

Predatory Behavior and Competition Among Laboratory-housed Largemouth and Smallmouth Bass

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ABSTRACT: Single and mixed-species groupings of largemouth (*Micropterus salmoides*) and smallmouth (*M. dolomieu*) bass were studied in order to document behavioral patterns associated with locating, capturing and ingesting prey, and to evaluate differential responses to a regime of forced competition for limited food. The analyses focused on the behavioral differences associated with (a) different prey species; (b) prey size, and (c) microhabitat. Cinematography aided in the identification of species-specific searching and prey-pursuit behavioral patterns. Both species were able to capture prey using different combinations and sequences of basic functional jaw and head movements. Differences in the relative lengths of jaw bones were not reflected in a difference in the total range of prey sizes consumed by adults of the two species, but rather appeared to affect the efficiency by which various feeding modes were performed (e.g., biting, engulfing and suction). Under the competitive feeding regime, largemouth bass captured significantly higher proportions of large prey and fewer small prey than smallmouth bass in the mixed-species subadult groups. Adult basses exhibited no significant difference in the frequencies of prey captures on the basis of prey size, but did capture prey at significantly different rates from four microhabitats in the mixed-species group compared to the conspecific groups. Adult basses of the two species also exhibited significant differences between groups (mixed vs. single species) in the relative proportions of feeding modes used in capturing prey. For each species, there was a significant relationship between the proportions of the feeding modes used and the microhabitats where prey were seized. The microhabitat niche overlap value was $\emptyset = 0.91$ for the single species adult groups and $\emptyset = .77$ for the mixed-species adult group. Subadult basses did not separate spatially, but rather exhibited lower niche overlap for the prey size dimension in the mixed-species groups ($\emptyset = .74$), compared to the single species groups ($\emptyset = .95$). No significant pattern of differential prey captures between bass species was observed on the basis of the five prey species offered. The relationships between morphology, environment foraging efficiency, and behavioral variability are discussed with reference to their potential roles in natural settings.

INTRODUCTION

A number of approaches have been employed in the study of fish foraging behavior, with most studies focusing on a single level of biological organization. For example, numerous studies of natural populations have sought information on food resource utilization patterns, generally in attempts to determine seasonal, ontogenetic or interspecific effects (Keast, 1978; George and Hadley, 1979, and many others). A number of laboratory studies have isolated the behavioral components of prey capture and handling behavior of fishes through the aid of high-speed cinematography (Alexander, 1970; Nyberg, 1971) and electromyography (Liem, 1980; Lauder, 1983). Few studies, however, have critically assessed the effects of the components of individual foraging behavior in relation to ecological problems. Direct field observations of fish feeding behavior are infrequent, relying on the synchronous union of highly transparent water, access to the aquatic medium by the observer, and either relatively frequent feeding bouts by the fishes (e.g., herbivorous coral reef fishes; Lobel and Ogden, 1981) or relatively chance sightings of rare feeding events (e.g., piscivorous fishes; MacKaye, 1981). Though fewer in number, studies integrating laboratory observations of fish behavior with information from natural populations have provided valuable insights into the behavioral compo-

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nents underlying ecological processes (Stein, 1977; Werner, 1977; Lobel and Ogden, 1981; Mittelbach, 1981; Werner *et al.*, 1977).

Generalized fish predators pose particularly interesting problems for both functional morphologists and ecologists. For example, Nyberg (1971) demonstrated how the relatively primitive Acanthopterygian jaw structure of the largemouth bass (Centrarchidae) is used to produce a variable feeding repertoire. Liem (1980) showed that the variable feeding behavior of several species of the Cichlidae are derived from a relatively specialized trophic morphology.

The ecologies of sympatric generalized predators (*i.e.*, those lacking trophic specialization and using a broad spectrum of prey) provide excellent test cases for competition theory. Despite recent arguments concerning the relative magnitude and periodic frequency of competition within natural communities (Schoener, 1982), patterns of differential resource use among sympatric organisms continue to influence our understanding of the factors influencing the local distribution, abundance and behavior of organisms. Sympatric freshwater fishes have frequently been shown to exhibit ecological segregation via partitioning of food resources (Starrett, 1950; Flemer and Woolcott, 1966; Moyle, 1973; and others) and microhabitat (Mendelson, 1975; Werner and Hall, 1976; Werner *et al.*, 1977; Gorman and Karr, 1978; Baker and Ross, 1981; and others). Several studies have shown that dietary differences were largely the result of differences in foraging habitats (Nilsson, 1960; Johannes and Larkin, 1961; Keast, 1978; George and Hadley, 1979; Paine *et al.*, 1982; Surat *et al.*, 1982). Yet relatively few studies have focused on the behavioral components of niche partitioning among fishes. While the components of interference competition are relatively easy to observe (aggressive behavior), the mechanisms of exploitation competition (resource depletion) are much less obvious. Differential foraging efficiencies among competing freshwater fishes have been shown to result in asymmetrical exploitation of microhabitats or habitat patches within experimental tanks (Schutz and Northcote, 1972) and ponds (Werner and Hall, 1977, 1979). If major morphological and behavioral differences are evident between potentially competing species, reasonable predictions about the polarization of differential resource use patterns are possible (Keast and Webb, 1966; Gatz, 1979a, 1979b). But if character divergence is small (as between congeners), the mechanisms producing ecological segregation may be subtle, where a suite of minor differences in morphology and behavior produce significant patterns of resource partitioning. The direction and magnitude of niche shifts should be less predictable in species with large niche breadths (Van Valen and Grant, 1970).

This study examines the foraging behavior of *Micropterus salmoides* and *M. dolomieu* under a forced competition feeding regime in an attempt to integrate behavioral data with existing ecological information. These predatory freshwater fishes are extremely similar morphologically, wide-ranging, and generalists in both microhabitat and food utilization. The largemouth bass *M. salmoides* occurs in a variety of habitats from Minnesota to Quebec and S to Tamaulipas, Mexico, and from Virginia through Florida on the Atlantic coast (also widely introduced worldwide; Robbins and MacCrimmon, 1974). The species occurs primarily in lentic and lower gradient lotic systems, often in association with rooted aquatic macrophytes or emergent vegetation (Trautman, 1981). As adults, largemouth bass are largely piscivorous, but the utilization of crustaceans, insects, amphibians and other small vertebrates is well-documented. The smallmouth bass *M. dolomieu* also occurs in a variety of habitats from Minnesota to Quebec and S to Arkansas and northern Alabama (also widely introduced elsewhere). Most commonly, smallmouth bass are encountered in intermediate gradient streams with quiet pools fed by fast riffles, and in lakes, often in association with rocky shoals. The diet of the smallmouth bass is quite similar to that of the largemouth, although the former often exhibits a greater reliance on decapod crustaceans where these are abundant (Clady, 1974; Hubert, 1977). The two species co-occur in numerous lentic and lotic systems, especially streams having intermediate or alternating gradients and lacustrine environ-

ments, where the littoral zone is heterogeneous in habitat characteristics. In soft-bottomed, warm-water ponds, the smallmouth bass cannot compete with the largemouth, although populations persist in monospecific stockings (Bennett and Childers, 1957; Smitherman and Ramsey, 1972).

The present study was conceived with the following goals: (1) to document the full range of behavioral patterns involved with feeding for both species of black bass; (2) to produce an environment of intense competition for limited food resources within single and mixed-species groups within large aquaria; (3) to closely monitor the success of each species along three dimensions associated with the food resource (prey type, prey size, microhabitat); (4) to analyze the association between feeding behavior and individual success, and (5) to evaluate the relationship between morphology, behavior, and their implications for potential competitive settings among natural fish populations.

