

The Effects of Acute Temperature Change on Prey Capture Kinematics in Largemouth Bass, *Micropterus salmoides*

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The effects of temperature on prey capture kinematics were investigated in the Largemouth Bass, *Micropterus salmoides*. Five individuals were first acclimated to 22 C and then acutely exposed to temperatures of 15, 20, 25, and 30 C. At each temperature, feeding events were recorded using high-speed video at 500 frames s⁻¹. An analysis of variance on the five fastest feeding events from each individual at each temperature resulted in a significant trend for the fastest feeding events to occur at 25 C. This effect confirmed the expectation of thermal dependence of mouth opening movements, which was based on an inverse relationship between water viscosity and temperature and the assumption that temperatures outside optimum decrease muscular power and contraction rates. However, the Q₁₀ value between 15–25 C was only 1.28, well below the minimum expected value of 2.0. Thus, we suggest the possibility that Largemouth Bass partially compensate for the effects of acute temperature changes by recruiting additional motor units at lower temperatures. The capacity of Largemouth Bass to mitigate the impact of acute temperature change on muscle physiology and the physical properties of water may represent a physiological adaptation to a predatory lifestyle in a thermally variable environment.

MANY important physiological processes in ectothermic vertebrates are influenced by temperature. Acute temperature changes are known to affect metabolic rate (Cossins and Bowler, 1987), muscle contractile properties (Bennett, 1984; Rome and Sosnicki, 1990), muscle recruitment patterns involved in locomotion (Rome et al., 1990; Temple and Johnston, 1997), behavioral dynamics (Mautz et al., 1992; Xu et al., 2001), and feeding kinematics (Wintzer and Motta, 2004) in fishes and other ectothermic vertebrates (Johnston and Temple, 2002). A common finding is that rate processes in muscles are fastest at some intermediate optimal temperature (Rome and Sosnicki, 1990). This effect of temperature on muscle performance has notable impacts on whole animal behaviors. For example, sprinting in lizards and fast-start swimming behaviors in fish typically are slower when temperatures fall below the thermal optimum for species acclimated to warm temperatures (Mautz et al., 1992; Beddow et al., 1995). However, when performing other routine behaviors, ectotherms have shown an ability to modulate muscular recruitment in order to maintain relatively constant speeds or patterns of locomotor kinematics, despite the dependence of muscle contractile properties on temperature (Johnston et al., 1977; John-Alder and Bennett, 1981; Rome and Swank, 2001).

These relationships between temperature and locomotion in ectotherms have been well documented in the literature. Although feeding behaviors are equally vulnerable to changes in

temperature, the kinematics of feeding under variable thermal conditions have received scant attention (Wintzer and Motta, 2004). The known effects of temperature on muscle contractile properties can be expected to have consequences for the mouth opening and buccal expansion movements that occur during suction feeding because, as with patterns of locomotion, these actions involve rapid muscular movements (Carroll, 2004). The thermal dependence of water viscosity also may affect prey capture kinematics by slowing suction feeding at lower temperatures, given that the dynamic viscosity of water increases markedly as temperature declines. For example, at 10 C, water is 30% more viscous than at 20 C (Fox and McDonald, 1992).

Previous work on Bluegill Sunfish, *Lepomis macrochirus*, has shown that temperature affects the timing of several jaw movements during feeding (Wintzer and Motta, 2004). When feeding on pieces of earthworm, Bluegill Sunfish exhibit slower prey capture kinematics at lower temperatures. In the present study, we further explore the effects of acute temperature change on prey capture kinematics in a study with Largemouth Bass, *Micropterus salmoides* (Lacépède). Unlike in the previous study, however, we challenged the Largemouth Bass with more elusive prey, as suction feeders are known to exhibit faster strikes when feeding on elusive prey items (Norton and Brainerd, 1993; Nemeth, 1997). We then examined the effect of acute temperature change on the fastest strike times recorded for five individuals at four experimental

temperatures. We analyzed the fastest strike times because suction feeding movements involve rapid muscle contractions and substantial effort (Carroll, 2004) and may reflect near-maximal effort by the Largemouth Bass.

