

## Kinematic Analysis of Suction Feeding in the Nurse Shark, *Ginglymostoma cirratum* (Orectolobiformes, Ginglymostomatidae)

PHILIP J. MOTTA, ROBERT E. HUETER, TIMOTHY C. TRICAS, AND ADAM P. SUMMERS

**Inertial suction feeding is known to occur in some sharks, but the sequence and temporal kinematics of head and jaw movements have not been defined. We investigated the feeding kinematics of a suction feeding shark, the nurse shark *Ginglymostoma cirratum*, to test for differences in the timing and magnitude of feeding components with other shark taxa when sharks were fed pieces of bony fish. Thirteen kinematic variables were measured from high-speed video recordings. Food capture in this species consists of expansive, compressive, and recovery phases, as in most other sharks, but there is little or no cranial elevation. Mean time to maximum gape (32 msec) is the fastest recorded for an elasmobranch fish. Other relatively rapid events include mandibular depression (26 msec), elevation (66 msec), and total bite time (100 msec). Buccal valves assist the unidirectional flow of water into the mouth and out of the gill chambers. Food capture under these experimental conditions appears to be a stereotyped modal action pattern but with significant interindividual variability in timing of kinematic events. *Ginglymostoma cirratum* exhibits a suite of specializations for inertial suction feeding that include (1) the formation of a small, anteriorly directed mouth that is approximately round and laterally enclosed by modified labial cartilages; (2) small teeth; (3) buccal valves to prevent the backflow of water; and (4) extremely rapid buccal expansion. Sharks that capture food by inertial suction have faster and more stereotyped capture behavior than sharks that primarily ram feed. Inertial suction feeding, which has evolved multiple times in sharks, represents an example of functional convergence with inertial suction feeding bony fishes.**

**T**HE feeding apparatus of vertebrates is a complex mechanical system with obvious importance to fitness. Understanding the dynamics of the prey capture mechanism in an evolutionary framework gives insight into the constraints and flexibility that govern changes in this key system (Lauder, 1990). Studies of cartilaginous fishes, bony fishes, amphibians, and reptiles have produced evolutionary hypotheses regarding the transition from aquatic to terrestrial prey capture (Lauder, 1985; Lauder and Reilly, 1994; Wilga et al., 2000). Sharks, skates, and rays (elasmobranchs) possess a radically different suspensorium and jaw structure from that of the bony fishes. In spite of the structural differences, elasmobranchs and bony fishes have evolved a similar suite of prey capture mechanisms including suction, grasping, biting, gouging, and filter feeding (Moss, 1977; Motta and Wilga, 2001).

Aquatic prey capture in sharks and bony fishes may be accomplished through ram, biting, or suction. Ram feeding, which occurs when the predator overswims the prey, may encompass feeding events that establish a continuous current in the mouth and over the gills. This occurs in the filter feeding basking shark *Cetorhinus maximus* or when the predator approaches the

prey with an open mouth resulting in some anterior or lateral displacement of water, such as in the white shark *Carcharodon carcharias* (Diamond, 1985; Tricas and McCosker, 1984; Sims, 2000). Biting, which may accompany ram, occurs when a shark swims toward the prey, stops, and then bites or removes pieces off the prey, such as in the cookiecutter shark *Isistius brasiliensis* (LeBoeuf et al., 1987; Motta and Wilga, 2001).

The mechanics and function of suction feeding are controversial (Muller et al., 1982; Norton and Brainerd, 1993; Van Damme and Aerts, 1997). The clearest terminology is that of Van Damme and Aerts (1997), who suggest that suction feeding includes a continuum of behaviors ranging from sucking in just enough water to keep the prey item from escaping as the predator swims over it (compensatory suction) to the entrainment of the prey item in a column of water that is transported toward the motionless predator (inertial suction). Bony fishes specialized for inertial suction feeding typically have a small, laterally enclosed mouth, protrusible upper jaw, reduced dentition, and strongly developed abductor muscles. Buccal expansion is large and rapid, and there is a wave of expansion and subsequent compression that travels

posteriorly such that the engulfed body of water and prey is carried into and through the buccal cavity (Lauder, 1980a; Muller et al., 1982; Liem, 1993). However, suction feeding in sharks and rays has only been investigated in a few species (Wu, 1994; Ferry-Graham, 1998; Pretlow-Edmonds, 1999). Buccal expansion is rapid and includes the use of labial cartilages and upper jaw protrusion to form a somewhat round and laterally enclosed mouth that is small to intermediate in size, and an anterior to posterior wave of expansion and compression draws the food into the mouth (Ferry-Graham, 1998; Wilga and Motta, 1998a).

