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Behavioral and Morphological Consequences of Rearing Florida Largemouth Bass with Non-Elusive Prey

Alpa Patel Wintzer

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Behavioral and Morphological Consequences of Rearing Florida Largemouth Bass with Non-Elusive Prey

by

Alpa Patel Wintzer

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science
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Alpa Patel Wintzer

ABSTRACT

(1) Hatchery-reared Florida largemouth bass, *Micropterus salmoides floridanus*, feed on inert pellet food while their wild counterparts capture elusive prey. Differences in levels of prey elusivity often mandate the use of alternate methods of prey capture and are accompanied by a related phenotypic change.

(2) This study investigates (a) differences between the prey capture kinematics and strike modes of hatchery and wild juvenile Florida largemouth bass raised on pellets and live prey, and (b) whether elusivity-based variation in prey capture translates to a phenotypic and functional change during skull development.

(3) Analysis of high-speed videography demonstrates that wild bass capture live prey with very rapid movements and large excursions. Hatchery bass of the same age, raised and feeding on pellets, however, used slower kinematics with smaller excursions, yielding strikes with a higher degree of suction.

(4) Capture events of hatchery bass fed live prey for the first time were characterized by movements that were faster than their wild counterparts, but had smaller excursion measurements and resulted in a decreased level of capture success. After five exposures to elusive mosquito fish, hatchery bass adapted their behaviors to capture prey at the kinematic level of wild bass.
(5) The developmental pattern of the skull was conserved between hatchery and wild bass until 80-99mm TL. At this point, wild bass quickly developed morphological changes of the jaw apparatus including a more fusiform head and elongated jaw structures. Natural development in hatchery bass, however, was retarded at this size. Post-release, the skulls of hatchery fish converged towards those of wild bass by 135mm TL. Despite this variation in skull development, no theoretical advantage in food capture was found between these two groups.

(6) It is likely that a lack of experience in live prey capture might constrain hatchery bass from utilizing the total functional potential of their specialized morphology, and therefore, exposure to elusive prey should be enforced in rearing-techniques of hatchery fishes in order to improve the low post-stock survival rates of this species.
General Background

Form and Function

Functional morphology links an organism’s anatomical form with its biological role (Bock 1980). This type of relationship is especially pronounced in the feeding structures of fishes, as they do not facilitate the process of prey acquisition or handling with the use of appendages. The result is often a form which may be highly derived to feed upon a specific prey type. Specializations in feeding can occur in a variety of associated structures, including dentition (Fryer and Iles 1972; Motta 1988), mouth orientation (Winemiller 1991), length of the digestive tract (Bowen 1983), head shape (Meyer 1987), and cranial osteology (Anker 1974; Muller 1987; Westneat 1990). While such specializations may lead to an increased efficiency in feeding events on a particular prey type, they may, depending upon the degree of specialization, constrain an organism’s ability to exploit alternate food sources, hence restricting it to its realized feeding niche (Wainwright 1988).

Feeding

A single bite during feeding in aquatic vertebrates can be divided into four discrete phases (Liem 1978; Lauder 1980). During the preparatory phase, the volume in the buccal cavity is decreased. This action occurs via the protraction of the hyoid, raising the floor of the buccal cavity, and the medial movement of the suspensorium, resulting in an overall lateral compression of the cranial region (Lauder 1985). The expansive phase follows, with a rapid expansion of the buccal cavity, as the cranium moves dorsally and
the mandible is depressed. The buccal volume is also increased with the depression of
the hyoid and the abduction of the palatoquadrate (Liem 1978). Next, the compressive
phase is marked by a decrease in buccal volume, with mandible elevation, protraction of
the hyoid and the palatoquadrate, and the adduction of the suspensorium (Lauder 1985).
Finally, during the recovery phase, cranial bones are returned to their normal positions.

Three modes of prey capture, ram, biting, and suction, have been identified which
may utilize the four-phase feeding sequence (Liem 1980) and differ in the timing of
kinematic events. During ram feeding, the predator’s body accelerates towards the prey,
engulfing it (Rand and Lauder 1981; Norton and Brainerd 1993; Wainwright et al. 2001).
During this motion, the ascending process of the premaxilla protrudes outwards in
modern teleosts, aiding in capture (Norton 1991). In this feeding mode, the prey remains
stationary, while the predator moves (Norton and Brainerd 1993). Biting, or
manipulation, occurs when a fish uses its jaws to cut a piece out of a larger prey item or
to feed on prey that is attached to the substrate (Norton and Brainerd 1993; Motta et al.
1997). In suction feeding, a rapid expansion of the buccal cavity leads to a rapid decrease
in buccal pressure. This action draws water and the prey item into the mouth (Lauder
1985; Wainwright et al. 2001). The predator remains relatively still in this feeding mode,
while the prey item moves (Norton and Brainerd 1993). As most fishes are able to
modulate their method of prey capture, Norton and Brainerd (1993) described a
continuum of feeding modes in fishes, with pure examples of ram feeding and suction
feeding as its endpoints.
Phenotypic Plasticity

Phenotypic plasticity is the act of producing a different morphology as the result of variations in environmental conditions. This change could, indeed, allow an organism to adapt to the new conditions it experiences, but this is not necessarily true of all plasticity events (Stearns 1989; Witte et al. 1984). Phenotypic plasticity in osteological structures is possible in vertebrates largely due to the dynamic properties of bone tissue (Lanyon and Rubin 1985; Wimberger 1991). According to Wolf’s law, the shape and density of bone can be remodeled as a result of a repetitive motion and its associated loading strains (Lanyon and Rubin 1985). Studies on various fish species indicate that teleosts exhibit a wide variety of changes in morphology in response to environmental stimuli, such as variation in ocular structures due to altered photic conditions (Zeutsius et al. 1984; Van Der Meer and Anker 1986), an increase or decrease in body depth dependant upon the presence of predators (Holopainen et al. 1997), changes in the pharyngeal jaw as a result of prey type (Hoogerhound 1986), and plasticity of the buccal jaws owing to different methods of prey capture (Witte et al. 1984; Patel unpublished data).

Behavioral Plasticity

Behavioral plasticity involves an adaptive modification of typical behavioral patterns in response to a change or stimulus in the environment. This type of plasticity if often associated with learning, as the behavior is repeated and the efficiency of the action increases (Meyer 1986). In the case of feeding, for example, a behaviorally flexible fish will become more adept at detecting and capturing prey with experience (Colgan et. al. 1986; Meyer 1986). Specifically, fishes have been found to modify nocturnal foraging...
strategies when light intensity is altered (Beers and Culp 1990), change their method of prey processing in response to differences in prey hardness (Irish, 1983), and utilize varying modes of prey capture in response to prey with different levels of evasiveness (Coughlin and Strickler 1990).

Ontogeny

A change in an organism’s morphology, behavior, or ecology during development is a type of ontogenetic shift. Ontogeny of diet, including both prey type and size, is typical in most fish species, with the purpose of increasing growth rates to minimize the risk of predation and maximize reproductive ability (Grossman 1980). A switch in diet is often coupled with a change in the morphology of structures involved in feeding (Hernandez and Motta 1997; Wainwright and Richard 1995; Cook 1996). These modifications to morphology can have a large influence on the ontogeny of feeding behavior. If an organism’s morphology has not completed its development, it might impose restrictions on the efficiency of a particular mode of prey capture that will be suitable to employ once the morphological development has been completed (Luczkovich et al. 1995). Thus, the morphology can dictate the method of prey capture that is employed (Coughlin 1991; Cook 1996).

Fisheries

Fishing is one of the oldest practices in human history, and attempts at managing fisheries date back as far as the Roman Empire (Welcomme 2001). Until recently, most thought of fisheries management in the same approach as Lackey (1979), who defined it as “the practice of analyzing, making and implementing decisions to maintain or alter the structure dynamics and interaction of habitat, aquatic biota, and man to achieve human
goals and objectives through aquatic resources.” With management adopting this anthropocentric viewpoint, aquatic ecosystems were suffering. By 1997, 75% of the most commonly collected marine fishes were being over-harvested (Garcia and Newton 1997). In addition, most freshwater bodies were being exploited beyond their optimal levels (FAO 1999). These findings prompted a more balanced management strategy, in which policies covered both the issues of conservation and sustainability in order to reap the long-term benefits that aquatic resources can provide (Welcomme 2001).

There are many types of fisheries, including those for specialized for food, ornamental species, bait species, fry, and insect and pest control (Welcomme 2001), but none have the social ties nor the financial influx of recreational fisheries. These programs are more ecologically “kind” than other fisheries, as recreational fisheries do not include mass collections. Also, while some fishers may eat their catches, the majority return the fish to the water, generally unharmed (Welcomme 2001). Policies further protect the sustainability of this activity by imposing limits on the number and the size of particular species that can be taken, and restrictions are placed upon the type of collecting gear that can be utilized (Welcomme 2001). Finally, attempts are made to stock hatchery-raised target species into systems where recreational fishing takes place. This is done to account for the reduced spawning attributed to individuals that have been removed, thus maintaining the environment’s ecological balance (Templeton 1995).

