

Modulation in feeding kinematics and motor pattern of the nurse shark *Ginglymostoma cirratum*

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Synopsis

Studies of feeding in bony fishes have almost universally demonstrated the ability of individuals to modulate their method of capture in response to differing stimuli. Preliminary evidence indicates that morphologically specialized inertial suction feeding sharks are the most likely fishes to lack inherent modulatory ability. We examined the ability of the nurse shark, *Ginglymostoma cirratum*, to modulate its feeding behavior based on different food types and sizes. *G. cirratum* is an inertial suction feeding fish that is apparently stereotyped in its food capture behavior. Electromyography showed no statistical difference between feeding motor patterns based on food type (squid or fish) or size (gape width or twice gape width), although there were slight inter-individual differences in the onset of muscle firing for some muscles. Kinematic analysis showed a statistical difference in variables associated with durations for different food types, with the durations for all variables being faster for squid bites than fish bites, but no difference based on the size of the food item. This apparent lack of modulation may be associated with specialization of the morphology and behavior of *G. cirratum* for obligate suction prey capture. This functional specialization constrains the method in which *G. cirratum* captures prey but does not appear to result in dietary specialization. An unusual post capture spit-suck manipulation allows this shark to handle and ingest large prey.

Introduction

Studies of feeding performance provide a crucial link between morphology and its ecological and fitness consequences in vertebrates (Reilly et al. 1992, Bouton et al. 1998, Wainwright et al. 2001, Waltzek & Wainwright 2003). An almost universal finding after more than three decades of research is that aquatically feeding vertebrates exhibit intra- and inter-individual variability in kinematic and motor patterns as well as the ability to modulate or alter these patterns in response to differing food

type, size, elusivity, and presentation (Liem 1978, Lauder 1981, Muller & Osse 1984, Friel & Wainwright 1999, Ferry-Graham et al. 2001, Motta & Wilga 2001), with some notable exceptions (Ferry-Graham 1997, 1998a, b, Edmonds et al. 2001). However, the vast majority of these studies have been on bony fishes (Norton 1995, Nemeth 1997).

Modulation is the ability of an organism to consistently alter its behavior pattern in response to differing stimuli (Liem 1978, 1979). Although inter-individual variability in kinematic and motor

patterns has been repeatedly found during elasmobranch feeding (Motta & Wilga 2001), modulation has been systematically examined in relatively few species of elasmobranchs (Table 1). A study of juvenile leopard sharks, *Triakis semifasciata*, found no evidence of modulation based on prey size or elusivity, although it was suggested that these sharks may be able to modulate the degree of suction used in prey capture to compensate for prey size (Ferry-Graham 1998a). Juvenile swellsharks *Cephaloscyllium ventriosum* also failed to demonstrate modulation with differing food size (Ferry-Graham 1997). Horn sharks *Heterodontus francisci* apparently do not modulate prey capture kinematics when offered one food type differing in its accessibility (Edmonds et al. 2001). Wilga & Motta (1998a) reported modulation in motor activity between feeding phases in the Atlantic guitarfish *Rhinobatos lentiginosus* but modulation was not examined for different food types, sizes, or elusivity. Other feeding studies have noted the apparent ability of various sharks, primarily ram feeding carcharhinid and lamnid sharks, to modulate prey capture based on differing food presentation, size, or type (Moss 1972, Tricas & McCosker 1984, Frazzetta & Prange 1987). It has been proposed that small food items should elicit suction feeding behaviors in sharks while larger prey items should elicit ram feeding and biting behaviors (Frazzetta & Prange 1987). Furthermore, previous studies on suction feeding sharks have utilized prey sizes that were gape sized or smaller (Edmonds et al. 2002, Motta et al. 2002, Robinson & Motta 2002).

These findings led Motta & Wilga (2001), Robinson & Motta (2002), and Motta et al. (2002) to propose that a lack of modulatory ability is more likely to be found in the morphologically specialized benthic inertial suction feeding sharks including the horn shark *Heterodontus francisci* and nurse shark *G. cirratum*, in which prey capture appears to be a stereotyped modal action pattern. The motor patterns of these species have yet to be examined (Edmonds et al. 2001, Motta et al. 2002, Robinson & Motta 2002).

The goal of this study is therefore to examine modulation of kinematic and motor patterns during inertial suction food capture in *G. cirratum* in response to different sizes and types of food.

Table 1. Summary of studies addressing modulation elasmobranchs.

