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THERMAL TOLERANCES OF FRESHWATER MUSSELS AND THEIR HOST FISHES: SPECIES INTERACTIONS IN A CHANGING CLIMATE

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ABSTRACT

Rising environmental temperatures result from changes in land use and global climate and can cause significant shifts in the composition and distribution of species within communities. In freshwater systems, the larval life stage, glochidia, of Unionida mussels develops as an obligate parasite on host fish gills or fins before transforming into the juvenile stage and dropping to the sediment to complete the life cycle. Because of the relationship between freshwater mussels and their often specific host fish species, mussels are not only limited by their own variable thermal tolerances, but also by those of their host fish. Our intent was to compile data from available literature regarding thermal sensitivities of eight species of freshwater mussels and their host fishes, to determine if the community structure of these systems is at risk from rising environmental temperatures. Mussels were both more and less thermally sensitive than specific host fish species (2.9 °C mean absolute difference between mussel and host; range = 0 – 6.8 °C). In 62% of mussel-host fish comparisons, freshwater mussels were more thermally tolerant than their hosts (3.4 °C mean difference; range = 0.2 – 6.8 °C), suggesting that some mussels are effectively more stenothermic than tolerance criteria indicate, which may pose additional environmental risk. Further analysis revealed that variation in mussel thermal tolerance could not be attributed to mussel acclimation temperature, species, life stage, or mean host fish thermal tolerance, suggesting that mussel thermal tolerance is controlled by multiple interacting and complex factors. Our findings in this meta-analysis suggest that thermal effects of anthropogenic landscape alteration and climate change may be compounded for freshwater mussels via their obligate life cycle interaction with fish and highlight the importance of considering global change effects in a community context.

KEY WORDS Host fish, Stream community, Thermal tolerance, Unionidae

INTRODUCTION

Stream and river temperatures have been increasing, with a mean temperature increase of 0.009 – 0.077 °C per year in United States waters (Kaushal et al., 2010). Rising environmental temperatures can cause significant shifts in the composition and distribution of species within communities (Smith et al., 2006). Aquatic systems are much more constrained than are terrestrial systems in the ways in which organisms can respond to warming, and therefore, thermal effects may be more pronounced (Shuter & Post, 1990). Because of this, and also because changes in temperature unrelated to climate change in stream ecosystems have

been well documented (Feller, 1981; Hewlett & Fortson, 1982), aquatic ecosystems are ideal model systems to study the ecological consequences of climate change.

Freshwater mussels (Order Unionida) fulfill their considerable role in the aquatic community by converting particulate matter from the water column into a food source for other organisms (Vaughn et al., 2004; Howard & Cuffey, 2006). The freshwater mussel family Unionidae is suffering a high rate of extinction; nearly 70% of North America's 297 species are extinct or vulnerable to extinction (Bogan, 1993; Williams et al., 1993; Graf & Cummings, 2007). The most notable

cause of decline in freshwater mussels is habitat degradation; other impacts include water withdrawal for industry, pollution, and urbanization (Bogan, 2008).

Freshwater mussels are a threatened taxon due in part to their unique life history strategies. They rely on host fish to complete their life cycle with a larval life stage, glochidia, that must infest the gills or fins of host fish as obligate parasites before transforming into the juvenile life stage and dropping to the sediment to continue development into benthic-dwelling adults (e.g., Watters, 2007).

Because of the relationship between mussels and their host fishes, freshwater mussels are not only potentially affected by their own variable thermal tolerance limits, but also by those of their host fish (Biro et al., 2007; Daufresne & Boet, 2007; Schmutz et al., 2007; Steingraeber et al., 2007). Although species interactions could be important in the ability of species to respond to climate change (Walther et al., 2002), this dynamic remains poorly explored for freshwater mussels (Spooner et al., 2011). Because some unionid mussels are host specific and may have different environmental requirements than their hosts, they represent an ideal case to explore the extent to which species interactions can and will mediate responses to climate change. The freshwater mussel-host fish relationship is a fitting model to explore both climate change in an aquatic context and interspecies relationships in the context of global change.

To elucidate the linkage between climate change and freshwater mussel survival, we collected representative thermal tolerance data for eight species of mussels as well as their host fishes. We then used these data to compare the thermal tolerances of these two groups of interacting organisms and propose scenarios of population and functional changes related to rising environmental temperatures.

METHODS

We compiled thermal tolerance data for glochidia of eight freshwater mussel species and seven species of juvenile freshwater mussels (Pandolfo et al., 2010). The mussel species represent two tribes (Lampsilini, Quadrulini) from the Ambleminae subfamily and one tribe (Anodontini) of the Unioninae subfamily: Fatmucket (*Lampsilis siliquoidea* (Barnes, 1823)), Pink Heelsplitter (*Potamilus alatus* (Say, 1817)), Black Sandshell (*Ligumia recta* (Lamarck, 1819)), Butterfly (*Ellipsaria lineolata* (Rafinesque, 1820)), Eastern Creekshell (*Villosa delumbis* (Conrad, 1834)), Washboard (*Megaloniais nervosa* (Rafinesque, 1820)), White Heelsplitter (*Lasmigona complanata* (Barnes, 1823)), and Brook Floater (*Alasmidonta varicosa* (Lamarck, 1819)) (Turgeon et al., 1998).

