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Corresponding long-term shifts in stream temperature and invasive fish migration

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Abstract

By investigating historic trapping records of invasive sea lamprey (*Petromyzon marinus*) throughout tributaries to the Laurentian Great Lakes, we found that upstream spawning migration timing was highly correlated with stream temperatures over large spatial and temporal scales. Furthermore, several streams in our study exceeded a critical spring thermal threshold (i.e., 15°C) and experienced peak spawning migration up to 30 days earlier than the 1980s, whereas others were relatively unchanged. Streams exhibiting warming trends and earlier migration were spatially clustered and generally found on the leeward side of the Great Lakes where the lakes most affect local climate. These findings highlight that all streams are not equally impacted by climate change and represent, to our knowledge, the first observation linking long-term changes in stream temperatures to shifts in migration timing of an invasive fish. Earlier sea lamprey migration in Great Lakes tributaries may improve young of the year growth and survival, but not limit their spatial distribution, making sea lamprey control more challenging.

Introduction

Global climate change has had increasingly strong effects on environmental patterns during the past several decades (Dale et al. 2001; Vaughan et al. 2003; Chen et al. 2006). In aquatic systems, climate change is predicted to alter fish thermal habitat regimes (Magnuson et al. 1990; Magnuson et al. 1997; Ficke et al. 2007), growth rates and recruitment (Hill and Magnuson 1990; Pörtner et al. 2001), as well as migration and spawning timing (Holmes 1990; Isaak et al. 2012). Many of these predictions have since been validated. For example, shifts in thermal habitat regimes have been shown to occur for freshwater fishes in Wisconsin (Lyons et al. 2010) as well as pelagic (Murawski 1993) and benthic (Perry et al. 2005) marine fishes around the world. Additionally, historical otolith data show a change in growth rates of marine fish as a result of warming sea temperatures (Thresher et al. 2007). Increased sea surface temperatures in the Sargasso Sea have been shown to cause a decrease in primary productivity, indirectly decreasing glass eel (*Anguilla* spp.) recruitment (Bonhommeau et al. 2008). Changes in migration timing of salmonids due to warming streams have been documented in the Pacific Northwest (Quinn and Adams 1996; Quinn et al. 1997). These studies, among others, provide evidence that warming climates are affecting ecological and biological processes in aquatic systems, but we suggest that managers also need to consider how aquatic invasive species and their control are influenced by warming temperatures (Hellmann et al. 2008; Rahel and Olden 2008), including changes in migration timing.

Invasive sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes is a useful species for evaluating the impact of warming streams on fish migration, because various stages of the sea lamprey life cycle have been shown to be highly temperature-dependent including egg development and larval growth (Holmes and Lin 1994), the timing of metamorphosis (Holmes et

al. 1994), and the adult spawning migration (Binder et al. 2010). Due to their devastating effects on the Great Lakes Fishery in the 1900s, the sea lamprey has been of particular interest in many ecological studies (Christie and Goddard 2003; Hansen et al. 2016) including a long-term and geographically broad data set describing sea lamprey spawning migrations (Mullett et al. 2003).

Here, we evaluated the long-term data set describing stream temperatures and sea lamprey trap catches to determine which streams throughout the Great Lakes have warmed and if sea lamprey migration timing has shifted in warming streams. We hypothesized that sea lamprey migration timing is largely driven by stream temperature (Binder and McDonald 2008; Binder et al. 2010), and as such, if stream temperatures have warmed earlier each spring, sea lamprey migration timing would have shifted correspondingly. Specifically, three predictions were evaluated as a test for our hypothesis: (1) sea lamprey migration timing would be highly correlated with stream temperature, (2) streams throughout the Great Lakes Basin warmed earlier each spring, and (3) in response to earlier stream warming, sea lamprey run timing also occurred earlier each spring.

Methods

Data Set

The Great Lakes Fishery Commission, which organizes sea lamprey control in the Great Lakes, provided access to the long-term data set describing adult sea lamprey trap catch (Mullett et al. 2003). Sustained and systematic trapping efforts began in the 1970s and have occurred at more than 118 trapping sites located throughout the Great Lakes Basin, primarily using portable traps installed below dams, or dam-integrated traps. The data set includes the species and number of individuals trapped at each site as well as water temperature on days that each trapping site

was checked. Full details of the sampling methods are described in Mullett et al. (2003). For this study, we assumed that trap catch mirrors migration timing, because the location and timing of trap deployment is specifically targeting adults migrating upstream to spawn.