Study	Species	Dominant feeding Style	Prey type and size	Feeding variable	Modulation tested	Modulation detected
Ferry-Graham (1997)	<i>Cephaloscyllium ventriosum</i>	Ram	Gape width and half-gape width pieces of cut smelt and shrimp	Preysize	Kinematics	No
Ferry-Graham (1998a)	<i>Triakis semifasciata</i>	Ram with suction component	Gape width and half-gape width cut shrimp, 1–2 cm live earthworm section, 1–4 cm live mud shrimp	Prey size, prey elusivity	Kinematics	No
Wilga and Motta (1998a)	<i>Rhinobatos lentiginosus</i>	Suction	Shrimp		Kinematics and Motor Pattern	No – Kinematics Yes – Motor Pattern
Edmonds et al. (2001)	<i>Heterodontus francisci</i>	Suction	4 cm cut squid	Prey accessibility	Kinematics	No

The nurse shark *G. cirratum* (Bonaterre 1788) (Orectolobiformes; Ginglymostomidae) is widely distributed throughout tropical and sub-tropical coastal waters on both sides of the Atlantic and in the Eastern Pacific (Compagno 2001). Its diet consists primarily of benthic invertebrates and fishes (Gudger 1921, Castro 2000, Compagno 2001). *G. cirratum* has a suite of characteristics suited for suction feeding. Robust and reinforced labial cartilages frame the terminal mouth when open, creating a small, nearly circular opening which is thought to be most efficient for suction generation (Wu 1994, Motta et al. 2002, Robinson & Motta 2002). The nurse shark has small, non-serrated tricuspid homodont teeth suited for grasping prey, but less so for cutting or tearing (Cappetta 1987, Williams 2001). A robust jaw and hyoid apparatus accommodates the apparently hypertrophied jaw abductor muscles (Moss 1965, Wu 1994), with which these animals are capable of extremely rapid buccal expansion occurring on average in 32 ms (Motta et al. 2002).

Materials and methods

Kinematics

We trained eight juvenile *G. cirratum* (Total Length 61.0–110.0 cm; mean 85.3 cm) to feed in a 2.4 m diameter, 1400 l semicircular tank with a 0.5 by 1.7 m acrylic window at Mote Marine Laboratory, Sarasota, Florida and in a similar tank at the University of South Florida, Tampa, Florida. We maintained the animals on a diet of dead Atlantic thread herring, *Opisthonema oglinum*, and squid, *Loligo* sp., three times a week. During experiments, the sharks readily fed on these two food types in two size classes: approximately gape width, and approximately twice gape width. The animals were not fed for a minimum of 48 h prior to each experiment.

We recorded high-speed video on the first two animals NAC HSV200 at 200 fields sec^{-1} and recorded the remaining six with a Redlake PCI 1000 digital camera at 250 frames sec^{-1} . We acquired lateral and ventral views of the shark feeding in the same frame by using a mirror platform set at 45° beneath the animal. We filmed a minimum of five bites for each food type and size.

Food items were presented randomly to avoid the potential confounding effect of satiation on motor patterns and kinematics. Each shark was recorded multiple times for kinematic variables prior to a final filming session with concurrent electromyography. We analyzed a total of 156 bites from the video footage for kinematic analysis. Some filmed bites were eliminated from analysis because the start of lower jaw depression was obscured.

We measured and analyzed eleven kinematic variables of food capture for each food type and size. Events following food capture were not analyzed, as post-capture events often lasted longer than the Redlake camera recorded and the shark typically swam off-field with the food item before manipulating and swallowing the food.

We designated the field prior to the start of lower jaw depression as time zero. The kinematic duration variables that were measured were: (1) time to mandible depression – from time zero to the field where ventral movement of the mandible stops; (2) time to maximum gape – from time zero to maximum gape; (3) gape duration – time jaws are held agape; (4) time to mandible elevation – from end of maximum gape to the field where dorsal movement of the mandible stops; and (5) bite duration – from time zero to the field where dorsal movement of the mandible stops. Movement of the hyoid could not be measured because it was masked by contraction of the hypaxial musculature. Palatoquadrate protrusion could not be measured because the palatoquadrate was obscured by extension of the labial cartilages. To measure distance and angle data, we captured selected video images from each animal and analyzed them using SigmaScan Pro 4.01 (SPSS Inc.). Variables that were measured using landmarks were: (1) gape width – from the anterior-most point of the mandible to the anterior-most point of the palatoquadrate at maximum gape; (2) resting jaw angle – at time zero the angle formed by the anterior-most points of the palatoquadrate and mandible, using the bottom of the medial labial cartilage as the vertex; (3) jaw angle at maximum gape; (4) resting cranial angle – at time zero the angle formed by a point on the dorsal surface above the first gill slit and the tip of the rostrum, with a point on the dorsal surface above the eye serving as the vertex; (5) cranial angle at maximum

gape – as in (4) but measured at maximum gape; and (6) total cranial elevation angle – the difference between maximum cranial angle and resting cranial angle.