Thermal tolerances for the freshwater mussels were designated by median lethal temperatures (LT50s) (Pandolfo et al., 2010). Host fish were identified for the eight species of freshwater mussels according to the Ohio State University Mussel/Host database (Cummings & Watters, 2002) and by personal communication with propagation experts; only findings that observed juvenile metamorphosis in nature or in laboratory studies were included (Table 1). Thermal tolerance data for host fish species were collected from several sources. Lethal threshold temperatures (incipient lethal temperature; ILT) from the Environmental Protection Agency's Water Quality Criteria (1972) and Wismer & Christie (1987) were used when available, as these data coincided most directly with the LT50 measure used for freshwater mussels. For species where no lethal threshold was available, critical thermal maximum temperatures (CTmax), using loss of equilibrium as an endpoint, were derived from Beitinger et al. (2000) and Wismer & Christie (1987). For species where ILT or CTmax were not available, upper thermal tolerance limit (UTTTL) data were applied from Eaton et al. (1995).

Upper thermal tolerances for host fish were plotted with freshwater mussel LT50s against acclimation temperature for each freshwater mussel species (Figure 1). In most instances, fish thermal tolerance increased linearly with increasing acclimation temperature, providing a reasonable indication of the upper thermal threshold for a species. However, the freshwater mussel thermal tolerances were not linearly related to acclimation temperature (Pandolfo et al., 2010). Because there was no significant effect of acclimation on freshwater mussel thermal tolerances, we were unable to conduct statistical comparisons on the linear regressions. Therefore, we qualitatively compared mussel thermal tolerances with fish thermal tolerances. If mussel tolerance was generally less than corresponding fish thermal tolerance (i.e., plotted points fell to the left), then the mussels were considered less thermally tolerant than the fish hosts and vice versa.

We also compared mean fish ILTs to mean mussel LT50s for the species with suitable data. To coincide with freshwater mussel LT50s, only fish ILTs for acclimation temperatures within the range of 22 – 27 °C were used. We conducted 29 species-specific comparisons between thermal tolerance means (e.g., mean Fatmucket versus mean Largemouth Bass, *Micropterus salmoides*), with comparisons possible for 6 of the 8 mussel species (Fatmucket, Black Sandshell, White Heelsplitter, Washboard, Brook Floater, and Eastern Creekshell). For each comparison, relative and absolute differences were calculated.

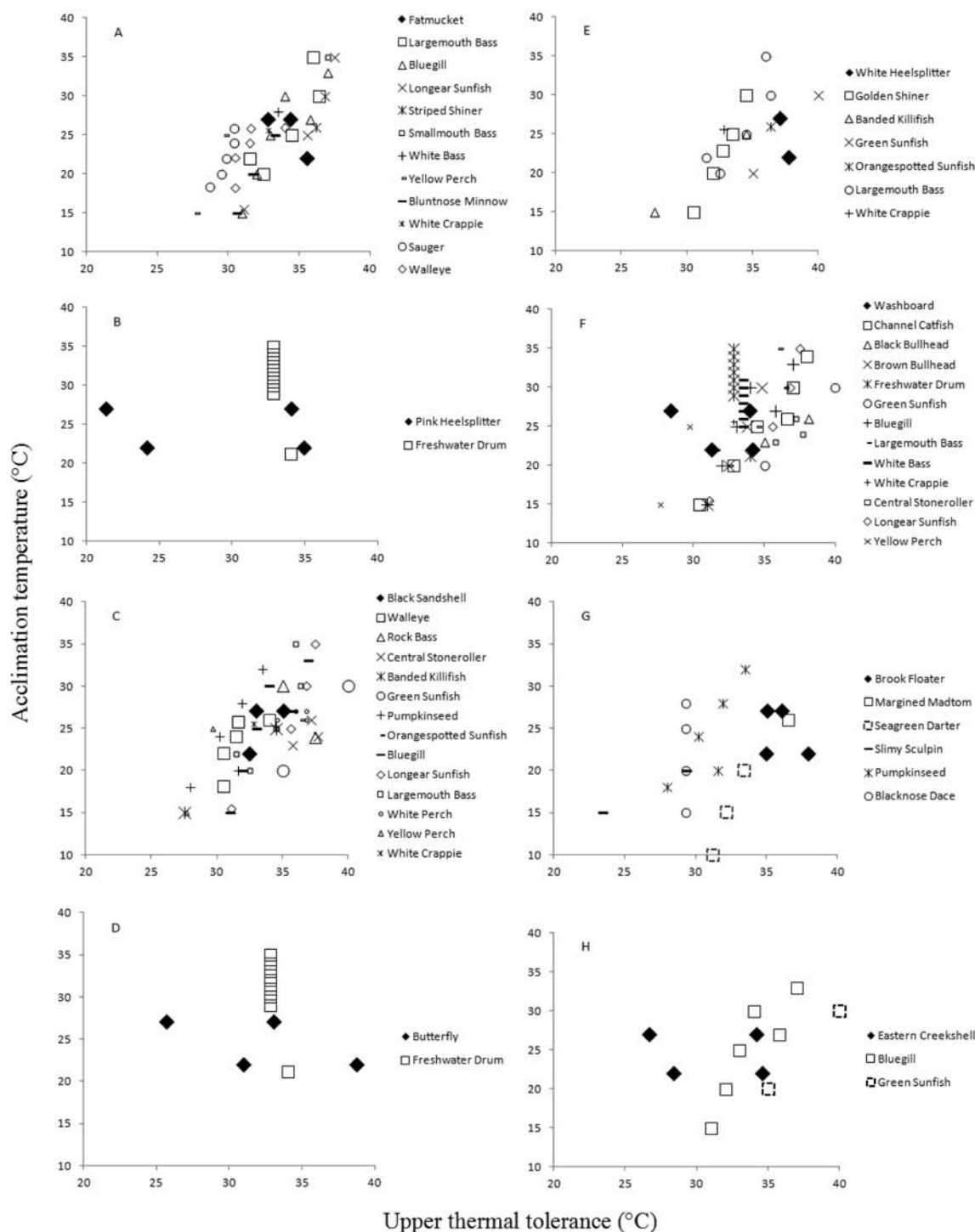


FIGURE 1

Upper thermal tolerances of eight species of freshwater mussels and their host fish. Each mussel species is graphed in a separate panel with its host fish: Fatmucket (A), Pink Heelsplitter (B), Black Sandshell (C), Butterfly (D), White Heelsplitter (E), Washboard (F), Brook Floater (G), and Eastern Creekshell (H). Freshwater mussels are denoted by the large diamond (◆), fish used to transform mussels from Pandolfo et al. (2010) are denoted by the large square (□).

