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A kinematic investigation into the feeding behavior of the Goliath grouper *Epinephelus itajara*

A. B. Collins · P. J. Motta

Abstract Goliath grouper *Epinephelus itajara* suffered significant overfishing in the United States until they were protected from harvest in 1990. As the population recovers, interactions between Goliath grouper and anglers have increased, and are often reported to management agencies as complaints after grouper predation upon hooked fish. Goliath grouper are generally characterized as opportunistic predators capable of consuming a wide variety of prey types; however, minimal data are available regarding the prey capture behavior of this species. Kinematic analyses of adult Goliath grouper feeding events demonstrated the capacity of individuals to modulate feeding behavior based upon the mobility and position of 'prey' items. Mobile epibenthic food (tethered swimming fish) elicited larger maximum gapes, faster times to food capture, shorter times to mouth closing, and more rapid total bite durations than food items that were not moving (cut dead bait). Feeding sequences involving mobile food items were characterized by a significantly higher degree of ram feeding behavior, while immobile food elicited primarily suction feeding and were preceded by a slower and closer approach to the food item prior to the onset of mouth opening. The findings are discussed in light of predation upon angled species and demonstrate the ability of Goliath grouper to adjust their feeding strategy based upon prey type and condition. This behavior likely allows for the exploitation of a wide variety of prey and provides an expansive dietary breadth for these opportunistic predators.

Keywords Ram-suction · Feeding · Behavior · Opportunistic predator · Goliath grouper

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Introduction

Fish feeding has been the focus of a large body of research over the past century due to the ecological, evolutionary and economic implications of prey selection and capture behavior. Understanding what and how fish eat is of critical importance when describing community structure, trophic relationships and population dynamics within aquatic systems (Hixon 1991; Beukers-Stewart and Jones 2004; Matich et al. 2011). Analysis of the morphological components and mechanisms of prey capture can also provide insight regarding phylogenetic relationships among species and the success and performance of particular taxa over evolutionary time (Wiens 1977; Liem 1980; Wimberger 1991; Motta and Kotrschal 1992; Liem 1993; Ferry-Graham

et al. 2002a, 2002b). For economically important species, predator-prey relationships and feeding behavior can be translated and applied to enhance aquaculture (Wintzer and Motta 2005; Mahjoub et al. 2008) or contribute to the success of commercial and recreational fishing strategies (Wolf and Chislett 1974; High 1980; Wraith et al. 2013).

Prey capture among fishes is typically categorized as biting, ram or suction, and most species can utilize a combination of these tactics to capture prey (Liem 1980; Van Leeuwen and Muller 1984; Norton 1991; Ferry-Graham et al. 2002a, 2002b; Motta 2004). Biting involves using the jaws and teeth to rip prey from its location (e.g., the substrate) (Norton 1995; Clifton and Motta 1998). Ram feeding occurs when a predator rapidly approaches and engulfs a prey item (Liem 1980; Norton 1991; Nemeth 1997a, 1997b; Wainwright et al. 2001). Suction feeding is characterized by rapid opening of the mouth that creates a significant subambient pressure within the buccal cavity, sucking prey into the predator's mouth with relatively little forward motion by the predator (Lauder 1980; Muller et al. 1982; Van Leeuwen and Muller 1984; Carroll et al. 2004; Higham et al. 2006; Wainwright and Day 2007). The majority of teleost fishes utilize suction to capture prey (Liem 1980; Muller and Osse 1984; Carroll et al. 2004), but modulation of feeding behavior is not uncommon and many predators will adjust their prey capture technique in response to prey type, prey size or environmental conditions. For example, faster mouth opening may occur when feeding upon elusive, mobile prey (Coughlin and Strickler 1990; Wainwright et al. 2001; Holzman et al. 2007), and wider maximum gapes may be achieved if the predator is presented with larger prey (Wainwright et al. 2001). Additionally, fish may locate prey faster and feed more rapidly when competition is perceived to be high (Stoner and Ottmar 2004; Pfeiffenberger and Motta 2011). The capacity to alter feeding behavior in response to varying conditions likely influences fitness at the individual level by expanding dietary breadth and increasing feeding opportunities (Liem 1980; Sanderson 1991).

Goliath grouper (*Epinephelus itajara,* Lichtenstein 1822) are one of the world's largest groupers (Craig et al. 2011), and can attain sizes exceeding 400 kg and two meters in total length (Bullock et al. 1992). Like many large, long-lived species, Goliath grouper have suffered significant population declines throughout their geographic range (Musick et al. 2000) and are currently listed as critically endangered on the IUCN Red List (Pusack and Graham 2009). The species was protected from all harvest within United States waters in 1990 (GMFMC 1990; SAFMC 1990) and is beginning to exhibit signs of recovery, especially along the southwest coast of Florida (Cass-Calay and Schmidt 2009; Koenig et al. 2011). Increasing interactions between Goliath groupers and anglers have recently become a source of contention among some groups, and anglers report that Goliath groupers are becoming a 'nuisance' species in some areas due to their propensity to take anglers' bait and 'steal' hooked fish (Fleshler 2011; Kelly 2011; Frias-Torres 2012).

The feeding mechanics of Goliath grouper have not previously been described, although the expansive buccal cavity is characteristic of species specialized for volume suction feeding (Lauder 1980; Weaver 1996; Wainwright et al. 2001; Carroll et al. 2004; Westneat 2005) and they are typically characterized as suction feeders (Gerhardinger et al. 2006; Koenig and Coleman 2009). Goliath grouper are reported to feed primarily upon benthic crustaceans (Longley and Hildebrand 1941; Randall 1967; Randall 1983; Bullock and Smith 1991; Heemstra and Randall 1993; Koenig and Coleman 2009) but fish are not uncommon prey (Randall 1983; Bullock and Smith 1991) and both teleost and elasmobranch species have been identified within their stomach contents (Randall 1967), as well as sea turtles (Yeiser et al. 2008) and octopus (Bullock and Smith 1991). The majority of fish prey identified to date consists of slower moving or benthic associated species (i.e. cowfish *Acanthostracion* spp., pufferfish *Sphoeroides* spp., catfish *Bagridae marinus* and stingrays *Dasyatis* spp.), which supports contentions that Goliath grouper are relatively sedentary ambush predators (Sadovy and Eklund 1999). However, feeding in the water column upon schools of baitfish (e.g., Clupeidae, Carangidae) as well as upon hooked fish being reeled in by anglers or shot by spearfishers is regularly observed (Gerhardinger et al. 2006; Phelan 2008; Collins pers. obs.). Their wide dietary berth and aggressive attacks upon hooked and struggling live fish suggest that Goliath grouper are capable of modifying their feeding behavior to take advantage of alternate prey opportunities.