The underlying supposition of stocking programs is that fishes raised in a hatchery setting will make a successful transition into the systems in which they are stocked (Vinyard 1982). However, as in the case of the largemouth bass, *Micropterus salmoides*, this assumption is not always found to be true. Largemouth bass, due to their
popularity as a sport fish, have been cultured and stocked in the United States for more than 100 years (Rosenblum et al. 1994). From 1996-1999, for example, more than 130,000 fingerlings were stocked into sites around Florida alone (FFWCC 1999). Despite this large stocking effort, experiments have shown that survival of bass fingerlings is typically poor, with some systems yielding survival estimates of less than 1% (Porak et al. 2002).

Many theories have been put forth in an effort to understand this poor survival. Loska (1982) suggested that the small sizes of the fingerlings at the time of stocking make them more susceptible to predation. Next, a dietary imbalance from pellet foods used in hatcheries may be related to liver abnormalities (Porak et al. 2002). Finally, Colgan et al. (1986) concluded that the lack of experience of hatchery-raised bass feeding on live forage fishes may be linked to poor feeding success and ultimately low survival rates.

**Study Organism**

The largest member of the family Centrarchidae (Nyberg 1971), the largemouth bass is native to the continent of North America (MacCrimmon and Robbins 1975). In North America, their range extends from southern Canada south to the peninsular tip of Florida (MacCrimmon and Robbins 1975), and west to northeastern Mexico (Hoyer and Canfield 1994). Introductions for sport and food purposes, however, have lead to a world-wide distribution (Hoyer and Canfield 1994).

A subspecies, *M. s. floridanus* (Lesuer), is recognized in peninsular Florida (Bailey and Hubbs 1949) (Fig. 1). This form differs from the northern largemouth bass, *M. s. salmoides* (Lacépède), in terms of maximum attainable size, with *M. s. floridanus*...
typically being larger (Bailey and Hubbs 1949). In addition, these two subspecies vary in the number of scale rows found on the cheek, the number of scales above, along, and below the lateral line, and the number of scales around the caudal peduncle. Character indices also indicate that *M. s. floridanus* possess smaller scales (Bailey and Hubbs 1949). Finally, a slight difference in coloration and pattern can be observed, with *M. s. floridanus* having a lighter and narrower lateral stripe on the caudal peduncle. Near the head, this stripe breaks up into a series of dashed blotches on *M. s. floridanus*, while it generally remains intact in *M. s. salmoides* (Bailey and Hubbs 1949).

Florida largemouth bass spawn between January and May (Hoyer and Canfield 1994). Males construct nests approximately twice their length (Hoyer and Canfield 1994), which females enter, laying eggs that adhere to the nest’s surface. These eggs are then externally fertilized by the male, who guards the nest from predators (Heidinger 1976; Hoyer and Canfield 1994). Fry remain in the nest area during their early development and feed primarily on zooplankton and aquatic insects (Huskey and Turingan 2001). Next, a niche shift occurs as the young-of-the-year (YOY) bass move from the nest to vegetated littoral zones (Olsen 1996). A change in diet is coupled with this change in habitat, and crustaceans, insects, and fishes are consumed (Huskey and Turingan 2001). As growth of the bass ensues, and predation is no longer a threat, bass leave the littoral zone and forage primarily for fish (Huskey and Turingan 2001) throughout the entire system.

Florida largemouth bass raised in hatcheries undergo dietary shifts on very different prey types than their wild counterparts. Standard feed training of hatchery-
Figure 1. Juvenile Florida largemouth bass, *Micropterus salmoides floridanus*
raised bass is a two phase process. At the beginning of phase I, fry are fed a krill-based
Biotrainer meal at a rate of 150g of meal per kg of bodyweight per day. Over the next 8
days, the bass are gradually trained to feed only on Biodiet Starter #3, a fish-based
crumble. During phase II, bass are gradually converted to feed on Biodiet Grower
1.5mm sinking pellets. Once this transition has been completed, fingerlings are graded to
reduce competition and cannibalism, and are moved to grow-out ponds. The fingerlings
are corralled between mesh barriers, which reduce natural foraging and facilitate feeding.
In the ponds, bass are fed 5 times per day for the first 7 days with Biodiet Grower 1.5mm
pellets at a rate of 15% of the total estimated biomass. For the next 4 days, the feeding
rate is gradually reduced to 10% of the biomass. Once reached, this feeding regimen is
maintained for 2 weeks. This process is repeated feeding the bass first 7.5% and then 5%
of the estimated biomass. One week before release the fingerlings’ diet is supplemented
with minnows. Individuals are stocked at approximately 100mmTL (all information from
Rich Stout, personal communication).

Prey capture in *M. salmoides* has been observed towards both ends of the ram-
suction continuum (Nyberg 1971; Sass and Motta 2002). This variation has been linked
to prey type, location (Nyberg 1971), and satiation (Sass and Motta 2002). The primary
mode of feeding in *M. salmoides*, however, is ram feeding (Norton and Brainerd 1993).

**Objectives**

The goal of this study is to investigate a new theory behind the poor survival rates
found with stocked *M. salmoides* fingerlings. Hatchery and wild bass, as described
above, subside on diets with different levels of evasiveness. These differences likely
warrant the utilization of specific modes of prey capture, which, with repetitive and
consistent loading regimes on the bones of the skull, may translate to phenotypic differences in the osteology of the feeding structures. When hatchery-raised bass are then released during stocking, they may be constrained by their morphology when attempting to capture elusive wild prey. If, however, bass are able to modify their prey capture behavior in a short amount of time, they may learn to feed on available prey types, and make a successful transition into their new environment. If hatchery bass cannot adjust their behavior rapidly enough, they may be vulnerable to starvation. Ultimately, the findings of this work will be used to offer management strategies for this fishery.
Chapter 1: Predator experience: A kinematic comparison of the ontogeny of prey capture in hatchery and wild Florida largemouth bass *Micropterus salmoides floridanus*

Introduction

Naïveté has the potential to be costly. Hatchery-reared fishes are traditionally maintained on a diet of pelleted foods while in captivity and, therefore, are inexperienced in capturing live prey (Vinyard 1982; Colgan et al. 1986; Brown & Laland 2002). Studies have found that these fishes often consume pellet-like items, such as stones, rather than pursuing live prey (Ermbak & Hasse 1983; Ellis et al. 2002). When they do attempt to feed on elusive prey, hatchery fishes are slower to attack (Sundström & Johnsson 2001), have a lower rate of successful capture, and are less efficient at consuming prey (Sundström & Johnsson 2001) than wild fishes. Findings such as these indicate that this behavioural deficit is correlated to the high rates of post-stock mortality documented for hatchery fishes (Brown & Laland 2002).

The largemouth bass, *Micropterus salmoides* (Lacepède), is the largest species in the Centrarchidae family (Nyberg 1971). Due to their popularity as a sport fish, they have been cultured and stocked in the United States for over 100 years (Rosenblum et al. 1994). Despite this large stocking effort, studies have shown that the survival of largemouth bass fingerlings is often poor, with some systems yielding survival estimates of less than 1% (Porak et al. 2002).
The present study examines this problem in light of prey capture kinematics. By quantifying capture behaviour, we can understand exactly how discrete elements of prey capture differ between hatchery and wild Florida largemouth bass, *Micropterus salmoides floridanus* (Lesuer). The following questions are addressed: (1) How do the “baseline” capture kinematics (i.e., hatchery bass feeding on pelleted foods and wild individuals capturing live fish prey) differ between hatchery and wild bass? (2) How do these “baseline” capture kinematics of wild bass compare to those of hatchery bass feeding on novel live prey? and (3) How long does it take for hatchery bass offered live prey to learn to use prey capture kinematics identical to their experienced wild counterparts? Additionally, implications of these results for fisheries management are discussed.

**Materials and Methods**

**Experimental animals**

Forty haphazardly chosen hatchery-reared Florida largemouth bass *Micropterus salmoides floridanus* from each of the four size classes under investigation (20-39, 40-59, 60-79, 80-99 mm total length (*L*<sub>T</sub>; size classes 1, 2, 3, and 4, respectively) were collected at the Richloam Fish Hatchery (Sumter County, Florida). These specimens were spawned by bass from one or a combination of the following systems: Lakes Cypress, Johns (Lake County, Florida), and Okeechobee (Okeechobee, Glades, Hendry, St. Lucie, Martin and Palm Beach Counties, Florida). In hatchery situations, these bass are released at approximately 100 mm *L*<sub>T</sub>. Forty wild bass from each size class were also collected from Lake Walk-in-the-Water using a seine net and from Lakes Mudd and Parker (all Polk County, Florida) via electrofishing from May to August 2001.
The specimens were housed at the University of South Florida’s aquarium facility, with wild bass kept at densities that approximated those found during collection (.01-.05g of biomass/L), and hatchery bass in separate tanks at 6g of biomass/L, typical of hatcheries. Density levels were regulated by partitioning off an appropriate-sized section of the tank. As is typical protocol in Florida, hatchery bass in size class 1 were fed at a rate of 17g crumble (BioDiet Trainer)/kg of biomass/day, while size classes 2, 3, and 4 fed on 1.5mm pellets (BioDiet Grower) at rates of 7.5%, 10%, and 15% of biomass/day, respectively. Wild bass were maintained on a diet of mosquito fish, *Gambusia holbrooki* (Girard), with body depths of approximately 40-60% of the maximum vertical gape of the bass to limit any effects of prey size on prey capture (Werner 1974; Richard & Wainwright 1995). Prey was offered twice daily until satiation. In addition, a 12hr light:12hr dark cycle was maintained and water temperature was 24ºC (Wintzer & Motta 2004). All maintenance and research was performed with University of South Florida Institutional Animal Care and Use Committee approval (#2066).