For the same subset of data that was used to examine quantitative differences in mussel and fish thermal tolerances (six mussel species), a fixed-effects generalized linear model was used to assess the effects of mussel acclimation temperature, species, life stage, and host fish thermal tolerance on freshwater mussel thermal tolerances (SAS PROC GLM, version 9.2, SAS Institute Inc., Cary, North Carolina). Host fish thermal tolerance was incorporated into the model as a mean among fish species of host fish tolerance for each mussel species. Because host fish thermal tolerance was determined by mussel species, species and host fish thermal tolerance were confounded variables (i.e., one mean fish tolerance datum for each mussel species). To reduce covariate redundancy, species was omitted from the model and host fish thermal tolerance was retained to represent the effect of host fish thermal tolerance among mussel species.

RESULTS

LT50s were available for glochidia and juvenile freshwater mussels at two acclimation temperatures (Table 2) (Pandolfo et al., 2010). For both life stages, the overall LT50s ranged from 21.4 °C to 42.6 °C with a mean of 33.1 °C. Fish thermal tolerance values ranged from 23.5 °C to 38.1 °C with a mean of 33.1 °C (Table 1). Fish thermal tolerance varied according to acclimation temperature, as well as the method used to determine the tolerance value.

Relative thermal tolerance between freshwater mussels and their corresponding host fish varied among mussel species, and for some mussels, it varied among host fish species. Fatmucket appeared more thermally tolerant than Sauger (*Sander canadensis*) and Yellow Perch (*Perca flavescens*). Pink Heelsplitter and Butterfly shared the same host fish, Freshwater Drum (*Aplodinotus grunniens*), which had limited thermal tolerance data available. Both Pink Heelsplitter and Butterfly had a wider LT50 range than Freshwater Drum's UTTL, though more data are needed. Black Sandshell appeared more thermally tolerant than Yellow Perch, and more sensitive than Orangespotted Sunfish (*Lepomis humilis*) and Central Stoneroller (*Camposoma anomalum*). White Heelsplitter was more thermally tolerant than Largemouth Bass (*Micropterus salmoides*), Golden Shiner (*Notemigonus crysoleucas*), White Crappie (*Pomoxis annularis*), and Banded Killifish (*Fundulus diaphanus*). Washboard was less thermally tolerant than Green Sunfish (*Lepomis cyanellus*), Black Bullhead (*Ameiurus melas*), and Central Stoneroller. Brook Floater was more thermally tolerant than Slimy Sculpin (*Cottus cognatus*), Blacknose Dace (*Rhinichthys atratulus*), and Pumpkinseed (*Lepomis gibbosus*). Eastern Creekshell in this study (Pandolfo et al., 2010)

were transformed by a hybrid Bluegill-Green Sunfish (*Lepomis macrochirus* x *L. cyanellus*); therefore, thermal tolerance data were considered for both species, because data were not available for the hybrid. Eastern Creekshell appeared to be similarly tolerant to both Bluegill and Green Sunfish; but, it remains unclear where the hybrid's thermal tolerance would occur.

Among mussel–fish relationships for which comparable thermal tolerance data were available, the mean of absolute differences between tolerances for mussels and corresponding host fish was 2.9 °C (n = 29, range = 0 – 6.8 °C). Mussels were more thermally tolerant than their host fish in 18 of 29 comparisons (62%), and among those, the mean difference was 3.4 °C (range = 0.2 – 6.8 °C). Fatmucket, Black Sandshell, White Heelsplitter, and Brook Floater were more tolerant than their hosts in the majority of comparisons. Fatmucket was more thermally tolerant than Largemouth Bass, Yellow Perch, Bluntnose Minnow, Sauger, and Walleye and less tolerant than Bluegill and Longear Sunfish. Black Sandshell was more tolerant than Walleye, Banded Killifish, Pumpkinseed, Bluegill, Longear Sunfish, Largemouth Bass, and Yellow Perch and less tolerant than only Rock Bass. White Heelsplitter was more thermally tolerant in all three comparisons to Golden Shiner, Banded Killifish, and Largemouth Bass. Brook Floater was also more tolerant in both comparisons to Pumpkinseed and Blacknose Dace. Eastern Creekshell was only compared with Bluegill, and it was less tolerant than that species. Only Washboard demonstrated a strong trend of lower thermal tolerance than the majority of its hosts. Channel Catfish, Black Bullhead, Brown Bullhead, Bluegill, Largemouth Bass, and Longear Sunfish were all more thermally tolerant than Washboard, and the mussel was only more tolerant than Yellow Perch. In those cases where the fish host is more thermally tolerant than the mussel, tolerance differed by a mean of 2.2 °C (range = 0.1 – 3.6 °C).

