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# Modulation of Prey-Capture Kinematics and Suction Feeding Performance in Smallmouth Bass, *Micropterus Dolomieu*

Andrea Sejdic

Western Kentucky University, [andrea.sejdic293@topper.wku.edu](mailto:andrea.sejdic293@topper.wku.edu)

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MODULATION OF PREY-CAPTURE KINEMATICS AND SUCTION FEEDING  
PERFORMANCE IN SMALLMOUTH BASS, *MICROPTERUS DOLOMIEU*

A Thesis  
Presented to  
The Faculty of the Department of Biology  
Western Kentucky University  
Bowling Green, Kentucky

In Partial Fulfillment  
Of the Requirements for the Degree  
Master of Science

By  
Andrea Sejdic

May 2016

MODULATION OF PREY-CAPTURE KINEMATICS AND SUCTION FEEDING  
PERFORMANCE IN SMALLMOUTH BASS, *MICROPTERUS DOLOMIEU*

Date Recommended

4/22/16



Dr. Steve Huskey, Director of Thesis

Dr. Michael Collyer

Dr. Philip Lienesch

 4/25/16  
Dean, Graduate Studies and Research      Date

I dedicate this thesis to my fiancé and my family. Your constant love and support has led me to this point. Thank you so much.

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MODULATION OF PREY-CAPTURE KINEMATICS AND SUCTION FEEDING  
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Andrea Sejdic

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Directed by: Dr. Steve Huskey, Dr. Michael Collyer, and Dr. Phil Lienesch

Department of Biology

Western Kentucky University

The feeding behavior of fishes is a topic that has piqued the interests of many researchers given the dynamic and ancestral nature of aquatic prey-capture. This study examines aquatic feeding in terms of the suction and ram components of feeding in smallmouth bass, *Micropterus dolomieu*, and how they modulate their kinematic behavior when attacking pelagic and benthic prey.

Relative to other *Micropterus* genera, the reduced gape in smallmouth bass suggests they may create considerable suction pressure – stronger subambient pressure pulled through a smaller opening creates greater velocity. Suction feeding is useful when feeding on benthic prey, such as crayfish. Ram feeding is utilized when capturing pelagic prey, such as goldfish, because prey swimming in the water column can be overtaken with body speed. Prey-capture experiments using high-speed cinematography and pressure transducers were conducted to determine if smallmouth bass modulate their feeding performance between pelagic and benthic prey items.

Results indicate that smallmouth bass modulate their behavior to include both aspects of ram and suction feeding when presented with differing prey, utilizing greater ram when feeding in the water column and stronger suction when feeding off the substrate (MANCOVA,  $p < 0.0001$ ).

Because feeding behaviors of smallmouth bass have implications for ecosystem health, which is driven by trophic food web dynamics, insight into the prey-capture behaviors utilized by smallmouth bass may provide more information for fisheries managers when managing the overall health and stability of these ecosystems.

## INTRODUCTION

Fish occupy every conceivable aquatic habitat and feed on every imaginable type of prey to survive. Specialist fish are characterized by their limited range of prey items (e.g., a piscivore or a planktivore) and presence in certain habitats with little successful occupation of other habitats; whereas generalist fish demonstrate a greater repertoire of prey consumed (e.g., omnivorous fish) and the habitats in which they dwell (Feary 2007). Also, ontogenetic niche and diet shifts may occur in fish between their larval, juvenile, and adult life stages where they switch from being a generalist larva or juvenile to a specialist adult (van Leeuwen et al. 2013). Their complex jaw architecture provides fish with the necessary jaw mechanisms and structures needed for the environment in which they dwell, and forces the animal to live within the biomechanical limitations fitted to a respective environment and/or prey type (Lauder 1991); this is known as an organism's ecomorphology (Motta and Kotrschall 1992). As such, there is a strong ecomorphological relationship that has evolved yielding diverse feeding mechanisms, specialized structures, and/or novel behaviors to capture prey (Motta and Kotrschall 1992; Motta et al. 1995).

During hydrodynamic feeding, the quick expansion of the fish's cranial skeleton, thus expanding the buccal cavity, is a necessity in order to induce water flow containing the prey into the mouth (Carroll and Wainwright 2009). When feeding with a large gape, it may take the fish longer to expand its buccal cavity, slowing down the gape cycle and producing a weaker suction pressure. A buccal cavity expanded at the same rate but pulled through a smaller gape should produce greater flow velocity and more successful prey-capture. Furthermore, a buccal cavity expanded more quickly *and* pulled through a

smaller gape should maximize water flow into the mouth (Carroll et al. 2004). These different suction pressures can be measured as subambient pressure inside of the buccal cavity given the hydrodynamic nature of aquatic feeding (van Leeuwen and Muller 1983) and comes about as a result of the complex nature of fish mouths.

Jaw mechanisms of centrarchid fishes have many mobile parts (Wainwright and Richard 1995). The specifics of their kinematics are determined by many factors, including: gape size, standard length of the fish and its prey, the type of prey they are consuming (Wainwright et al. 2001; Day et al. 2005; Wainwright et al. 2007), and the environment in which they are feeding (Savino and Stein 1982). Another important influence on the effectiveness of prey-capture is an individual's mouth size and shape, because these two morphological characteristics will affect the speed at which water enters the mouth during a feeding event (Lauder 1983; Lauder and Clark 1984; Nemeth 1997). Individual morphological characteristics strongly influence a predator in terms of different constraints, such as gape size, that limit them in capturing various sized prey (Nemeth 1997). Small gape sizes indicate that the movements of the jaw and head will create rapid rates of intake (Lauder 1980b; Wainwright and Richard 1995). This signifies that a quick jaw opening will create a high velocity of intake when focused on a specific area (Carroll et al. 2004; Higham 2011). Conversely, large gapes are beneficial in allowing a fish to capture a larger prey item, and would take longer to open; therefore, the velocity may be significantly less than that of a fish with a smaller gape (Carroll et al. 2004).

The hydrodynamics of prey-capture in fish predators are defined by the unidirectional flow of water in through their mouth and out through their operculi

(Lauder 1980b; Lauder 1983; Van Wassenbergh and Aerts 2009). The pressure gradient will always be lower inside of the mouth in comparison to the fluid environment outside of the buccal cavity to ensure that when the fish opens its mouth, the surrounding water will rush inside (Lauder 1980a; Lauder 1980b). Kinematics will always influence hydrodynamics, meaning the amount and speed of jaw expansion will determine the amount and velocity of fluid flow (Day et al. 2005, Higham et al. 2006b). The ability of fish to capture large prey items increases with the size of their jaws; however, that decreases the amount of suction force that can be generated (Muller et al. 1982; Carroll et al. 2004). Larger prey are captured in a larger volume of water but usually require a great ram component to be successful (van Leeuwen and Muller 1983). Conversely, small gapes allow for stronger subambient pressure generation to ensure prey-capture and create a buccal volume large enough to rapidly draw smaller, benthic prey in (Carroll et al. 2004). The volume of water (that will eventually be drawn into the buccal cavity) that the prey is suspended in, as well as the subambient pressure generated within the buccal cavity, are both determinants of prey-capture success and feeding performance (Higham et al. 2006a; Carroll and Wainwright 2009).

Although prey-capture is limited by kinematics and hydrodynamics, fish may alter their motor patterns when feeding on different prey types and, thus, utilize modulation (Nyberg 1971; Norton and Brainerd 1993; Nemeth 1997). Modulation is the ability of a fish predator to modify kinematic and pressure outputs by adjusting its feeding performance (Sass and Motta 2002) and may happen between different prey-capture events (Nyberg 1971). For fish predators living in habitats that provide both benthic and pelagic prey, the predators should be able to modulate their gape, as well as

the speed at which they open their mouths, given the type of prey they are capturing (Day et al. 2005). With the ability to modulate their feeding performance, fish should be able to increase their prey-capture success rate because the range of the prey they have the ability to ingest would significantly increase (Norton and Brainerd 1993; Nemeth 1997). For example, modulation in feeding kinematics and attack strategies were correlated with the size and evasiveness of given prey by *Hexagrammos decagrammus* (Nemeth 1997). The different types of feeding strategies utilized most often would be ram feeding and suction feeding, and the ability of a predator to modulate between those two strategies would benefit them greatly when feeding on prey imposing different constraints (e.g., benthic vs. pelagic prey) (Nyberg 1971; Day et al. 2005).

Suction feeding and ram feeding fall onto a behavioral continuum (Nyberg 1971; Norton and Brainerd 1993) to account for the different feeding methods that must be employed with different types of prey. Ram feeding encompasses the propulsion of the entire body of a fish predator to overcome its prey item with the use of a wide gape that generates weaker buccal subambient pressure gradients (Lauder and Liem 1981; Higham et al. 2006a). Ram feeding is associated with a large gape size, the generation of weaker subambient pressure, and a larger, slower volume of water drawn in during prey-capture events (Higham et al. 2006a; Carroll and Wainwright 2009). Suction feeding denotes fish that create significant negative pressure in their buccal cavity to suck in prey (Norton and Brainerd 1993; Day et al. 2005; Higham et al. 2006a); they generate a large enough pressure gradient, in relation to the surrounding environment, to overcome prey escape maneuvers (Muller et al. 1982; Carroll et al. 2004). This mode of feeding is linked to smaller gape sizes and less volume of water pulled into the buccal cavity during prey-

capture events, though more directed in its application (Higham et al. 2006a; Carroll and Wainwright 2009), as well as lower jaw depression and elevation of the head in order to create the buccal cavity expansion that causes water and the prey item to rush into the fish's mouth (Grubich and Wainwright 1997; Carroll and Wainwright 2009). It also includes jaw protrusion which allows the mouth to get closer to the prey without the predator having to move closer (Higham 2011). This is important during suction feeding because it enhances the force of suction on the given area by creating a more circular oral jaw opening (Higham 2011). Jaw protrusion also serves to close the distance between predator and prey at the moment of the strike, which can be considered a component of ram feeding. Another factor that affects the success of suction feeding is the distance of the prey from the mouth; the speed of water being sucked in is highest at the mouth aperture and decreases very quickly away from the mouth, therefore suction feeding is most effective when prey is close to the mouth of the fish predator (Higham 2011). Fish are often categorized as discrete ram or suction feeders; although more accurately, the majority of fish fall within a continuum of ram to suction feeding (Nyberg 1971; Norton and Brainerd 1993; Wainwright et al. 2007) and may utilize bits of each during a prey-capture event.

During feeding, fish may employ both ram and suction feeding to increase prey-capture success (Wainwright et al. 2001). Swimming may decrease suction performance; therefore, when capturing pelagic prey, fish may have to employ a ram feeding technique (Nyberg 1971; van Leeuwen and Muller 1983; Higham 2005). When fish swim, they create a bow wave directly in front of them (Nyberg 1971; Lauder and Clark 1984), which acts in decreasing the pressure difference between the inside of the buccal cavity

and the outer fluid environment, thus decreasing the chance of producing high subambient pressure (van Leeuwen 1984; Higham et al. 2005). Suction performance and kinematics in terms of modulation are aligned with the level of elusiveness of the given prey item (Nemeth 1997). The ability to modulate is based on the surrounding environment; whether the fish has to swim in the pelagic zone or focus on a benthic substrate and/or vegetation to successfully capture prey (Grubich and Wainwright 1997; Norton and Brainerd 1993). Before prey-capture can be achieved, there are methods of orientation and positioning that are employed by both the predator and prey (Nyberg 1971).

