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The effects of temperature change on the hatching success and larval survival of largemouth bass *Micropterus salmoides* and smallmouth bass *Micropterus dolomieu*

S. J. LANDSMAN*†, A. J. GINGERICH†‡, D. P. PHILIPP†‡
AND C. D. SUSKI†‡§

**Department of Integrative Biology, University of Illinois, 286 Morrill Hall, 505 S. Goodwin Ave., Urbana, Illinois 61801, U.S.A.*, †*Illinois Natural History Survey, Institute of Natural Resource Sustainability, University of Illinois, 1816 S. Oak St., Champaign, Illinois 61820, U.S.A.* and ‡*Department of Natural Resources and Environmental Science, University of Illinois, Turner Hall, 1102 S. Goodwin Ave., Urbana, Illinois 61801, U.S.A.*

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In this study, the effects of abrupt temperature change on the hatching success and larval survival of eggs, yolk-sac larvae (YSL) and larvae above nest (LAN), for both largemouth bass *Micropterus salmoides* and smallmouth bass *Micropterus dolomieu* were quantified. Temperature had a significant effect on hatching success and time to 50% mortality, with large heat shocks causing accelerated mortality. The temperature changes shown to influence survival of all life stages, however, were beyond what is typically experienced in the wild. *Micropterus salmoides* had greater egg hatching success rates and increased survival rates at YSL and LAN stages, relative to *M. dolomieu*. Additionally, egg hatching success and survival of LAN varied across nests within the study. These findings suggest that temperature alone may not account for variations in year-class strength and may emphasize the need for protection of the nest-guarding male *Micropterus* spp. to ensure recruitment.

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Key words: distribution; range; recruitment; year class.

INTRODUCTION

Water temperature plays an important role in the lives of fishes and is considered to be an ecological resource, similar to food, habitat and access to mates, which can influence individual fitness (Magnuson *et al.*, 1979). When temperature varies away from the optimal for an organism, this may act as a stressor and impair physiological and behavioural activities (Fry, 1947; Beyers & Rice, 2002; Donaldson *et al.*, 2008). For larval fishes, water temperature can influence growth rates (Shuter *et al.*, 1980; Leggett & Deblois, 1994), swimming performance and predator avoidance (Leggett *et al.*, 1984; Pepin, 1991; Blaxter, 1992), as well as metabolic rate (Blaxter, 1992; Kamler, 2008) and cellular function (Somero & Hofmann, 1997). Large, abrupt changes in temperature can induce significant larval mortality events that, in turn,

§Author to whom correspondence should be addressed. Tel.: +1 217 244 2237; email: suski@illinois.edu

can have profound effects on year-class strength (Fry, 1947; Badenhuizen, 1969; Lamadrid-Rose & Boehlert, 1988; Myers, 1998; Planque & Frédou, 1999).

Smallmouth bass *Micropterus dolomieu* Lacépède 1802 and largemouth bass *Micropterus salmoides* (Lacépède 1802) are two sympatric fish congeners found in temperate North American lakes and rivers that serve as excellent model species to quantify the effects of temperature change on offspring survival and contributions to year-class strength. In the spring, as water temperature approaches 15° C, males of both species begin to construct highly visible, bowl-shaped nests in the littoral zones of lakes and rivers (Beeman, 1924; Kramer & Smith, 1962; Allan & Romero, 1975). Females of both species, after being courted by the male, enter the nest and lay up to several thousand eggs (Kramer & Smith, 1962; Raffetto *et al.*, 1990), after which they leave. Parental care is the sole responsibility of the male, and that obligation can last up to 5–6 weeks for *M. dolomieu* and up to 4–5 weeks for *M. salmoides* (Coble, 1975). This lengthy paternal investment serves to increase the likelihood of offspring survival and continues until offspring become independent of male care (Ridgway & Friesen, 1992). Because guarding males of both species fail to feed regularly and rely mostly on the consumption of accumulated lipid reserves to fuel parental care activities (Coble, 1975; Hinch & Collins, 1991; Gillooly & Baylis, 1999; Mackereth *et al.*, 1999), the parental care period can cause declines in energy reserves.

