

A comparison of prey capture kinematics in hatchery and wild *Micropterus salmoides floridanus*: effects of ontogeny and experience

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Analysis of high-speed videography demonstrated that juvenile wild Florida largemouth bass *Micropterus salmoides floridanus* captured live prey with very rapid movements and large excursions. Hatchery fish of the same age, raised on pelleted feed, however, used slower kinematics with smaller excursions, yielding strikes with a higher degree of 'suction'. Capture events of hatchery Florida largemouth bass fed live prey for the first time were characterized by movements that had smaller excursion measurements than wild fish and resulted in a decreased level of capture success. After five exposures to elusive mosquitofish *Gambusia holbrooki*, hatchery Florida largemouth bass adapted their behaviour to capture prey at the kinematic level of wild fish.

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Key words: *Centrarchidae*; fisheries; learning; ram-suction index; survival.

INTRODUCTION

Naïvety 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). Feeding ecology studies have found that these fishes often consume pellet-like items, such as stones, rather than pursuing live prey (Ersbak & Haase, 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 with 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 centrarchid family (Nyberg, 1971). Due to their popularity as a sport fish, they have been cultured and stocked in the U.S. for >100 years (Rosenblum

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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 <1% (Porak *et al.*, 2002).

The present study examined this problem in light of prey capture kinematics. By quantifying capture behaviour, any differences in the discrete elements of prey capture between hatchery and wild Florida largemouth bass *Micropterus salmoides floridanus* (LeSueur) (Bailey & Hubbs, 1949) could be determined. The following questions were addressed: (1) How do the 'baseline' capture kinematics (*i.e.* hatchery Florida largemouth bass feeding on pelleted foods and wild individuals capturing live fish prey) differ between hatchery and wild fish? (2) How do these 'baseline' capture kinematics of wild Florida largemouth bass compare to those of hatchery fish feeding on novel live prey? (3) How long does it take for hatchery Florida largemouth 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 from each of the four size classes under investigation (20–39, 40–59, 60–79, 80–99 mm total length L_T ; size classes 1, 2, 3, and 4, respectively) were collected at the Richloam Fish Hatchery (Sumter County, Florida). These specimens were spawned by fish 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 fish are released at *c.* 100 mm L_T . Forty wild Florida largemouth bass from each size class were also collected from Lake Walk-in-the-Water using a seine and from Lakes Mudd and Parker (all Polk County, Florida) by electrofishing from May to August 2001.

The specimens were housed at the University of South Florida's aquarium facility, with wild Florida largemouth bass kept at densities that approximated those found during collection (0.01 to 0.05 g biomass l^{-1}), and hatchery fish in separate tanks at 6 g biomass l^{-1} , typical of hatcheries. Density levels were regulated by partitioning off an appropriate-sized section of the tank. As is typical protocol in Florida, hatchery fish in size class 1 were fed at a rate of 17 g crumble (BioDiet Trainer) per kg of biomass per day, while size classes 2, 3 and 4 were fed on 1.5 mm pellets (BioDiet Grower) at rates of 7.5, 10, and 15% of biomass day^{-1} , respectively. Wild Florida largemouth bass were maintained on a diet of mosquitofish *Gambusia holbrooki* (Girard), with body depths of *c.* 40–60% of the maximum vertical gape of the Florida largemouth 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 12 L : 12 D cycle was maintained and water temperature was 24° C (Wintzer & Motta, 2004). All maintenance and experiments were performed with University of South Florida Institutional Animal Care and Use Committee approval (#2066). Additionally, the experimental design of this study attempted to minimize the number of live prey used (Huntingford, 1984)

VIDEOGRAPHY

In an effort to encourage active feeding during filming sessions, food was withheld from both types of fish for a 24 h period prior to filming. Feeding sequences were filmed in the holding tanks at 500 fields s^{-1} 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 analysed filming events.

As Florida largemouth 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 $6.5 \times 4.0 \times 6.5$ cm section of the aquarium using a piece of clear perforated Plexiglass, so that the individual could still receive visual and chemical cues from the other fish in the tank. This partitioned section maintained an appropriate stocking density.

For each filming event of baseline feeding by Florida largemouth bass in size class 1, a single mosquitofish for wild Florida largemouth bass, or pellet for hatchery fish, 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 mosquitofish or pellet and to ensure the focal animal captured a prey or food item. Care was taken to note which Florida largemouth bass consumed the prey items to avoid satiation effects (Sass & Motta, 2002). A single prey capture was filmed from 15 Florida largemouth bass per four size classes and diet (mosquitofish and pellet), for a total of 120 captures.

To investigate the ability of hatchery fish to feed on novel live prey, the hatchery fish from the previous study were subsequently filmed during their initial experience capturing mosquitofish 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 prey capture from 12 Florida largemouth bass in size class 2 was recorded, while 15 bites were recorded from each of size class 3 and 4, yielding a total of 42 prey capture events. Ideally, the converse design with wild Florida largemouth 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, five hatchery-raised fish from each size class were removed from the tanks after the novel prey filming had been completed. Fish in the same size class were housed together in smaller tanks, to maintain appropriate hatchery densities. Prey capture on live mosquitofish 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 (two to three mosquitofish per Florida largemouth bass per filming day).

VIDEO ANALYSIS

Successful feeding sequences were analysed 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 travelled by the bass from the start of mandible depression (time zero) until prey capture; (6) distance moved by the prey, the total distance travelled 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 maintained; (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; (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. Ln transformations were applied to non-normal data sets. The data were regressed against L_T 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 Florida largemouth bass to capture live mosquitofish. Thus, this size class was omitted from statistical analyses for that experiment. Additionally, only 12 hatchery Florida largemouth bass in size class 2 successfully captured mosquitofish. In this case, the data generation function of SYSTAT 10 (SPSS Inc.) was utilized to create three 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 (PC) 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. These axes were chosen because they explained the greatest amount of variance for these data sets, while the impact of the remaining axes was negligible. 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. Bonferroni corrections were not used during data analysis in order to decrease the chance of making type II errors (Cabin & Mitchell, 2000; Moran, 2003). An α -level of $P = 0.05$ was used to determine differences in all statistics for this study.

