RESEARCH ARTICLE

Prey Capture Behavior of Native vs. Nonnative Fishes: A Case Study From the Colorado River Drainage Basin (USA)

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ABSTRACT

The Colorado River drainage basin is home to a diverse but imperiled fish fauna; one putative challenge facing natives is competition with nonnatives. We examined fishes from Colorado River tributaries to address the following questions: Do natives and nonnatives from the same trophic guild consume the same prey items? Will a given species alter its behavior when presented with different prey types? Do different species procure the same prey types *via* similar feeding behaviors? Roundtail chub (*Gila robusta*) and smallmouth bass (*Micropterus dolomieu*), midwater predators, and Sonora sucker (*Catostomus insignis*) and common carp (*Cyprinus carpio*), benthic omnivores, were offered six ecologically relevant prey types in more than 600 laboratory trials. Native species consumed a broader array of prey than nonnatives, and species from a given trophic guild demonstrated functional convergence in key aspects of feeding behavior. For example, roundtail chub and smallmouth bass consume prey attached to the substrate by biting, then ripping the prey from its point of attachment; in contrast, Sonora sucker remove attached prey via scraping. When presented with different prey types, common carp, roundtail chub, and smallmouth bass altered their prey capture behavior by modifying strike distance, gape, and angle of attack. Gape varied among the species examined here, with smallmouth bass demonstrating the largest functional and anatomical gape at a given body size. Because fish predators are gape-limited, smallmouth bass will be able to consume a variety of large prey items in the wild, including large, invasive crayfish and young roundtail chub—their presumptive trophic competitors. *J. Exp. Zool. 317:103–116, 2012.* © 2012 Wiley Periodicals, Inc.

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The Colorado River basin drainage is home to a broad assemblage of native fish species. However, anthropogenic alteration of freshwater habitats in the Southwestern United States threatens the existence of these fishes, and the introduction of nonnative species is considered a major factor in their decline (Meffe, '85; Tyus and Saunders, 2000; Minckley et al., 2003; Clarkson et al., 2005). Most introduced species are game or food fishes—popular with anglers, but hypothesized to have a negative impact on natives through direct predation and competition for food resources (Rinne, '96). However, despite the putative role of resource competition in the decline of native populations, there has been little assessment of the ability of nonnative and native fishes to exploit available prey types—even though

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the ability to capture and consume a given food resource may be key to understanding the ecological role of a species. Correspondingly, very few studies have examined the physiological and behavioral basis of prey capture behavior of native fishes of the southwest.

We seek to fill this gap by describing the strike and capture behaviors of native and nonnative fishes from Colorado River tributaries: roundtail chub (*Gila robusta*), Sonora sucker (*Catostomus insignis*), smallmouth bass (*Micropterus dolomieu*), and common carp (*Cyprinus carpio*). These species were selected because they coexist in tributaries of the Colorado River (including Fossil Creek and the Verde River, AZ) and represent two trophic guilds: midwater predator (roundtail chub and smallmouth bass) and benthic omnivore (Sonora sucker and common carp). Smallmouth bass are midwater predators in streams (Poe et al., '92) and diet data suggest that, in small tributaries where native Colorado Pikeminnow (*Ptychocheilus lucius*) are absent, roundtail chub will function as top predators (Minckley, '73). Similarly, Sonora sucker and common carp are both considered opportunistic, benthic omnivores (Schreiber and Minckley, '81; Vilizzi and Walker, '99). By comparing the functional biology of feeding in native and nonnative species with likely trophic overlap, we seek to understand the behavioral and physiological underpinnings of prey selection, capture tactics, realized trophic niche, and feeding success in the wild.

To this end, we conducted laboratory feeding trials wherein ecologically relevant prey were offered to individuals representing each of these four species. Using direct observation and digital recordings of feeding trials, we monitored acceptance or rejection of each prey type, evaluated overall feeding success on a given prey type, and quantified the movements that generate feeding behaviors. With these experiments, we address three interrelated questions. (1) Do native and nonnative fishes from the same trophic guild attack and consume the same subset of prey types? These diet breadth data will be used to evaluate the fundamental niche of each species in light of potential competitive interactions in natural habitats. (2) Will a given species alter its behavior when presented with different prey types? Some fishes modulate prey capture to procure a variety of food resources (Liem, '79); however, other species may be unable to alter feeding behavior when presented with a variety of food challenges (Gibb and Ferry-Graham, 2005). (3) Do different species procure the same prey types *via* similar feeding behaviors? To answer this, we compare feeding behavior across the four species to determine if similar patterns of movement are used to capture particular prey items. For example, all benthivores may consume algae from the substrate *via* scraping; alternately, one benthivore may scrape the substrate, while another may remove algae by biting and tearing. Such behavioral similarities in unrelated species would provide support for the evolutionary hypothesis that fish that occupy the same trophic guild (e.g., benthic omnivore) have evolved functionally convergent mechanisms to exploit similar prey types commonly found in most freshwater environments.

METHODS

Selection, Acquisition, and Care of Study Species

The roundtail chub *G. robusta* (Baird and Girard, 1853), a cyprinid (Cypriniformes) and midwater predator (Schreiber and Minckley, '81; Rees et al., 2005) typically inhabits pools, runs, and rapids of small- to medium-sized rivers (Minckley, '73; Sublette et al., '90) in the Colorado River system. Roundtail chubs appear to be opportunistic feeders, consuming aquatic insects, algae, small fish, and occasionally fish eggs (Neve, '76; Schreiber and Minckley, '81; Sublette et al., '90; Quist et al., 2006)—as well as terrestrial organisms such as lizards and insects that fall into the water (Rinne and Minckley, '91); Quist et al., 2006). The Sonora sucker *C. insignis* (Baird and Girard, 1854) is a member of the Catostomidae (Cypriniformes) and congregates in deeper and slower moving pools of water in rivers of similar size (Minckley, '73; Sublette et al., '90). Sonora suckers appear to be opportunistic, omnivorous benthic feeders, consuming invertebrates, algae, plant debris, and seeds (Minckley, '73; Schreiber and Minckley, '81). Both roundtail chub and Sonora sucker are considered to be "species of concern" by the United States Fish and Wildlife Service.

Smallmouth bass *M. dolomieu* (Lacepède, 1802), a Centrarchid (Perciformes) carnivore (Dauwalter and Fisher, 2008), are endemic to the central and eastern U S (Scott and Crossman, '73) and will consume fish, crayfish, annelids, and various aquatic invertebrates (Bestgen et al., 2008; Dauwalter and Fisher, 2008; Kuhlmann et al., 2008). Smallmouth bass were introduced to tributaries and reservoirs of the Colorado River in Arizona almost 100 years ago (Scott and Crossman, '73) and are stocked as sport fish (Sharma and Jackson, 2008) across North America. Common carp *C. carpio* (Linnaeus, 1758), another cyprinid (Cypriniformes), originated in Asia and Eastern Europe (Zhou et al., 2003), but have become established in the Verde River and many other bodies of water in the southwest as a food fish and for pest control (Lourdes Ruiz-Gomez et al., 2008). Common carp are benthic omnivores that consume a variety of food types, including vegetation, insects, eggs, detritus, and, occasionally, larval fish (Sibbing, '88; Vilizzi and Walker, '99; Carpenter and Mueller, 2008; Ojuok et al., 2008).