Inertial suction feeding is hypothesized to be the ancestral form of prey capture for the bony fishes (Lauder, 1985). In contrast, fossil evidence and observations of morphologically similar, but extant sharks indicate that the ancestral prey capture behavior in elasmobranchs probably involved grasping the prey whole or tearing pieces from it, with minimal upper jaw protrusion or suction. Many of these Paleozoic sharks had a grasping dentition, long slitlike jaw and amphistylic jaw suspension that permitted little upper jaw kinesis (Schaeffer, 1967; Moy-Thomas and Miles, 1971; Maisey, 1980). A variety of extant elasmobranchs use inertial suction to some degree as their primary feeding method [spiny dogfish *Squalus acanthias* (Wilga and Motta, 1998a); leopard shark *Triakis semifasciata* (Russo, 1975; Talent, 1976; Ferry-Graham, 1998); wobbegong *Orectolobus maculatus*, nurse shark *G. cirratum*, and whale shark *Rhincodon typus* (Wu, 1994; Clark and Nelson, 1997; Robinson and Motta, 2002); horn shark *Heterodontus francisci* (Strong, 1989; Pretlow-Edmonds, 1999; Edmonds et al., 2001); guitarfish *Rhinobatos lentiginosus* (Wilga and Motta, 1998b); and perhaps the angel shark *Squatina californica* (Fouts and Nelson, 1999)]. Inertial suction feeding elasmobranchs are found in at least eight families, often nested within clades that contain ram and compensatory suction feeders, indicating that inertial suction feeding has evolved independently in several elasmobranch lineages (Fig. 1) (Motta and Wilga, 2001). However, functional convergence of inertial suction feeding in sharks has received little attention (Moss, 1977; Motta and Wilga, 1999).

Orectolobiformes, which include the nurse sharks and wobbegongs, are considered specialized inertial suction feeders based on their anatomy and feeding kinematics (Moss, 1977; Wu, 1994; Motta and Wilga, 1999). *Ginglymostoma cirratum* is common to shallow waters throughout the West Indies and south Florida, where it feeds on small fishes and crustaceans (Compag-

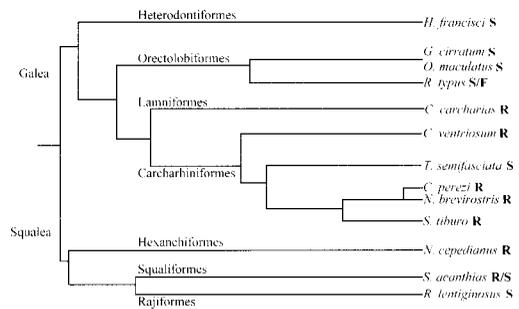


Fig. 1. Phylogeny of neoselachians according to Shirai (1996) with placement of *Carcharhinus perezii* according to G. J. P. Naylor (pers. comm.) incorporating prey capture types (R = ram feeding; S = suction feeding; S/F = suction filter feeding) based on the following kinematic studies: *Heterodontus francisci* = Edmonds et al. (2001); *Ginglymostoma cirratum* = this study and Robinson and Motta (2002); *Orectolobus maculatus* = Wu (1994); *Rhincodon typus* = Clark and Nelson (1997); *Carcharodon carcharias* = Tricas and McCosker (1984); *Cephaloscyllium ventriosum* = Ferry-Graham (1997); *Triakis semifasciata* = Ferry-Graham (1998); *Carcharhinus perezii* = Motta and Wilga (2001); *Negaprion brevirostris* = Motta et al. (1997); *Sphyrna tiburo* = Wilga and Motta (2000); *Notorynchus cepedianus* = personal observation (PJM); *Squalus acanthias* = Wilga and Motta (1998a); *Rhinobatos lentiginosus* = Wilga and Motta (1998b).

no, 1984; Castro, 2000). This benthic shark routinely uses inertial suction, generating pressures as low as  $-760$  mm Hg, to capture its prey (Tanaka, 1973; Robinson and Motta, 2002).

