

# The effects of temperature on prey-capture kinematics of the bluegill (*Lepomis macrochirus*): implications for feeding studies

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**Abstract:** Research with ectothermic organisms has demonstrated that temperature is positively correlated with an individual's power output during locomotion. This study investigates the effect of temperature on another aspect of power output, prey-capture kinematics, of the bluegill (*Lepomis macrochirus* Rafinesque, 1819). Feeding sequences for two treatments of four sunfish were filmed at three temperatures (18, 24, and 30 °C) with one treatment (A) experiencing an increasing range of temperatures and the other (B) experiencing a decreasing temperature range. Directional temperatures affected prey-capture kinematics. The time required to achieve maximum lower jaw depression and maximum gape, as well as the duration of maximum gape, time to close the mouth (from the point of maximum gape), and the total bite duration, increased as water temperature decreased. In addition, both the time to maximum gape and the time to maximum lower jaw depression were longer at 18 °C for individuals in treatment A than those in treatment B. These results indicate that water temperature can bias the results of feeding studies employing kinematics that do not control for its effects as well as those that make comparisons across such studies which utilize different temperatures and taxa.

**Résumé :** La recherche sur les organismes ectothermes a démontré qu'il existe une corrélation entre la température d'un individu et son rendement de puissance durant la locomotion. Notre étude examine l'effet de la température sur un autre aspect du rendement de puissance, la cinématique de la capture des proies, chez le crapet arlequin (*Lepomis macrochirus* Rafinesque, 1819). Nous avons filmé des séquences de quatre crapets en train de s'alimenter dans deux conditions et à trois températures (18, 24 et 30 °C); les conditions sont (A) une gamme de températures croissantes et (B) une gamme de températures décroissantes. Le sens du changement de température affecte la cinématique de la capture des proies. Le temps nécessaire pour obtenir la dépression maximale de la mâchoire inférieure et l'ouverture maximale de la bouche, ainsi que la durée de l'ouverture maximale, le temps nécessaire pour fermer la bouche (depuis le moment d'ouverture maximale) et la durée totale de la morsure, augmentent à mesure que la température de l'eau décroît. De plus, le temps requis pour l'ouverture maximale de la bouche et la dépression maximale de la mâchoire inférieure est plus long à 18 °C chez les individus soumis aux conditions A que chez ceux soumis aux conditions B. Ces résultats indiquent que la température de l'eau peut fausser les résultats d'études de l'alimentation qui utilisent une cinématique qui ne tient pas compte des effets de la température; il en est de même des études qui font des comparaisons impliquant diverses températures et taxons.

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## Introduction

Studies on the feeding morphology and kinematics of lower vertebrates are common, as they offer a clearer understanding of the evolution of feeding mechanisms in higher taxa (Lauder 1982; Reilly 1995; Motta and Wilga 1999). Unfortunately, as these study organisms are often ectotherms, abiotic factors can affect their physiological processes, ultimately altering performance levels. This type of limitation, in terms of functional power output, has been an

intensely studied aspect in the field of thermal biology. Studies have documented that colder temperatures are related to decreased performance levels while jumping (Miller 1982; Renaud and Stevens 1983; Whitehead et al. 1989), swimming (Beamish 1981; Navas et al. 1999; Wilson et al. 2000), and running (Huey 1982; Marsh and Bennet 1985; Else and Bennett 1987).

With such an extensive focus on the relationship of temperature and functional power output during locomotion, one may wonder how temperature affects other aspects of an organism's power output, such as prey capture. Although previous research has already addressed this general question, it has only been investigated at the level of feeding performance (i.e., percentage of successful strikes; Greenwald 1974; Beddow et al. 1995) and number of prey items consumed per unit time (Stevens 1988a, 1988b; Buentello et al. 2000), both of which decreased at colder temperatures.

The details of prey-capture kinematics of ectothermic organisms have yet to be examined in light of the influence of temperature. This experiment investigates the relationship

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between prey-capture kinematics in the bluegill (*Lepomis macrochirus* Rafinesque, 1819) and temperature and discusses the possible implications of these findings with regard to the comparison of kinematic feeding studies that have been performed at different temperatures or with different species.