Largemouth Bass are a widespread piscivorous freshwater fish found in the temperate waters of North America. Like most teleosts, they capture prey using a combination of ram and suction feeding. As a Largemouth Bass swims towards its prey, it initiates buccal expansion and mouth opening to draw the prey into its mouth (Svanback et al., 2002). Although there are a number of cranial muscles involved in feeding, the anterior epaxial musculature that attaches onto the posterodorsal surface of the skull provides the primary power input (Van Leeuwen and Muller, 1983; Lauder, 1985; De Visser and Barel, 1998; Carroll et al., 2004; Carroll and Wainwright, 2006). The sternohyoideus muscle acts antagonistically to the epaxial muscles, and in some feeding events it contributes significant power to the strike (Carroll, 2004; Carroll and Wainwright, 2006). The epaxial muscles cause dorsal rotation of the cranium while ventral muscles antagonistically depress the hyoid apparatus to expand the buccal cavity laterally (Sanford and Wainwright, 2002). The process of buccal expansion can occur in less than 30 milliseconds (Sanford and Wainwright, 2002) and is believed to be limited by available muscular power (Carroll, 2004). Because the rate of buccal expansion is rapid, suction feeders experience substantial hydrodynamic loading, which is reflected by sharp pressure changes inside the buccal cavity. Buccal pressure can peak at more than 25 kPa below ambient in Largemouth Bass (Carroll et al., 2004).

Based on the rapid nature of suction feeding, we expect that when Largemouth Bass feed at temperatures below or above their optimum, the rate of mouth opening during prey capture will be slower. This prediction is founded upon two expectations. First, the contractile properties of Largemouth Bass cranial muscles are assumed to be strongly affected by temperature, as is typically found in teleost fishes (Kolok, 1992; Beddow and Johnston, 1995; Johnson and Bennett, 1995; Johnston and Temple, 2002). Second, temperature changes will result in changes in water viscosity, which will affect the hydrodynamic loading of an expanding head during suction feeding because higher dynamic viscosity will beget higher drag forces. At lower temperatures, the fish will require increased muscular power in order to overcome increased resistance to the jaw movement through water and maintain a constant kinematic pattern (Rome et al., 1984;

Fuiman and Batty, 1997; Hunt von Herbing, 2002). Because suction feeding is limited by available muscular power Largemouth Bass may not be able to overcome the effect of temperature on muscle properties and may exhibit slower prey capture movements at temperatures outside of their thermal optimum.

MATERIALS AND METHODS

Study animal.—Largemouth Bass were chosen for this study because of their aggressive feeding behavior in captivity (Richard and Wainwright, 1995; Sanford and Wainwright, 2002; Svanback et al., 2002). Five individuals were collected from Putah Creek in Yolo County, California, where the water temperature was 15.6 C and temperatures can range from about zero to 46.1 C annually. The individuals were numbered 1–5 with standard lengths of 157, 185, 185, 185, and 190 mm, respectively, and were housed separately in 100 L aquaria. They were acclimated to room temperature at 21–23 C for three weeks, as the preferred temperature for this warm water species is approximately 22 C (Cincotta and Stauffer, 1984). The individuals were maintained on a mixed diet of frozen Squid (*Loligo opalescens*), live Goldfish (*Carassius auratus*), and Mosquitofish (*Gambusia affinis*) before and between experiments. Live Goldfish, approximately 30-mm long, were used as prey items during the experiments.

Prior to feeding experiments, the temperature in each tank was adjusted to one of the four test temperatures: 15, 20, 25, and 30 C. These temperatures were chosen to represent a large fraction of the potential range of thermal variation typical of North American temperate lakes where Largemouth Bass commonly occur (Savitz et al., 1996; Beletsky and Schwab, 2001). Aquarium water temperature was cooled by placing bags of ice directly in the tank water. This process lasted about 90 minutes for adjusting to both 15 and 20 C. Video recording began once the temperature reached the desired experimental temperature. Reduced amounts of the ice were kept in the tanks for the duration of the filming sessions to maintain the experimental temperatures ± 1 C. Heating the tanks to temperatures above the acclimation temperature was done with commercial 25-Watt aquarium heaters. Heating to 25 C required 60–90 minutes before video recording began. Heating to 30 C required ten hours. Because the temperature adjustment time required for 30 C was longer than for the other temperatures, we explored the possible influence of an extended acclimation period by maintaining four of the five individuals