METHODS

Single-species (conspecific) and mixed-species (heterospecific) groups of largemouth and smallmouth bass were established in large laboratory aquaria containing simulated components of natural aquatic habitats. Videotapes and motion pictures were employed in the analysis of behavioral sequences and the determination of the success rates of individual bass in capturing limited numbers of prey organisms introduced into the tanks.

Experimental animals. — Both species of black bass were seined from Four Mile Creek in Butler Co., Ohio, and electroshocked from Acton Lake in Preble Co., Ohio, in March 1980 and early September 1981. Eight additional largemouth bass were collected by angling in a farm pond in Preble County and three smallmouth bass were obtained from Indian Creek, Butler County, in September 1981. Fishes were taken immediately into the laboratory and placed into separate 20-liter opaque plastic containers (fishes < 165 mm TL) or into large, aerated fiberglass troughs, and isolated by opaque partitions (fishes > 165 mm TL). The fishes were kept in isolation at 12 ± 2 C and were not fed for 1 week, thus permitting the complete passage of all gut contents. Following the week of isolation, total length and weight of each fish was taken.

The fishes were then placed into the experimental tanks in one of two groups: conspecific or heterospecific. In the heterospecific groups, individuals of each species were size-matched by total length (Table 1). Experimental fishes used in 1980 were considered "subadults" based on *post mortem* examination of opercular bones for annuli and comparisons with published data on growth rates for the two species in the region (Brown, 1960; Clark, 1960). Fishes used in 1981 were "adults" based on the same criteria. The adult groups consisted of four fish per tank rather than six (subadult groups) in an attempt to equalize fish biomass. It was not possible to totally eliminate size discrep-

TABLE 1. — Total lengths (mm) of fishes in each experimental group at the onset of the study. (Some fishes of "adult" groups were probably sexually immature 2 year olds)

Treatment group		Individual <i>M. dolomieu</i>				Individual <i>M. salmoides</i>				
Subadults										
Conspecific group	Ia	102	100	98	96	80	79			
	Ib							174	164	160 145 145 138
Heterospecific group	Ia	165	165	126				157	155	125
	Ib	110	102	100				124	110	102
Adults										
Conspecific group	IIa	178	175	170	167					
	IIb							190	188	187 180
Heterospecific group	II	252	245					225	208	

ancies in the groups, and these differences, along with differences in individual color patterns, were used as a means of identifying individuals.

Experimental tanks.—Each group was held in aerated, aged tap water for 70 days in separate 1140-liter wooden tanks, each with a 2.5 X 0.6 m glass-viewing window on one side. The tanks contained an 8-cm layer of rinsed sand. Two simulated microhabitats were placed in the center of each tank 60 cm apart along the long axis. One microhabitat consisted of bunched artificial plants (similar to *Vallisneria*) averaging 40 cm in height and rooted in the substrate. The other microhabitat in each tank was a simulated rock shoal comprised of a pile of cobble (Cummins, 1962) which contained numerous spaces, potentially usable by small benthic prey. Each tank received overhead lighting from two fluorescent bulbs (8608 lux). Each treatment group was maintained on a 12:12 LD cycle (0600-1800) to simulate spring and autumn daylengths. Water temperature varied between 17 and 25 C. Wooden dowel rods were fastened to the back wall of each tank in a vertical position, 20 cm apart, to serve as reference points in the determination of predator attack velocities.

Feeding regime.—Each treatment group was provided one prey item per resident every 48 hr at 1600 hr. The prey were introduced in two groups of three (to subadults) or two (to adults) prey. Some basses consumed more prey than others on a given feeding date. Prey items consisted of locally collected fishes, *i.e.*, *Notropis whipplei*, *Semotilus atromaculatus*, *Pimephales notatus*, *Etheostoma caeruleum* and crayfish (*Orconectes rusticus*). Only one prey species was presented on a given feeding date, and the order of presentation was randomized. Prey were divided into two size categories for each treatment group and the size intervals were based on the size of the smallest tank resident. On each feeding date, half of the introduced prey were small (prey/predator TL ratio between .2 and .33) and half were large (prey/predator TL ratio between .33 and .5). All of the prey were introduced into the experimental tanks via flushing with water through opaque plastic tubes secured diagonally to the back wall of each tank. The bottoms of the tubes were positioned just above the rocky shoals and within the vegetation. The order of presentation (large vs. small prey; rocks vs. vegetation) was randomized on each feeding date. Any prey not consumed after 3 min were removed from the experimental tanks (generally these were prey hidden from the predator's view and thus sequences could not be filmed if discovered by the predator at a later time).

Individual feeding rates were expected to be unequal under the competitive feeding regime. Therefore once per week, prey (*Pimephales*) were introduced directly at the water's surface near the center of each tank, and all basses were permitted to feed until satiated. This insured that any individuals that had not captured prey during the previous week would obtain sufficient nutrition for adequate health during the experiment. The observation that basses normally ate from 2-8 *Pimephales*, depending on size, indicated that the regular feeding ration for the filmed sequences was indeed limiting food intake severely.

Data collection and analysis.—Additional lighting was used during filming of predatory behavior. Two flood lamps were positioned at the extreme ends of each tank, producing an additional 1076 lux (measured at the center of each tank with a light meter). This did not appear to affect bass or prey behavior. Videotaping (Sony) and motion picture filming at 54 frames/sec (Braun Super 8) were used to record searching and predatory behavior. A Lafayette Super 8 motion picture analyzer was used to examine filmed predation sequences on a frame-by-frame basis.

As one additional quantitative measure of species differences in the manner of prey pursuit, the predator's longitudinal body axis angle was determined at the moment of initial contact with prey. The longitudinal body axis angle was defined as the angle formed between the horizontal plane and an imaginary line running from the fish's eye to the center of the caudal peduncle. This was recorded by tracing the vector from the projector viewing screen and measuring the deviation from horizontal (0°) with a protractor.

The G-test of independence (Sokal and Rohlf, 1981) and niche overlap values (Schoener, 1974) were used in analyzing prey capture and behavioral data. Of the 1080 prey introduced into the experimental tanks during the study, 756 prey captures were recorded on videotape or motion picture film. Consequently, all statistical comparisons are assumed to use random samples from a larger universe of potential data points.

Prey handling studies. — To analyze components of prey handling behavior (basic functional morphology and the effects of prey size, position, etc.), a second series of observations was made on six additional adult smallmouth and five additional adult largemouth bass during November–December 1980. These fishes were housed individually in 1140-liter wooden or metal tanks containing aerated tap water at $14 \pm 3\text{C}$. Each bass was presented one prey item at 48–120 hr intervals. The prey were of various lengths and species. These included the species used in the experimental feeding regime (except *Etheostoma*), as well as *Catostomus commersoni*, *Camptostoma anomalum*, *Moxostoma anisurum*, *Notropis cornutus*, *Pimephales promelas*. Prey handling was videotaped and observed directly. A stopwatch was used to measure the duration of prey handling, which was defined as the time interval from the seizure of prey until its complete passage through the pharynx as indicated by a return to normal rhythmic ventilation.