## Materials and methods

### Videography

Four bluegill were obtained by hook and line from a residential pond in Hillsborough County, Florida, in October of 2001 at a water temperature of approximately 24 °C. The fish (mean standard length 10.25 cm, range 9.9–11.0 cm) were maintained on a diet of earthworms (*Lumbricus* sp.) and housed in a 208-L aquarium with a small number of aquarium plants as refuge. The water temperature was maintained at 18 °C.

After a 2-week acclimation period, feeding sequences were filmed using a Redlake PCI-1000 high-speed digital video system (250 frames/s). Ambient indoor fluorescent lighting provided all of the illumination used for filming. During these sessions, a 5.0-cm grid was positioned behind the aquarium for scale and pieces of *Lumbricus* sp., approximately one half of the fish's gape, were offered in the water column after they were dropped onto the water's surface and began to sink towards the bottom of the tank. Only capture sequences in which an individual fed in a position lateral to the camera were used for analysis. To avoid satiation effects, individuals were fed no more than eight pieces of *Lumbricus* sp. during the filming session (Sass and Motta 2002). All bites were recorded during a single filming session at each study temperature. After 24 h at 18 °C, the temperature was gradually increased with immersion heaters to 24 °C over a 48-h period and maintained at that temperature for 24 h. Feeding events were again recorded, and the temperature was increased a second time to 30 °C over a 48-h period followed by the further recording of bites. This increasing temperature treatment is referred to as treatment A.

This procedure was repeated with four different individuals (mean standard length 11.48 cm, range 10.6–12.3 cm); however, the initial acclimation temperature for this portion of the study was 30 °C. In this treatment (treatment B), the temperature was decreased twice (to 24 and 18 °C, both over 48-h intervals) using a water chiller, with each temperature maintained for a 24-h period, and feeding events recorded at each temperature. Water temperatures utilized in this study fall within the natural temperature range of this species (Page and Burr 1991). All maintenance and research was performed under a protocol approved by the University of South Florida's Institutional Animal Care and Use Committee (No. 1987).

### Video analysis

Redlake MotionScope imaging software version 2.21.1 (Redlake 1997) was used to analyze prey-capture kinematics from the feeding sequences. Five bites per individual were analyzed at each temperature for five kinematic variables, all of which are typical descriptors of a basic bite sequence (Gillis and Lauder 1995; Sass and Motta 2002; Carroll and Wainwright 2003): (1) time to maximum lower jaw depression

(milliseconds) is measured from the initial opening of the mouth to the time at which the distance from the anterior tip of the mandible to the anterior margin of the eye is the greatest; (2) time to maximum gape (milliseconds) is measured from the initial opening of the mouth to the time at which the greatest measured distance between the anterior-most tips of the upper and lower jaws is achieved; (3) duration of maximum gape (milliseconds) is the length of time that the jaws are held in the position of maximum gape prior to mouth closing; (4) time to jaw closure (milliseconds) is the time taken for the jaws to fully close on the prey item from the end of maximum gape; and (5) total bite duration (milliseconds) is the time elapsed between the initial opening and final closing of the fish's mouth.

### Data analysis

Normality and equality of variance were tested for each data set using Kolmogorov–Smirnov and Levene's median tests, respectively.  $\log_{10}$  transformations were applied in cases for which the data were non-normal. Data sets for the variable duration of maximum gape could not be normalized despite transformation. To compensate, a more stringent  $p$  value ( $p = 0.01$  versus  $p = 0.05$ ) was adopted for tests involving these data. In addition, all data sets were compared against the fishes' standard lengths using Spearman's rank order correlation statistic to identify any size effects biasing the data.

To examine the effect of temperature on prey-capture kinematics, separate one-way repeated measures ANOVAs were performed for each treatment, A and B. A Tukey's multiple comparisons test was then run to pinpoint the source of any variance. The mean value for each group of five replicate bites per individual for each study temperature was used for these analyses to avoid pseudoreplication. Because the data for each fish had been reduced, tests for individual variability could not be concomitantly tested in the repeated measures ANOVA. In addition, one-way ANOVAs were applied to the full data sets (no means taken) for each study temperature within each treatment to identify differences among individual fish. Furthermore, one-way ANOVAs were performed between the means of identical kinematic variables at a particular temperature between both directional temperature treatments to find differences resulting from the direction of temperature change (increasing versus decreasing). All analyses were performed using SigmaStat version 2.03 (SPSS, Inc. 1997) and SYSTAT version 10 (SPSS, Inc. 2000).