Variation among mussel thermal tolerances could not be significantly attributed to mussel acclimation temperature, life stage, or mean host fish thermal tolerance. Though host fish thermal tolerance accounted for the largest source of variation in the model, the effect was not significant (p = 0.098). Acclimation temperature was also not a significant factor (p = 0.275), nor was mussel life stage (p = 0.773). Acclimation temperature and life stage were not expected to be significant effects, based on related previous analyses of the data (Pandolfo et al., 2010).

DISCUSSION

Although we cannot conclude that host fish thermal tolerance significantly affects freshwater mussel

thermal tolerance, host fish thermal tolerance was the most explanatory variable in our model. Despite the limited sample sizes and power of our analysis, we found a nearly significant effect ($p < 0.10$). As additional data become available for meta-analyses such as these, we suspect that a significant relationship may be revealed, reflecting the intrinsic species interactions involved in mussel thermal tolerance that varies among mussel species. The qualitative comparisons presented here demonstrated that, for the species examined, freshwater mussels generally have a thermal tolerance that is similar to or slightly greater than the thermal tolerance of their host fishes. In that prevalent case where a fish host is more stenothermic than the parasitizing mussel, the effective thermal tolerance of the mussel is reduced by the obligate relationship with the fish. However, these results and conclusion are based on an examination of acute thermal thresholds which may not adequately express the complexity of potential climate change scenarios.

As a response to global climate change, decreasing mussel survival may be a function of not only first order temperature or flow effects, but also of changing interactions with their host fishes (Spooner et al., 2011). Mussel population dynamics can also be impacted if increased water temperatures decrease the infestation success of glochidia on the host fish or if too few mussels are recruited to reproductive maturity to maintain the population. The mussels examined in our comparative study are dependent on predominantly coolwater and warmwater assemblage species as their hosts (Stefan et al., 1995), and therefore, we can potentially classify these mussels based on the classification of their hosts. Though not included in our study, mussel species exist that occupy cold headwater streams that are thermally buffered, relative to coolwater or warmwater stream habitats, and therefore, they parasitize coldwater fish as hosts (Bogan, 2002). These mussels are most likely to be adversely affected by global climate change and stream warming. It is also possible that mussels or fish that appear more heat tolerant may actually be more at risk from climate change because heat tolerant species may be living closer to their thermal limits (Tomanek & Somero, 1999). Evidence exists that some fish species are already encountering temperatures at their upper lethal limit in North America (Eaton et al., 1995; Caissie, 2006).

The bulk of aquatic thermal tolerance testing to date has been conducted on fish (e.g., Beiting et al., 2000). From such studies, we have gained insight on the effects of temperature on basic physiological processes (van Dijk et al., 1999; Widmer et al., 2006; Fontaine et al., 2007). Increases in environmental temperature have also been shown to adversely affect

fish assemblages (e.g., Keleher & Rahel, 1996; Peterson & Kwak, 1999; Flebbe et al., 2006). One long term study found that an increase of 1.5 °C in the average water temperature in the Upper Rhone River caused southern fish species to displace northern fish species (Daufresne et al., 2004). The increase of southern warmwater fish into the range of the northern cooler water fish was consistent with predictions based on latitudinal, altitudinal, and stream order gradient hypotheses (Brown, 1971; Vannote et al., 1980).

Studies with mollusks have found, as in those with fish, that increases in temperature can affect various physiological functions, including immune condition (Chen et al., 2007), filtration rate (Schulte, 1975; Han et al., 2008), oxygen consumption (Newell et al., 1977; Han et al., 2008), excretion rates (Han et al., 2008), and growth (Han et al., 2008). To a degree, increased energy input (e.g., through filtration) may compensate for increased metabolic demands, but there appears to be a thermal limit above which the positive relationship between temperature and physiological function plateaus or becomes negative due to increasing energetic costs (Schulte, 1975; Newell et al., 1977). Rising temperatures have been associated with alterations in reproduction in the marine bivalve *Macoma balthica* (Philippart et al., 2003) and increased spawning in marine *Perna canaliculus* and *Mytilus galloprovincialis* (Petes et al., 2007). In addition to the findings on sublethal effects of thermal stress, a number of studies have addressed acute thermal limits (Ansell et al., 1980; Iwanyzki & McCauley, 1993; Urban, 1994; Pandolfo et al., 2010). Laboratory tests have shown that viability of glochidia can vary widely even at a common temperature among species belonging to the same tribe (Cope et al., 2008). Laboratory tests also show that increasing temperature causes a decrease in glochidial viability (Jansen et al., 2001; Zimmerman & Neves, 2002; Akiyama & Iwakuma, 2007).

The obligate parasite-host relationship between freshwater mussels and fish provides an insightful example of how the loss of one species in a community can initiate cascading effects for additional species. These cascades may lead to chains of extinction among any number of species that interact in a critical manner. In perhaps the clearest case of coextinction in the literature, severe reductions in populations of the Eel Grass *Zostera marina* drove the host-specific Eelgrass Limpet, *Lottia alveus*, to extinction (Carlton et al., 1991). Changes in environmental temperatures can also cause asynchrony in species interactions. Increased temperature caused the bivalve *Macoma balthica* to adjust its reproductive schedule which led to asynchrony with the presence of phytoplankton and shrimp necessary for juvenile survival (Philippart et al.,

2003). For freshwater mussels, asynchrony with the presence of host fish could lead to a collapse of mismatched populations.