Electromyography

We used six of the eight *G. cirratum* for electromyography (EMG) studies. Specimens were anesthetized with 0.1 g l⁻¹ tricaine methanesulfonate (MS-222). Up to twelve cranial muscles per experiment were implanted with bipolar electrodes inserted via 23 gauge hypodermic needles similar to the protocol of Motta et al. (1997). We implanted electrodes in the anterior division of the preorbitalis, quadratomandibularis, interhyoideus, intermandibularis, levator hyomandibularis, coracobranchialis, coracoarcualis, coracomandibularis, coracohyoideus, and epaxialis (for descriptive anatomy see Motta & Wilga 1999). The electrodes were differentially amplified (1000×, AM Systems Inc., Model 1700) and bandpass (100–3000 Hz) and notch (60 Hz) filtered. We recorded signals simultaneously on a Yokogawa DL416 digital oscilloscope and pulse code modulator (AR Vetter MV 520) that recorded to VHS tape. One channel on the pulse code modulator recorded a digital pulse synchronized with a pulsing LED that was recorded by the high-speed camera.

We converted EMG data from analog to digital signals using a Cambridge Electronics Design (CED) 1400+ analog-digital converter and downloaded to computer. We then analyzed the food capture sequences using Spike2 and a custom EMG analysis program (Cambridge Electronics Design, Ltd.). All sequences were referenced with respect to jaw opening as determined from the video. The variables measured were onset of muscle firing with respect to onset of jaw opening and duration of muscle activity.

We commenced feeding experiments approximately 1 h following recovery from surgery after the animal resumed normal swimming and respiratory behaviors. Food was offered on wooden tongs with the longest dimension of the food item parallel to the mouth of the animal. We fed the animals to satiation, therefore there was not always an equal number of trials for both food types and sizes. The food item was held loosely in the

tongs and released prior to the prey capture in most cases. In some cases the animal removed the food item directly from the tongs before it could be released. Following the experiment we sacrificed all six animals via an overdose of MS-222 in order for us to verify electrode placement via dissection, following University of South Florida and Mote Marine Laboratory Institutional Animal Care and Use guidelines (USF IACUC #1734). The stomach contents of three individuals were dissected out for qualitative observation. We used a total of 28 bites for EMG analysis. As not all muscles implanted fire in all cases and as all muscles could not be implanted in all individuals, the data used for analysis is a composite of multiple bites from individual animals. A minimum of three bites from three animals for each treatment type was used. In some cases, there were not sufficient bites to statistically analyze effects of food type and/or food size for certain muscles and they were excluded from analysis.

Statistical analysis

We regressed all kinematic variables against total lengths to investigate for size-dependent differences. As there was no significant relationship between size and any of the kinematic variables the original data were further analyzed.

Normality and equality of variance assumptions were tested respectively by the Kolmogorov-Smirnov normality test and the Levene Median test using SigmaStat 2.03 (SPSS Inc.). Due to the fact that kinematic variables were not likely independent of each other, a principal components analysis (PCA) was performed using a correlation matrix. Obstruction and non-lateral footage resulted in missing values for some of the landmark variables. These missing values were replaced via Systat 9 (SPSS Inc.) using regression substitution and a correlation matrix to determine missing values. The resulting PCA component scores were analyzed via MANOVA and significant component scores were tested with univariate *F* tests using individual, food type, and food size as factors. Due to the highly unbalanced design of the electromyographic data a PCA was not feasible, therefore, we ran one-way ANOVAs for each electromyographic variable. The factors that were examined were individual, food type, and food size. A post-hoc Tukey's multiple

comparison test was performed to test all pairwise comparisons (Zar 1999). We used non-parametric Kruskal-Wallis ANOVA on ranks in cases in which assumptions of normality and heterogeneity of variance could not be met by transformation. We used Dunnett's multiple comparison test for significant ANOVA on ranks. Two-way or three-way ANOVA was not possible due to sample size and the unbalanced design due to missing data in some cells, so interaction effects could not be directly determined. A sequential Bonferroni correction was not applied to the data due to its effect of increasing Type II error (Cabin & Mitchell 2000, Moran 2003).