**Videography**

In an effort to encourage active feeding during filming sessions, food was withheld from both types of bass for a 24 hour period prior to filming. Feeding sequences were filmed in the holding tanks at 500 fields/sec with a Redlake PCI-1000 Motionscope camera. A grid was positioned behind the tanks for scale and fish fed in a position lateral to the camera during all filming events.

As bass were filmed in groups of appropriate density, their marking patterns were used to identify individuals in order to avoid pseudoreplication of recording multiple bite sequences from the same fish. The patterns from the smallest size class, however, were
difficult to discern from one another, and hence, these filming sessions involved a single fish separated in a 6.5 cm x 4.0 cm x 6.5 cm section of the aquarium using a piece of clear perforated Plexiglas, so that the individual could still receive visual and chemical cues from the other bass in the tank. This partitioned section maintained an appropriate stocking density.

For each filming event of baseline feeding by *M. salmoides floridanus* in size class 1, a single mosquito fish, for wild bass, or pellet, for hatchery bass, was introduced per trial. As the individuals in size classes 2-4 were not fed in isolation, three prey or food items were simultaneously introduced to randomly chosen locations within the aquarium. This was done to minimize competition for one mosquito fish or pellet and to ensure the focal animal captured a prey or food item. Care was taken to note which bass consumed the prey items to avoid satiation effects (Sass & Motta, 2002). A single bite was filmed from fifteen bass per four size classes and diet (mosquito fish and pellet), for a total of 120 bites.

To investigate the ability of hatchery bass to feed on novel live prey, the hatchery bass from the previous study were subsequently filmed during their initial experience capturing mosquito fish using the same experimental set-up. Individuals in size class 1 could not capture live prey during their initial attempts and, thus, were excluded from this portion of the study. A single bite from 12 bass in size class 2 were recorded, while fifteen bites were taken from each of size class 3 and 4, yielding a total of 42 prey capture events. Ideally, the converse design with wild bass feeding on pellets would have been instructive, but these fish refused to capture this food type.
In order to investigate the effect of experience on capture behaviour with, five hatchery-raised bass from each size class were removed from the tanks after the novel prey filming had been completed. Fishes in the same size class were housed together in smaller tanks, to maintain appropriate hatchery densities. Prey capture on live mosquito fish was filmed every other day for a total of six filming sessions, including the initial feeding on novel prey. Fish in this portion of the study, were only fed during filming sessions, during which individuals were fed to satiation (2-3 mosquito fish per bass per filming day).

**Video analysis**

Successful feeding sequences were analyzed using Redlake MotionScope 2.21 imaging software (Redlake MotionScope Inc.) and Jandel SigmaScan Pro 4 (SPSS Inc.). Kinematic variables of cranial excursions, measured in mm and degrees, included: (1) Maximum gape distance, the point at which the measured distance between the tips of the upper and lower jaws is greatest; (2) Maximum premaxilla protrusion, the greatest distance from the anterior point of the protruded premaxilla to the anterior margin of the eye; (3) Maximum hyoid depression, the difference between the resting and maximum hyoid depression distances, measured from the ventral margin of the eye; (4) Maximum head elevation, the greatest angle from the tip of the rostrum to the anterior base of the dorsal fin to the dorsal portion of the base of the pectoral fin; (5) Distance moved by the predator, the total distance traveled by the bass from the start of mandible depression (time zero) until prey capture; and (6) Distance moved by the prey, the total distance traveled by the prey or food item from time zero until prey capture.
The following timing and duration variables were expressed in ms relative to time zero, the start of mandible depression: (1) Time to maximum gape, time until maximum gape distance is reached; (2) Duration of maximum gape, the length of time that the maximum gape position is held; (3) Time to maximum premaxilla protrusion, time until premaxillary protrusion is at its greatest; (4) Time to start hyoid depression, the time to the beginning of a ventral motion of the hyoid; (5) Time to maximum hyoid depression, the time until hyoid depression is at its greatest; (6) Duration of hyoid depression, the total length of time for which the hyoid is depressed; (7) Time to close mouth, from the end of duration of maximum gape until the mouth is completely closed after prey capture; (8) Time to capture, the time at which the prey item completely enters the mouth; and (9) Total bite duration, the time elapsed between the initial opening and final closing of the fish’s mouth. Additionally, the number of strikes required for all successful prey captures was recorded.

Data analysis

All data were tested for normality and equality of variance using Kolmogorov-Smirnov and Levene median tests, respectively. Natural log transformations were applied to non-normal data sets. The data were regressed against total lengths of individual fish, and the resultant size-removed residuals were used in all further analyses. The data set for the novel prey experiment was unbalanced due to the inability of size class 1 hatchery-reared bass to capture live mosquitofish. Thus, this size class was omitted from statistical analyses for that experiment. Additionally, only 12 hatchery bass in size class 2 successfully captured mosquito fish. In this case, the data generation function of
SYSTAT 10 (SPSS Inc.) was utilized to create 3 values, resulting in a sample size of 15 individuals for a balanced design.

In order to reduce the data sets for the studies on baseline and novel prey captures, they were partitioned along orthogonal axes using principal component analyses performed with all of the kinematic variables. MANOVAs on the factor loading scores of PC axes I and II for the baseline study, and PC axes I and III for the data on novel prey capture were then used to find differences between and among diet and size class in multivariate space. To determine if there was an effect of diet or size class on a single PC axis, an ANOVA was run for each axis using factor-loading scores. On axes where significant differences were found, two-way ANOVAs (diet and size class) were performed on size-removed kinematic variables. A Tukey post hoc test was then run to pinpoint the source of any variance. An a-level of $p=0.05$ was used to determine differences in all statistics for this study. To avoid type II error, Bonferroni corrections were not utilized in analyses (Cabin & Mitchell 2000; Moran 2003).

Plots of the distance traveled by the predator against the distance traveled by the prey were created to visualize movement and to examine the feeding mode of these fishes. In addition, a calculation of the degree of strike mode (Sass & Motta 2002) was made for each individual using the ram-suction index (RSI) formula from Norton & Brainerd (1993):

$$\text{RSI} = \frac{(D_{\text{predator}} - D_{\text{prey}})}{(D_{\text{predator}} + D_{\text{prey}})}$$

where $D_{\text{predator}}$ is the distance moved by the predator, and $D_{\text{prey}}$ is the distance moved by the prey. A sequence in which the predator moves while the prey remains still, for example, is classified as pure ram feeding and would yield an RSI value of +1. The
opposite scenario is termed pure suction and has an RSI value of -1. These designations are the endpoints of a continuum with varying degrees of ram and suction in between (Norton & Brainerd 1993).

In the study on prey capture and experience, there were fish in size class 1, which did not feed on the first and second filming days. Additionally, some individuals in size class 2 did not capture prey on filming day 2. Due to this unbalanced design, t-tests were performed within each size class. These analyses compared each kinematic variable, using all five bites on a single successful filming day (all five fish feeding), against five randomly chosen bites from the wild bass data set of the appropriate size class. Wild *M. salmoides* were considered to be the efficiency standard against which to compare inexperienced hatchery bass. These data sets were compared at every filming date until the kinematic variables were no longer statistically different between wild and hatchery bass. A Kruskal-Wallis one-way ANOVA on ranks, followed by a Tukey post hoc test, compared the length of time, in days of exposure to live prey, to approach the values of wild bass among the four size classes. All analyses were performed using SigmaStat 2.03 and SYSTAT 10 (both SPSS Inc.).

**Results**

*Baseline Prey Capture Kinematics*

Wild bass capturing mosquito fish began the strike with an S-start, had shorter timing and duration variables, and typically greater values for excursions than hatchery bass feeding on pellets, although the distance moved by the food item was greater for hatchery bass (Fig. 2a; Table 1a). Separation was clear in multivariate space (Wilk's-Λ
Figure 2. Principle components analysis of kinematic variables for feeding events of (a) wild *M. salmoides floridanus* capturing mosquito fish and hatchery-reared *M. salmoides floridanus* capturing pellets and (b) naïve hatchery-reared and experienced wild *M. salmoides floridanus* capturing mosquito fish.
Table 1. Principal component loading scores for feeding events of (a) wild *M. salmoides floridanus* capturing mosquito fish and hatchery-reared *M. salmoides floridanus* capturing pellets and (b) wild and hatchery-reared *M. salmoides floridanus* capturing mosquito fish. Bolded values indicate axis assignment.

