

Climate impacts on landlocked sea lamprey: Implications for host-parasite interactions and invasive species management

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Abstract. Altered thermal regimes under climate change may influence host-parasite interactions and invasive species, both potentially impacting valuable ecosystem services. There is considerable interest in how parasite life cycle rates, growth, and impacts on hosts will change under altered environmental temperatures. Likewise, transformed thermal regimes may reduce natural resistance and barriers preventing establishment of invasive species or alter the range and impacts of established exotic species. The Laurentian Great Lakes are some of the most invaded ecosystems and have been profoundly shaped by exotic species. Invasion by the parasitic sea lamprey (*Petromyzon marinus*) contributed to major declines in many Great Lakes fish populations. In Lake Superior, substantial progress has been made towards controlling invasive sea lamprey and rehabilitating native fish populations. Surface water temperatures in Lake Superior have been increasing rapidly since 1980 presenting a new challenge for management. Here we test how thermal changes in Lake Superior have impacted the feeding and growth of the parasitic sea lamprey. Sea lamprey have increased in size corresponding with longer durations of thermal habitat (i.e., longer growing seasons) for their preferred hosts. To compare regional differences in sea lamprey feeding and growth rates, we used a bioenergetics model with temperature estimates from a lake-wide hydrodynamic model hindcast from 1979–2006. Spatial differences in patterns of warming across the lake result in regionally different predictions for increases in sea lamprey feeding rates and size. These predictions were matched by data from adult sea lamprey spawning in streams draining into these different thermal regions. Larger sea lampreys will be more fecund and have increased feeding rates, thus increasing mortality among host fishes. Resource management should consider these climate driven regional impacts when allocating resources to sea lamprey control efforts. Under new and evolving thermal regimes, successful management systems may need to be restructured for changing phenology, growth, and shifts in host-parasite systems towards greater impacts on host populations.

Key words: adaptive management; climate change; Great Lakes; host; invasive species; Lake Superior; lake trout; parasite; sea lamprey.

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INTRODUCTION

Global climate change, particularly its effects on thermal regimes available to organisms, is predicted to alter phenology, species distributions, growth potentials, and trophic interactions (Walther et al. 2002). Two major concerns for future climate change are how these changes will impact host-parasite interactions (Elliot et al. 2002) and invasive species (Hellmann et al. 2008). Host-parasite interactions may be influenced by elevated environmental temperatures through changes to life cycle completion rates, parasite growth and subsequent impacts on host survival (Macnab and Barber 2012). Parasite life cycles are complex and altered thermal regimes could have varying effects from potentially reduced larval and host survival, to increased larval development rates (Molnár et al. 2013). For at least a part of their life cycle, parasites rely on the temperatures provided through their host's behavioral thermoregulation or internal metabolism (Elliot et al. 2002). Therefore, parasites using ectotherms as hosts may be more strongly affected by changing thermal regimes (Thomas and Blanford 2003, Macnab and Barber 2012). Determining how host-parasite interactions will change under altered climatic conditions, and predicting the ecological consequences, will be important for minimizing parasite and disease impacts on ecosystems. Additionally, host-parasite interactions may be particularly strong in systems where novel parasites are introduced to hosts (Holmes 1996, Meeus et al. 2011).

Changes in species invasion patterns and potential impacts are another major concern for future climate change (Hellmann et al. 2008). Changing thermal and precipitation regimes may influence the natural barriers and filters against invasive species (Rahel and Olden 2008). Additionally, climate change may render conditions more advantageous for some invasive species that are already present or managed at low levels, resulting in new threats for the future (Hellmann et al. 2008). Invasive species are managed in fundamentally different ways than native species (i.e., control vs. conservation; Hellmann et al. 2008). Understanding changes in natural barriers to invasion, shifts in spatial distributions, and growth or impact potentials will be critical for adaptive ecosystem manage-

ment in the future.

While many ecosystems have been profoundly impacted through species invasion, few have been more fundamentally changed than the Laurentian Great Lakes (Ricciardi 2006). Species invasions, subsequent restoration efforts (Kitchell and Sass 2008), and climate change (Austin and Colman 2008) have had extensive effects on food web interactions in the Great Lakes. Among the most impactful invasions of the Great Lakes is the parasitic sea lamprey (*Petromyzon marinus*). Coupled with fisheries exploitation, sea lamprey drove native large-bodied fishes to low abundances (Smith and Tibbles 1980, Bronte et al. 2003). As a result of a highly successful lampicide treatment program and development of new control measures, sea lamprey abundance has declined by 90–95% (Christie and Goddard 2003). Small populations of sea lamprey continue to derive from the survivors of ongoing treatment programs.

While management and restoration efforts have proceeded for native fish communities in all five Great Lakes, Lake Superior has realized the most substantial recovery. As a result of sea lamprey control and commercial fisheries management, many of Lake Superior's native fish populations have reached levels approximating restoration goals (Negus and Schreiner 2008). Based on catch rates of commercial fisheries and stock assessments, the relative abundance of lake trout (*Salvelinus namaycush*) and other potential host fishes increased several-fold during the period of 1960–1985 and have since remained at high levels (Bronte et al. 2003; Fig. 1). In addition, stocking of non-native Pacific salmon species have created substantial, self-sustaining populations. These abundant populations of large-bodied fishes all serve as potential hosts for sea lamprey, and offer a plentiful food source for surviving sea lampreys (Kitchell and Sass 2008).