Results

Feeding behavior

The nurse shark *G. cirratum* captured food in all cases using inertial suction. The food item was visibly drawn to the mouth of the animal following

rapid buccal expansion. Food capture followed the same basic pattern beginning with mandible depression (Figure 1). In 74% of the bites there was a slight delay between end of mandible depression (45 ms \pm 2.58) and maximum gape (56 ms \pm 3.92), which was due to minor cranial elevation (1.6 \pm 0.7). The mouth was held agape for a time (66 ms \pm 5.07) before the mandible was elevated (53 ms \pm 2.58) and the twice gape-size food was grasped between the anterior teeth, or the gape-size food sucked directly into the buccal cavity (Figure 1). Smaller food items were apparently swallowed whole without processing by the teeth as evidenced by examination of stomach contents following three of the EMG experiments. Large food items were often held between the jaws and then manipulated. This manipulation consisted of one or both of the following behaviors: reorientation of the food item along its long axis, and/or repeated spit and suction behaviors termed 'spit-suck manipulation.'

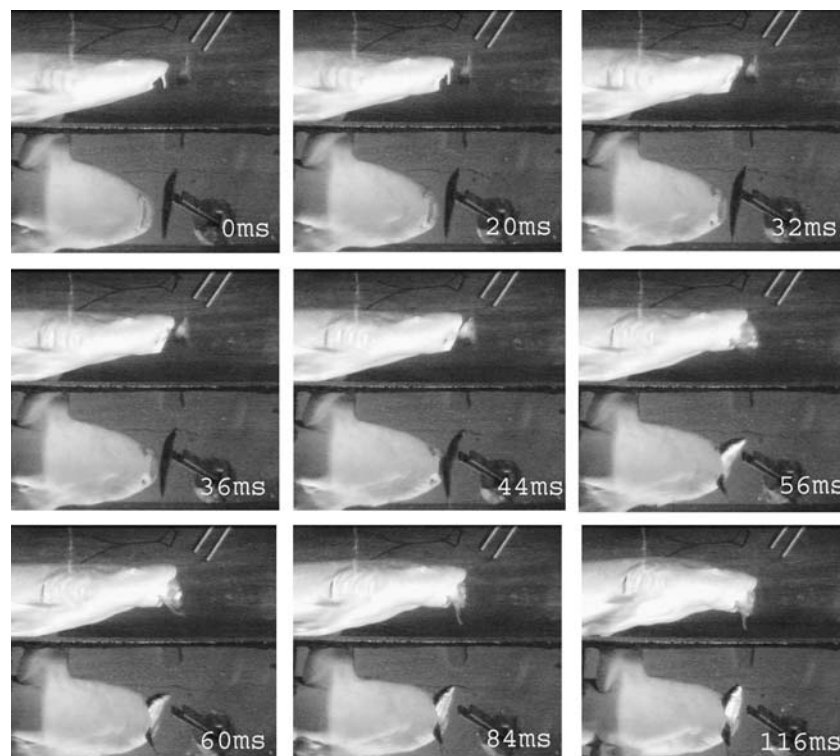


Figure 1. Kinematic profile of feeding in a nurse shark *Ginglymostoma cirratum*. Durations indicated are for this specific bite and not the mean for this behavior. Sequence begins with lower jaw depression at 0 ms. End of mandible depression occurs at 32 ms and maximum gape occurs at 36 ms. The food is drawn to the mouth via inertial suction and is lodged at 56 ms, preventing complete jaw closure. Mandible elevation begins at 60 ms and stops by 84 ms.

Reorientation of the food item consisted of either the animal dropping the food item and reacquiring it, or the animal actively expelling the item from its mouth and then sucking it back in. In some instances, food was reoriented along its longitudinal axis and transported through the buccal cavity into the stomach in a single suction event. Spit-suck manipulation consisted of the repeated alteration of suction and spitting behaviors such that the food item came partially out of the mouth and was then sucked back in. Qualitative observation of stomach contents indicated that fish were shredded during spit-suck manipulation but squid were relatively intact.

Modulation of kinematic variables

There was no distinct separation of the variables by food type or size in kinematic space (Figure 2). The principal component analysis separated the kinematic variables into three components that explained 69.29% of the variance. Principal component 1 (PC1) explained 36.96% of the variance, principal component 2 (PC2) explained a further 18.97% of the variance, and principal component 3 (PC3) accounted for 13.35% of the variance (Figure 2). All duration variables loaded positively on PC1 with all loading values higher than 0.7. Resting jaw angle and jaw angle at maximum gape loaded positively on PC2 with loading values of 0.709 and 0.728, respectively, while resting cranial angle and cranial angle at maximum gape loaded negatively on PC2 with loading values of -0.617 and -0.613, respectively. Gape width loaded positively on PC3 with a loading of 0.581.

