

The effects of satiation on strike mode and prey capture kinematics in the largemouth bass, *Micropterus salmoides*

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Synopsis

The feeding mechanism and kinematics of prey capture have been studied in many fishes. However, the effects of satiation on the strike mode and prey capture kinematics have never been directly measured. We analyze 12 kinematic variables to determine the effects of satiation on prey capture in five largemouth bass, *Micropterus salmoides*, by using high speed videography. We also present the first experimental test for modulatory capabilities in response to satiation, by using the ram-suction index. Significant changes in the kinematic variables of maximum lower jaw depression, maximum gape distance, maximum hyoid depression, time to maximum hyoid depression, and time from maximum hyoid depression to recovery were seen with the effects of satiation. Change in the kinematic variables imply a decrease in jaw opening velocity and the magnitude of suction velocity created during repetitive strikes by *M. salmoides* with increasing satiation. The bass primarily uses a ram strike mode, with some suction bites occasionally. Ram-suction index analyses suggests that *M. salmoides* does not modulate strike mode in response to satiation. However, the bass modulate prey capture kinematics without altering strike mode with the effects of satiation. Prey capture success decreases in each bass, as the probability of a successful prey capture event becomes lower, with increasing satiation. These findings demonstrate that satiation can have major effects on prey capture kinematics and future studies of feeding kinematics should account for satiation in their analyses.

Introduction

The feeding mechanisms in fishes have been studied extensively during the last thirty years (e.g., Alexander 1970, Lauder & Liem 1981, Wainwright & Lauder 1986, Norton 1995). However, the majority of studies on the functional morphology of the feeding apparatus and kinematics of prey capture in fishes have not explicitly addressed satiation in their analyses. For example, many studies have not mentioned the number of feeding events used in their analyses (e.g., Norton & Brainerd 1993, Nemeth 1997b) or have noted the number of feeding sequences analyzed, but failed to mention the total number recorded (e.g., Lauder 1980, 1981, Gillis & Lauder 1995). Thus, the degree of preda-

tor satiation in strikes used to characterize the feeding mechanism is unknown. Satiation, may be defined as, 'to satisfy (an appetite or desire) fully' or 'to satisfy to excess, or filled to satisfaction' (American College Heritage Dictionary 1993). The only study to our knowledge that has accounted for satiation in the analysis is by Wainwright & Lauder (1986), who used randomization to ensure that there would be no systematic influences of satiation on the results. Although Lauder (1980) noted that buccal pressure magnitude varied inversely with degree of predator satiation in *Lepomis*, the effects of satiation on strike mode and prey capture kinematics in a teleost over the course of a series of feeding events has never been directly measured.

Modulation or the ability of a predator to consistently change kinematic, electromyographic, and pressure profiles of jaw function to varying feeding conditions has been noted in many fishes (Nyberg 1971, Elshoud-Oldenhauve & Osse 1976, Liem 1978, 1980b, Lauder & Liem 1980, Nemeth 1997a,b). Most studies have reported modulation to occur in response to varying prey locations, sizes, and types (Ballintijn et al. 1972, Liem 1978, 1980b, Lauder 1981, 1983a). Although Nyberg (1971) observed modulation in *Micropterus salmoides* in response to differing prey types and locations, the effects of satiation on modulation of strike mode and prey capture kinematics in this or any other aquatic feeding vertebrate has not been studied.

Three major strike modes have been described in fishes; suction feeding, ram feeding, and biting or manipulation (Liem 1980a). Furthermore, ram feeding and suction feeding have been considered endpoints of a continuum (Norton & Brainerd 1993). Inertial suction occurs when the predator remains relatively stationary and rapidly expands the mouth to suck in prey items (Werner & Hall 1974). Inertial suction allows a variable strike distance which may be determined by the relative masses of the predator and prey, the rapidity of mouth cavity expansion, the relative size of the gape, and the volume change of the expanding mouth cavity (Lauder 1980, Muller & Osse 1984, Norton & Brainerd 1993). During suction feeding, negative buccal pressure is caused by rapid expansion of the buccal cavity created by simultaneous elevation of the neurocranium, lateral expansion of the suspensoria, and depression of the floor of the mouth via the hyoid bar (Lauder 1980, 1983b, Muller & Osse 1984, Wainwright & Lauder 1992).

During ram feeding, the predator overcomes the prey by rapid acceleration of the body, often aided by explosive protrusion of the premaxilla (Lauder & Liem 1981, Rand & Lauder 1981, Westneat & Wainwright 1989). According to Norton & Brainerd (1993), a pure ram strike occurs only when the predator moves and the prey does not.

In the past, many studies have focused on body morphology as an ecomorphological predictor of strike mode in fishes (e.g., Keast & Webb 1966, Webb 1984b, Norton & Brainerd 1993, Norton 1991, 1995, Motta et al. 1995). Suction feeding predators are thought to be best suited by having an agile locomotory complex including laterally positioned pectoral fins and a laterally compressed body which allows fine tuning of the predators position prior to the strike

(Webb 1984a, 1988). One key to the success of a ram feeding predator is a large gape (Norton 1991). Along with increased gape size, speed is also essential for ram feeding and it is likely that ram feeding predators have locomotory adaptations that maximize the ability of the predator to accelerate and reach high attack velocities (Norton 1995). Specializations for ram feeding include a subcarangiform body, a thick caudal peduncle, posterior extensions of the median fins, and a flexible body allowing large amplitude propulsive movements (Webb 1984a).

Largemouth bass have morphological attributes of both ram and suction feeders that span the range of these ecomorphological feeding predictors, therefore it is possible that *M. salmoides* could modulate its prey capture behavior to effectively use ram, suction, or a combination of the two modes depending on the degree of predator satiation, although Norton & Brainerd (1993) found that bass primarily used ram based feeding when presented with differing prey types. We expect that *M. salmoides* will use a more energetically demanding ram-dominated strike mode early in the feeding bout, but will modulate its feeding to a less energetically costly suction-based mode as the bass approach satiation (Norton & Brainerd 1993).

The specific goals of this study are: (1) to characterize the effects of satiation on kinematic determinants of prey capture in the largemouth bass, *M. salmoides*; (2) to determine whether the strike mode (e.g., ram, suction) is modulated due to the effects of satiation; and (3) to determine the effects of satiation on prey capture success.