To ensure we were using the most complete and robust trapping data, we only included streams with data from at least 30 years spanning from 1984 or earlier through 2014 or later. To better ensure trapping efforts did not miss the migration peak, we excluded years that had the highest sea lamprey catch on the first or last day the trap was checked. Additionally, the trap site must have been checked a minimum of 5 times each year. The average number of trap checks per site per season was 29.4 and the average trap deployment length was 44.9 days (Table 1), during which the vast majority of adult sea lamprey were surveyed each year (Mullett et al. 2003).

Given these selection criteria, our subset included 29 streams total, 8 streams located in Canada and 21 streams located in the United States (Table 1).

Analysis

For the analysis, we chose variables most relevant to sea lamprey biology. Previous studies found that sea lamprey migration peaks when stream temperatures reach approximately 15°C (Applegate 1950; Binder et al. 2010). Subsequently, we used the Julian day at which streams each year first reached 15°C ($D_{15^{\circ}\text{C}}$) to represent spring temperature conditions. Because trap catches within a year were often not normally distributed, we used the Julian day when 50% of the total annual trap catch occurred ($D_{50\%}$) to represent the timing of peak spawning migration for a given year.

To test our first prediction that sea lamprey migration timing would be highly correlated with stream temperature, we determined if $D_{50\%}$ was influenced by $D_{15^{\circ}\text{C}}$ using a general linear

mixed model. In this case, we ran a single analysis using data from our 29 study streams with stream identity as a random effect.

To test our second prediction that streams throughout the Great Lakes Basin warmed earlier each spring, we determined if $D_{15^{\circ}\text{C}}$ decreased over our study period using a general linear model. To determine if streams differed in their changes over time, our model included stream identity and the interaction between stream identity and year as factors. To better evaluate changes in individual streams, we used a simple slope analysis to test whether temperature changes for a given stream differed significantly from zero. Using these slopes (i.e., mean annual change in $D_{15^{\circ}\text{C}}$) from each study stream, we ran a spatial autocorrelation analysis to determine whether geographic clustering existed among streams based on whether or not they experienced temperature shifts over time.

To test our third prediction that in response to earlier stream warming, sea lamprey run timing also occurred earlier each spring, we determined if $D_{50\%}$ decreased over our study period using a general linear model, which again included stream identity and the interaction between stream identity and year as factors. As with the second prediction, we used a simple slope analysis to evaluate shifts in sea lamprey migration timing for each stream and a spatial autocorrelation analysis to determine whether geographic clustering exists among streams based on whether or not they experienced shifts sea lamprey migration timing. To determine if a relationship exists between the magnitude of changes in $D_{15^{\circ}\text{C}}$ and $D_{50\%}$, we ran a final linear regression using magnitude of change in $D_{15^{\circ}\text{C}}$ as the independent variable and magnitude of change in $D_{50\%}$ as the dependent variable.

All analyses were performed in R (3.2.3). We ran spatial autocorrelation analyses using the Moran.I function within the APE (4.0) R package (Paradis et al. 2004). Figures were created

with the ggplot2 (2.2.1) R package (Wickham 2009) with the exception of the maps, which were created using arcMap.

Results

Prediction 1 was supported; sea lamprey migration timing was highly correlated with stream temperature across streams. When streams reached 15°C earlier in the year, the timing of when 50% of the sea lamprey migrated tended to occur earlier in the year, and vice versa ($F_{1,875} = 467.11, p < 0.01$). The relationship was consistent across the latitudinal gradient of the entire Great Lakes Basin, with $D_{15^{\circ}\text{C}}$ explaining 61% of the overall variance in $D_{50\%}$ (Figure 1).

Prediction 2 was partially supported; we found stream warming to be variable both over time and across streams (stream-by-year interaction: $F_{29,875} = 50.76, p < 0.01$). While the majority of streams in our analysis trended toward earlier spring warming, some had no change, and one stream even warmed significantly later in the year (Figure 2a; plots for individual streams are provided in Figure S1). Additionally, streams with similar warming trends were clustered spatially in several areas throughout the Great Lakes Basin (Moran's $I = 0.20, p = 0.01$; Figure 2a). Most streams exhibiting earlier warming were located on the leeward (eastern) side of the Great Lakes (Figure 2a).