Plots of the distance travelled by the predator against the distance travelled by the prey were created to visualize movement and to examine the feeding mode of these fish. In addition, a calculation of the degree of strike mode (Sass & Motta, 2002) was made for each individual using the 'ram-suction' index (I_{RS}) formula from Norton & Brainerd (1993): $I_{RS} = (D_{\text{predator}} - D_{\text{prey}}) (D_{\text{predator}} + D_{\text{prey}})^{-1}$, where D_{predator} is the distance moved by the predator and D_{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 I_{RS} value of +1. The opposite situation is termed pure 'suction' and has an I_{RS} 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 paired *t*-tests were performed within each size class. These analyses compared each kinematic variable, using all five prey captures on a single successful filming day (all five fish feeding), against five randomly chosen bites from the wild Florida largemouth bass data set of the appropriate size class. Wild *M. s. floridanus* were considered to be the efficiency standard against which to compare inexperienced hatchery fish. These data sets were compared at every filming date until the kinematic variables were no longer statistically different between wild and hatchery fish. 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 Florida largemouth 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 Florida largemouth bass capturing mosquitofish began the strike with an 'S'-start, had shorter timing and duration variables, and typically greater values for excursions than hatchery fish feeding on pellets, although the distance moved by the food item was greater for hatchery fish. Additionally, wild Florida largemouth bass struck at live prey more times before capture than hatchery fish capturing pellets [Fig. 1(a) and Tables I(a) and II]. Separation was clear in multivariate space (Wilk's- Λ $F_{6,222}$, $P < 0.001$), and significant effects of diet ($P \leq 0.001$), size class ($P \leq 0.001$) 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 three of the four 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 showed that larger Florida largemouth bass generally made greater excursions and had longer timing and duration values. Within a size class, wild fish usually had greater excursion distances and shorter timing and duration values than hatchery bass (Fig. 2). Also, very short timing and duration measurements for gape variables were recorded for hatchery fish in size class 2, while long timing and duration values of these same variables were observed for hatchery fish in size class 3 (Fig. 2).

While both wild and hatchery Florida largemouth bass generally feed *via* ram-capture, hatchery fish feeding on pellets utilized 'suction' to a higher degree at all size classes. Wild fish used more ram as they grew larger, while hatchery fish employed the highest level of ram feeding at the smallest size (Fig. 3).

CAPTURE OF NOVEL PREY

Data for both experienced wild and naïve hatchery Florida largemouth bass feeding on mosquitofish were different in multivariate space (Wilk's- Λ $F_{4,166}$, $P < 0.033$) [Fig. 1(b)]. Hatchery fish typically utilized a weak curvature of the body as a strike posture, had smaller distances for excursion variables, smaller values for timing and duration measurements (probably as a result of the small excursions), and performed more strikes to capture their prey than wild fish [Tables I(b) and III]. Two-way ANOVAs on PC axes I and III showed an effect of diet ($P < 0.001$ for both) and the interaction of diet and size class for PC axis I only ($P = 0.046$). Some of these trends for hatchery fish capturing live prey were different to those while capturing pellets. Although the small excursion distances were maintained during both diet treatments, capture events by

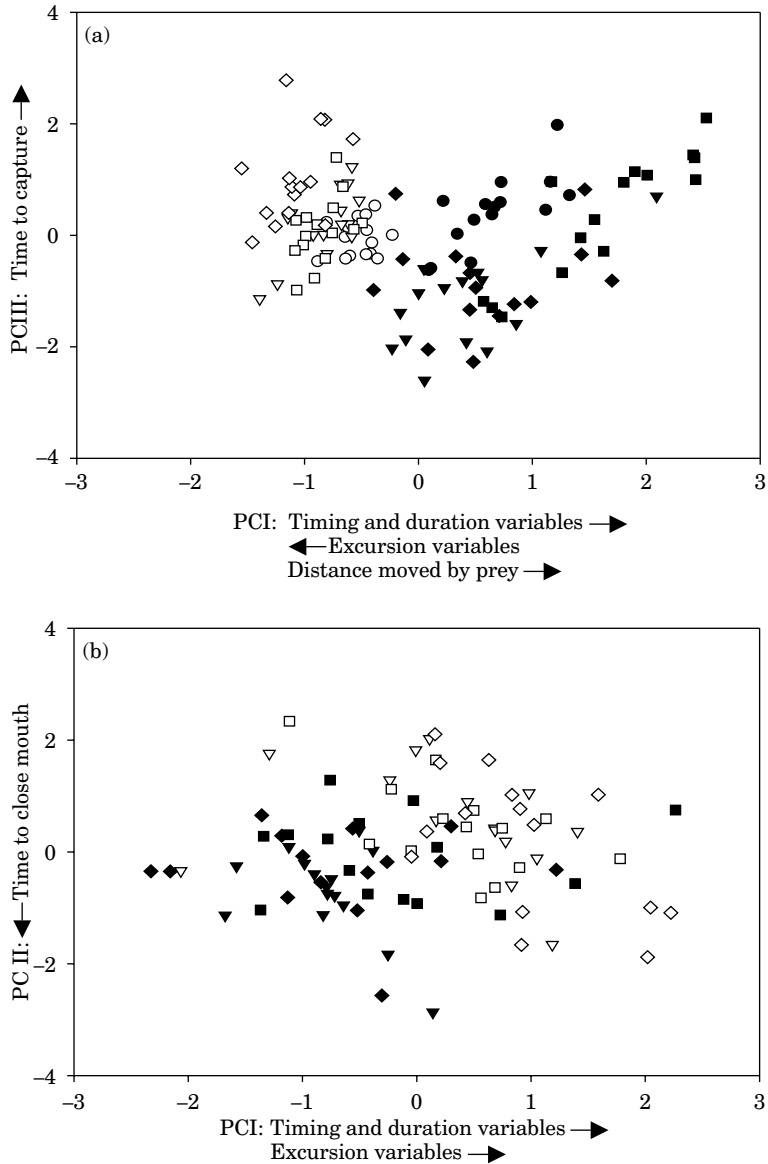


FIG. 1. Principle components analysis of kinematic variables for feeding events of (a) wild *Micropterus salmoides floridanus* capturing mosquito fish and hatchery-reared *M. s. floridanus* capturing pellets and (b) naïve hatchery-reared and experienced wild *M. s. floridanus* capturing mosquito fish. Data for fish in size class 1 are not included in (b), as hatchery fish could not catch live prey at this age. (○, ▽, □, ◇: wild Florida largemouth bass size classes 1, 2, 3 and 4, respectively; ●, ▼, ■, ◆: hatchery fish size classes 1, 2, 3 and 4, respectively)

hatchery Florida largemouth bass involving pellets had longer timing and duration values and required fewer strikes.