During the reproductive period, developing broods can be exposed to a variety of different environmental stressors, such as wind events and cold fronts, that can result in siltation, physical alteration of nest habitat and abrupt and rapid temperature changes (Kramer & Smith, 1962; Allan & Romero, 1975; Goff, 1986; Steinhart *et al.*, 2005). Premature brood abandonment by male *M. dolomieu* and *M. salmoides* has been observed following temperature changes as small as 2° C (Rawson, 1945; Henderson & Foster, 1957) and can be exacerbated if temperatures drop below 15° C (Latta, 1963). Similarly, Suski & Ridgway (2007) showed that, in Lake Opeongo, Ontario, Canada, abrupt changes in temperature following storm events were the primary cause of premature abandonment for nest-guarding *M. dolomieu* when considered along with other variables including exposure of nests to wave action, accumulated degree days at time of spawning and male size. Premature abandonment by a nest-guarding male may result in the total loss of that brood through predation (Neves, 1975; Philipp *et al.*, 1997; Suski & Philipp, 2004), which has the potential to negatively affect year-class strength (Kramer & Smith, 1962; Coutant, 1975; Myers & Barrowman, 1996; Myers, 2002; Devries *et al.*, 2009). Currently, it is not known if premature parental abandonment following abrupt fluctuations in water temperature results from negative effects of low temperature on offspring survival, on the willingness or ability of parental males to continue with care of their broods, or through a combination of these two potential mechanisms (Allan & Romero, 1975; Suski & Ridgway, 2007).

The majority of past work examining the forces that control larval mortality and recruitment for *M. dolomieu* and *M. salmoides* has focused on the contribution of eggs and late juvenile stages (*i.e.* YOY) to year-class strength, with limited information concerning the factors influencing the survival of larval stages (Parkos & Wahl, 2002). Furthermore, most recruitment studies involving fishes from the genus *Micropterus* have focused on *M. salmoides*, with a paucity of information existing for factors controlling year-class strength in *M. dolomieu* (Devries *et al.*, 2009). On the basis of this background, the goals of the current study were to: (1) determine

how *M. dolomieu* and *M. salmoides* egg hatching success and larval survival rates were influenced by abrupt changes in temperature, and (2) assess species-specific differences and stage-specific trends in survival rates following abrupt temperature changes of varying magnitudes. The experimental approach employed by this study allowed for a comparison not only of multiple life stages within two species but also across multiple nests within a population.

MATERIALS AND METHODS

STUDY SITE

This study was conducted at the Queen's University Biological Station (QUBS) on Lake Opinicon, Ontario, Canada (44° 34' N; 76° 19' W) from 13 May to 12 June 2008. Lake Opinicon is a 787 ha mesotrophic lake that contains self-sustaining *M. dolomieu* and *M. salmoides* populations (Keast, 1970).

METHODS

Littoral zone snorkel surveys were performed to locate nests with male *M. salmoides* and *M. dolomieu* guarding unhatched eggs (<3 days old). Because these species mate assortatively by size (Ridgway *et al.*, 1991; Wiegmann & Baylis, 1995; Philipp *et al.*, 1997; Suski & Philipp, 2004), large female fish might produce offspring of higher 'quality' than smaller conspecifics (Birkeland & Dayton, 2005), and the number of eggs guarded by a nesting male correlates positively with size (Philipp *et al.*, 1997; Suski & Philipp, 2004), attempts to control for the effects of allometry were made by excluding nesting males that were disproportionately large (>450 mm total length, L_T) or small (<300 mm L_T). In addition, nests were often >1 km away from each other, reducing the likelihood that a single female may have deposited eggs into multiple nests in this study. Once a suitably sized nesting male of either species was located, it was marked with an individually numbered nest tag and the location was drawn on a map of the site. Nest depth was estimated visually and ranged from 0.5 to 3.0 m, consistent with nest depths of these species in other systems (Beeman, 1924; Kramer & Smith, 1962; Bozek *et al.*, 2002; Suski *et al.*, 2003) and in Lake Opinicon (Philipp *et al.*, 1997; D. P. Philipp, unpubl. data). Following discovery of a nest, the snorkeller captured the nesting male with conventional fishing gear and brought the fish to a boat where L_T was measured to the nearest mm, and the fish was then held in a closed cooler of lake water.