Climate change presents a new challenge to management in Lake Superior. Mean annual surface water temperatures have increased over the last century and with an advancing rate since around 1980 (Austin and Colman 2007, 2008, Desai et al. 2009; Fig. 1). Since 1985, Lake Superior, the world's largest lake by area, has warmed by $1.21 \pm 0.68^\circ\text{C}$ per decade (Austin and Colman 2007, Desai et al. 2009). These physical

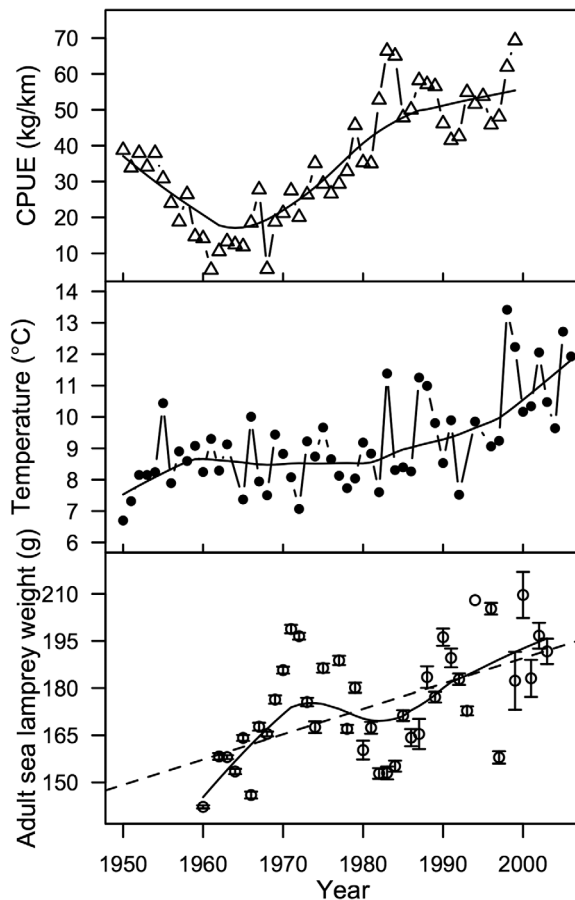


Fig. 1. Catch per unit effort (CPUE) of lake trout (top; redrawn from Bronte et al. 2003), mean average annual surface water temperature (middle; data redrawn from Austin and Coleman 2008), and average adult sea lamprey weight (bottom; redrawn based on Jorgensen and Kitchell 2005b), in Lake Superior during the period of 1960–2006. Solid lines in each data set are fits from a local regression curve. The dashed line in the bottom panel represents the ordinary least squares line of best fit.

changes in Lake Superior are likely impacting ecological interactions, but these effects for many fish species including sea lamprey are not well studied.

Sea lamprey are the apex predator in the Lake Superior food web and have strong top-down ecological impacts (Schmidt et al. 2009). Average sizes of spawning adult sea lampreys have increased from about 150 grams in 1960 to greater than 200 grams in recent records (Jorgen-

sen and Kitchell 2005b, Moody et al. 2011; Fig. 1). This trend is of significant management concern as large sea lampreys consume more blood, kill more host fishes, and are more fecund. The observed trend in sea lamprey size developed as a density-dependent response to reduced sea lamprey abundance and consequent increase in available hosts after sea lamprey control began in 1960 (Bronte et al. 2003, Jorgensen and Kitchell 2005a; Fig. 1). Sea lamprey host density has been stable in Lake Superior since 1980 (Fig. 1), yet average sea lamprey sizes continue to increase (Fig. 1). We posit that warming waters in Lake Superior have driven the observed trend in sea lamprey sizes since 1980. The optimal temperature for feeding and growth of sea lamprey, 18°C (Kitchell and Breck 1980), is generally warmer than that of its preferred host species lake trout (10°C) and Chinook salmon (*Oncorhynchus tshawytscha*; 13°C). As a parasite, sea lamprey occupy the thermal habitat of their host. Since 1980, climate change has significantly increased the amount of preferred thermal habitat available to these host fishes and created longer growing seasons (Cline et al. 2013). We expect sea lamprey feeding and growth to respond to these changes (Kitchell et al., *in press*).

Sea lamprey sizes are highly variable from year to year, yet the drivers of this variability are poorly understood. Inter-annual and spatial variability of temperature effects are substantial and likely contribute to variability in sea lamprey size. Here we test how thermal changes in Lake Superior have impacted the feeding rates and growth of sea lamprey. We evaluate the influence of spatial and temporal heterogeneity in lake thermal characteristics on sea lamprey size. To assess observed changes in regional sea lamprey size we compare spawning adult sizes from spatially distinct river systems across Lake Superior. We then apply high-resolution hydrodynamic and bioenergetics models to evaluate changes in regional feeding rates and growth of sea lamprey between 1979 and 2006.