Two-way ANOVAs for each kinematic variable indicated diet related differences for all variables except time to start hyoid depression, time to close the

TABLE I. Principal component loading scores for feeding events of (a) wild *Micropterus salmoides floridanus* capturing mosquito fish and hatchery-reared *M. s. floridanus* capturing pellets and (b) wild and hatchery-reared *M. s. floridanus* capturing mosquito fish. Values in bold indicate axis assignment

(a) Kinematic variable	Factor 1	Factor 3
Time to capture (ms)	0.842	-0.026
Time to maximum premaxilla protrusion (ms)	0.811	0.126
Time to maximum hyoid depression (ms)	0.808	0.158
Time to maximum gape (ms)	0.791	0.090
Distance moved by predator (mm)	0.687	0.296
Total bite duration (ms)	0.677	-0.676
Maximum gape distance (mm)	0.641	0.152
Duration of hyoid depression (ms)	0.587	-0.239
Maximum hyoid depression (mm)	0.585	0.056
Time to start hyoid depression (ms)	0.489	0.099
Distance moved by prey (mm)	0.393	0.186
Maximum head elevation (degrees)	0.449	0.308
Maximum premaxilla protrusion (mm)	0.500	0.040
Duration of maximum gape (ms)	0.408	-0.240
Time to close mouth (ms)	0.058	-0.871
Per cent of total variance explained	37.128	11.698
(b) Kinematic variable	Factor 1	Factor 2
Time to maximum hyoid depression (ms)	0.847	0.239
Duration of hyoid depression (ms)	0.834	-0.124
Maximum gape distance (mm)	-0.823	0.492
Maximum hyoid depression (mm)	-0.819	0.360
Total bite duration (ms)	0.814	0.248
Time to maximum gape (ms)	0.764	0.458
Time to maximum premaxilla protrusion (ms)	0.758	0.447
Time to start hyoid depression (ms)	0.738	0.155
Time to close mouth (ms)	0.731	0.159
Distance moved by predator (mm)	-0.702	0.519
Maximum premaxilla protrusion (mm)	-0.595	0.513
Duration of maximum gape (ms)	0.578	0.300
Maximum head elevation (degrees)	-0.531	0.243
Distance moved by prey (mm)	0.432	-0.346
Time to capture (ms)	0.365	0.697
Per cent of total variance explained	49.648	15.002

mouth and total bite duration (Table III). Tukey *post hoc* tests showed similar results as that found in the baseline capture, in that larger size classes typically had larger excursions, longer timing and duration values and took fewer strikes than smaller individuals. Within a size class, wild fish had greater excursion distances than hatchery fish.

Plots of distances moved by predator and prey again showed that ram-capture was the dominant type of prey capture for both hatchery and wild fish feeding on mosquitofish. Although hatchery Florida largemouth bass utilized a greater level

TABLE II. ANOVA results for kinematic variables during prey capture events of wild *Micropterus salmoides floridanus* capturing mosquito fish and hatchery-reared *M. s. floridanus* feeding on pellets

Kinematic variable	Diet				Size class				P
	Mean \pm s.e.		Hatchery		Mean \pm s.e.		Diet		
	Wild	1	2	3	4	Size class	Interaction		
Maximum gape distance (mm)	8.7 \pm 0.4	5.0 \pm 0.3	4.1 \pm 0.2	5.5 \pm 0.3	7.4 \pm 0.4	10.4 \pm 0.6	<0.001**	<0.001**	<0.001**
Maximum premaxilla protrusion (mm)	5.3 \pm 0.2	4.5 \pm 0.2	3.3 \pm 0.1	4.3 \pm 0.2	5.2 \pm 0.1	6.8 \pm 0.1	<0.001**	0.003**	<0.001**
Maximum hyoid depression (mm)	4.8 \pm 0.2	2.4 \pm 0.1	1.8 \pm 0.1	3.0 \pm 0.2	4.2 \pm 0.4	5.4 \pm 0.3	<0.001**	0.303	<0.001**
Maximum head elevation (degrees)	47.6 \pm 0.8	43.6 \pm 0.8	41.5 \pm 0.7	46.3 \pm 1.1	44.5 \pm 1.0	50.0 \pm 1.2	<0.001**	0.009**	0.022*
Distance moved by predator (mm)	23.7 \pm 2.1	5.2 \pm 0.5	6.8 \pm 1.4	10.0 \pm 1.4	14.1 \pm 2.1	26.9 \pm 3.7	<0.001**	0.001**	<0.001**
Distance moved by prey (mm)	1.7 \pm 0.1	3.4 \pm 0.3	1.1 \pm 0.2	2.4 \pm 0.3	2.9 \pm 0.3	3.8 \pm 0.4	<0.001**	0.022*	<0.001**
Time to maximum gape (ms)	13.3 \pm 0.4	18.3 \pm 0.7	14.7 \pm 0.9	12.9 \pm 0.9	18.2 \pm 1.0	17.3 \pm 0.7	<0.001**	<0.001**	0.006**
Duration of maximum gape (ms)	6.4 \pm 0.5	10.5 \pm 0.9	4.8 \pm 0.2	6.3 \pm 0.5	11.7 \pm 1.6	10.9 \pm 0.8	<0.001**	0.018*	<0.001**
Time to maximum premaxilla protrusion (ms)	13.1 \pm 0.4	18.4 \pm 0.8	14.4 \pm 0.9	12.9 \pm 0.9	18.7 \pm 1.2	17.1 \pm 0.7	<0.001**	<0.001**	0.005**
Time to start hyoid depression (ms)	7.6 \pm 0.3	13.6 \pm 0.6	9.8 \pm 0.9	10.8 \pm 0.9	11.2 \pm 1.0	10.7 \pm 0.6	<0.001**	0.505	<0.001**
Time to maximum hyoid depression (ms)	16.8 \pm 0.6	25.7 \pm 1.0	16.9 \pm 1.1	18.3 \pm 1.2	25.1 \pm 1.5	24.7 \pm 1.1	<0.001**	0.025*	0.165
Duration of hyoid depression (ms)	30.1 \pm 1.5	66.4 \pm 2.4	36.2 \pm 3.3	42.3 \pm 3.8	53.8 \pm 5.1	60.6 \pm 3.9	<0.001**	0.821	0.067
Time to capture (ms)	18.4 \pm 0.9	19.9 \pm 1.0	14.9 \pm 0.6	14.5 \pm 0.8	22.7 \pm 1.5	24.3 \pm 1.3	0.356	0.002**	<0.001**
Time to close mouth (ms)	11.6 \pm 0.7	39.3 \pm 4.5	20.1 \pm 2.5	12.6 \pm 1.2	44.3 \pm 8.4	24.7 \pm 3.6	<0.001**	<0.001**	<0.001**
Total bite duration (ms)	31.2 \pm 1.1	68.0 \pm 5.3	39.6 \pm 3.2	31.9 \pm 1.9	74.2 \pm 9.8	52.8 \pm 4.3	<0.001**	<0.001**	<0.001**
Total number of strikes	1.3 \pm 0.1	1.1 \pm 0.0	1.3 \pm 0.1	1.2 \pm 0.1	1.2 \pm 0.1	1.0 \pm 0.0	0.027*	0.135	0.587