RESULTS

Foraging behavior. — The foraging behavior of largemouth and smallmouth bass was consistently different in several components. The substrate searching behavior of the largemouth bass involved discrete, jerky swimming patterns with the head lowered and caudal fin raised so that both eyes were fixed upon an area directly in front of the fish's snout (Fig. 1). Smallmouth bass generally swam in a horizontal position near the substrate with the back arched somewhat, and the snout lowered so that prey could be detected using both eyes. Often the fish would tilt its dorsoventral axis away from vertical, apparently facilitating lateral substrate scanning with one eye (Fig. 1). The swimming patterns of the two bass species also differed during prey pursuit, particularly during surface strikes. Largemouth bass frequently remained near the surface while chasing elusive surface prey such as *Notropis*. Largemouth bass surface-foraging involved a series of chases, strikes (accelerated velocity toward prey at close range), reorientation to fleeing prey, and additional strikes. During surface strikes, adult smallmouth bass spent much less time positioned near the surface (intervals rarely exceeded 2.0 sec). Smallmouth bass attacks were characterized by the visual tracking of prey from a position low in the water column, a relatively slow pursuit from a comparable depth, and terminated by a smooth, rapid rise to the surface in an attempt to intercept the fleeing prey. If a miss occurred, adult smallmouth bass always returned to a position low in the water column to relocate prey. It was difficult to distinguish between a pursuit phase and an accelerated strike phase during smallmouth bass attacks.

The longitudinal body axis angle at the moment of initial contact with prey was different for the two species ($F = 11.65$, $df = 1$, $P < .0001$). Smallmouth bass tended to remain more horizontal while attacking prey ($\bar{x} = 15.4^\circ$, $SD = 13.02$, $N = 158$, subadults; $\bar{x} = 15.4^\circ$, $SD = 11.27$, $N = 118$, adults). The mean angle was 23.1° ($SD = 17.05$, $N = 238$) for subadult largemouth bass and 22.7° ($SD = 17.17$, $N = 135$) for adults.

Jaw movements during feeding. — For both species, three major jaw movement patterns (biting, engulfing and sucking) were detected. Two additional, intermediate jaw movements, engulf/bite and suction/engulf, were observed much less frequently. Descriptions of the sequence of movements among the major functional jaw and head elements characterizing each feeding mode are illustrated in Figure 2. The present analysis was limited to the principal functional head structures readily observed on film and videotape. More detailed discussions of anatomical features involved in teleost feeding are available elsewhere (Alexander, 1967; 1970; Liem, 1967, 1980; Lauder, 1983). Biting occurred when prey were simply seized and held between the mandibles and maxillae. Engulfing involved enclosure of the prey within the buccal cavity as the predator passed through

the area with jaws fully open, premaxillae fully extended, and operculae flared. Suction occurred when a prey item was drawn into the buccal cavity by means of the jaw and head element movements specified in Figure 2. The biting mode appeared equivalent to Alexander's (1967) method (i), suction equals method (ii), and engulf/bite appeared similar to method (iii). These observations also corroborate the findings of Nyberg (1971) but add the bite and engulf/bite modes to the largemouth bass feeding repertoire. Due to their low frequency of occurrence ($N = 24$ among all experimental fishes), the two intermediate feeding modes were combined with engulfing for the statistical analyses.

The mean attack velocities associated with the three major feeding modes were as follows: bite = 83.9 cm/sec ($SD = 65.4$), engulf = 103.9 cm/sec ($SD = 59.9$), and suction = 60.9 cm/sec ($SD = 46.4$); values are for all experimental fishes combined. There was no significant difference between the attack velocities of adult largemouth and smallmouth bass. Subadults did differ, however ($t = 2.51$; $df = 29$; $P < .05$); subadult

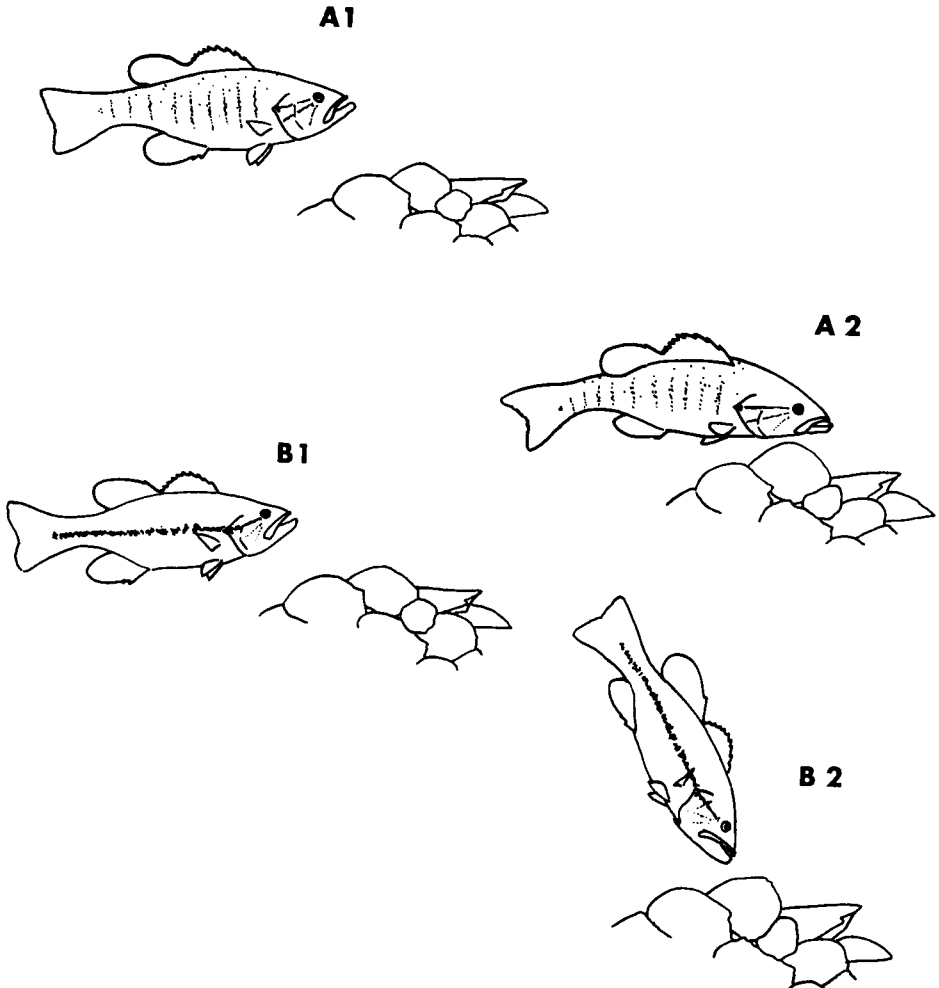


Fig. 1. — Typical substrate searching postures of *M. dolomieu* (A) and *M. salmoides* (B)

largemouth bass averaged 89.7 cm/sec (SD = 61.9) and smallmouth bass 106.2 cm/sec (SD = 73.1) during attacks.

There was no significant difference between the bass species for the position of the prey in the jaws during the initial grasp (Table 2). The region of the prey's body initially seized by the predator depended primarily upon the orientation and direction of movement of the prey relative to the predator. One exception involved the capture of crayfish resting on the substrate, in which a bass often positioned itself behind the prey, seizing its abdomen via the bite mode (66% of *Orconectes* captures), or often with suction in the case of largemouth bass captures of small crayfish. Of 13 attacks initially directed at the cephalothorax, only three were actually ingested headfirst. Crayfish were frequently rejected and recaptured from midwater by the bass, irrespective of whether they were attacked frontally or from behind.