METHODS

Study system

Lake Superior is an ultra-oligotrophic lake with a surface area of 82,100 km². It is the largest lake on Earth by surface area, third largest by

volume, has a mean depth of about 150 m and a maximum depth of 407 m. Up to 40% of Lake Superior's surface is covered by ice in winter (Assel 2005). Historically, mean annual surface temperatures have ranged from about 6°C to about 12°C (Austin and Colman 2007). Since 1980, ice cover has declined by about 50% and surface temperatures have risen by about 3°C (Austin and Colman 2007, 2008, Desai et al. 2009). The fish community in Lake Superior has a total of 86 known species, 71 of which are native and 15 are non-native including both invasive and introduced species (Ebener 2007). Cold water, low ion concentrations, and low productivity have prevented many of the prolific invaders found in the lower Great Lakes from successfully colonizing many regions of Lake Superior (Great Lakes Fisheries Commission, <http://www.glf.org>). As in each of the other Great Lakes, control of invasive sea lamprey and restoration of native fish communities are management priorities (Kitchell and Sass 2008; Great Lakes Fisheries Commission, <http://www.glf.org>).

Sea lamprey life cycle and ecology

Sea lamprey are anadromous and semelparous. They begin their life cycle by commonly spending 3–6 years (but as many as 16) in a filter-feeding larval stage buried in soft sediments of streams, rivers, and some shallow bays (Applegate 1950, Potter 1980; Great Lakes Fishery Commission, <http://www.glf.org>). When larvae attain an appropriate length and sufficient lipid reserves they undergo metamorphosis, develop a parasitic oral disc, and emigrate to the lake as juveniles. Here they attach to host fishes and rasp a hole in the skin to feed on blood and fluids. The parasitic or juvenile phase typically lasts from 12 to 18 months, during which an individual sea lamprey often kills several large-bodied host fishes (Applegate 1950). In spring, juvenile sea lamprey become sexually mature and migrate into streams as adults where they spawn and die.

Sea lamprey populations are controlled using lampricides on their larval stage. Streams are treated on a rotating cycle of assessment and treatment. Most streams receive treatments on a four-year cycle to prevent larvae from metamorphosing and migrating to the lake. Treatment goals are for 99% effectiveness however in

practice 5–10% of larval sea lamprey survive to their juvenile stage (Great Lakes Fishery Commission, <http://www.glf.org>).

Data acquisition and empirical analyses

To assess changes in adult sea lamprey size we used long-term monitoring data collected by the US Fish and Wildlife Service (USFWS) in all US waters of the Lake Superior. Since 1960, adult sea lamprey have been monitored in 23 Lake Superior tributaries. Each spring, USFWS uses electrical and mechanical barriers, and screw traps to collect adult sea lamprey for estimates of relative abundance and adult sizes. Not all tributaries have been continuously monitored, but the spatial distribution of catches throughout time captures the large-scale spatial heterogeneity from east to west. The longest consistent records of adult sea lamprey size come from the Bad, Rock, and Tahquamenon rivers (20, 29, and 28 years, respectively). For a lake-wide adult sea lamprey size estimate, we used the arithmetic average of adult sea lamprey weight across all monitored streams for each year (Jorgensen and Kitchell 2005a, 2005b).

To evaluate the influence of water temperatures on sea lamprey size, we compared the average size of adult sea lamprey collected in tributary streams between 1980–2008 with average summer (June–August) surface temperatures of Lake Superior lagged by one year. Observed water temperatures are based on daily records of Lake Superior surface temperature data from the NOAA mid-lake buoys available from the National Data Buoy Center (www.ndbc.noaa.gov). Sea lamprey move from the lake into tributaries to spawn in the spring following 12–18 months in their parasitic stage. They do not exhibit homing, but return to a stream near where they mature (Bergstedt and Seelye 1995). Accordingly, we developed thermal histories based on water temperatures lagged by one year (e.g., sea lamprey returning in April 2009 spent the summer of 2008 in the lake). These observed temperatures are not location specific to the tributaries. They represent an average lake-wide condition to compare between years.

A unique feature of parasites such as sea lamprey is that they cannot behaviorally thermoregulate; they must grow under the thermal regime of their hosts. Lake trout are commonly

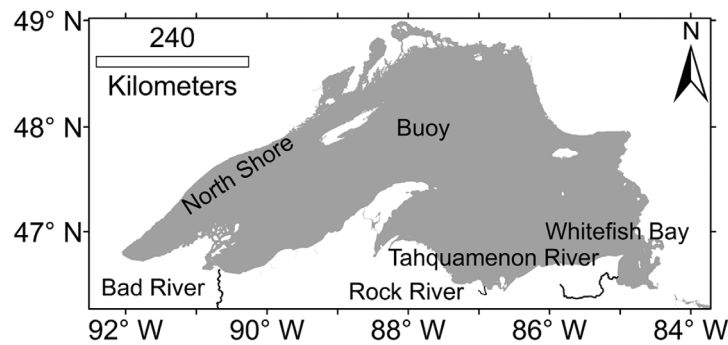


Fig. 2. Map of Lake Superior. Specific rivers used in our analysis and regions referenced within this study are labeled. “Bouy” indicates the position of the National Oceanic and Atmospheric Administration’s automated buoy that provides observed surface water temperatures used in this study.