During prey capture many fishes demonstrate inherent intra- and interindividual variability in their kinematic and motor activity patterns, in addition to the ability to modulate or alter these patterns in response to differing food types and presentations (Liem, 1980a; Wainwright and Turingan, 1993; Nemeth, 1997). Variability may occur independently of the ability to modulate and may occur among feedings within a food category (Liem, 1978; Chu, 1989; Ferry-Graham, 1997). There is ample evidence of extensive variation of prey capture kinematics and motor patterns within species of sharks and rays (Motta et al., 1997; Wilga and Motta, 1998a; Ferry-Graham, 1998), but it is unclear whether an apparently morphologically specialized obligate suction feeding shark such as *G. cirratum* would demonstrate variability and what effect if any this would have on prey capture ability.

In this study, we investigated the kinematics of suction food capture in *G. cirratum* and compared it to food capture in other elasmobranchs. Our goals were to (1) determine to what extent *G. cirratum* relies on inertial suction feeding when presented with one food type; (2)

describe the kinematic pattern of suction food capture; (3) compare the kinematics of feeding to those of other cartilaginous and bony fishes; and (4) investigate interindividual variability in food capture kinematics and discuss this in light of prey capture.

#### MATERIALS AND METHODS

*Experimental procedure.*—Specimens of juvenile *G. cirratum* were collected in Florida Bay north of the Florida Keys and held at Mote Marine Laboratory, Sarasota, Florida, in 5 m diameter circular holding tanks with natural seawater. Four males and one female, ranging from 64–98 cm total length (mean = 78, SD = 13 cm), were used in the experiments. These immature sharks probably included age class 3+ years and older, although there are no published studies on *G. cirratum* aging prior to year 3 (Carrier and Luer, 1990; J. Castro, pers. comm.). An additional 85 cm TL female was video recorded to prepare the composite photograph of prey capture and to digitize the kinematic profile of a prey capture event. Approximately two weeks prior to the experiments, each animal was transferred to a 2.4 m diameter, 1400-liter semicircular tank with a 0.5 × 1.7 m acrylic window and fed cut pieces of fish three times a week. Water temperature in the experimental tank ranged from 26–29° C. Pieces of filets of Atlantic thread herring (*Opisthonema oglinum*) and crevalle jack (*Caranx hippos*) were cut to approximately half the mouth diameter (mouth diameter ranged from 4–8 cm) and placed on the floor of the tank or on a platform. Prey refers here to dietary items captured by natural feeding, and food refers to pieces of or whole food items offered under experimental conditions. Food size was approximately 2.5 × 3 × 1 cm for most bites. The animal was either conditioned to take the food from the floor of the tank in front of the window, or on a small plexiglass platform raised approximately 25 cm off the tank floor. In the latter case the shark sucked the food through a 2.5-cm hole in the clear plexiglass wall of the platform. In many cases, the shark remained stationary and propped on its pectoral fins as it took the food. Sharks became satiated after 22–44 bites, refusing further food.

All experimental sharks were filmed during feeding with a high-speed video camera (NAC HSV-200, 200 fps) or a Photosonics 1-PL camera (200 fps). A mirror placed at a 45-degree angle below the transparent floor of the tank provided a simultaneous ventral view of the shark in

some of the experiments. Illumination was provided with approximately 3000 watts of quartz-halogen lights. Because electromyographic experiments were being conducted simultaneously on these sharks, they had bipolar fine wire electrodes (0.06 mm diameter alloy wire) implanted in their cranial muscles. Motta et al. (1997) determined that implantation of electromyographic leads in the lemon shark *Negaprion brevirostris* did not affect feeding kinematics. The 85-cm TL female *G. cirratum* used for the food capture sequence and kinematic profile of prey capture was videotaped at 250 fps with a Redlake PCI-1000 digital camera illuminated by 300 watts of quartz-halogen light.