There was a significant relationship ($G = 61.11$, $df = 6$, $P < .001$) between the place of capture in the fishes' environment and the frequencies of the three major jaw movements used by both species when all age and treatment groups were combined. Smallmouth bass most frequently used biting to capture prey within vegetation. They frequently attacked from close range, grasped a portion of the prey's body, and extracted prey from the vegetation by rapidly jerking the head dorsolaterally and bending the body. By contrast, the largemouth bass frequently lunged directly into the vegetation from any distance and used a variety of jaw movements in grasping prey (most frequently suction). Largemouth bass most often exhibited suction during bottom cap-

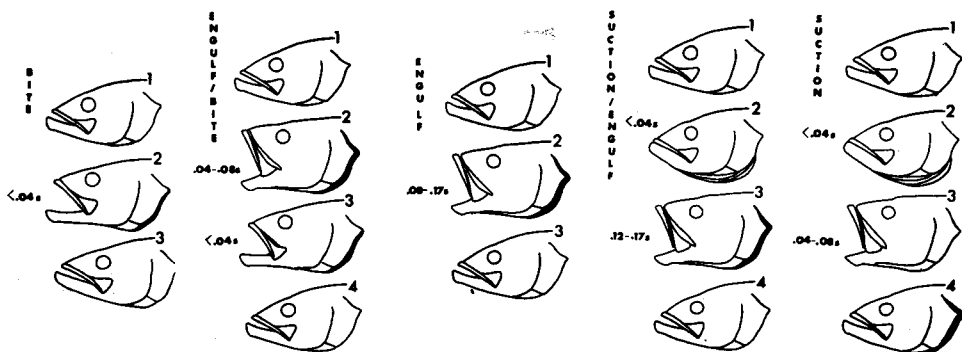


Fig. 2.—The jaw movement patterns involved in prey capture by *Micropterus* (the duration of the jaws agape is designated in hundredths of seconds). BITE: 1—normal “resting”; 2—jaws open but incompletely, opercula abduct and flare, hyoid minimally depressed (prey is held in jaws); 3—jaws close and opercula adduct (may follow period of prey handling). ENGULF/BITE: 1—resting; 2—jaws open completely, premaxilla and maxilla extend forward, opercula abduct and flare, hyoid depresses; 3—jaws close, hyoid raises, opercula remain flared (the bass passes over the prey); 4—jaws close and opercula adduct (prey is held in jaws). ENGULF: 1—resting; 2—jaws open completely, premaxilla and maxilla extend forward, opercula abduct and flare, hyoid depresses (prey is enveloped in buccal cavity as bass passes over it); 3—jaws close followed by opercular adduction. SUCTION/ENGULF: 1—resting; 2—jaws close and opercula adduct, hyoid depression begins, followed by opercular abduction, branchiostegal membranes unfold as opercular seal is maintained; 3—jaws open completely, premaxilla and maxilla extend forward, hyoid depresses completely, followed by opercular flaring (prey not completely sucked into buccal are enveloped as bass passes over it); 4—jaws close, hyoid raises, followed by opercular adduction. SUCTION: 1—resting; 2—jaws close and opercula adduct, hyoid depresses, followed by opercular abduction, branchiostegal membranes unfold as opercular seal is maintained; 3—jaws open, premaxilla and maxilla extend forward, hyoid depresses completely (prey is drawn into buccal cavity by suction); 4—jaws close, followed by hyoid raising and opercular flaring and adduction (see Nyberg, 1971, for more details of suction feeding in *M. salmoides*)

tures, whereas smallmouth bass generally used biting (Table 3). Subadult and adult smallmouth bass frequently initiated bottom strikes from distances of 0.5-1.0 m, approaching at relatively high velocities, jamming their open jaws against sand or rocks and pinning prey to the substrate. During attacks on crayfish hidden within the rocky shoals, smallmouth bass used either suction or biting, in which a portion of the prey was grasped and jerked out with movements similar to those described for vegetation biting sequences. Largemouth bass always used suction during rocky shoal captures; however, biting was used during several captures of crayfish over open sand substrate. Largemouth bass and adult smallmouth bass attacking prey in midwater exhibited engulfing behavior in over 50% of the filmed sequences (N = 75). Subadult smallmouth bass exhibited biting more often in midwater captures; however, it should be noted that filmed samples of jaw movements were low for this group due to the combined effects of their relatively small size and high pursuit velocities.

Effects of competition.—Of 120 prey presented to the adult heterospecific group, 54 were captured by largemouth and 53 were captured by smallmouth bass. In one subadult heterospecific group, the total number of prey captured by each species was not significantly different (68 for *Micropterus salmoides* and 62 for *M. dolomieu* of 180 introduced prey); however, the replicate group favored prey capture by the largemouth bass (94 for *M. salmoides* and 33 for *M. dolomieu* of 180 introduced prey).

There was no significant relationship between the size category of prey (for all prey species combined) and capture frequencies for adults of the two bass species ($G = 1.14$, $df = 1$, $P = .28$). Prey selection on the basis of size was demonstrated by subadult basses

TABLE 2.—Percentages of prey capture positions at the moment of initial grasp by each black bass species (frequency values are in parentheses)

Prey position	Subadults		Adults	
	<i>M. salmoides</i>	<i>M. dolomieu</i>	<i>M. salmoides</i>	<i>M. dolomieu</i>
head-first	33.7 (98)	39.0 (71)	41.9 (36)	42.3 (37)
midbody	12.1 (34)	10.5 (20)	14.5 (13)	11.9 (10)
tail-first	54.2 (102)	50.5 (77)	43.6 (58)	45.8 (48)
	$X^2 = .616$; $df = 2$; $P = .735$		$X^2 = .638$; $df = 2$; $P = .727$	

TABLE 3.—The percentages of jaw movements used by black bass capturing prey in different regions of the water column (B = Bite, E = Engulf, S = Suction)

Capture place	Subadults						Adults					
	<i>M. salmoides</i>			<i>M. dolomieu</i>			<i>M. salmoides</i>			<i>M. dolomieu</i>		
	B	E	S	B	E	S	B	E	S	B	E	S
Bottom	5.0	15.0	80.0	88.2	5.9	5.9	24.1	27.6	48.3	46.1	23.1	30.8
Midwater	11.8	58.8	29.4	80.0	20.0	0.0	15.6	68.7	14.6	18.5	66.7	14.8
Vegetation	9.1	27.3	63.6	100.0	0.0	0.0	33.3	12.5	54.2	85.7	7.1	7.1
Surface	50.0	0.0	50.0	100.0	0.0	0.0	0.0	10.0	90.0	75.0	0.0	25.0
	$G = 14.25$; $df = 6$; $P = .027$			$G = 2.60$; $df = 6$; $P = .86$			$G = 31.71$; $df = 6$; $P < .001$			$G = 29.03$; $df = 6$; $P < .001$		

housed heterospecifically; largemouth bass selected the larger size class more frequently (Table 4). A comparison of niche overlaps for the two species for the prey size dimension yielded $\emptyset = .94$ for adult conspecific groups (if conspecifically housed basses had captured all introduced prey, overlap would equal 1), $\emptyset = .90$ for the adult heterospecific group, $\emptyset = .95$ for subadult conspecific groups, and $\emptyset = .74$ for subadult heterospecific groups. Again, the analysis indicates some degree of food partitioning on the basis of size for small basses but not larger basses in the heterospecific associations.

The two bass species did not differ in their proficiency at capturing different prey organisms under the experimental conditions. G-tests revealed no significant relationships between the prey species and the number of prey captured by individual bass or bass species in any of the treatment groups.