The goal of this study was to provide a general baseline description of Goliath grouper prey capture behavior and to assess whether Goliath grouper modulate feeding behavior in response to varied prey types

and presentations. Previous studies have demonstrated that predation events upon elusive prey may elicit increased ram behavior (e.g., Norton 1991), larger gape width (e.g, Wainwright et al. 2001), and faster approach and strike velocities (e.g. Nemeth 1997a, 1997b). We hypothesized that immobile and benthic prey would elicit suction feeding, and that more mobile and elevated prey would result in a behavioral shift toward ram feeding. A description of Goliath grouper feeding behavior may allow for future innovative suggestions to decrease the probability of catching this species and reduce predation upon hooked fish, and should assist with better understanding the interaction between Goliath grouper and anglers.

Methods

Experimental trials took place in situ at artificial reefs in the central eastern Gulf of Mexico that exhibited consistent Goliath grouper presence throughout the year (Collins et al. 2015). Site depths ranged between 20 and 30 m. Feeding trials took place during the summer (June – August) when bottom water temperatures were between 27 and 30°C, and were only attempted when horizontal visibility was greater than 5 m.

Feeding trials

Monofilament line (225 kg test), hereafter referred to as the 'mainline,' was attached to a weight positioned on the bottom. The mainline was marked in 200 mm increments (to provide scale) and connected to a subsurface buoy that kept it suspended vertically (Fig. 1). Prey items were measured (length and width, mm) and threaded with a short piece (10–20 cm) of cotton line through their approximate center of mass that provided an easy "break-away" component so that Goliath grouper would not ingest anything other than the attached prey item. The cotton thread was connected to a 20 cm section of lightweight monofilament (5 kg test) secured to a stainless steel gangion that could be snapped on to the mainline.

Prey items, hereafter referred to as 'food' for consistency, were classified as 'mobile' (live grunt *Haemulon* spp.) or 'immobile' (cut dead bait; either *Euthynnus alletteratus* or *Sphyraena barracuda*). Mobile food was attached to the main line at least two meters from the bottom in order to keep the food swimming (Fig. 1).
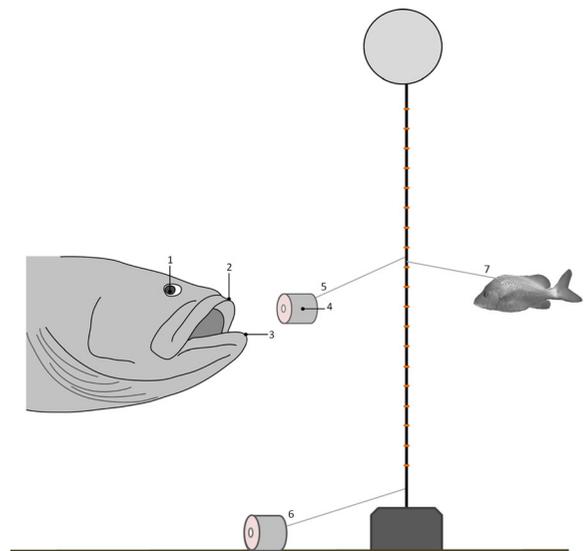

Fig. 1 Kinematic analyses of feeding sequences for Goliath grouper *Epinephelus itajara* were performed by tracking the following landmarks: (1) midpoint of the eye; (2) anterior point of the premaxilla; (3) anterior point of the lower jaw; and (4) estimated center of mass of the food item. Food items were attached to a weighted line that was marked in 200 mm increments and was suspended vertically by a subsurface buoy. Immobile food items were presented as elevated (5) or benthic (6), and mobile food (7) was tethered to the line at least 2 m from the substrate

Mobile food that was not consumed within five minutes was removed from the line and released. Immobile food was also attached to the main line and was presented either on the substrate (benthic) or suspended from the main line at least two meters above the bottom (elevated; Fig. 1). All food items (mobile and immobile) were generally the same size and ranged from 100 × 100 mm to 100 × 330 mm (width × length; mean = 219 × 100 mm; Table 1).

Goliath grouper ranged in size from 1100 to 2070 mm TL ($n = 26$; mean ± S.E. = 1475 ± 39 mm). Only one feeding strike was evaluated for each individual, resulting in a total of 11 individual feeding sequences upon mobile food, and 15 individual feeding sequences upon immobile food (9 individuals fed upon elevated immobile items and 6 fed upon benthic immobile items; Table 1). Goliath grouper mature between 1100 and 1350 mm (Bullock et al. 1992), so based on the size range of recorded individuals it is assumed that all feeding sequences were for adult fish. Goliath grouper were recorded and measured prior to presenting the food item using a custom-made laser apparatus that was attached to an underwater video camera (Sony Handycam, HDR-550 CX, 60 frames

Table 1 Kinematic and timing variables assessed through video analysis of feeding sequences for 26 individual Goliath Grouper *Epinephelus itajara*, separated by food type (mobile or immobile). The *Immobile* food group was additionally split further and separated by position within the water column (elevated or benthic) and these results are presented within the shaded columns. Variable abbreviations indicate predator total length (TL), stalking duration (StD), food distance at the onset of predator mouth opening (FDMO), maximum gape (MG), distance moved by the predator (D_{pred}), distance moved by the food (D_{food}), time to food capture (TTFC), time to maximum gape (TTMG), time to close mouth (TTCM) and total bite duration (TBD).