used as hosts by sea lamprey in the Great Lakes (Schneider et al. 1996). Lake trout in Lake Superior have three main ecotypes: the lean, the humper, and the Siscowet. Each ecotype has different ecology and preferred temperatures. The lean lake trout ecotype is a primary host of sea lamprey and exhibits behavioral thermoregulation during periods of summer stratification with a median temperature preference of about 10°C (Christie and Regier 1988, Mattes and Madsen 2004). This host was chosen because it is a known preferred host for sea lamprey, has been the subject of extensive laboratory and field studies (Bence et al. 2003), and is the target of economically important commercial, recreational, and treaty fisheries in Lake Superior. Based on the generality from laboratory studies of preferred temperature and observed distributions in the field, Trumpickas et al. (2009) used the duration of days greater than or equal to 10°C as a basis for analyzing climate change impacts in the Great Lakes. To evaluate lake-wide growing season, we plotted adult sea lamprey size against one year lagged observed days $\geq 10^\circ\text{C}$ from the mid-lake buoy and analyzed the fit using least squares regression. Multiple lags between size and temperature data were assessed using a cross-correlation analysis, however only a 1-year lag had strong correlation with adult sea lamprey size.

To examine the influence of spatial heterogeneity in regional water temperature on sea lamprey size we analyzed inter-annual trends of returning adult sea lamprey size from three major spawning streams; the Bad, Rock, and

Tahquamenon Rivers (Fig. 2 for river locations). These three sites represent a gradient from east to west and offer distinct differences in annual temperature conditions. We tested for differences in intercepts and slopes between streams using ANCOVA on the mean adult sea lamprey size migrating into each stream across all years.

Modeling approaches

We used the hydrodynamic model of Bennington et al. (2010) to evaluate spatial and temporal heterogeneity in water temperatures and growing seasons across the lake from 1979–2006. The Lake Superior version of this modeling approach derives from the MIT general ocean circulation model (Marshall et al. 1997a, 1997b) configured to the bathymetry of Lake Superior (Schwab and Sellers 1996). The model uses several atmospheric variables such as air temperature, wind speed, incoming radiation, relative humidity, and ice cover to drive deterministic heat exchange modules. This results in time-evolving, three-dimensional temperature estimates. Here we use only surface temperatures. The model offers high horizontal spatial resolution at 2×2 km grid cells. This model has been rigorously vetted and compared with observed temperatures (Bennington et al. 2010). Biases in over-lake atmospheric conditions cause the model to modestly overestimate temperatures in cold years while no known bias exists in warm years (Bennington et al. 2010). Therefore tests of warming effects are conservative estimates of true changes in conditions (Cline et al. 2013). At the time of model run, the latest year with lake ice data needed for

model forcing was 2006.

To assess the impacts of regional differences in warming rates on sea lamprey growth and feeding, we developed estimates of feeding and growth rates based on the Wisconsin bioenergetics model (Hanson et al. 1997). The bioenergetics model uses initial weight, final weight, diet composition, physiological parameters (Kitchell and Breck 1980), and annual thermal history to drive an energy balance module to predict feeding rate and subsequent growth. The resulting total weight gain is expressed in a value of “*P*” which scales from 0 to 1.0 as the proportion of maximum possible feeding required to accomplish the observed final weight of spawning adults. Sea lamprey specific physiological parameters, diet composition, and dietary energy densities were derived from laboratory studies (Farmer and Beamish 1973, Farmer et al. 1977), used by Kitchell and Breck (1980) and altered by the addition of ontogenetic changes in energy density (Cochran et al. 2003).

We forced the bioenergetics model with three-dimensional time-evolving temperature fields from the lake-wide hydrodynamic model of Bennington et al. (2010) to assess changes in sea lamprey growth and feeding rates due to variation in thermal conditions. Using the annual thermal histories from each grid cell in the hydrodynamic model, we estimate total blood consumption required to achieve the observed growth for sea lamprey returning to spawn in streams. Assuming a lean lake trout host, all temperatures $\geq 10^{\circ}\text{C}$ were set to 10°C to mimic the thermoregulation observed in this species. Initial weight was set at 10 g for newly metamorphosed juvenile sea lamprey leaving natal streams based on results from Lake Superior tributaries (Applegate 1950, Kitchell and Breck 1980). For bioenergetics model simulations we employed a constant *P*-value of 0.8, which corresponds to the feeding requirements for average sized sea lamprey to reach the observed sizes given average thermal conditions.

