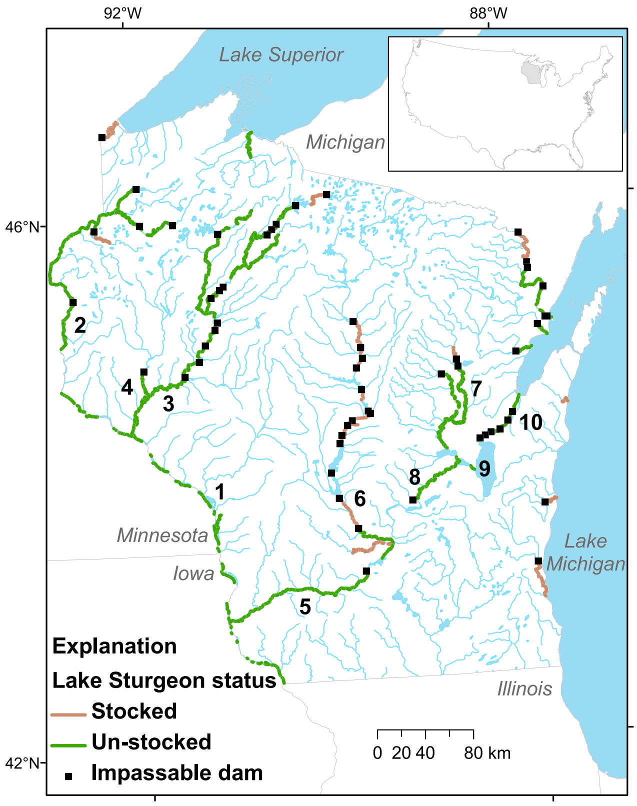

Fig. 1. Map of Wisconsin showing riverine areas occupied by Lake Sturgeon (*Acipenser fulvescens*). Suitable lake areas are not shown in this and subsequent figures. Brown = areas where hatchery-raised juvenile Lake Sturgeon have been stocked during the last 20 years; green = no stocking has occurred. Dark squares = impassable dams. Rivers and lakes mentioned in the text are indicated by numbers: 1 = Mississippi River, 2 = St. Croix River, 3 = Chippewa River, 4 = Red Cedar River, 5 = Lower Wisconsin River, 6 = Middle Wisconsin River, 7 = Lower Wolf River, 8 = Upper Fox River, 9 = Lake Winnebago, 10 = Lower Fox River

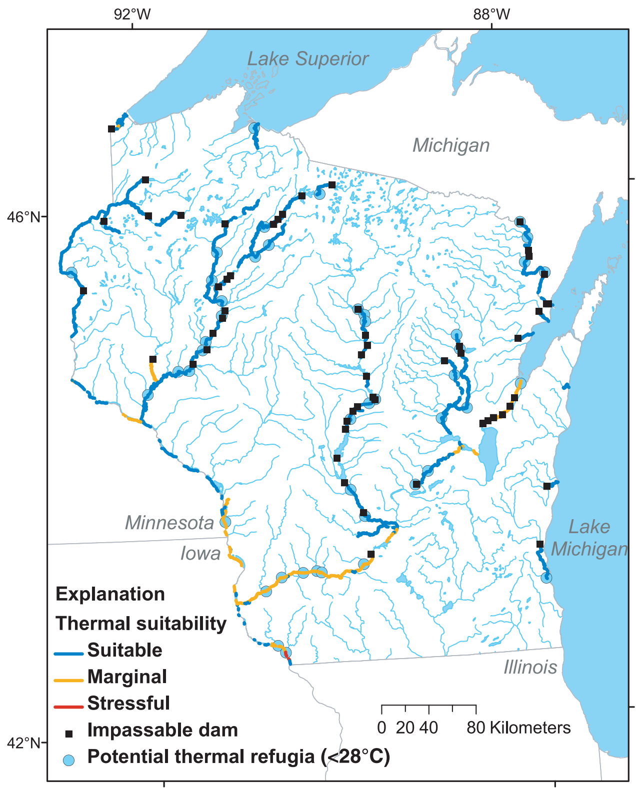

Fig. 2. Map of Wisconsin showing present (1990–2008) thermal suitability as herein defined, of Lake Sturgeon riverine habitats. Blue = areas thermally suitable (average max. daily mean water temperature <28°C), orange-yellow = thermally 'marginal' areas (28–30°C), red = thermally 'stressful' areas (>30°C). Dark squares = impassable dams. Light blue circles = tributaries that might be suitable thermal refugia (<28°C)