Prediction 3 was partially supported; as with $D_{15^{\circ}\text{C}}$, changes in $D_{50\%}$ over time differed among streams (stream-by-year interaction: $F_{28,847} = 2.61, p < 0.01$; Figure 2b; plots for individual streams are provided in Figure S2). Observed changes in $D_{50\%}$ were further related to those of $D_{15^{\circ}\text{C}}$, such that streams that experienced earlier warming were more likely to experience 50% migration earlier as well ($R^2 = 0.59, F_{1,27} = 39.29, p < 0.01$; Figure 3). In fact, the one stream that experienced significantly later warming also experienced later dates of 50%

142 migration. Further, streams where sea lamprey were migrating earlier in the year were spatially
143 clustered (Moran's $I = 0.30$, $p < 0.01$; Figure 2b) and located on the leeward (eastern) side of the
144 Great Lakes, similar to that observed for $D_{15^{\circ}\text{C}}$.

146 Discussion

147 Our study revealed a strong relationship between spring stream temperatures and sea
148 lamprey migration timing across the Great Lakes Basin over the last several decades. We found
149 that the sea lamprey spawning migration tended to occur earlier in streams that reached 15°C
150 earlier in the year compared to those that reached 15°C later in the year. These findings are
151 consistent with previous studies that have shown the general influence of temperature on
152 locomotor activity (Binder and McDonald 2008) and the specific temperature at which peak
153 migration occurs (Applegate 1950; Binder et al. 2010). Here we show how these effects of
154 temperature act in a consistent fashion over the large spatial extent of the Great Lakes Basin.
155 While our analysis showed a strong correlation between stream temperature and sea lamprey
156 migration timing, some variability in migration timing was left unexplained, suggesting that our
157 surrogate of run timing (trap catch) had inherent sampling variability or that environmental
158 factors in addition to river temperature influence run timing. For example, Binder et al. (2010)
159 found that the rate at which temperature rise in the spring can also affect migration timing.
160 Future analyses, particularly those that are building predictive models of migration timing,
161 should consider the speed of spring warming and other variables (e.g., photoperiod, lunar cycles,
162 lake temperature, larval pheromone). Additionally, warmer temperatures could increase larval
163 productivity in some streams, and because adult sea lamprey use chemical cues released by
164 larvae to locate streams with suitable spawning habitat (Vrieze and Sorensen 2001; Meckley et

al. 2014), increased larval productivity could influence migration timing. However, the influence of pheromones and other factors on migration timing is likely to be much less than temperature given the findings of other studies (Applegate 1950; Wagner et al. 2009; Meckley et al. 2014).

The direction and magnitude of change in both water temperature and sea lamprey migration timing was variable among our study streams. How global climate change is expected to influence a stream depends on several factors, including local climate, hydrology, and geomorphology (Milly et al. 2005; Nelson et al. 2009). While our study was not designed to identify the underlying drivers of stream temperature changes, the nature of the spatial clustering we observed suggests a regional factor, such as local climate, is important. The location of these clusters in relation to the Great Lakes may also be informative. We found streams exhibiting warming trends and earlier migration were generally found on the leeward (eastern) side of the Great Lakes. Interestingly, regional climate models of the Great Lakes Basin (e.g., Gula and Peltier 2012; Xue et al. 2017) in combination with long-term field observations (e.g., Mason et al. 2016) have identified differences in climate change between windward and leeward sides of the lakes, resulting from feedbacks between the lakes and the atmosphere. These differences are particularly large for snowfall and snowpack (Gula and Peltier 2012, Demaria et al. 2016), which are relevant variables to our study because they directly impact the spring warming of streams (Smith and Lavis 1975, Kobayashi 1985). The role that snow and other Great Lakes-influenced climate variables play in our observed spatial clusters, while outside the scope of this study, is an intriguing question that warrants further investigation as it may be broadly informative to how stream ecosystems around large lakes will be affected by climate change.

The relatively broad range of magnitudes of change in sea lamprey migration timing demonstrates the complexity of how streams are influenced by the effects of climate change.