Reasonable uncertainty exists in the values of parameters used to drive the model and input initial weights. For example, several sizes have been reported for recently metamorphosed juvenile sea lamprey. Those range from 3 to 10 g (Applegate 1950, Holmes and Youson 1998, Youson 2003). Additionally, considerable diver-

sity exists in the timing of migration of juveniles from their natal streams into the lake (Holmes et al. 1994, Holmes and Youson 1998). Therefore we have not presented exact estimates of blood consumption or growth. Rather, we simulated average sea lamprey feeding rates and growth for the period 1979–1984 and the period 2001–2006 using the same initial weight, *P*-values, and 12-month life history strategy. These two periods provide contrast between the previous cooler conditions and recent warmer conditions while averaging variation from interannual differences. Results are reported in terms of grams of blood consumed per sea lamprey over its parasitic phase, a critical measure of their impact on host fishes. We then present the outcome of these simulations as the percent change in total blood consumption per sea lamprey over their parasitic phase for each grid cell between the pre-warming conditions (1979–1984) and the current period (2001–2006). This method integrates over the numerous possible simulations using different values for juvenile sea lamprey starting weight, diverse possible life history strategies, and potential proportion of maximum consumption rates (*P*). Based on simulations, a change in any one of these parameters would only slightly change reported values in Fig. 6 (i.e., by $<1\%$), but not the overall distribution of changes, the focus of this study.

All data analysis and bioenergetics modeling was done using R (R Development Core Team 2013). Some of the figures presented herein are redrawn from data presented in published reports. In each case, we provide attribution to the original source.

RESULTS

The observed average adult sea lamprey size increased 12% from about 170 g to about 190 g between 1980 and 2008 (Fig. 1). Over this same period average summer water temperatures varied from about 8°C to more than 10°C (Fig. 1). While summer water temperatures have increased significantly since 1980 (Fig. 1), there was no significant relationship between adult sea lamprey size and mean summer water temperatures ($R^2 = 0.06$, $p = 0.187$). Mean length of the growing season, i.e., days $\geq 10^{\circ}\text{C}$, increased by more than 10 days per decade between 1980 and

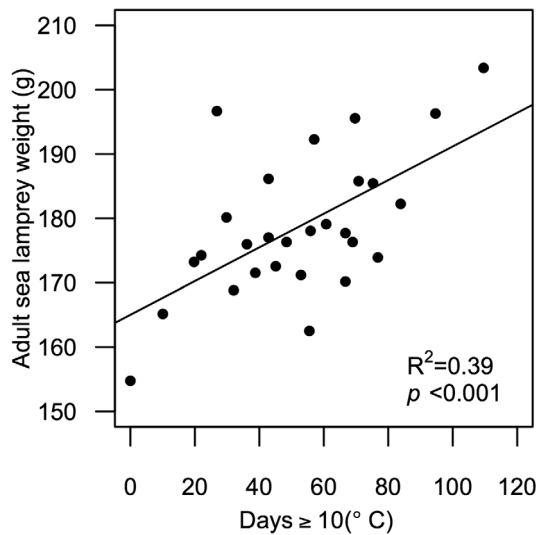


Fig. 3. Mean adult sea lamprey weight as a function of the number of days where surface temperatures are $\geq 10^{\circ}\text{C}$ from the mid-lake buoy for the period of 1980–2008 in Lake Superior. Dashed line represents least squares line of best fit.

2008 but ranged from 0 to as many as 110 (Fig. 3). Adult sea lamprey size significantly increased with longer growing seasons ($R^2 = 0.34$, $p < 0.001$; Fig. 3).

Within any given year substantial spatial variation exists in returning sea lamprey size observed across Lake Superior. As an example, we present observed average sea lamprey size returning to three systems, the Bad, Rock, and Tahquamenon Rivers representing a gradient from west to east in Fig. 4 (see locations in Fig. 2). All three rivers exhibit significant increases in sea lamprey size between 1980 and 2008 ($p = 0.006$). There is no significant difference in the rates of increase in sea lamprey size among rivers over this period (ANCOVA: $df = 2$, $F = 0.396$, $p = 0.67$). The average weight of adult sea lampreys returning to these three rivers are significantly different from each other (ANCOVA: $df = 2$, $F = 28.107$, $p < 0.001$). These differences reflect this gradient from east to west as sea lamprey returning to the Tahquamenon River are on average 17 g larger than sea lampreys returning to the Rock River which are on average 18 g larger than those in the Bad River (Fig. 4). Even with extremely large sample sizes (Bad: $n = 2555$, Rock: $n = 10914$, Tahqua-