Kinematic or timing variable	Mobile Mean ± S.E.	Immobile Mean ± S.E.	*Immobile Elevated Mean ± S.E.*	*Immobile Benthic Mean ± S.E.*
Predator TL (mm)	1422 ± 63	1501 ± 50.1	*1485 ± 94.1*	*1630 ± 39.6*
Food length (mm)	281 ± 10.4	163 ± 13.9	*152 ± 19.3*	*205 ± 36*
StD (s)	8.1 ± 1.9	12.3 ± 2.3	*14.2 ± 4.9*	*16.4 ± 4.7*
FDMO (mm)	221 ± 12.2	54 ± 12.6	*71.9 ± 17.7*	*38 ± 17*
MG (mm)	317 ± 32	161 ± 6.5	*156 ± 10.4*	*176 ± 21*
D_{pred} (mm)	273 ± 15	33 ± 10.4	*52.6 ± 16.4*	*13.8 ± 8.8*
D_{food} (mm)	52 ± 11	96 ± 11.1	*100 ± 6.9*	*90 ± 27.2*
TTFC (ms)	77 ± 7.5	137 ± 12.6	*123 ± 16.7*	*180 ± 39*
TTMG (ms)	121 ± 6.7	173 ± 13.3	*148 ± 21.7*	*227 ± 26*
TTCM (ms)	124 ± 9.8	265 ± 58.3	*200 ± 15.7*	*494 ± 23*
TBD (ms)	246 ± 15.9	442 ± 60.2	*349 ± 30.0*	*667 ± 21*
Number of individual bites (n)	11	15	*9*	*6*

per second) that was operated by an underwater observer. The lasers projected equidistant points (200 mm apart) onto the body of the Goliath grouper and still frames in which the fish was perpendicular to the optical axis of the camera were used to calculate TL to the nearest cm. Furthermore, head length for each individual was calculated as the distance between the anterior tip of the retracted premaxilla and the posterior edge of the operculum.

Two high definition video cameras (GoPro HD HeroII, modified with an Oculus flat lens to minimize distortion) were placed orthogonal to each other and positioned four meters from the main line by divers. Cameras recorded at 60 fields per second and were positioned so that the food was centered within the field of view. When possible, a third high definition camera (Sony Handycam, HDR-550 CX, 60 fields per second) held by an underwater observer approximately four meters from the food was also used to film feeding sequences. This additional videography was not always feasible, however, since Goliath grouper would not feed consistently in the presence of divers. Multiple recordings of the same feeding event from different positions allowed for a greater likelihood that fish would be recorded feeding perpendicular to the camera. The best representative lateral view (e.g., Fig. 1) of each feeding event was selected for analysis of feeding kinematics.

All experimental procedures were performed with the approval of the University of South Florida Institutional Animal Care and Use Committee (permits #3210 and #3887).

Kinematics

Feeding sequences were analyzed using the program Tracker (version 4.84, © 2014, www.cabrillo.edu/~dbrown/tracker). For each feeding sequence, the following landmarks were tracked from the video frame before the onset of mouth opening until the frame after the mouth closed: (1) center of the eye of the predator (COE), (2) anterior tip of the predator's premaxilla (APM), (3) anterior tip of the predator's lower jaw (ALJ), and (4) estimated geometric center of mass of the food item (COM) (Fig. 1). Using these landmarks, the following kinematic variables were assessed: (1) maximum gape (MG): the maximum distance between the anterior tip of the premaxilla and the anterior tip of the lower jaw during food capture; (2) time to maximum gape (TTMG): the length of time from onset of mouth opening until maximum gape was obtained; (3) time to food capture (TTFC): the time between the onset of mouth opening and the point at which the center of mass of the food item passed through the anterior gape of the predator; (4) time to close mouth (TTCM): the time

between the end of maximum gape and the jaws returning to a closed position; and (5) total bite duration (TBD): the time from the onset of mouth opening until the mouth closed. Stalking duration (StD) was calculated as the time between orientation of the predator to the food item (the point at which the head oriented to the food item and began approach) and the onset of mouth opening. Food distance from the predator at the onset of mouth opening (FDMO) was calculated as the distance between the center of mass of the food item and the anterior tip of the premaxilla. Distance moved by the predator (D_{pred}) was calculated as the total distance travelled by the predator (measured at the center of the eye) from the onset of jaw opening until the center of mass of the food passed through the anterior gape. Distance moved by the food (D_{food}) was calculated as the total distance travelled by the estimated center of mass of the food from the onset of predator jaw opening until passing through the anterior gape of the predator (vertical line between the anterior tip of the premaxilla and the lower jaw). For feeding events upon immobile food, suction distance was calculated as the distance between the center of mass of the food and the anterior tip of the premaxilla for the frame in which the food item began to move toward the predator.

Data analysis

The distances moved by the predator were plotted against the distances moved by the food item for all feeding sequences. In addition, these distances were used to calculate a value of "ram-suction" index (I_{RS}; Norton and Brainerd 1993), where

$$I_{RS} = (D_{predator} - D_{food})/(D_{predator} + D_{food}).$$

Calculation of I_{RS} allowed for a description of the strike mode and designation of individual feeding behavior along the 'ram-suction' continuum (Norton and Brainerd 1993; Sass and Motta 2002; Oufiero et al. 2012), where an I_{RS} value = +1.0 is indicative of complete ram feeding and alternately, an I_{RS} value = −1.0 designates pure suction. Suction distance was expressed as a percentage of total length, head length, and maximum vertical gape. Kinematic variable data were assessed for equality of variance (using Levene's test) and for normality (using the Shapiro-Wilk test) and were log-transformed when necessary to meet the assumptions of normality and equal variance. Linear

regressions were performed to test for relationships between predator total length and the variables as defined above: StD, MG, TTMG, TTFC, TTCM, and TBD. To assess whether I_{RS} values or any of these kinematic variables exhibited a relationship to food type (mobile vs. immobile) or food position (benthic vs. elevated; for immobile food only), t-tests were performed to identify differences between groups. The above statistical analyses were performed using the program SigmaPlot (version 12.5, Systat Software, San Jose, CA). Principal component analysis (PCA) was used to resolve correlated kinematic variables as related to food type and position (mobile, immobile benthic and immobile elevated). PCA was conducted using the FACTOR procedure and SAS software, and the first five principal components were rotated using the varimax option to ease interpretability (SAS Institute Inc. 2006). Major axes (principal components) were identified by eigenvalues >1 and scores for each feeding event were plotted in three-dimensional principal component space.