While the male was absent, the snorkeller placed a clear 1 m² acetate sheet, divided into 2 cm² cells, on top of the nest and outlined the egg mass with a grease pencil. The number of eggs was counted in three 2 cm² cells (at the centre of the egg mass, mid-way to the edge, and at the edge) and these values were averaged. This average egg count (per 2 cm² cell) was scaled up to the area of the egg mass to estimate the total number of eggs for each nest (Raffetto *et al.*, 1990). Approximately 100 eggs were transferred to a glass jar filled with lake water using a kitchen turkey baster and placed in an insulated cooler. A weather monitoring station at QUBS, which recorded lake temperature every 60 min (Campbell Scientific thermocouple probes, Model 105T; www.campbellsci.com) indicated that, on the days of egg collections at the time of day when eggs were collected, mean \pm s.e. water temperature at 0.2 and 3.3 m depth was 17.3 \pm 0.1 and 16.4 \pm 0.1° C, respectively. For the entire 2008 nesting season (6 May to 17 June), temperatures averaged 18.3 \pm 0.1° C at 0.2 m and 17.6 \pm 0.1° C at 3.3 m depth. Examination of three successive years (2006, 2007 and 2008) of temperature data during the nesting period (*i.e.* 6 May to 17 June) showed that the largest hourly increases and decreases in water temperature were 1.34 and 1.02° C at 0.2 m, and 2.48 and 2.75° C at 3.3 m depth, respectively. Once egg collection was complete, males were released on top of their nests and brood-guarding resumed within 2 min. The snorkeller remained at the nest while the male was absent, to deter brood predation. Eggs

were transported by boat to the aquatic facility at QUBS. No more than 2 h elapsed from the collection of eggs to their arrival at the aquatic facility.

To quantify the effects of acute temperature change on egg survival, 10 eggs from each nest were distributed into five 100 ml perforated plastic cups (50 eggs total) that were filled with lake water from aerated water baths adjusted to each different temperature. Water temperature in each bath was held constant using 50 W aquarium heaters or temperature-controlled refrigerated cooling units outfitted with external cooling coils of polyethylene tubing. The mean \pm s.e. temperature of the treatments was 30 (30.3 ± 0.2), 25 (25.1 ± 0.2), 20 (18.7 ± 0.3), 15 (14.8 ± 0.1) and 10° C (9.9 ± 0.2 ° C). Cups with eggs were placed into these water baths, causing an abrupt temperature shock. When the lake's mean surface temperature on collection days was taken into account, temperature changes were -7 , -2 , $+3$, $+8$ and $+13$ ° C for eggs in the 10, 15, 20, 25 and 30° C treatments, respectively. Approximately 10% of each bath was exchanged with fresh lake water every 24–36 h to minimize accumulation of wastes. Mean dissolved oxygen readings were taken regularly (YSI 85, Yellow Springs Instruments; www.ysi.com) and were mean \pm s.e. 13.6 ± 0.1 , 11.6 ± 0.1 , 10.5 ± 0.1 , 9.3 ± 0.1 and 6.7 ± 0.1 mg l⁻¹ for the 10, 15, 20, 25 and 30° C water baths, respectively; these values are well above lethal limits for *M. salmoides* and *M. dolomieu* eggs (Spoor, 1977, 1984).