188 Previous studies on migration timing of migratory fishes also showed a wide range in
189 magnitudes of change (Quinn and Adams 1996; Quinn et al. 1997; Robards and Quinn 2002;
190 Juanes et al. 2004); however, their small number of study streams across a relatively smaller
191 geographic area caused, in many instances, conflicting results among studies. Our more inclusive
192 study allowed us to better capture the wide range of variability in migration shifts experienced by
193 streams, therefore our results show consistencies with many previous studies that may have
194 conflicting results compared to one another. For example, American shad (*Alosa sapidissima*) in
195 the Columbia River Basin and Atlantic salmon (*Salmo salar*) in northern New England were
196 found to have relatively large shifts to earlier migration, ranging from -0.4 to -0.9 days per year
197 over several decades (Quinn and Adams 1996; Juanes et al. 2004). In comparison, we found six
198 streams where sea lamprey migration timing was earlier than -0.4 days per year. Additionally,
199 Sockeye salmon (*Oncorhynchus nerka*) in the Columbia River Basin had relatively small shifts
200 to earlier migration, ranging from -0.13 to -0.23 days per year over several decades (Quinn and
201 Adams 1996; Quinn et al. 1997). In comparison, we found eight streams with earlier sea lamprey
202 migration ranging from -0.1 to -0.3 days per year. Finally, steelhead (*Oncorhynchus mykiss*) at a
203 location in the Columbia River Basin were actually found to migrate up to 21 days later (0.44
204 days per year) over several decades (Robards and Quinn 2002), which again is consistent with
205 our results as we found six streams with later sea lamprey migration ranging from 0.14 to 0.64
206 days per year. The observed discrepancies in migration shifts between sea lamprey in the Great
207 Lakes Basin, sockeye salmon (Quinn and Adams 1996), and Atlantic salmon (Juanes et al. 2004)
208 again highlight the idea that local climates may be an important factor in determining a stream's
209 sensitivity to larger-scale global climate change. These discrepancies are likely also influenced
210 by differences in species life history. For instance, Quinn and Adams (1996) suggest that

differences in migration shifts of sockeye salmon and American shad in the Columbia River Basin may actually be driven by differences in their natural histories. Shad spawn shortly after they enter rivers, so their larvae experience very similar stream conditions as the spawning adults, which could have driven the evolution of greater behavioral plasticity to changing environments (Quinn and Adams 1996). Sea lamprey also spawn shortly after they enter rivers (Applegate 1950), suggesting their life history may be important to their sensitivity to changes in stream temperature.

A shift in migration timing for Great Lakes sea lamprey populations could make controlling this species and protecting the 7 billion dollar-a-year fishery even more difficult. Earlier spawning means earlier egg hatching, giving larval sea lamprey a longer period of time to develop and grow prior to their first winter, especially in northern latitude streams such as the St. Marys River. This change could not only potentially increase a stream's production of metamorphosing sea lamprey, but metamorphosis could occur a year sooner than historically observed. Typically 3-6 years is required for sea lamprey larvae in the Great Lakes to metamorphose to the parasitic stage (Beamish and Potter 1975; Quintella et al. 2003). As a result, chemical treatments to control larval sea lamprey populations may need to occur a year sooner in those streams that are more sensitive to warming as the effects of climate change continue. Furthermore, metamorphosed sea lamprey that survive the sea lamprey control program will likely cause more damage to the fishery under climate warming scenarios. For example, Cline et al. (2014) correlated the warming of the Great Lakes with increased parasitic sea lamprey growth rates. Larger parasitic sea lamprey are likely to have a much greater impact on fish populations throughout the lakes, but may not experience higher natural mortality rates like other fast growing fishes (grow fast and die young; Pauly 1980), because the duration of the

parasitic life stage, when most growth occurs, is fixed between 12 to 18 months and adult sea lamprey die after spawning (Applegate 1950). Under current warming trends, we do not expect many Great Lakes tributaries would become too warm to support sea lamprey given that they can tolerate temperatures up to 30°C (Potter 1980), and in their native range, sea lamprey occupy streams as far south as Florida in North America and southern Spain in Europe (Hansen et al. 2016).

Given the large spatial and temporal scale of this study, some aspects of the design were not ideal, but do not necessarily discount the observation of warming streams and earlier run timing of sea lamprey. A possible deficiency was that sea lamprey control actively applies selective lampricides to Great Lakes tributaries to kill larval sea lamprey, including the streams where adult sea lamprey are trapped (Christie and Goddard 2003). Lampricide application could have two consequences for our analysis. First, adult sea lamprey populations may have declined through our time series and low abundance adult sea lamprey populations may have different migration phenologies. However, we think this scenario is unlikely because although sea lamprey populations are 90% lower than historic highs, major declines in population occurred during the 1960s; adult sea lamprey populations have been relatively stable through our time series (Sullivan et al. 2015). Second, lampricide treatment will kill adult sea lamprey if applied during the spawning migration. While lampricide treatment could have occurred on some of our study streams during some years, applications generally occur once every four years during the summer and fall, which would be after the trapping period. Also, our data inclusion criteria would have prevented us from using data from years when trap catch was very low. A deficiency of our spatial analysis was that some geographic regions of the Great Lakes have not been consistently trapped due to their remoteness or lack of suitable tributaries for trapping. These

areas include as northern Lake Superior, western Lake Michigan, and eastern Lake Huron. Additional trapping data from all areas of the Great Lakes, especially additional windward locations in the upper Great Lakes, would have further strengthened evidence of spatial clustering.