A number of scenarios warrant consideration to examine the interactions of freshwater mussels with host fishes in the context of climate change (Figure 2). The thermal tolerance of freshwater mussels can potentially be higher, lower, or similar to their host fish. Each of these possibilities may lead to very different outcomes, each with distinct implications for conservation and management of freshwater mussels. If freshwater mussels and their host fishes have similar thermal tolerances, then no species interaction effects are expected to compound any adverse effects from climate change. This does not imply that climate change does not pose a risk to mussels or their hosts, but that they are expected to respond in similar manners, and therefore their relationship can be conserved. However, even if host fish remain within range of freshwater mussels, glochidia may not transform successfully outside an optimal temperature range (Roberts & Barnhart, 1999).

An important consideration is that freshwater mussels are more constrained in their mobility than are their host fish. Freshwater mussels do not have the option to relocate, and must be able to tolerate local environmental conditions to survive (Golladay et al., 2004). As temperature increases, some fish species may shift their distribution as a response, with warmwater species moving into cooler habitats, or relocating to lower order streams. Because freshwater fish are able to detect differences in water temperature and relocate to cooler water when available, the fish may more easily alter their distribution outside of the range of the freshwater mussels that rely on them (Kaya et al., 1977; Headrick & Carline, 1993; Schaefer et al., 2003). In this scenario, the thermal tolerance criteria for mussels do not indicate their effective vulnerability to temperature rise unless those thresholds for host fish are also considered. If this occurs, mussels may be able to parasitize other more tolerant fish species as alternate hosts. However, most mussel species specialize with one or only a few fish species as hosts, but specificity varies among species (Haag & Warren, 2003). In general, freshwater mussels become locally adapted to their host fish and experience greater transformation success with fish in their native habitat than with fish from other areas (Rogers et al., 2001).

Another scenario is that if the host fish have thermal tolerances greater than the dependent mussels, the fish will not need to relocate to cooler habitat. The possibility remains in this scenario that through typical fish movement, mussels may be dispersed

to cooler habitats where they will be more suited for survival. However, if this is not the case, mussel populations may decline due to decreased glochidial infestation success or thermal mortality of mussels of all life stages, despite the presence of their host fish. If mussel populations become too small and fragmented, sperm may not reach females during the spawning season, and such populations will be unable to contribute genetically (Downing et al., 1993; Strayer et al., 2004; McLain & Ross, 2005).

Organisms can adapt to environmental changes in two ways: changes within individuals (phenotypic plasticity) or evolutionary changes (Berteaux et al., 2004). However, freshwater mussel adaptation may be limited due to their extended life span, as species with long generation times respond relatively slowly to environmental changes (Berteaux et al., 2004; Rowe, 2008). In addition, recruitment does not necessarily occur annually; for instance, a population study of the freshwater mussel Ebonyshell, *Fusconaia ebena* (Lea, 1831), found successful recruitment only once every 5 to 10 years (Payne & Miller, 2000). Thus, the population dynamics of freshwater mussels are complex, and populations may exhibit negative growth and highly variable recruitment, while long-lived individuals thrive (Strayer et al., 2004).

Aquatic species may also have to cope with the shifting distributions of more thermally tolerant non-indigenous species (Stachowicz et al., 2002; Carveth et al., 2006), and land-use changes can combine with climate change effects to the detriment of aquatic organisms (Peterson & Kwak, 1999). Environmental temperature rise may result in unexpected changes in ecosystems as regime shifts occur (Hsieh et al., 2005), and the many factors involved in climate change may interact in a synergistic fashion (Portner et al., 2005). In fact, alterations in flow regime as a result of changing precipitation patterns may be at least as threatening to aquatic species as increasing temperatures (Peterson & Kwak, 1999).

Our analysis highlights the importance of considering global change effects in a community context, but additional research is required to fully understand and plan for climate change and the thermal tolerance dynamics of freshwater mussels and their host fish. More data are needed on thermal tolerances of specific host fish-mussel pairs, the transformation success rate with alternate hosts, and local and broad-scale influences of flow and land cover before it is possible to determine which of the proposed scenario outcomes is most plausible among freshwater mussel species (Figure 2). Surveys of mussel assemblage structure along temperature gradients would provide critical information, as