Results

Total length of the grouper did not affect the stalking duration (StD; range: 2.7–49.7 s, mean = 11.9 s; $p = 0.76$, df = 24), maximum gape (MG; range: 114–460 mm; mean = 223.1 s; $p = 0.62$, df = 24), time to food capture (TTFC; range: 34–300 s; mean = 114 s; $p = 0.98$, df = 24), time to maximum gape (TTMG; range: 70–300 s; mean = 152 s; $p = 0.95$, df = 24), time to close mouth (TTCM; range: 67–1370 s; mean = 226 s; $p = 0.25$, df = 24), or total bite duration (TBD; range: 134–1635 s; mean = 379 s; $p = 0.32$, df = 24). Consequently, all individuals were grouped together for the remaining analyses. Feeding behavior of Goliath grouper was significantly affected by the activity level of the food (Table 1). Principal component analysis identified three major axes (eigenvalues >1.0), which together explained 89% of the variability among feeding events on mobile and immobile food (Table 2, Fig. 2). Mobile food elicited significantly larger maximum gapes, shorter capture times, shorter times to maximum gape, faster mouth closing and more rapid bite durations overall than those involving immobile food ($p < 0.05$; df = 24; Fig. 2 and Fig. 3). Stalking durations (time between orientation to food and the onset of mouth opening) lasted up to 50 s, and were generally shorter when approaching mobile food (Table 1),

Table 2 Results from principal components analysis (PCA) examining the correlation of kinematic variables during feeding events upon all food types (mobile, immobile benthic and immobile epibenthic). Kinematic variables assessed were (1) stalking duration (StD); (2) maximum gape (MG); (3) time to food capture (TTFC); (4) time to maximum gape (TTMG); (5) time to close mouth (TTCM); and (6) total bite duration (TBD)

Kinematic variable	PC1	PC2	PC3	PC4	PC5
StD (s)	0.1989	0.2114	-0.1822	0.9394	0.0019
MG (mm)	-0.1258	-0.1156	0.9714	-0.1651	-0.0013
TTFC (ms)	0.2134	0.9327	-0.1246	0.2168	-0.1487
TTMG (ms)	0.4163	0.8702	-0.0851	0.1237	0.2168
TTCM (ms)	0.9586	0.2127	-0.1086	0.1547	-0.0116
TBD (ms)	0.9137	0.3559	-0.1109	0.1586	0.0327
Variance explained	2.0279	1.8570	1.0236	1.0212	0.0703
Proportion of variance explained	0.5983	0.1610	0.1323	0.0974	0.0110
Cumulative variance explained	0.5983	0.7593	0.8916	0.9890	1.0000

although there was not a significant statistical difference ($p = 0.064$, df = 24). All feeding sequences on mobile food were more characteristic of ram feeding (Fig. 4a) and I_{RS} ranged +0.46 to +1.0 (Fig. 4b). When presented with immobile food, Goliath grouper approached more slowly, exhibited smaller maximum gapes, longer capture times and greater bite durations (Fig. 2, Fig. 3), and almost all feeding sequences upon immobile food demonstrated suction feeding (I_{RS} ranged −1.0 to +0.16; Fig. 4b). All attacks upon mobile food involved continuous forward motion by the grouper through the feeding sequence, while attacks upon immobile food typically involved an initial approach to the food item, followed by an abrupt stop in front of the food before the onset of mouth opening. Additionally, Goliath grouper began to open their mouth from farther away when feeding upon mobile food (range: 122–262 mm; mean = 221 mm), but minimized the distance between their mouth and the food prior to suction feeding upon immobile items (range: 1–120 mm; mean = 54 mm; $p < 0.001$, df = 24; Fig. 3a). During feeding events upon immobile food, mouth opening was initiated at a distance which corresponded to 0.001–29% of head length (mean distance at onset of mouth opening =12.6%). This was in contrast to feeding events upon mobile food, where mouth opening was