Roundtail chub, Sonora sucker, and smallmouth bass were collected from Fossil Creek, AZ by electrofishing, netting, and angling. Common carp—present in the lower reaches of Fossil Creek where it meets the Verde River, but much more difficult to obtain *via* standard collection methods, were purchased from a commercial supplier. Fish were acclimated to lab conditions for at least 2 weeks, while housed individually in 38 or 76 L tanks at 22–25°C. Photoperiod was maintained on a 14:8 light:dark cycle. Fish were fed commercial food pellets

Table 1. Prey acceptance and capture success for *G. robusta* (roundtail chub), *C. insignis* (Sonora sucker), *M. dolomieu* (smallmouth bass), and *C. carpio* (common carp).

Species	Prey type	Trials	Attacks	Acceptance (Percent)	Successful attacks	Failed attacks	Success (Percent)
G. robusta	Algae	18	15	83	10	5	67
G. robusta	Benthic attached	24	24	100	23	1	96
G. robusta	Benthic elusive	29	29	100	26	3	90
G. robusta	Midwater nonelusive	37	37	100	37	0	100
G. robusta	Midwater elusive	31	31	100	29	2	94
G. robusta	Crayfish	30	30	100	26	4	87
C insignis	Algae	21	21	100	20	1	95
C insignis	Benthic attached	21	21	100	20	1	95
C insignis	Benthic elusive	19	12	63	9	3	75
C insignis	Midwater nonelusive	19	14	73	13	1	93
C. insignis	Midwater elusive	18	0	0	0	0	0
C. insignis	Crayfish	18	1	5	0	1	0
M. dolomieu	Algae	18	0	0	0	0	0
M. dolomieu	Benthic attached	24	15	63	14	1	93
M. dolomieu	Benthic elusive	29	0	0	0	0	0
M. dolomieu	Midwater nonelusive	37	25	67	25	0	100
M. dolomieu	Midwater elusive	31	22	70	22	0	100
M. dolomieu	Crayfish	30	21	70	19	2	90
C. carpio	Algae	18	15	83	15	0	100
C. carpio	Benthic attached	24	18	75	18	0	100
C. carpio	Benthic Elusive	29	0	0	0	0	0
C. carpio	Midwater nonelusive	37	18	49	18	0	100
C. carpio	Midwater elusive	31	0	0	0	0	0
C. carpio	Crayfish	30	0	0	0	0	0

Table 2. Anatomical measurements (mean±SD) for specimens of *G. robusta (*roundtail chub), *C. insignis* (Sonora sucker), *M. dolomieu* (smallmouth bass), and *C. carpio* (common carp).

Species	*N*	Total length (cm)	Fork length (cm)	Head length (cm)	Anatomical gape (cm)
G. robusta	6	14.5 ± 3.5	14.0 ± 3.5	3.2 ± 1.4	1.5 ± 0.7
C. insignis	6	11.6 ± 0.6	10.5 ± 0.5	2.5 ± 0.1	1.7 ± 0.7
M. dolomieu	6	26.1 ± 1.6	24.8 ± 1.8	7.1 ± 0.9	3.9 ± 0.3
C. carpio	6	28.5 ± 0.5	25.9 ± 0.6	6.4 ± 0.2	2.7 ± 0.5

when in holding tanks and six individuals representing each species were offered six different food items during feeding trials (Table 1). After the feeding trials, individuals were sacrificed using a lethal dose of buffered tricane methansulfonate solution (3.0 g per 1,000 ml H_2O) and preserved by freezing for subsequent morphological measurements (Table 2). All procedures were conducted under the auspices of the Northern Arizona Institutional Animal Care and Use Committee (protocol #07-014) and in accordance with state and federal permits and policies.

Laboratory Feeding Trials

Prior to the feeding trials, a fish was removed from its holding tank and placed in a feeding arena that consisted of a 75.7 L glass aquarium containing dechlorinated tap water. The aquarium used as an arena contained no gravel, rocks, plants, or other structures because the purpose of the chamber was to facilitate encounters between fish and their potential prey; water quality was maintained in the feeding arena with an external canister filter. Fish were given 48 hr to acclimate to the experimental arena and were fasted during this time. During the feeding trials, digital video images were recorded from a lateral view (camera body axis perpendicular to the front surface of the tank) using a high-speed digital camera (Phantom V5, Vision Research, Inc., Wayne, NJ, USA) recording at 1,000 frames-per-second. This digital system was used to record images of fish attacking, capturing, and processing the prey items.

During feeding trials, fish were offered six different ecologically relevant prey items (Table 1). These included: filamentous algae/periphyton attached to rocks (hereafter, *algae*), "bloodworms" (nymphs of *Chironomus sp.*) that were artificially attached to the substrate (a model for an attached prey item, such as a caddis fly nymph; hereafter, *benthic attached*), live invertebrate nymphs (damselfly nymphs, *Odonata sp.*) resting on the substrate (hereafter, *benthic elusive*), pieces of bloodworm (nymphs of *Chironomus sp.),* or commercial food pellets (additional details given in Results) presented in the water column (hereafter, *midwater nonelusive*); live fish in the water column (hereafter, *midwater elusive*), and live crayfish (*Orconectes virilis,* a crayfish species introduced to Arizona and present throughout the state; hereafter, *crayfish*) on the substrate.

During the course of the experiment, 623 feeding trials were conducted on 24 individuals ($n = 6$ per species) representing the four species (Table 1). Prey items were introduced to the experimental arenas in a randomly generated order and fish were allowed a minimum of 3 min to either accept, as indicated by the initiation of an attack, or reject, as indicated by the failure of the fish to attack, the prey. If a fish accepted the prey item, the attack itself was then determined to be a success or a failure, where a success was defined as the fish capturing and consuming the prey item and a failure occurred when a fish was unable to ingest a prey item after it attacked. Prey types were introduced randomly, however, once enough kinematic data had been obtained for a given prey type (see below), it was removed from the random rotation and was not offered again. In addition, prey types rejected on one day would be offered again on a subsequent day. Thus, a fish would eventually receive a less desirable prey type that had been previously rejected (e.g., algae) as the *only* food item offered during a given feeding trial. In this manner, acceptance and feeding success were determined for six individuals of each species for each prey type. If a fish accepted a prey item, three to five events were recorded for that individual, and three events were subsequently quantified to ascertain values for various kinematic variables.