Fish predators must adjust their approach and attack velocities depending on the type of prey present, whereas the prey must respond with their own escape strategies whether they are on the benthos or in the water column (Nyberg 1971; Norton and Brainerd 1993). With benthic prey, the fish predators dramatically slow their approach and get very close to the prey (Nyberg 1971). This dramatic reduction in approach velocity provides the predator ample opportunity to adjust their feeding kinematics and suction pressure, thereby increasing their attack success (Nyberg 1971; Nemeth 1997). Benthic prey, conversely, provide another obstacle to the fish predator whilst employing their defense mechanisms (Nemeth 1997; Copp and Jamon 2001). Crayfish, for example, are considered grasping prey and they either cling to the substratum or employ defensive turning/swimming when being approached by a predator (Wine and Krasne 1972; Norton 1991; Copp and Jamon 2001). Because the predator cannot determine what defensive mechanism the crayfish will implement due to the elusiveness of crayfish, the predator must modulate its cranial kinematics to ensure successful prey-capture (Nemeth 1997;



Nyberg 1997; Wine and Krasne 1972). Given that the predator greatly reduces its approach velocity and gets closer to its benthic prey, this allows for the utilization of rapid cranial kinematics and attack velocity, which produces stronger suction and ultimately, more successful prey-capture (Svanback et al. 2002; Higham 2011).

Conversely, if a predator is feeding on prey in the water column it would have to employ a fast approach velocity to overtake its prey and ensure successful capture (Norton 1991; Tran et al. 2010). Pelagic prey, such as small fish, provide predators with different elusive strategies than benthic prey (Wainwright and Lauder 1986; Norton 1991; Huskey 2003). Some of these strategies include different visual indicators, such as a false eyespot, that assist the prey in escape (Lonnstedt et al. 2013). Other features, such as the relative position of their prey's eyes and tail, assist the predator in determining the direction in which its fish prey is swimming, and thusly, the predator adjusts its point of attack and increases its velocity as necessary to ensure success (Norton 1991; Tran et al. 2010). Given that fish prey rapidly swim away from a predator, this action necessitates that the predator quickly increase its approach and attack velocities and modulate its cranial kinematics, creating less suction but a wider gape, to ensure successful capture (Norton and Brainerd 1993; Nemeth 1997; Sass and Motta 2002; Day et al. 2005).

The smallmouth bass, *Micropterus dolomieu*, in the order Perciformes and family Centrarchidae, is a prevalent freshwater fish in rivers, streams, and rocky bodies of water (Edwards et al. 1983; Near et al. 2004; Zipkin et al. 2008). These top-level predators are native to the central and eastern United States, though the species has been introduced to the western United States, as well as Japan and South Africa, among others (Near et al. 2004; Carey et al. 2011). Smallmouth bass prefer cool and clear river habitats with

abundant shade and cover (Edwards et al. 1983). These surroundings provide optimal conditions regarding protective cover in terms of rocks, trees, and boulders from which to launch attacks (Edwards et al. 1983). In this environment, the smallmouth is exposed to many different types of prey items, both pelagic (i.e., in the water column) and benthic (i.e., in/on the substratum). This species is a top-level predator that has been observed performing ram feeding and suction feeding when acquiring small prey from pelagic and benthic areas of water, respectively (Winemiller 1985; Near et al. 2004; Carey et al. 2011). As juveniles, smallmouth bass are primarily benthic foragers that have been documented feeding on invertebrates and this aspect of benthic feeding continues into adulthood (Sabo et al. 1996). Their prey repertoire as adults ranges from benthic invertebrates to pelagic fish (Near et al. 2004). Given the various types of prey they consume, smallmouth bass would have to modulate their behavior when feeding on fish swimming away, in comparison to crayfish, specifically *Procambarus clarkii*, employing their stand-and-fight defense mechanism on the bottom (Stein 1976; Stein 1977; Copp and Jamon 2001).

Other centrarchid fish, such as *Micropterus salmoides*, largemouth bass, have been observed utilizing similar feeding strategies. Largemouth bass primarily lunge at their prey with a wide gape and employ little suction in pelagic regions of water given their piscivorous diet (Winemiller and Taylor 1985; Huskey 2003). Conversely, *Lepomis* species are centrarchids with small gape sizes that employ high subambient pressures (Lauder 1980b). In the Centrarchidae family, black basses of the *Micropterus* genus have been identified as piscivorous, meaning they predominately prey on other fish (Huskey and Turingan 2001; Collar et al. 2008). Piscivores have been described as predators with

gape limitations that consume their fish prey whole employing mainly ram feeding techniques in prey-capture (Hambright 1991). Piscivorous fish, such as largemouth bass, have the advantage of a large, fusiform body and a large gape to allow for more effective ram feeding on their fish prey (Keast 1985; Norton and Brainerd 1993). *Lepomis* are sister taxa to *Micropterus* (Awise and Smith 1977; Near et al. 2003) and are found to have smaller, laterally compressed, bodies and employ great amounts of suction through a significantly reduced gape to capture their prey (Nyberg 1971; Lauder 1980b; Norton and Brainerd 1993; Carroll et al. 2004).

Smallmouth bass have a smaller gape than largemouth bass with a similar fusiform body shape, but a larger gape than bluegill sunfish (Nemeth 1997; Carroll and Wainwright 2009). All other things being equal, which is a major assumption of this research, smallmouth bass should produce stronger suction than largemouth bass because the water is being pulled through a smaller mouth opening. This would be very useful when feeding on crayfish in the benthic environment where ram feeding is impossible. Smallmouth bass prey on benthic-dwelling invertebrates as much as, or even more than, they prey on fish in the water column (Edwards et al. 1983). These individuals should modulate their kinematic and suction performance based on the different constraints of their prey; they are expected to utilize ram feeding on fish in the pelagic zone and suction feeding on crayfish in the benthic zone.

Small fish, i.e. goldfish (*Carassius auratus*) that were used in this study, try to swim away from the smallmouth bass predator coercing the bass to then utilize quick body propulsion to lunge into their prey, attacking quickly and efficiently utilizing ram feeding (Rand and Lauder 1981). Because of the pelagic nature of goldfish prey,

smallmouth bass may choose to increase their approach velocity, thus decreasing their ability to generate stronger suction pressure, in essence ramming their bodies into their prey with a wide gape (Lauder 1980b). Crayfish are more elusive prey, in comparison to goldfish, given that crayfish manage to cling onto the substrate and can swim forward or backwards during an escape response reducing their predictability (Copp and Jamon 2000). Crayfish should cause smallmouth to employ a stronger suction force in order to ensure successful prey-capture from the benthos (Lauder 1980b; Copp and Jamon 2000; Copp and Jamon 2001). Because crayfish are on the benthos and not swimming in the water column, this should require smallmouth bass to employ faster attack kinematics, rather than approach kinematics (i.e., more suction than ram), resulting in stronger suction pressure when acquiring their crayfish prey (Lauder 1980b).

This study examined prey-capture kinematics and suction performance in smallmouth bass putting emphasis on their ability to modulate, or adjust, their feeding performance when presented with benthic and pelagic prey items. This research will grant further insight into the feeding behavior of smallmouth bass. These bass are expected to employ a significant amount of suction pressure when feeding on benthic crayfish and should display a ram feeding technique, weaker suction pressure in comparison to crayfish, when capturing their goldfish prey in the water column. Both of these feeding techniques are on a continuum scale and this research will provide information regarding where smallmouth bass fall on this ram to suction feeding continuum (Norton and Brainerd 1993). More knowledge about their feeding behavior and modulation could help to identify where they fall on the suction feeding continuum and whether, evolutionarily, they present feeding performances that are more closely

related to their ram feeding or suction feeding relatives (Awise and Smith 1977). This research grants further insight into the biomechanics, kinematics, and hydrodynamic properties associated with smallmouth bass suction feeding performance.

## HYPOTHESIS

I hypothesize that the smallmouth bass will employ stronger suction pressure and faster kinematics that will be advantageous in capturing benthic-dwelling prey and, conversely, a ram feeding technique, with weaker suction and slower kinematics, utilized in capturing their pelagic prey.

## METHODS

### *Fish Capture and Husbandry*

This research was conducted in the Engineering and Biological Sciences building on Western Kentucky University's main campus. The smallmouth bass were collected in Clear Fork Creek in Rockfield, Kentucky, and were transferred to the Functional Morphology Laboratory within three hours of capture. The six bass were housed individually in 75 liter aquaria. In the lab they were subjected to a photoperiod of ambient day and night length provided by external windows. Whisper power filters provided constant filtration of the 20°C water.

Upon first arrival to the lab, fish acclimated to their new surroundings. During this period they were fed mainly non-elusive earthworms and were put on a consistent

feeding schedule of three times per week. As the fish became more acclimated to their new surroundings, goldfish (*Carassius auratus*) and crayfish (*Procambarus clarkii*) were introduced to their diet. Introducing these prey items kept the bass accustomed to actively pursuing elusive prey types found in their natural habitat and all bass were of a size known to consume both fish and crayfish prey in the wild (Clady 1984; Sharma et al. 2009). Bass sizes were as follows: 148 mm, 153 mm, 168 mm, 172 mm, 176 mm, and 197 mm.

The variety of benthic and pelagic prey provided a better understanding of how smallmouth bass employ different techniques of prey-capture given the differing feeding constraints created by the prey. High-speed video sequences and suction pressure were recorded at every feeding event once the fish became accustomed to the schedule. For each feeding the fish were presented with either goldfish swimming in the pelagic region of water, or crayfish living on rocks in the benthos, to determine how smallmouth bass modulate their behavior during prey-capture. Prey size was standardized at 40-50 mm lengths and up to four prey items were presented to the smallmouth bass at each feeding event to avoid the effects of satiation on feeding performance (Wainwright and Lauder 1986; Sass and Motta 2002).

### *Surgical Manipulation*

In conducting this study the fish were submerged in a bath of 1 mg L<sup>-1</sup> MS-222, tricaine methanesulfonate, until they lost consciousness. A series of hypodermic needles was then used to create a hole in the rostrum into the buccal cavity; a plastic cannula was mounted through this hole and secured with a small collar. The fish recovered in their

original tanks as the MS-222 was washed off of their gills. Bass were allowed to recover for at least one week before being used in feeding trials. For each feeding trial, an individual was taken out of its tank, a Millar SPR-407 pressure transducer was secured through its cannula, and the bass was then returned to its tank to recover from the stress. After observation for a short period of time, the same implantation process was performed on the other fish. The fish were then presented with prey and their kinematic and suction performances were simultaneously recorded.