in the 15 and 20 C treatments overnight and then recording additional feedings on the second day. This allowed us to ask if a longer acclimation period at both 15 and 20 C affected the focal variables analyzed in this study. There was a two to four day period between treatments to allow for recovery. During this period, Largemouth Bass were kept at room temperature. Fish were always not fed for the two days prior to a recording session to increase hunger levels and motivation.

All video recordings occurred in the same aquaria in which the bass were maintained to reduce stress, maximize motivation levels, and encourage the aggressive nature of feeding behavior. The five individuals were each subjected to a different sequence of the test temperatures. For example, Individual #1 underwent treatments in the following order: 30, 25, 20, and 15 C, whereas Individual #4 experienced the treatments as follows: 25, 30, 20, and 15 C. To minimize satiation effects, recording sessions ended when the individuals no longer achieved peak gape during prey capture (Sass and Motta, 2002). Filming sessions generally lasted one to two hours during which 8–20 sequences were recorded.

Measuring and analyzing prey capture kinematics.—Feeding sequences were recorded at 500 frames s^{-1} using a NAC (Simi Valley, CA) Memrecam Ci high-speed video system with a shutter speed of 1/3000 s. The camera was positioned with a lateral view of the Largemouth Bass approximately 1.5 m from the aquarium. To scale the images, a single frame of a ruler was recorded in the position where prey capture events occurred. Two 600-W floodlights were used to illuminate the tanks during filming but the lights were turned off between feedings to minimize their impact on aquarium water temperature. During filming, the individual was encouraged to one end of the tank using a plastic ruler. The Goldfish was held at the base of the head and introduced to the aquarium at the end of the tank away from the predator to ensure adequate time for both predator and prey to react to the interaction. When the individual spotted the prey, both the Largemouth Bass and the Goldfish were released simultaneously. Once both the prey and Largemouth Bass were released, the Largemouth Bass responded immediately with rapid swimming and prey capture.

Using ScionImage software, two landmarks were manually digitized from video frames: the anterior tip of the premaxilla and the anterior tip of the lower jaw. These points were used to measure gape distance during prey capture in

each frame beginning before the onset of mouth opening until shortly after peak gape distance was achieved. Two kinematic variables were generated from these data for further analysis: peak gape distance and time to peak gape distance (Richard and Wainwright, 1995; Sanford and Wainwright, 2002; Svanback et al., 2002). Although studies of prey capture kinematics in fishes often include additional movements, we focused on mouth opening time because it has been shown to be more highly correlated with suction pressure than any other externally visible skull motion (Sanford and Wainwright, 2002; Svanback et al., 2002) and it is highly correlated with the fluid speed that is generated by suction feeding centrarchids (Day et al., 2005). When peak gape is achieved during a strike, time to peak gape represents a simple kinematic metric that is the best known indicator of the major mechanical consequences of suction performance, suction pressure and fluid speed. Time to peak gape distance was measured as the time in milliseconds from 20% of peak gape to the first frame where peak gape distance was visible. Twenty percent of peak gape was used because the initial stages of mouth opening have been shown to be highly variable in duration (Sanford and Wainwright, 2002). Peak gape distance and time to peak gape distance were measured in 323 strike sequences from the five individuals for an average sample size of 16 prey capture sequences per fish at each temperature.

We wanted to evaluate the effect of temperature on the fastest time to peak gape distance, but it is known that choosing the single fastest time in performance trials creates awkward statistical issues with the behavior of observations from the tail of a distribution (Losos et al., 2002). To deal with this issue, we selected the five fastest times to peak gape from the first day of feeding trials for each Largemouth Bass at each temperature. The null hypothesis of no effect of temperature on the time to peak gape distance was tested using a repeated measures two-way analysis of variance (ANOVA) with temperature as the fixed factor, and individual as the random factor (Sokal and Rohlf, 1981). All of the interaction terms generated by the repeated measures were also inspected.