A relationship between the treatment group (hetero- vs. conspecific) and the frequency of prey captures from various regions in the tanks existed for adult largemouth bass (Table 5; $G = 11.84$, $df = 3$, $P < .01$). Adult smallmouth bass exhibited differences in the frequencies of prey captures in different regions of the tanks when treatment groups were compared (Table 5); however, these were just above the chosen limit of statistical significance ($G = 7.53$, $df = 3$, $P = .056$). These data suggest that the location (microhabitat) of prey capture provided a basis for the subdivision of limited food resources provided for adults. The overlap values for the two species for foraging region were $\emptyset = .91$ for adult conspecific groups and $\emptyset = .77$ for the adult heterospecific group. Both species captured relatively fewer prey from vegetation and more from the surface in the adult heterospecific group (Table 5). Adult largemouth bass captured proportionately fewer prey from the substrate and more from midwater in the heterospecific compared to the conspecific group, while the opposite was observed for adult smallmouth bass.

Subadult basses did not demonstrate a significant relationship between the region of prey capture and the treatment condition ($G = 2.97$ and 5.76 for largemouth and smallmouth bass, respectively; $df = 3$; $P = .40$, $.12$; Table 5). Overlap for microhabitat was $\emptyset = .88$ for subadult conspecific groups and $\emptyset = .87$ for subadult heterospecific groups.

Since a relationship between the feeding mode (jaw movement sequences) and capture region within the tanks had been previously established, statistical analyses of feeding mode by species and treatment group were performed. A significant interdependence existed between the jaw movements used in feeding and the bass species when all

TABLE 4.—The percentages of prey size classes captured by bass species in heterospecific groups (P values based on G, 1 df; frequency values are in parentheses)

	Replicate	Species	Large prey	Small prey	P
Adults	II	<i>M. salmoides</i>	53.7 (29)	46.3 (25)	.28
		<i>M. dolomieu</i>	43.4 (23)	56.6 (30)	
Subadults	Ia	<i>M. salmoides</i>	60.3 (41)	39.7 (27)	< .01
		<i>M. dolomieu</i>	38.7 (24)	61.3 (38)	
	Ib	<i>M. salmoides</i>	56.4 (53)	43.6 (41)	< .001
		<i>M. dolomieu</i>	18.2 (6)	81.8 (27)	

treatment groups were combined ($G = 51.85$, $df = 2$, $P < .001$). An analysis of the jaw movements used in feeding and the treatment group (hetero- vs. conspecific) yielded a significant relationship for both adult largemouth ($G = 6.12$, $df = 2$, $P < .05$) and smallmouth bass ($G = 9.16$, $df = 2$, $P < .01$, Table 6). Adult largemouth bass in heterospecific groups used suction more often and bites less often than when in conspecific groups (Table 6). Adult smallmouth bass also used suction feeding more often in the heterospecific group but used the engulf feeding mode less often when housed heterospecifically (Table 6). Biting was the predominant feeding mode used by heterospecifically grouped, adult smallmouth bass. Conspecifically grouped, adult smallmouth bass used biting and engulfing in equal proportions. Subadult basses exhibited very similar trends in comparisons of feeding mode frequencies between treatment groups, but these were not statistically significant (Table 6). These data suggest that adult basses may have maximized their rates of food intake by using the feeding modes that provide them a relative advantage (in terms of efficiency) over the other species in certain microhabitats. Interspecific differences in the use of feeding modes should have been associated with differences in feeding efficiencies since the artificial competitive setting forced the basses to feed swiftly in order to obtain a portion of the limited food supply.

Prey handling. — The description of prey handling behavior that follows is based on an analysis of filmed and videotaped sequences in the experimental treatment groups as well as 88 additional observations on 11 basses collected in November 1981. Prey smaller than 25% of the predator's total length were ingested via rhythmic contractions of the bass's pharyngeal musculature. These were virtually identical in the two species. For intermediate (prey/predator TL ratio $> .25$ but $< .33$) and large (ratio $> .33$) prey, the ventilation movements and pharyngeal contractions appeared much more irregular in the duration of alternative contraction and relaxation intervals, particularly in the largemouth bass. In both species, there was a visible lowering and posterior movement of the pectoral girdle accompanied by contractions of the dorsal head musculature. Movements of the jaws and operculae were accompanied by a reduction in the ventila-

TABLE 5. — The percentage of prey captured from various microhabitats by bass in conspecific and heterospecific groups (p values based on G, 3 df; frequency values are in parentheses)

	Species	Treatment	Substrate	Midwater	Vegetation	Surface	P
Adults	<i>M. salmoides</i>	conspecific	30.3 (27)	34.8 (31)	30.3 (27)	4.49 (4)	< .01
		heterospecific	26.7 (16)	41.7 (25)	13.3 (8)	18.3 (11)	
	<i>M. dolomieu</i>	conspecific	29.1 (23)	40.5 (32)	22.8 (18)	7.6 (6)	.056
		heterospecific	46.1 (24)	30.8 (16)	9.6 (5)	13.5 (7)	
Subadults	<i>M. salmoides</i>	conspecific	37.7 (49)	31.5 (41)	22.3 (29)	8.5 (11)	.40
		heterospecific	33.8 (52)	26.0 (40)	30.5 (47)	9.7 (15)	
	<i>M. dolomieu</i>	conspecific	35.7 (35)	39.8 (39)	12.2 (12)	12.2 (12)	.12
		heterospecific	37.2 (35)	35.1 (33)	22.3 (21)	5.3 (5)	

tion rate during the handling of large size class prey. There was no significant difference in the position of prey within the basses' jaws (*i.e.*, head, tail, midbody) during ingestion of small and intermediate size classes (Nov. - Dec. 1980 observations): however, large prey were grasped by the head or midbody and ingested headfirst in 73% of the cases. Largemouth bass often rested on the substrate with their fins erect while handling large (TL ratio > .33) prey. While resting on the substrate, the pelvic, anal and lower lobe of the caudal fin were generally the only portions of the fish in contact with the substrate. Smallmouth bass rarely rested on the bottom while handling prey, but generally remained stationary in the water column. The five individually housed largemouth and six smallmouth bass exhibited no difference in the upper limits for the prey sizes that could be ingested (Fig. 3). Only cypriniform prey were included in this analysis in order to standardize the comparisons since there is a marked effect of perciform spiny fin rays on ingestion by predators (Hoogland *et al.*, 1956).

The duration of prey handling can be used as an indicator of the energetic cost associated with ingesting prey of various sizes (Werner, 1977). Although the slopes of the two regressions were similar ($F = 4.64$, $df = 1, 23$, $P > .05$), the duration of prey handling was at a minimum for a prey/predator TL ratio of 0.22 for smallmouth and 0.31-0.32 for largemouth bass (Fig. 4). Prey smaller than prey/predator TL ratio 0.2 appeared to be more difficult to handle than slightly larger prey (TL ratio .2-.32 depending on the bass species) due to the jerking head movements required for directing small prey to the esophagus. Prey larger than a TL ratio of .32 required additional time, and perhaps energy expenditure, for the proper alignment of prey, ingestion and compensation for interference with normal ventilation. For subadults and adults of both species, ventilation rates increased following the completion of prey handling (Fig. 5), suggesting the presence of a lactic acid surfeit after prey pursuit, capture and handling. Ventilation rates were significantly affected by the stage of prey handling in adult basses ($F = 10.16$, $df = 2$, $P < .001$) but not significantly in subadults.