### *High Speed Cinematography and Pressure Measurements*

Every feeding event was recorded at 500 frames per second with a Redlake high-speed digital video camera. MiDAS software, version 2.0, (Xcitex, Inc.), was used to generate a pressure trace and imageJ software, version 1.48 (NIH, USA), was used to analyze the videos for kinematic variables. Only videos perpendicular to the camera were utilized for later analyses as they provided clear images with no parallax. A Millar SPR-407 pressure transducer was secured through the cannula in the fish's rostrum; it was utilized in measuring the pressure inside of the buccal cavity during each feeding event in synchronization with the videos. In preparation to feeding, the bass shuts its operculum and raises the floor of the mouth in order to create the greatest volume change during feeding. The buccal cavity immediately expands and causes negative pressure. This induces the suction that allows the fish to pull in prey as its mouth opens (Norton and Brainerd 1993; Carroll et al. 2004). Data from the pressure transducer was recorded and MiDAS software generated a pressure trace. Peak negative pressure, event duration, and rate of change were recorded for later analyses.

Key kinematic variables were analyzed using imageJ software and were modeled after Huskey (2003). These variables included: maximum gape height (mm), approach velocity (mm/ms), attack velocity (mm/ms), predator-prey distance (mm), and hyoid depression (mm). Maximum gape height was measured at maximum mouth opening from the anterior point of the premaxilla to the lower jaw tip. Approach and attack velocities were measured as the distance (mm) traveled over time (ms) and the average velocities were recorded. Approach velocities were measured 60 ms before Time 0 (the time of mouth opening) to Time 0. Attack velocities were measured from Time 0 to the time the prey entirely entered the mouth. Predator-prey distance was measured as the distance from the tip of the bass' lower jaw to the point of the prey nearest the predator at Time 0. Hyoid depression was measured from the middle of the eye to the floor of the bass' mouth.

Timing variables (ms) were measured from Time 0 to the time at which maximum gape, peak subambient pressure, maximum hyoid depression, and maximum cranial elevation occurred. The entire gape cycle (ms) from Time 0 to successful prey-capture, as indicated by the time of jaw closure, was included as well. Angles of cranial elevation (in radians) were measured at Time 0, peak subambient pressure, and maximum gape height as an angle from the base of the pectoral fin, to the first dorsal fin spine, to the tip of the rostrum.

### *Data Analysis*

The statistical software environment *R* (R Core Team 2015) and package *geomorph* (Adams et al. 2014; Adams et al. 2015) were used in the statistical analysis. A



multivariate analysis of covariance (MANCOVA), implementing a Randomized Residual Permutation Procedure (RRPP) and 10,000 iterations, was used (Adams et al. 2014; Adams et al. 2015, Collyer et al. 2015).

A Procrustes (squared) distances from a linear model (procD lm) analyzed the independent variable of prey type and the covariate of bass standard length (SL, mm) as individual functions of the dependent variables, as well as taking into account the interaction between the independent variable and the covariate.

An advanced procD lm compared the full and reduced models (Adams et al. 2015) where the reduced model disregarded interactions among and within variables, and the full model took into account interactions between variables. Angles between slope vectors and pairwise distances between slope vectors were analyzed to determine the difference in the amount of slope change between the covariate of bass SL (Collyer et al. 2015). An advanced procD lm was essentially used for pairwise comparisons; it tested whether slope-prey interaction was significant. If the interaction was significant, slopes were compared, and if the interaction was not significant, least squares means (LS means) were compared. All statistics were completed utilizing an alpha = 0.05 level.

A confounding variable in this experiment could be that bass were feeding on prey in an aquarium setting rather than in a natural environment. Glass walls provided by the fish tanks could cause a difference in water dynamics, specifically, if a goldfish swims to the corner of the tank as the smallmouth bass is approaching it, the smallmouth would have to employ different feeding techniques, i.e. stronger suction or reduced ram, to acquire the prey. To control for this, the goldfish were released in the middle of the water column by hand. This ensured that the smallmouth bass had to employ a ram

feeding behavior, as it would in its natural environment, when acquiring fish prey.

Releasing the goldfish in the middle of the tank by hand also ensured a lateral view of the feeding event for filming purposes and kinematic measurements.

This same method of releasing the prey item in the middle of a tank did not work for a crayfish however, because the smallmouth would capture the crayfish as it dropped down through the water column. Therefore, to control for this, the crayfish was placed beside a rocky substrate in the middle of the tank in a position that provided the semblance of protection that crayfish require in their natural habitat, but not so much to be visually obscured from the smallmouth predator or the high speed video camera. This forced the smallmouth to decrease its approach velocity, and utilize stronger suction to capture the crayfish from the substrate, as it would in the wild.

## RESULTS

A total of 278 feeding events (158 goldfish; 120 crayfish) from six bass were recorded.

### *Pressure and Kinematics*

A univariate analysis of covariance, ANCOVA, using a RRPP revealed that prey item, SL of the bass, and the interaction between prey item and SL significantly impacted peak subambient pressure (Table 1). Because of the significance, a pairwise comparison was performed ( $F=16.307$ ,  $z\text{-score}=8.9416$ , and  $p=0.00015$ ).

Figure 1 shows that as bass get larger, the amount of pressure they produced while feeding on crayfish increased, whereas the amount of pressure produced while

feeding on goldfish decreased. Smallmouth bass produced stronger peak subambient pressure when feeding on crayfish (Figure 1).

A MANCOVA utilizing a RRPP was performed on the kinematic variables of peak subambient pressure, maximum gape, approach velocity, attack velocity, predator-prey distance, and hyoid depression. This procedure revealed that prey item, SL, and the interaction between the two was significant (Table 2). A pairwise comparison was performed ( $F=12.74$ ,  $z\text{-score}=7.4416$ ,  $p=0.00025$ ). Slope distance ( $0.5737426$ ,  $p=0.0025$ ) and slope angles ( $102.2283^\circ$ ,  $p=0.00535$ ) indicated that bass SL was significant.

As smallmouth bass got larger, gape size increased (Figure 2); however, this plot also revealed that regardless of that increase, smallmouth were continually feeding on goldfish with a wider gape than when feeding on crayfish. Figures 3 and 4 show a similar trend in approach and attack velocities in that bass exhibited greater velocity when feeding on goldfish. Approach and attack velocities showed trends of decrease as bass SL increased when feeding on goldfish, and both velocities showed an increase as bass SL increased when feeding on crayfish. Predator-prey distance differed in that bass were further away from goldfish and closer to crayfish (Figure 5) as they initiated their strike. As bass SL increased, the proximity of bass to goldfish increased and the proximity to crayfish decreased; however, Figure 5 also shows that bass constantly remained closer to crayfish as they attacked. Figure 6 illustrates that bass had a greater hyoid depression when feeding on goldfish regardless of SL.

### *Timing Variables*

Time 0 to maximum gape, Time 0 to peak subambient pressure, Time 0 to maximum hyoid depression, Time 0 to maximum cranial elevation, and the length of the entire gape cycle from Time 0 to successful prey-capture were assessed using a MANCOVA with RRPP (Table 3). Pairwise distances between LS means were assessed because of the significance of prey item, but not SL or the interaction between prey item and SL. The LS means (28.4262,  $p=0.51185$ ) indicate that prey type changed the timing variables between bass, but did so consistently for differently sized smallmouth bass.

As indicated by Figures 7 through 11, bass gape cycles were shorter when feeding on crayfish than when feeding on goldfish: their entire gape cycle was shorter than that of goldfish (Figure 7), they reached maximum gape more quickly (Figure 8), they reached peak subambient pressure more quickly (Figure 9), their time to maximum hyoid depression happened sooner (Figure 10), and they approached maximum cranial elevation more quickly (Figure 11).

#### *Angles of Cranial Elevation*

Cranial elevation at Time 0, peak subambient pressure, and maximum gape were evaluated using a MANCOVA with RRPP (Table 4). Pairwise distances between LS means were assessed because the covariate of SL and the interaction between prey item and SL were not significant, whereas prey item was significant (Table 4). The LS means (0.1901,  $p=0.5016$ ) indicate that prey type changed the angles of cranial elevation consistently regardless of different sizes of bass.

Cranial elevation at Time 0 was significant ( $p=0.0299$ ); however, this was not meaningful ( $R^2=0.038$ ) and is illustrated in Figure 12. Figure 13 illustrates that bass

consistently produced a greater cranial elevation angle at peak subambient pressure when feeding on goldfish. Cranial elevation at maximum gape was larger for bass feeding on goldfish as well (Figure 14).

## DISCUSSION

The results of this study suggest smallmouth bass utilize highly variable kinematics when presented with different functional prey-types and are consistent with the hypothesis that smallmouth bass utilize stronger peak subambient pressure when feeding on benthic prey and weaker pressure when feeding on open-water prey, therefore utilizing modulation.

### *Pressure and Kinematics*

The interaction between prey item and SL was statistically significant (ANCOVA,  $p < 0.0001$ ) in terms of peak subambient pressure and provided that smallmouth bass produce stronger subambient pressure when feeding on crayfish than on goldfish. Interestingly, Figure 1 shows that during crayfish feeding events, as bass SL increases, peak subambient pressure increases as well, suggesting that larger bass are capable of generating stronger suction pressure, a point that contradicts a previous study on snook (Wainwright et al. 2006). Suction pressure decreases with size during goldfish feeding events, likely due to the fact that larger bass are capable of swimming at faster speeds thus reducing the need for suction during what are predominately ram prey-

capture events. In the largest bass, the variation between peak pressures on goldfish vs crayfish is very large.

The interaction between prey item and SL was significant (MANCOVA,  $p < 0.0002$ ) for the dependent variables of peak pressure, maximum gape, approach velocity, attack velocity, predator-prey distance, and hyoid depression. The variation was largest due to differing prey types ( $R^2 = 0.42588$ ,  $P < 0.0001$ ), which signifies that different prey types were the predominant factors affecting the differences in peak pressure and kinematic performance in smallmouth bass.

Overall maximum gape increased with bass SL; however, the rate of change between maximum gape, SL of the bass, and the different prey items remained the same (Figure 2). Maximum gape was larger in bass during goldfish feeding events and smaller in bass during crayfish feeding events. Hyoid depression (Figure 6) provided a similar trend. As bass SL increased, hyoid depression increased, and smallmouth depressed their hyoid more when feeding on goldfish than on crayfish.

Figure 3 indicates that smallmouth bass approached their goldfish prey more quickly than their crayfish prey. A greater approach and attack velocity, in addition to a wider gape, when feeding in the pelagic zone indicates ram feeding (Carroll et al. 2004). Interestingly, comparing the slope and data points of crayfish for approach (Figure 3) and attack (Figure 4) velocities, there is a subtle difference suggesting that smallmouth bass had a very slow approach velocity when nearing their crayfish prey, but an increased attack velocity to ensure successful capture.

Figure 5 indicates that smallmouth bass were closer to crayfish than goldfish at Time 0, which was intuitive given the different defense mechanisms employed by the

prey items. Crayfish were more unpredictable in their escape vs defense strategies (Copp and Jamon 2001) and predatory bass had to get close enough to utilize the method of suction feeding that would ensure successful capture. Ram feeding on crayfish is simply not an option because they reside on the substrate. Goldfish, however, were located in the water column and provided bass with visual indicators of the direction in which they were swimming, e.g., eyes and tail, which allowed the smallmouth predators to more easily predict their escape direction and overtake them with a wide gape and high approach and attack velocity (Norton 1991).