The MANOVA indicated significant effects for food type and individual (Table 2). For food type the only component that was significantly different according to the univariate *F*-test was PC1 upon which the duration variables loaded. In all cases, duration variables were shorter for squid than fish. The bite duration for squid averaged $133 \text{ ms} \pm 12.07$ as compared to $178 \text{ ms} \pm 10.17$ for fish. Mandible depression averaged $38 \text{ ms} \pm 4.60$ for squid and $49 \text{ ms} \pm 3.08$ for fish. The time to maximum gape was $45 \text{ ms} \pm 4.66$ for squid and $62 \text{ ms} \pm 5.19$ for fish, with gape durations of $45 \text{ ms} \pm 5.09$ and $76 \text{ ms} \pm 6.77$, respectively. The only duration variable with similar values was the duration of mandible elevation,

which was $54 \text{ ms} \pm 5.51$ for squid and $55 \text{ ms} \pm 3.31$ for fish. Inter-individual variability was significant for PC3 upon which gape width loaded. Larger individuals had a larger gape width, although regression of gape width against individual size was not significant. Although the MANOVA for food size was not significant ($p = 0.087$), the univariate *F*-test suggested there was a significant effect on PC1 ($p = 0.001$). Interaction effects for individuals, food type, and food size could not be determined due to collinearity of the treatments and interaction effects.

Electromyography

The mean onset times and durations for each implanted muscle were used to determine a mean motor pattern for all bites combined (Figure 3). There were no significant differences between food types or sizes for any of the EMG variables, however individual differences were found for five EMG variables. These differences were found in onset of muscle firing for the coracobranchialis ($F = 4.903$, $df = 2$, $p = 0.03$), coracomandibularis ($H = 6.751$, $df = 2$, $p = 0.034$), epaxialis ($F = 56.660$, $df = 2$, $p = 0.001$), interhyoideus ($F = 4.634$, $df = 2$, $p = 0.035$), and quadratomandibularis ($F = 6.395$, $df = 2$, $p = 0.014$). The remaining EMG variables, both onset times and durations of activity, were not significantly different among individuals.

Discussion

The nurse shark *G. cirratum* is an inertial suction feeder with stereotyped prey capture kinematics. Suction prey capture is characterized by rapid buccal expansion similar to that of other suction feeding elasmobranchs (Ferry-Graham 1997, 1998a, b, Edmonds et al. 2001, Motta et al. 2002, Robinson & Motta 2002). Prey capture is characterized by an anterior-to-posterior expansion of the buccopharyngeal cavity.

Similar to *H. francisci* and *T. semifasciata* that capture food by suction and a combination of suction and ram, cranial elevation does not appear to be an integral component of suction feeding in nurse sharks (Ferry-Graham 1998a, Edmonds et al. 2001). In 35% of the bites, the total cranial angle at maximum gape was negative, indicating

that at maximum gape the head of the animal was depressed relative to its position prior to jaw opening. Cranial elevation, which is markedly

greater in ram-feeding sharks, is thought to be useful for increasing the gape during feeding, repositioning the sub-terminal mouth towards the