(a)

<table>
<thead>
<tr>
<th>Kinematic variable</th>
<th>Factor 1</th>
<th>Factor 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to capture (ms)</td>
<td>0.842</td>
<td>-0.026</td>
</tr>
<tr>
<td>Time to maximum premaxilla protrusion (ms)</td>
<td>0.811</td>
<td>0.126</td>
</tr>
<tr>
<td>Time to maximum hyoid depression (ms)</td>
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</tr>
<tr>
<td>Time to maximum gape (ms)</td>
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</tr>
<tr>
<td>Distance moved by predator (mm)</td>
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</tr>
<tr>
<td>Total bite duration (ms)</td>
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<td>-0.676</td>
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<td>Maximum gape distance (mm)</td>
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<td>0.152</td>
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<tr>
<td>Duration of hyoid depression (ms)</td>
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<td>-0.239</td>
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<td>Maximum hyoid depression (mm)</td>
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<td>0.056</td>
</tr>
<tr>
<td>Time to start hyoid depression (ms)</td>
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<td>Distance moved by prey (mm)</td>
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<td>0.186</td>
</tr>
<tr>
<td>Maximum head elevation (degrees)</td>
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<td>0.308</td>
</tr>
<tr>
<td>Maximum premaxilla protrusion (mm)</td>
<td>0.500</td>
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<tr>
<td>Duration of maximum gape (ms)</td>
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<tr>
<td>Time to close mouth (ms)</td>
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<td>-0.871</td>
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</table>

% of total variance explained 37.128 11.698

(b)

<table>
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<tr>
<th>Kinematic variable</th>
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<td>Duration of hyoid depression (ms)</td>
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<td>Maximum gape distance (mm)</td>
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<td>Time to maximum premaxilla protrusion (ms)</td>
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<td>0.447</td>
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<td>Time to start hyoid depression (ms)</td>
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<td>0.155</td>
</tr>
<tr>
<td>Time to close mouth (ms)</td>
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<td>0.159</td>
</tr>
<tr>
<td>Distance moved by predator (mm)</td>
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<td>0.519</td>
</tr>
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<td>Maximum premaxilla protrusion (mm)</td>
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<td>Duration of maximum gape (ms)</td>
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<td>-0.346</td>
</tr>
<tr>
<td>Time to capture (ms)</td>
<td>0.365</td>
<td>0.697</td>
</tr>
</tbody>
</table>

% of total variance explained 49.648 15.002
F_{6,222}=19.082; \ p=<0.001), \ and \ significant \ effects \ of \ diet \ (p=<0.001), \ size \ class \\
(p=<0.001), \ and \ their \ interaction \ (p=<0.001) \ were \ detected \ on \ both \ axes.

Two-way ANOVAs for each variable indicated diet related differences for all 
kinematic measurements except time to capture (Table II). Differences due to size class 
were found for all kinematic measurements except for 3 of the 4 variables involving the 
hyoid. Similarly, differences were found in the interaction effects for all variables except 
time to reach maximum hyoid depression and duration of hyoid depression (Table II). 
Tukey tests show that larger bass generally make greater excursions and have longer 
timing and duration values. Within a size class, wild bass usually had greater excursion 
distances and shorter timing and duration values than hatchery bass (Figure 2). Also, very 
short timing and duration measurements for gape variables were recorded for hatchery 
bass in size class 2, while long timing and duration values of these same variables were 
observed for hatchery bass in size class 3 (Figure 2).

While both wild and hatchery bass generally feed via ram-capture, hatchery fish 
feeding on pellets utilize suction to a higher degree at all size classes. Wild bass use more 
ram as they grow larger, while hatchery bass employ the highest level of ram feeding at 
the smallest size (Figure 3).

Capture of novel prey

Data for both experienced wild bass and naïve hatchery bass feeding on mosquito 
fish were different in multivariate space (Wilk's-\Lambda \ F_{4,166}=2.689; \ p=<0.033) (Figure 1b). 
Wild bass typically utilized a weak curvature of the body as a strike posture, had greater 
distances for excursion variables and larger values for timing and duration measurements 
(Table 1b, III). Two-way ANOVAs on PC axes I and III showed an effect of diet
Figure 3. Kinematic profiles of select variables for wild *M. salmoides floridanus* capturing mosquito fish and hatchery-reared *M. salmoides floridanus* capturing pellets within four size classes.
Table 2. ANOVA results for kinematic variables during prey capture events of wild *M. salmoides floridanus* capturing mosquito fish and hatchery-reared *M. salmoides floridanus* feeding on pellets. *p*≤0.05, **p*≤0.01

<table>
<thead>
<tr>
<th>Kinematic variable</th>
<th>Diet mean(SE)</th>
<th>Size class mean(SE)</th>
<th>p-value</th>
<th>Size class</th>
<th>Interaction</th>
</tr>
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<tbody>
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<td></td>
<td>Wild</td>
<td>Hatchery</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Maximum gape distance (mm)</td>
<td>8.7(0.4)</td>
<td>5.0(0.3)</td>
<td>4.1(0.2)</td>
<td>5.5(0.3)</td>
<td>7.4(0.4)</td>
</tr>
<tr>
<td>Maximum premaxilla protrusion (mm)</td>
<td>5.3(0.2)</td>
<td>4.5(0.2)</td>
<td>3.3(0.1)</td>
<td>4.3(0.2)</td>
<td>5.2(0.1)</td>
</tr>
<tr>
<td>Maximum hyoid depression (mm)</td>
<td>4.8(0.2)</td>
<td>2.4(0.1)</td>
<td>1.8(0.1)</td>
<td>3.0(0.2)</td>
<td>4.2(0.4)</td>
</tr>
<tr>
<td>Maximum head elevation (degrees)</td>
<td>47.6(0.8)</td>
<td>43.6(0.8)</td>
<td>41.5(0.7)</td>
<td>46.3(1.1)</td>
<td>44.5(1.0)</td>
</tr>
<tr>
<td>Distance moved by predator (mm)</td>
<td>23.7(2.1)</td>
<td>5.2(0.5)</td>
<td>6.8(1.4)</td>
<td>10.0(1.4)</td>
<td>14.1(2.1)</td>
</tr>
<tr>
<td>Distance moved by prey (mm)</td>
<td>1.7(0.1)</td>
<td>3.4(0.3)</td>
<td>1.1(0.2)</td>
<td>2.4(0.3)</td>
<td>2.9(0.3)</td>
</tr>
<tr>
<td>Time to maximum gape (ms)</td>
<td>13.3(0.4)</td>
<td>18.3(0.7)</td>
<td>14.7(0.9)</td>
<td>12.9(0.9)</td>
<td>18.2(1.0)</td>
</tr>
<tr>
<td>Duration of maximum gape (ms)</td>
<td>6.4(0.5)</td>
<td>10.5(0.9)</td>
<td>4.8(0.2)</td>
<td>6.3(0.5)</td>
<td>11.7(1.6)</td>
</tr>
<tr>
<td>Time to maximum premaxilla protrusion (ms)</td>
<td>13.1(0.4)</td>
<td>18.4(0.8)</td>
<td>14.4(0.9)</td>
<td>12.9(0.9)</td>
<td>18.7(1.2)</td>
</tr>
<tr>
<td>Time to start hyoid depression (ms)</td>
<td>7.6(0.3)</td>
<td>13.6(0.6)</td>
<td>9.8(0.9)</td>
<td>10.8(0.9)</td>
<td>11.2(1.0)</td>
</tr>
<tr>
<td>Time to maximum hyoid depression (ms)</td>
<td>16.8(0.6)</td>
<td>25.7(1.0)</td>
<td>16.9(1.1)</td>
<td>18.3(1.2)</td>
<td>25.1(1.5)</td>
</tr>
<tr>
<td>Duration of hyoid depression (ms)</td>
<td>30.1(1.5)</td>
<td>66.4(2.4)</td>
<td>36.2(3.3)</td>
<td>42.3(3.8)</td>
<td>53.8(5.1)</td>
</tr>
<tr>
<td>Time to capture (ms)</td>
<td>18.4(0.9)</td>
<td>19.9(1.0)</td>
<td>14.9(0.6)</td>
<td>14.5(0.8)</td>
<td>22.7(1.5)</td>
</tr>
<tr>
<td>Time to close mouth (ms)</td>
<td>11.6(0.7)</td>
<td>39.3(4.5)</td>
<td>20.1(2.5)</td>
<td>12.6(1.2)</td>
<td>44.3(8.4)</td>
</tr>
<tr>
<td>Total bite duration (ms)</td>
<td>31.2(1.1)</td>
<td>68.0(5.3)</td>
<td>39.6(3.2)</td>
<td>31.9(1.9)</td>
<td>74.2(9.8)</td>
</tr>
<tr>
<td>Total number of strikes</td>
<td>1.3(0.1)</td>
<td>1.1(0.0)</td>
<td>1.3(0.1)</td>
<td>1.2(0.1)</td>
<td>1.2(0.1)</td>
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</table>
Figure 4. Scatterplots of the distance moved by the prey versus the distance moved by the prey for feeding events of wild *M. salmoides floridanus* capturing mosquito fish and hatchery-reared *M. salmoides floridanus* capturing pellets within four size classes.
(p=<0.001 for both) and the interaction of diet and size class for PC axis I only (p=0.046).

Two-way ANOVAs for each kinematic variable indicated diet related differences for all variables except time to start hyoid depression, time to close the mouth, and total bite duration (Table III). Tukey post hoc tests show similar results as that found in the baseline capture, in that larger size classes typically have larger excursions, longer timing and duration values, and take fewer strikes than smaller individuals. Within a size class, wild bass had greater excursion distances than hatchery bass.

Predator-prey movement plots again show that, ram-capture is the dominant type of prey capture for both hatchery and wild bass feeding on mosquito fish. Although hatchery bass utilize a greater level of ram feeding while feeding on live mosquito fish than on pellets, wild individuals still use more ram in all size classes (Figure 4).

Prey capture and experience

Hatchery bass, feeding on mosquito fish prey, had similar feeding kinematics to wild bass of the same size class within five exposures (10-15 total captures per bass) (Table IV). A non-parametric Kruskal-Wallis ANOVA for all combined kinematic variables revealed differences in these times among size classes (d.f.=3; H=23.738; p=<0.001). Size classes 1 vs. 2 and 3 vs. 4, however, did not differ, and hatchery individuals in size classes 3 and 4 had feeding kinematics similar to wild bass more quickly than those in the two smaller size classes (Table IV).