From the resulting digital images, we used eight kinematic variables to quantify various aspects of prey capture; all variables were measured manually from anatomical landmarks using the computer program DIDGE (developed by Alistair Cullum, Creighton University, Omaha, Nebraska, USA). To quantify movements of the jaws of the predator during the capture of the prey, we measured maximum functional gape (hereafter, maximum *gape*; the maximum distance between jaws during the feeding event), *time to maximum gape* (time required to achieve gape after the onset of mouth opening), maximum *gape angle* (largest angle created by the upper and lower jaws during the gape), and duration of the entire gape cycle (time required for the mouth to cycle from closed to opened to closed again during prey capture; hereafter, *gape cycle time*). We also measured the following variables that quantified the fish's strike, beginning at the onset of the predator's lunge toward the prey, on the prey items: *strike distance* (distance between predator and prey at onset of strike), *strike time* (time between onset of strike and contact with prey), *attack angle* (angle of the predator's body relative to a line parallel to the substrate, where a positive angle indicates that the head of the fish is closer to the surface and the tail is closer to the substrate), and the distance the prey moved toward the fish, or *prey movement* during the strike (a simple metric of the suction pressure produced by the predator during the feeding event). For each individual, for a given kinematic variable, we calculated the average (arithmetic mean) value of all feeding trials where that individual consumed a particular prey type and this value was used for statistical analysis.

Statistical Analyses of Kinematic Data

Kinematic data collected during the feeding trials generated a matrix of 95 data rows (six individuals per species, between three and six prey types per individual, and the mean value for a given individual on a given prey type), with eight kinematic variables measured to quantify feeding behavior (as described above). Because the data for the kinematic variables were not normally distributed, they were transformed using the Box-Cox technique (Sakia, '92) prior to hypothesis testing. Data were transformed using the statistical software package JMP v.9; all other statistical analyses were conducted using SPSS v.19. After data were transformed, they were used to test specific hypotheses generated by two of the questions that framed this study (see Introduction). Hypothesis 1: feeding behavior differs among the four species. Hypothesis 2: a given species will alter its behavior when presented with different prey types.

To address Hypothesis 1, all feeding events for a given individual (across all prey types) were used to construct an average (arithmetic mean) feeding event for that individual; this generated a data matrix with 24 rows of data (four species and six individuals per species), which was then input into a Principal Component Analysis (PCA). The PCA allowed us to simultaneously examine all eight kinematic variables and reduce them to a small number of factors, which are compound variables. The PCA was conducted using the correlation matrix and varimax rotation; factors with an eigenvalue greater than one were retained as important axes of variation and variables with component loadings greater than 0.6 (or less than −0.6) were considered significant for a given factor. The factors generated by the PCA were then used to test the predictions of Hypothesis 1. However, the individuals representing the four species examined here were not identical in body or head size (Table 1).

To assess potential size effects, we used Analysis of Covariance (ANCOVA) and considered head length (deemed the best overall metric for the size of the feeding apparatus) as the covariate. Although some of the species considered here did not overlap with one another in head size, most anatomical features of the cranium (including mouth gape) scale proportionally with size as fishes grow across juvenile and adult size ranges; this relationship has been demonstrated for the species examined here or in close relatives (Richard and Wainwright, '95; Vilizzi and Walker, '99; Portz and Tyus, 2004). Thus, we accept the a priori assumption that the ANCOVA is based on a valid scaling relationship across the size ranges considered here. Individual ANCOVAs were initially run on two PCA factors (dependent variables) considering three potential effects: *species*, *size*, and *species x size* (interaction term). However, because the interaction term was nonsignificant (see Results), it was removed from the model (Engqvist, 2005). In addition, subsequent evaluation of the ANOVA considering potential effects of *size* and *species* revealed that *size* was not a significant covariate (see Results), so this term was also removed from the model. Thus, after rejecting the hypothesis that the compound kinematic variables evaluated here are correlated with size, we performed one-way ANOVA to evaluate the data for potential effects of *species*.

To assess Hypothesis 2, the original dataset (95 data rows containing data for all species, all individuals, and mean kinematic values for a given individual on a particular prey type) was subdivided into four datasets containing only the data rows pertaining a given species; the number of data rows for each species varied depending on the number of prey types accepted. The dataset for each species was analyzed using PCA to consolidate the eight kinematic variables into a few compound variables (as described above), and the resultant factors were examined using one-way ANOVA to consider the potential effects of *prey type*.

Morphological Analysis

After the feeding trials, individual fish were euthanized and total length (TL), fork length, head length (HL), and anatomical gape were determined (Table 1). Anatomical measurements were taken as follows: TL was measured from the anterior tip of the upper jaw to the tip of caudal fin; *fork length* was measured from the anterior tip of the upper jaw to fork in caudal fin; or HL was measured from the anterior tip of the upper jaw to the caudal edge of operculum; *anatomical gape* was the maximum distance between the tip of the upper jaw and the tip of the lower jaw when the oral jaws were manually abducted. Using these measurements of head length and anatomical gape, we employed Analysis of Covariance (ANCOVA, as described in detail above) to determine if intrinsic differences in anatomical gape were present among the four species included in the study and to ascertain if these differences could account for observed differences in functional gape (i.e., the gape produced during a feeding event) across species (Huskey and Turingan, 2001). The ANCOVA initially considered three potential effects: *species*, *size*, and *species x size*; however, the interaction was removed from the ANCOVA model because it was not significant (see Results)—leaving only potential effects of *species* and *size*.

Based on analysis of the kinematic data, we generated the a posteriori hypothesis that anatomical gape limits functional gape (or maximum gape) during prey capture for these four species. To assess this hypothesis, we performed ANCOVA using the kinematic variable maximum gape with *species* as the main effect and anatomical gape as a covariate. Again, the interaction term was not significant, so it was removed from the model leaving only potential effects of *species* and the anatomical covariate (see Results).

RESULTS

Behavioral Observations, Prey Item Acceptance, and Capture Success

When offered a particular prey type, fish from a given species typically accepted this prey item a majority of the time (>60% acceptance) or rejected it entirely (0% acceptance). In addition, items that were accepted were typically captured successfully (>60% success). Exceptions to this overall pattern are noted below (see also Table 2).

Roundtail chub accepted, successfully captured, and consumed all prey items offered to them (Table 2). Most individuals willingly fed on algae; when doing so, they appeared to make small, probing bites and usually consumed at least some of the plant material. Roundtail chub consistently consumed benthic-attached prey using a bite coupled with a side-to-side jerking motion to tear food from the substrate. Roundtail chub successfully located and consumed benthic elusive prey, even when these prey attempted to hide. Roundtail chub also readily consumed prey in the water column, both elusive and nonelusive (Fig. 1). Roundtail chub were consistently willing to attack small crayfish—usually by approaching from behind in an attempt to swallow the crayfish tail first.