## Results

No correlation was detected between standard length and any of the kinematic variables measured in this study (Spearman's rank order correlation,  $p$ -value range = 0.053–0.997). Additionally, no difference was found between individual fish in either treatment A or B. There was, however, a significant effect of temperature for each variable (Table 1). Tukey's post hoc test revealed that the lowest temperature had slower times to reach maximum lower jaw depression and maximum gape, as well as time to jaw closure, compared with bites at the two higher temperatures, which did not differ significantly in any case. The remaining kinematic

**Table 1.** Temperature results of one-way repeated measures ANOVAs for each kinematic variable measured during prey capture by bluegill, *Lepomis macrochirus*, in both differential temperature treatments, A (increasing temperatures) and B (decreasing temperatures).

	Temperature (°C)	Treatment A*			Treatment B*		
		(ms)	$F_{[2,6]}$	$p$	(ms)	$F_{[2,6]}$	$p$
Time to maximum lower jaw depression	18	32.2±1.8	11.352	0.009	25.0±0.9	6.157	0.035
	24	25.2±0.9			22.0±0.8		
	30	22.4±0.8			19.8±0.6		
Time to maximum gape	18	35.0±2.0	8.062	0.020	27.7±0.9	8.039	0.020
	24	26.8±1.5			24.2±1.1		
	30	25.0±1.5			21.6±0.8		
Duration of maximum gape	18	22.6±1.2	33.174	<0.001	26.6±1.4	31.621	<0.001
	24	13.8±0.9			14.4±1.1		
	30	10.2±0.5			9.4±0.4		
Time to jaw closure	18	24.6±1.7	35.969	<0.001	38.5±3.1	17.521	0.003
	24	13.4±1.5			24.8±1.5		
	30	12.4±1.4			20.6±1.3		
Total bite duration	18	82.2±2.6	39.003	<0.001	92.8±3.0	192.931	<0.001
	24	54.0±1.5			63.4±1.7		
	30	47.6±1.5			51.6±1.6		

**Note:**  $\alpha = 0.010$  for the duration of maximum gape and  $\alpha = 0.050$  for all other variables;  $N = 4$  individuals per treatment.

\*Values are means  $\pm$  SE.

**Table 2.** Results of Tukey's post hoc comparisons of kinematic variables measured in *L. macrochirus* feeding at three different water temperatures during directional temperature treatments A (increasing temperatures) and B (decreasing temperatures).

	Treatment	$p$ values		
		18 vs. 24 °C	24 vs. 30 °C	18 vs. 30 °C
Time to maximum lower jaw depression	A	0.038	ns	0.009
	B	0.040	ns	0.030
Time to maximum gape	A	0.049	ns	0.022
	B	0.042	ns	0.017
Duration of maximum gape	A	0.003	0.008	<0.001
	B	0.004	0.004	<0.001
Time to jaw closure	A	0.001	ns	<0.001
	B	0.012	ns	0.003
Total bite duration	A	0.001	0.012	<0.001
	B	<0.001	0.004	<0.001

**Note:**  $\alpha = 0.010$  for the duration of maximum gape and  $\alpha = 0.050$  for all other variables; ns, not significant;  $N = 4$  individuals per treatment.

variables, duration of maximum gape and total bite duration, were different at every temperature treatment, showing a similar negative correlation (Table 2). Finally, the time taken to reach maximum gape was slower at 18 °C for treatment A than for treatment B (ANOVA,  $F_{[1,6]} = 6.777$ ,  $p = 0.040$ ), as well as time to maximum lower jaw depression (ANOVA,  $F_{[1,6]} = 9.969$ ,  $p = 0.020$ ).

## Discussion

The results of this study demonstrate that both temperature and directional temperature change influence the prey-capture kinematics of *L. macrochirus*. Although the exact physiological explanations for these results are not known, some possible reasons may be drawn from past research involving temperature and ectotherm function. Although the results of this study may indeed be related to neural system function (Preuss and Faber 2003), the focus will be placed on temperature and muscle physiology.