Because the 30 C treatment involved a slower transition to the experimental temperature than any of the other temperature treatments, we were concerned that the additional time could affect the feeding response. To evaluate this possibility, we compared the effect of temperature on the kinematic variables measured between the first day of recording, when temperature adjustments occurred in 90 minutes, and the next day, when

TABLE 1. REPEATED MEASURES TWO-WAY ANOVA FOR THE EFFECT OF TEMPERATURE ON PEAK GAPE DISTANCE IN *Micropterus salmoides*.

Source (Between subjects)	df	Mean squares	F-ratio	P
Temperature	1	0.002	0.003	0.955
Individual bass	1	2.68	5.38	0.04
Temp * Individual	1	0.012	0.024	0.878
Error	16	0.498		
Source (Within subjects)	df	Mean squares	F-ratio	P
A	4	0.153	2.446	0.055
A * Individual	4	0.138	2.214	0.077
A * Temp	4	0.081	1.307	0.34
A * Temp * Individual	4	0.111	1.79	0.21
Error	64	0.062		

the fish had been maintained at either the 15 or 20 C temperature treatment for 24 hours. We asked whether feedings recorded after a 90-minute transition to the treatment temperature change had the same peak gape distance and time to peak gape as feedings recorded the following day. These statistical comparisons were run on 15 and 20 C separately, and the design was a two-way ANOVA with individual crossed with experimental day.

Thermal dependence of time to peak gape was calculated using the standard temperature coefficient (Q_{10}) across each 5 C temperature change and across 15–25 C to facilitate comparisons to values in the literature. The Q_{10} is the proportional change in a rate per 10 C increment (Cossins and Bowler, 1987). For example, a Q_{10} of 2 would indicate a doubling in rate with a 10 C increment.

RESULTS

The experimental individuals demonstrated aggressive feeding behavior during recording sessions. Approximately 10% of prey capture attempts failed since the Goldfish sometimes evaded capture. The overall average peak gape distance at 15, 20, 25, and 30 C were 2.575, 2.59, 2.533, and 2.587 cm, respectively. In the repeated measures ANOVA on peak gape distance there were no significant effects of temperature, although a significant difference among individuals was found due to variation in body size (Table 1). The overall means of the five fastest times for each individual at the four temperatures were 23.3, 22.4, 18.2, and 22.0 ms respectively (Fig. 1). The repeated measures two-way ANOVA revealed a significant temperature effect on the fastest times to peak gape with a confidence level of 0.05 ($P < 0.001$; Table 2).

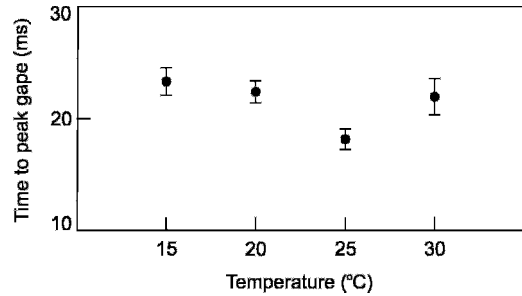


Fig. 1. The means \pm SE of the five fastest times to peak gape distance from each of the five Largemouth Bass at four experimental temperatures.

Post hoc tests between the 25 C value and each of the other temperatures were all non-significant except the comparison between 15 and 25 C, which was significant at $P = 0.05$. The Q_{10} values from 15–20, 20–25, and 25–30 C were 1.08, 1.53 and 0.68, respectively. From 15–25 C, the Q_{10} was 1.28. Separate repeated measures ANOVAs for 15 and 20 C that compared time to peak gape and peak gape distance measured on day one and on day two at these temperatures were all non-significant for the day effect. There was no indication that the time to peak gape was different after 24 hours acclimation than after 90 minutes, suggesting that the longer thermal adjustment period required for 30 C did not invoke a bias in the response.

DISCUSSION

We found a moderate but significant effect of temperature on time to peak gape. Largemouth Bass showed their fastest strikes at 25 C with time becoming longer as temperature diverged from this intermediate value. Although temperature influenced time to open the mouth, the effect

TABLE 2. REPEATED MEASURES TWO-WAY ANOVA ON TIME TO PEAK GAPE DISTANCE IN *Micropterus salmoides*.

