

# Diet-induced phenotypic plasticity in the skull morphology of hatchery-reared Florida largemouth bass, *Micropterus salmoides floridanus*

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**Abstract** – 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. This study examines whether elusivity-based variation in prey capture translates to a phenotypic change during skull development, and if this change results in a functional difference in the feeding mechanism. The developmental pattern of the skull was conserved between hatchery and wild bass until 80–99 mm 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 135 mm TL. Despite variation in skull development, no theoretical advantage in food capture was found between these two groups.

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**Un resumen en español se incluye detrás del texto principal de este artículo.**

## Introduction

The physical remodelling of the bones (Lanyon & Rubin 1985) and musculature (Goldspink & 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 (Turinigan et al. 1995). This change is especially prevalent in younger individuals, as their osteological development is not yet complete (Hinton & 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 flor-*

*idanus* (LeSeuer), reared in hatchery systems are maintained on inert pellet food, while their wild counterparts catch live prey, including insects, crustaceans and small fishes (Huskey & Turingan 2001). Research on the feeding behaviours of these groups has demonstrated a higher degree of inertial suction employed by hatchery bass when compared with the ram-dominated prey capture of wild individuals (Wintzer 2004). This study investigates the hypothesis that these alternate methods of prey 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 poststock survival of this species.

## Material and methods

### Specimens

Forty haphazardly chosen Florida largemouth bass, *M. salmoides floridanus*, were obtained from the Richloam Fish Hatchery (Sumter County, Florida) between May and July 2001. Individuals spanned a size range of 20–99 mm 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 40 *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 10 individuals.

Finally, 10 largemouth bass, five wild and five poststocked, 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 to 135 mm TL (size class 5). These stocked fish were previously released at approximately 100 mm TL prior to capture.

All fish in size classes 1–4 were killed with an overdose of tricaine methanesulphonate (MS-222) and preserved in a buffered formalin solution. After 1 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 & Uhler 1977). The skulls of bass in size class 5, because of their larger size, were prepared using dermestid beetles, *Dermestes maculatus* (DeGeer).

Fifteen landmarks (Table 1, Fig. 1) 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

Table 1. Descriptions of landmark locations used in a geometric morphometric analysis of skull shape of *Micropterus salmoides floridanus*.

Landmark	Location
1	Articulation of the opercle and hyomandibula
2	Posterior-most point of the operculum
3	Ventral articulation of the opercle and preopercle
4	Articulation of the interopercle and subopercle
5	Posterior-most aspect of the lower jaw
6	Quadrate-articular joint
7	Posterior-most region of the supramaxilla
8	Posteroventral region of the maxilla
9	Posterior-most region of the dentigerous arm of the premaxilla
10	Anterior-most aspect of the lower jaw
11	Anterior-most point of the dentigerous arm of the premaxilla
12	Dorsal extent of the ascending process of the premaxilla
13	Dorsal tip of the hyomandibula
14	Dorsal-most point of the cranium
15	Ventral-most point on the skull

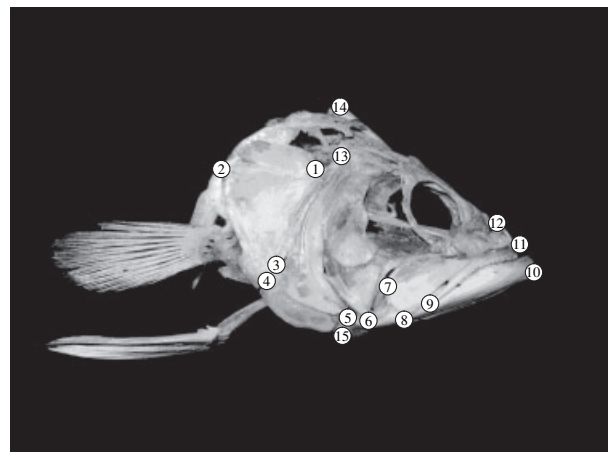


Fig. 1. Landmarks used to study shape change between hatchery and wild largemouth bass *Micropterus salmoides floridanus* through ontogeny.

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 & Richtsmeier 2001). This process decreases the amount of variance associated with nonshape disparities in landmarks, such as geometric scale (Rohlf & Slice 1990; Kassam et al. 2003). Principal components analysis (PCA) 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 because of allometric growth during ontogeny.