Discussion

Baseline prey capture kinematics
Wild-caught juvenile largemouth bass feeding on *G. holbrooki* exhibited behaviors associated with ram feeding and high capture success. Strikes began with S-postured fast starts minimizing the prey’s reaction time to escape.
Table 3. ANOVA results for kinematic variables during prey capture events of wild and hatchery-reared *M. salmoides floridanus* capturing mosquito fish.  *p<0.05, **p<0.01

<table>
<thead>
<tr>
<th>Kinematic variable</th>
<th>Diet mean(SE)</th>
<th>Size class mean(SE)</th>
<th>p-value</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Wild</td>
<td>Hatchery</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>Diet</td>
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<td>Maximum gape distance (mm)</td>
<td>10.0(0.4)</td>
<td>8.7(0.3)</td>
<td>6.9(0.1)</td>
<td>9.1(0.2)</td>
<td>11.9(0.3)</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Maximum premaxilla protrusion (mm)</td>
<td>5.9(0.2)</td>
<td>5.5(0.2)</td>
<td>4.4(0.1)</td>
<td>5.6(0.1)</td>
<td>7.0(0.1)</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Maximum hyoid depression (mm)</td>
<td>5.7(0.2)</td>
<td>4.8(0.2)</td>
<td>3.5(0.1)</td>
<td>5.6(0.1)</td>
<td>6.6(0.2)</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Maximum head elevation (degrees)</td>
<td>50.0(0.7)</td>
<td>44.9(0.7)</td>
<td>45.0(1.0)</td>
<td>46.9(0.8)</td>
<td>50.0(0.9)</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Distance moved by predator (mm)</td>
<td>27.9(2.3)</td>
<td>16.0(1.0)</td>
<td>13.4(1.1)</td>
<td>20.1(1.4)</td>
<td>32.8(2.9)</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Distance moved by prey (mm)</td>
<td>1.9(0.2)</td>
<td>2.5(0.1)</td>
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<td>Time to maximum gape (ms)</td>
<td>14.0(0.4)</td>
<td>12.4(0.6)</td>
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<td>0.012*</td>
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<td>5.2(0.3)</td>
<td>9.5(0.7)</td>
<td>0.031*</td>
</tr>
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<td>Time to maximum premaxilla protrusion (ms)</td>
<td>13.9(0.4)</td>
<td>11.9(0.6)</td>
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<td>14.2(0.7)</td>
<td>14.0(0.6)</td>
<td>0.003**</td>
</tr>
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<td>Time to start hyoid depression (ms)</td>
<td>8.3(0.3)</td>
<td>8.9(0.5)</td>
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<td>9.1(0.5)</td>
<td>9.5(0.6)</td>
<td>0.435</td>
</tr>
<tr>
<td>Time to maximum hyoid depression (ms)</td>
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<td>17.4(0.8)</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Duration of hyoid depression (ms)</td>
<td>33.5(1.7)</td>
<td>26.6(0.8)</td>
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<td>28.3(1.1)</td>
<td>37.5(1.9)</td>
<td>&lt;0.001**</td>
</tr>
<tr>
<td>Time to capture (ms)</td>
<td>20.0(1.1)</td>
<td>16.7(0.7)</td>
<td>14.4(0.6)</td>
<td>17.9(0.7)</td>
<td>22.7(1.5)</td>
<td>0.003**</td>
</tr>
<tr>
<td>Time to close mouth (ms)</td>
<td>12.0(0.8)</td>
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<td>12.6(0.7)</td>
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<td>Total bite duration (ms)</td>
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<td>Total number of strikes</td>
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<td>1.6(0.1)</td>
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<td>1.1(0.1)</td>
<td>0.006**</td>
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</table>
Figure 5. Scatterplots of the distance moved by the prey versus the distance moved by the prey for feeding events of naïve hatchery-reared and experienced wild *M. salmoides floridanus* capturing mosquito fish within 3 size classes.
Table 4. Number of exposures to live prey required for capture kinematic measurements of hatchery-reared *M. salmoides floridanus* learning to feed on mosquito fish to become equivalent to wild *M. salmoides floridanus* capturing mosquito fish.

<table>
<thead>
<tr>
<th>Kinematic variable</th>
<th>Size class 1</th>
<th>Size class 2</th>
<th>Size class 3</th>
<th>Size class 4</th>
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<td>1</td>
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<tr>
<td>Maximum premaxilla protrusion (mm)</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Maximum hyoid depression (mm)</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Maximum head elevation (degrees)</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Distance moved by predator (mm)</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Distance moved by prey (mm)</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Time to maximum gape (ms)</td>
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<td>3</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Duration of maximum gape (ms)</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Time to maximum premaxilla protrusion (ms)</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Time to start hyoid depression (ms)</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Time to maximum hyoid depression (ms)</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Duration of hyoid depression (ms)</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Time to capture (ms)</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Time to close mouth (ms)</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total bite duration (ms)</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total number of strikes</td>
<td>5</td>
<td>5</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Mean number of exposures</td>
<td>3.2</td>
<td>3.4</td>
<td>2.0</td>
<td>1.6</td>
</tr>
</tbody>
</table>
(Weihs & Webb 1983, Porter & Motta 2004). The utilization of rapid kinematic variables and large buccal expansion serves multiple purposes. A fast and full expansion of the buccal cavity, could yield minimal obstruction of water flowing into the mouth and out through the gills during approach (Nyberg 1971), reducing the effects of drag, and facilitating compensatory suction (Van Damme & Aerts 1997). Large cranial excursions also result in an enlarged “catching area” (Norton 1991), and in the case of premaxillary protrusion, the jaws are brought closer in proximity to the prey (Ferry-Graham et al. 2001; Waltzek & Wainwright 2003). Additionally, a rapid closure of the mouth minimizes prey escape. This increased effort during the capture of elusive prey should be employed to maximize a predator’s energetic profitability (Bolnick & Ferry-Graham 2002). Other fishes, including the kelp greenling, *Hexagrammos decagrammus*, (Nemeth 1997), the blue-green damselfish, *Chromis viridis*, (Coughlin & Strickler 1990), and several cottid species (Norton 1991) have been documented to alter their feeding regimes towards this ram-dominated mode while capturing evasive prey.

Prey capture events of hatchery-reared *M. salmoides floridanus* feeding on pellets were characterized by a larger degree of suction than bites in which their wild counterparts capture elusive prey. Bass approached the pellets without assuming a specialized attack posture prior to a strike. Additionally, they traveled a distance during the strike that was approximately five times less than their wild counterparts in approximately the same amount of time. This behavior reduces the strength of bow wave formation in front of the fish’s mouth. Because the motion of this pressure wave acts in the opposite direction as flow into the buccal cavity, a decrease in its strength will yield a larger resultant degree of suction pressure (Ferry-Graham et al. 2003). Slower values of
timing variables (e.g., time to maximum gape and time to maximum hyoid depression) facilitate a longer duration of negative buccal pressure, resulting in less subambient pressure, and increasing the time taken to reach the minimum pressure (Svanbäck et al. 2002). These behaviors suggest that the fish have adopted a different feeding behavior for this non elusive food. Contrary to previous hypotheses (Muller et al. 1982; van Leeuwen & Muller 1984), Svanbäck et al. (2002) found that large excursions made during a bite were not strongly correlated with the level of subambient suction pressure. Large excursions of the buccal cavity and hyoid were not necessary to capture pellet food. Thus, the smaller excursions documented during the capture of pellets did not inhibit feeding. When the energetic savings of these small excursions and slow timings are paired with the near 100% capture success, hatchery bass feeding on pellets generally exhibit an energetically efficient technique for reaping the maximum benefit for their efforts (Bolnick & Ferry-Graham 2002).

Effects of size

Variables for timings and excursions were positively related to the total length of wild juvenile bass. The association between predator size and linear excursion distances can be attributed to geometric similarity of head morphology (Richard & Wainwright 1995; Hernández 2000). Longer values for duration variables for larger fishes have been observed in both bony fishes and elasmobranchs, and have been attributed to the negative relationship between the contraction speed of sarcomeres in the feeding musculature and body size (Richard & Wainwright 1995, Robinson & Motta 2002). Overall, these slower motions lead to a longer time to capture with size, but the success of the feeding sequence was unaltered, as the number of strikes required to capture prey was not related to size.
While hatchery bass feeding on pellets appeared to be constrained by geometric similarity and sarcomere physiology, this relationship was poorly defined due to a high degree of variability in the duration and timing of gape variables, which were short in size class 2 and very long in size class 3. The fast time to capture and short duration that the mouth is held open in size class 2 may be related to the natural development of aggressive behavior in largemouth bass, beginning at approximately 35mm $L_T$, a phenomenon which has been found to develop even under laboratory conditions (Brown 1985). For wild bass, the onset of this behavior has been correlated with the break up of sibling groups and the beginning of solitary life (Cole & Noakes 1980; Brown 1985). Bass in hatchery systems, however, are unable to disperse, which may lead to more aggression resulting in greater competition for food. Thus, the fast captures by bass in size class 2 may be most efficient for successful feeding. The extremely long time required to capture prey and to close the mouth seen in size class 3 defy explanation in the light of increased aggression. Prey capture kinematics can be influenced by the predator’s cranial morphology during ontogenetic development (Luczkovich et al. 1995), however, geometric shape analysis has demonstrated that there is no physical variation in the feeding osteology of hatchery bass in size classes 2 and 3. Alternatively, there is a small chance that the hatchery bass at this size class were siblings, leading to a founder’s effect. Genetics have been shown to affect both aggression levels (Berejikian et al. 1996) and feeding in fishes (Williamson 1983). Regardless of the source of variability in prey capture behavior employed by hatchery bass feeding on pellets, there was no difference in the number of strikes required to capture food across size, indicating a high success rate at all ages studied.
**Novel prey capture and learning with increased experience**