*, $P \leq 0.050$, **, $P \leq 0.001$.

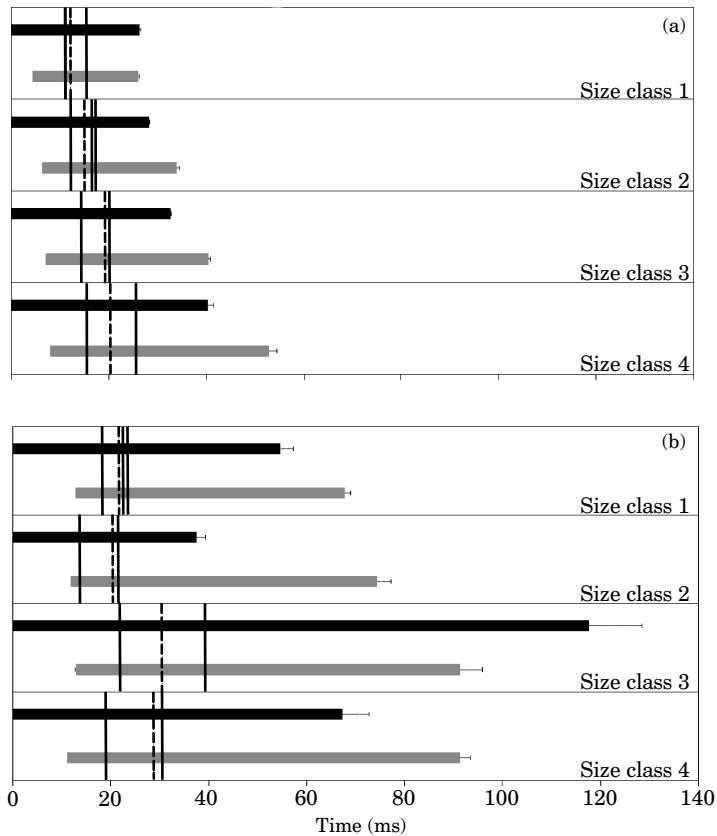


FIG. 2. Kinematic profiles of select variables for (a) wild *Micropterus salmoides floridanus* capturing mosquito fish and (b) hatchery-reared *M. s. floridanus* capturing pellets within four size classes. Variables include total bite duration (■), duration of hyoid depression (▒), maximum gape distance (—) and maximum hyoid depression (----).

of ram feeding while feeding on live mosquitofish than on pellets, wild individuals still used more ram in all size classes (Fig. 4).

PREY CAPTURE AND EXPERIENCE

Hatchery Florida largemouth bass, feeding on mosquitofish, had similar feeding kinematics to wild fish of the same size class within 10–15 total captures per fish (Table IV). A non-parametric Kruskal–Wallis ANOVA for all combined kinematic variables revealed differences in these times among size classes (d.f. = 3, $P < 0.001$). Size classes 1 v. 2 and 3 v. 4, however, did not differ. In addition, hatchery individuals in size classes 3 and 4 assumed more rapidly the feeding kinematics of wild fish than those in the two smaller size classes (Table IV).