Hyoid depression was greater in smallmouth bass when feeding on goldfish than crayfish (Figure 6) and stayed consistent with smaller and larger sized bass. The results of hyoid depression furthermore indicated modulation in smallmouth bass, and stay consistent with the results of the previous kinematic variables. Bass appear to maximize hyoid depression in an attempt to maximize their entire mouth cavity for use during ram feeding.

### *Timing Variables*

The results of the timing variables in this study showed that prey type (MANCOVA,  $p < 0.0001$ ) affected timing variables regardless of the SL of the bass, and did so consistently for smaller and larger sizes of bass. SL was not statistically significant when it came to timing differences between different prey-capture events, indicating that bass modulated their kinematics due to only prey type. Because crayfish are benthic prey, smallmouth bass had to modulate their behaviors to ensure successful capture. They accomplished this by shortening the length of their gape cycles (Figure 7) and by getting

closer to their prey at the onset of the attack (Figure 5). Bass were further away from goldfish prey at the onset of their gape cycle, and they had to use a greater approach velocity with a greater maximum gape which lengthened their overall gape cycle.

Shorter gape cycles paired with stronger subambient pressure (Figure 1), smaller maximum gape (Figure 2), and slower approach velocity (Figure 3) indicate suction feeding; whereas longer gape cycles, weaker subambient pressure, large maximum gape, and fast approach velocity signify ram feeding (Carroll et al. 2004; Svanback et al. 2002). The timing data are consistent with the kinematic variables indicating modulation in smallmouth bass. These results indicate that ram feeding on pelagic fish takes a longer amount of time than suction feeding on benthic invertebrates.

#### *Angles of Cranial Elevation*

SL, as well as the interaction between SL and prey item, was not significant when it came to angles of cranial elevation; however, prey item was significant (Table 4). Figure 12 does not demonstrate much variation in angles of elevation at Time 0, showing significance but not meaningful enough to consider. Angles at peak suction (Figure 13) and maximum gape (Figure 14) were greater when bass fed on goldfish and the angles increased with bass SL. This indicates that, regardless of different sizes, bass increase their cranial elevation when ram feeding to ensure prey-capture by covering as much area as they can; whereas when feeding on crayfish, they maximize their capture efficiency by pinpointing the crayfish in the benthos with a lesser angle of cranial elevation and stronger suction. These data are consistent with maximum gape (Figure 2); as



smallmouth bass get larger, their maximum gape gets larger, which alters the maximum cranial elevation.

Smallmouth fed on crayfish more quickly utilizing smaller angles of cranial elevation, and took a longer time feeding on goldfish with the use of larger angles of cranial elevation, consistent with Higham (2011). The closer smallmouth bass were to their prey, the smaller their gape heights and angles of cranial elevation, and the stronger their suction pressure; the further away bass were, the larger their gape heights and angles of cranial elevation, which worked to weaken their suction pressure. This further indicates modulation in these bass.

### *General Conclusions*

The relationship between pressure and kinematics equip smallmouth bass with the most effective method of prey-capture given the varying prey. The differences of pressure and kinematics between feeding events is evidence of bass utilizing suction when feeding on crayfish: stronger peak subambient pressure, smaller gape, smaller hyoid depression, shorter predator-prey distance, slower approach velocity, and greater attack velocity in comparison to the approach velocity. The variation is also evidence of ram when feeding on goldfish: weaker peak subambient pressure, larger maximum gape, larger hyoid depression, longer predator-prey distance, fast approach velocity, and fast attack velocity. These data indicate that smallmouth bass modulate their behaviors given varying prey in the benthos and pelagic regions of water.

Pressure and kinematics interplay during feeding events to ensure that bass effectively modulate their feeding behaviors to suit the constraints of their varying

pelagic (goldfish) and benthic (crayfish) prey items. The ability of fish predators to modulate their feeding behavior is often an indication of consuming an increased diversity of prey items, which should increase the chance of successfully capturing those prey items (Nemeth 1997).

Modulation is often indicative of a diverse feeding repertoire and an increase in prey-capture success in individual fish; having the ability to modulate kinematic, hydrodynamic, and feeding behaviors should provide for a greater range of potential prey and expand habitat occupancy (Nemeth 1997). Given the results of this study it is safe to conclude that smallmouth bass modulate their kinematics and suction performance relative to the prey they are trying to capture.

### *Ecological Implications*

Feeding behaviors of smallmouth bass have implications for fisheries management and ecosystem health. Ecosystem health is driven by trophic food web dynamics and insight into the prey-capture techniques utilized by top-level predators may provide more information when managing the overall health and stability of ecosystems (Holmlund and Hammer 1999; Rahel 2004). Fishing causes reduction in ecosystem health, due to species being removed from the system and throwing off the balance of the trophic food web. Therefore, to once again provide balance to the ecosystem, managers often stock fish (Buynak et al. 1991).

Smallmouth bass are largely and commonly managed by fisheries for harvest by anglers (Funk and Fleener 1974; Rahel 2004; Baldrige and Lodge 2013). Being more perceptive of their feeding behavior and abilities to modulate between prey could be of

help to fishery and/or hatchery managers in methods of feeding their fish before introducing them into the wild.

Once introduced to a freshwater ecosystem, given that they are exposed to natural prey, smallmouth bass spread fairly rapidly and have the ability to reduce or displace native fish populations (Rahel 2004; Zanden and Olden 2008). The ability to modulate between benthic invertebrate prey and pelagic fish prey suggests the likely inclusion of a vast prey repertoire, which further indicates more diverse potential habitat occupancy (Carey et al. 2011). However, pellet fed smallmouth bass that are raised in aquaculture for introduction/stocking, would not be very successful once introduced to an ecosystem with differing types of elusive prey (Ehrlich et al. 1989); therefore, smallmouth bass must be exposed to all of the prey items in their feeding repertoire prior to introduction to new ecosystems in order to ensure they have developed the necessary behaviors to achieve success in the wild.

There was little known about the prey-capture kinematics and suction feeding performance in smallmouth bass, but the results of this study indicate that smallmouth are very successful predators that have the ability to adjust to the constraints of different prey types and different habitats (pelagic vs. benthic). The ability of smallmouth bass to modulate their predatory behavior likely underlies their occupancy of diverse freshwater habitats and their consumption of assorted prey. In the words of James A. Henshall, “Inch for inch and pound for pound, the gamest fish that swims.”

## LITERATURE CITED

- Adams, D. C., Collyer, M. L., and Otarola-Castillo, E. 2014. R: package, *geomorph*: Software for geometric morphometric analysis.
- Adams, D. C., Collyer, M. L., and Sherratt, E. 2015. *Geomorph*: Software for geometric morphometric analyses. R package version 2.1.6. <http://cran.r-project.org/web/packages/geomorph/index.html>.
- Avise, J. C. and Smith, M. H. 1977. Gene frequency comparisons between sunfish (Centrarchidae) populations at various stages of evolutionary divergence. *Systematic Zoology* 26: 319-335.
- Baldrige, A. K. and Lodge, D. M. 2013. Intraguild predation between spawning smallmouth bass (*Micropterus dolomieu*) and nest-raiding crayfish (*Orconectes rusticus*): implications for bass nesting success. *Freshwater Biology* 58: 2355-2365.
- Buynak, G. L., Kornman, L. E., Surmont, A., and Mitchell, B. 1991. Evaluation of a smallmouth bass stocking program in a Kentucky reservoir. *North American Journal of Fisheries Management* 11: 293-297.
- Carey, M. P., Sanderson, B. L., Friesen T. A., Basrnas, K. A., and Olden, J. D. 2011. Smallmouth bass in the Pacific Northwest: a threat to native species; a benefit for anglers. *Reviews in Fisheries Science* 19: 305-315.
- Carroll, A. M., Wainwright, P. C., Huskey, S. H., Collar, D. C., and Turingan, R. G. 2004. Morphology predicts suction feeding performance in centrarchids. *The Journal of Experimental Biology* 207: 3873-3881.

- Carroll, A. M. and Wainwright, P. C. 2009. Energetic limitations on suction feeding performance in centrarchid fishes. *The Journal of Experimental Biology* 212: 3241-3251.
- Case, J. E., Westneat, M. W., and Marshall, C. D. Feeding biomechanics of juvenile red snapper (*Lutjanus campechanus*) from the northwestern Gulf of Mexico. *The Journal of Experimental Biology* 211: 3826-3835.
- Clady, M. D. 1974. Food habits of yellow perch, smallmouth bass, and largemouth bass in two unproductive lakes in northern Michigan. *The American Midland Naturalist* 91: 453-459.
- Collar, D. C., O'Meara B. C., Wainwright, P. C., and Near, T. J. 2008. Piscivory limits diversification of feeding morphology in centrarchid fishes. *Evolution* 63: 1557-1573.
- Collyer, M. L., Sekora, D. J., and Adams, D. C. 2015. A method for analysis of phenotypic change for phenotypes described by high-dimensional data. *Heredity*. 115: 357-365.
- Copp, N. H. and Jamon, M. 2000. The defense response in crayfish: behavior and kinematics. *Biomechanics in Animal Behavior* 275-290. Oxford BIOS Scientific Publishers
- Copp, N. H. and Jamon, M. 2001. Kinematics of rotation in place during defense turning in the crayfish *Procambrus clarkii*. *The Journal of Experimental Biology* 204: 471-486.
- Day, S. W., Higham, T. E., Cheer, A. Y., and Wainwright, P. C. 2005. Spatial and temporal patterns of water flow generated by suction-feeding bluegill sunfish

- Lepomis macrochirus* resolved by particle image velocimetry. *The Journal of Experimental Biology* 208: 2661-2671.
- Edwards, E. A., G. Gebhart, and Maughan, O. E. 1983. Habitat suitability information: Smallmouth bass. U.S. Department of the Interior, *Fish Wildlife Services* 36: 9-47.
- Ehrlich, K. F., Cantin, M. C., Rust, M. B., and Grant, B. 1989. Growth and survival of larval and postlarval smallmouth bass fed a commercially prepared dry feed and/or *Artemia* nauplii. *Journal of the World Aquaculture Society* 20: 1-6.
- Feary, D. 2007. The influence of resource specialization on the response of reef fish to coral disturbance. *Marine Biology* 153: 153-161.
- Funk, J. L. and Fleener, G. G. The fishery of a Missouri Ozark stream, big piney river, and the effects of stocking fingerling smallmouth bass. *Transactions of the American Fisheries Society* 103: 757-771.
- Grubich, J. R. and Wainwright, P. C. 1997. Motor basis of suction feeding performance in largemouth bass. *The Journal of Experimental Biology* 277: 1-13.
- Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: Role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120: 500-508.
- Higham, T. E., Day, S. W., and Wainwright, P. C. 2005. Sucking while swimming: evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. *The Journal of Experimental Biology* 208: 2653-2660.