At 8 to 12 h intervals, all cups were inspected and the number of surviving eggs was recorded. Dead eggs were identified by opaque colouration with fungal growth and were removed using a transfer pipette. To remove analytical bias associated with disproportionately long or short survival rates, monitoring stopped once mortality reached 50% (*i.e.* analyses used time to 50% mortality; McCormick & Wegner, 1981). An egg was considered to have hatched when a tail was visible and locomotion was observed.

The collection and monitoring procedure described above was repeated two additional times later in the season for the same individuals, if possible, to document the effect of temperature change on the survival of yolk-sac larvae (YSL, *c.* 1–2 days after hatching), as well as pigmented larvae that had begun to hover above the nest, but had not yet left the nest area (LAN, *c.* 10 days post-hatch). To boost sample sizes, one *M. dolomieu* nest ($n = 10$) and four *M. salmoides* nests ($n = 15$) beyond those already sampled were used at the YSL stage. Due to premature abandonment by brood-guarding males during the LAN stage, sample sizes were reduced to $n = 8$ for *M. dolomieu* and $n = 3$ for *M. salmoides*. When these two stages were collected, surface temperature at 0.2 and 3.3 m was 16.4 ± 0.2 and 17.8 ± 0.1 ° C, respectively. In this case, the 10, 15, 20, 25 and 30° C baths resulted in temperature changes of -6 , -1 , $+4$, $+9$ and $+14$ ° C at the YSL stage and -8 , -3 , $+2$, $+7$ and $+12$ ° C at the LAN stage. It was possible to use YSL from all the same males as those sampled during the egg stage. During laboratory assessment of survival for larvae, dead larvae were identified by lack of movement, rigid posture, grey colouration and were removed with a transfer pipette. Observations of YSL and LAN occurred every 8 to 12 h until 50% mortality was reached so as to eliminate biasing data by including inordinately long survival times and in keeping with methods used in similar studies (McCormick & Wegner, 1981). When 50% mortality within a cup was reached between inspection intervals, mortality was estimated to have occurred at the midpoint between the intervals.

Male size and egg counts were compared across species with a *t*-test (Zar, 1999). Increases in mean hourly water temperature at 0.2 and 3.3 m depth across the spawning period (6 May to 17 June) for three consecutive years (2006, 2007 and 2008) were assessed using linear regression analyses (Zar, 1999). A mixed-model ANCOVA was used to examine the influence of different covariates on egg hatching success and time to 50% larval mortality at the YSL and LAN stages (Bennington & Thayne, 1994; Zar, 1999). For these models, the main effects were species and temperature; nest was entered as a random effect because the nests used in the study were drawn from a larger population of nests within the lake (Bennington & Thayne, 1994; Zar, 1999). When the interaction was significant, or if the interaction was not significant but at least one of the main effects was significant, a Tukey–Kramer honestly significant difference (HSD) *post hoc* test was used to separate all means (Zar, 1999). Analysis of egg hatching success was performed following arc-sine square-root transformations to account for data collected as proportions. Preliminary analyses revealed that egg count was not a covariate that had a significant influence on hatching success or mortality rates ($P > 0.05$) and subsequently was excluded from all future models. Male size was also intentionally excluded

from analyses, not only because of the strong positive relationship between male size and egg count (Suski & Philipp, 2004) but also because this study was intentionally designed to standardize male size across nests and across species. All data were analysed using JMP 7.0 (SAS Institute, Inc.; www.sas.com), means are reported \pm s.e. where appropriate, and the level of significance (α) for all tests was $P \leq 0.05$.

RESULTS

PARENTAL MALE SIZE AND EGG COUNT

The size of nesting males did not differ significantly between species (t -test, $t = -1.0$, d.f. = 24, $P > 0.05$), with the mean \pm s.e. L_T of males sampled being 382 ± 10 mm ($n = 15$) for *M. salmoides* and 367 ± 12 mm ($n = 10$) for *M. dolomieu*. Furthermore, egg counts between species did not differ significantly (t -test, $t = -1.0$, d.f. = 23, $P > 0.05$). The mean \pm s.e. egg count for nesting *M. salmoides* ($n = 14$) was 3800 ± 450 eggs and ranged from 1200 to 6900 eggs. *Micropterus dolomieu* produced broods averaging 3100 ± 420 eggs, with individual values ranging from 2200 to 6200 eggs.