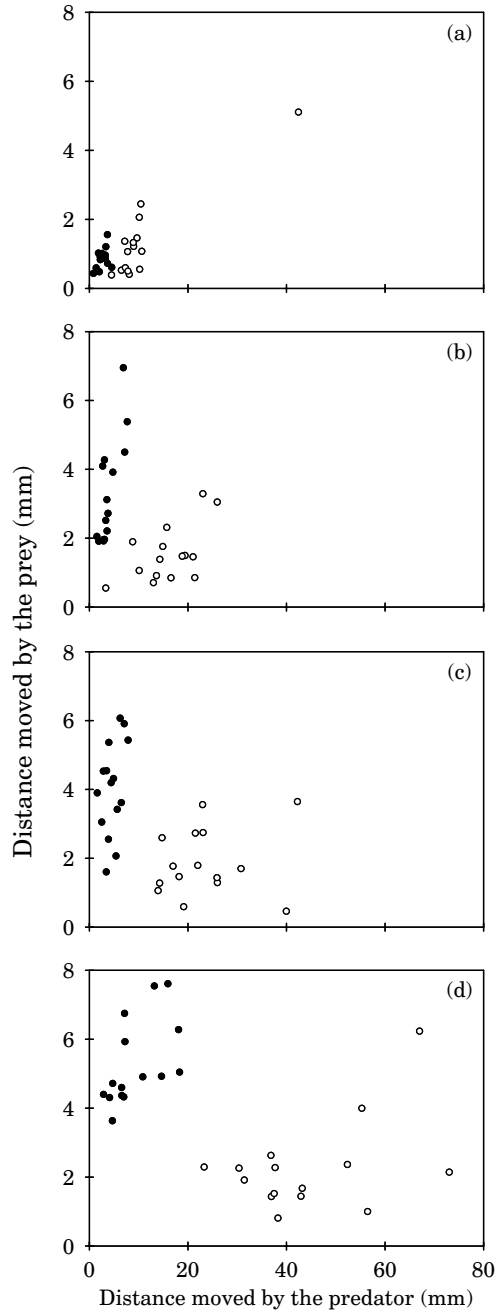


FIG. 3. Scatter plots of the distance moved by wild (○) and hatchery *Micropterus salmoides floridanus* (●) and the distance moved by the prey for feeding events of wild *M. s. floridanus* capturing mosquito fish and hatchery-reared *M. s. floridanus* capturing pellets within four size classes: (a) 1, (b) 2, (c) 3 and (d) 4. The mean 'ram-suction' indices (I_{RS}) were: (a) wild 0.789 and hatchery 0.504, (b) wild 0.819 and hatchery 0.092, (c) wild 0.845 and hatchery 0.069, and (d) wild 0.901 and hatchery 0.218.

TABLE III. ANOVA results for kinematic variables during prey capture events of wild and hatchery-reared *Micropterus salmoides floridanus* capturing mosquito fish

Kinematic variable	Diet				Size class			P
	Wild		Hatchery		Mean \pm S.E.			
	2	3	4	Diet	Size class	Interaction		
Maximum gape distance (mm)	10.0 \pm 0.4	8.7 \pm 0.3	6.9 \pm 0.1	9.1 \pm 0.2	11.9 \pm 0.3	<0.001**	0.031*	<0.001**
Maximum premaxilla protrusion (mm)	5.9 \pm 0.2	5.5 \pm 0.2	4.4 \pm 0.1	5.6 \pm 0.1	7.0 \pm 0.1	<0.001**	0.160	<0.001**
Maximum hyoid depression (mm)	5.7 \pm 0.2	4.8 \pm 0.2	3.5 \pm 0.1	5.6 \pm 0.1	6.6 \pm 0.2	<0.001**	<0.001**	0.523
Maximum head elevation (degrees)	50.0 \pm 0.7	44.9 \pm 0.7	45.0 \pm 1.0	46.9 \pm 0.8	50.0 \pm 0.9	<0.001**	0.684	0.002**
Distance moved by predator (mm)	27.9 \pm 2.3	16.0 \pm 1.0	13.4 \pm 1.1	20.1 \pm 1.4	32.8 \pm 2.9	<0.001**	0.469	0.124
Distance moved by prey (mm)	1.9 \pm 0.2	2.5 \pm 0.1	1.8 \pm 1.4	2.3 \pm 0.2	2.4 \pm 0.2	0.011*	0.583	0.447
Time to maximum gape (ms)	14.0 \pm 0.4	12.4 \pm 0.6	11.0 \pm 0.5	14.6 \pm 0.7	14.1 \pm 0.6	0.012*	0.030*	0.193
Duration of maximum gape (ms)	7.0 \pm 0.6	6.1 \pm 0.4	5.0 \pm 0.2	5.2 \pm 0.3	9.5 \pm 0.7	0.031*	<0.001**	0.612
Time to maximum premaxilla protrusion (ms)	13.9 \pm 0.4	11.9 \pm 0.6	10.5 \pm 0.5	14.2 \pm 0.7	14.0 \pm 0.6	0.003**	0.025*	0.259
Time to start hyoid depression (ms)	8.3 \pm 0.3	8.9 \pm 0.5	7.2 \pm 0.3	9.1 \pm 0.5	9.5 \pm 0.6	0.435	0.247	0.223
Time to maximum hyoid depression (ms)	18.4 \pm 0.6	14.4 \pm 0.6	14.0 \pm 0.6	17.8 \pm 0.8	17.4 \pm 0.8	<0.001**	0.018*	0.084
Duration of hyoid depression (ms)	33.5 \pm 1.7	26.6 \pm 0.8	24.1 \pm 0.9	28.33 \pm 1.1	37.5 \pm 1.9	<0.001**	0.245	0.163
Time to capture (ms)	20.0 \pm 1.1	16.7 \pm 0.7	14.4 \pm 0.6	17.9 \pm 0.7	22.7 \pm 1.5	0.003**	0.641	0.010**
Time to close mouth (ms)	12.0 \pm 0.8	13.7 \pm 0.5	12.0 \pm 0.8	12.6 \pm 0.7	14.0 \pm 0.9	0.081	0.898	0.362
Total bite duration (ms)	33.0 \pm 1.3	32.2 \pm 0.9	27.9 \pm 0.8	32.3 \pm 0.9	37.7 \pm 1.5	0.497	0.701	0.326
Total number of strikes	1.2 \pm 0.8	1.6 \pm 0.1	1.7 \pm 0.2	1.4 \pm 0.1	1.1 \pm 0.1	0.006**	0.110	0.133

*, $P \leq 0.050$; **, $P \leq 0.001$.