Sonora sucker accepted and consumed algae more readily than roundtail chub (Table 2), but also appeared to use their mouths to probe for other food items present within the filaments. Individuals of this species willingly consumed benthic-attached prey, typically by swimming over the top of the prey item and using repeated movements of the jaws to suck and/or scrape at the food item until it was removed from the substrate. Sonora sucker readily consumed benthic elusive prey; to do this they utilized a similar behavior as that employed to procure benthic-attached items. Midwater, nonelusive prey were also accepted and consumed (Table 2), but this appeared to be challenging for these fish—it took individuals longer to detect and identify prey, relative to roundtail chub or smallmouth bass, and a sucker would spend a considerable time positioning itself over the prey in order to protrude its mouth downward onto the prey item (Fig. 1). With the exception of one anomalous (and

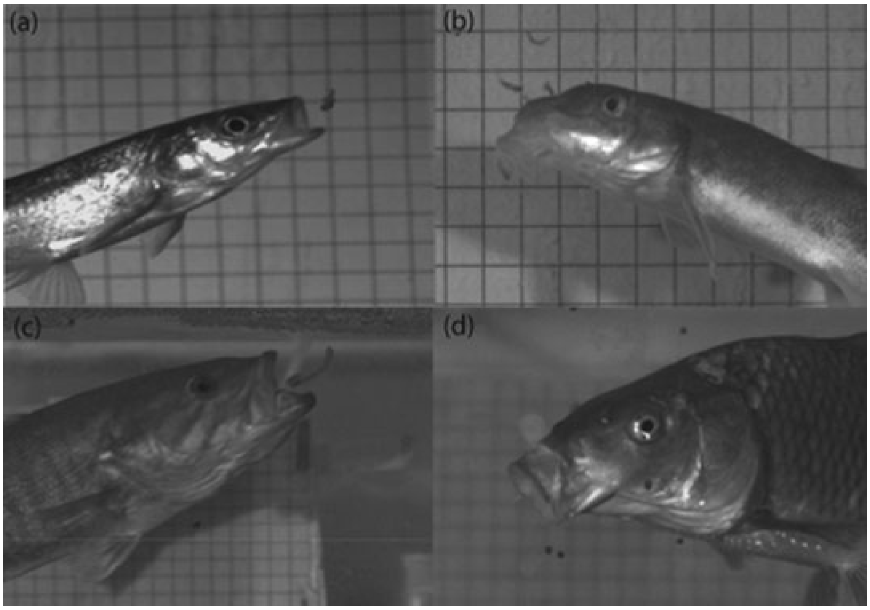

Figure 1. All four study species readily consume nonelusive prey items in the water column: (A) *G. robusta* (roundtail chub), (B) *C. insignis* (Sonora sucker), (C) *M. dolomieu* (smallmouth bass), and (D) *C. carpio* (common carp). Note that common carp and Sonora sucker position the head over the prey item during food capture.

unsuccessful) crayfish attack, Sonora sucker completely rejected both midwater elusive fish and crayfish (Table 2).

Smallmouth bass consistently rejected algae as a food item (Table 2). Smallmouth bass accepted and consumed benthic-attached prey immediately upon detecting the food item; however, it appeared that this prey item was detected only after it was physically agitated by water movement—this water movement was generated by the bass swimming about the tank. Once an attached prey item was captured between the upper and lower jaws, smallmouth bass would use a side-to-side jerking motion (similar to that demonstrated by roundtail chub) to remove the food item. Smallmouth bass consistently rejected benthic elusive prey (Table 2), likely because these prey were small and relatively immobile—which appeared to render them difficult for bass to detect. Both midwater nonelusive and midwater elusive prey items were accepted, and both prey types elicited similar behavioral responses in smallmouth bass: once an individual fish detected the prey item, it would rush toward the prey, mouth held agape, to engulf the food (Fig. 1). Smallmouth bass also aggressively attacked crayfish, even though some of the crayfish were so large that multiple bites were required for the fish to process and swallow the prey. In addition, if a bass missed during the initial strike, the crayfish often tried to escape into the water column, at which point the bass would strike again—successfully capturing and consuming the crayfish.

Most common carp accepted algae (Table 2), and often took multiple, sequential bites during a single feeding trial. Common carp readily accepted and captured benthic-attached prey items, typically by swimming over top of the food item and then using quick, repeated, ventrally directed bites to remove the prey from the substrate. Benthic elusive invertebrates, however, were consistently rejected (Table 2). Common carp accepted midwater nonelusive prey, although they were distinct from the other three species in their feeding behavior on this prey type in two ways. First, carp rejected *Chironomus sp.* larvae when presented in the water column (whereas all other species accepted this prey item); thus, to obtain midwater-feeding events for this species, it was necessary to offer carp food pellets (Fig. 1). [We note that our findings for this study (see Results) reveal that the important criteria to generate a distinct behavioral response are the location of the prey and how elusive it is; other workers who have conducted similar experiments using different model systems and reached the same conclusion (Ferry-Graham et al., 2001; Ferry-Graham et al., 2002). Thus, commercial food pellets presented in the water column should not elicit different capture behavior relative to other midwater nonelusive food items.] Second, even when offered pellets, carp still accepted this food type at a lower rate ($<50\%$ acceptance) than any other food type in any other species (all other food types for all other species showed $>60\%$ acceptance). When procuring midwater prey, carp utilized a

Table 3. Variable loadings for Factors 1 and 2 generated by Principal Component Analysis (PCA) when all four species are considered together; see text for additional details. Variables that loaded heavily for a given factor (more than 0.6 or less than −0.6) are indicated with an asterisk.

Variance	Factor 1 (46%)	Factor 2 (33%)
Strike distance	.935*	−.207
Strike duration	.732*	.046
Prey movement	.924*	−.284
Maximum gape	.910*	.223
Time to maximum gape	.246	.908*
Gape cycle time	−.053	.962*
Gape angle	−.574	.619*
Angle of attack	.452	−.555

similar behavior to that observed for Sonora sucker—a fish would tilt the head and body back so that the mouthparts could extend down into the water column to engulf the food (Fig. 1). Common carp consistently rejected both midwater elusive prey (live fish) and crayfish (Table 2).

Species Effects

A PCA of the data for all four species resulted in two factors that together summarized 79% of the variance (Table 3). Factor 1 was weighted by predator strike distance, strike time (or strike duration), maximum gape, and prey movement during the feeding event. Factor 2 was weighted by variables quantifying the timing of mouth movements (time to maximum gape, gape cycle time) and the apparent gape angle produced during mouth opening. When these two factors were examined with ANCOVA (considering head length as a covariate), the interaction term was not significant (df 3,16; Factor 1 $F = 0.2$, Factor 2 $F = 2.2$) and was removed from the model. Once the interaction term was removed, ANCOVA for Factors 1 and 2 both revealed a significant effect of *species*, but no effect of *size* (df 1,19; Factor 1 $F = 3.9$, Factor 2 $F = 2.8$). Based on this result, one-way ANOVA was used to evaluate the dependent variables for potential *species* effects; this analysis revealed that there was a significant *species* effect for both PCA factors (df 3,20; Factor 1, $F = 42.0$, Factor 2, $F = 25.1$; in both cases, $P > 0.001$). Based on post hoc analysis (Tukey tests), Factor 1 distinguishes all species from one another, except Sonora sucker and roundtail chub, and generates a clear separation between natives and nonnatives along this axis (Fig. 2). Factor 2 tends to separate benthic and midwater feeders (Fig. 2), although smallmouth bass and common carp cannot be distinguished from one another. Relative to native species, nonnative species tended to strike at the prey from farther away (this generated a correspondingly longer strike time), opened their mouths to form a greater gape, and sucked the prey into their mouths across a larger distance. When compared with midwater feeders, benthic feeders tended to have slower mouth movements and produced a greater gape angle when procuring food.