Fig. 2 Symbols represent scores identified through principal component analysis of individual feeding events upon mobile (●; live grunt *Haemulon* spp.), immobile elevated (○; suspended dead bait) or immobile benthic (◓; dead bait on the substrate) food. Kinematic variables that contribute to observed differences are indicated along each major axis (major axes were identified as those with eigenvalues >1; see text and Table 2 for details)
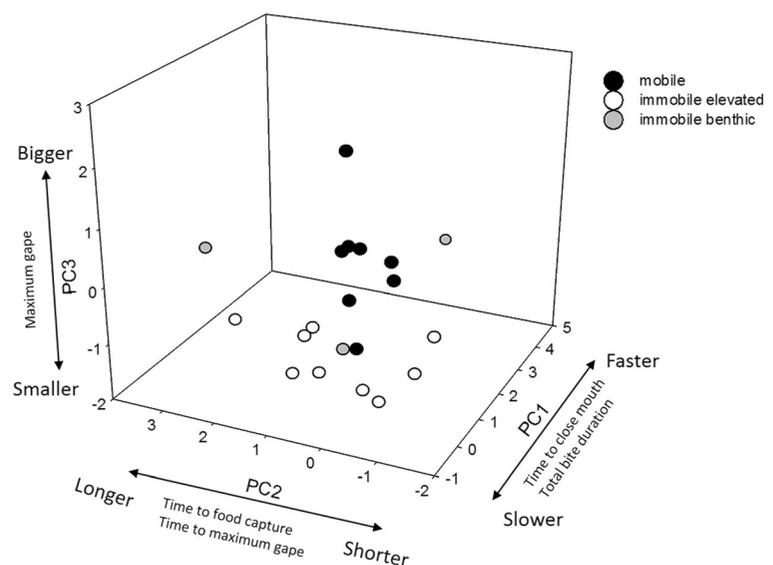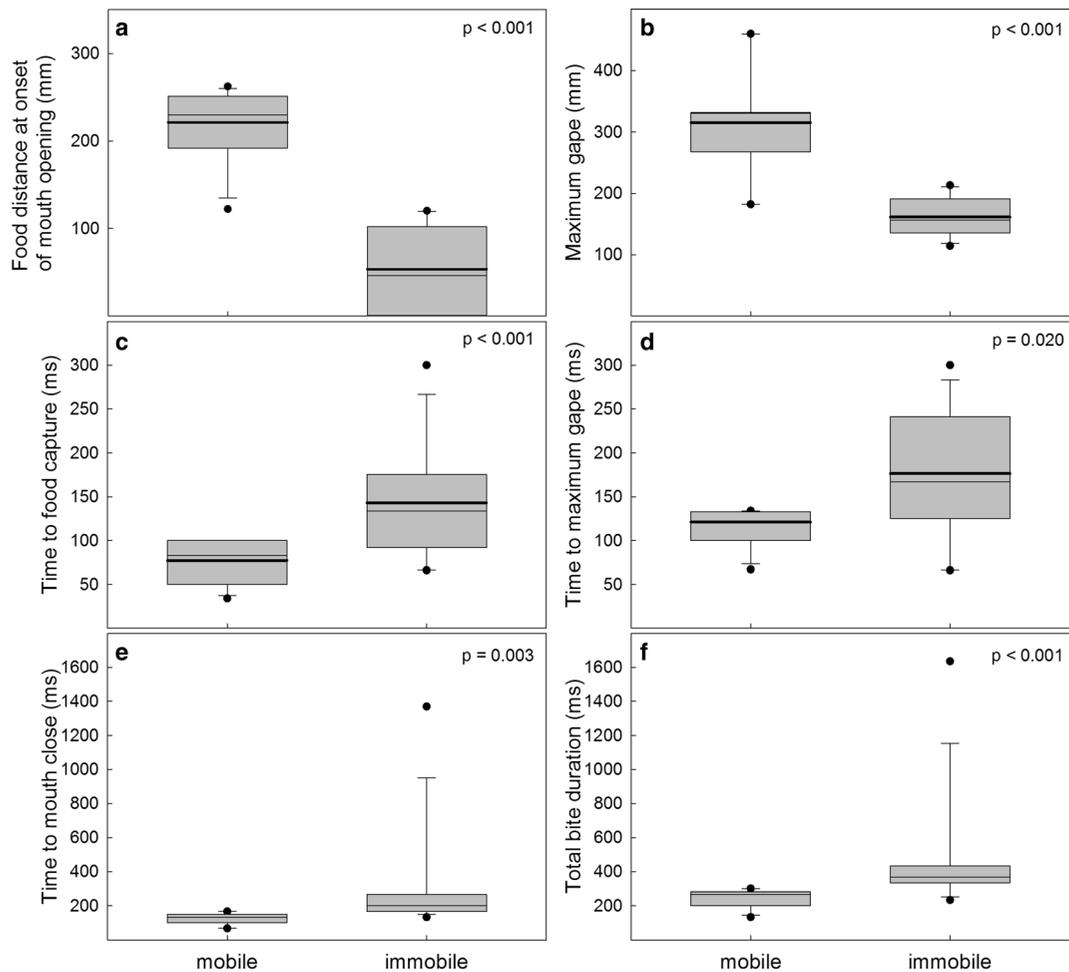
Fig. 3 Kinematic variables recorded during Goliath grouper *Epinephelus itajara* feeding events on mobile ($n = 11$) and immobile ($n = 15$) food. Only variables for which significant differences were observed are presented: (**a**) distance of the food from the anterior tip of the premaxilla at the onset of mouth opening ($t = 9.3$; df = 24); (**b**) maximum gape, the maximum distance between the anterior tip of the premaxilla and the anterior tip of the lower jaw($t = 2.44$, df = 24); (**c**) time to food capture, the time between the onset of mouth opening and the center of mass passing through the jaws ($t = 2.90$, df = 24); (**d**) time to maximum gape, the time between the onset of mouth opening and achieving maximum gape($t = 2.28$, df = 24); (**e**) time to mouth close, the time between the end of maximum gape and the jaws returning to a closed position ($t = 2.13$, df = 24); and (**f**) total bite duration, the time between the onset of mouth opening and the jaws returning to the closed position ($t = 2.86$, df = 24). The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside of the 95% confidence intervals. Results of t-test comparisons are displayed in the upper right corner of each graph

initiated at a distance of 25–68% of predator head length (mean distance =57%).

Suction distances for feeding sequences upon either category of immobile food (epibenthic and benthic) ranged from 0 to 120 mm (mean = 53.5 ± 12.3 S.E.), corresponding with a mean of 3.4% of total length (± 0.1% S.E.; range = 0–7.9%), 12.2% of head length (± 2.8% S.E.; range = 0–28.6%) and 29.4% of maximum gape (± 7.7% S.E.; range = 0–65.4%). Feeding

sequences upon immobile, elevated food elicited faster times to maximum gape, faster times to close the mouth and shorter bite durations than immobile benthic food ($p < 0.05$, df = 13; Fig. 5); however, no significant differences were observed between the two immobile food presentations for the following variables: predator distance from the food at the onset of mouth opening, stalking period, maximum gape, and food capture time. Both immobile food presentations elicited feeding that