Material and methods

Experimental animals and design

The kinematics of prey capture events were examined using five largemouth bass, *Micropterus salmoides floridanus* (Centrarchidae), collected by hook and line from a residential pond in Hillsborough County, Florida. The bass were acclimated to laboratory water and temperature (25°C) and were each housed in separate 95 l aquaria at a photoperiod of approximately 12 h daylight and 12 h darkness. The size of the fish ranged from 29 to 34 cm total length (Table 1). The narrow range of bass lengths mitigated the effects of scale that were noted in the feeding behavior of largemouth bass (Richard & Wainwright 1995, Wainwright & Richard 1995).

Table 1. Total length and total, maximum, minimum, average, and standard error of prey consumed per feeding event for each largemouth bass, *Micropterus salmoides*, studied.

Bass	Total length (cm)	Total # of strikes	Maximum	Minimum	Average	Standard error (\pm)
A	31.4	226	26	18	22.6	0.945
B	31.5	267	39	15	26.7	2.805
C	33.5	511	73	39	51.1	3.623
D	30.7	219	25	17	21.9	0.809
E	29.1	390	51	27	39	2.558

The bass were fed a diet of eastern mosquitofish, *Gambusia holbrooki* (Poeciliidae), ranging in total length from 3.5 to 4.5 cm. Mosquitofish size range was kept consistent to avoid prey size effects on prey capture, which were noted by Werner (1974). Mosquitofish were captured by dipnet in the same pond from which the bass were taken. The bass were conditioned to consume mosquitofish dropped through a 2.2 cm diameter clear tube when lights were turned on. The tube was positioned in the center of the tank, with the bottom of the tube 10 cm from the tank bottom.

Feeding events were conducted every three days until ten feeding bouts were recorded for each bass. No maintenance feedings were conducted between feeding events. Each bass was fed one mosquitofish at approximately one minute intervals until satiated. Satiation was considered to be complete when the introduced prey item was not consumed within two minutes. A one minute interval between prey introductions was used to negate any effects of muscle fatigue on the results (Granzier et al. 1983). Mosquitofish prey were randomly selected from a separate 95 l feeder aquarium. Only prey fish that were alive and active were used for the feedings. Prior to dropping the mosquitofish into the tank, weight and total length were recorded for each. The number of mosquitofish eaten in one feeding bout ranged from 15 to 73 (Table 1). After ten feeding bouts had been recorded, each bass was killed with an overdose of MS-222 (tricaine methanesulfonate) according to the University of South Florida Animal Care and Use Committee guidelines, standard measurements were recorded, and the specimen was preserved in 10% formalin.

Videography

All bass were filmed during feeding with a single video camera (NAC HSV-200, 200 fields s^{-1}), in lateral view with a 5 cm^2 background grid. Lighting was provided by approximately 3000 W of quartz-halogen lights.

Only those feedings in which the bass was in full lateral view throughout the strike were considered acceptable for analysis. Any feedings in which the tube interfered with prey capture were not analyzed.

Video analysis

Fifty prey capture bouts (ten per bass) resulting in 1613 separate strikes were analyzed field-by-field by downloading images with Video Blaster (Creative Laboratories, Inc.), SigmaScan Image (Jandel Scientific, Inc.), and a Panasonic AG1970 VCR. Of the 1613 strikes, the number of analyzed strikes was less (Table 2). Strike mode refers to the ram or suction method of prey capture, whereas prey capture kinematics refers to the twelve measured morphological and timing variables that define jaw opening and closure. For this study, 'gape cycle' was defined as the duration from the start of the expansive phase (initial jaw depression) to the end of the compressive phase (jaw closure on the prey). Time zero was defined as the field immediately preceding the field containing the first movement of the lower jaw tip at the beginning of jaw depression. This study focuses on the initial strike terminating with the initial jaw closure and does not include subsequent prey manipulation or transport. Twelve kinematic variables (eight timing, two linear distances, and two angular measurements) were measured from all acceptable sequences: (1) maximum gape distance, in cm; (2) time to maximum gape, in ms; (3) time from maximum gape to jaw closure on the prey, in ms; (4) gape cycle duration, in ms; (5) maximum hyoid depression, in cm; (6) time to maximum hyoid depression, in ms; (7) time from maximum hyoid depression to recovery of the anatomical elements of the feeding apparatus, in ms; (8) maximum head elevation, in degrees; (9) time to maximum head elevation, in ms; (10) maximum lower jaw depression, in degrees; (11) time to maximum lower jaw depression, in ms; and (12) time from maximum lower jaw depression to jaw closure,

Table 2. Statistics for linear regressions of kinematic variable vs. prey consumed for five largemouth bass, *Micropterus salmoides*. Asterisks next to p-values denote significance at the Bonferroni corrected α of 0.004.

