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The effects of intraspecific competition on the prey capture behavior and kinematics of the bluegill sunfish, *Lepomis macrochirus*

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Abstract Competition has broad effects on fish and specifically the effects of competition on the prey capture kinematics and behavior are important for the assessment of future prey capture studies in bony fishes. Prey capture kinematics and behavior in bony fishes have been shown to be affected by temperature and satiation. The densities at which bony fish are kept have also been shown to affect their growth, behavior, prey selection, feeding and physiology. We investigated how density induced intraspecific competition for food affects the prey capture kinematics of juvenile bluegill sunfish, *Lepomis macrochirus*. High speed video was utilized to film five bold individuals feeding at three different densities representing different levels of intraspecific competition. We hypothesized that: (1) the feeding kinematics will be faster at higher levels of competition compared to lower levels of competition, and (2) bluegill should shift from more suction-based feeding towards more ram-based feeding with increasing levels of competition in order to outcompete conspecifics for a prey item. We found that, with increased intraspecific competition, prey capture became faster, involving more rapid jaw opening and therefore greater inertial suction, shorter mouth closing times, and shorter gape cycles. Furthermore, the attack velocity of the fish increased with increasing competition, however a shift towards primarily ram based feeding was not confirmed. Our study demonstrates that prey capture kinematics are affected by the presence of conspecifics and future studies need to consider the effects of competition on prey capture kinematics.

Keywords Prey capture kinematics · Competition · Bluegill · Density · Ram-suction

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Introduction

Competition for food in fishes has been extensively studied for decades (Werner and Hall 1979; Mittelbach 1981; Ehlinger 1990; Taborsky 1998) demonstrating that fish compete for food resources by exploitation, scramble and contest competition (Ward et al. 2006). Consequently, to successfully compete for food, rapid acquisition of the prey is crucial. Previous research on the effects of fish density and size on the feeding behavior of Pacific halibut *Hippoglossus stenolepis,* found that fish at higher densities will locate and consume the prey in less time than

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conspecifics at lower predator densities (Stoner and Ottmar 2004). However, the effects of competition on prey capture kinematics of fishes have not been investigated.

Fishes can capture food by ram, suction, or biting, or a combination of the three (Liem 1980; Norton and Brainerd 1993). During prey capture, modulation of prey capture kinematics of bony fishes occurs in response to position, size and elusiveness of prey (Nyberg 1971; Wainwright and Lauder 1986; Nemeth 1997a). Ram feeding involves high attack velocities to overtake the prey item whereas suction feeding involves lower attack velocities and precise positioning to suck the prey item into the mouth and usually a combination of these two feeding modes is utilized by fish (Nemeth 1997a, b; Higham 2007). With increasing intraspecific competition, we would expect predators, such as the bluegill sunfish *Lepomis macrochirus*, to approach the prey at higher attack velocities and to capture the prey without braking before employing a more ram dominated prey capture.

Bluegill sunfish, *Lepomis macrochirus* Rafinesque 1819 are native to and widespread in North America. Bluegill sunfish are considered one of the highest performing suction feeders (Carroll et al. 2004) and have been the focus of extensive research in prey capture kinematics and performance (Gillis and Lauder 1995; Ferry-Graham et al. 2003; Higham et al. 2005a; Higham et al. 2006; Holzman et al. 2008) and feeding ecology (Werner 1977; Mittelbach 1981; Osenberg et al. 1988; Savino et al. 1992; Brogowski et al. 2005). Increased intraspecific competition for food has been assumed to affect the growth of bluegill living in high density populations (Wiener and Hanneman 1982) which is further supported by the general assumption that almost all conspecifics compete for food and habitat since they occupy the same niche (Ward et al. 2006).

Previous studies have shown that temperature (Wintzer and Motta 2004; Devries et al. 2006), satiation (Sass and Motta 2002), prey type (Norton 1991) and body size (Richard and Wainwright 1995) can affect the prey capture kinematics of fishes, and that higher stocking densities and competition reduce the growth and survival rate of fishes (Houde 1977; Anderson et al. 2002).