HATCHING SUCCESS

Temperature change significantly influenced the proportion of eggs that hatched for both species (ANCOVA; Table I). Hatching success was at least 70% when water temperature differed from ambient by -7 , -2 , $+3$ and $+8^\circ$ C. At the most extreme $+13^\circ$ C warm-water treatment, however, hatching success decreased by nearly 40 and 50% for *M. salmoides* and *M. dolomieu*, respectively. Records from the spawning seasons for 2006 to 2008 indicate that the largest hourly increase or decrease in temperature was $<3^\circ$ C, a temperature change that the data indicate these species' offspring could tolerate. In addition, differences in hatching success between species were significant with *M. salmoides* exhibiting greater hatching success across all treatments than did *M. dolomieu*. Analyses also revealed that hatching success varied across individual nests (ANCOVA; Table I).

LARVAL SURVIVAL, YSL STAGE

The YSL mortality was highly affected by the magnitude of temperature change to which larvae were exposed (ANCOVA; Table I). Both species survived for >14 days (336 h) following abrupt exposure to the extreme temperature -6° C below ambient lake temperature, or more than twice the largest hourly decrease noted between 2006 and 2008. Notable decline in survival, however, occurred following temperature changes above ambient, with significant differences in all three times to reach 50% mortality [$P < 0.05$; Fig. 1(a)]. Similar trends in times to 50% mortality were revealed by the lack of differences in mortality times between species (ANCOVA; Table I), though it should be noted that the effect was marginally non-significant and that in three of the five treatments *M. salmoides* attained 50% mortality several hours after *M. dolomieu* [Fig. 1(a)]. Additionally, nest had no effect on time to 50% mortality of YSL (ANCOVA; Table I).

TABLE I. Results of ANCOVA examining the effects of nest (random), species and temperature change on the egg hatching success and time for 50% mortality of yolk-sac larvae and larvae above nest for *Micropterus dolomieu* and *Micropterus salmoides*

Stage	Source	d.f.	SS	F	P
Egg hatching success	Whole model	27	19.6	4.5	<0.05
	Nest	18	12.9	4.5	<0.05
	Species	1	1.3	8.5	<0.05
	Temperature	4	5.5	8.5	<0.05
	Species × temperature	4	0.4	0.6	>0.05
	Error	72	11.6		
Yolk-sac larvae time to 50% mortality	Whole model	32	2 695 126.3	10.7	<0.05
	Nest	23	144 255.0	0.8	>0.05
	Species	1	23 515.9	3.0	>0.05
	Temperature	4	2 421 989.0	76.9	<0.05
	Species × temperature	4	21 517.0	0.7	>0.05
	Error	92			
Larvae above nest time to 50% mortality	Whole model	18	35 774.1	20.7	<0.05
	Nest	9	1042.2	10.8	<0.05
	Species	1	412.4	4.3	0.05
	Temperature	4	5508.8	57.3	<0.05
	Species × temperature	4	76.1	0.8	>0.05
	Error	36			

SS, sum of squares.

LARVAL SURVIVAL, LAN STAGE

Similar to the YSL stage, *M. salmoides* and *M. dolomieu*, LAN mortality was highly influenced by temperature change (ANCOVA; Table I). In contrast, however, the only temperature treatment to result in significantly lowered time to 50% mortality was the extreme warm-water temperature change of +12° C above ambient. Larvae of both species survived for 48–72 h in temperature exposures of –8, –3C, +2 and +7° C below or above ambient, but survived for <4 h at +12° C above ambient [Fig. 1(b)]. Again, thermal records for spawning seasons between 2006 and 2008 indicate that the greatest hourly increases and decreases in water temperature, namely of 2.48 or 2.75° C, respectively, could be tolerated by later stages of offspring development. Species had a significant affect on larval mortality, with *M. salmoides* requiring more time to reach 50% mortality than *M. dolomieu* LAN (ANCOVA; Table I). Variation in time to 50% mortality of LAN also varied across individual nests (ANCOVA; Table I).