Kinematic variable	Bass	N	Slope	y-intercept	r ²	p-value
Gape cycle (ms)	A	107	0.523	65.989	0.0122	0.258
	B	133	0.221	65.928	0.00462	0.437
	C	305	0.756	50.892	0.117	<0.001*
	D	110	1.026	62.902	0.0401	0.036
	E	288	0.708	40.486	0.112	<0.001*
Maximum gape distance (cm)	A	104	-0.0408	4.027	0.173	<0.001*
	B	129	-0.0276	3.817	0.141	<0.001*
	C	299	-0.0172	3.163	0.0971	<0.001*
	D	109	-0.0636	3.939	0.226	<0.001*
	E	288	-0.0087	3.159	0.0248	<0.001*
Time to maximum gape distance (ms)	A	107	-0.0317	22.167	0.00133	0.71
	B	134	0.0733	22.537	0.024	0.074
	C	304	0.0137	20.142	0.00389	0.278
	D	110	0.0219	20.902	0.00124	0.715
	E	288	0.00472	19.576	0.000587	0.682
Time from maximum gape to jaw closure (ms)	A	107	0.592	43.232	0.0182	0.166
	B	134	-0.0979	46.545	0.00117	0.694
	C	304	0.711	31.317	0.114	<0.001*
	D	110	1.07	40.939	0.0489	0.02
	E	288	0.704	21.169	0.115	<0.001*
Maximum hyoid depression (cm)	A	79	-0.02003	4.942	0.0596	0.0453
	B	101	-0.0288	5.211	0.219	<0.001*
	C	199	-0.00867	4.7215	0.03856	0.00544
	D	78	-0.0576	5.309	0.323	<0.001*
	E	224	-0.0095	3.948	0.042	0.002*
Time to maximum hyoid depression (ms)	A	84	0.456	24.816	0.226	<0.001*
	B	110	0.258	28.281	0.184	<0.001*
	C	200	0.242	29.571	0.215	<0.001*
	D	90	0.403	26.077	0.194	<0.001*
	E	225	0.157	25.912	0.175	<0.001*
Time from maximum hyoid depression to recovery (ms)	A	81	2.73	99.38	0.116	0.002*
	B	96	0.8026	144.277	0.0382	0.0563
	C	194	0.635	114.648	0.0511	0.002*
	D	73	0.6448	135.349	0.0075	0.4659
	E	217	0.946	86.215	0.102	<0.001*
Maximum head elevation (degrees)	A	63	-0.0878	58.664	0.00593	0.548
	B	88	0.0638	56.315	0.00572	0.484
	C	183	-0.0375	57.501	0.00285	0.473
	D	59	0.702	43.831	0.251	<0.001*
	E	213	0.0411	58.308	0.00157	0.566
Time to maximum head elevation (ms)	A	107	-0.0317	22.167	0.00133	0.71
	B	135	0.0739	22.573	0.0241	0.072
	C	304	0.0137	20.142	0.00389	0.278
	D	110	0.0219	20.902	0.00124	0.715
	E	288	0.00472	19.576	0.00059	0.682
Maximum lower jaw depression (degrees)	A	80	-0.917	107.855	0.349	<0.001*
	B	97	-0.706	107.649	0.317	<0.001*
	C	246	-0.504	96.426	0.25	<0.001*
	D	84	-1.51	114.417	0.444	<0.001*
	E	244	-0.31	102.762	0.0793	<0.001*
Time to maximum lower jaw depression (ms)	A	107	0.00384	20.753	0.00002	0.96
	B	134	0.0634	21.916	0.0188	0.114
	C	304	0.0168	19.767	0.00458	0.239
	D	110	0.0675	20.324	0.0113	0.269
	E	288	0.0376	18.311	0.0257	0.006

Table 2. (Continued)

Kinematic variable	Bass	N	Slope	y-intercept	r ²	p-value
Maximum lower jaw depression to jaw closure (ms)	A	107	0.557	44.647	0.0153	0.205
	B	134	0.151	43.221	0.00283	0.542
	C	305	0.741	31.068	0.12	<0.001*
	D	110	1.024	41.517	0.0451	0.026
	E	288	0.68	22.228	0.112	<0.001*

in ms. Gape distance was measured, from the lateral view, as the vertical linear distance between the most anterior points of the upper and lower jaw at maximum gape. Maximum hyoid depression was the perpendicular distance between the ventral-most point of the eye and the most ventral point of the mouth floor at peak hyoid depression. Maximum head elevation was measured as the angle between the first dorsal fin spine and the dorsal tip of the premaxilla and a line from the first dorsal fin spine to the origin of the first pectoral fin ray at maximum gape distance. Maximum lower jaw depression was measured as the angle between a line from the jaw hinge to the posterior-most point of the eye and a line from the jaw hinge to the anterior tip of the mandible. Maximum lower jaw depression represents the total angular excursion of lower jaw movement at maximum gape distance (see figure 1 in Richard & Wainwright 1995 for illustration of linear and angular measurements). All measurements were taken from the lateral view of the fish except for gape cycle duration, where in addition to lateral view, frontal views were also included when applicable.

Ram-suction index

In addition to the twelve kinematic variables, ram-suction index (RSI) values were calculated by the method of Norton & Brainerd (1993) for every clearly visible strike. Acceptable images were downloaded to computer using Video Blaster (Creative Laboratories, Inc.) and x, y coordinates were calculated using SigmaScan Image (Jandel Scientific, Inc.) RSI values were used to test for modulation in the strike mode (ram and suction) of bass over the course of a feeding bout to satiation. The RSI allows strikes to be placed along a ram/suction feeding continuum based on the relative movements of the predator and prey during a strike (Norton 1995). RSI values were calculated by recording the coordinates of both the predator and the prey at the start of the strike (time zero) and the coordinates of the predator and prey (from the point on the prey most distant from the predator) at the last field before the

prey disappeared into the predator's mouth. The premaxilla was used as the landmark for the quantification of the coordinates of the predator since no significant difference was noted between using the landmark of the eye or premaxilla by Norton & Brainerd (1993) in *M. salmoides*. These coordinates were then used to determine the net distance moved by the predator and by the prey during the strike. The RSI is given by:

$$RSI = (D_{\text{Predator}} - D_{\text{Prey}}) / (D_{\text{Predator}} + D_{\text{Prey}}),$$

where D_{Predator} is the net distance moved by the predator and D_{Prey} is the net distance moved by the prey. The index ranges from +1, a pure ram strike in which only the predator moves, to -1, a pure suction strike in which only the prey moves.

Analysis of prey capture success

An analysis of the effects of satiation on foraging success was conducted. For each clearly visible strike, a capture or miss was tallied. For the purpose of this study, a capture was defined as any strike in which the prey was fully captured and ingested on the initial attempt. A miss was any feeding attempt where the prey was: (1) not successfully captured on the initial attempt; or (2) captured on the initial attempt, but later escaped. Although the prey may have been captured later within the two minute satiation interval after the initial attempt, a miss was still tallied. Ecologically, a miss on the initial attempt may signify unsuccessful foraging under normal conditions as the prey may find refuge or escape following the strike. However, under the conditions of this study, the aquaria provided no refuge and the prey could be easily captured later.