Source (Between subjects)	df	Mean squares	F-ratio	P
Temperature	1	783.22	5.01	0.05
Individual bass	1	0.95	0.006	0.939
Temp * Individual	1	38.42	0.025	0.625
Error	16	155.02		
Source (Within subjects)	df	Mean squares	F-ratio	P
A	4	36.9	0.65	0.63
A * Individual	4	24.5	0.43	0.79
A * Temp	4	27.9	0.49	0.74
A * Temp * Individual	4	18.8	0.33	0.86
Error	64	57		

was more subtle than expected from previous studies of similar systems. This result is reflected in the relatively low Q_{10} values.

The muscles that power the expansive phase of feeding in Largemouth Bass are likely to be strongly influenced by temperature. Research on teleost muscle has consistently found substantial thermal dependence of power capacity, with *in vitro* preparations typically showing Q_{10} values of 2.0 or greater at temperatures below the optimum (Rome, 1990; Rome et al., 2000; Johnston and Temple, 2002). For fishes, Q_{10} values for the rate of twitch contractions are about 2.0 or greater when acclimation temperatures are not at the lower end of the species' tolerance curve (Johnson and Bennett, 1995; Temple and Johnston, 1997; Johnston and Temple, 2002).

The changes in water viscosity due to reduced temperatures increased drag resistance to jaw rotation and buccal expansion during prey capture motions. To overcome the effect of water viscosity on jaw movement, the individuals in this study would have required greater muscular power simply to generate constant kinematic patterns at lower temperatures. Based on this expectation and the assumed thermal dependence of muscular power production, dropping the temperature from 25 to 15 C was anticipated to result in at least a doubling of time to peak gape in Largemouth Bass. Instead, time to peak gape only increased from 18.2 ms at 25 C to 23.3 ms at 15 C, or a Q_{10} of 1.28, which is well below the expected Q_{10} value of approximately 2.0.

Although a direct measure of temperature effects on muscle contractile properties in Largemouth Bass will be an important goal in future research, the modest Q_{10} values in this study suggest that time to peak gape distance was not entirely limited by the effects of temperature on contractile speeds or available muscle power. Given the expectation that muscle contractile properties are thermally dependent, we suggest that at temperatures away from 25 C, the individuals could have increased motor unit recruitment to maintain kinematics and to create the suction power required to catch elusive prey. Such a scenario would also require that, during prey capture, Largemouth Bass did not fully activate their jaw abducting muscles at temperatures closer to 25 C (Grubich and Wainwright, 1997). This potential pattern of muscular modulation would partly compensate for the more severe influence of muscle contractile properties and water viscosity on feeding behavior.

One important issue surrounding the interpretation of our results is whether the strikes that we evaluated in our study represented maximal

effort on the part of the fish. The times that we report for gape opening, 22.4 ms at 20 C and 18.2 ms at 25 C, compare favorably to values in the literature at temperatures ranging from 21–23 C. One previous report of average time to peak gape distance for slightly larger size Largemouth Bass feeding on fish prey was 35 ms (Sanford and Wainwright, 2002). Over 95% of 200 prey capture events analyzed by Svanback et al. (2002) were longer than 30 ms, again with specimens that were about 3 cm larger than the fish used in the present study. Although it is always difficult to evaluate whether animals are exerting maximal effort in behavioral experiments, our overall means of the five fastest strikes for fish at each temperature were fast relative to previously published values, suggesting that the individuals were at least approaching maximal effort in these strikes.