DISCUSSION

Year-class strength and recruitment of fishes can be strongly influenced by temperature change during egg and larval development (Rombough, 1996). In a review

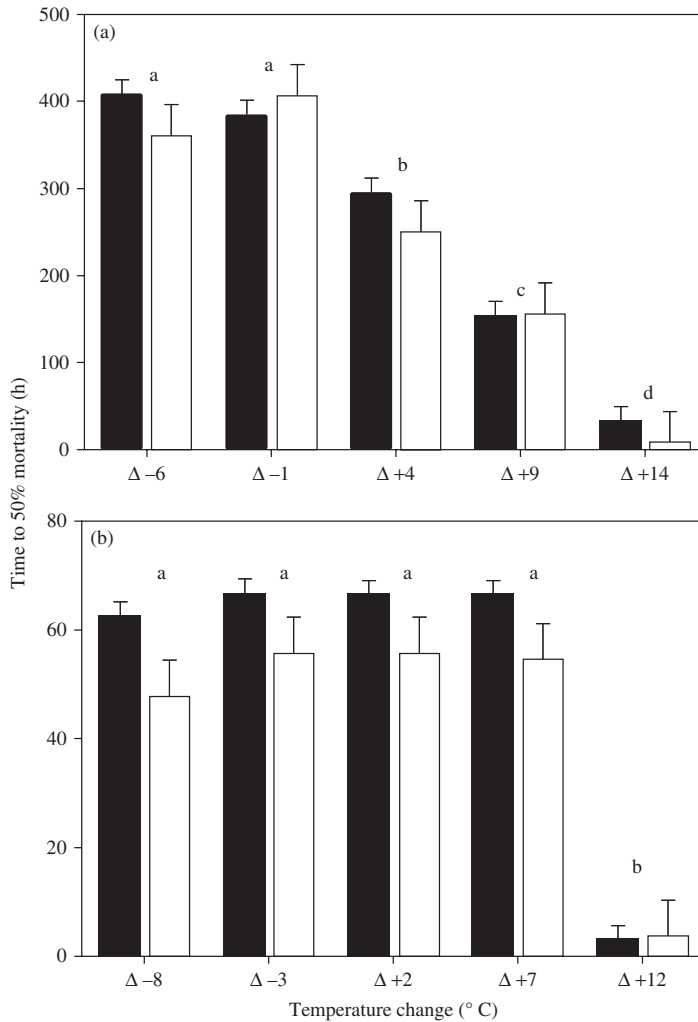


FIG. 1. Mean \pm S.E. time required to reach 50% mortality for *Micropterus salmoides* (■) and *Micropterus dolomieu* (□) in (a) yolk-sac larvae and (b) larvae above nest following five different treatments of abrupt temperature change. Samples sizes were $n = 15$ nests and $n = 10$ nests at the yolk-sac larvae stage, and $n = 3$ nests and $n = 8$ nests at the larvae above nest stage for each species, respectively. The magnitude of change in temperature was relative to the mean \pm S.E. water temperature at the time of collection, namely 16.4 ± 0.2 and $17.8 \pm 0.1^{\circ}\text{C}$ for yolk-sac larvae and larvae above nest, respectively. This resulted in temperature changes of -6 , -1 , $+4$, $+9$ and $+14^{\circ}\text{C}$ at the yolk-sac larvae stage and -8 , -3 , $+2$, $+7$ and $+12^{\circ}\text{C}$ at the larvae above nest stage for the 10, 15, 20, 25 and 30°C temperature treatments, respectively. Lower case letters above bars refer to differences in hatching success for different temperatures across both species [Tukey–Kramer honestly significant difference (HSD) *post hoc* test, $P < 0.05$].