Statistical analyses

All kinematic variables were plotted as Model I linear regressions with more than one value of Y for

each value of X (Sokal & Rohlf 1981). Statistical significance was determined by ANOVA (SigmaStat Version 2.0, Jandel Scientific, Inc.). The linear regressions were plotted as the kinematic variable (dependent variable) vs. prey consumed (independent variable) for each bass to determine the relationship between the kinematic variable and the effect of satiation (prey consumed). A Bonferroni correction was applied to the experiment-wise error rate ($\alpha = 0.05$) to reduce the probability of Type I errors. The null hypothesis was rejected at the $\alpha = 0.004$ level after the Bonferroni correction (0.05/12 kinematic variables) (Rice 1989). For all significant kinematic variables, a repeated measures ANOVA was conducted to determine when satiation (number of prey consumed) began to cause significant changes in the magnitude and timing of the kinematic variables. Statistical differences were concluded at the $\alpha = 0.05$ level.

Ram-suction index values were plotted in two ways for each bass to determine if modulation of the strike mode (ram and suction) was occurring with satiation. First, Model I linear regressions with more than one value of Y for each X were plotted for each bass, with the independent variable being prey consumed and the dependent variable being RSI value (Sokal & Rohlf 1981). A maximum of ten RSI values were possible for each X, ranging from a minimum of -1 to a maximum of $+1$. Statistical significance was determined by ANOVA at the $\alpha = 0.05$ level (SigmaStat Version 2.0, Jandel Scientific, Inc.). Second, average RSI values for each prey consumed category were calculated for each bass. RSI average values were displayed as scatter plots to look for trends not seen through regression analysis of the strike mode of bass.

The effects of satiation on prey capture success were assessed using logistic regression (Systat 9.0, SPSS, Inc.). In the ten feeding bouts from each bass, individual strikes were used as the qualitative dependent variable, where a capture = 1 and a miss = 0. Prey consumed was used as the continuous independent variable. Prey capture success was analyzed as the probability of a successful prey capture event at each specific prey consumed category. Statistical significance was determined by a chi-square test ($\alpha = 0.05$).

Results

Kinematic variables

Five of the twelve kinematic variables examined (two linear distances, two timing, and one angular

measurement) showed significant trends with the effect of satiation (Table 2, Figure 1). The variables of maximum gape distance, time to maximum hyoid depression, and maximum lower jaw depression were significant for all five bass. A significant relationship for bass B, D, and E was seen between prey consumed and maximum hyoid depression, whereas time from maximum hyoid depression to recovery showed a significant relationship with the effects of satiation in bass A, C, and E. Although significant, the r^2 values were mostly low implying a poor fit of the line. Maximum lower jaw depression, maximum gape distance, and maximum hyoid depression decreased with increasing number of prey consumed (Figures 1–3). Maximum gape distance decreased from approximately 4.0 to 2.5 cm from the beginning of the feeding event until satiation (Figure 1). Maximum lower jaw depression and maximum hyoid depression decreased from approximately 110 to 80 degrees and 4.8 to 3.5 cm, respectively. In contrast, significant temporal variables increased in duration with the effects of satiation (Figures 1,2c,3c). Time to maximum hyoid depression increased from approximately 26.9 ms at the beginning of the feeding event to 40 ms when satiation was concluded. The time from maximum hyoid depression to recovery increased from approximately 100 to 150 ms. Maximum hyoid depression durations appear as discrete rows due to the minimal camera resolution of ± 5 ms. In the additional seven kinematic variables analyzed (gape cycle duration, time to maximum gape, time from maximum gape to jaw closure, maximum head elevation, time to maximum head elevation, time to maximum lower jaw depression, time from maximum lower jaw depression to jaw closure), no significant trends were found between the kinematic variable and predator satiation for all five bass.

Significant changes in the magnitude and timing of the kinematic variables throughout the course of a feeding bout were highly variable. Bass satiation (number of prey consumed) ranged from 9 to 49 mosquitofish before changes in the significant kinematic variables occurred for all five bass.

Analysis of the ram-suction index

No significant trends were found when prey consumed was regressed against the RSI value for the five bass (mean p-value = 0.378). From scatterplot analysis, it was observed that the bass primarily used ram feeding, regardless of the effect of satiation; however some bites were closer to the suction end of the ram/suction