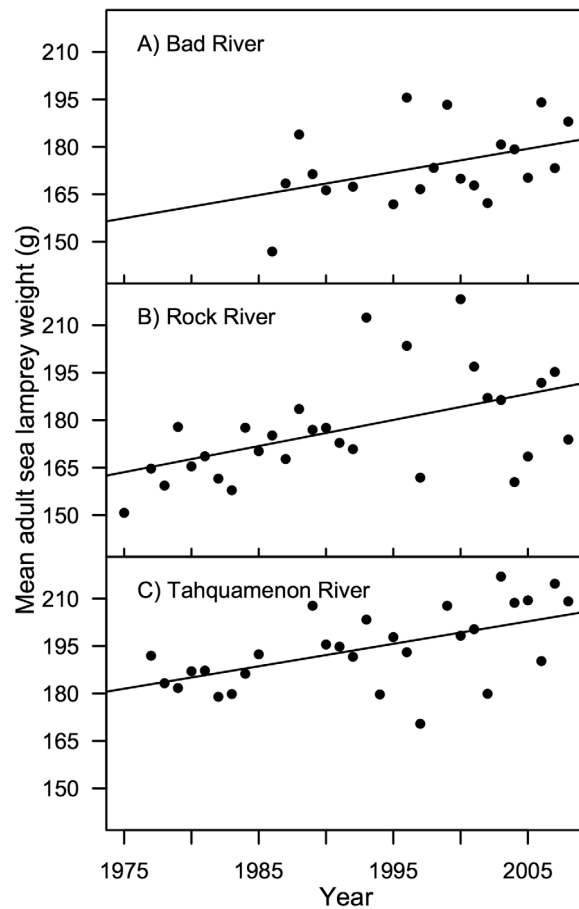


Fig. 4. Mean adult weight for spawning sea lamprey returning to (A) the Bad River, (B) Rock River, and (C) Tahquamenon River of Lake Superior during the period 1975–2008. Lines represent least squares regressions. (Bad River: $R^2 = 0.17$, $p = 0.04$; Rock River: $R^2 = 0.23$, $p = 0.005$; Tahquamenon River: $R^2 = 0.30$, $p = 0.001$).

menon: $n = 4316$) the inter-annual variability in adult sea lamprey sizes is very large varying by more than 50 g in consecutive years. However, R^2 values are all significant ($p < 0.05$ for each river; Fig. 4).

To synthesize spatial variability and climate change effects we selected a subset of years that represent the period when pronounced temperature increases began (1979–1984) and contrasted average temperature conditions with those of the most recently documented period (2001–2006). In an average year the extent of days $\geq 10^{\circ}\text{C}$ varies spatially from less than 75 in the north shore and

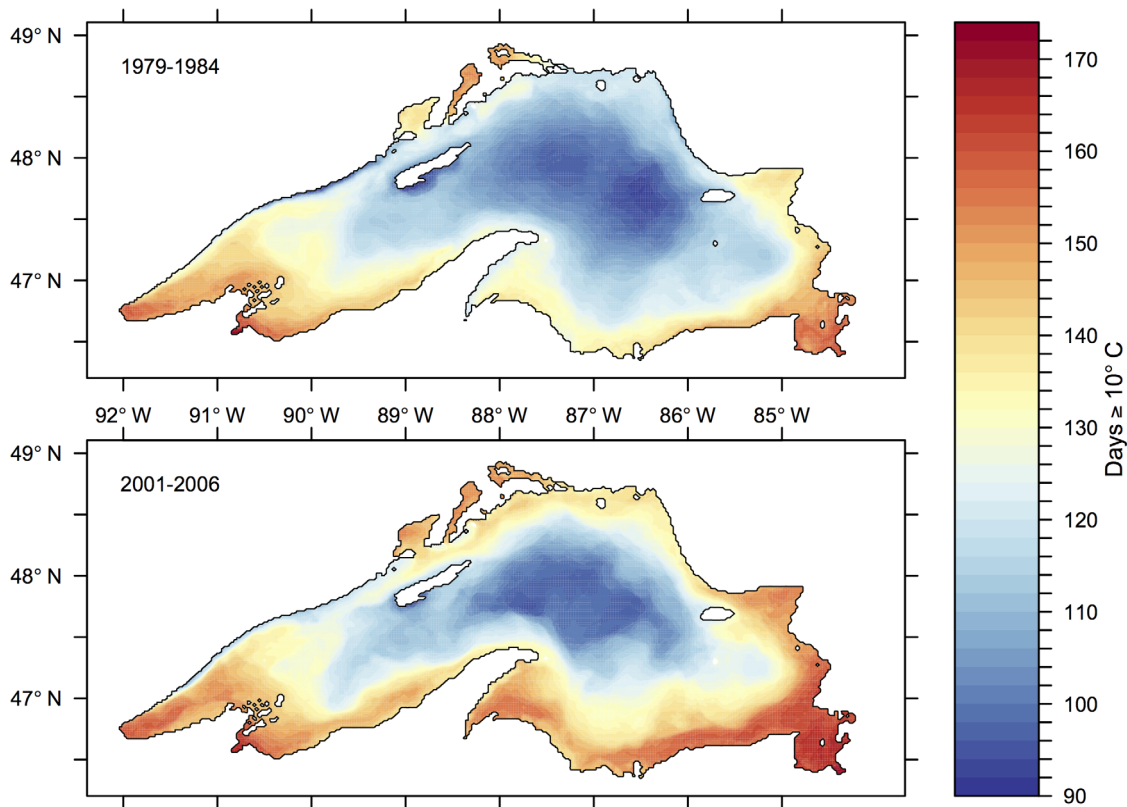


Fig. 5. Spatial distributions of days $\geq 10^{\circ}\text{C}$ in the surface waters of Lake Superior. The top panel represents the average of the years 1979–1984 and the bottom panel the years of 2001–2006.