- Higham, T. E., Day, S. W., and Wainwright, P. C. 2006a. Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *The Journal of Experimental Biology* 209: 2713-2725.
- Higham, T. E., Day, S. W., and Wainwright, P. C. 2006b. The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes. *The Journal of Experimental Biology* 209: 3281-3287.
- Higham, T. E. 2011. Feeding mechanics. *Encyclopedia of Fish Physiology: From Genome to Environment* 1: 597-602.
- Holmlund, C. M. and Hammer, M. 1999. Ecosystem services generated by fish populations. *Ecological Economics* 29: 253-268.
- Holzman, R., Day, S. W., Wainwright, P. C. 2007. Timing is everything: coordination of strike kinematics affects the force exerted by suction feeding fish on attached prey. *The Journal of Experimental Biology* 210: 3328-3336.
- Huskey, S. H. and Turingan, R. G. 2001. Variation in prey-resource utilization and oral jaw gape between two populations of largemouth bass, *Micropterus salmoides*. *Environmental Biology of Fishes* 61: 185-194.
- Huskey, S. H. 2003. Functional and morphological bases of intraspecific variation in the feeding ecomorphology of largemouth bass, *Micropterus salmoides*. Ph.D. dissertation, Florida Institute of Technology.
- Keast, A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. *Environmental Biology of Fishes* 12: 119-129.

- Lauder, G. V. 1980a. Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *Journal of Morphology* 163: 283-317.
- Lauder, G. V. 1980b. The suction feeding mechanism in sunfishes (*Lepomis*): and experimental analysis. *The Journal of Experimental Biology* 88: 49-72.
- Lauder, G. V. 1983. Prey capture hydrodynamics in fishes: experimental tests of two models. *The Journal of Experimental Biology* 104: 1-13.
- Lauder, G. V. and Clark, B. D. 1984. Water flow patterns during prey-capture by teleost fishes. *The Journal of Experimental Biology* 113: 143-150.
- Lauder, G. V. 1991. Biomechanics and evolution: integrating physical and historical biology in the study of complex systems. *Ecological Morphology: Integrative Organismal Biology*: 1-16.
- Lauder, G.V., and Liem, K.F. 1981. Prey capture by *Luciocephalus pulcher*: implications for models of jaw protrusion in teleost fish. *Environmental Biology of Fishes* 6: 257-268.
- Lonnstedt, O. M., McCormick, M. I., and Chivers, D. P. 2013. Predator-induced changes in the growth of eyes and false eyespots. *Scientific Reports* 3: 2259.
- Motta, P. J. and Kotrschall, K. M. 1992. Correlative, experimental, and comparative evolutionary approaches in ecomorphology. *Netherlands Journal of Zoology* 42: 400-415.
- Motta, P. J., Norton, S. F., and Luczkovich, J. J. 1995. Perspectives on the ecomorphology of bony fishes. *Environmental Biology of Fishes* 44: 11-20.



- Muller, M. Osse, J. W. M., and Verhagen, J. H. G. 1982. A quantitative hydrodynamical model of suction feeding in fish. *Journal of Theoretical Biology* 95: 49-75.
- Near, T. J., Bolnick, D. I., and Wainwright, P. C. 2004. Investigating phylogenetic relationships of sunfishes and black basses (Actinopterygii: Centrarchidae) using DNA sequences from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 32: 344-357.
- Nemeth, D. H. 1997. Modulation of attack behavior and its effects on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *The Journal of Experimental Biology* 200: 2155-2164.
- Norton, S. F. 1991. Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology* 72: 1807-1819.
- Norton, S. F. and Brainerd, E. L. 1993. Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *The Journal of Experimental Biology* 176: 11-29.
- Nyberg, D. W. 1971. Prey capture in the largemouth bass. *The American Midland Naturalist* 86: 129-142.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rahel, F. J. 2004. Unauthorized fish introductions: fisheries management of the people, for the people, or by the people? *American Fisheries Society Symposium* 44:431-443.

- Rand, D. M. and Lauder, G. V. 1981. Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor behavior. *Canadian Journal of Zoology* 59: 1072-1078.
- Richard, B.A., and Wainwright, P.C. 1995. Scaling the feeding mechanisms of largemouth bass (*Micropterus salmoides*): kinematics of prey-capture. *The Journal of Experimental Biology* 198: 419-433.
- Sabo, M. J., Orth, D. J., and Pert, E. J. 1996. Effects of stream microhabitat characteristics on rate of net energy gain by juvenile smallmouth bass, *Micropterus dolomieu*. *Environmental Biology of Fishes* 46: 393-403.
- Sass, G. G. and Motta, P. J. 2002. The effects of satiation on strike mode and prey-capture kinematics in the largemouth bass, *Micropterus salmoides*. *Environmental Biology of Fishes* 65: 441-454.
- Savino, J. F. and Stein, R. A. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* 111: 255-266.
- Sharma, S., Herborg, L. M., and Therriault, T. W. 2009. Predicting introduction, establishment, and potential impacts of smallmouth bass. *Diversity and Distributions* 15: 831-840.
- Stein, R. A. 1976. Behavioral response of crayfish to a fish predator. *Ecology* 57: 751-761.
- Stein, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58: 1237-1253.

- Svanback, R., Wainwright, P. C., and Ferry-Graham, L. A. 2002. Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. *Physiological and Biochemical Zoology* 75: 532-543
- Tran, H. Q., Mehta, R. S., and Wainwright, P. C. 2010. Effects of ram speed on prey-capture kinematics of juvenile Indo-Pacific tarpon, *Megalops cyprinoides*. *Zoology* 113: 75-84.
- van Leeuwen, A., Huss, M., Gardmark, A., Casini, M., Vitale, F., Hjelm, J., Persson, L., and Roos, A.M. 2013. Predators with multiple ontogenetic niche shifts have limited potential for population growth and top-down control of their prey. *The American Naturalist* 182 (1): 53-66.
- van Leeuwen, J. L and Muller, M. 1983. The recordings and interpretation of pressure in prey sucking fish. *Netherlands Journal of Zoology* 33: 425-475.
- van Leeuwen, J. L. 1984. A quantitative study of flow in prey-capture by rainbow trout, with general consideration of the actinopterygian feeding mechanism. *Transactions of the Zoological Society of London* 37: 21-77.
- Van Wassenbergh, S. and Aerts, O. 2009. Aquatic suction feeding dynamics: insights from computational modelling. *Journal of the Royal Society Interface* 6: 149-158.
- Wainwright, P. C. and Lauder, G. V. 1986. Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zoological Journal of the Linnaean Society* 88: 217-228.
- Wainwright, P. C. and Richard, B. A. 1995. Scaling the feeding mechanism of the largemouth bass (*Micropterus salmoides*): motor pattern. *The Journal of Experimental Biology* 198: 1161-1171.

- Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carroll, A. M., Hulsey, C. D., and Grubich, J. R. 2001. Evaluating the use of ram and suction during prey-capture by cichlid fishes. *The Journal of Experimental Biology* 204: 3039-3051.
- Wainwright, P. C., Huskey, S. H., Turingan, R. G., and Carroll, D. C. 2006. Ontogeny of suction feeding capacity in snook, *Centropomus undecimalis*. *Journal of Experimental Zoology* 305A: 246-252.
- Wainwright, P. C., Carroll, A. M., Collar, D. C., Day, S. W., Higham, T. E., and Holzman, R. A. 2007. Suction feeding mechanics, performance, and diversity in fishes. *Integrative and Comparative Biology* 47: 96-106.
- Wine, J. and Krasne, F. B. 1972. The organization of escape behavior in the crayfish. *The Journal of Experimental Biology* 56: 1-18.
- Winemiller, K. O. and Taylor, D. H. 1985. Predatory behavior and competition among laboratory-housed largemouth and smallmouth bass. *The American Midland Naturalist* 117: 148-166.
- Zanden, M. J. V. and Olden, J. D. 2008. A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1512-1522.
- Zipkin, E. F., Sullivan, P. J., Cooch, E. G., Kraft, C. E., Shuter, B. J., and Weidel, B. C. 2008. Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition? *Canadian Journal of Fisheries and Aquatic Sciences* 65: 2279-2292.

**Table 1.** ANCOVA table for the dependent variable of peak subambient pressure (kPa) implementing a Randomized Residual Permutation Procedure (RRPP). Alpha value of 0.05.

	df	SS	MS	R <sup>2</sup>	F	Z	P-value
Prey Item	1	3253.9	3253.9	0.42588	218.230	55.071	0.0001
SL	1	102.7	102.7	0.01344	6.885	3.668	0.0117
Prey Item*SL	1	243.1	243.1	0.03182	16.307	8.977	0.0001
Residuals	271	4040.7	14.9				
Total	274	7640.4					

**Table 2.** MANCOVA table with the dependent variables of peak subambient pressure (kPa), maximum gape (mm), approach velocity (mm ms<sup>-1</sup>), attack velocity (mm ms<sup>-1</sup>), predator-prey distance (mm), and hyoid depression (mm). RRPP implemented. Alpha value of 0.05.

	df	SS	MS	R <sup>2</sup>	F	Z	P-value
Prey Item	1	41288	41288	0.64240	270.9762	45.424	0.0001
SL	1	1082	1082	0.01683	7.1012	4.061	0.0068
Prey Item*SL	1	1941	1941	0.03020	12.7399	7.462	0.0002
Residuals	131	19960	152				
Total	134	64271					

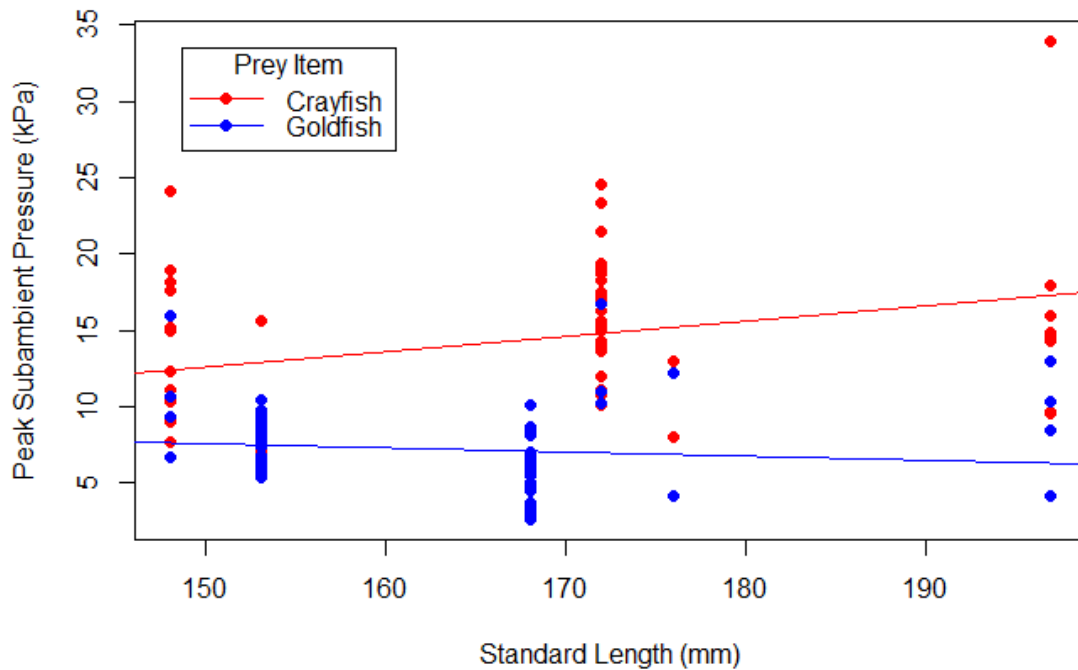
**Table 3.** MANCOVA table implemented using an RRPP on the dependent timing variables of the entire gape cycle, Time 0 to maximum gape, Time 0 to peak subambient pressure, Time 0 to maximum hyoid depression, and Time 0 to maximum cranial elevation. Alpha value of 0.05.