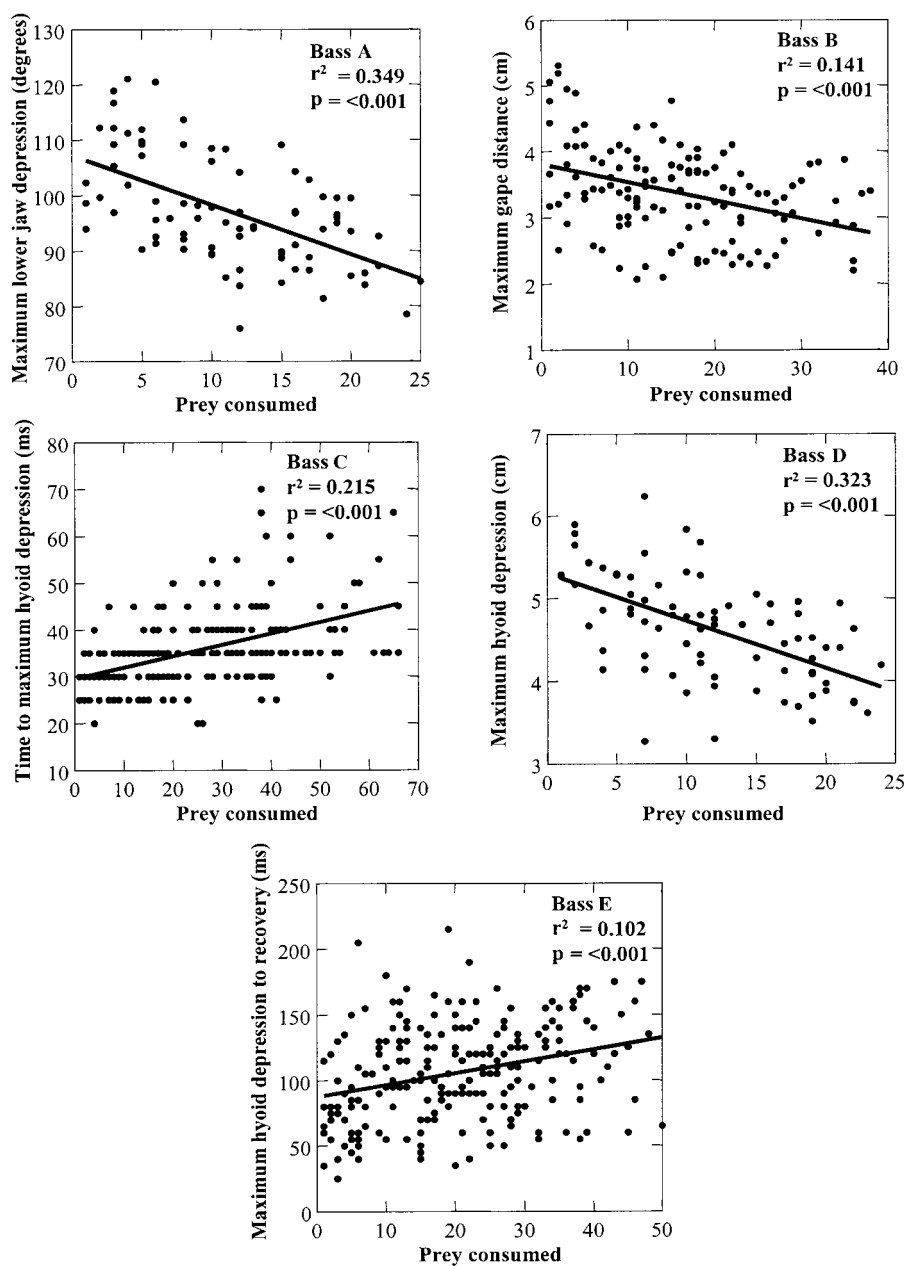


Figure 1. Linear regressions of kinematic variables showing significant trends vs. prey consumed for five representative largemouth bass, *Micropterus salmoides*.

continuum (Figure 4). Although primarily ram, no strikes indicated pure ram (+1) or pure suction (-1) according to the index, indicating a degree of predator and prey movement within every strike analyzed. No modulation of strike mode was observed in any of the bass, in that, there was no consistent change from ram to suction (or vice versa) as predicted.

Prey capture success

The effects of satiation on prey capture success were examined for each bass by examining the probability of a successful prey capture event for each successive prey consumed. For each bass, the probability of a successful prey capture on the initial attempt decreased

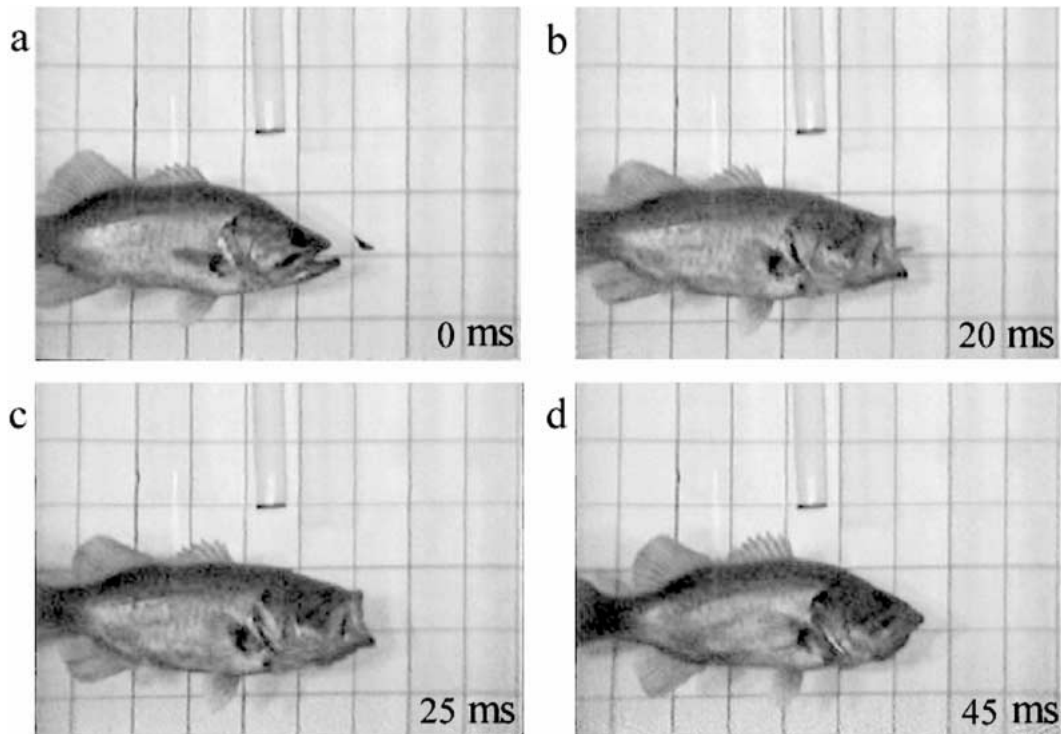


Figure 2. Representative strike from early in the feeding event of largemouth bass *C. Micropterus salmoides* (a = initial mouth opening, b = maximum gape distance and prey entering the mouth, c = maximum hyoid depression, and d = mouth closure on the prey).

with increasing predator satiation (Figure 5). That is, as each bass consumed more prey individuals, it became less successful in capturing the prey. The probability of prey capture success decreased significantly ($p < 0.05$) for all five bass with the effects of satiation (Table 3).

Discussion

Implications of kinematic analysis

Largemouth bass decreased the speed of mouth opening and also opened the mouth less as they became satiated. Time to reach maximum gape in *M. salmoides* did not change with satiation. A decrease in maximum gape distance with constant time duration suggests a decrease in jaw opening velocity with the effects of satiation. The decrease in jaw opening velocity observed in the expansive phase of *M. salmoides* may suggest a decrease in the rate of contraction of the jaw opening muscles: the levator operculi, epaxialis, sternohyoideus, and levator arcus palatini

(Osse 1969, Wainwright & Lauder 1986, Wainwright et al. 1989, Grubich & Wainwright 1997).

In a study of *Lepomis*, Lauder (1980) noted that buccal pressure magnitude varied inversely with the degree of predator satiation. The creation of subambient pressure within the buccal cavity is the result of simultaneous elevation of the neurocranium, lateral expansion of the suspensoria, depression of the mandible, and depression of the floor of the mouth via the hyoid bar (Muller & Osse 1984, Wainwright & Lauder 1992). The magnitude of negative pressure created in the buccal cavity during a strike has implications for the amount of suction force generated by the predator. Therefore, it can be inferred that less suction force was generated by *Lepomis* with increasing satiation.