During their initial exposure to *G. holbrooki* prey, hatchery bass employed an intermediate degree of suction compared to wild bass capturing mosquito fish and hatchery bass feeding on pellets. Feeding events began with a pre-strike posture that was marked by a weak curvature of the body. Porter & Motta (2004) found that Florida gar, *Lepisosteus platyrhincus*, using a similar type of strike behavior, had slower attack velocities than great barracuda, *Sphyraena barracuda*, which use a more-compacted S-start like that of wild bass capturing mosquito fish. While the timings of capture variables were rapid, the small cranial excursions, possibly an artifact of feeding on non-elusive food (Janssen 1977; Vinyard 1982), are not beneficial in the capture of elusive prey (Norton 1991). This is reflected in the large number of strikes required to capture novel mosquito fish prey.

After five feeding exposures, involving capture of approximately 10-15 live mosquito fish per study animal, hatchery bass adopted capture behaviors kinematically similar to wild bass. The number of strikes required to successfully capture prey also decreased. Sundström & Johnsson (2001) found that after six exposures, hatchery-reared trout, *Salmo trutta*, had still not attained the level of foraging efficiency and prey consumption of wild trout. Ellis et al. (2002) noted that turbot, *Scophthalmus maximus*, raised in hatcheries developed these same traits to the level of wild turbot in nine days. The results of this study show that juvenile largemouth bass are behaviorally flexible and can adjust quickly compared to other species during feeding events and introduction of live, elusive prey to hatchery fish days prior to release may facilitate more natural feeding behaviors at least from a kinematic perspective.
Some aspects of feeding behavior, such as an attraction to live stimulus (Olla et al. 1998) and the snapping at prey during captures (Kieffer & Clogan 1992), are likely innate to predators such as the largemouth bass at any age. Yet, the ability to adjust these behaviors with increased exposure to prey appears to be related to the size of the fish. Many studies have attributed similar results to learning (see Brown & Laland 2001 for a review). Previous work with largemouth bass has shown no difference in the learning rate of stimulus avoidance between juveniles (145 mm $L_T$) and adults (Coble et al. 1985). Clear differences in the time required for hatchery-reared bass to adapt their feeding kinematics to those of their wild counterpart’s show that bass in size classes 1 and 2 are slower to adjust their capture behavior than individuals in size classes 3 and 4. Although learning is likely a large component of the behavioral change seen with experience, one must also consider the consequences of additional factors, including a more developed sensory-motor system with age (Colgan et al. 1986) and the interaction between fish size and the physical properties of the aquatic medium (Hernández 2000), both of which can greatly enhance feeding ability in larger individuals.

Implications for fisheries

Hatchery raised largemouth bass took only five exposures (10-15 captures) to assume prey capture kinematics of wild bass feeding on elusive prey. In a post-stock situation, the encounter rate of bass with live prey could be very high. However, competition for live prey by other wild bass could reduce the ability to encounter and capture live, elusive prey, therefore resulting in starvation and poor survival of hatchery raised fish. Due to the apparently short time of size class 4 bass to adopt predatory behaviors more akin to wild bass, fish of this size class should be fed elusive natural
prey, such as species that they would encountered in natural systems, for 10-15 days prior to release. This suggestion covers a conservative range because capture success in laboratory studies is often artificially increased (Nyberg 1971). Additionally, recent work with social enhancement of hatchery stocks by adding experienced individuals to tanks, have shown very promising results (Olla & Davis 1989; Sundström & Johnsson 2001; Brown & Laland 2002) in decreasing the time required for survival behaviors to be modified. The simultaneous implementation of these techniques may prove beneficial by further reducing the time required to improve prey capture.

In summary, the level of prey elusivity warrants largemouth bass to use different methods for prey capture in hatchery and wild environments. Wild bass utilize a ram-based feeding mode with quick motions and large excursions, and hatchery bass use slower movements and limited excursions to capture prey with some suction. In addition, hatchery-reared bass fed live prey for the first time captured prey less effectively than their wild counterparts, but adapted their behaviors to capture prey at the kinematic level of wild bass after five exposures. Experience, therefore, plays an important role in prey capture development and should be enforced in the rearing-techniques of hatchery fishes.

**Introduction**

The physical remodeling of the bones (Lanyon and Rubin 1985) and musculature (Goldspink and Howells 1974) associated with feeding has been found in response to specific characteristics of a fish’s diet, including prey hardness (Greenwood 1965), nutritional content (Wimberger 1993), and elusivity (Turingan et al. 1995). This change is especially prevalent in younger individuals, as their osteological development is not yet compete (Hinton and McNamara 1984) and generally results in a morphology that is better suited to the capture of a specific prey type (Wainwright 1999).

As is the common protocol for many fish species, Florida largemouth bass, *Micropterus salmoides floridanus*, reared in hatchery systems are maintained on inert pellet food, while their wild counterparts catch live prey, including insects, crustaceans, and small fishes (Huskey and Turingan 2001). Research on the feeding behaviors of these groups has demonstrated a higher degree of inertial suction employed by hatchery bass as compared to the ram-dominated prey capture of wild individuals. This study investigates the hypothesis that these alternate methods of capture, warranted by level of prey elusivity, should be associated with a concomitant change in the morphology of young hatchery bass. In addition, this potential deviation from the expected
developmental trajectory of wild individuals will be examined in relation to the poor post-stock survival of this species.

Materials and Methods

Specimens

Forty haphazardly chosen Florida largemouth bass (Lesuer), *M. salmoides floridanus*, were obtained from the Richloam Fish Hatchery (Sumter County, Florida) between May and July 2001. Individuals spanned a size range of 20-99mm TL, with 10 fish in each of four size classes (20-39, 40-59, 60-79, 80-99 mm TL; size classes 1, 2, 3, and 4, respectively). These specimens had a mixed genetic background, resulting from in-house matings of parents from one or a combination of Lake Cypress, Lake Johns (both Lake County, Florida), and Lake Okeechobee (Okeechobee, Glades, Hendry, St. Lucie, Martin and Palm Beach Counties, Florida).

An additional forty *M. salmoides floridanus* were collected from natural, unstocked systems, including Lake Walk-in-the-Water, Lake Mudd, and Lake Parker (all Polk County, Florida) via seining and electrofishing from May to August 2001. These bass could also be divided into size classes 1-4, each with ten individuals.

Finally, ten largemouth bass, five wild and five post-stocked, were collected by electrofishing from Lake Talquin (Gadsen and Leon Counties, Florida) in June 2002 and May 2003. These fish were larger in size, ranging from 120-135mm TL (size class 5). These stocked fish were previously released at approximately 100mm TL prior to capture.

All fish in size classes 1-4 were euthanatized with an overdose of tricine methanesulfonate (MS-222) and preserved in a buffered formalin solution. After one
week, the specimens were transferred to 70% isopropyl alcohol until further use. The bass from size class 5 were frozen in water.

**Skull shape analysis**

Geometric morphometric shape analysis was used to detect phenotypic variation in the skull during the development of hatchery bass, using their wild counterparts as a baseline. Five hatchery and five wild bass from each size class 1-4 were cleared with trypsin digestion, and their cartilage and bone were differentially stained (Dingerkus and Uhler 1977). The skulls of bass in size class 5, due to their larger size, were prepared using dermestid beetles, *Dermestes maculates*.

Fifteen landmarks (Table 5, Fig. 6) were chosen on the skull to give a detailed overview of head shape. The coordinate locations for these landmarks were digitized on lateral-view photographs for all 50 specimens using tpsDig. CoordGen6 was then used to transform the raw landmarks into Bookstein Coordinates (Bookstein 1991), which were scaled to a baseline with landmarks 2 and 10 as its endpoints. Procrustes superimposition technique was applied to the Bookstein Coordinates, using translation to match up the centroids and then rotation around this fixed point to best match homologous coordinates (Lele and Richtsmeier 2001). This process decreases the amount of variance associated with non-shape disparities in landmarks, such as geometric scale (Rohlf and Slice 1990; Kassam et al. 2003). Principal components analysis then was performed on the Bookstein coordinates, using a correlation matrix, in PCAGen6 in order to visualize differences within and between diet (hatchery/wild) and size class. The PCA also allowed us to follow any shape differences due to allometric growth during ontogeny.
Figure 6. Landmarks used to study shape change between hatchery and wild largemouth bass, *M. salmoides floridanus*, through ontogeny.
Table 5. Descriptions of landmark locations used in a geometric morphometric analysis of skull shape of *Micropterus salmoides floridanus*.