	df	SS	MS	R <sup>2</sup>	F	Z	P-value
Prey Item	1	26731	26731.5	0.227043	38.8749	18.8449	0.0001
SL	1	134	134.3	0.001141	0.1953	0.1265	0.7874
Prey Item*SL	1	792	792.3	0.006730	1.1522	0.7334	0.2808
Residuals	131	90079	687.6				
Total	134	117737					

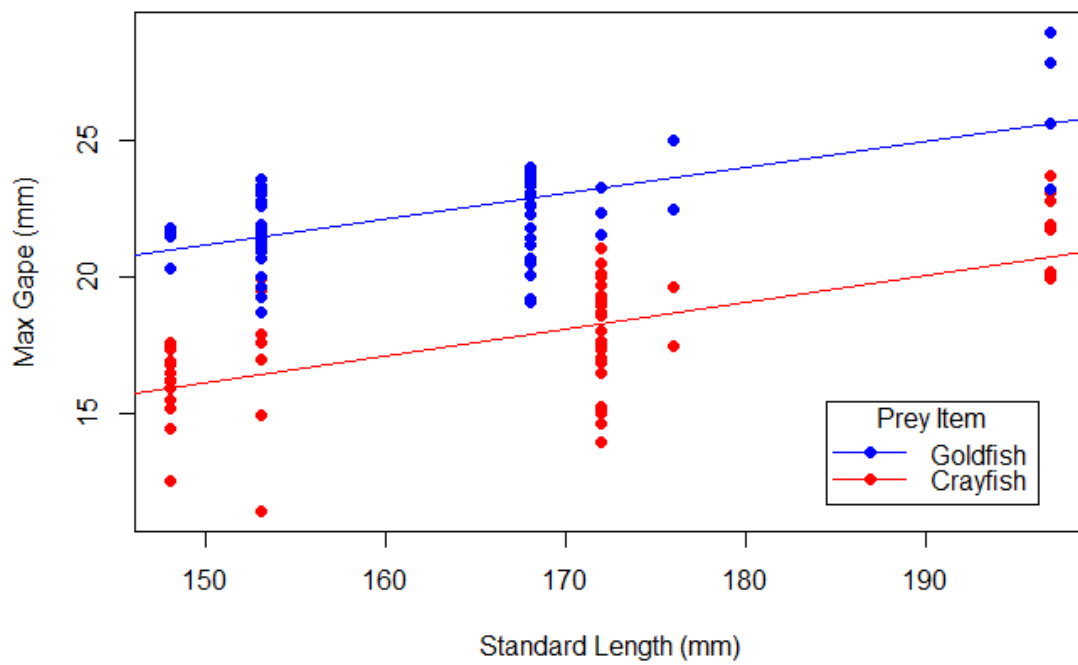
**Table 4.** MANCOVA table using an RRPP on the dependent variables of cranial elevations at Time 0, peak subambient pressure, and maximum gape (in radians). Alpha value of 0.05.

	df	SS	MS	R <sup>2</sup>	F	Z	P-value
Prey Item	1	1.08929	1.08929	0.79477	464.3783	50.876	0.0001
SL	1	1.00133	1.00133	0.00097	0.5670	0.413	0.5699
Prey Item*SL	1	0.00081	0.00081	0.00059	0.3439	0.257	0.7359
Residuals	119	0.27914	0.00235				
Total	122	1.37056					

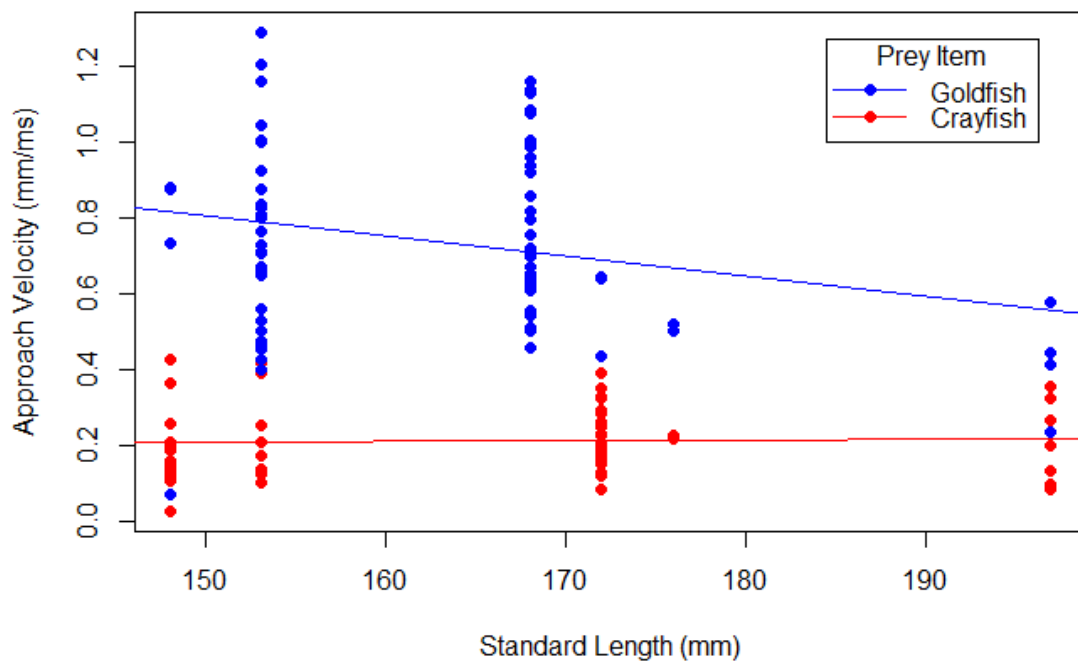




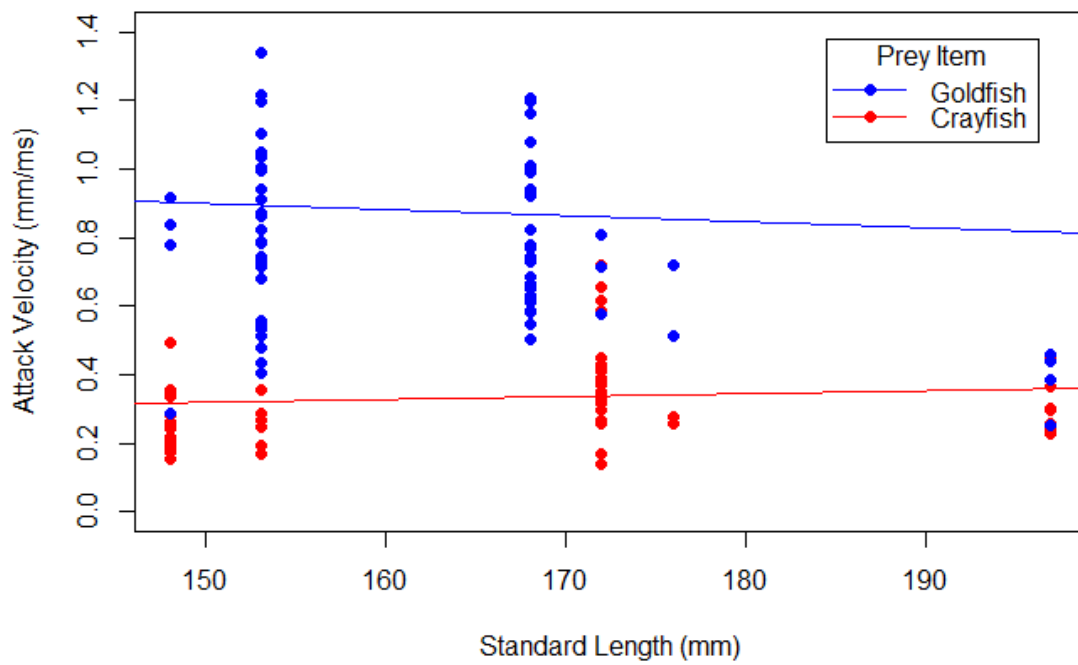
**Figure 1.** Linear model illustrating the variation in peak subambient pressure (kPa) between feeding events on two prey types at different sizes of smallmouth bass (SL, mm). The red symbols represent the individual feeding events on crayfish, and the red line represents the relationship between standard length and peak subambient pressure when feeding on crayfish. The blue symbols represent the individual goldfish feeding events, and the blue line represents the relationship between standard length and peak subambient pressure when feeding on goldfish.



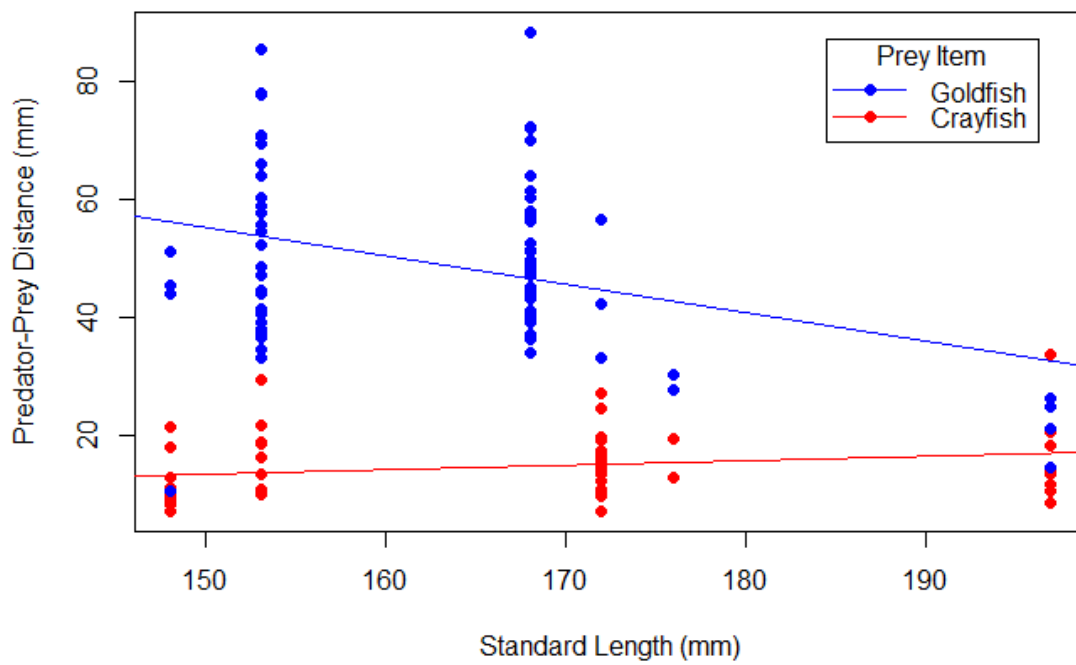
**Figure 2.** Linear model illustrating the variation in maximum gape (mm) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