The goal of this study is to examine the effects of intraspecific competition on the prey capture kinematics of bluegill sunfish. Specifically, it is hypothesized that: (1) bluegill sunfish will feed faster at higher levels of competition compared to lower levels of competition, and (2) bluegill sunfish will shift from primarily suction feeding towards more ram feeding with increasing levels of intraspecific competition. This study will address whether future studies should take into account the effects of competition on prey capture kinematics.

Materials and methods

Study organism

Thirty five juvenile bluegill sunfish (8.9–10.0 cm SL) were caught by cast netting from the Hillsborough River drainage in Hillsborough County, Florida, USA. The animals were housed in 40-liter aquaria individually at 22°C with a 12:12 light period and were acclimated for 2–4 weeks. The tanks were screened on the sides and the back with white paper such that the animals could not see each other. The front of the tank remained unscreened for acclimation of the animals to feed under camera lighting and while filming. Animals were fed daily with a mix of live and freeze-dried *Artemia* sp. through a clear vertically oriented PVC-tube (2.57 cm diameter) that was positioned in the center of the aquarium with its opening approximately 4 cm below the water surface.

Experimental procedures

To vary the levels of intraspecific competition, three microcosms with different numbers of conspecifics were established. In the aquarium lacking competition there was only one fish, low levels of competition were represented by the focal fish plus two other conspecifics, and high competition was represented by the focal fish plus four other conspecifics. Consequently, the most aggressive bluegill was selected as the focal fish for the trials. The focal fish was transferred to the filming tank alone or with other fish, depending on the induced competition level. All fish were housed individually in 40-liter aquaria before being moved to the filming tank (40-liters, 51 cm L×31 cm H×26 cm D at 22°C), which was screened on the sides and back such that the fish could only see the fish which were present in the filming tank. The fish were allowed to acclimate for 24 h after transfer and were not fed during this time, after which they were filmed.

Using two High-Speed cameras, a Redlake Motionscope PCI 2000S and a Redlake Motionscope PCI 500 (Redlake MASD, Inc., San Diego, CA, USA), five prey-capture events per treatment per focal fish were filmed at 250 fields per second to obtain a lateral and a dorsal view of the prey-capture event. The dorsal image was captured by one camera mounted vertically at 90° over the water surface and directly over the feeding tube. The second camera position in front of the aquarium recorded a lateral view of the focal fish during prey capture. The prey items, live *Artemia* sp. (average 0.5 cm length) were introduced one item at a time through the clear PVC tube suspended in the middle of the tank. Prey items were introduced approximately 5 min apart when the fish had moved away from the feeding tube. Only prey capture events in which the focal fish was lateral to the camera were used for analysis. A maximum of ten *Artemia* sp. were fed to the subject fish during any trial in order to eliminate possible effects of satiation on the prey capture kinematics (Sass and Motta 2002), although only the first five successful prey capture events were used for the analysis. Other fish present in the tank only consumed two prey items throughout all the trials. As five successful prey capture events were not always obtained on 1 day, filming resumed after 24 h, during which time the fish were not fed. After five successful filming events, each focal fish was returned to its individual holding tank alone. Each fish was only used for one competition level treatment and was then released or euthanized according to University protocol, except for the focal fish which experienced all competition levels. Each focal animal was filmed five times for three different competition treatments (no competition, low competition and high competition). This trial was repeated for a total of five focal fish ($n=5$). The focal animals were identified from conspecifics by individual differences in their color patterns and markings. Prey capture events in which the mouth of the animal touched the feeding tube were not considered successful prey capture events and were not accounted for since this might have an effect on the prey capture kinematics. Due to possible chemical cues left by the fish while filming, the water was completely changed after each filming session.