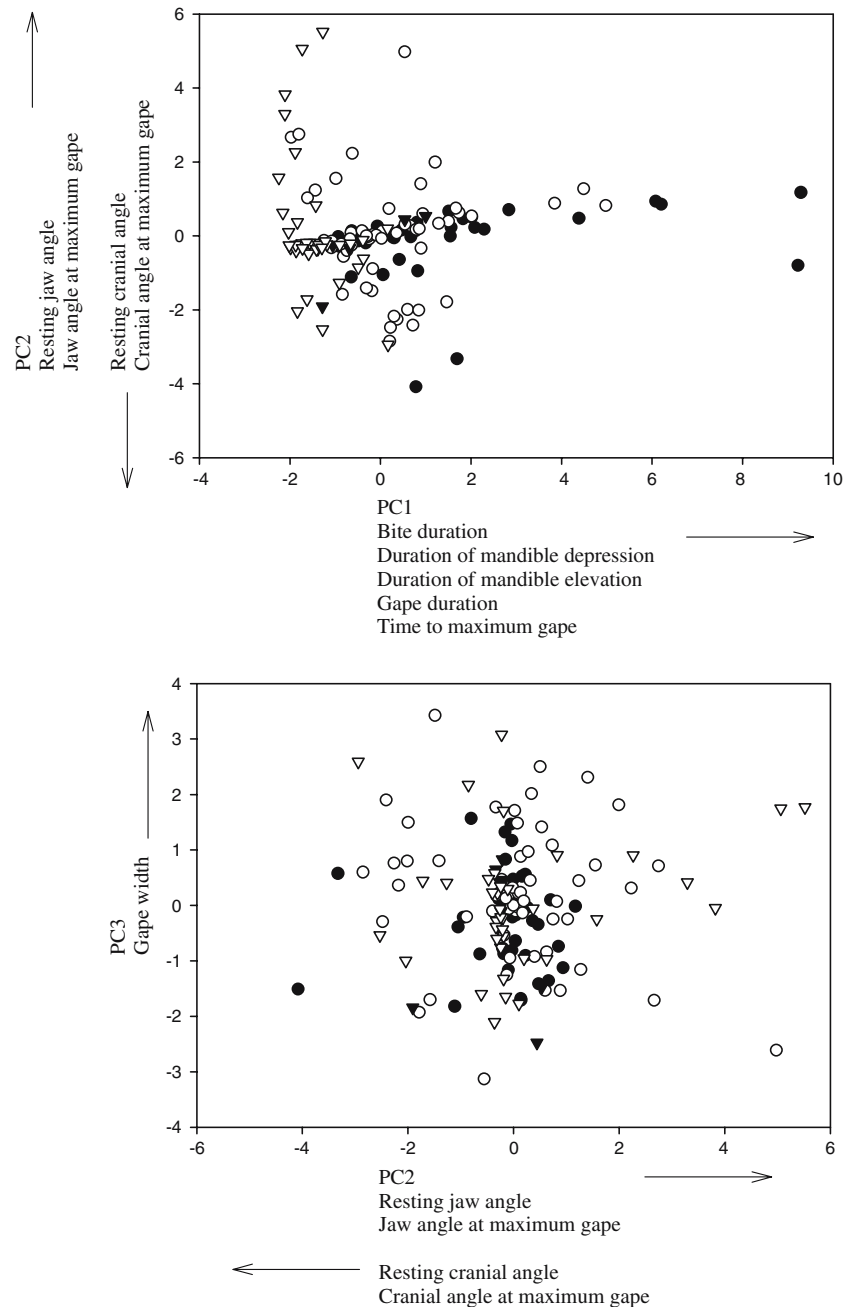


Figure 2. Plot of principal components for kinematic variables. Top graph indicates principal component 1 (PC1) versus principal component 2 (PC2). Bottom graph indicates principal component 2 (PC2) versus principal component 3 (PC3). Arrows indicate increasing magnitude of the loadings of the kinematic variables on the principal component axis. Closed circles indicate bites with gape-size fish. Open circles indicate bites with twice gape-size fish. Closed triangles indicate bites with gape-size squid. Open triangles indicate bites with twice gape-size squid.

Table 2. MANOVA values and univariate F tests for the principal components. Significant values indicated by bold type.

Treatment type	Effect				
	SS	Df	MS	F	p
<i>Food type</i>					
Univariate F tests	Wilks' Lambda = 0.798	F-Statistic = 11.025	df = 3, 131	Prob = 0.000	
Principal component 1	86.038	1	86.038	32.79	0.000
Error	348.978	133	2.624		
Principal component 2	0.721	1	0.721	0.392	0.532
Error	244.559	133	1.839		
Principal component 3	0.171	1	0.171	0.147	0.702
Error	154.701	133	1.163		
<i>Food size</i>					
Univariate F tests	Wilks' Lambda = 0.903	F-Statistic = 4.677	df = 3, 131	Prob = 0.087	
Principal component 1	30.793	1	30.793	11.736	0.001
Error	348.978	133	2.624		
Principal component 2	3.862	1	3.862	2.1	0.15
Error	244.559	133	1.839		
Principal component 3	0.002	1	0.002	0.001	0.97
Error	154.701	133	1.163		
<i>Individual</i>					
Univariate F tests	Wilks' Lambda = 0.708	F-Statistic = 2.292	df = 21, 376	Prob = 0.001	
Principal component 1	32.825	7	4.689	1.787	0.095
Error	348.978	133	2.624		
Principal component 2	22.203	7	3.172	1.725	0.108
Error	244.559	133	1.839		
Principal component 3	27.8	7	3.971	3.414	0.002
Error	154.701	133	1.163		

Results are separated by treatment type (food type, food size, and individual).