<table>
<thead>
<tr>
<th>Landmark</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>articulation of the opercle and hyomandibula</td>
</tr>
<tr>
<td>2</td>
<td>posterior-most point of the operculum</td>
</tr>
<tr>
<td>3</td>
<td>ventral articulation of the opercle and preopercle</td>
</tr>
<tr>
<td>4</td>
<td>articulation of the interopercle and subopercle</td>
</tr>
<tr>
<td>5</td>
<td>posterior-most aspect of the lower jaw</td>
</tr>
<tr>
<td>6</td>
<td>quadrate-articular joint</td>
</tr>
<tr>
<td>7</td>
<td>posterior-most region of the supramaxilla</td>
</tr>
<tr>
<td>8</td>
<td>posteroventral region of the maxilla</td>
</tr>
<tr>
<td>9</td>
<td>posterior-most region of the dentigerous arm of the premaxilla</td>
</tr>
<tr>
<td>10</td>
<td>anterior-most aspect of the lower jaw</td>
</tr>
<tr>
<td>11</td>
<td>anterior-most point of the dentigerous arm of the premaxilla</td>
</tr>
<tr>
<td>12</td>
<td>dorsal extent of the ascending process of the premaxilla</td>
</tr>
<tr>
<td>13</td>
<td>dorsal tip of the hyomandibula</td>
</tr>
<tr>
<td>14</td>
<td>dorsal-most point of the cranium</td>
</tr>
<tr>
<td>15</td>
<td>ventral-most point on the skull</td>
</tr>
</tbody>
</table>
A MANOVA was performed on the loading scores of the PCA to detect any effects of diet and size class (independent variables) on skull shape characteristics (dependent variables) in multivariate space. In addition, two-way ANOVAs were performed using the loading scores for each axis to detect the factors that had a strong influence on overall skull shape. To pinpoint where differences lie, resampling-based Goodall’s F-tests were performed for all combinations of diet and size class in TwoGroup6. An $\alpha$-level of $P=0.050$ was used to determine significance in this study. To avoid type II error, Bonferroni corrections were not utilized in analyses (Cabin & Mitchell 2000; Moran 2003).

The tpsDig program, by F.J. Rohlf, is available at http://life.bio.sunysb.edu/morph/. CoordGen6, PCAGen6, and TwoGroup6 by, H.D. Sheets, can be found at http://www2.canisius.edu/~sheets/morphsoft.html.

**Mechanical advantage**

Lever ratios were used to examine if a physical modification in morphology translated to a functionally relevant mechanical advantage during prey capture. Lower jaws were dissected out of the remaining 40 largemouth bass (5 hatchery and 5 wild individuals per size class 1-4). Jaws were bisected at the mandibular symphysis and photographed from a medial view. Pictures were then imported into Jandel SigmaScan Pro 4 (SPSS Inc.) to take lever arm measurements. Due to the anatomical complexity of the adductor mandibulae in *M. salmoides*, the endpoints of the closing in-lever arm have been fairly inconsistent in the literature. Therefore, three separate measurements were taken for this variable: from the center of the quadrate-articular (QA) joint to the 1) the
dorsoposterior margin of the coronoid process (Wainwright and Shaw 1999), 2) mid-point of the Aw subdivision insertion (Wainwright and Richard 1995), and 3) the insertion of a thick tendon from A2 and A3 subdivisions onto the medial aspect of the dentary (Fig. 7). The opening in-lever was measured from the QA joint to the attachment location of the interopercular ligament on the posterior margin of the retroarticular, while the out-lever was taken from the QA joint to the anterior-most tooth (Fig. 7).

The data sets were tested for normality and equality of variance using Kolmogorov-Smirnov and Levene median tests, respectively. Analyses of covariance (ANCOVA), with total length as the covariate, were performed to test for differences between hatchery and wild bass within each lever arm. Mechanical advantage ratios were taken by dividing each in-lever by the out-lever, and functional differences between these diets were examined with one-way ANOVAs within each ratio. Large ratios describe slow, force-based motions, while fast, velocity-based movements are associated with smaller values (Ferry-Graham and Lauder 2001). Finally, scaling was examined by calculating the slopes for plots of each lever arm and ratio versus the total length of the fish. To avoid type II error, Bonferroni corrections were not utilized in analyses (Cabin & Mitchell 2000; Moran 2003)

Results

Skull shape analysis

Quiver plots generated from principal components analysis indicate separation of skull shapes by a combination of age class and food type, with no complete separation by food type throughout all age classes. Skull shape loading positively on PC 1 (51% of variance) had a deeper, longer head, with oral jaw structures acting as the key
Figure 7. Medial view of a largemouth bass, *M. salmoides floridanus*, lower jaw illustrating the measurement points for lever arms.
Figure 8. Principal components analysis of Procrustes superimposed Bookstein coordinates of hatchery and wild largemouth bass, *M. salmoides floridanus*, in five size classes.
lengthening elements (Fig. 8). Characteristics that loaded positively on PC II (10% of variance) included an increased length of the ascending process of the premaxilla, a general deepening of the ventral skull landmarks, and a compression of the head at the dorsal-most landmark of the skull, point 14. Hatchery and wild individuals from size class 1 grouped together at intermediate and low values for PC I and II, respectively. Bass from both diets in size classes 2 and 3 and hatchery specimens from size class 4 clustered together at low PC I values and intermediate PC II values. Skull growth for wild individuals in size class 4 deviated at this point in development, loading intermediate and high for these axes. Morphologies then converge for size class 5, with both wild and hatchery fish falling high on PC I and intermediate on PC II (Fig. 8).

Combined scores for both PC axes indicated a clear separation in multivariate space (Wilk's-Λ F_{8,78}=3.028; p=<0.005). As determined by two-way ANOVAs, size class (p=<0.001) and a diet by size class interaction (p=0.002) were significant on PC I. Effects of diet (p=0.007) and size class (p=<0.001) were found on PC II. Goodall's F-test results indicate that the skull shapes of hatchery and wild *M. salmoides floridanus* within the same size class were the same in every case except size class 4 (Table 6).

*Mechanical advantage*

All size-removed lever arm measurements, except for the second closing in-lever, were significantly larger in wild *M. salmoides floridanus* when compared to their hatchery counterparts. The second closing in-lever was not different between these groups (Table 7). Mechanical advantage ratios were uniformly low for both hatchery and wild bass indicating a speed-efficient jaw opening and closing mechanism, with neither hatchery nor wild fish possessing a physical feeding advantage over the other
(Table 7). All lever arms scaled isometrically with the total length of the fish, while all of the mechanical advantage ratios showed no relationship with size, with slopes of zero (Table 7).

**Discussion**

*Phenotypic variation*

Skull development in wild largemouth bass followed a trajectory directed towards a morphology suited for ram feeding. Initially, individuals in size class 1 loaded at an intermediate level on PC I before loading more negatively in size class 2 and 3. This difference is due to the differential growth rates between the crania and oral jaws, a common phenomenon in fish development (Kelsch 1995; Koumoundouros et al. 1999; Gisbert et al. 2002). Size class 4 wild bass experienced a period of fast growth, which correlates to an ontogenetic diet change from benthic crustaceans to a majority of more evasive fishes (Keast 1985). These individuals developed long, more fusiform heads, with elongated jaw elements, including the dentary, maxilla, and the dentigerous arm of the premaxilla. Liem (1993) and Albertson et al. (2003) concluded that these characters are effective for ram capture, a strike mode commonly employed for elusive prey (Norton 1991). In addition, the longer ascending arm of the premaxilla enhances upper jaw protrusion, bringing the predator closer to its prey (Waltzek and Wainwright 2003). Overall, this specialization in design is linked to function during ontogeny, as bass in size class 4 have been found to employ the highest level of ram feeding among the four smallest size classes, with a mean RSI of 0.901 while capturing elusive mosquitofish, *Gambusia holbrooki*, prey. RSI values close to +1 indicate ram feeding, while those near -1 correspond to pure suction (Norton and Brainerd 1993). The skulls of bass in the
Table 6. Goodall’s F-test results for comparisons of skull shape of *M. salmoides floridanus* between each diet-size class group. Bolded values indicate comparisons of hatchery and wild bass within a single size class. *p<0.05, **p<0.01

<table>
<thead>
<tr>
<th></th>
<th>Hatchery sc1</th>
<th>Hatchery sc2</th>
<th>Hatchery sc3</th>
<th>Hatchery sc4</th>
<th>Hatchery sc5</th>
<th>Wild sc1</th>
<th>Wild sc2</th>
<th>Wild sc3</th>
<th>Wild sc4</th>
<th>Wild sc5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatchery sc1</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatchery sc2</td>
<td>0.010**</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatchery sc3</td>
<td>0.050*</td>
<td>0.190</td>
<td>0</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Hatchery sc4</td>
<td>0.040*</td>
<td>0.160</td>
<td>0.070</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hatchery sc5</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Wild sc1</td>
<td><strong>0.080</strong></td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild sc2</td>
<td>0.010**</td>
<td><strong>0.060</strong></td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild sc3</td>
<td>0.020*</td>
<td>0.100</td>
<td><strong>0.160</strong></td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.020*</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild sc4</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td><strong>0.010</strong></td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Wild sc5</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td><strong>0.600</strong></td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0.010**</td>
<td>0</td>
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</tbody>
</table>
Table 7. ANCOVA and ANOVA results comparing lever arms and mechanical advantage ratios, respectively, between hatchery and wild largemouth bass, *M. salmoides floridanus*. *p*≤0.05, **p*≤0.01