Data analysis

Feeding events were downloaded to a computer and analyzed using MaxTRAQ Software version 1.87 (Innovision Systems, Inc., Columbiaville, Michigan, USA). The following kinematic variables were analyzed from the lateral sequences: peak gape of the mouth (Peak Gape); time to open the mouth (T_{Open}); time to close the mouth once reaching peak gape (T_{Close}); and total time of the gape cycle (T_{Cycle}). Peak Gape is defined as the maximum distance between the two most anterior points on the upper and lower jaw during the prey-capture event. T_{Open}, as described by Sanford and Wainwright (2002) eliminates the variability of early mouth opening in bony fishes before prey-capture and is measured as the time from 20% to 95% of peak gape. T_{Close} is the time from reaching Peak Gape to closing the mouth and is measured from the field the mouth starts closing after reaching Peak Gape to the field at which the mouth reaches 20% of Peak Gape while closing. The 20% was selected in order to be consistent with the T_{Open} measurement and also to eliminate possible variation in mouth closing. The gape cycle is measured as the time from the field in which the mouth reaches 20% of Peak Gape while opening to the field in which the mouth reaches 20% of Peak Gape while closing. In addition to the kinematic data the lateral filming sequences were used to determine x and y coordinates for the predator and the prey to determine the distance moved by the predator and prey for each prey capture event (Norton and Brainerd 1993). The distances the predator and the prey ($D_{Predator}$ and D_{Prey}) moved in the time from reaching 20% of the peak gape while opening the mouth until the prey disappeared in the mouth of the predator were determined by tracking a spot on the opercle of the fish and the head of the *Artemia* sp. during the prey capture sequence. In addition, the velocities of the predator and the prey ($V_{Predator}$ and V_{Prey}) were determined for the duration of the prey capture event (T_{Prey}), which is determined as the time from when the mouth reaches 20% of the peak gape while opening the mouth until the prey disappears in the mouth of the predator. In addition, the running average for the change in velocity of the predator ($A_{Instantaneous}$) was determined for each field of 10 sequential fields before the prey entered the mouth of the predator and used to determine if the predator maintained, increased or decreased its velocity prior to prey capture for three subjects under the different competition levels. An increase in velocity between sequential fields therefore indicates the fish is accelerating, whereas a decrease indicates deceleration. In this manner the net acceleration or deceleration of the predator was calculated across the 10 fields. The small sample size of subjects occurred because this variable was determined post hoc after the video sequences had been trimmed in length.

To quantify the ram and suction components in the prey capture events, the velocity and the distance moved of the predator ($V_{Predator}$ and $D_{Predator}$) was used as an indicator for the ram component and the velocity and the distance moved of the prey (V_{Prey} and D_{Prey}) and the time to open the mouth (T_{Open}) as an indicator for the suction component.

Statistical analysis

All variables obtained in this study were subjected to a Two-Way Repeated Measures ANOVA using Sigmaplot Software version 11.0 (Systat Software, Inc., Chicago, Illinois, USA) to account for significant differences ($P<0.05$) across treatments in a model with repeated measurements for each focal animal. The research was approved and followed the guidelines set forth by the University of South Florida, Institutional Animal Care and Use Committee (IACUC protocol #W3402).

Results

Behavior

The bold focal fish exhibited aggressive behavior towards conspecifics once the feeding tube was placed over the tank. During low and high competition scenarios, the focal animals constantly bit the conspecifics and chased them away as they approached the feeding tube. When the prey was introduced into the filming tank, the focal animal would rapidly swim towards the prey, capture it and resume chasing away conspecifics which approached the feeding tube.