Prey-Type Effects within Species

Three of four species examined here varied their feeding behavior when presented with different prey types; the only species that did not demonstrate *prey-type* effects on feeding behavior was the Sonora sucker. For Sonora sucker, PCA of the feeding behavior of six individuals feeding on four prey types (crayfish and live fish were rejected) resulted in three Factors with eigenvalues greater than one (Table 4). However, none of these factors varied due to effects of *prey type* (Table 5; Fig. 3).

In contrast, common carp varied their behavior in response to different prey types, even though they were only willing to accept half of the prey types offered to them. PCA of the eight kinematic variables measured for six individuals consuming three prey types resulted in two factors—both of which varied with *prey type* (Tables 4 and 5). Midwater nonelusive prey elicited a different response (Tukey post hoc), which resulted in high scores for Factor 1 (Fig. 3).

Smallmouth bass also changed their behavior when feeding on different prey types. A PCA of the feeding behavior of six individuals feeding on the five accepted prey types generates two factors, only one of which (Factor 1) varies with *prey type* (Table 6). Bass also tended to respond differently to benthic-attached food (Tukey post hoc), which resulted in low scores for Factor 1 (Fig. 3).

Roundtail chub showed the most diet breadth in laboratory trials and they varied their behavior in a complex manner to procure all six prey types. The PCA summarizing feeding behavior for this species generated three factors; of these, Factors 2 and 3 varied with prey type, while Factor 1 did not. Factor 2 tended to separate prey items based on how elusive they were (with more elusive prey generating higher scores on Factor 2), whereas Factor 3 tended to separate prey based on physical location (with prey located on the substrate generating higher scores for Factor 3).

Prey-Type Effects across Species

A comparison of the PC loadings across the three species that altered behavior in response to prey type allows us to determine if key aspects of behavior are consistently modified in response to different prey stimuli. From this comparison, several patterns emerge. First, strike distance and gape (both maximum gape and gape angle) vary with prey type in a consistent manner for smallmouth bass, roundtail chub, and common carp (Table 5; Fig. 4) and these variables always load heavily on the first factor that describes variation that can be attributed to *prey-type* effect (Factor 1 for common carp and smallmouth bass, Factor 2 for roundtail chub). Prey in the water column are attacked from

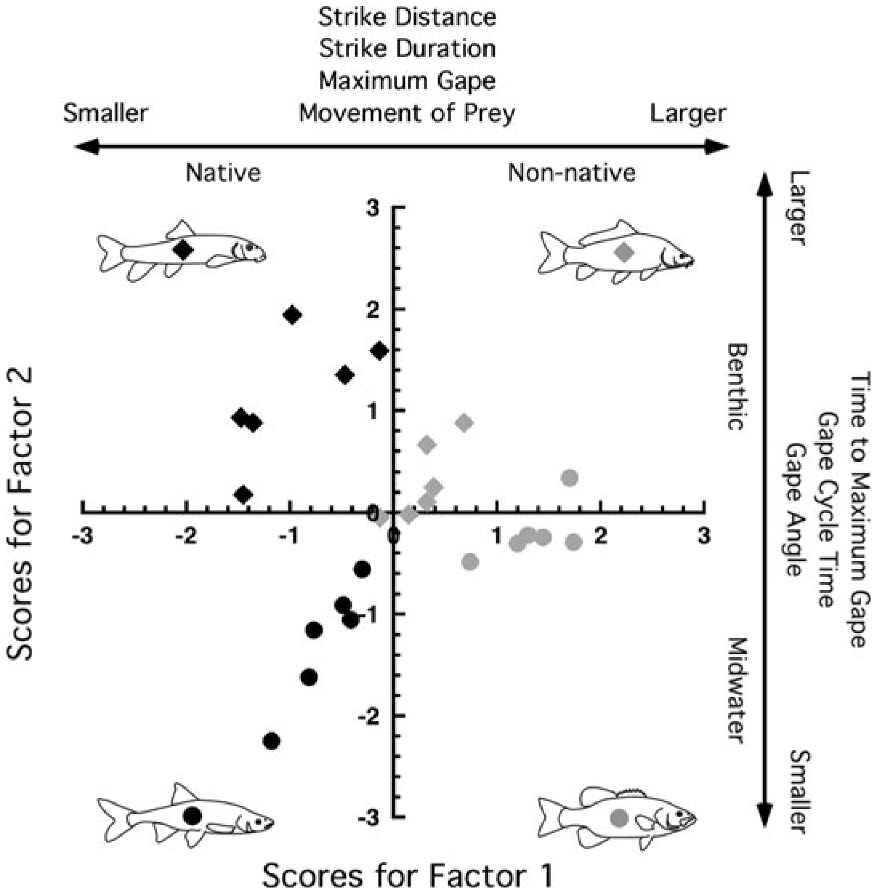

Figure 2. Factors 1 and 2 (compound variables generated using PCA, see Table 2 and text for details) quantify differences among the four species examined here. Each symbol represents the mean response for all prey types for one individual of a given species: Sonora sucker are indicated by black diamonds, roundtail chub by black circles, common carp by gray diamonds, and smallmouth bass by gray circles. Factor 1 tends to separate natives (black symbols) from nonnatives (gray symbols), whereas Factor 2 tends to separate benthic feeders (circles) from midwater feeders (diamonds). Kinematic variables that contribute to observed differences among species are indicated on the secondary x- and y-axis.

farther away and with a greater gape, relative to prey attached to the bottom (Fig. 4). Prey movement (that is, movement of the prey toward the predator) tended to vary with prey type across all three species (Fig. 4), but appeared in Factor 1 for common carp and smallmouth bass and in Factor 3 for roundtail chub (Table 5). Smallmouth bass and common carp were able to elicit large movements of the prey when feeding in the water column; in contrast, chub only were able to produce large movements of their prey when feeding from the substrate (Fig. 4). Angle of attack also varied in all three species, but again showed a complex pattern of distribution across the PCA factors (Table 5): roundtail chub and smallmouth bass tended to swim up toward prey when feeding in the water column, whereas common carp tended to tip their heads back (a behavior that will also generate a large angle of attack) when feeding on benthic-attached prey (Fig. 4). Somewhat surprisingly, timing variables were not modified by smallmouth bass or roundtail chub in a consistent manner in response to different prey types; only common carp altered the timing of the gape cycle to accommodate different food items (Table 5).