prey in a more terminal position, and possibly assisting in palatoquadrate protrusion (Moss 1972, Tricas & McCosker 1984, Frazzetta & Prange 1987, Frazzetta 1994, Motta et al. 2002). Cranial elevation would be a disadvantage in suction feeding sharks as a larger gape is less effective in suction feeding (Lauder 1983, Norton 1991, Norton & Brainerd 1993) and the terminal position of the mouth may preclude the necessity for cranial elevation (Motta et al. 2002). Spit-suck manipulation was observed in all but one of the individuals. This behavior was seen only for twice gape-size food. The teeth in nurse sharks are small and non-serrated (Goto 2000, Compagno 2001), which does not make them suited for tearing. It is possible that the teeth are instead used in spit-suck manipulation to grasp the food item, or the back and forth movement of the food item across the teeth results in shearing or rasping of the flesh. Spit-suck manipulation in nurse sharks has been observed to dismember food items including large

fish and crabs (Motta et al. 2002, personal observations).

Kinematic and electromyographic results support the hypothesis that *G. cirratum* is a stereotyped inertial suction feeder. The nurse shark *G. cirratum* does not appear to modulate its capture behavior based on food size, however slight modulation of capture kinematics may be present based on food type (Table 2).

The kinematic durations for all variables were longer for fish bites as compared to squid bites. This difference between food types in part may be attributable to the greater mass of fish compared to squid for equivalent sized pieces. Motor patterns indicated no apparent modulation for food size or type. The discrepancy between kinematics and motor patterns for food type may also be due to the lower sample size of the electromyographic data. Due to this low sample size, the statistical results of the electromyographic analysis must be viewed with caution. The overall motor pattern

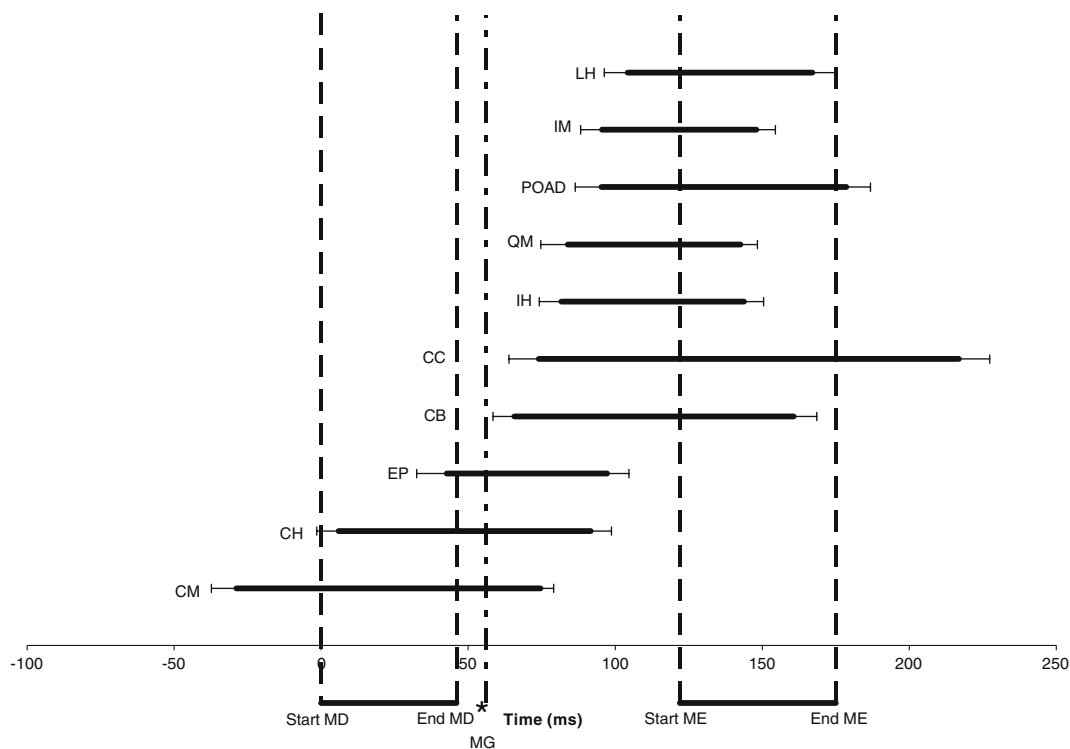


Figure 3. Compilation of muscle firing for the nurse shark *Ginglymostoma cirratum*, with standard error bars ($n = 6$ individuals; 34 bites total). Bars below the axis represent the overall kinematic profile. The first bar indicates duration of mandible depression and the second bar indicates duration of mandible elevation. The * represents maximum gape. MD, mandible depression; ME, mandible elevation; MG, maximum gape; CB, coracobranchialis; CC, coracoarcualis; CH, coracohyoideus; CM, coracomandibularis; EP, epaxialis; IH, interhyoideus; IM, intermandibularis; LH, levator hyomandibularis; POAD, anterior division of preorbitalis; QM, quadratomandibularis. Not all muscles were implanted or fired in all bites.