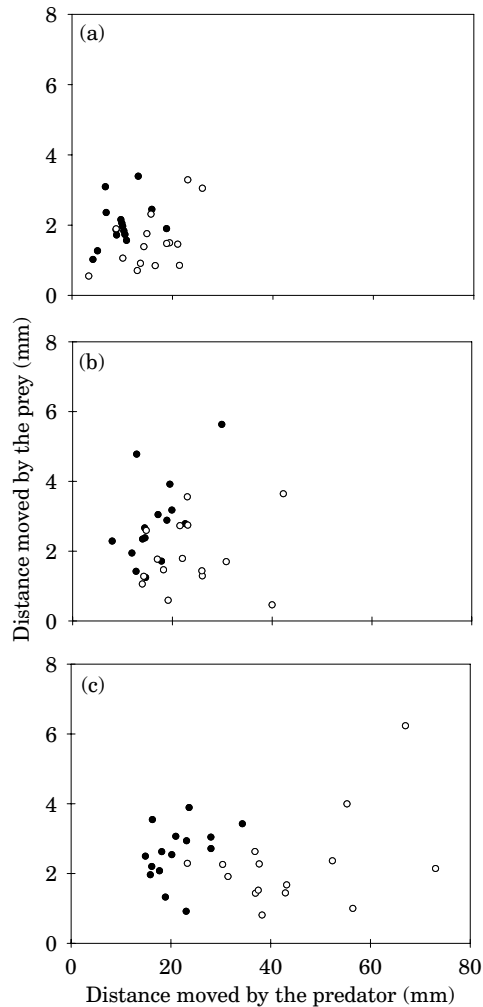


FIG. 4. Scatter plots of the distance moved by wild (○) and hatchery *Micropterus salmoides floridanus* (●) and the distance moved by the prey for feeding events of naïve hatchery-reared and experienced wild *M. s. floridanus* capturing mosquito fish within three size classes: (a) 2, (b) 3 and (c) 4. The mean 'ram-suction' indices (I_{RS}) were: (a) wild 0.819 and hatchery 0.618, (b) wild 0.845 and hatchery 0.709, and (c) wild 0.901 and hatchery 0.781.

DISCUSSION

BASELINE PREY CAPTURE KINEMATICS

Wild-caught juvenile Florida largemouth bass feeding on *G. holbrooki* exhibited behaviours associated with ram feeding and high capture success. Strikes began with S-postured fast starts minimizing the prey's reaction time to escape (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

TABLE IV. Number of exposures to live prey required for capture kinematic measurements of hatchery-reared *Micropterus salmoides floridanus* learning to feed on mosquito fish to become equivalent to wild *M. s. floridanus* capturing mosquito fish. Equivalence was determined by paired *t*-tests

Kinematic variable	Number of exposures to feed like wild fish			
	Size class			
	1	2	3	4
Maximum gape distance (mm)	3	3	1	1
Maximum premaxilla protrusion (mm)	3	3	1	1
Maximum hyoid depression (mm)	3	3	4	3
Maximum head elevation (degrees)	3	4	1	1
Distance moved by predator (mm)	3	3	1	1
Distance moved by prey (mm)	3	3	1	1
Time to maximum gape (ms)	4	3	5	1
Duration of maximum gape (ms)	3	3	3	3
Time to maximum premaxilla protrusion (ms)	3	3	1	1
Time to start hyoid depression (ms)	3	3	4	3
Time to maximum hyoid depression (ms)	3	5	1	1
Duration of hyoid depression (ms)	3	3	1	3
Time to capture (ms)	4	3	3	1
Time to close mouth (ms)	3	3	1	1
Total bite duration (ms)	3	4	1	1
Total number of strikes	5	5	3	3
Mean number of exposures	3.2	3.4	2.0	1.6

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* (Pallas) (Nemeth, 1997), the blue-green damselfish *Chromis viridis* (Cuvier) (Coughlin & Strickler, 1990), and several cottid (Norton, 1991) and cichlid (Wainwright *et al.*, 2001) species have been documented to alter their feeding regimes towards this ram-dominated mode while capturing evasive prey.

Prey capture events of hatchery-reared *M. s. floridanus* feeding on pellets were characterized by a larger degree of 'suction' than captures in which their wild counterparts capture elusive prey. Florida largemouth bass approached the pellets without assuming a specialized attack posture prior to a strike. Additionally, they travelled a distance during the strike that was approximately five times less than their wild counterparts in approximately the same amount of time. This behaviour could reduce 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). In comparison to prey captures involving rapid buccal expansion, longer durations of timing variables (*e.g.* time to maximum gape and time to maximum hyoid depression) result in a lower degree of maximum 'suction' pressure (Svanbäck *et al.*, 2002). In addition, the time required to achieve this lower pressure increases, as does the interval of time over which it may be sustained (Svanbäck *et al.*, 2002). These behaviours suggest that the fish have adopted a different feeding behaviour 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 prey capture 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 by juvenile Florida largemouth bass in this study. Thus, the smaller excursions documented during the capture of pellets did not inhibit feeding. When the energetic savings of these small excursions and longer timing values are paired with the near 100% capture success, hatchery fish 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 Florida largemouth 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 increasing size in *M. s. floridanus*, 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 fish 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 behaviour in Florida largemouth bass, beginning at *c.* 35 mm L_T , a phenomenon which has been found to develop in fishes even under laboratory conditions (Brown, 1985). For wild largemouth bass, the onset of this behaviour has been correlated with the break-up of sibling groups and the beginning of solitary life (Cole & Noakes, 1980; Brown, 1985). Largemouth bass in hatchery systems, however, are unable to disperse, which may lead to more aggression resulting in greater competition for food. Although these studies were performed using the northern subspecies of largemouth bass *Micropterus salmoides salmoides* (Lacepède), this behaviour might also be found in *M. S. floridanus*. Thus, the fast captures by Florida largemouth 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 Florida largemouth bass in size classes 2 and 3 (Wintzer, 2004). Alternatively, there is a small chance that the hatchery fish 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 behaviour employed by hatchery fish 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 Florida largemouth bass employed an intermediate degree of 'suction' compared to wild fish capturing mosquitofish and hatchery fish 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* Dekay using a similar type of strike behaviour, had slower attack velocities than great barracuda *Sphyrnaena barracuda* (Walbaum), which use a more-compacted S-start like that of wild bass capturing mosquitofish. The small cranial excursions witnessed, 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 mosquitofish prey by hatchery-reared Florida largemouth bass.

After five feeding exposures, involving capture of *c.* 10–15 live mosquitofish per study animal, hatchery fish adopted capture behaviours kinematically similar to wild fish. The number of strikes required to successfully capture prey also decreased. Sundström & Johnsson (2001) found that after six exposures, hatchery-reared brown trout *Salmo trutta* L. had still not attained the level of foraging efficiency and prey consumption of wild brown trout. Ellis *et al.* (2002) noted that turbot *Psetta maxima* (L.), raised in hatcheries, developed these same traits to the level of wild turbot in 9 days. The results of this study show that juvenile Florida largemouth bass are behaviourally 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 behaviours at least from a kinematic perspective.