TABLE 6. — The percent occurrence of feeding modes used during filmed prey captures by bass in conspecific and heterospecific groups (p values based on G, 2 df; frequency values are in parentheses)

	Species	Treatment	Bite	Engulf	Suction	P
Adults	<i>M. salmoides</i>	conspecific	27.6 (16)	37.9 (22)	34.5 (20)	< .05
		heterospecific	10.3 (4)	33.3 (13)	56.4 (22)	
	<i>M. dolomieu</i>	conspecific	44.7 (21)	44.7 (21)	10.6 (5)	< .01
		heterospecific	48.3 (14)	17.2 (5)	34.5 (10)	
Subadults	<i>M. salmoides</i>	conspecific	15.4 (4)	34.6 (9)	50.0 (13)	.24
		heterospecific	3.8 (1)	26.9 (7)	69.2 (18)	
	<i>M. dolomieu</i>	conspecific	76.9 (10)	15.4 (2)	7.7 (1)	.33
		heterospecific	94.1 (16)	5.9 (1)	0 (0)	

Jaw morphometry.—Premaxillary, maxillary and dentary bones from the skulls of 12 largemouth bass and 11 smallmouth bass were measured for a range of total lengths. In all cases the ratio of the jaw bone, as measured in a straight line from the most anterior to the most posterior point, to the basses' total length was constant (all $r = .99$). The slopes of the largemouth bass regressions (bone length vs. TL) were greater than those of the smallmouth bass for all three bones (Fig. 6). The length of all three jaw bones become a smaller proportion of the basses' body length as the fishes grow, and this occurs to a significantly greater extent in smallmouth bass (Fig. 6). The difference between the relative lengths of the three jaw bones of the two basses is negligible at total lengths less than 110 mm.

DISCUSSION

Largemouth and smallmouth bass exhibited few qualitative differences in the behavioral patterns involved in prey capture. Only substrate searching and the swimming patterns during prey pursuit appeared to be species-specific. The behavioral patterns exhibited during prey-grasping and ingestion were variable, yet qualitatively identical in the two species, differing only in their relative frequencies of occurrence within four microhabitats. The ability to grasp prey by a variety of means (Fig. 2) undoubtedly fa-

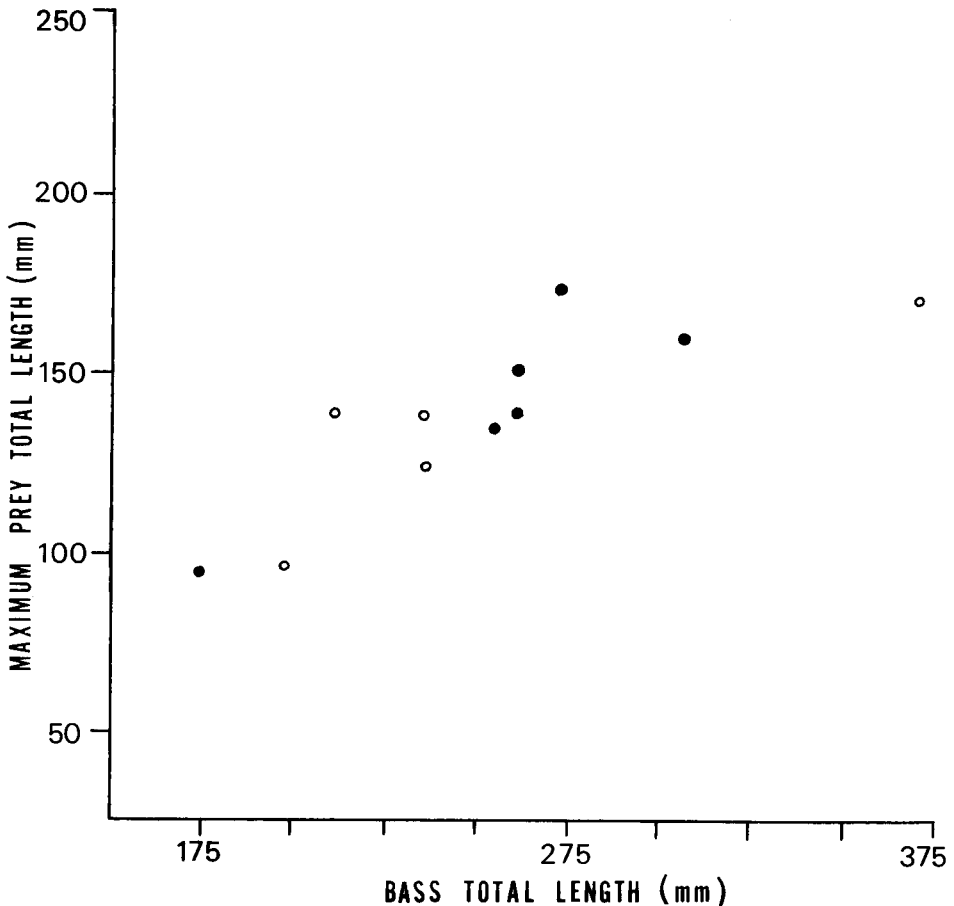


Fig. 3.—Maximum prey sizes ingested by *M. dolomieu* (closed circles) and *M. salmoides* (open circles) used for the prey handling observations

cilitates the successful capture of a relatively broad range of prey organisms in a variety of habitats. The diet breadth, habitat and geographical ranges of these economically and ecologically important fishes have been well-documented (for comprehensive reviews, see Robbins and MacCrimmon, 1974; Stroud and Clepper, 1975; Carlander, 1977).

The two species are quite similar on a morphological basis as well. The largemouth and smallmouth bass differ most significantly in background coloration, coloration pattern, the size and number of scales, maximum body size and jaw dimensions. The proportional difference between the jaw dimensions of the two species was shown to increase with size. We hypothesize that this difference in jaw dimensions is related more to differential efficiencies among the five foraging modes and less to optimal forage size, on the basis of four observations resulting from the current study: (1) No significant difference existed for the maximum size of cypriniform prey that could be ingested by the two bass species over the size range of individuals used for the prey-handling observations. This finding corroborates Lawrence's (1957) conclusion that the ingestion of prey is limited by the esophagus (*e.g.*, the cleithrum bones bordering the esophagus) of the largemouth bass rather than the gape diameter. (2) The relationship between the prey/predator length ratio and handling time was not significantly different between the two species. (3) Significant differences among the relative proportions of large and small size