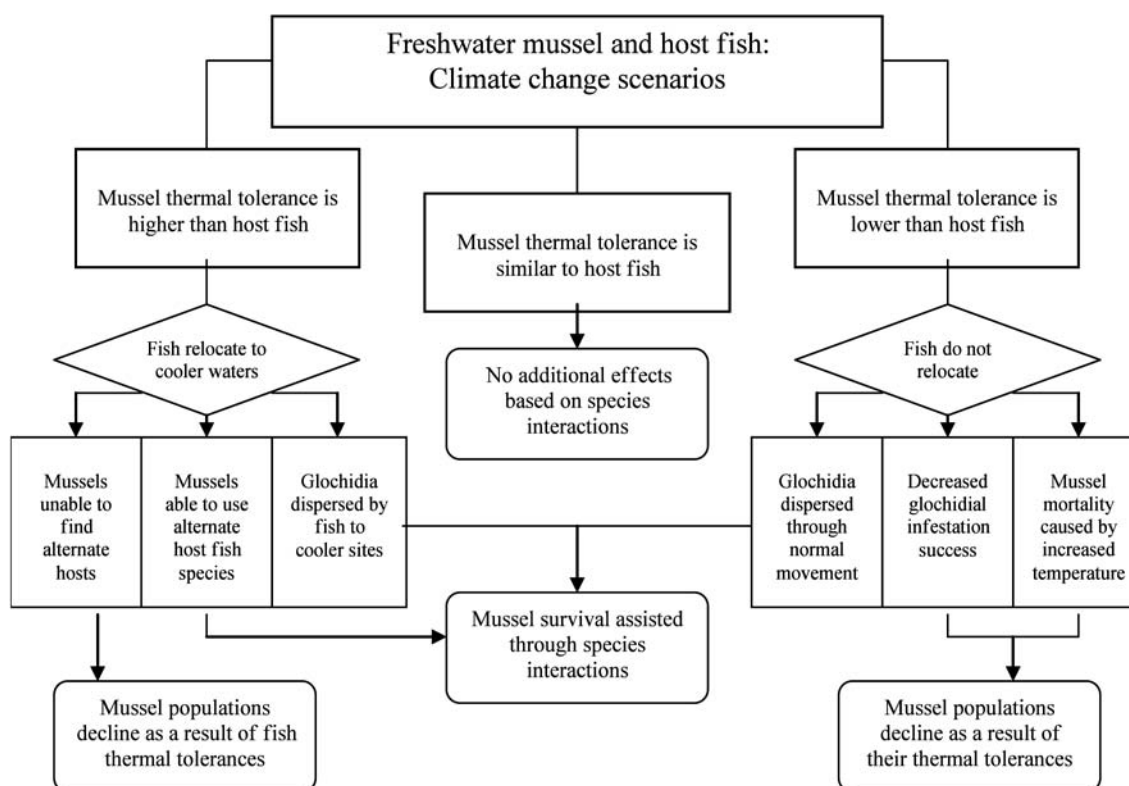


FIGURE 2

Flow diagram of potential interaction scenarios for freshwater mussels and their host fishes in the context of climate change.

would additional laboratory investigations of infestation success of glochidia on multiple fish species in relation to environmental temperature changes.

Research on climate change effects cannot be conducted for every species and community; therefore the focus must be on species with a disproportionately important function in their ecosystems (Bale et al., 2002). We further propose that freshwater mussels are a crucial fauna to study in the context of global change, not only because they are one of the most endangered aquatic faunal groups in North America, but also because of their unique life history strategies. Unionids provide a means for measuring the importance of species interactions as a component of climate change using a sensitive model species in aquatic systems—if freshwater mussels will not be our aquatic climate change canary, which fauna will?

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TABLE 1

Thermal tolerance data compiled from literature for freshwater fish species that serve as hosts for freshwater mussels. All temperatures are °C; acclimation temperature is in parentheses. ILT=incipient lethal temperature, CTmax=critical thermal maximum, UTTL=upper thermal tolerance limit.

Freshwater mussel	Host fish	Fish species name	Thermal tolerance	Method	Source
Fatmucket (<i>Lampsilis siliquoidea</i>)	Largemouth Bass ¹	<i>Micropterus salmoides</i>	32.5 (20)	ILT	EPA 1972
			31.5 (22)	ILT	EPA 1972
			34.5 (25)	ILT	EPA 1972
			36.4 (30)	ILT	EPA 1972
			36 (35)	ILT	Wisner and Christie 1987
	Bluegill	<i>Lepomis macrochirus</i>	31 (15)	ILT	Wisner and Christie 1987
			32 (20)	ILT	Wisner and Christie 1987
			33 (25)	ILT	Wisner and Christie 1987
			35.8 (27)	ILT	Wisner and Christie 1987
			34 (30)	ILT	Wisner and Christie 1987
			37 (33)	ILT	Wisner and Christie 1987
			31.1 (15.5)	ILT	Wisner and Christie 1987
	Longear Sunfish	<i>Lepomis megalotis</i>	35.6 (25)	ILT	EPA 1972
			36.8 (30)	ILT	EPA 1972
			37.5 (35)	ILT	EPA 1972
			36.2 (26)	CTmax	Beitinger et al. 2000
	Striped Shiner	<i>Luxilus chrysocephalis</i>	37 (35)	ILT	Wisner and Christie 1987
	Smallmouth Bass	<i>Micropterus dolomieu</i>	33.5 (28)	UTTL	Eaton et al. 1995
	White Bass	<i>Morone chrysops</i>	27.7 (15)	ILT	EPA 1972
	Yellow Perch	<i>Perca flavescens</i>	29.7 (25)	ILT	EPA 1972
	Bluntnose Minnow	<i>Pimephales notatus</i>	30.6 (15)	ILT	EPA 1972
			31.7 (20)	ILT	EPA 1972
			33.3 (25)	ILT	EPA 1972
			32.8 (25.6)	UTTL	Eaton et al. 1995
	White Crappie Sauger	<i>Pomoxis annularis</i> <i>Sander canadensis</i>	28.7 (18.3)	ILT	Wisner and Christie 1987
			29.5 (19.9)	ILT	Wisner and Christie 1987
			29.9 (22)	ILT	Wisner and Christie 1987
			30.4 (23.9)	ILT	Wisner and Christie 1987
			30.4 (25.8)	ILT	Wisner and Christie 1987
	Walleye	<i>Stizostedion (Sander) vitreum</i>	30.5 (18.2)	ILT	Wisner and Christie 1987
			30.5 (22.1)	ILT	Wisner and Christie 1987
			31.5 (24)	ILT	Wisner and Christie 1987
			31.6 (25.8)	ILT	Wisner and Christie 1987
			34 (26)	ILT	Wisner and Christie 1987
Pink Heelsplitter (<i>Potamilius alatus</i>)	Freshwater Drum ¹	<i>Aplodinotus grunniens</i>	34 (21.2)	CTmax	Wisner and Christie 1987
			32.8 (29-35)	ILT	Wisner and Christie 1987
Black Sandshell (<i>Ligumia recta</i>)	Walleye ¹	<i>Stizostedion (Sander) vitreum</i>	30.5 (18.2)	ILT	Wisner and Christie 1987
			30.5 (22.1)	ILT	Wisner and Christie 1987
			31.5 (24)	ILT	Wisner and Christie 1987
			31.6 (25.8)	ILT	Wisner and Christie 1987
			34 (26)	ILT	Wisner and Christie 1987
	Rock Bass	<i>Ambloplites rupestris</i>	37.5 (23.9)	ILT	Wisner and Christie 1987
			35 (30)	ILT	Wisner and Christie 1987
	Central Stoneroller	<i>Camptostoma anomalum</i>	35.8 (23)	CTmax	Beitinger et al. 2000
			37.7 (24)	CTmax	Beitinger et al. 2000
			37.2 (26)	CTmax	Beitinger et al. 2000
	Banded Killifish	<i>Fundulus diaphanus</i>	27.5 (15)	ILT	EPA 1972
	Green Sunfish	<i>Lepomis cyanellus</i>	34.5 (25)	ILT	Wisner and Christie 1987
			35 (20)	ILT	Wisner and Christie 1987
	Pumpkinseed	<i>Lepomis gibbosus</i>	40 (30)	ILT	Wisner and Christie 1987
			28 (18)	ILT	Wisner and Christie 1987
			31.6 (20)	ILT	Wisner and Christie 1987
			30.2 (24)	ILT	Wisner and Christie 1987
			31.9 (28)	ILT	Wisner and Christie 1987
			33.5 (32)	ILT	Wisner and Christie 1987