Morphological Analyses

Smallmouth bass had the largest anatomical gape of the four species, while Sonora sucker had the smallest anatomical gape. After the removal of the nonsignificant interaction term (df 3,16; $F = 1.6$), ANCOVA examining this relationship across species was significant (*size* effect, df 1,19, $F = 20.9$, $P < 0.001$; *species* effect, df 3,19, $F = 4.4$, $p < 0.05$). Based on estimated marginal

Table 4. Variable loadings for Factors 1, 2, and 3 (where appropriate) generated by Principal Component Analysis (PCA) when datasets from the four species are considered individually (see text for additional details). Only factors with eigenvalues greater than one are included; variables that loaded heavily for a given factor (more than 0.6 or less than −0.6) are indicated with an asterisk. Factors that did not vary with *prey type* (according to ANOVA, see Table 6 and text) are indicated in gray. Variables that consistently loaded heavily across species within factors that showed *prey-type* effects are indicated in bold.

	Smallmouth bass		Roundtail chub			Common carp		Sonora sucker		
Variance	Factor 1 46%	Factor 2 26%	Factor 1 34%	Factor 2 27%	Factor 3 18%	Factor 1 59%	Factor 2 19%	Factor 1 32%	Factor 2 28%	Factor 3 13%
Strike distance	**.894***	.075	.030	**.799***	−.233	**.893***	.126	.920*	−.006	−.207
Strike duration	.330	.810*	.923	−.017	.218	.319	.891*	.795*	−.129	.340
Prey movement	**.634***	.370	.097	.296	.819*	.811*	.404	.836*	−.248	.108
Maximum gape	**.920***	.154	−.072	**.914***	−.022	**.889***	.322	.691*	.428	−.292
Time to maximum gape	.245	.891*	.922	.093	−.047	.349	.760*	.009	.199	.929*
Gape cycle time	−.264	.910*	.951	−.100	.053	.447	.850*	.315	.847*	.157
Gape angle	**.804***	−.106	.022	**.690***	.259	**.757***	.053	−.206	.688*	.131
Angle of attack	**.620***	.122	−.075	.318	**−.854***	.103	**−.796***	.183	−.844*	.014

Table 5. *F*-values from ANOVA for effect of *prey type* on compound kinematic variables (Factors 1, 2, and 3 [where appropriate] as generated by Principal Component Analysis (PCA, see Table 4) that quantify feeding behavior in the four study species (see text for additional details).

	Sonora sucker df 3,16	Common carp df 2,14	Smallmouth bass df 3,18	Roundtail chub df 5,29
Factor 1	0.14	11.2**	27.2**	2.1
Factor 2	2.7	7.8*	0.2	9.5**
Factor 3	3.1	NA	NA	10.3**

*$P < 0.01$; **$P < 0.001$. NA = Not Applicable.

means, individuals with a common head size of 4.8 cm would have the following gape sizes: smallmouth bass = 3.1 cm; roundtail chub = 2.3 cm; common carp = 2.1 cm; Sonora sucker = 1.5 cm. Smallmouth bass and Sonora sucker had anatomical gapes that were significantly different from all other species, while roundtail chub and common carp were not different from one another.

Functional gape during feeding, as measured by maximum gape, appears to be limited by anatomical gape, and gape varies among species. The ANCOVA for maximum gape using anatomical gape as a covariate yields no significant interaction term (df 3,16; $F = 3.2$), but there is a significant correlation between functional and anatomical gape (df 1,19, $F = 12.7$, $P < 0.01$)—which indicates that gape measured from anatomical manipulation of a specimen *is* predictive of actual gape produced during a feeding event. In addition, there were significant differences among species for this relationship (df 3,19, $F = 7.8$, $P < 0.001$), which reveals that some species come closer to reaching maximum anatomical gape during prey capture, relative to other species.

DISCUSSION

The four species considered here currently co-exist in streams and rivers of the Colorado River basin drainage. Yet, until now, little was known about how these fish attack, capture, and consume food resources present in these habitats. Through behavioral, morphological, and kinematic analysis, we have determined how these four species respond when presented with different prey types and defined the suites of movements used to capture them. These findings yield predications as to how various prey types may be exploited in the wild.

We found that the native predator, roundtail chub, accepted and consumed a wider variety of prey than the nonnative predator, smallmouth bass. Roundtail chub were willing to eat attached algae and appeared to probe for other food items within it; smallmouth bass, in contrast, never consumed algae, nor were they willing to search for invertebrates residing within the filaments. Smallmouth bass are considered true carnivores (Sublette et al., ’90; Dauwalter and Fisher, 2008), which explains their lack of interest in herbivorous material. However, smallmouth bass also rejected damselfly nymphs, which are common benthic macroinvertebrates, while roundtail chub readily consumed them. Although both species include benthic invertebrates in their diets in the wild (Minckley, ’73; Neve, ’76; Sublette et al., ’90; Quist et al., 2006; Dauwalter and Fisher, 2008), smallmouth