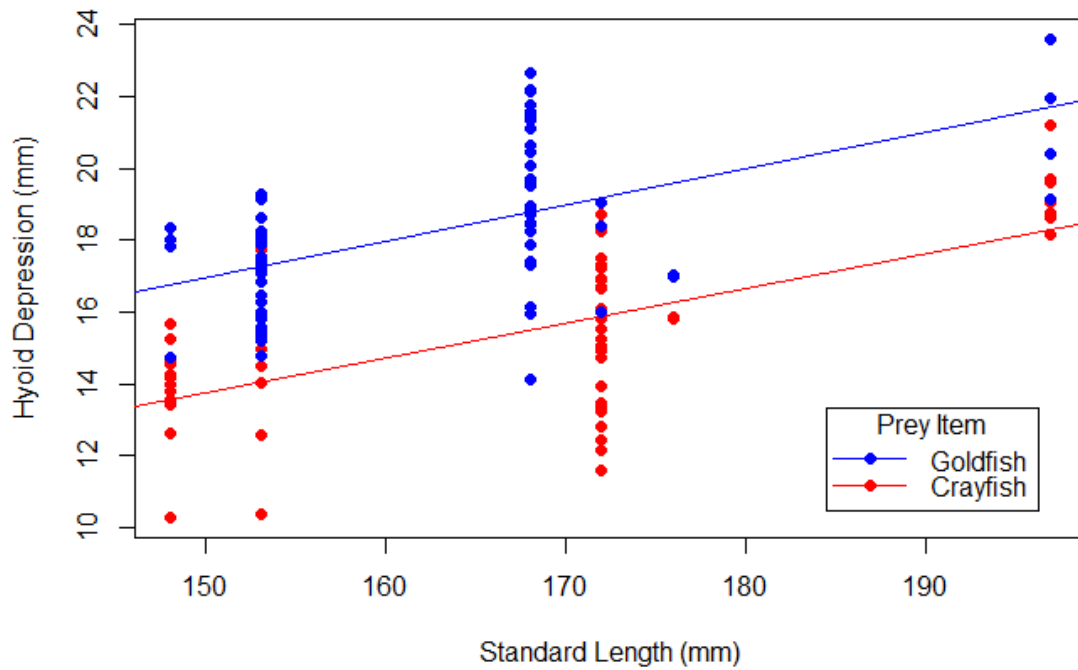
**Figure 3.** Linear model illustrating the variation in approach velocity (mm/ms) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



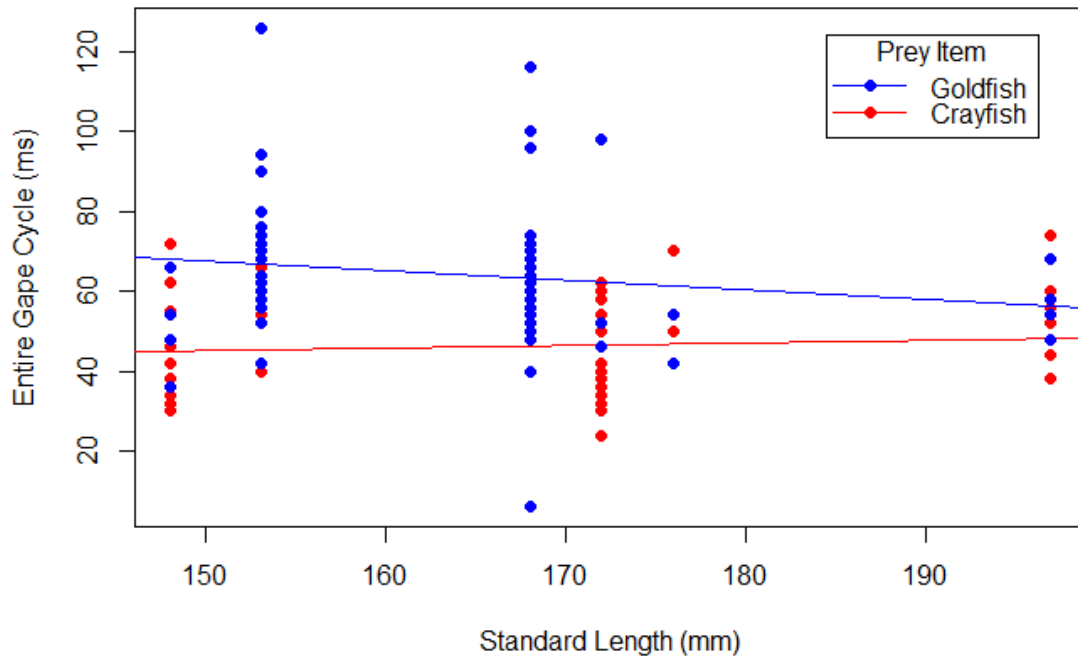
**Figure 4.** Linear model illustrating the variation in attack velocity (mm/ms) between feeding events on two prey items. The symbols and lines represented in this plot are the same as depicted in Figure 1.



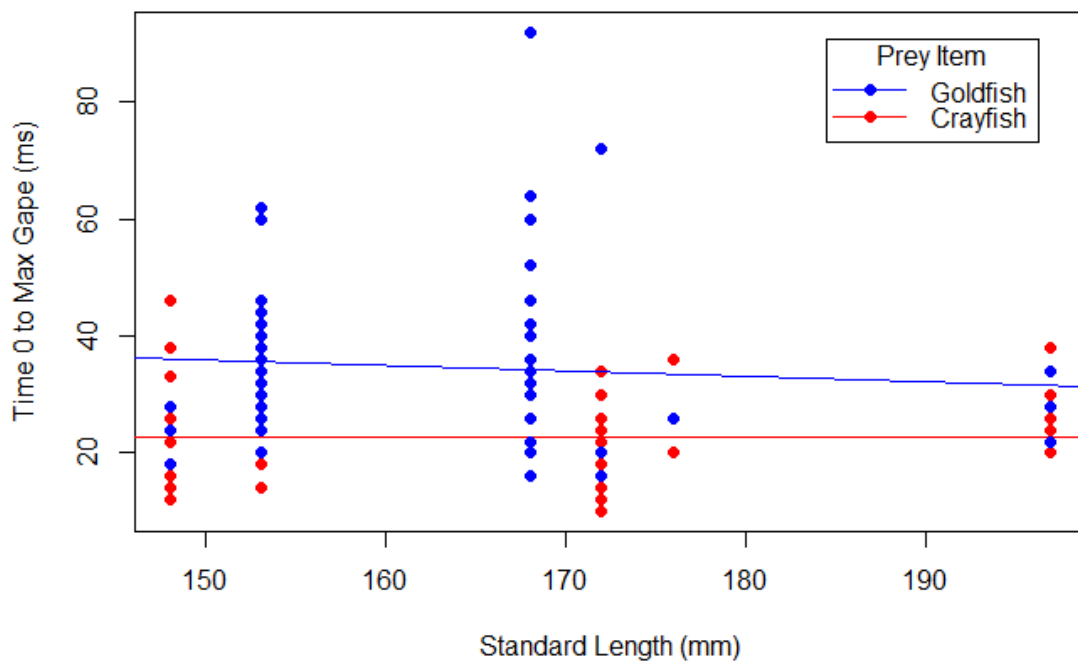
**Figure 5.** Linear model illustrating the variation in predator-prey distance (mm) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



**Figure 6.** Linear model illustrating the variation in hyoid depression (mm) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.

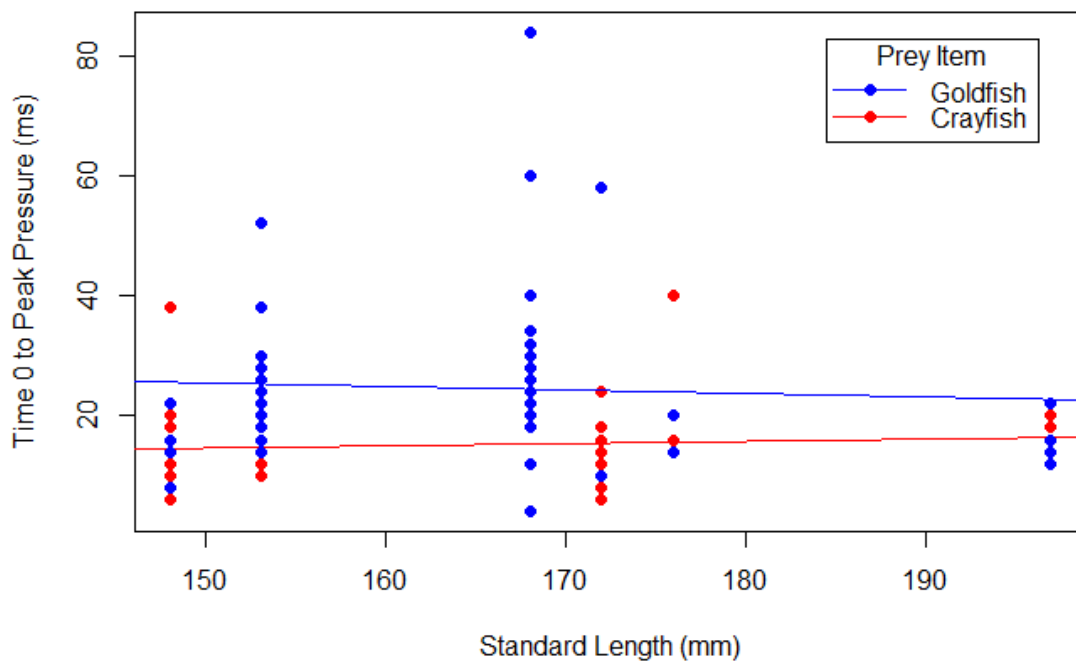


**Figure 7.** Linear model illustrating the variations in the entire gape cycles (ms) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.