Data analysis

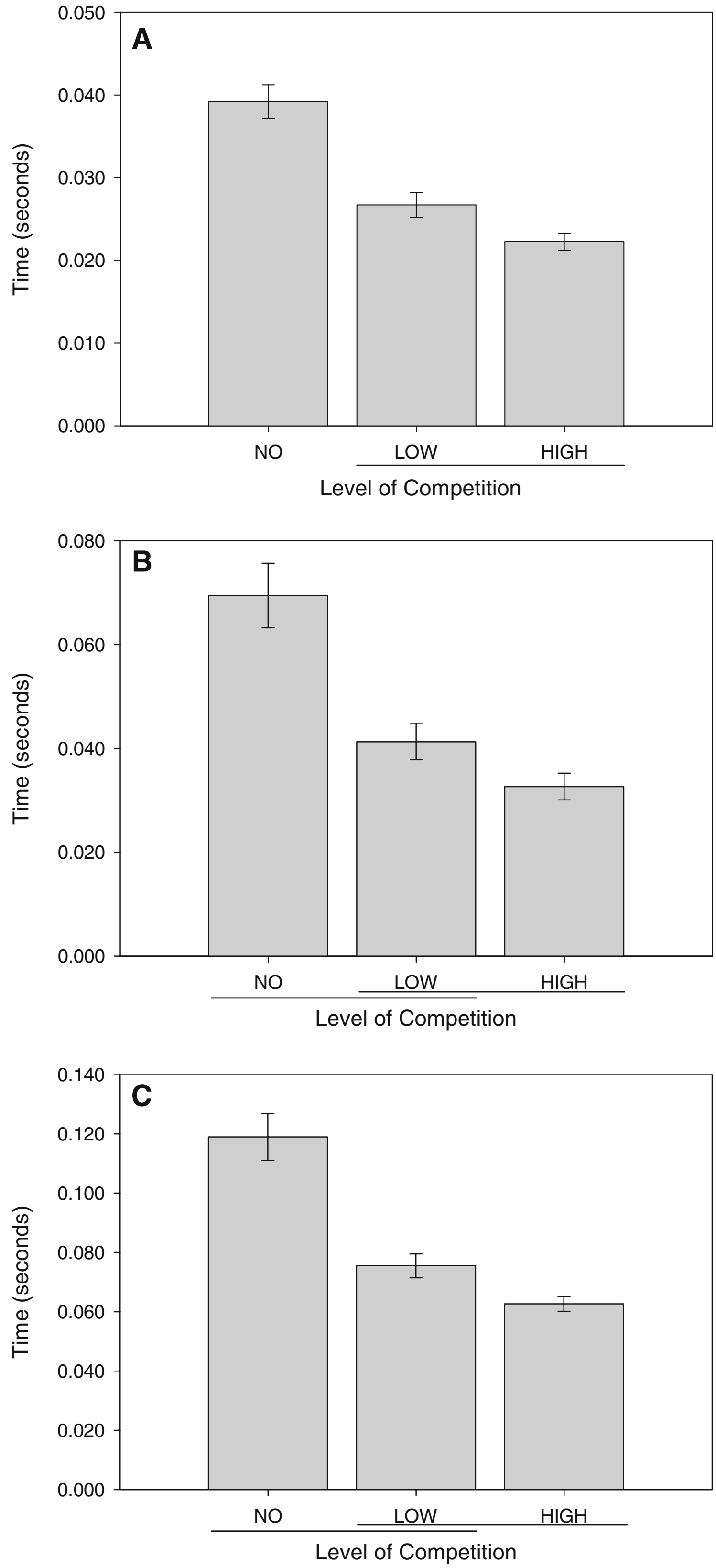
Two-Way Repeated Measures ANOVA revealed that increased intraspecific competition resulted in significant differences ($P<0.05$) in six out of nine variables measured in the bold individuals (Table 1) in this study. The field specific velocity ($A_{Instantaneous}$) failed normality even with transformation and underwent a nonparametric Friedman's Repeated Measures ANOVA on Ranks. Time to open the mouth (T_{Open}) decreased with increasing competition, when comparing no competition to low competition ($P=0.011$) and no competition to high competition ($P=0.003$); Time to close mouth (T_{Close}) and the gape cycle (T_{Cycle}) decreased as well when comparing no to high competition ($P=0.023$; Fig. 1). Peak Gape showed no significant difference with increasing competition.

The distance of the prey (D_{Prey}; Fig. 2) decreased with increasing intraspecific competition, being different when comparing no competition to low competition ($P=0.040$) and no competition to high competition ($P=0.003$), whereas the distance of the predator ($D_{Predator}$; Fig. 3) showed no significant differences across treatments. The velocity of the prey (V_{Prey}; Table 1) showed no significant differences with increasing competition, however the velocity of the predator ($V_{Predator}$; Fig. 2) increased with increasing intraspecific competition being different when comparing no competition to low competition ($P=0.033$) and no competition to high competition ($P=0.005$). The duration of the prey capture event (T_{Prey}; Fig. 2) decreased with increasing intraspecific competition,

Table 1 Average values for kinematic variables during prey capture for five *Lepomis macrochirus*. Values are for five feeding events each. Superscript letters denote significant differences across treatments.*indicate variables with significant differences ($P<0.05$), (ns) indicates no significant difference