<table>
<thead>
<tr>
<th>Lever arm</th>
<th>Mean (SE) hatchery</th>
<th>Mean (SE) wild</th>
<th>Slope hatchery</th>
<th>Slope wild</th>
<th>d.f.</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Opening in-lever</td>
<td>1.087 (0.030)</td>
<td>1.198 (0.030)</td>
<td>0.91</td>
<td>1.10</td>
<td>1.37</td>
<td>6.605</td>
<td>0.014*</td>
</tr>
<tr>
<td>Closing in-lever1</td>
<td>2.296 (0.061)</td>
<td>2.514 (0.061)</td>
<td>0.90</td>
<td>1.10</td>
<td>1.37</td>
<td>6.426</td>
<td>0.016*</td>
</tr>
<tr>
<td>Closing in-lever2</td>
<td>1.609 (0.062)</td>
<td>1.771 (0.062)</td>
<td>0.95</td>
<td>1.20</td>
<td>1.37</td>
<td>3.388</td>
<td>0.074</td>
</tr>
<tr>
<td>Closing in-lever3</td>
<td>1.775 (0.047)</td>
<td>1.935 (0.047)</td>
<td>0.91</td>
<td>1.10</td>
<td>1.37</td>
<td>5.750</td>
<td>0.022*</td>
</tr>
<tr>
<td>Out-lever</td>
<td>8.130 (0.130)</td>
<td>8.875 (0.130)</td>
<td>0.91</td>
<td>1.10</td>
<td>1.37</td>
<td>16.287</td>
<td>&lt;0.001**</td>
</tr>
</tbody>
</table>

**Mechanical advantage**

<table>
<thead>
<tr>
<th></th>
<th>Mean (SE) hatchery</th>
<th>Mean (SE) wild</th>
<th>Slope hatchery</th>
<th>Slope wild</th>
<th>d.f.</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jaw opening ratio</td>
<td>0.133 (0.002)</td>
<td>0.135 (0.002)</td>
<td>0.00</td>
<td>0.00</td>
<td>1.38</td>
<td>0.420</td>
<td>0.521</td>
</tr>
<tr>
<td>Jaw closing ratio 1</td>
<td>0.281 (0.005)</td>
<td>0.282 (0.005)</td>
<td>0.00</td>
<td>0.00</td>
<td>1.38</td>
<td>0.069</td>
<td>0.795</td>
</tr>
<tr>
<td>Jaw closing ratio 2</td>
<td>0.196 (0.006)</td>
<td>0.196 (0.006)</td>
<td>0.00</td>
<td>0.00</td>
<td>1.38</td>
<td>&lt;0.001</td>
<td>0.989</td>
</tr>
<tr>
<td>Jaw closing ratio 3</td>
<td>0.220 (0.005)</td>
<td>0.217 (0.005)</td>
<td>0.00</td>
<td>0.00</td>
<td>1.38</td>
<td>0.187</td>
<td>0.668</td>
</tr>
</tbody>
</table>
largest size class 5 exhibit further morphological specialization towards ram feeding with a continued lengthening of the head. This is concomitant with the greater component of their diet being composed of more elusive prey (Huskey and Turingan 2001).

Hatchery bass followed a modified growth pattern of skull development compared to their wild counterparts. The path of the developmental trajectory was conserved between these two groups until size class 4, at which point normal development appeared to be retarded. The resultant morphology maintained by size class 4 hatchery bass, included a deeper, shorter head and a shorter ascending process of the premaxilla. A similar disruption of heterochrony was seen by Meyer (1987) in the cichlid Cichlasoma managuense maintained on inert flake food diets when compared to their nauplii-fed cohorts. Likewise, coho salmon, Oncorhynchus kisutch, reared in hatcheries were found to exhibit a reduced head length, possibly due to diet (Hard et al. 2000). This type of morphology is better suited for feeding with a larger component of suction (Albertson et al. 2003), allowing hatchery bass in size class 4 to capture inert pellet food with an average RSI value of 0.218. After release into natural systems, the hatchery bass probably reverted to ram capture of elusive live prey resulting in altered loading patterns on the developing bones such that the morphology of size class 5 hatchery fish converge with wild fish (Fig. 3). Meyer (1987) observed such a diet-induced convergence in morphology when, in the same experiment discussed above, the fishes with the flake food diet were switched to the nauplii diet. A similar convergence in head morphology has also been documented between wild and post-released Atlantic salmon, Salmo salar (Fleming et al. 1994).
Although diet has been linked to skull plasticity in previous studies (Wimberger 1991; Day et al. 1994; Hegrenes 2001), additional factors may have also affected the results of this study. Morphological abnormalities, for example, are more common in hatchery stocks than in wild fishes (Romanov 1984) due to a lack of natural selection in these systems (Barahona-Fernandes 1982). Similarly, nutritional differences in diet can affect trends in phenotypic plasticity (Wimberger 1993). Both of these factors, however, result in random patterns of morphological variation (Day et al. 1994) instead of those consistent with the expected changes due to prey capture and probably did not have a large influence over these results. Finally, the basis for phenotypic plasticity has historically been divided into two related components: environment and genetics (Brannon 1993). As the wild and hatchery bass used in this study are not genetic cohorts, it is likely that there was some effect of genotype on the data collected. As this factor was not specifically tested, it is not possible to know its exact impact on plasticity. The results of this study, however, are in accord with those from similar research, in which sibling groups are fed alternate diets (Meyer 1987; Wimberger 1991). Thus, it appears that environmental factors were probably dominant in shaping the observed plasticity (Turingan et al. 1995; Cutwa and Turingan 2000).

**Functional similarity**

Florida largemouth bass reared in hatchery systems are not physically constrained by diet-induced skull plasticity incurred during development. While the individual lever arm measurements were, in fact, different between the hatchery and wild groups (except for opening in-lever 2), all jaw elements in *M. salmoides*, as has been documented in other studies (Richard and Wainwright 1995; Wainwright and Shaw 1999), scale
isometrically with an increase in total length. Thus, once lever ratios are calculated, any
difference in function is effectively cancelled out, and both groups had velocity-based
mechanical advantage ratios. These findings are consistent with similar ratios calculated
for largemouth bass in previous studies (Richard and Wainwright 1995; Wainwright and
Richard 1995).

Although mechanical advantage investigations did not reveal any physical
constraints in jaw function between hatchery and wild bass, there are several unmeasured
factors that may have negative implications for hatchery bass survival. Diet-regulated
feeding mode, for example, has been thought to influence body shape in Geophagus
cichlids (Wimberger 1992). Ram feeders, such as M. salmoides floridanus, are fusiform
in shape and possess a low aspect-ratio caudal fin (Norton and Brainerd 1993). Body
shape can be closely related to prey capture (Webb 1984), and hence, a large change from
this specialized form could have implications for successful feeding by hatchery-reared
bass. Furthermore, the mass of the adductor mandibulae muscle has been correlated to
diet, despite a lack of lever arm significance (Cutwa and Turingan 2000), demonstrating
that these morphological aspects can be independent and exert individual effects. Finally,
research on the plasticity of neural development in hatchery-reared rainbow trout, O.
mykiss, has shown that cultured fishes have underdeveloped regions of the brain,
including the optic tectum and telencephalon, which are related to feeding (Marchetti and
Nevitt 2003). Given these considerations, diet-induced plasticity has the potential to
introduce physical constraints to aspects of prey capture in anatomical regions other than
the oral jaws.
**Implications for fisheries**

The functional mechanisms of feeding investigated in this study did not demonstrate physical constraints in the use of the lower jaw during prey capture. It is likely, however, that this species is behaviorally constrained. This stems from a lack of experience with live prey capture in hatchery systems (Colgan et al. 1986). It has been found that hatchery-reared Florida largemouth bass utilized slow prey capture kinematics with small cranial excursions to capture pellet food. Wild bass, however, obtained live prey with rapid motions and large excursions. When the hatchery bass were exposed to live prey for the first time, they used faster movements than their wild counterparts, coupled with small excursion distances, yielding a low level of capture success. Thus, despite the fact that there is an equal degree morphologically-based potential function between these groups, hatchery bass are only conditioned to exploit a lesser, realized function. After five exposures to live prey (2-3 capture events per exposure), however, hatchery bass used capture kinematics identical to wild individuals. These results show both the high degree of behavioral plasticity inherent to these animals and the need to expose Florida largemouth bass to live prey items while in the hatchery. This would minimize the difference in experience of capturing live prey between wild and hatchery bass, increasing the chances of post-stock survival in this species.

The results of this study should not be directly applied to other fisheries, as the degree of inducible phenotypic plasticity can vary among species (Day et al. 1994) due to differences in the level of developmental canalization (Meyer 1987). Additionally, many hatchery species show allometric growth of the cranial and mouth regions (Kelsch 1995; Koumoundouros et al. 1999; Gisbert et al. 2002). Thus, jaw plasticity in other species
could potentially place physical limitations on hatchery fishes during feeding. Behavioral plasticity can also vary among species (Coble et al. 1985). Ultimately, the functional implications of prey elusivity on skull development should be investigated at the species level, as both phenotypic and behavioral plasticity are factors that could affect the post-stock survival of hatchery fishes.
References


Loska, P.M. (1982). A literature review on the stocking of black basses (Micropterus spp.) in reservoirs and streams. Georgia Department of Natural Resources, Game and Fish Division, Atlanta.