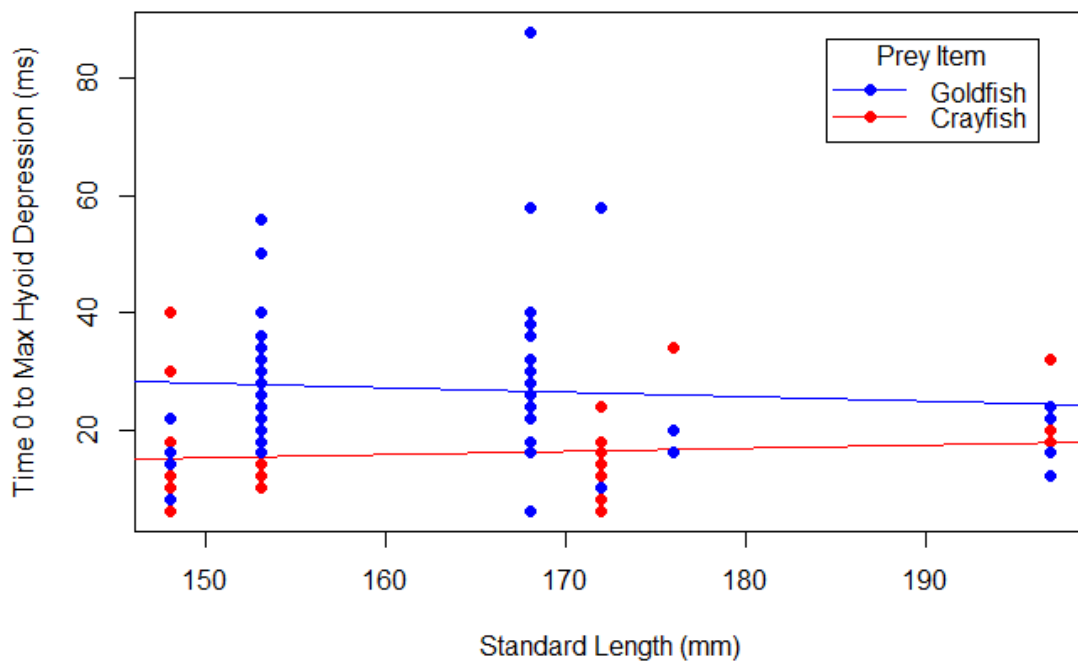


**Figure 8.** Linear model illustrating the variations in timing, from Time 0 to the time at maximum gape (ms), between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.

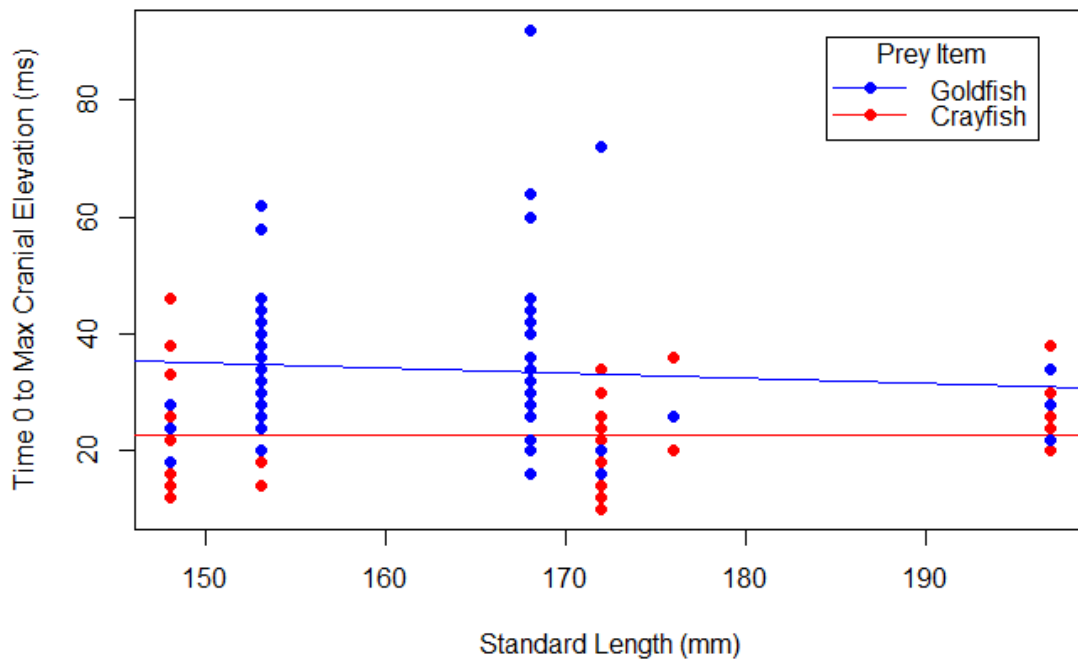




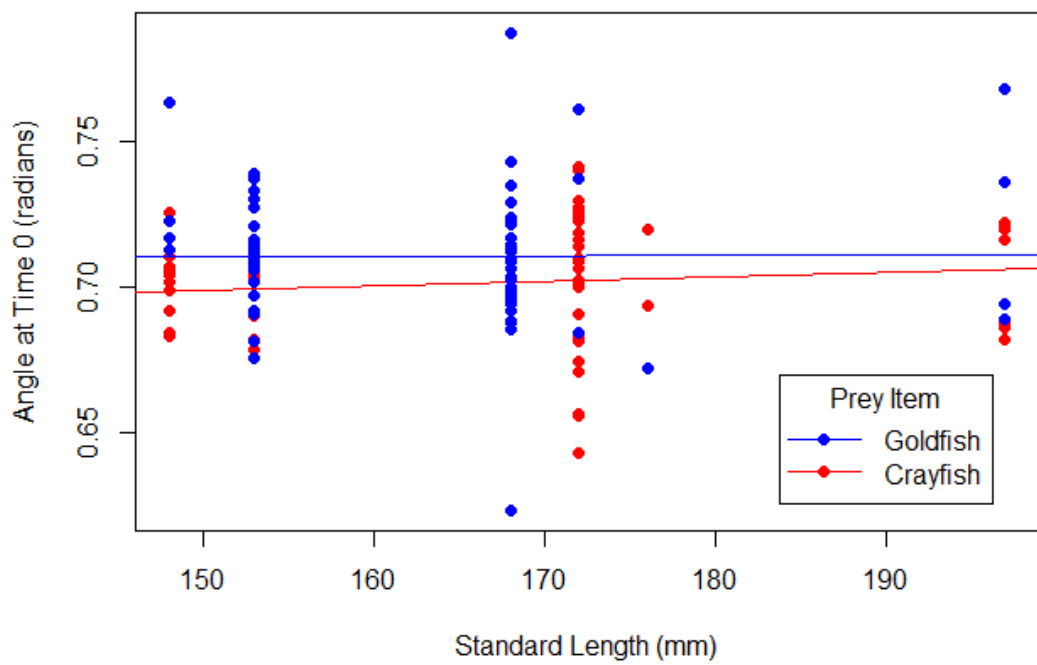
**Figure 9.** Linear model illustrating the variations in timing, from Time 0 to the time at peak subambient pressure (ms), between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



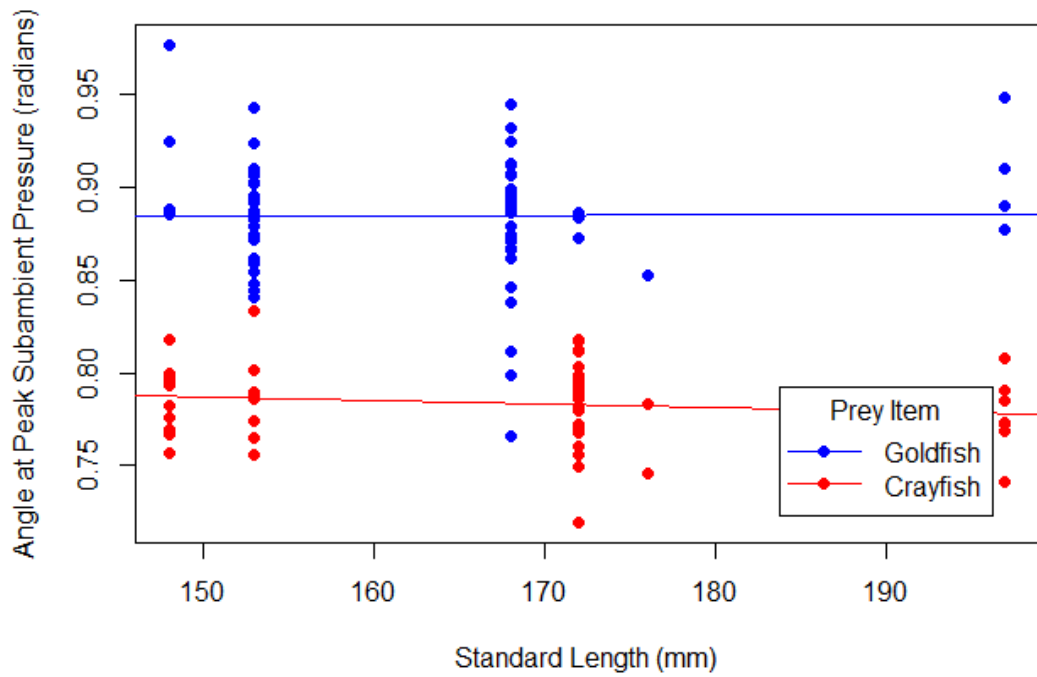
**Figure 10.** Linear model illustrating the variations in timing, from Time 0 to the time at maximum hyoid depression (ms), between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



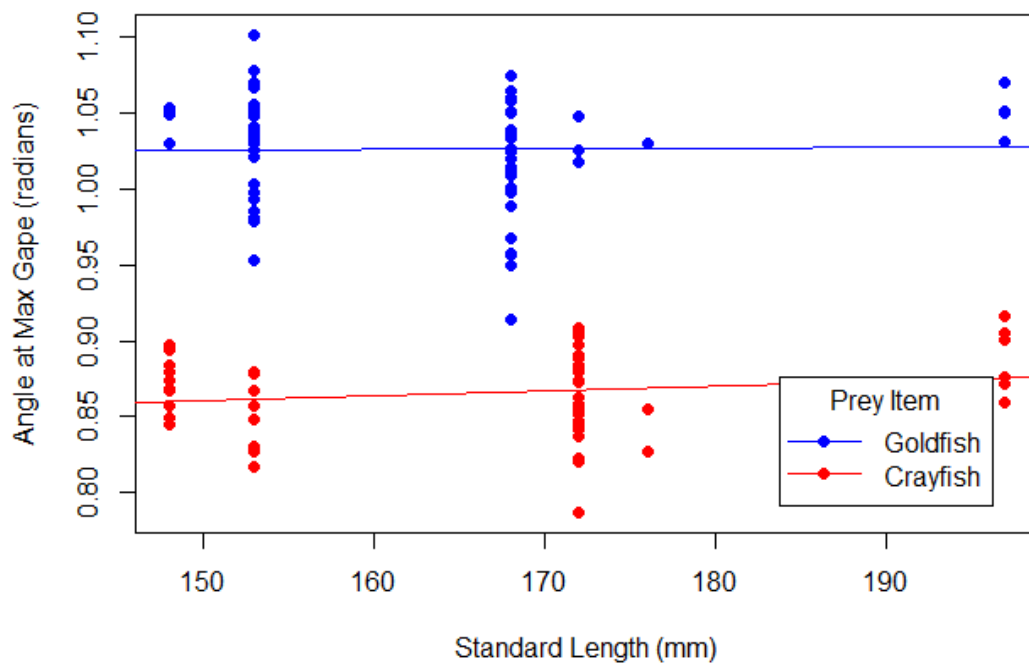
**Figure 11.** Linear model illustrating the variations in timing, from Time 0 to the time at maximum cranial elevation (ms), between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



**Figure 12.** Linear model illustrating the variations in the angle of cranial elevation at Time 0 (radians) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



**Figure 13.** Linear model illustrating the variations in the angle of cranial elevation at peak subambient pressure (radians) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.



**Figure 14.** Linear model illustrating the variations in the angle of cranial elevation at maximum gape (radians) between feeding events on two prey types. The symbols and lines represented in this plot are the same as depicted in Figure 1.