Variable	Level of competition		
	No	Low	High
T_{Open}* (ms)	39^{A}	27^{B}	22^{B}
T_{Close}* (ms)	69^{A}	$41^{A, B}$	33^{B}
T_{Cycle}* (ms)	119^{A}	$76^{A, B}$	63^{B}
$D_{Predator}^{(ns)}$ (cm)	0.6	0.7	0.7
D_{Prey}* (cm)	0.3^{A}	0.2^{B}	0.1^{B}
$V_{Predator}$* (cm s^{-1})	14.0^{A}	24.7^{B}	30.7^{B}
$V_{Prey}^{(ns)}$ (cm s^{-1})	6.4	5.9	3.9
$A_{Instantaneous}$* (cm s^{-1})	-10.4^{A}	$+2.6^{A, B}$	$+7.2^{B}$
T_{Prey}* (ms)	41^{A}	30^{B}	23^{B}
Peak Gape$^{(ns)}$ (cm)	0.783	0.907	0.897

Fig. 1 Average values and ±1 SE for **a**) time to open the mouth (T_{Open}), **b**) time to close the mouth (T_{Close}) and **c**) the gape cycle (T_{Cycle}) during prey capture for five *Lepomis macrochirus*, at three levels of competition. The lines denote no significant difference between treatments



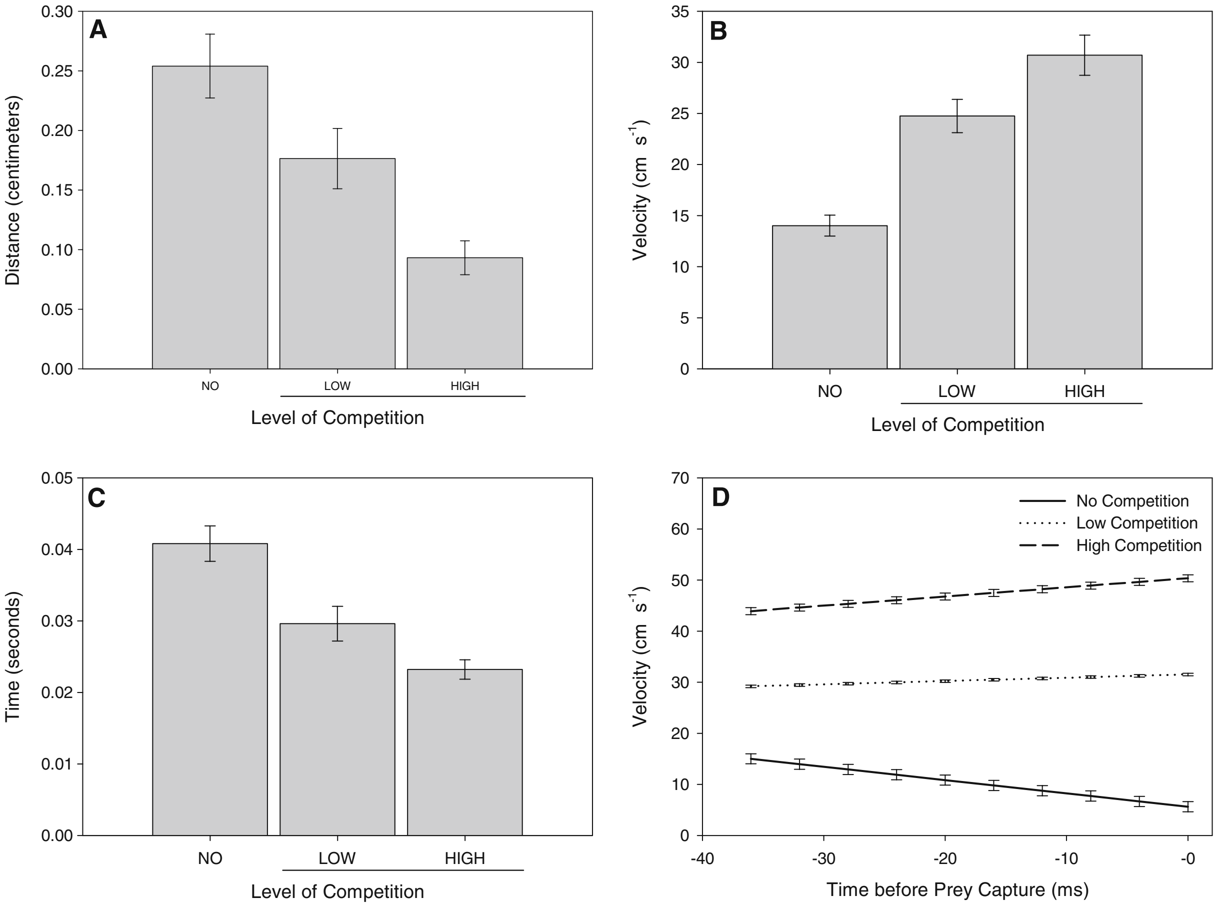
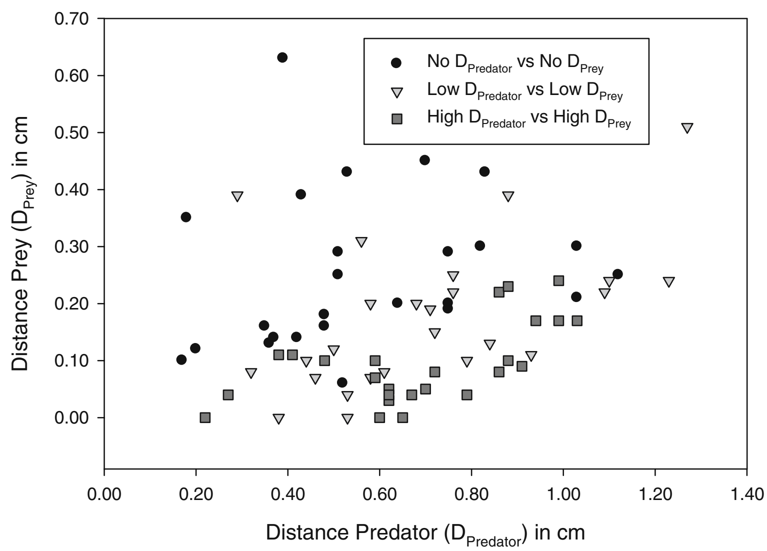