mid lake regions, to more than 150 in some regions of the southern shore (Fig. 5). There is a general gradient from cooler waters in the west to warmer waters in the east that is strongly pronounced by approximately 40% greater days $\geq 10^{\circ}\text{C}$ in the Whitefish Bay region than along the north shore across all years (Fig. 5). Climate warming has occurred asymmetrically across the lake (Fig. 5). Available days $\geq 10^{\circ}\text{C}$ have changed very little in the western arm between 1979 and 2006. Specific regions such as along the north shore are cooling while some warm regions such as Whitefish Bay have continued to have long durations of days $\geq 10^{\circ}\text{C}$. In contrast, days $\geq 10^{\circ}\text{C}$ along the north eastern shore have increased about 20% from 110 to about 130 days. Along the southern shore large areas that had 110–130 days $\geq 10^{\circ}\text{C}$ in the early period, more recently have 130–150 (Fig. 5).

We offer a more specific analysis of the effects of changing temperature by using the bioener-

getics model to estimate blood consumed by individual sea lamprey in order to accomplish the observed growth. As a test of regional and climate effects on sea lamprey size, we simulated sea lamprey feeding and growth lake-wide using spatially distinct thermal profiles for the periods of 1979–1984 and 2001–2006. We calculate the percent change in total annual blood consumption as climate change had differentially warmed across Lake Superior. From the early to the later period, average sea lamprey blood consumption increased lake-wide about 5%. There is substantial spatial heterogeneity in the changes in feeding rates resulting for warming waters. The southwestern regions of the lake show little change in sea lamprey blood consumption with warming and may have even declined slightly from cool upwelling events (Fig. 6). Changes in blood consumption owing to climate are mostly concentrated in the eastern half of the lake. In three areas dispersed along the southeastern

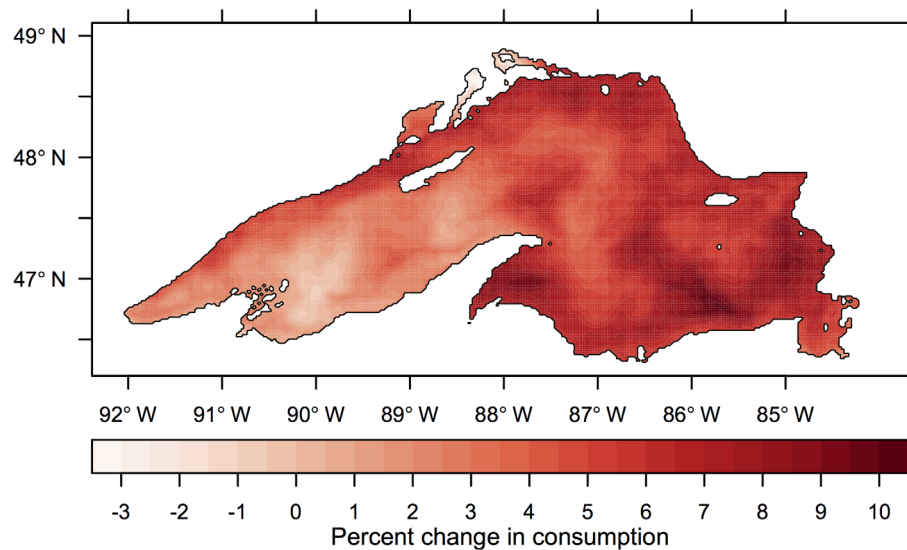


Fig. 6. Spatial distribution of changes in sea lamprey total consumption over their parasitic phase in Lake Superior between the time periods of 1979–1984 and 2001–2006.

shore, blood consumption has increased by >10% in the last three decades (Fig. 6).

DISCUSSION

Increasing water temperatures and spatial heterogeneity in warming across Lake Superior has influenced parasitic sea lamprey feeding and growth. Our results illustrate that adult sea lamprey sizes and feeding rates have increased in concert with the lake-wide warming occurring since 1980. However, increasing adult sea lamprey size closely corresponds with increased availability of optimal thermal habitat for their primary host species, not simply warmer surface waters. Differential warming rates across space also corresponds to regional differences in sea lamprey size returning to spawning streams. While unexplained variance in sea lamprey size remains, changes in average adult sea lamprey size correlate with longer growing seasons which represent increased feeding and growth with warming waters. These changes pose challenges for future sea lamprey management.

Larger sea lampreys can have two important effects on host species. First, vulnerability to direct mortality increases as the ratio of host size to sea lamprey size declines and sea lamprey feeding exceeds blood renewal rates for smaller

hosts (Kitchell 1990, Jorgensen and Kitchell 2005a). Attack rates should increase if more hosts are killed by larger sea lamprey and new hosts are sought. Second, indirect mortality owing to infection (Swink 2003, Madenjian et al. 2008) and wounding rates should also increase. Those expectations are supported by recent reports from Lake Superior where wounding rates are increasing while sea lamprey population densities have been maintained at low levels (Ebener 2007) and lake trout abundance has remained high (Bronte et al. 2003).