Wisconsin to become thermally marginal or stressful. Of the 48 river-lake networks, 47 have at least one river segment where at least one GCM predicts water temperatures to exceed 28°C, and 21 of these have at least one segment predicted by at least one GCM to be above 30°C. Nineteen of these networks have tributaries that are predicted not to exceed 28°C and thus may be suitable as thermal refugia. Fourteen networks, including the six short contiguous networks in the Lower Fox River (38.3 km total) plus eight short (2.6–31.5 km) contiguous networks (98.3 km total) in the Middle Wisconsin River are predicted by either 12 or all 13 of the GCM to have all of their river segments above 28°C. Only two of these networks, both in the middle Wisconsin River and totaling 43.0 km, have a tributary predicted to remain cool enough to be suitable as a thermal refuge. Excluding these two networks gives 12 networks across two rivers totaling 93.6 km that are projected to be likely to have marginal thermal habitat throughout and no access to thermal refugia. None of these 12 networks are predicted to have all of their segments above 30°C by more than three GCM.

Discussion

Although analyses of the impacts of climate change on the broad-scale distribution and habitat suitability for freshwater fishes are becoming more common (reviewed in Comte et al., 2013), there appear to have been no previous thermal modeling studies on the potential effects of climate change on any North American sturgeon species, including the Lake Sturgeon. However, thermal modeling studies from Europe on five sturgeon species predicted that four of the species would be reduced in abundance and distribution because of warmer water temperatures (Lassalle et al., 2008; Lassalle and Rochard, 2009). In a systematic expert-knowledge assessment based on the vulnerability of California fishes to climate change, two of the three sturgeon species known from the state were judged highly vulnerable to extirpation, and the third species as being less vulnerable (Moyle et al., 2013).

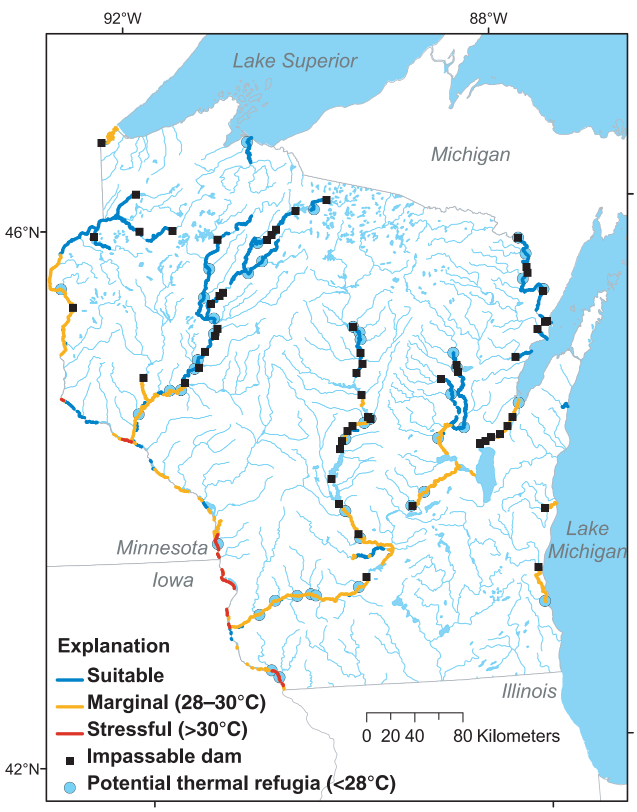

Fig. 3. Map of Wisconsin showing the predicted future (2046–2065) thermal suitability, as herein defined, of Lake Sturgeon riverine habitats. Blue = areas predicted to be thermally suitable by seven or more downscaled Global Climate Models; orange-yellow = 'marginal'; red = 'stressful'. Dark squares = impassable dams. Light blue circles = tributaries that might be suitable thermal refugia

Similar to results in Europe, findings from this study predict that thermally suitable river habitat for Lake Sturgeon will decline in Wisconsin in the future because of climate warming. There is uncertainty about the magnitude of decline because of different results from different GCM, but even the most optimistic projections have the amount of marginal thermal habitat as defined herein as nearly doubling, and the amount of stressful habitat increasing more than five-fold. The most pessimistic projections have almost all the river habitat in the state becoming marginal, with nearly half becoming stressful. Note, however, that Lake Sturgeon temperature tolerance is poorly known and that we may be overestimating the thermal sensitivity of the species and hence overestimating declines in thermal habitat suitability.