Fig. 2 Average values and ±1 SE for **a**) the distance the prey moved during prey capture (D_{Prey}), **b**) the velocity of the predator during prey capture ($V_{Predator}$) and **c**) the duration of the prey capture event (T_{Prey}) for five *Lepomis macrochirus*. **d**) Average velocity for ten fields prior to prey capture ±1 SE for three *Lepomis macrochirus*. The lines in figures A, B, and C denote no significant differences between treatments

Fig. 3 The distances moved by predator ($D_{Predator}$) and prey (D_{Prey}) during prey capture plotted against each other at three levels of competition for five *Lepomis macrochirus*



being different when comparing no competition to low competition (P=0.035) and no competition to high competition (P=0.005). The average change in velocity of the predator for ten fields prior to prey capture ($A_{Instantaneous}$; Fig. 2) increased (+7.2 cm s^{-1}) significantly with increasing levels of competition, indicating acceleration at high levels of competition, no significant change in velocity (+2.6 cm s^{-1}) at low competition and a negative change in velocity (−10.4 cm s^{-1}), at no competition indicating deceleration of the focal fish (P=0.028).

Discussion

This study, the first to investigate the effects of intraspecific competition on the prey capture kinematics in fish, demonstrates that bluegill sunfish exhibit faster mouth opening and closing times, shorter gape cycles and an increase in predator approach velocity with increasing levels of intraspecific competition. In contrast to previous studies, prey capture kinematics have been shown to become slower (time to reach maximum gape and lower jaw depression, time to close the mouth) and last longer (duration of bite) at lower water temperatures (Wintzer and Motta 2004; Devries et al. 2006) and prey capture kinematics are slower (lower jaw depression, max gape distance, hyoid depression and recovery) with increasing satiation (Sass and Motta 2002). However, this is the first study to reveal that intraspecific competition for food modulates prey capture kinematics in fishes.