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.

The tpsDig program, by F.J. Rohlf, is available at <http://life.bio.sunysb.edu/morph/>. CoordGen6, PCA-Gen6, 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 (five hatchery and five 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 SigmaScan Pro 4 (SPSS Inc., Chicago, IL, USA) 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 (please see descriptions below). Therefore, three separate measurements were taken for this variable: from the center of the quadrate-articular (QA) joint to the (i) the dorsoposterior margin of the coronoid process (Wainwright & Shaw 1999), (ii) mid-point of the Aw subdivision insertion (Wainwright & Richard 1995), and (iii) the insertion of a thick tendon from A2 and A3 subdivisions onto the medial aspect of the dentary (Fig. 2). 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. 2).

The data sets were tested for normality and equality of variance using Kolmogorov–Smirnov and Levene

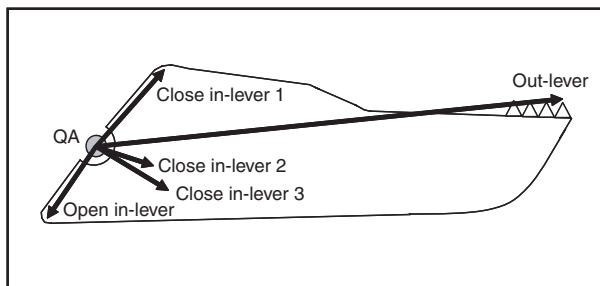


Fig. 2. Medial view of a largemouth bass *Micropterus salmoides floridanus* lower jaw illustrating the measurement points for lever arms (QA = quadrate-articular joint).

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 & 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.

## Results

### Skull shape analysis

Quiver plots generated from PCA indicate separation of skull shapes by a combination of size class and food type, with no complete separation by food type throughout all size classes. Skull shape loading positively on PCI (51% of variance) had a deeper, longer head, with oral jaw structures acting as the key lengthening elements (Fig. 3). Characteristics that loaded positively on PCII (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 PCI and PCII respectively. Bass from both diets in size classes 2 and 3 and hatchery specimens from size class 4 clustered together at low PCI values and intermediate PCII 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 PCI and intermediate on PCII (Fig. 3).

Combined scores for both PC axes indicated a clear separation in multivariate space (Wilk's- $\Lambda$   $F_{8,78} = 3.028$ ;  $P \leq 0.005$ ). As determined by two-way ANOVAS, size class ( $P \leq 0.001$ ) and a diet by size class interaction ( $P = 0.002$ ) were significant on PCI. Effects of diet ( $P = 0.007$ ) and size class ( $P \leq 0.001$ ) were found on PCII. 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 2).

### 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 with

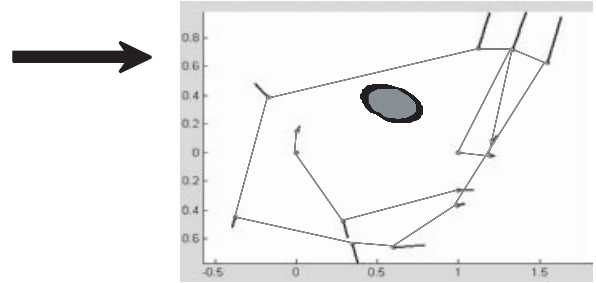
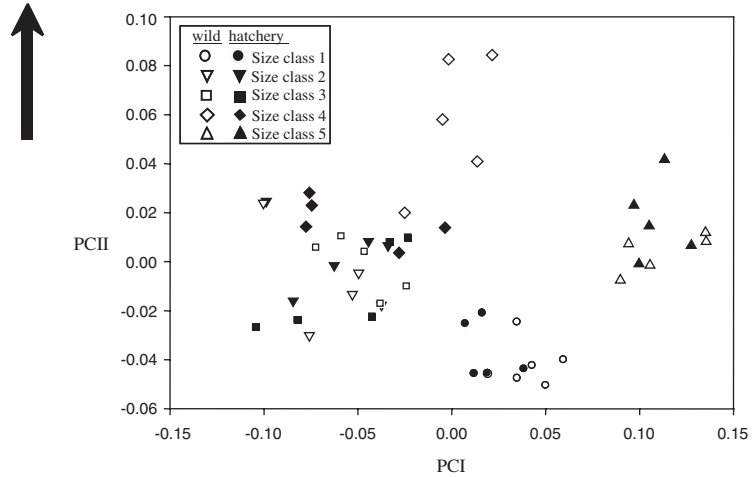
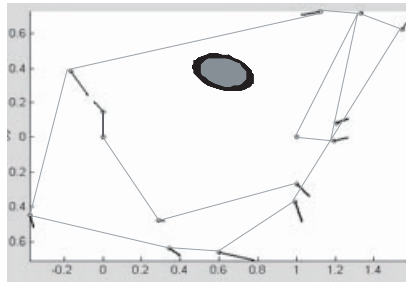