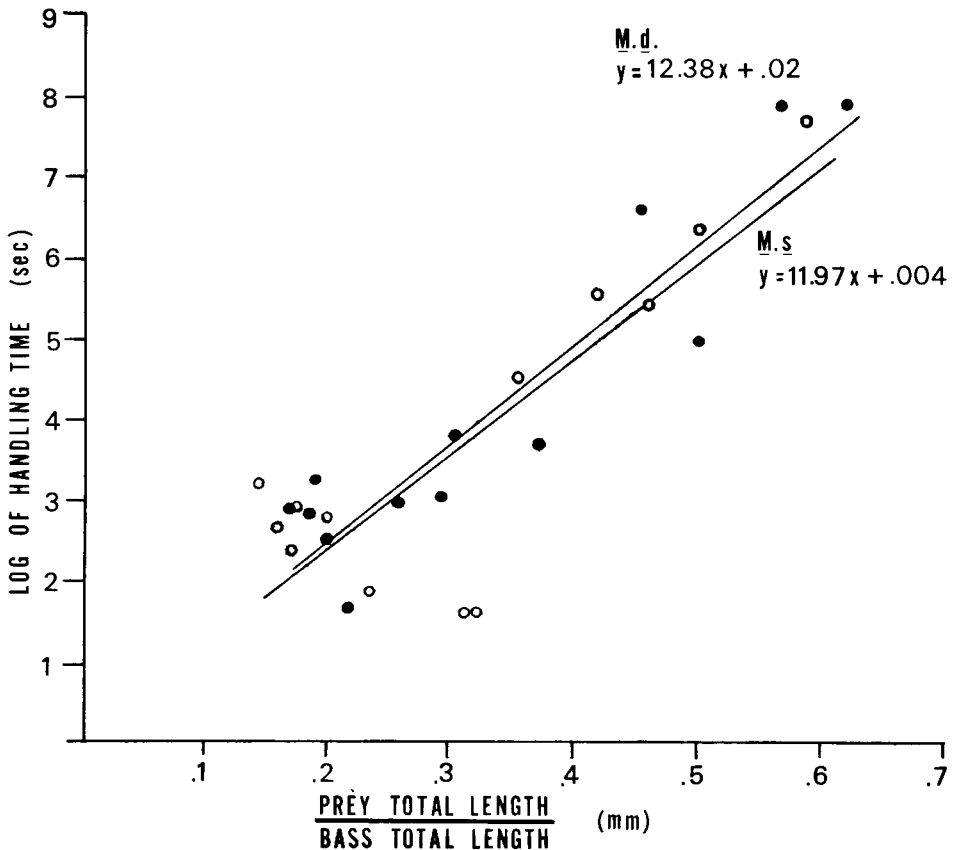


Fig. 4. — Semilog plot of handling time for 27 prey to predator length ratios involving *M. dolomieu* [closed circles ($r = .93$, $P < .01$)] and *M. salmoides* [open circles ($r = .83$, $P < .01$)]

class prey were observed only in the subadult heterospecific groups, when the differences in jaw dimensions were negligible. (4) A significant relationship between treatment group and the frequency of prey captures by various feeding modes existed among adult basses (smaller basses exhibited statistically nonsignificant trends among feeding mode frequencies).

The most striking difference among basses of all treatment groups was the greater reliance upon biting for successful prey capture by smallmouth bass. Largemouth bass always exhibited suction and engulfing, more frequently than the biting mode of prey capture. The data implicate relative interspecific differences in the efficiency of prey capture via biting, engulfing and suction. The larger jaw dimensions of the largemouth bass undoubtedly facilitate more efficient prey capture via engulfing. A larger gape and buccal volume should permit the bass to fully envelope larger prey, as well as compensate for small miscalculations during engulf attacks on evasive, small prey. The effect of relative jaw dimensions on suction and biting efficiency is less obvious, but probably involves buccal cavity volume in the case of the former and jaw strength in the latter. Nyberg (1971) described the elements of suction feeding in the largemouth bass in detail. Effective suction feeding relies upon the generation of negative pressure within the orobranchial chamber prior to jaw opening (Alexander, 1970). The large orobranchial chamber of the largemouth bass apparently provides for effective suction feeding despite its comparatively large gape (*i.e.*, more precisely directed suction is accomplished by a small gape diameter as observed in smaller centrarchids). The success of bass suction feeding is dependent upon drawing prey into the buccal cavity via a rapid burst of jaw

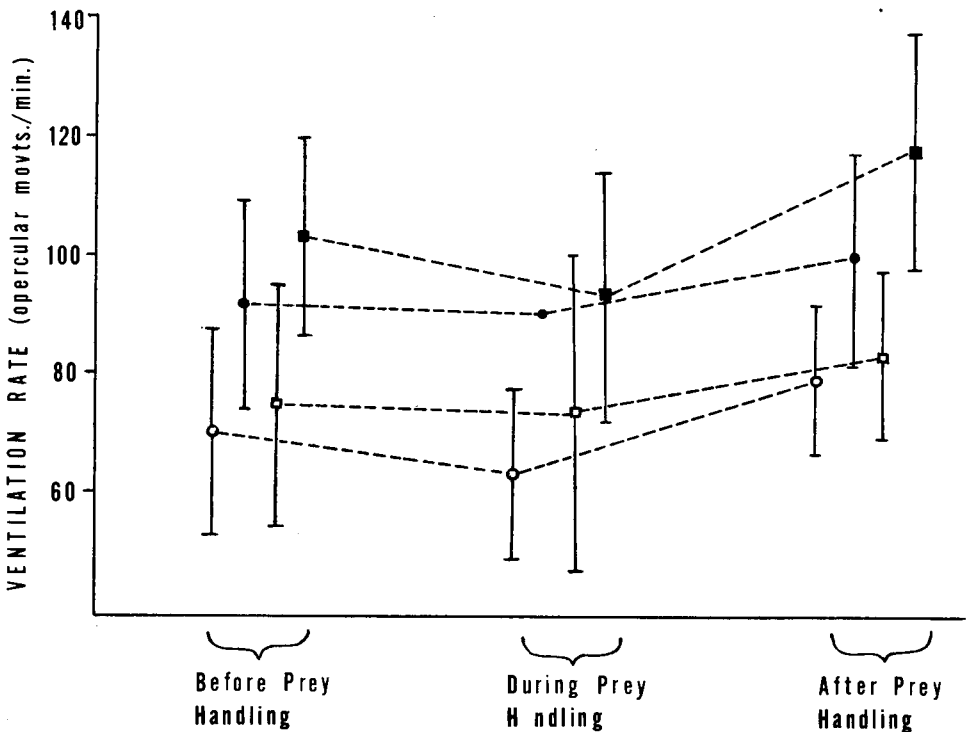


Fig. 5. — Mean ventilation rates for subadult *M. dolomieu* (closed circles), subadult *M. salmoides* (open circles), adult *M. dolomieu* (closed squares), and adult *M. salmoides* (open squares) at various stages of prey handling (+ 1 sd)

opening at close range. Frequently, sand and debris were sucked into the buccal cavity along with prey, indicating an inability to direct the area of suction with a high degree of precision. These observations parallel Alexander's (1970) findings that *Ictalurus melas* and *Taurulus bubalis*, two teleosts with comparatively large gape diameters, generated the greatest relative increases in orobranchial chamber volume among eight fishes studied. We suggest that, compared to smallmouth bass, the largemouth bass possesses the more developed head morphology for engulfing and undirected, burst suction feeding.

It is unknown whether or not this enhanced engulf and suction feeding is associated with a decrease in the strength of the jaws for holding prey during the biting mode of feeding. Predatory teleost fishes known to be powerful biters (*i.e.*, piranhas of the Characidae, jacks of the Carangidae, bluefish of the Pomatomidae, etc.) possess compact jaws and a steeply sloping forehead for muscle attachment. We hypothesize that smallmouth bass possess relatively stronger, more compact jaws than largemouth bass, and that a trade-off exists between strength and gape diameter (and perhaps maximum orobranchial chamber volume). The ability of smallmouth to grasp and jerk crayfish from within rock crevices was previously noted. Laboratory studies, in which predators