Fig. 4 **a** Distances moved by Goliath grouper *Epinephelus itajara* plotted against distances moved by food items during feeding events upon mobile (●; live grunt *Haemulon* spp.) or immobile (○; dead bait; white symbols) food, and **b** Ram-suction index (I_{RS}) values calculated for these feeding events. There was a significant difference in I_{RS} between groups ($p < 0.001$, df = 24). The dotted line indicates the point on the continuum where feeding becomes biased in the direction of either pure ram (+1.0) or pure suction (−1.0)
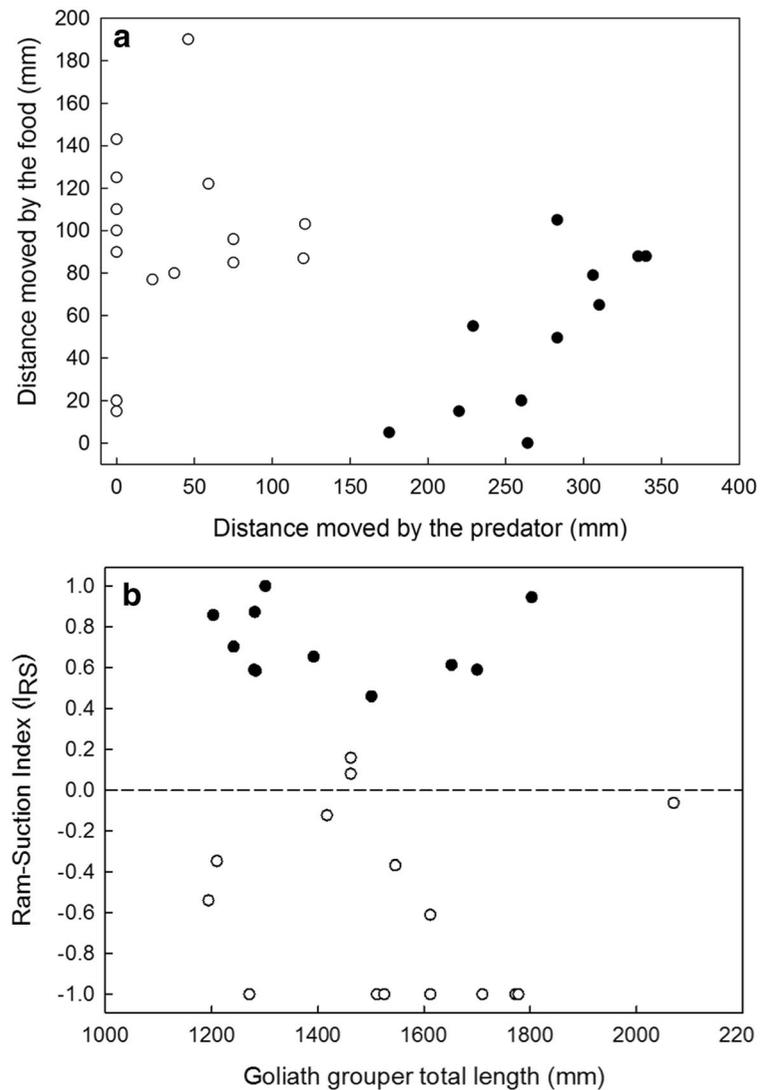
was typically characteristic of suction feeding (Fig. 6a), with I_{RS} values that ranged from −1.0 to +0.16 for elevated immobile food, and from −1.0 to −0.37 for benthic immobile food (Fig. 6b). There was not a significant difference in I_{RS} values between these two groups ($p = 0.094$, df = 13).

Discussion

Most groupers are ambush predators (Burnett-Herkes 1975; Parrish 1987; Bullock and Smith 1991) that often engulf prey through suction feeding (Thompson and Munro 1978, Viladiu et al. 1999; Burns 2009); however,

this family is ecologically diverse and there are many grouper species that actively chase down prey and exhibit prey capture behavior that is characteristic of ram feeding (Wainwright and Bellwood 2002; Oufiero et al. 2012). Goliath groupers have been characterized as ambush suction feeders that prey predominantly upon slow moving benthic fishes and crustaceans (Sadovy and Eklund 1999; Koenig and Coleman 2009), but increasing reports of predation by Goliath grouper upon hooked fish during angling events indicate that they are capable of modulating their feeding behavior to take advantage of scavenging opportunities. During this study, mobile food elicited faster approaches, wider maximum gapes, and more rapid capture than immobile
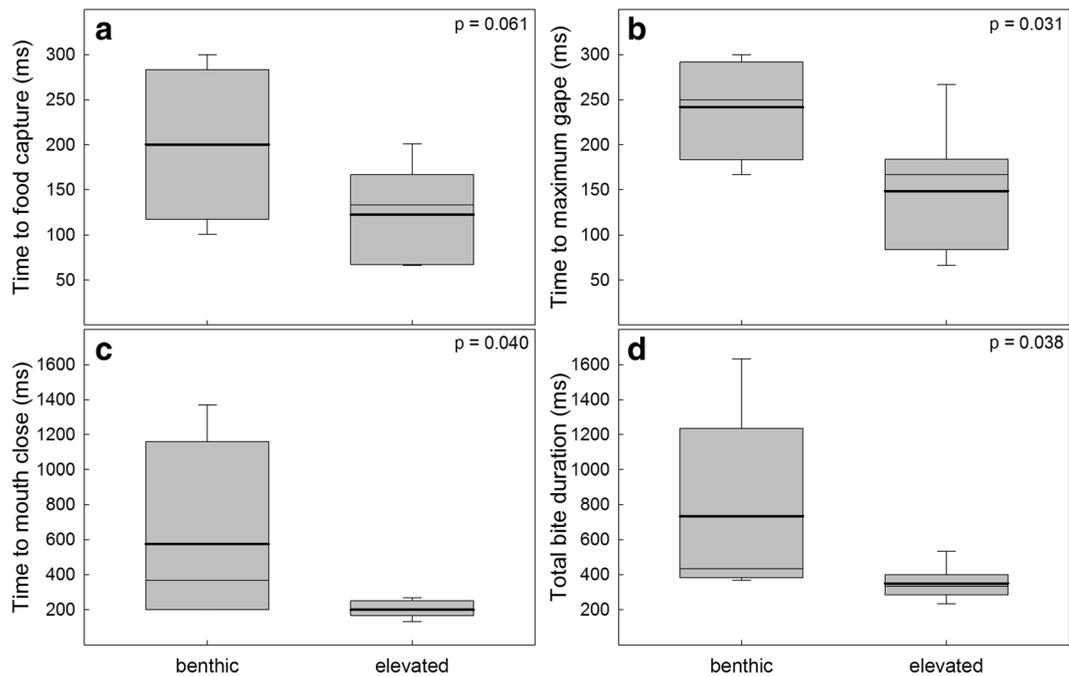
Fig. 5 Kinematic variables recorded during Goliath grouper *Epinephelus itajara* feeding events on immobile food that were positioned on the ground (benthic, $n = 6$) or in the water column (elevated; $n = 9$). Only variables that contributed heavily are presented in this figure: (**a**) time to food capture, the time between the onset of mouth opening and the center of mass passing through the jaws ($t = 2.08$, df = 13); (**b**) time to maximum gape, the time between the onset of mouth opening and achieving maximum gape($t = 2.47$, df = 13); (**c**) time to mouth close, the time between the end of maximum gape and the jaws returning to a closed position ($t = 2.37$, df = 13); and (**d**) total bite duration, the time between the onset of mouth opening and the jaws returning to the closed position ($t = 2.53$, df = 13). The mean of each data set is represented by the bold solid line, the median by the thin line, the boxes indicate the interquartile range, and 95% confidence intervals are contained within the error bars. The bold dots indicate observations that fall outside of the 95% confidence intervals. Results of t-test comparisons are listed in the upper right corner of each graph

food. Furthermore, for strikes upon immobile food, feeding behavior shifted with food position, and epibenthic items elicited faster strikes and shorter bite durations than food positioned on the ground.