Fast start behaviors in fish are a useful comparison to the current study because, as with rapid strikes in Largemouth Bass, fast start behaviors are viewed as a maximal effort behavior limited by available muscle power (Johnson and Bennett, 1995; Johnson et al., 1998; Temple and Johnston, 1998). In cases where acclimation temperatures were well within the fish tolerance curve, Q_{10} values for fast start velocity across acute temperature changes ranged from 1.2 in Killifish, *Fundulus heteroclitus* (Lacepede), to 2.81 in the Long-Spined Sea Scorpion, *Taurulus bubalus* (Gratzianov), and the overall mean of eight species was 1.75 (Temple and Johnston, 1997). When these values are compared to the current study, the Q_{10} value of 1.28 for time to peak gape distance between 15–25 C falls within the lower end of the range of results for fast start velocity. Changes in muscle recruitment patterns may account for this trend in both fast start and suction feeding behaviors. There is precedence for this concept. Fishes and other ectothermic vertebrates have been shown to alter muscle recruitment patterns during locomotion in order to compensate for the thermal dependence of contractile properties (Marsh and Bennett, 1986; Rome and Swank, 2001). Perhaps the best documented response to changes in thermal environment is that as locomotor speeds increase, the point at which different muscle fiber types recruit also changes depending on temperature (Marsh and Bennett, 1985; Jayne et al., 1990; Rome and Swank, 2001). This common mechanism for muscle modulation in locomotion could account for the minimal effect of temperature on suction feeding behaviors in Largemouth Bass.

The effect of temperature on prey capture kinematics has also been measured in the

Bluegill Sunfish, *Lepomis macrochirus* (Wintzer and Motta, 2004), another centrarchid fish from North America. The individuals were fed pieces of earthworm. Between 18 and 24 C, Q_{10} values of 1.56 and 1.25 were calculated for time to maximum gape, with an increase and decrease in temperature, respectively. Thus, under somewhat less demanding feeding conditions, Bluegill Sunfish exhibited a pattern similar to the results found in this study for Largemouth Bass, suggesting that a thermal dependence of prey capture kinematics may be general at least for this family of temperate freshwater fishes. However, this inference merits further exploration of temperature effects on feeding in other species of Centrarchidae.

Many freshwater fish species encounter natural thermal variation in lake habitats (Cooke et al., 2003). Seasonal fluctuations in water temperature can readily span 10–15 C, and spatial variation in temperature of temperate bodies of water can be nearly as extreme (Allender and Saylor, 1979; Marcogliese and Esch, 1992; Cooke et al., 2004). For example, surface water temperatures can vary as much as 10–15 C during periods of upwelling (Beletsky and Schwab, 2001), and stratification can produce sharp thermoclines with temperature drops up to 20 C (Marcogliese and Esch, 1992). Largemouth Bass might be exposed to these fluctuations in the course of a single 24 hr period, as they tend to travel considerable distances over potentially large thermal gradients to forage, spawn, and avoid predators (Winter, 1977; Mesing and Wicker, 1986).

Because Largemouth Bass often inhabit thermally variable environments, the finding that time to peak gape distance is only slightly affected by temperature may have implications for the trophic ecology of this species. Previous studies with Largemouth Bass show that kinematic speed during prey capture is positively correlated with the magnitude of suction pressure (Sanford and Wainwright, 2002; Svanback et al., 2002). When Largemouth Bass and other perciform species feed on more elusive prey, such as fish, they exhibit stronger suction pressures than when they feed on less elusive prey (Norton and Brainerd, 1993). Although temperature changes did significantly affect time to mouth opening in this study, the presence of unexpectedly low Q_{10} values indicates a possible compensation mechanism on the part of the fish to reduce the impact of temperature changes on skull movement during feeding. If muscle performance was the only factor controlling suction feeding performance, at colder temperatures, the time to mouth opening would be slower and

Largemouth Bass may not be able to generate the suction pressures required to capture elusive prey. Thus, the apparent capacity of Largemouth Bass to partially mitigate temperature effects on muscle performance and water viscosity may represent a behavioral adaptation to the lifestyle of a predator that hunts in thermally variable habitats on a short time scale. In addition, Largemouth Bass have a wide thermal tolerance range and can resist acute temperature changes as great as 20 C (Venables et al., 1978). This capability further substantiates the possibility that Largemouth Bass have acquired adaptations to deal with acute temperature changes in their environment. However, future studies examining *in vivo* and *in vitro* muscle activity in variable temperature regimes should be conducted in order to further investigate potential mechanisms of thermal compensation in Largemouth Bass.

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