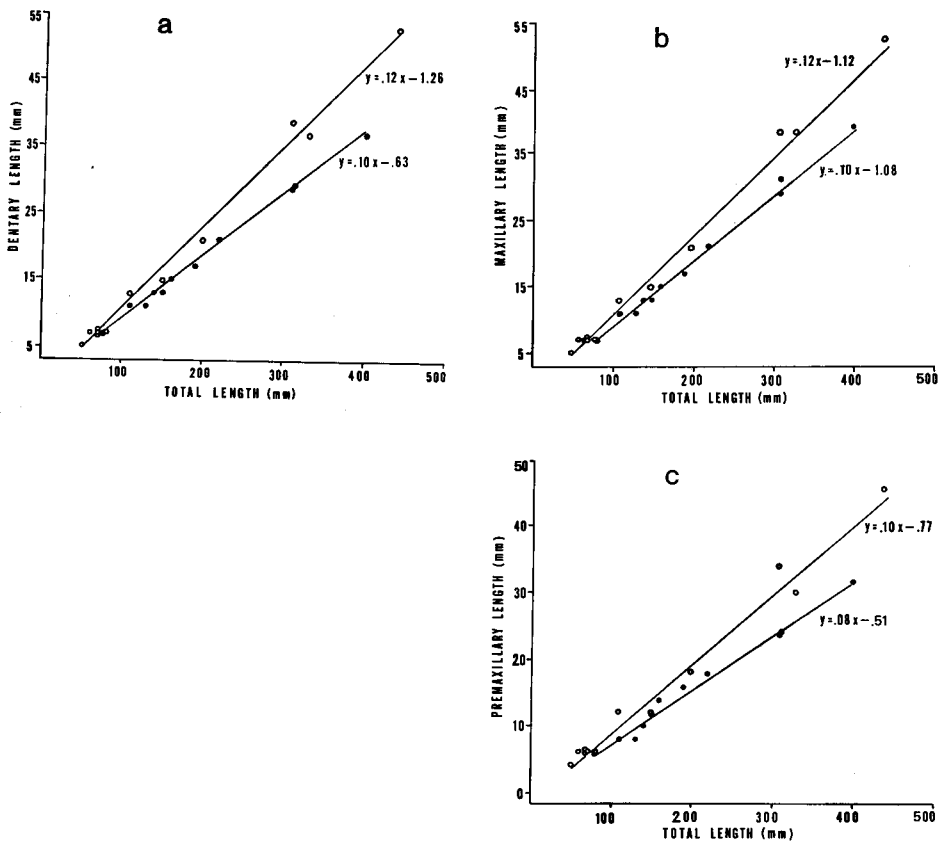


Fig. 6.—Linear regressions for the relative lengths of (A) dentary, (B) maxillary, and (C) premaxillary bones of *M. salmoides* (open circles) and *M. dolomieu* (closed circles) ($r = .99$ in all cases). The regression slopes were different between the two bass species in each case: (A) $F = 29.00$, $df = 1, 19$, $P < .001$; (B) $F = 29.00$, $df = 1, 19$, $P < .001$; (C) $F = 6.28$, $df = 1, 19$, $P < .025$; (Snedecor and Cochran, 1967)

are presented prey affixed to a pressure-sensitive device, could directly test the hypothesis.

Two alternative hypotheses may account for the observed interspecific differences in morphology and behavior. The traits may have a largely innate basis, having evolved under conditions of allopatry with each species restricted to geographical zones dominated by different aquatic habitats. Following this scenario, the resource segregation observed among contemporary sympatric bass populations may be based largely on previously evolved innate behavioral differences, and past or present competition need not be inferred (e.g., selective segregation *sensu* Brian, 1956). Schutz and Northcote (1972) concluded that both behavioral differences observed in the laboratory and ecological differences among cutthroat trout *Salmo clarki* and Dolly Varden *Salvelinus malma*, were due to innate morphological and behavioral differences. Species-specific differences in morphology and behavior were found to play a major role in the replacement of planktivorous brook silverside, *Labidesthes sicculus*, by inland silverside, *Menidia beryllina*, in Lake Texoma (McComas and Drenner, 1982). The more recently introduced *Menidia* possess a more protrusible jaw apparatus, which was apparently more effective in capturing elusive copepods in the novel lentic environment.

Alternatively, the phenotypic and ecological differences observed between black bass species may have resulted from interspecific competition among sympatric populations (e.g., interactive segregation *sensu* Brian, 1956). The demonstration of niche shifts, or compression, among sympatric organisms under conditions of resource limitation is strong evidence for contemporary interactive segregation (Werner and Hall, 1976, 1977, 1979). The statistical analyses of capture frequencies for the two bass species revealed a significant relationship between treatment group and prey size for small predators, and treatment group and microhabitat and feeding behavior for larger basses. These results, together with the corresponding niche overlap value differences, provide evidence for potential mechanisms for niche shifts between these species under appropriate conditions of resource limitation. Caution should be exercised in this interpretation, since the number of individual predators employed in the adult treatment groups was small, even though a large number of predation sequences were recorded. Further evidence concerning the viability of behaviorally mediated, interactive segregation among natural populations of black basses awaits future laboratory studies of similar and alternative designs, since there is currently no capability for observing feeding behavior in sufficient detail in the field.

Schutz and Northcote (1972) argued that the distinction between selective and interactive segregation may be difficult or impossible to determine among potentially competing populations experiencing continuous evolutionary differentiation upon contact. Yet by their own criterion, interactive segregation is inferred from the occurrence of niche shifts when single and mixed-species groups are compared. Werner and Hall (1976, 1977, 1979) provided perhaps the best evidence of niche shifts for fishes in their experiments on sunfishes in ponds. A brief review of major features of the ecology and distribution of largemouth and smallmouth bass supports a model of interactive segregation where the two species co-occur under conditions of appropriate density (i.e., where populations have not been significantly reduced to low levels by overfishing, winter freezes, pollution, etc.).

Within the broad zone of sympatry exhibited by the two species (both historical and contemporary), the largemouth bass is most frequently encountered in the lower gradient and slower, backwater regions of drainage systems, including vegetated littoral zones of the Great Lakes (Robbins and MacCrimmon, 1974). Smallmouth bass are more common in clear, comparatively higher gradient regions of streams and rocky, wave-swept littoral regions of the Great Lakes. Many of the morphological and behavioral differences observed during our study can be interpreted as adaptive for successful prey capture in the habitats characteristic of the zones where each species is clearly the predominant *Micropterus* form. Smallmouth bass tended to remain relatively horizontal,

strike in continuous sweeps, remain near the substrate, and exhibit biting during prey captures. Each of these traits would benefit efficient feeding in an environment with significant water current velocity. For example, any deviation from a horizontal body axis angle, with the fish's snout facing directly into a significant water current, increases drag on the fish's body and minimizes the advantage of a fusiform body plan. The biting mode of prey capture may be more effective in environments with water current flow, since the advantage of suction and engulfing would be reduced by the increase in drag (in effect, the drag on a slow-moving fish in a fast current would approximate the drag experienced by a fish swimming very rapidly in no current). Interestingly, active predatory fishes in high gradient, montane streams exhibit little suction capability and no premaxillary protrusion (e.g., salmoniforms). As in this study, Nyberg (1971) observed relatively lower attack velocities during largemouth bass suction feeding. He also noted that extremely fast predators such as barracuda (*Sphyræna* spp.) exhibit a lack of premaxillary protrusion and suction ability, since these require a comparatively high degree of accuracy and would add little to the overall attack velocity. The use of the biting mode by smallmouth bass appeared to be relatively inefficient as a means of capturing prey from within vegetation. Frequently, smallmouth bass were observed to firmly grasp prey along with strands of vegetation, only to lose the prey during subsequent manipulations. Conversely, largemouth bass generally sucked prey from within vegetation with relatively few incidents of escape.

Whether or not interactive segregation among black basses occurs in contact zones and regions of intermediate or heterogenous environments remains to be demonstrated in the field. Diet studies have revealed a high degree of similarity where the species are sympatric (Clady, 1974; Bohn, 1975; Hubert, 1977). Our study demonstrated that the feeding behavior of the largemouth bass is even more variable than previously described (Nyberg, 1971). The results strongly suggest that variability in the feeding behavior of black basses facilitates more efficient prey capture from a variety of different microhabitats. The success of worldwide introductions of both species is evidence of the viability of this behaviorally variable, generalist feeding strategy.

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