TABLE 1
(cont.)

Freshwater mussel	Host fish	Fish species name	Thermal tolerance	Method	Source
Black Sandshell (<i>Ligumia recta</i>) continued	Orangespotted Sunfish	<i>Lepomis humilis</i>	36.4 (26)	CTmax	Beitinger et al. 2000
		<i>Lepomis macrochirus</i>	31 (15)	ILT	Wisner and Christie 1987
	Bluegill	<i>Lepomis macrochirus</i>	32 (20)	ILT	Wisner and Christie 1987
			33 (25)	ILT	Wisner and Christie 1987
			35.8 (27)	ILT	Wisner and Christie 1987
			34 (30)	ILT	Wisner and Christie 1987
			37 (33)	ILT	Wisner and Christie 1987
			31.1 (15.5)	ILT	Wisner and Christie 1987
	Longear Sunfish	<i>Lepomis megalotis</i>	35.6 (25)	ILT	EPA 1972
			36.8 (30)	ILT	EPA 1972
			37.5 (35)	ILT	EPA 1972
			32.5 (20)	ILT	EPA 1972
	Largemouth Bass	<i>Micropterus salmoides</i>	31.5 (22)	ILT	EPA 1972
			34.5 (25)	ILT	EPA 1972
			36.4 (30)	ILT	EPA 1972
			36 (35)	ILT	Wisner and Christie 1987
	White Perch	<i>Morone americana</i>	34.6 (25-26)	ILT	Wisner and Christie 1987
			36.8 (26-27)	ILT	Wisner and Christie 1987
			36 (27)	ILT	Wisner and Christie 1987
			27.7 (15)	ILT	EPA 1972
	Yellow Perch	<i>Perca flavescens</i>	29.7 (25)	ILT	EPA 1972
	White Crappie	<i>Pomoxis annularis</i>	32.8 (25.6)	UTTIL	Eaton et al. 1995
Butterfly (<i>Ellipsaria lineolata</i>)	Freshwater Drum ¹	<i>Aplodinotus grunniens</i>	34 (21.2)	CTmax	Wisner and Christie 1987
			32.8 (29-35)	ILT	Wisner and Christie 1987
White Heelsplitter (<i>Lasmigona complanata</i>)	Golden Shiner ¹	<i>Notemigonus crysoleucas</i>	30.5 (15)	ILT	EPA 1972
			32 (20)	ILT	EPA 1972
			32.7 (22.8)	ILT	Wisner and Christie 1987
			33.5 (25)	ILT	EPA 1972
			34.5 (30)	ILT	EPA 1972
			27.5 (15)	ILT	EPA 1972
	Banded Killifish	<i>Fundulus diaphanus</i>	34.5 (25)	ILT	Wisner and Christie 1987
	Green Sunfish	<i>Lepomis cyanellus</i>	35 (20)	ILT	Wisner and Christie 1987
			40 (30)	ILT	Wisner and Christie 1987
	Orangespotted Sunfish	<i>Lepomis humilis</i>	36.4 (26)	CTmax	Beitinger et al. 2000
	Largemouth Bass	<i>Micropterus salmoides</i>	32.5 (20)	ILT	EPA 1972
			31.5 (22)	ILT	EPA 1972
			34.5 (25)	ILT	EPA 1972
			36.4 (30)	ILT	EPA 1972
			36 (35)	ILT	Wisner and Christie 1987
			32.8 (25.6)	UTTIL	Eaton et al. 1995
Washboard (<i>Megalaniais nervosa</i>)	Channel Catfish ¹	<i>Ictalurus punctatus</i>	30.4 (15)	ILT	EPA 1972
			32.8 (20)	ILT	EPA 1972
			34.5 (25)	ILT	EPA 1972
			36.6 (26)	ILT	Wisner and Christie 1987
			37 (30)	ILT	EPA 1972
			38 (34)	ILT	Wisner and Christie 1987
	Black Bullhead	<i>Ameiurus melas</i>	35 (23)	ILT	Wisner and Christie 1987
			38.1 (26)	CTmax	Beitinger et al. 2000
	Brown Bullhead	<i>Ameiurus nebulosus</i>	31 (15)	ILT	EPA 1972
			32.5 (20)	ILT	EPA 1972
			33.8 (25)	ILT	EPA 1972
			34.8 (30)	ILT	EPA 1972
			41 (35)	ILT	Wisner and Christie 1987
			34 (21.2)	CTmax	Wisner and Christie 1987
	Freshwater Drum	<i>Aplodinotus grunniens</i>	32.8 (29-35)	ILT	Wisner and Christie 1987
			35 (20)	ILT	Wisner and Christie 1987
	Green Sunfish	<i>Lepomis cyanellus</i>	40 (30)	ILT	Wisner and Christie 1987
			31 (15)	ILT	Wisner and Christie 1987
	Bluegill	<i>Lepomis macrochirus</i>	32 (20)	ILT	Wisner and Christie 1987
			33 (25)	ILT	Wisner and Christie 1987
			35.8 (27)	ILT	Wisner and Christie 1987
			34 (30)	ILT	Wisner and Christie 1987
			37 (33)	ILT	Wisner and Christie 1987