In the Great Lakes, as stream and lake temperatures increase due to the effects of predicted climate change, fish production is predicted to increase due to improvements in temperature dependent biological processes such as egg development, larval growth rates, and metabolic rates (Hill and Magnuson 1990; Holmes and Youson 1997; Magnuson et al. 1997). Increased production of valued fishes would be beneficial to economies worldwide, but increased production of invasive species could negate these gains. Shifts in migration and reproduction timing may have large implications for the control and viability of invasive and valued fish populations worldwide (Rahel et al. 2008). Natural resource managers and policy makers may better protect aquatic resources by considering changes in aquatic communities over large geographic and temporal scales to determine whether fishes, either invasive or valued, have been showing changes in reproduction timing.

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Table 1. For the 29 streams used in our analyses, this table shows the associated lake and country, the total number of sea lamprey catch data entries, the range of years trapped, the total number of years trapped, and the average number of days the traps were set per year.

Tributary	Lake, Country	Total number of data entries	Range of years trapped	Number of years trapped within range	Average trap deployment (days)
Betsie River	Michigan, US	1099	1978-2015	37	56.2
Betsy River	Superior, US	684	1977-2015	38	43.9
Boardman River	Michigan, US	882	1978-2015	37	49.3
Bowmanville Creek	Ontario, CA	915	1981-2015	35	43.9
Carp Lake River	Michigan, US	961	1979-2015	36	48.2
Carp River	Superior, CA	588	1975-2014	33	40.2
Cattaraugus Creek	Erie, US	914	1980-2015	36	33.9
Cheboygan River	Huron, US	1624	1977-2015	39	52.2
Duffins Creek	Ontario, CA	1019	1981-2015	35	52.9
Echo River	Huron, CA	979	1980-2015	31	52
Graham Creek	Ontario, CA	751	1981-2014	31	52.4
Grand River	Erie, US	396	1978-2015	33	24
Grindstone Creek	Ontario, US	488	1978-2014	34	37.2
Humber River	Ontario, CA	2059	1981-2015	35	60.8
Jordan River	Michigan, US	951	1978-2014	36	52.4
Little Salmon River	Ontario, US	425	1978-2014	35	31.9
Manistique River	Michigan, US	1301	1977-2015	39	44.4
Menominee River	Michigan, US	771	1977-2014	38	41.7
Middle River	Superior, US	464	1984-2015	32	33.1
Miners River	Superior, US	349	1979-2014	36	27.4
Ocqueoc River	Huron, US	1361	1981-2015	35	54.5
Peshtigo River	Michigan, US	1066	1977-2015	39	46.7
Rock River	Superior, US	1552	1975-2015	41	59.7
St Joseph River	Michigan, US	805	1978-2015	37	42.4
St Marys River	Huron, US	1332	1977-2015	39	46.1
Sterling Creek	Ontario, US	919	1980-2015	36	43.3
Stokely Creek	Superior, CA	250	1981-2014	30	27.1
Tahquamenon River	Superior, US	1081	1977-2015	39	47.7
Thessalon River	Huron, CA	2194	1980-2015	36	56.6

Figure Captions

Figure 1. The relationship between the Julian day on which stream temperature first reached 15°C ($D_{15^{\circ}\text{C}}$) and the Julian day on which 50% trap catch occurred ($D_{50\%}$); the solid line represents a regression line of the linear relationship.

Figure 2. Maps showing the 29 trap locations used in our analyses. Colors indicate slopes of Julian day on which stream temperature reached 15°C ($D_{15^{\circ}\text{C}}$) vs. year (panel A) and of Julian day on which 50% trap catch occurred ($D_{50\%}$) vs. year (panel B). Map source: Great Lakes Information Network (GLIN).

Figure 3. The relationship between the magnitude of change in Julian day on which stream temperature reached 15°C ($D_{15^{\circ}\text{C}}$) and the magnitude of change in Julian day on which 50% trap catch occurred ($D_{50\%}$) for each of our 29 streams; the solid line represents a regression line of the linear relationship.

Figure 1

Figure 2

Figure 3