of both marine and freshwater species, Rombough (1996) suggested that temperature changes of $\pm 6^{\circ}\text{C}$ were the maximum that fish eggs could tolerate without incurring significant negative effects on year-class strength. Furthermore, $\pm 2^{\circ}\text{C}$ changes in water temperature during the egg stage for Atlantic cod *Gadus morhua* L. 1758

(thermal tolerance range from -1.8 to 12.0°C ; Valerio *et al.*, 1992) can generate 1000-fold variations in recruitment (Planque & Frédou, 1999). The eggs of *M. salmoides* and *M. dolomieu*, collected from multiple nests within a population, proved to be quite resilient to temperature change because reductions in hatching success only occurred when eggs received a thermal shock of $+13^{\circ}\text{C}$ above ambient, with no significant decline in hatching success following exposure to cold water, although inter-nest differences in hatching success were observed. This finding is similar to that of McCormick & Wegner (1981) who showed that the hatching success of *M. salmoides* eggs pooled from several parents declined only when exposed to temperatures $>30^{\circ}\text{C}$. In contrast, Webster (1948) reported that the survival of *M. dolomieu* eggs was unaffected by temperature changes of $+24^{\circ}\text{C}$ using eggs from a single nest in Cayuga Lake, New York. Because both Webster (1948) and McCormick & Wegner (1981) evaluated effects using eggs from a single nest, however, it is possible that their results were unintentionally confounded by the use of eggs that were particularly resilient to temperature change. The present study used nests from various areas of the lake, often >1 km apart, thus reducing the likelihood that a single female deposited eggs into multiple sampled nests. Also, previous work with *M. dolomieu* has shown that relatively few nests provide the majority of offspring in a year class, emphasizing differences in offspring survival across nests (Gross & Kapuscinski, 1997).

Mortality of eggs and larvae following acute temperature that increases probably results from elevated metabolic rates, causing accelerated consumption of energy stores (Coutant, 1975; Boulekbache *et al.*, 1989; Blaxter, 1992) or from thermal degradation of proteins that impart a direct effect on cell functions such as substrate binding activity and stress protein synthesis (McCarthy & Houlihan, 1997; Somero & Hofmann, 1997). Exposure to the cold probably reduces metabolic rates of eggs and larvae, thereby prolonging their survival following thermal change rather than inducing mortality (Coutant, 1975; Blaxter, 1992). The current study, therefore, demonstrates that eggs and larvae of both *M. salmoides* and *M. dolomieu* are resilient to acute temperature changes as survival amidst cold-water temperature shocks was greater than at warm-water shocks, with this result varying across nests within a population.

It is important to differentiate variations in water temperature in the marine environment with those that may occur in freshwater. The heat capacity of oceans is far greater than smaller freshwater bodies and, therefore, marine fishes are less likely to experience abrupt temperature changes of the magnitude experienced by freshwater fishes. This could make marine fishes more susceptible to mortality following modest temperature changes (Houde, 1994); over evolutionary time scales, the exposure of *M. dolomieu* and *M. salmoides* eggs to fluctuating temperature may have resulted in increased tolerance to such fluctuations. In the present study, the observed maximum hourly increase and decrease in Lake Opinicon's water temperature between 6 May and June 17 of 2006 to 2008 was 2.48 and 2.75°C , respectively. The experimental conditions exposed eggs and larvae to a change in temperature that was several times as great as the maximum hourly increase noted during 2006 to 2008, with little effect on mortality rates. Together, findings demonstrate the thermal resilience of both *M. dolomieu* and *M. salmoides* eggs across a range of temperatures.