The negative correlation between temperature and several timing and duration variables associated with prey capture may be related to enzyme physiology. Several studies have documented that the relationship of temperature to enzyme activity is wholly complex, with different enzymes exhibiting an increase, decrease, or even no change in reaction rate with decreasing temperatures (Hochachka and Somero 1971; Hazel and Prosser 1974; Shaklee et al. 1977). It is possible that some enzymes associated with the production of energy in the bluegill experienced such a decrease in reaction rate, functioning more slowly at colder temperatures. Hochachka and Somero (1971) attributed this type of retardation to an overall kinetic energy reduction of the reactants as well as a decline in enzyme-substrate affinity. Thus, at higher temperatures, enzymes involved in muscle contraction, such as ATPase and those utilized in the management of calcium, might increase the rates of any involved reactions (Herring 1994; Rome 1995). This could result in an increase in the maximum contraction speed, allowing for greater force gen-

eration and, ultimately, a more powerful output. Rome and Swank (1992), for example, found such an increase in force generation during muscle shortening between 10 and 20 °C while studying the locomotory muscles in scup, *Stenotomus chrysops* (L., 1766), as did Langfeld et al. (1989) while working with shorthorn sculpin, *Myoxocephalus scorpius* (L., 1758), between 1 and 12 °C. Similarly, the sartorius muscle of the leopard frog (*Rana pipiens* Schreber, 1782) also demonstrated an increase in shortening velocity and power output from 5 to 25 °C (Rome 1983).

The lack of a difference for the majority of kinematic variables between 24 and 30 °C in this study may be related to a thermal plateau in regard to a temperature–function association (Knowles and Weigl 1990). This trend had also been documented for the jumping distance of the green frog (*Rana clamitans* Latr., 1801) and *R. pipiens* at 10 and 25 °C (Huey 1975; Tracy 1976) and for the northern cricket frog (*Acris crepitans* Baird, 1854) between 20 and 30 °C (Knowles and Weigl 1990). Additionally, both the acceleration and mean average velocity of striking gopher snakes (*Pituophis catenifer affinis* Hallowell, 1852) showed little variation between 27 and 33 °C (Greenwald 1974). Greenwald (1974) attributed this pattern to the absolute optimal functioning of neuromuscular pathways at these temperatures, whereas at lower temperatures, an impairment of function is witnessed.

The longer times to reach both maximum gape and maximum lower jaw depression for treatment A compared with treatment B at 18 °C are likely related to acclimation temperature. The same result was found for the mean maximum jumping distance of the wood frog (*Rana sylvatica* LeConte, 1825) with cold-acclimated individuals typically jumping shorter distances than their warm-acclimated counterparts (Knowles and Weigl 1990). Similarly, Stevens (1988a) found a decrease in feeding performance in cold-acclimated American toads (*Bufo americanus* Holbrook, 1836). These differences may be the result of the rate of acclimation of certain enzymes utilized during the opening of the mouth in *L. macrochirus*. It has been found, for example, that the rate of acclimation of the critical thermal maxima in *R. pipiens* and giant toads, *Bufo marinus* (L., 1758), took up to 36 h longer in cold-acclimated individuals compared with those that were warm-acclimated (Brattstrom and Lawrence 1962), suggesting a slower rate of thermal compensation in which the biochemical properties of an individual have been somewhat remodeled in an effort to better fit environmental conditions (Hazel and Prosser 1974; Shaklee et al. 1977).

In addition, the effects of temperature acclimation may depend on the muscle fiber type composition. In the head of perch (*Perca fluviatilis* L., 1758), muscles such as the sternohyoideus and the posterior portion of the levator operculi, both of which are involved in rapid jaw opening, are composed of white (fast, anaerobic) and pink (fast, aerobic–anaerobic) fibers. The adductor operculi and the anterior section of the levator operculi, however, are cranial muscles involved in both fast jaw opening and sustained respiration containing red (slow aerobic) fibers (Akster and Osse 1978). Hochachka (1967) reported that colder acclimation temperatures resulted in the favoring of non-mitochondrial modes of metabolism (but see Shaklee et al. 1977). Thus, slower activities of the red aerobic fiber types found in jaw opening and

respiratory muscles could lend to the slower times to reach maximum gape and lower jaw depression.

In general, the results of acclimation studies show that the initial temperature of acclimation has no effect on ectothermic function, as is seen in the remaining kinematic variables. The jump distance of *B. americanus* (Renaud and Stevens 1983), the swimming velocity of the African clawed frog, *Xenopus laevis* (Daudin, 1802) (Miller 1982), and the power output of *R. pipiens* sartorius (Rome 1983) are all examples. In these cases, thermal compensation may have taken place or the muscles involved might be of the white fiber type.