Fig. 3. Principal components analysis of Procrustes superimposed Bookstein coordinates of hatchery and wild largemouth bass *Micropterus salmoides floridanus* in five size classes. Quiver plots (dark lines) indicate the direction and magnitude of landmark change at the positive end of the corresponding axis. Grey/black ovals indicate the approximate position of the eye.

Table 2. Goodall's *F*-test results for comparisons of skull shape between each diet-size class group.

		Hatchery					Wild				
		sc1	sc2	sc3	sc4	sc5	sc1	sc2	sc3	sc4	sc5
Hatchery	sc1	0									
	sc2	0.010**	0								
	sc3	0.050*	0.190	0							
	sc4	0.040*	0.160	0.070	0						
	sc5	0.010**	0.010**	0.010**	0.010**	0					
Wild	sc1	<b>0.080</b>	0.010**	0.010**	0.010**	0.010**	0				
	sc2	0.010**	<b>0.060</b>	0.010**	0.010**	0.010**	0.010**	0			
	sc3	0.020*	0.100	<b>0.160</b>	0.010**	0.010**	0.010**	0.020*	0		
	sc4	0.010**	0.010**	0.010**	<b>0.010**</b>	0.010**	0.010**	0.010**	0.010**	0	
	sc5	0.010**	0.010**	0.010**	0.010**	<b>0.600</b>	0.010**	0.010**	0.010**	0.010**	0

Values in bold indicate comparisons of hatchery and wild bass *Micropterus salmoides floridanus* within a single size class.

sc, size class.

\* $P \leq 0.05$ , \*\* $P \leq 0.01$ .

their hatchery counterparts. The second closing in-lever was not different between these groups (Table 3). 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

Table 3. ANCOVA (TL as covariate) and anova results comparing lever arms and mechanical advantage ratios respectively between hatchery and wild largemouth bass *Micropterus salmoides floridanus*.

	Mean (SE)		Slope		d.f.	F-value	P-value
	Hatchery	Wild	Hatchery	Wild			
<b>Lever arm</b>							
Opening in-lever	1.087 (0.030)	1.198 (0.030)	0.91	1.10	1,37	6.605	0.014*
Closing in-lever 1	2.296 (0.061)	2.514 (0.061)	0.90	1.10	1,37	6.426	0.016*
Closing in-lever 2	1.609 (0.062)	1.771 (0.062)	0.95	1.20	1,37	3.388	0.074
Closing in-lever 3	1.775 (0.047)	1.935 (0.047)	0.91	1.10	1,37	5.750	0.022*
Out-lever	8.130 (0.130)	8.875 (0.130)	0.91	1.10	1,37	16.287	<0.001**
<b>Mechanical advantage</b>							
Jaw opening ratio	0.133 (0.002)	0.135 (0.002)	0.00	0.00	1,38	0.420	0.521
Jaw closing ratio 1	0.281 (0.005)	0.282 (0.005)	0.00	0.00	1,38	0.069	0.795
Jaw closing ratio 2	0.196 (0.006)	0.196 (0.006)	0.00	0.00	1,38	<0.001	0.989
Jaw closing ratio 3	0.220 (0.005)	0.217 (0.005)	0.00	0.00	1,38	0.187	0.668

Slope indicates variable scaling with growth.

\* $P \leq 0.05$ , \*\* $P \leq 0.01$ .

possessing a physical feeding advantage over the other (Table 3). 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 3).