Some aspects of feeding behaviour, such as an attraction to live stimulus (Olla *et al.*, 1998) and the snapping at prey during captures (Kieffer & Colgan, 1992), are probably innate to predators such as the largemouth bass at any age. Yet, the ability to adjust these behaviours with increased exposure to prey appears to be related to the size of the fish. Many studies have attributed similar results to learning (Brown & Laland, 2001). 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 Florida largemouth bass to adapt their feeding kinematics to those of their wild counterparts show that fish in size classes 1 and 2 are slower to adjust their capture behaviour than individuals in size classes 3 and 4. Although learning is probably a large component of the behavioural change seen with experience, the consequences of additional factors must be considered, 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), or even the development of keener maneuverability, all of which can greatly enhance feeding ability in larger individuals.

It should be noted that this study merely estimated the utilization of 'suction' during prey capture (distance moved by the prey) rather than empirically measuring it (Wainwright *et al.*, 2001). As a result, certain characteristics of the prey may have caused some variation in the data. While the masses of pellets and mosquitofish were comparable (A.P. Wintzer, unpubl. data), the round shape of the pellet may experience added pressure drag compared to the more streamlined mosquitofish (Vogel, 2003), and thus will be more easily entrained in the 'suction' force. Other factors which were un-controlled within the experimental design, including the position of the prey relative to the flow, the extension of fins, and evasive movements, could also have an effect upon the ability of a fish to 'suck' prey into the mouth. To truly quantify 'suction' pressure during such feeding events, further research involving the cranial implantation of a pressure transducer (Svanbäck *et al.*, 2002) into hatchery and wild fish or the use of Digital Particle Image Velocimetry (Ferry-Graham *et al.*, 2003) would be necessary.

IMPLICATIONS FOR FISHERIES

Hatchery raised Florida largemouth bass took only five exposures (10–15 captures) to assume prey capture kinematics of wild fish feeding on elusive prey. In a post-stock situation, the encounter rate of fish with live prey could be very high. Competition for live prey by other wild Florida largemouth bass, however, 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 fish to adopt predatory behaviours more akin to wild fish, fish of this size class should be fed elusive prey species that they would encounter 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). Largemouth bass growth rates are also strongly influenced by switching from invertebrate feeding to piscivory, another possible benefit of early training on elusive natural prey such as fishes (Olson, 1996). 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 behaviours to be

modified. The simultaneous implementation of these techniques may prove beneficial by further reducing the time required to improve prey capture.

Wintzer (2004) documented that structures in the skull associated with feeding followed different growth trajectories for wild and hatchery Florida largemouth bass beginning at size class 4. At this stage, wild fish developed characters suitable for ram feeding, such as a more fusiform head and lengthened jaw elements (Liem, 1993; Norton, 1995). Hatchery fish at this size, however, showed retardation in growth, and retained a skull shape common to 'suction' feeders, including a deeper, shorter head (Otten, 1983; Liem, 1993). The skulls of post-release hatchery Florida largemouth bass converged towards those of wild fish by 135 mm L_T , probably due to a common diet. Although variation in skull development existed, no theoretical difference in function was found between these two groups, upon examination of mechanical advantage of the mandible. Despite this lack of a correlation, there are additional unmeasured morphological factors (e.g. body shape and muscle mass) that may have negative implications for the survival of hatchery fish and which should be explored.

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References

- Bailey, R. M. & Hubbs, C. L. (1949). The black basses (*Micropterus*) of Florida, with description of a new species. *University of Michigan Museum of Zoology Occasional Papers* **516**, 1–40.
- Berejikian, B. A., Mathews, S. B. & Quinn, T. P. (1996). The effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 2004–2014.
- Bolnick, D. I. & Ferry-Graham, L. A. (2002). Optimizing prey-capture behaviour to maximize expected net benefit. *Evolutionary Ecology Research* **4**, 843–855.
- Brown, C. & Laland, K. (2001). Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology* **59**, 471–493. doi: 10.1006/jfbi.2000.1689
- Brown, C. & Laland, K. (2002). Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon. *Journal of Fish Biology* **61**, 987–998. doi: 10.1006/jfbi.2003.2114
- Brown, J. A. (1985). The adaptive significance of behavioural ontogeny in some centrarchid fishes. *Environmental Biology of Fishes* **13**, 25–34.
- Cabin, R. J. & Mitchell, R. J. (2000). To Bonferroni or not to Bonferroni: When and how are the questions. *Bulletin of the Ecological Society of America* **81**, 246–248.
- Coble, D. W., Farabee, G. B. & Anderson, R. O. (1985). Comparative learning ability of selected fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 791–796.
- Cole, K. S. & Noakes, D. L. G. (1980). Development of early social behavior of rainbow trout, *Salmo gairdneri* (Pisces, Salmonidae). *Behavioural Processes* **5**, 97–112.
- Colgan, P. W., Brown, J. A. & Oratti, S. D. (1986). Role of diet and experience in the development of feeding behavior in largemouth bass, *Micropterus salmoides*. *Journal of Fish Biology* **28**, 161–170.