TABLE 1
(cont.)

	Host fish	Fish species name	Thermal tolerance	Method	Source
Washboard (<i>Megalaniais nervosa</i>) continued	Largemouth Bass	<i>Micropterus salmoides</i>	32.5 (20)	ILT	EPA 1972
			31.5 (22)	ILT	EPA 1972
			34.5 (25)	ILT	EPA 1972
			36.4 (30)	ILT	EPA 1972
			36 (35)	ILT	Wisner and Christie 1987
	White Bass	<i>Morone chrysops</i>	33.5 (25-31)	UTTL	Eaton et al. 1995
	White Crappie	<i>Pomoxis annularis</i>	32.8 (25.6)	UTTL	Eaton et al. 1995
	Central Stoneroller	<i>Camptostoma anomalum</i>	35.8 (23)	CTmax	Beitinger et al. 2000
			37.7 (24)	CTmax	Beitinger et al. 2000
			37.2 (26)	CTmax	Beitinger et al. 2000
	Longear Sunfish	<i>Lepomis megalotis</i>	31.1 (15.5)	ILT	Wisner and Christie 1987
			35.6 (25)	ILT	EPA 1972
			36.8 (30)	ILT	EPA 1972
			37.5 (35)	ILT	EPA 1972
	Yellow Perch	<i>Perca flavescens</i>	27.7 (15)	ILT	EPA 1972
			29.7 (25)	ILT	EPA 1972
Brook Floater (<i>Alasmodonta varicosa</i>)	Margined Madtom ¹	<i>Noturus insignis</i> ²	36.5 (26)	CTmax	Beitinger et al. 2000
	Seagreen Darter ¹	<i>Etheostoma thalassinum</i> ³	31.2 (10)	CTmax	Beitinger et al. 2000
			32.2 (15)	CTmax	Wisner and Christie 1987
			33.4 (20)	CTmax	Beitinger et al. 2000
	Slimy Sculpin	<i>Cottus cognatus</i>	23.5 (15)	ILT	Wisner and Christie 1987
			29.4 (20)	CTmax	Wisner and Christie 1987
	Pumpkinseed	<i>Lepomis gibbosus</i>	28 (18)	ILT	Wisner and Christie 1987
			31.6 (20)	ILT	Wisner and Christie 1987
			30.2 (24)	ILT	Wisner and Christie 1987
			31.9 (28)	ILT	Wisner and Christie 1987
			33.5 (32)	ILT	Wisner and Christie 1987
			29.3 (15)	ILT	Wisner and Christie 1987
			29.3 (20)	ILT	EPA 1972
	Blacknose Dace	<i>Rhinichthys atratulus</i>	29.3 (25)	ILT	EPA 1972
			29.3 (28)	ILT	EPA 1972
Eastern Creekshell (<i>Villosa delumbis</i>)	Hybrid Bluegill ¹	<i>Lepomis machrochirus cyanellus</i>			
	Bluegill	<i>Lepomis macrochirus</i>	31 (15)	ILT	Wisner and Christie 1987
			32 (20)	ILT	Wisner and Christie 1987
			33 (25)	ILT	Wisner and Christie 1987
			35.8 (27)	ILT	Wisner and Christie 1987
			34 (30)	ILT	Wisner and Christie 1987
	Green Sunfish	<i>Lepomis cyanellus</i>	37 (33)	ILT	Wisner and Christie 1987
			35 (20)	ILT	Wisner and Christie 1987
			40 (30)	ILT	Wisner and Christie 1987

¹Fish used to transform juvenile mussels from Pandolfo et al. (2010).

²Thermal data for Slender Madtom (*Noturus exilis*).

³Thermal data for Greenside Darter (*Etheostoma blennioides*).

TABLE 2

Freshwater mussel thermal tolerance data. LT50s for glochidia (24 h) and juvenile (96 h) mussels at 22 °C and 27 °C acclimation temperatures (Pandolfo et al. 2010). All LT50s reported as °C.

Species	LT50			
	Glochidia		Juveniles	
	22 °C Acclimation	27 °C Acclimation	22 °C Acclimation	27 °C Acclimation
<i>Lampsilis siliquoidea</i>		32.8	35.6	34.4
<i>Potamilus alatus</i>	24.2	21.4	35.0	34.1
<i>Ligumia recta</i>	42.6	33.0	32.5	35.1
<i>Ellipsaria lineolata</i>	31.0	25.7	38.8	33.1
<i>Lasmigona complanata</i>	37.8	37.1		
<i>Megalonaias nervosa</i>	31.3	28.4	34.2	34.0
<i>Alasmidonta varicosa</i>	38.0	36.1	35.0	35.1
<i>Villosa delumbis</i>	28.4	26.7	34.6	34.2