Despite the substantial projected increase in marginal and stressful thermal habitat caused by climate change, most river-lake networks are forecast to have upstream or downstream river reaches or large tributaries that will remain thermally suitable in the future under most GCM. These areas could act as thermal refugia, perhaps allowing Lake Sturgeon populations to avoid high water temperatures even if a portion of their habitat were to become thermally less suitable. Lake Sturgeon are highly mobile and can undertake long spawning migrations through rivers and lakes (Lyons and Kempinger, 1992; Auer, 1999; Knights et al., 2002; Bott et al., 2009; Homola et al., 2012); they can traverse dams if regularly operated navigation locks or appropriate fish passage facilities are present (Knights et al., 2002; Kynard et al., 2008; Thiem et al., 2011). These attributes suggest that Lake Sturgeon could move long distances from less to more suitable thermal habitats within a network. However, some studies have found that tagged Lake Sturgeon remain in localized areas during the summer (Fortin et al., 1993; Borkholder et al., 2002; Knights et al., 2002); if this is a general characteristic of the species, then individuals within reaches that might become thermally less suitable might be unlikely to encounter thermal refugia, especially if the refugia were distant and thermal cues were lacking. If that were the case, populations within the network might be affected despite the presence of accessible thermal refugia.

Lake Sturgeon populations are predicted to be most vulnerable in 14 short river-lake networks. Six of these networks in the Lower Fox River are already estimated to be thermally marginal for Lake Sturgeon under present climate conditions; eight more short networks in the Middle Wisconsin

River are also predicted to become marginal because of climate warming. Only two of the Wisconsin River networks have tributaries that could act as thermal refugia. Thus, the future of Lake Sturgeon may be uncertain in these 12 networks.

Lake Sturgeon population persistence in isolated short networks may be inherently uncertain even if thermal conditions were to remain suitable. One study suggests that the species may need up to 250–300 km of unobstructed river habitat to thrive (Auer, 1996b). Of the 48 networks in Wisconsin, only two, the Mississippi River and the Upper Fox/Lower Wolf/Winnebago, have more than 250 km of river habitat. Populations in networks with fewer than 25 km of river habitat (i.e. <10% of the amount suggested by Auer, 1996b), which encompasses 31 of the 48 networks in Wisconsin, could represent population sinks that persist only because of stocking or migrants from viable populations upstream. For example, the six lower Fox River networks are immediately downstream from the largest Lake Sturgeon population in the state in the Upper Fox/Lower Wolf/Winnebago network (Bruch, 1999), and tagged Lake Sturgeon from the Upper Fox/Lower Wolf/Winnebago network have been captured in the Lower Fox River networks (Lyons and Kempinger, 1992). The eight Middle Wisconsin River networks lost their Lake Sturgeon populations in the early 1900s because of pollution and dams (Becker, 1983). Annual stocking to restore the species began in the 1990s and is ongoing, but it is too early to determine if self-sustaining populations will develop (Lyons et al., 2000).

If Auer's (1996b) conclusions on lengths of unobstructed river are generally applicable, then even under current climate conditions most of Wisconsin's river-lake networks may have Lake Sturgeon populations with uncertain long-term prospects because of limited river habitat. The potential increase of less suitable thermal conditions owing to climate change might make the persistence of Lake Sturgeon populations in these networks even less likely. Short networks are caused by dams that isolate populations by blocking upstream movement. If Lake Sturgeon in isolated short networks were given access to longer and more thermally suitable reaches via fish passage or translocation, their long-term population prospects might be improved. Fish passage or translocation could also provide access to thermal refugia as river segments warmed in response to climate change, although the likelihood of Lake Sturgeon finding and moving to these refugia remains uncertain. Improving connectivity among isolated river reaches could be considered as a possible component of Lake Sturgeon conservation in general and of adaptation to climate change in particular (Palmer et al., 2009).

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