- Coughlin, D. J. & Strickler, J. R. (1990). Zooplankton capture by a coral reef fish: an adaptive response to evasive prey. *Environmental Biology of Fishes* **29**, 35–42.
- Ellis, T., Hughes, R. N. & Howell, B. R. (2002). Artificial dietary regime may impair subsequent foraging behaviour of hatchery-reared turbot released into the natural environment. *Journal of Fish Biology* **61**, 252–264. doi: 10.1006/jfbi.2002.2041
- Ersbak, K. & Haase, B. (1983). Nutritional deprivation after stocking as a possible mechanism leading to mortality in stream-stocked brook trout. *North American Journal of Fisheries Management* **3**, 142–151.
- Ferry-Graham, L. A., Wainwright, P. C. & Belwood, D. R. (2001). Prey capture in long-jawed butterflyfishes (Chaetodontidae): the functional basis of novel feeding habits. *Journal of Experimental Marine Biology and Ecology* **256**, 167–184.
- Ferry-Graham, L. A., Wainwright, P. C. & Lauder, G. V. (2003). Quantification of flow during suction feeding in bluegill sunfish. *Zoology* **106**, 159–168.
- Hernández, L. P. (2000). Intraspecific scaling of feeding mechanics in an ontogenetic series of zebrafish, *Danio rerio*. *Journal of Experimental Biology* **203**, 3033–3043.
- Huntingford, F. A. (1984). Some ethical issues raised by studies of predation and aggression. *Animal Behaviour* **32**, 210–215.
- Janssen, J. (1977). Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes *Coregonus hoyi* and *C. artedii*. *Journal of the Fisheries Research Board of Canada* **35**, 249–253.
- Kieffer, J. D. & Colgan, P. W. (1992). The role of learning in fish behavior. *Reviews in Fish Biology and Fisheries* **2**, 125–143.
- van Leeuwen, J. L. & Muller, M. (1984). Optimum sucking techniques for predatory fish. *Transactions of the Zoological Society of London* **37**, 137–169.
- Liem, K. F. (1993). Ecomorphology of the teleostean skull. In *The Skull*, Vol. 3 (Hanken, J. & Hall, B. K., eds), pp. 422–452. Chicago, IL: The University of Chicago Press.
- Luczkovich, J. J., Norton, S. F. & Gilmore, Jr., R. G. (1995). The influence of oral anatomy on prey selection during the ontogeny of two percoid fishes, *Lagodon rhomboides* and *Centropomus undecimalis*. *Environmental Biology of Fishes* **44**, 79–95.
- Moran, M. D. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**, 403–405.
- Muller, M., Osse, J. W. M. & Verhagen, J. H. G. (1982). A quantitative hydrodynamical model of suction feeding in fish. *Journal of Theoretical Biology* **95**, 49–79.
- Nemeth, D. H. (1997). Modulation of attack behaviour and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *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. (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. *Environmental Biology of Fishes* **44**, 61–78.
- Norton, S. F. & Brainerd, E. L. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *Journal of Experimental Biology* **176**, 11–29.
- Nyberg, D. W. (1971). Prey capture in the largemouth bass. *American Midland Naturalist* **86**, 128–144.
- Olla, B. L. & Davis, M. W. (1989). The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. *Aquaculture* **76**, 209–214.
- Olla, B. L., Davis, M. W. & Ryer, C. H. (1998). Understanding how the hatchery environment represses or promotes the development of behavioural survival skills. *Bulletin of Marine Science* **62**, 531–550.
- Olson, M. H. (1996). Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. *Ecology* **77**, 179–190.
- Otten, E. (1983). The jaw mechanism during growth of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Netherlands Journal of Zoology* **33**, 55–98.

- Porak, W. F., Johnson, W. E., Crawford, S., Schoeb, D. F., Schoeb, T. R., Stout, R. B., Krause, R. A. & DeMauro, R. A. (2002). Factors affecting survival of largemouth bass raised on artificial diets and stocked into Florida lakes. *American Fisheries Society Symposium* **31**, 649–665.
- Porter, H. T. & Motta, P. J. (2004). A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redbfin needlefish (*Strongylura notata*), and great barracuda (*Sphyræna barracuda*). *Marine Biology* **145**, 989–1000. doi: 10.1007/s00227-004-1380-0
- Richard, B. A. & Wainwright, P. C. (1995). Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *Journal of Experimental Biology* **198**, 419–433.
- Robinson, M. P. & Motta, P. J. (2002). Patterns of growth and effects of scale on the feeding kinematics of the nurse shark (*Ginglymostoma cirratum*). *Journal of Zoology, London* **256**, 449–462.
- Rosenblum, P. M., Brandt, T. M., Mayes, K. B. & Hutson, P. (1994). Annual cycles of growth and reproduction in hatchery-reared Florida largemouth bass, *Micropterus salmoides floridanus*, raised on forage or pelleted diets. *Journal of Fish Biology* **44**, 1045–1059.
- Sass, G. G. & 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.
- Sundström, L. F. & Johnsson, J. I. (2001). Experience and social environment influence the ability of young brown trout to forage on live novel prey. *Animal Behaviour* **61**, 249–255.
- Svanbäck, R., Wainwright, P. C. & Ferry-Graham, L. A. (2002). Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. *Physiological and Biochemical Zoology* **75**, 532–543.
- Van Damme, J. & Aerts, P. (1997). Kinematics and functional morphology of aquatic feeding in Australian side-necked turtles (Pleurodira; Chelodina). *Journal of Morphology* **233**, 113–125.
- Vinyard, G. L. (1982). Feeding success of hatchery-reared kokanee salmon when presented with zooplankton prey. *Progressive Fish-Culturist* **44**, 37–39.
- Vogel, S. (2003). *Comparative Biomechanics: Life's Physical World*. Princeton, NJ: Princeton University Press.
- Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carroll, A. M., Hulsey, C. D. & Grubich, J. R. (2001). Evaluating the use of ram and suction during prey capture by cichlid fishes. *Journal of Experimental Biology* **204**, 3039–3051.
- Waltzek, T. B. & Wainwright, P. C. (2003). Functional morphology of extreme jaw protrusion in neotropical cichlids. *Journal of Morphology* **257**, 96–106.
- Weihls, D. & Webb, P. W. (1983). Optimization of locomotion. In *Fish Biomechanics*. (Webb, P. W. & Weihls, D., eds), pp. 339–371. New York: Praeger.
- Werner, E. E. (1974). The fish size, prey size, handling time relation in several sunfishes and some implications. *Journal of the Fisheries Research Board of Canada* **31**, 1531–1536.
- Williamson, J. H. (1983). Comparing training success of two strains of largemouth bass. *Progressive Fish-Culturist* **45**, 3–7.
- Wintzer, A. P. (2004). Behavioral and morphological consequences of rearing Florida largemouth bass with non-elusive prey. Master's thesis. University of South Florida, Tampa. (Also available at <http://www.lib.usf.edu/ETD-db/theses/available/etd-07152004-151704/>).
- Wintzer, A. P. & Motta, P. J. (2004). The effects of temperature on prey capture kinematics of the bluegill sunfish, *Lepomis macrochirus*: implications for feeding studies. *Canadian Journal of Zoology* **82**, 794–799.