## 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 PCI before loading more negatively in size class 2 and 3. This difference is because of 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 a shallow supraoccipital crest, elongated jaw elements, including the dentary, maxilla and the dentigerous arm of the premaxilla. Liem (1993) and Norton (1995) concluded that these characters are effective for ram capture, a strike mode commonly employed for elusive prey (Norton 1991). In addition, a longer ascending arm of the premaxilla enhances upper jaw protrusion, bringing the predator closer to its prey (Waltzek & 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 ram-suction index (RSI) of 0.901 while capturing elusive mosquitofish, *Gambusia holbrooki* (Girard), prey (Wintzer

2004). RSI values close to +1 indicate ram feeding, while those near -1 correspond to pure suction (Norton & Brainerd 1993). The skulls of bass in the 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 & Turingan 2001).

Hatchery bass followed a modified growth pattern of skull development compared with 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. A similar disruption of heterochrony was seen by Meyer (1987) in the cichlid, *Cichlasoma managuense* (Günther), maintained on inert flake food diets when compared with their nauplii-fed cohorts. The resultant morphology maintained by size class 4 hatchery bass, included a deeper, shorter head, including a higher supraoccipital crest, and shorter jaw elements, including the mandible, maxilla and dentigerous arm of the premaxilla. This type of morphology is better suited for feeding with a larger component of suction (Otten 1983; Liem 1993), allowing hatchery bass in size class 4 to capture inert pellet food with an average RSI value of 0.218 (Wintzer 2004). A shorter ascending process of the premaxilla was also noted in size class 4 hatchery bass. Witte (1984) found that tank-reared *Haplochromis squamipinnis* (Regan) cichlids also had a reduced ascending process of the premaxilla compared with wild individuals, noting that it was likely because of a higher degree of bite force utilized by the domesticated group. Pellet foods are hard and, as a result, hatchery bass might also employ a stronger bite during capture and processing than wild bass. Additionally, hatchery bass had a shorter articulating process of the lower jaw, another characteristic of fishes which utilize

biting during feeding (Otten 1983; Wainwright 1999). 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 a diet of nauplii. A similar convergence in head morphology has also been documented between wild and postreleased Atlantic salmon, *Salmo salar* (Linnaeus) (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) because of 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 because of 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 & 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 & Wainwright 1995; Wainwright & 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 & Wainwright 1995; Wainwright & 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 & 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 & 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, *Oncorhynchus mykiss* (Walbaum), has shown that cultured fishes have underdeveloped regions of the brain, including the optic tectum and telencephalon, which are related to feeding (Marchetti & 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 behaviourally constrained. This stems from a lack of experience with live prey capture in hatchery systems (Colgan et al. 1986; Wintzer 2004). Wintzer (2004) 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 of 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) over a 10-day period, however, hatchery bass used capture kinematics identical to wild individuals. These results show both the high degree of behavioural 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 poststock 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) because of 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. Behavioural 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 behavioural plasticity are factors that could affect the poststock survival of hatchery fishes.

## Resumen

1. Los individuos de *Micropterus salmoides floridanus* criados en cautividad se alimentan de cápsulas inertes de comida mientras que sus congéneres salvajes capturan presas elusivas. A menudo diferencias en los niveles de elusividad de las presas permiten la utilización de métodos alternativos para capturar presas. Este estudio examina si la variación basada en la elusividad de la captura de presas se traduce en un cambio fenotípico durante el desarrollo del cráneo y si este cambio resulta en una diferencia funcional en el mecanismo de alimentación.

2. El patrón de desarrollo del cráneo se mantuvo entre individuos criados en cautividad y en individuos salvajes hasta los 80–99 mm longitud total. En este punto, los individuos salvajes desarrollaron rápidamente cambios en el aparato mandibular incluyendo una cabeza más fusiforme y estructuras mandibulares más alargadas. Sin embargo, en individuos de cautiverio, el desarrollo natural se retrasó en este tamaño.

3. Tras una suelta, los cráneos de individuos procedentes de cautiverio convergieron hacia los individuos salvajes en los 135 mm longitud total. A pesar de la variación en el desarrollo del cráneo, no encontramos ninguna ventaja teórica en la captura de alimento entre estos dos grupos.

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