### Implications for feeding studies

Many species inhabit environments that exhibit extensive fluctuations in temperature; therefore, multiple kinematic feeding studies performed with a single species may also encompass a wide array of temperatures while still producing biologically meaningful data. Past research examining various aspects of feeding in the bluegill, for example, which live in a thermal range of approximately 0–36 °C (Page and Burr 1991), have also been performed at many study temperatures: electromyographic recordings of feeding musculature to examine modulation of feeding behavior on different prey types at 17 °C (Wainwright and Lauder 1986), electromyographic recordings of feeding musculature and observations of gill movement as a proxy for buccal pressure change at 18 °C (Lauder et al. 1986), feeding kinematics (prey capture versus prey transport) at 19 ± 1.5 °C (Gillis and Lauder 1995), correlating morphology and feeding kinematics at 20–23 °C (Wainwright and Shaw 1999), and measurement of opercular bone strain during feeding at 25 °C (Lauder and Lanyon 1980). Although each of these studies provides us with important information on its own, this research shows that an accurate comparison of kinematic results across these works may not be possible because of the lack of temperature standardization.

Kinematic studies of lower vertebrate feeding have been performed on myriad of taxa living in a multitude of thermal ranges. As research on specific species is performed at temperatures appropriate for their ecology, there can be great variability in the applied temperature across kinematic studies of different species: fringed turtle, *Chelus fimbriatus* (Schneider, 1783), at 27 °C (Lemell et al. 2002); snapping turtle, *Chelydra serpentina* (L., 1758), at 19.5 ± 1.5 °C (Lauder and Prendergast 1992); phyllomedusine tree frogs at 20–24 °C (Gray and Nishikawa 1995); ambystomatid salamanders at 17 °C (Lauder and Shaffer 1985); nurse sharks, *Ginglymostoma cirratum* (Bonnaterre, 1788), at 26–29 °C (Motta et al. 2002); swell sharks, *Cephaloscyllium ventriosum* (Garman, 1880), at 18 ± 0.5 °C (Ferry-Graham 1998); and cheeklined wrasse, *Oxycheilinus diagrammus* (Lacépède 1801), at 23 ± 2 °C (Ferry-Graham et al. 2001). Knowing that there can be differences in prey-capture kinematics for a single species within its natural temperature range and that temperature ranges may vary from taxa to taxa, can we safely compare kinematic data from organisms inhabiting dissimilar thermal ranges? In an extreme example, the Antarctic bald notothen, *Pagothenia borchgrevinki* (Boulenger, 1902), is able to achieve its maximum cruising speed at a temperature of –0.8 °C, while the largemouth bass, *Micro-*

*pterus salmoides* (Lacepède, 1802), a temperate species, reaches its maximum cruising speed between 25 and 30 °C (Johnston and Ball 1997). With the possibility for such severe differences, it becomes clear that we must exhibit caution when making comparisons of studies across taxa with different thermal regimes.

In summary, this study showed that prey-capture kinematics in the bluegill may vary with both temperature and the direction of temperature change. Feeding-associated variables involved with opening and closing the mouth increased significantly in duration with decreasing water temperature. Furthermore, kinematic durations involved with opening the mouth differed between cold- and warm-acclimated fish at the lowest temperature investigated.

Although most research on prey capture of fishes has been performed at biologically relevant temperatures, these temperatures can differ greatly depending on the ecology of the organism. To compare among such studies, we have to be cognizant of this relationship between temperature and feeding kinematics. Therefore, it is important to (i) investigate the kinematics of fishes, or other ectothermic vertebrates, at a biologically meaningful temperature and at different temperatures that the animal would experience (e.g., summer versus winter), (ii) be aware, when comparing different studies utilizing a common species, that temperature may have profound effects on its feeding kinematics, and (iii) consider additional effects that temperature might have on feeding studies. For instance, consideration might also be given to the possible increase in ambient temperature resulting from high-wattage illumination utilized during high-speed videography. This may be particularly pertinent for studies such as those involving larval fishes in very small filming tanks, which could increase in temperature at a relatively rapid pace. Ultimately, gaining a better understanding of the relationship between feeding and temperature will lead to greater standardization both within and across kinematic research, resulting in findings with a higher level of accuracy.

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