Flexibility in feeding behavior is indicative of a diverse diet (Liem 1980; McKaye and Marsh 1983; Norton 1991), and the capacity to modulate prey capture strategy may significantly influence growth and survival at the individual level by expanding dietary breadth and increasing feeding opportunities (Liem 1980; Sanderson 1991). Modulation of feeding behavior as a response to differing prey conditions has been demonstrated for multiple species. For example, largemouth bass (*Micropterus salmoides*) switch from ram to suction feeding when visibility is inhibited (Gardiner and Motta 2012), and also will increase ram-feeding behavior when presented with elusive prey (Wintzer and Motta 2005). Elusive prey has also been shown to elicit increased ram behavior

in sculpins (Cottidae; Norton 1991), larger gape width and increased ram distance in cichlids (Wainwright et al. 2001), and faster approach and strike velocities in the kelp greenling *Hexagrammos decagrammus* (Nemeth 1997a, 1997b). Wider gapes and faster mouth closing times reduce the chance of prey escaping (Motta et al. 2002), so the most effective predation strategies upon evasive prey should include rapid approaches, shorter bite times and larger maximum gapes.

Categorizing prey capture behavior as either ram or suction has long been used to describe fish feeding strategies (Alexander 1967; Nyberg 1971; Van Leeuwen and Muller 1984; Wainwright and Lauder 1986; Norton 1991). Most fishes utilize a combination of both ram and suction, placing them somewhere along a 'ram-suction' continuum (e.g., Norton and Brainerd 1993; Wainwright and Richard 1995; Nemeth 1997a, 1997b; Van Damme and Aerts 1997; Higham et al.
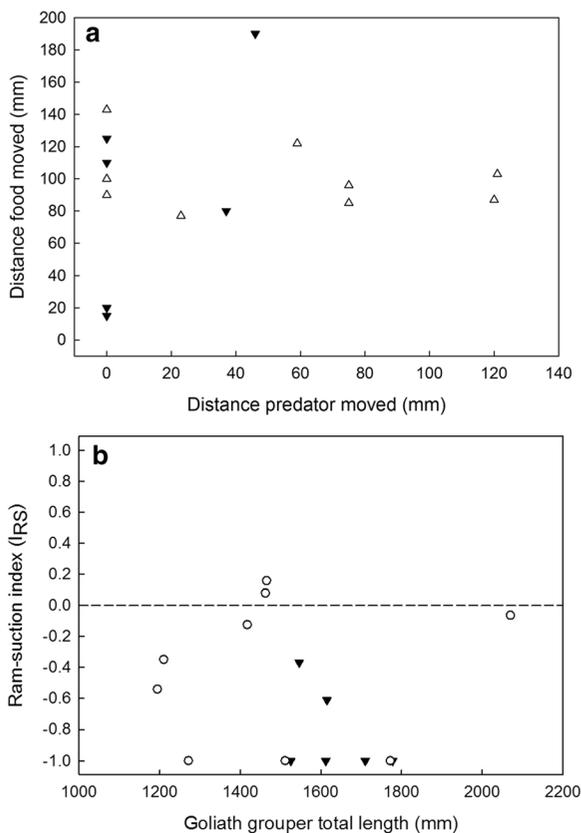
Fig. 6 a Distances moved by Goliath grouper *Epinephelus itajara* plotted against distances moved by food items during feeding events upon immobile benthic (●) or elevated (○) food, and **b** Ram-suction index (I_{RS}) values calculated for these feeding events. There was not a significant difference in I_{RS} between groups (df = 13; $p = 0.094$)

2005; Flammang et al. 2009). The ram suction index (Norton and Brainerd 1993) provides a relatively easy way to compare feeding behaviors, both among and within species (Gibb 1997; Nemeth 1997a, 1997b; Ferry-Graham 1998; Sass and Motta 2002; Wintzer and Motta 2005). Calculated I_{RS} values for Goliath grouper spanned the full ram-suction continuum during this study, providing evidence of their ability to adjust their prey capture strategy based upon the situation. When presented with live, active food, all Goliath grouper demonstrated I_{RS} values characteristic of ram feeding (i.e., $I_{RS} > 0.0$), and exhibited forward movement to engulf the swimming fish. In contrast, non-moving food items, regardless of their position within the water column (epibenthic vs. benthic), typically elicited I_{RS} values indicative of suction feeding (< 0.0). While estimates of I_{RS} provide an index value and thus are not meant to provide an exact measure of feeding

performance on their own (Wainwright et al. 2001), the index can be especially useful during attempts to demonstrate how fish adjust their feeding behavior in response to differing prey opportunities. The I_{RS} values calculated herein were supported by an assessment of the actual distances moved by food and predator during alternate scenarios: distances moved by the food items were much greater than distances moved by the Goliath grouper when presented with immobile food, while the opposite was true for mobile food.

Goliath grouper suction feeding was preempted by slow approaches and often, a complete halt in forward motion prior to mouth opening, which was directly followed by the food being rapidly sucked into the mouth. Additionally, suction feeding sequences exhibited significantly shorter distances between predator's mouth and the food at the onset of mouth opening (mean distance =3.5% of total length versus 16% of total length during ram feeding). Similarly, largemouth bass (mean standard length = 235 mm) initiated suction feeding at small distances of 0.4–26.6 mm (mean = 10.1 mm versus 44.8 mm for ram feeding; Svanback et al. 2002), which corresponded to <1–11% (mean ~ 4.3%) of predator standard length. Slow approaches during suction feeding are likely an attempt to reduce the "bow wave" created by forward motion of the head – the reduction of which should allow for greater suction pressure on the prey item (Ferry-Graham et al. 2003; Wintzer and Motta 2005). Furthermore, the capacity for effective suction decreases with distance from the target (Muller et al. 1982; Norton and Brainerd 1993; Wainwright et al. 2001; Day et al. 2005), so suction feeding at close range should increase efficiency (Gibb and Ferry-Graham 2005), especially for non-elusive prey that is unlikely to escape (Higham et al. 2006). Suction distances during feeding sequences upon immobile food ranged between 0 and 120 mm (mean = 53.5 mm), corresponding to <1–8% of predator total length (mean = 3.4%), < 1–29% of predator head length (mean = 12.2%), and <1–65.4% of maximum gape (mean = 29.4%). Bluegill sunfish *Lepomis macrochirus*, are specialized suction feeders (Gillis and Lauder 1995; Carroll et al. 2004), and Holzman et al. (2007) demonstrated that individuals (156–178 mm SL) would initiate strikes upon tethered shrimp from an average of ~10 mm away (~6% of predator SL). Suction feeding perch (*Perca fluviatilis* L.) between 60 and 200 mm TL displayed suction distances ~7–12 mm (6–11% of predator TL), and larger perch had longer suction distances than smaller perch