Despite the dominant use of ram feeding by the largemouth bass under these experimental conditions, a variable degree of suction was also used, as determined from the RS (Figure 4). The decrease in jaw opening velocity observed in this study over the course of a feeding bout suggests that the amount of suction force generated by the bass decreases with increasing satiation as noted by Lauder (1980). Furthermore,

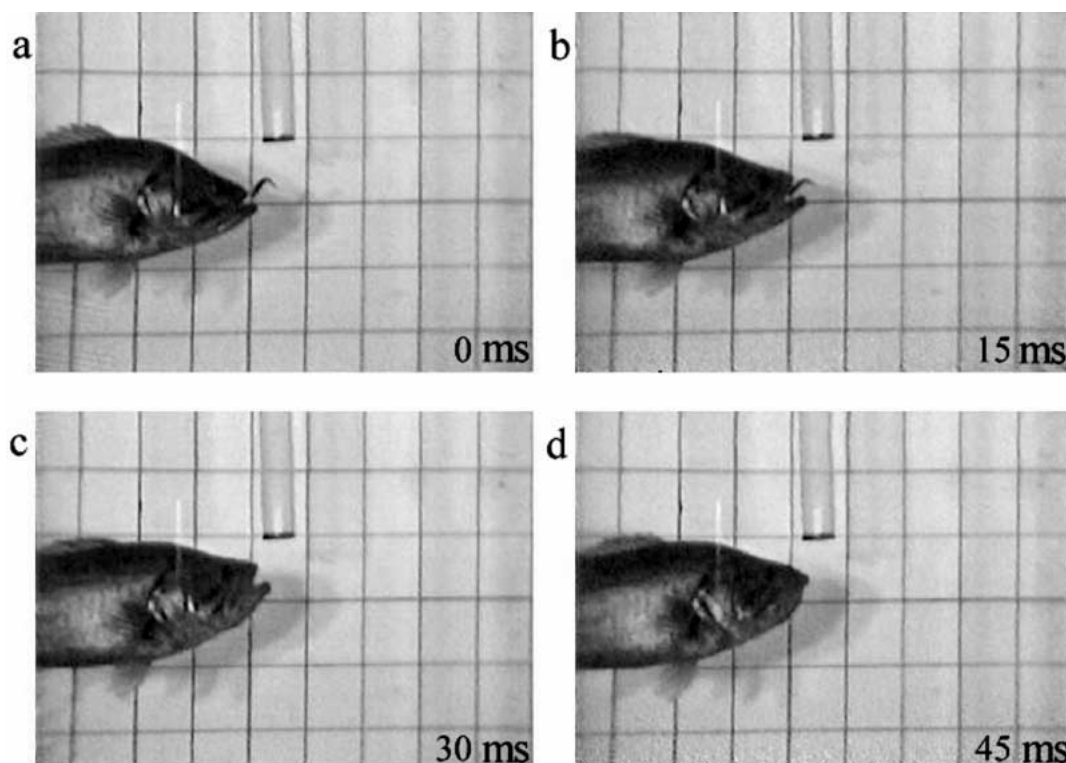


Figure 3. Representative strike from late in the feeding event of largemouth bass *C. Micropterus salmoides* (a = initial mouth opening, b = maximum gape distance and prey entering the mouth, c = maximum hyoid depression, and d = mouth closure on the prey).

in the bass, maximum gape distance and maximum hyoid depression were inversely proportional to the degree of predator satiation (Figure 1). The decreasing angular excursion of the mandible with increasing satiation implies that the movement of the lower jaw contributed most to the decrease in maximum gape distance. A decrease in the magnitude of mouth opening and hyoid depression will decrease the amount of water drawn into the buccal and opercular cavities during a suction feeding event (Alexander 1970, Muller et al. 1982). If the predator's attack produces less suction during the strike, the distance from which the prey may be pulled into the mouth decreases, and the predator may need to increase the ram component of its attack to forage successfully. However, in this study it did not apparently increase the ram component (Figure 4), rather, prey capture success decreased with satiation.

Three measures of hyoid movement showed significant changes as a function of satiation. Mechanisms that increase the suction velocity of a strike may include increasing the volume change in the buccal cavity and

increasing the rate of buccal expansion (Lauder 1983b, Norton & Brainerd 1993). Therefore, a decrease in maximum hyoid depression and an increase in time to maximum hyoid depression further suggests that *M. salmoides* is generating less suction velocity with the increasing effects of satiation. The time required for the recovery of the anatomical elements of the feeding apparatus became greater as *M. salmoides* approached satiation (Figure 1). Under natural conditions when prey may be readily available, the increased duration of recovery in the feeding apparatus may hinder the speed at which a predator can forage upon abundant prey when satiated.

Numerous studies of the feeding mechanism in fishes have not explicitly addressed the effects of satiation in their analyses (Norton & Brainerd 1993, Motta et al. 1997, Nemeth 1997b). Interestingly, with satiation, two obligate suction feeding nurse sharks, *Ginglymostoma cirratum*, showed a different pattern. One shark actually increased the speed of jaw opening as it consumed over 40 pieces of food to become satiated, while the second shark showed no change (Motta et al. 2002).