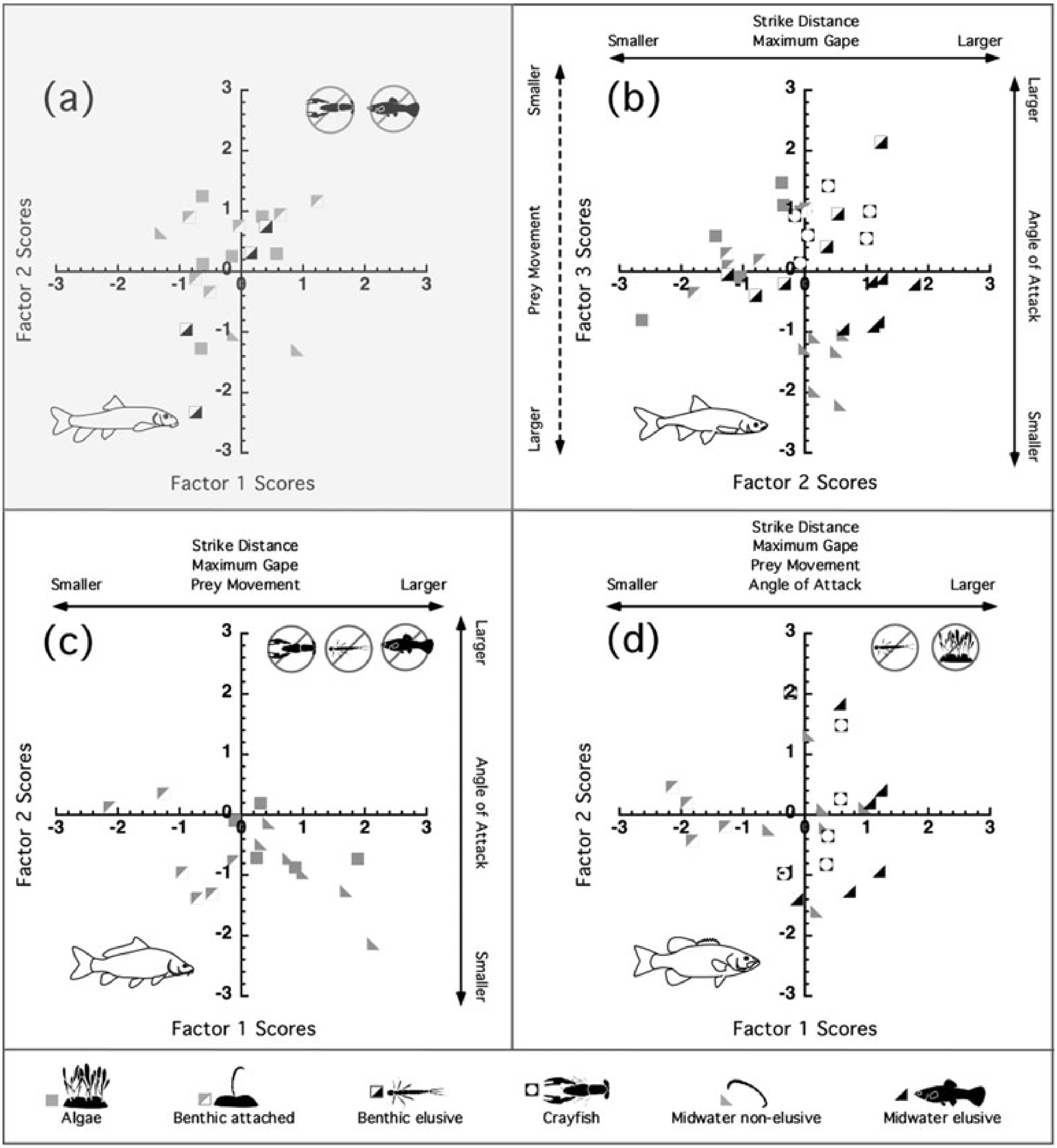

Figure 3. Graphical representation of axes of variation present in the feeding behavior of the four species examined in this study. Each graph represents two factors (which are compound variables) generated by PCA of the feeding events for a single species; when possible, factors that varied due to the effect of *prey type* are shown on the x- and y-axis (see Table 4 and text for additional details). Sonora sucker (A) are presented in a gray box to indicate that no factor varied with prey type in this analysis. In contrast, roundtail chub (B), common carp (C), and smallmouth bass (D) all varied their feeding behavior to facilitate the consumption of different prey items. Kinematic variables that contribute to observed differences among prey types are indicated on the secondary x- and y-axes, where appropriate. Strike distance and gape variables consistently appeared on the first axes of variation associated with prey-type effects; attack angle and prey movement also varied with prey type, but in a more complex manner.

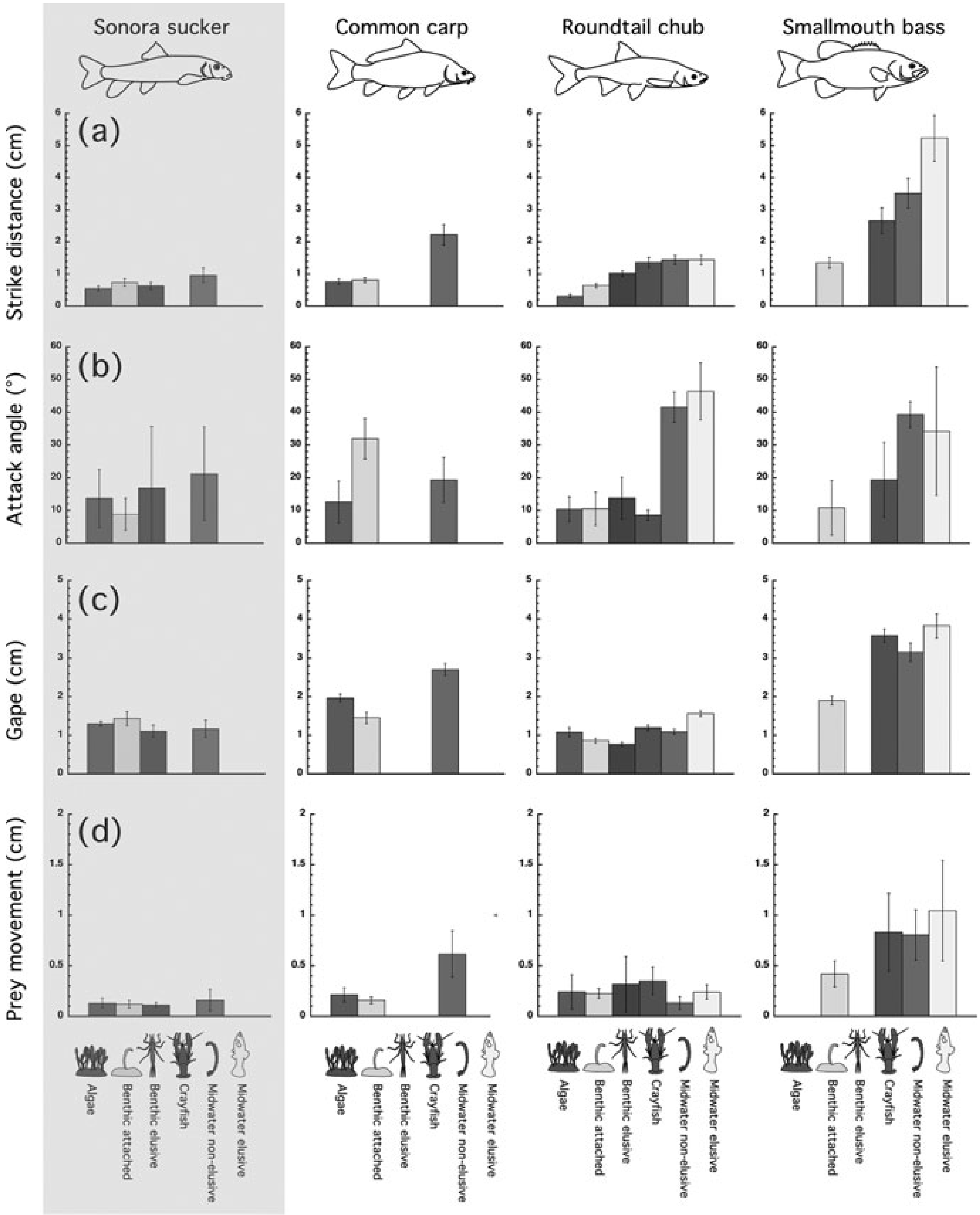

Figure 4. Three species of fish alter their behavior when consuming different prey items; however, Sonora sucker (shown in gray box at far left) did not alter their behavior in a consistent manner when presented with different prey items. Roundtail chub and smallmouth bass (at right) tended to increase strike distance (A), attack angle (B), and gape (C) when feeding on more elusive prey items in the water column. Common carp (center left), however, changed attack angle when feeding on benthic-attached prey. Smallmouth bass produced more prey movement (a metric of suction) when feeding on elusive prey in the water column; in contrast, roundtail chub produced more prey movement (D) when capturing prey items from the substrate. Each column represents the arithmetic mean of a given variable for a particular prey type; error bars represent the standard error of the mean.

bass appeared unable to detect a benthic invertebrate unless it was actively moving on the substrate or in the water column. In fact, damselfly larvae that have evolved in habitats where centrarchid fishes are present will remain immobile more often than damselfly larvae that have evolved in similar, but fishless, habitats (McPeek, '90). Roundtail chub, in contrast, spent considerable time foraging along the bottom and readily located prey on the substrate, even when these prey items were immobile. In addition, we find that roundtail chub appear to be most effective at producing suction when feeding from the substrate, whereas smallmouth bass produce the most suction when feeding in the water column. This last, in combination with the marked difference in the response of these two species to live damselfly larvae in the laboratory environment, yields the prediction that free-living roundtail chub actively forage along the substrate seeking macroinvertebrates, whereas free-living smallmouth bass are more likely to procure macroinvertebrates during seasonal periods of emergence, as they migrate through the water column to reach the surface.