Competition in fishes has been widely studied, including competition for food (Booth and Beretta 2004; Schleuter and Eckmann 2006; Ward et al. 2006), habitat (Almany 2004; Hasegawa and Maekawa 2006; Kahl and Radke 2006) and reproduction (Taborsky 1998; Stoltz and Neff 2006; Plath et al. 2008). Bluegill sunfish competing for the prey item in this study exhibited two forms of food competition: scramble and contest competition. In scramble competition the focal fish reaches the prey item before other fish, whereas in contest competition the focal fish aggressively displaces its competitors while pursuing the prey item (Ward et al. 2006). Under both levels of competition the focal bluegill sunfish reached the *Artemia* sp. prey first, and chased away conspecifics which were approaching the feeding tube.

During suction feeding the rapid expansion of the buccal cavity generates a flow of water into the mouth of the fish (Liem 1980; Norton and Brainerd 1993; Carroll et al. 2004; Day et al. 2005) and faster mouth opening times, as observed in this study (Fig. 1), can be interpreted as an increase in buccal expansion rate which leads to lower sub-ambient pressures within the buccal cavity and higher flow speeds of the water in front of the mouth (Sanford and Wainwright 2002), therefore indicating an increase in inertial suction force with increasing levels of competition. Fish may perform compensatory suction to counter the bow wave generated by the increased velocities of the predator (Van Damme and Aerts 1997; Ferry-Graham et al. 2003; Higham et al. 2005a), which could move the prey away from the approaching predator. A recent study on bluegill sunfish demonstrated the formation of this bow wave when approaching prey and how suction feeding reverses the flow and draws the prey into the mouth (Holzman and Wainwright 2009). Therefore, more rapid mouth opening with increased competition may be related to the increased velocity of the predator and the need for greater compensatory suction to counter the effects of a bow wave generated by faster velocities during prey capture. Faster mouth opening may also be due in part to the higher predator approach velocity and the force exerted on the opening mouth by the water.

The gape cycle was found to become shorter in duration with increasing levels of intraspecific competition, which indicate faster prey capture events. Therefore, the hypothesis that bluegill sunfish feed faster at higher levels of competition compared to lower levels of competition was confirmed.

Bluegill sunfish are characterized as ram and suction feeders (Carroll et al. 2004; Day et al. 2005; Higham et al. 2005b; Higham 2007) and utilized a combination of ram and suction during prey capture in this study. The bluegill sunfish exhibited higher approach velocities during the prey capture event ($V_{Predator}$ and $A_{Instantaneous}$) with increasing levels of intraspecific competition which are characteristic of ram feeders and are usually utilized when capturing elusive prey (Webb and Skadsen 1980; Norton 1991; Porter and Motta 2000). The increased velocity is indicative of an increase of the ram component during prey capture. However, the apparent increase in suction force with increasing competition is indicative of an increase in the suction component during prey capture. An increase in inertial suction force usually manifests itself by drawing the prey towards the mouth from a greater distance and at a higher velocity. However, the distance the prey moved decreased because the bluegill continued to accelerate as it approached the prey to engulf it. The velocity of the prey did not increase despite more rapid mouth opening because the fish was perhaps employing greater compensatory suction to overcome the bow wave it was generating in front of the mouth.

Therefore it is concluded that both the ram and suction components increased with increasing levels of competition, however it was not possible to confirm the second hypothesis that bluegill shift from using primarily suction feeding to ram feeding with increasing levels of competition.

Recent studies in fish behavior investigating the bold-shy continuum have found that fish exhibiting bold behavior are more willing to take risks (Wilson et al. 1993; Webster et al. 2009). Individuals displaying higher risk behavior increased their reproductive success as well as increasing predation risk which could lead to early mortality whereas shy individuals will exhibit behavior to avoid predation (Wilson et al. 1993; Webster et al. 2009). The focal bluegill sunfish in this study were selected for bold behavior and it is likely that the level of boldness could affect the prey capture kinematics, since the latency to attack prey has been shown to decrease in bold individuals (Webster et al. 2009). This suggests that bold animals may exhibit faster prey capture times compared to shy animals.

In conclusion, this study demonstrated that prey capture kinematics of bold bluegill sunfish are affected by the presence of conspecifics while competing for food. Increasing intraspecific competition resulted in faster mouth opening and closing, shorter gape cycle time and increased predator velocity during prey capture. However a shift from suction feeding towards ram feeding with increasing intraspecific competition was not confirmed in this study.

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