(Svanback and Eklov 2003). Similarly, van Wassenberg et al. (2006) showed that theoretical suction distance generally increased with catfish *Clarius gariepinus* head size, at least up to a suction distance of 100 mm (catfish ranged in size from 111 to 923 mm TL). In contrast, suction distances for nurse sharks (*Ginglymostoma cirratum*) were not affected by the total length of the shark (1000–1720 mm TL) and were typically only ~30 mm (1.7–3% of TL) (Motta et al. 2008). The suction distances observed within this study (1–120 mm) are relatively small compared to the large size of Goliath grouper (> 1000 mm TL), but are comparable to those observed for other large and small fishes (Svanback and Eklov 2003; van Wassenberg et al. 2006; Motta et al. 2008). This is likely due to the hydrodynamic restrictions imposed during aquatic suction feeding, which limit the effectiveness of suction to relatively short distances from the mouth (Muller et al. 1982; Norton and Brainerd 1993; Wainwright et al. 2001; Day et al. 2005; Gibb and Ferry-Graham 2005).

Due to the forward motion required for ram feeding, benthic prey is most effectively captured through suction (Carroll et al. 2004; Day et al. 2005; Gibb and Ferry-Graham 2005; Nauwelaerts et al. 2007), and Goliath grouper exhibited suction for all benthic food items during this study. When immobile food items were elevated off of the bottom, Goliath grouper continued to exhibit suction feeding behavior but exhibited shorter times to maximum gape and mouth closing and shorter bite durations. Similar differences in feeding kinematics between benthic and midwater feeding have been observed for other fishes such as the European ruff *Gymnocephalus cernua* (Elshoud-Oldenhave and Osse 1976) and the Malawi cichlid *Petrotilapia tridentiger* (Liem 1980). The longer times to maximum gape, mouth closing and total bite durations during benthic feeding may be explained by an increased need to properly orient the mouth for good suction in order to work around substrate interference, or alternately, because the substrate may facilitate prey capture by providing an additional barrier to prey escape, the urgency to close the mouth may be reduced.

The morphology of specialized suction feeding teleosts [e.g., butterflyfishes (Motta 1988), seahorses (Bergert and Wainwright 1997), bluegill sunfish (Carroll et al. 2004)] is typically exemplified by small mouths, reduced dentition and deep bodies (Muller and Osse 1984; Norton and Brainerd 1993; Clifton and Motta 1998). In contrast, specialized 'ram' feeders are characterized by large mouths, relatively large teeth and more streamlined bodies that are efficient at rapidly overtaking prey (Rand and Lauder 1981; Webb 1984; Porter and Motta 2004; Grubich et al. 2008). Goliath grouper have large mouths, exhibiting a maximum vertical gape at least 15% of total body length, but possess small villiform teeth and have bodies that are not suggestive of high cruising speed. A large mouth increases the size range of potential prey (Keast 1985; Werner 1974; Wainwright and Richard 1995) but may also decrease suction performance (Muller et al. 1982; Van Leeuwen and Muller 1984; Liem 1990). Oufiero et al. (2012)) suggested that species with low morphological potential for suction may exhibit a range of attack behaviors. Feeding behavior by Goliath grouper demonstrated that they are capable of exhibiting a range of prey capture strategies and will adapt prey capture mechanisms in response to different situations. While their morphology is not predictive of a specialized ram feeder, they are capable of short explosive bursts of speed (Bullock and Smith 1991) and will overtake fish struggling on a line that presents allows for easy capture and provides an additional food opportunity.

Based upon the results herein, we suspect that these types of prey items are likely consumed primarily through suction feeding. However, more elusive, mobile prey is still represented within their diet and they are likely consumed during short bursts of ram-dominated feeding. The ability to modulate feeding behavior, combined with their large gape, allow Goliath grouper to consume a wide variety of prey. Along the west coast of Florida, Goliath grouper are most commonly associated with artificial reefs (Koenig et al. 2011; Collins et al. 2015). Artificial reefs are favored fishing areas for many anglers, and as the Goliath grouper population recovers, the interaction between this species and anglers is likely to increase. Angled fish that are struggling on a hook and line immediately above resident habitat present a readily exploitable food opportunity. Predation upon these items increases the potential for incidental catch and release of Goliath grouper, and attacks upon hooked prey may also result in fishing gear entanglement or ingestion. Burns (2009) demonstrated a difference in survival after hooking (using circle hooks) for two species of reef fish (Red grouper *E. morio* and Red snapper, *Lutjanus campechanus*) and based this upon their feeding mechanism. Specifically, Red Grouper fed primarily through suction, followed by a period of prey manipulation within the buccal cavity that resulted in a

higher proportion of mouth hooks, a lower incidence of gut hooking, and reduced the overall catch and release mortality for this species. Conversely, Red Snapper displayed fast biting behavior that resulted in a higher incidence of gut hooking because they swallowed prey more rapidly. For Goliath grouper, rapid ram-based predation upon struggling fish that are being reeled in may increase the incidence of gut hooking as well as the ingestion of hooks and the associated fishing gear. Predation upon dead bait is likely more suction-based, which should favor being hooked in mouth or jaw rather than in the esophagus or stomach. Both scenarios are likely to increase as the population continues to recover, and further investigation into feeding behavior and the effects of catch and release upon Goliath groupers is warranted.

Conclusions

Mobile, elusive 'prey' elicited an increased capacity for ram feeding, and Goliath grouper exhibited larger maximum gapes and more rapid feeding sequences than when presented with immobile food. Immobile food was primarily consumed through suction, and strikes upon these items were characterized by slower, closer approaches, smaller maximum gapes and longer bite durations. The results reported herein demonstrate that Goliath grouper are capable of modulating feeding behavior based upon prey activity level and position within the water column.

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