sequence, however, is consistent with that of other elasmobranch motor patterns (Motta et al. 1997, Wilga and Motta 1998a). An exception is that the epaxialis fires at jaw opening in the lemon shark *Negaprion brevirostris*, a ram-feeder, and is associated with marked cranial elevation in that species as compared to *G. cirratum* which has negligible cranial elevation and no activity in the epaxialis at jaw opening (Motta et al. 1997).

The few studies in elasmobranchs that have systematically examined modulation have failed to demonstrate it during food capture (Ferry-Graham 1997, 1998a, b, Wilga & Motta 1998a, Edmonds et al. 2001). There are, however, reasons to be cautious about suggesting that modulation is absent in the elasmobranchs under investigation. First, most of these studies have been on benthic or epibenthic, primarily suction-feeding species (Wu 1994, Ferry-Graham 1997, 1998b, Wilga &

Motta 1998a, Edmonds et al. 2001). Motta & Wilga (2001) proposed that sharks that are more morphologically specialized for suction will have more stereotyped capture behavior and less modulation than ram feeding sharks, in part due to the rapid kinematics necessary for suction capture. However, fast suction feeding with apparent modulation of prey capture is employed by *Astatotilapia elegans*, a cichlid, which uses peripheral feedback control to abbreviate suction (Aerts 1990, Aerts & DeVree 1993). Secondly, some of these studies may not have provided food items that were different enough to require modulation of the feeding behavior. Ferry-Graham (1998a) suggested that the live prey items offered to juvenile *T. semifasciata* may not have been truly elusive, given the fact that all elusive prey items were captured. Modulation was not present in *C. ventriosum* based on only prey size

(Ferry-Graham 1997). The study on *H. francisci* utilized only one food type and examined differences in presentation (Edmonds et al. 2001). It appears plausible that food size would result in modulation of kinematics and motor patterns in *G. cirratum* due to differences in gape size required to ingest the food, as well as differing mass of the food. However, food size had no discernible effect on the kinematics of feeding in the *G. cirratum* with the possible exception of gape width. It is possible that food size did not differ sufficiently to result in modulation. *G. cirratum* primarily takes small bony fishes (<20 cm) in waters off the east coast of Florida and the Bahamas, suggesting that food sizes used in this study were as large as those naturally found for nurse sharks (Castro 2000).

Although there were no differences detected during capture, it is possible that modulation occurs in the manipulation sequence based on food size. Spit-suck manipulation, during which the shark repositioned and sometimes dismembered the food, occurred only with food items that were twice gape size.

The consistency of the feeding behavior suggests that nurse sharks are functional specialists *sensu* Ferry-Graham et al. (2002). Morphologically, *G. cirratum* has a small, anteriorly directed and laterally enclosed mouth, large labial cartilages braced against the upper jaw, a buccal valve to prevent backflow of water out of the mouth, teeth reduced in size, and apparently hypertrophied jaw abductor muscles (Moss 1965, 1977, Motta et al. 2002, Motta & Wilga 1999). Combined with rapid buccal expansion, *G. cirratum* is morphologically suited for suction capture and is an apparent obligate suction feeder based on all observations to date (Tanaka 1973, Robinson & Motta 2002, Motta et al. 2002, this study). Due to their reduced, non-serrated dentition nurse sharks are not likely to be able to cut or tear pieces out of larger prey items, limiting prey size but not prey type as reflected by their wide dietary breadth, which includes teleosts, crustaceans, cephalopods, and other invertebrates (Gudger 1921, Castro 2000, Compagno 2001).

Although modulation was not present with respect to food type or size, inter-individual variation was found with gape width and the firing patterns of a few muscles. Variation among individuals is a common finding of feeding studies in lower

vertebrates such as fish and salamanders (Shaffer & Lauder 1985, 1986, Wainwright & Lauder 1986, Reilly & Lauder 1989, Reilly & Lauder 1990, Lauder & Shaffer 1993, Gillis & Lauder 1994, 1995, Reilly 1996) and inter-individual variation has been found in other elasmobranchs (Motta et al. 1997, Ferry-Graham 1997, Wilga & Motta 1998a, b).

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