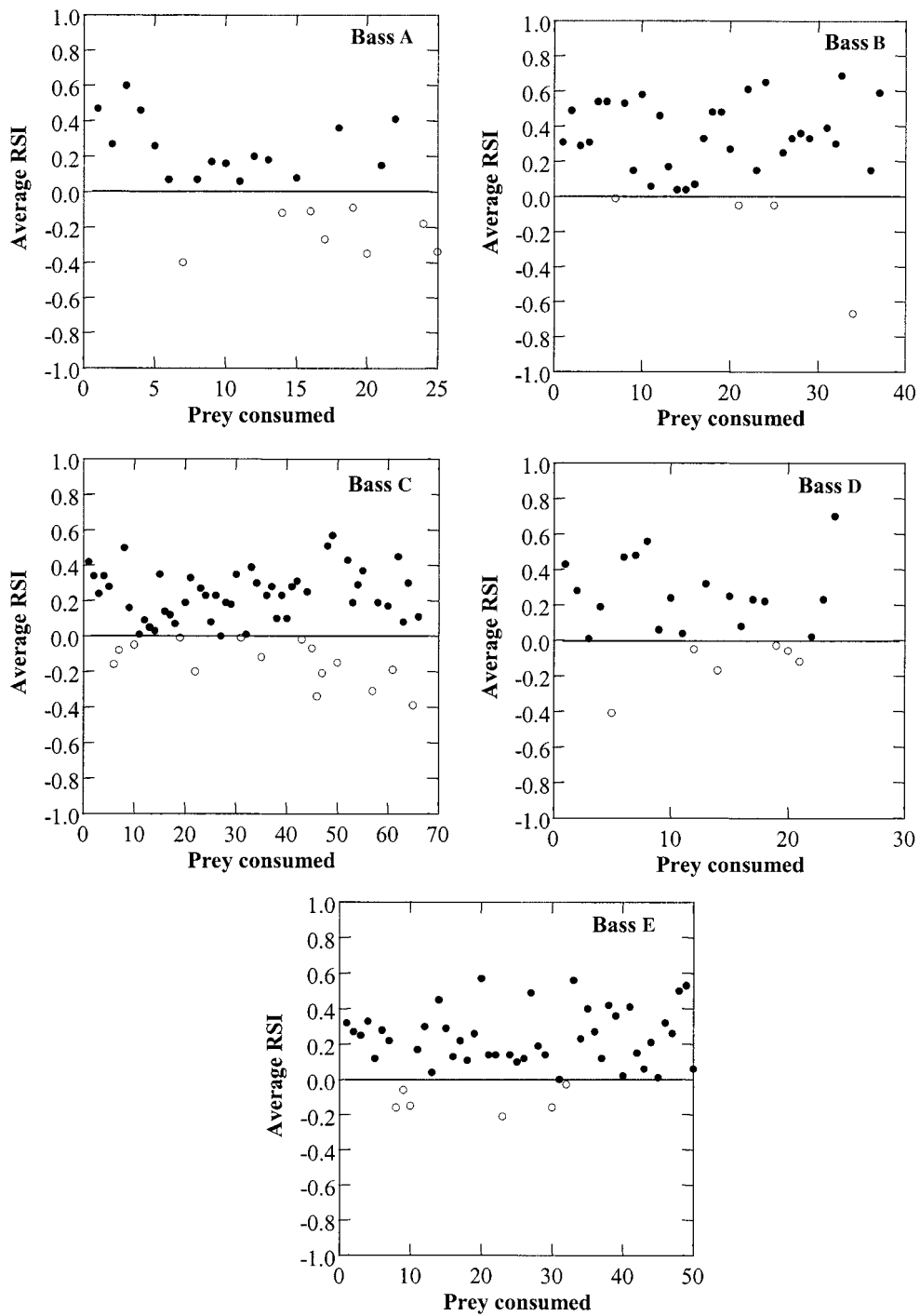


Figure 4. Scatterplot of RSI average value vs. prey consumed for five largemouth bass, *Micropterus salmoides*. Open circles denote suction-dominated feeding. Dark circles represent ram-dominated feeding.

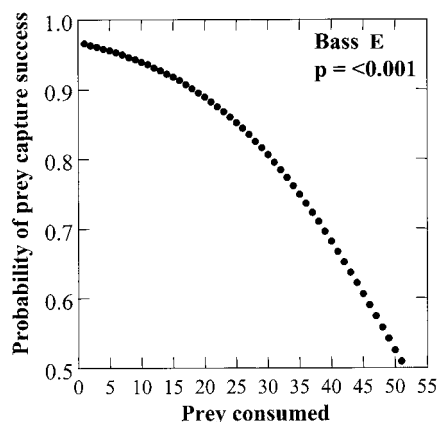


Figure 5. Logistic regression of the probability of prey capture success vs. prey consumed for a representative largemouth bass, *Micropterus salmoides*. Note: all other largemouth bass studied showed similar patterns of decreasing prey capture success with increasing number of prey consumed.

Table 3. Statistics for logistic regressions of the probability of prey capture success vs. prey consumed for five largemouth bass, *Micropterus salmoides*. Asterisks next to p-value denote significance at the $\alpha = 0.05$ level. N represents the number of prey consumed for each bass.

Bass	N	Constant	Coefficient	Odds ratio	χ^2 -value	p-value
A	26	3.062	-0.151	0.86	31.579	<0.001*
B	39	1.963	-0.036	0.965	5.235	0.022*
C	66	2.695	-0.043	0.958	38	<0.001*
D	25	3.151	-0.136	0.873	23.664	<0.001*
E	51	3.4	-0.066	0.936	29.806	<0.001*

Results of this study indicate observable changes in the feeding kinematics of the largemouth bass with the effects of satiation. Therefore, future kinematic studies of fish feeding should consider satiation effects in their characterization and analysis of the feeding mechanism. To determine when satiation begins to influence prey capture kinematics, we conducted a repeated measures ANOVA for all significant kinematic variables. The point at which satiation begins to influence the kinematics of prey capture is highly variable among kinematic variables and individual bass (range 9–49 prey consumed). Nevertheless, we suggest using a conservative estimate of the first ten consecutive bites in future studies to avoid any confounding effects of satiation. Indeed, numerous studies in the past have limited the number of prey consumed consecutively to this range (Cook 1996, Nemeth 1997a,b).

Modulation of strike mode

The bass primarily employed ram feeding regardless of the degree of satiation. No significant trend was observed when RSI value was plotted against prey consumed for each bass; however the analysis of RSI average value per prey consumed revealed the ram-dominated pattern (Figure 4). Therefore, no modulation of strike mode was observed in these bass under the experimental conditions in that the bass did not consistently change from ram to suction or vice versa with satiation. Although modulation was not observed in the strike mode of *M. salmoides*, modulation was noted in prey capture kinematics as five of the twelve kinematic variables showed consistent changes with satiation. This suggests that bass are responding to satiation effects through kinematic changes in jaw function while still using a ram-feeding pattern. Occasionally the bites were suction dominated; however, due to the limitations of the RSI in accurately accounting for movement of elusive prey away from the predator, it is possible that these data underestimate the ram component of the strikes used by the fish.