As evidenced by the historic collapse of fish communities in the Great Lakes as well as stable isotope studies of the Lake Superior food web, sea lamprey is the apex predator of these ecosystems and has strong top-down effects (Schmidt et al. 2009). Currently, sea lampreys in Lake Superior are larger than ever and, therefore, have increased fecundity. As a result, more larval sea lamprey are produced, which could fuel an increase in the residual population of sea lamprey surviving 90% effective control efforts. The most recently estimated abundance at about 75,000 parasitic sea lampreys in Lake Superior (Heinrich et al. 2003). High abundance of hosts and effects of climate warming allows those individuals to feed and grow at more rapid rates. An additional consideration derives from Negus

and Schreiner (2008) reporting substantial decline in size at age for Chinook salmon over the past three decades. This decline has been attributed to an increased density of piscivores plus a resulting decline of forage fishes. The consequent decline in host size creates more vulnerability to direct mortality effects of larger sea lampreys. As larger sea lampreys exert more pressure on host species such as lake trout and salmon, we should expect growing evidence for effects expressed as a trophic cascade that passes down through the Lake Superior food web (Kitchell et al. 2000).

Unlike many anadromous fishes such as Pacific salmon (*Oncorhynchus* spp.), there is no evidence that sea lamprey return to a specific natal stream to spawn and complete their life-cycle (Bergstedt and Seelye 1995, Waldman et al. 2008). Mature sea lamprey use pheromone cues from larval sea lamprey rearing in streams to find suitable spawning environments (Vrieze and Sorensen 2001). Therefore, they often move into streams near where they reach adequate size and receive environmental cues for maturation. One potential limitation of the result presented in Fig. 6 is that a sea lamprey may not spend its entire life in one area, but could have reared under a different thermal regime. Sea lamprey exhibit 'regional panmixia' where they return to streams near where they enter the lake (Waldman et al. 2008). In this study, evidence for regional impacts of warming waters comes from spatial heterogeneity in observed sea lamprey size that corresponds with the general thermal patterns found across the lake (Figs. 4 and 5). Sea lamprey likely integrate over different temperature conditions and experience an average condition found within small regional areas.

Change in parasite growth is one response to warmer environmental temperatures, but changes in parasite phenology and life cycle completion rates may also have strong impacts on hosts. Sea lamprey have diverse life history strategies migrating from streams into lake between April and November depending on temperatures (Holmes et al. 1994, Holmes and Youson 1998). This results in a parasitic feeding stage of between 12 and 18 months prior to migration for spawning (Applegate 1950, Bergstedt and Swink 1995). Kitchell and Breck (1980) verified the 12-month life history assumption by using a

bioenergetics model fit to periodically observed sizes of sea lamprey collected by commercial fisheries in Lake Huron. The duration of the parasitic phase can be influenced by host choices. Different host thermal preferences create different thermal histories (Moody et al. 2011; Kitchell et al., *in press*). Major host fishes such as lean lake trout, siscowet lake trout, and Chinook salmon have different thermal preferences (10°C, 4°C, and 13°C, respectively) and vary in the duration and spatial extent of preferred thermal habitat across the lake and through time (Cline et al. 2013). This creates variable growing season lengths for parasitic sea lamprey attached to different hosts. Changing climate may also affect the growth, development, and phenology of the larval life-stage. Increased temperature is strongly related to shorter periods of egg incubation and increased larval sea lamprey growth (Holmes 1990, Holmes and Youson 1998). Therefore, altered thermal regimes may induce changes in the timing of juvenile and adult life stages that could have consequences for host-parasite interactions under a changing climate.

Much of the climate change literature reported to date extrapolates observed patterns in weather effects, phenological changes, and altered geographic distributions of selected organisms for future climate scenarios through use of large-scale global circulation models (e.g., Karl et al. 2009, Trumpickas et al. 2009). In contrast, the climate change effects on Lake Superior sea lamprey and their trophic interactions reported here derive from observed data and potential changes owing to currently increasing water temperatures. Warmer surface waters and resultant longer growing seasons in the Whitefish Bay region both lead to larger adult sea lamprey sizes (Figs. 5 and 6). While overall increase in adult sea lamprey size started with recovery of host populations (Jorgensen and Kitchell 2005a), we suggest that it has continued over the past three decades in response to extended periods of thermal stratification that promote greater durations of higher feeding and increased growth rates for sea lamprey.

Lessons from sea lamprey in Lake Superior presented here offer insights for management of invasive species and host-parasite systems in the future. Changing thermal regimes present challenges from new invaders, but as shown,

established or controlled species may undergo shifts in growth or timing that can impact the effectiveness of management or produce expansion of an established but low abundance exotic species. In host-parasite systems, changes in total food consumption, parasite growth, and reproductive success can strongly impact host populations. Additionally, changes in phenology and life-cycle can influence the effectiveness of current management protocols. Adaptive management strategies offer integrated approaches that can address resource management in ways that are tailored to the complexity of these challenges. This paper describes the basis for seeking ways to address climate change in Lake Superior. If costs of sea lamprey control must be restricted, the approach we present can guide identifying where overall effectiveness of sea lamprey control can be maximized in each of the Great Lakes.

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