For both species of *Micropterus*, the three stages of offspring displayed pronounced differences in their responses to temperature stress. Egg survival was at least 70% in

four of the five temperature treatments, and the time required to reach 50% mortality for LAN was 85% lower than the time required for 50% mortality of YSL. Pörtner & Knust (2007) argued that the reduction in animal performance at high temperature probably occurs because sufficient quantities of oxygen cannot be delivered to respiring tissues, due to a reduction in aerobic metabolic scope. Eggs obtain oxygen through passive diffusion across their capsule and do not need gills or blood to obtain and deliver oxygen, possibly causing improved thermal tolerance relative to more advanced stages of development (Rombough, 2007). Fish eggs consist of water, proteins and lipids (Brooks *et al.*, 1997), the last of which are consumed as eggs develop into YSL (Kamler, 2008), and this process is probably hastened as temperature increases (Pepin, 1991). In the current study, although YSL survival remained high during cold shocks, warm-water shocks caused significant decline in survival. An even more pronounced decline, however, was observed for LAN during exposure to the extreme warm-water shock, where time to 50% mortality was reached in <4 h as opposed to over 150 h for YSL. As such, *M. dolomieu* and *M. salmoides* eggs and YSL may have had greater energy reserves to fuel the accelerated metabolic rates relative to later stages (*i.e.* larger body sizes of LAN) that have consumed more of their lipid stores (Adams *et al.*, 2004; Kamler, 2008). In addition, later stages of development may consume remaining lipid reserves as their resting metabolic rates increase with body size (Gillooly *et al.*, 2001) This finding, however, contradicts previous work, suggesting that later stages of development can withstand extreme temperature better than earlier stages (Rombough, 1996).

The current study sought to compare hatching success and larval survival simultaneously between two congeners. Results indicated a species effect at both the egg and LAN stages, with *M. salmoides* offspring having greater hatching success or time to 50% mortality. Previous comparative work has shown that *M. salmoides* and *M. dolomieu* differ in early life-history characteristics of eggs and larvae, with *M. dolomieu* showing increased investment in offspring, producing larger embryos with longer hatching and longer incubation times, and subsequently larger larval sizes (Suski & Philipp, 2004; Cooke *et al.*, 2006; Devries *et al.*, 2009). Therefore, it might be expected that, due to these differences in egg and larvae characteristics (*e.g.* greater embryo and larval size), *M. dolomieu* offspring would show greater resilience to temperature change than *M. salmoides*, but current results indicate *M. salmoides* offspring survive better under difficult thermal conditions. The largest differences were shown at increased temperatures, which may be explained by the lower thermal preference of *M. dolomieu* (Kieffer & Cooke, 2009) and a more northerly geographic distribution than *M. salmoides* (Scott & Crossman, 1973). Although differences in vulnerability to handling stress associated with laboratory confinement may exist between the two species, results across the temperature treatments suggest that differences in realized thermal niche, observed thermal niche and thermal performance differ across life stages of these two species.

Because little mortality was observed across the various temperature treatments used in this study, it is probable that water temperature does not influence larval mortality in the wild but, instead, may affect offspring survival through other indirect effects. Variation in water temperature has been shown to cause negative, sublethal effects on the metabolism, motor function, growth and development of larval fishes, which can lead to reduced activity, swimming performance and an impaired ability to capture prey or escape predators, thereby leading to increased mortality (Blaxter,

1992). For broods of *M. salmoides* and *M. dolomieu*, survival at early life stages is highly influenced by the presence of the parental nest-guarding male. Several researchers have found that temperature change, particularly temperature decreases, can cause nesting males to abandon their broods (Rawson, 1945; Henderson & Foster, 1957; Suski & Ridgway, 2007), and this absence can lead to severe reductions in brood size (Neves, 1975). If, however, temperature fluctuations do not cause direct offspring mortality, then sustaining healthy *M. salmoides* and *M. dolomieu* populations may be influenced by protecting the nest-guarding male from anthropogenic disturbances, predominantly angling, which has been shown to induce premature abandonment *via* brood predation (Philipp *et al.*, 1997; Suski & Philipp, 2004). Nevertheless, it is still unclear why males abandon their broods despite, according to the present study, high offspring survival which would not negatively affect fitness. Therefore, future studies should focus on the mechanisms behind parental male abandonment, particularly at non-lethal temperatures.

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