Where roundtail chub and smallmouth bass demonstrated overlap in prey types, they also demonstrated convergence in the movements used to procure different prey types from the environment. For example, when attacking benthic-attached prey, both smallmouth bass and roundtail would approach slowly, bite the unattached region of the prey, and rip the prey from the substrate using a sharp tug. These two species were also similar in the kinematics of their attacks on specific prey types: when feeding on midwater prey, both roundtail chub and smallmouth bass would approach the prey from below (positive angle of attack), initiate the strike from far away (large strike distance), and produce a very large mouth opening (large maximum gape) when engulfing prey. In fact, for both species, kinematics varied consistently in response to where their prey items were located in the tank and how potentially elusive they were (Figs. 3 and 4); for example, a chironomid larvae triggered a different response when floating in the water column (midwater nonelusive) vs. when they were attached to the substrate (benthic attached). Roundtail chub and smallmouth bass also readily consumed crayfish. However, smallmouth bass were willing to consume crayfish that required multiple bites to process and swallow and often attacked crayfish from the anterior end, such that the head was engulfed first. Roundtail chub engulfed crayfish whole, typically attacked from the posterior end, and often retreated if the crayfish exhibited defensive behavior. In the wild, crayfish will quickly reach a body size refuge that protects them from predation by roundtail chub—but they will have to attain much larger body sizes to be protected from attacks by smallmouth bass.

The benthic omnivores also showed substantial overlap in the food items they would consume in a laboratory setting. Sonora sucker and common carp both captured nonelusive prey from the water column, but this behavior appeared to require substantial time and effort, relative to the procurement of benthic prey. During midwater feeding events for Sonora sucker and common carp, the head and mouth were carefully positioned directly over the food item to facilitate capture. Neither benthic omnivore species ever approached or attacked small prey fish in the water column; in fact, these species displayed no interest in midwater elusive prey items. And, although both species investigated crayfish sitting on the bottom, we only observed one crayfish attack (unsuccessful) by a Sonora sucker; crayfish are not likely to be included in the diets of either of these species in the wild (Hinojosa-Garro and Zambrano, 2004).

We found one difference in prey acceptance for the benthic omnivores: Sonora sucker would readily consume live, benthic macroinvertebrates, while the common carp examined here would not. In fact, Sonora sucker appeared to actively forage for invertebrates hiding in the algal filaments using a jaw probing behavior, whereas common carp simply tore off large clumps of algal filaments. These observations suggest that wild common carp typically encounter aquatic invertebrates incidentally when foraging for algae and detritus—however, further studies using wild-caught carp are needed to evaluate this hypothesis. Diet data for common carp that have invaded freshwater lakes suggest that juveniles readily consume microcrustaceans and very small macroinvertebrates, such as amphipods (García-Berthou, 2001). Larger macroinvertebrates, such as the damselfly larvae used as prey items here, are only included in the diet of very large, adult carp (Khan, 2003); thus, it is also possible that the common carp individuals examined here were simply too young or small to consume the large macroinvertebrates offered to them during feeding trials (Hinojosa-Garro and Zambrano, 2004). However, when evaluating potential competitive interactions between nonnative and native benthic omnivores, it is also necessary to consider the effects of foraging mode on the habitat. While foraging on the benthos, common carp uproot aquatic vegetation and increase water turbidity, thereby degrading the habitat and indirectly decreasing the number of macroinvertebrates (Matsuzaki et al., 2007).

Even though they demonstrated diet breadth by accepting four of six food items, Sonora sucker were the only species for which there was no *prey-type* effect on food-capture kinematics. In contrast, even though common carp may share some behavioral limitations with the Sonoran sucker—for both species, prey were consistently positioned below the head during capture and the jaw apparatus was always projected ventrally—carp were successfully able to change other aspects of their feeding behavior. We note that three of the species considered here (common carp, roundtail chub, and smallmouth bass) all modified key aspects of prey capture when feeding on different prey items—strike distance, gape, and body angle of attack. Only Sonora sucker did not alter this suite of behaviors when consuming different prey types. Future work will be necessary to determine if apparent inability to alter behavior when presented with different prey challenges is characteristic of the Sonora sucker or if it is a consequence of some as-yet-to-be-defined anatomical constraint imposed by catastomid jaw morphology.

Based on morphological and kinematic comparisons of these four species, smallmouth bass have the largest gape, Sonora sucker have the smallest gape, and roundtail chub and common carp are intermediate. Given that predatory fishes can only consume prey items small enough to fit between the upper and lower jaws (Hartman, '58; Hambright, '91), smallmouth bass may have a competitive advantage over roundtail chub because they are less likely to be limited in the size of prey they can consume. Correspondingly, some food resources may be functionally unavailable to native fishes because of gape limitation (Nilsson and Bronmark, 2000). For example, microcrustaceans will be consumed by small-mouthed and large-mouthed fishes alike, but larger aquatic invertebrates (including invasive crayfish) and most prey fishes can reach a size refuge to avoid being captured and consumed by predatory fishes. Thus, for a species with a small gape, like the roundtail chub, many prey items within its habitat may be simply too large to consume. In contrast, a species with a large gape, like the smallmouth bass, can consume large crayfish and even young roundtail chub—their likely trophic competitors.

We also note that nonnative fish species tended to initiate the strike from a greater distance away from the prey item, when compared with natives. This may indicate that nonnatives are more aggressive feeders, relative to natives. However, it is also possible that this pattern emerges because natives may rely more heavily on nonvisual cues when locating prey—which means a predator must be physically closer to the prey item in order to detect it.

In the Colorado River basin drainage, there has been an increase in nonnative fish populations and a simultaneous decline of native fish populations over the last 100 years (Bestgen and Propst, '89; Marsh and Douglas, '97; Brouder et al., 2006). Other factors not considered here certainly play a role in the extinction of native fishes, including, disease, habitat loss, flow-regime alteration, etc. (Gaicher et al., '80; Bestgen and Propst, '89; Marsh and Douglas, '97; Quist et al., 2006). In addition, nonnatives can cause habitat degradation and negatively affect native fishes through direct predation. However, based on the behavioral and functional data presented here, it is clear that sympatric native and nonnative species that occupy the same trophic guild (1) may experience overlap in their use of food resources within the habitat and (2) will employ functionally convergent behaviors when exploiting these resources—the resulting competition between native and nonnative fishes likely plays an underappreciated role in the decline of native fish populations throughout the American southwest.

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