The RSI is limited by its inability to distinguish pure ram feeding and its inability to predict a pure suction strike (-1) due to the incorporation of jaw protrusion into the forward motion of the predator (Summers 1993, Nemeth 1997b, Van Damme & Aerts 1997, Summers et al. 1998). While the RSI can predict pure suction strikes in primitive fishes that lack jaw protrusion, the largemouth bass clearly exhibits jaw protrusion in its strikes, which can be problematic for the RSI (Figure 2). In addition, as mentioned above, the RSI can severely underestimate the ram component of a strike on elusive prey (Norton & Brainerd 1993). For example, calculating the RSI in a strike in which an elusive prey is moving in the same direction as the advancing predator will always underestimate the ram component of a strike, implying a partial suction component when in fact there is none. In this scenario, a pure ram strike (+1) can never occur if the prey has a degree of elusivity. Nevertheless, the RSI quantifies relative predator movement to prey movement during the strike, and was therefore employed in this study.

The primary use of ram feeding may have implications for energetic trade-offs and the generation of less suction velocity by the predator with the effects of satiation. When the bass is hungry it expends more energy for prey capture due to a greater reliance on predator movement through ram as compared to suction. When considering energy expenditures involved with

prey capture, we can gain knowledge from bioenergetics models and models of fish foraging (Mittelbach 1981, Hanson et al.¹). Given that a fish will expend a similar amount of energy in the movement of jaw muscles during feeding, regardless of whether it uses ram or suction feeding, ram feeding must require greater energy expenditure due to swimming. From a bioenergetics standpoint, swimming uses energy and decreases the amount of energy allocated to growth with all other factors equal (Hanson et al.¹). Similarly, models of energy intake that take into account handling time and search time in making habitat decisions suggest that ram feeding is more energetically costly (Mittelbach 1981). For example, a ram feeding predator will spend more energy in the search and capture of elusive prey than a predator which does not expend much energy to capture non-elusive prey both in the search and capture of that prey. If suction velocity diminishes as the fish becomes satiated, this presumably diminishes the distance between the predator and prey at which suction feeding is successful (Lauder 1980). This in turn may translate into a continued reliance on ram with satiation, which is perhaps energetically more costly than suction feeding, which in the case of the bass is coupled with diminishing prey capture success.

In their study of feeding method employed by morphologically similar species of fishes on elusive and non-elusive prey, Norton & Brainerd (1993) found that *M. salmoides* predominantly employed ram feeding for both prey types. In support of their findings, this study presents evidence that *M. salmoides* can and does utilize predominantly ram feeding along with some suction feeding as part of its feeding repertoire on elusive prey.

The effects of satiation on foraging success

Prey capture success, as represented by the probability of a successful strike per consecutive prey consumed, decreased over the course of a feeding event to satiation. That is, each bass became less successful at capturing the prey on the initial attempt at increasing levels of satiation. This observation was expected as it is likely that the motivation of the bass would decrease as hunger levels diminish. Although prey capture success diminishes with increasing satiation, a high percentage of strikes are still successful on the initial attempt towards

the end of the feeding bout; this may be accounted for by the utilization of ram feeding seen in response to diminishing levels of suction velocity in the bass.

While we cannot discount that muscle fatigue contributed to the changes observed in the kinematic variables and prey capture success in this study, we feel that they are minor contributors. We believe that muscle fatigue was not a major variable influencing our findings because the total duration of each strike (mean 66 ms) was much shorter than the interval (one minute) allowed between each offer of a prey item during a feeding bout, allowing ample time for full recovery of the muscles used during a strike. The sternohyoideus, levator operculi, hyohyoideus, adductor mandibulae, levator arcus palatini, and adductor arcus palatini muscles are involved with jaw and suspensorial abduction and adduction in teleost fishes (Osse 1969). In the perch, *Perca fluviatilis*, the sternohyoideus consists of white, fast, anaerobic fibers and the levator operculi consists of similar white fibers in addition to pink fibers, which are fast twitch fibers with both aerobic and anaerobic capacity. White and pink fibers of the head are only active during fast movements such as feeding (Akster & Osse 1978). Barends (1979) and Barends et al. (1983) showed a similar division of the perch and rosy barb, *Barbus conchonioides*, adductor mandibulae into aerobic and anaerobic portions, but this muscle is more correctly classified as being composed of multiple fiber types, making the reduction to two fiber types an oversimplification. Regardless, the general pattern that emerges is that the anaerobic portions are primarily used for sporadic feeding movements (Herring 1994). During isometric contraction of red and white fibers isolated from the hyohyoideus of the carp, *Cyprinus carpio*, white fibers have shorter contraction and relaxation time than red fibers with a half relaxation time of 106 ms for white fibers (Granzier et al. 1983). However, white fibers are more susceptible to fatigue and showed a 50% drop in peak tension after approximately 20 tetani repeated two seconds apart. In the majority of teleosts, fast fibers are multiply innervated by more than one motor end plate and multiply innervated fibers are universal in jaw and trunk muscles in some teleosts (Johnston 1983, Herring 1994). Under natural feeding conditions multiply innervated fibers may not fatigue as rapidly as indicated above; different fibers may be active at different times and they may show graded responses as seen for the adductor operculi fibers of *Oreochromis mossambicus* (Flitney & Johnston 1979, Granzier et al. 1983). Although fatigue may be a factor

¹ Hanson, P.C., T.B. Johnson, D.E. Schindler & J.F. Kitchell. 1997. Fish bioenergetics 3.0. Sea Grant Technical Report, Wisconsin Sea Grant Institute, Madison 103 pp.

in *M. salmoides* after repeated captures spaced one minute apart, we believe this is less important than the effects of satiation.

In summary, jaw opening velocity and prey capture success decrease in bass with the effects of satiation. Consistent changes in the jaw movements of the bass with the effects of satiation suggest that bass modulate prey capture kinematics. However, no modulation of the strike mode was observed for *M. salmoides* with the effects of satiation, as ram feeding was primarily employed throughout the entire feeding event. The results of this study demonstrate the need to control for satiation in future studies of the feeding mechanisms in fishes. Although the influences of satiation may depend on the fish species studied and the prey item used, we recommend analyzing no more than ten consecutive strikes when studying prey capture kinematics in fishes.

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