*Data collection.*—Video images of the five experimental sharks were analyzed with a Panasonic AG-1970 video analyzer and monitor, and cine film with a LW Athena analysis projector. Only clear lateral images of capture bites were used for the analysis, and therefore 8–14 bites were analyzed per shark, totaling 53 bites in all. The following durations were determined for each bite by counting the number of fields/frames (1 field/frame = 5 msec) for each of the following kinematic events: (1) mandibular depression = start of mandibular depression to maximum mandibular depression; (2) mandibular elevation = maximum mandibular depression to end of mandible elevation; (3) mandibular total = total time for mandibular depression and elevation; (4) head onset = time from beginning of mandibular depression to beginning of head elevation, if there was head elevation; (5) head elevation = start of head elevation to maximum head elevation; (6) head depression = maximum head elevation to end of head depression; (7) head total = total time of head elevation and depression; (8) labial onset = time from start of mandibular depression to start of labial cartilage protrusion; (9) labial protrusion = start of labial protrusion to maximum labial protrusion; (10) labial retraction = maximum labial protrusion to complete labial retraction; (11) labial total = total time of labial protrusion and retraction; (12) maximum gape = start of mandibular depression to maximum gape; and (13) food enters mouth = start of mandibular depression until the food enters the mouth and is no longer visible. In lateral view, palatoquadrate protrusion was obscured by the protrusion of the labial cartilages, but was visible in more anterior views. Consequently the kinematics of palatoquadrate protrusion are only qualitatively described. Maximum hyoid depression could not be accurately determined on the majority of bites because of the ventral bulging

TABLE 1. KINEMATIC VARIABLES RECORDED FOR FIVE *Ginglymostoma cirratum* AND RESULTS OF THE ONE-WAY ANOVA OR KRUSKAL WALLIS AMONG SHARKS WITH KINEMATIC VARIABLES AS THE FACTORS. \* indicates values considered significant at  $P = 0.05$ , \*\* at  $P = 0.01$ , NS = not significant after sequential Bonferroni correction.

Factor	Mean $\pm$ SE (msec)	df	$F$ (ANOVA)	H (K-W)	$P$
Mandibular depression	26 $\pm$ 1	4		11.56	0.021*
Mandibular elevation	66 $\pm$ 4	4		23.86	<0.001**
Mandibular total	92 $\pm$ 4	4		24.74	<0.001**
Labial onset	8 $\pm$ 1	4		24.77	<0.001**
Labial protrusion	27 $\pm$ 2	4	3.95		0.008*
Labial retraction	65 $\pm$ 4	4	8.88		<0.001**
Labial total	92 $\pm$ 4	4		26.33	<0.001**
Maximum gape	32 $\pm$ 2	4	4.28		0.005*
Food enters mouth	36 $\pm$ 2	4	2.48		0.056 NS

of the buccopharyngeal cavity during suction feeding.

In addition, up to 42 sequential bites from individual feeding events were analyzed as above from two sharks that ate an unusual number of food items (Nurse 4 = 80 cm TL,  $n = 33$  bites; Nurse 5 = 79 cm TL,  $n = 31$  bites) to measure possible changes in duration of labial cartilage protrusion and retraction, and mandibular depression and elevation as the sharks became satiated. These variables were consistently obtainable from the video sequences for nearly all of the bites in a feeding sequence. Video images that were not suitable for analysis resulted in the difference between the total number of feeding bites (e.g., 42) and the number of bites analyzed (e.g., 33). Satiation, which occurred in about 1–2 h, was determined by the sharks refusing to take additional food items.

Because the sharks were conditioned to feed when the flood lights were turned on, two sharks in particular (Nurse 4 and 5) often approached the area where food was to be presented and commenced suction feeding behavior in the absence of any food. This provided us the opportunity to investigate stereotypy in feeding kinematics by comparing the duration of specific kinematic events (mandibular depression, mandibular elevation, mandibular total, labial onset, labial protrusion, labial retraction, labial total, maximum gape) of bites with food present versus absent. The bites with and without food occurred throughout the entire feeding trial and therefore were most likely not affected by any satiation effects on duration (see Results). In this manner, 12 bites with, and 12 bites without food were compared separately for each of the two sharks.

To construct a kinematic profile of cranial movements during suction capture, sequential video fields from a lateral view of a suction cap-

ture event were individually captured by the Redlake PCI-1000 software and analyzed with Sigma Scan Pro (SPSS Science). The following measurements were digitized every other field (0.008 sec) from the start of mandibular depression until the end of labial cartilage retraction (totaling 48 fields): (1) labial cartilage protrusion distance = the distance from the pupil to anterior margin of the medial labial cartilage; (2) gape distance = distance from the anterior margin of the mandible to anterior margin of upper labia; (3) hyobranchial depression distance = distance between the dorsal and ventral body surface one third the distance from the eye to the first gill slit; (4) mandibular depression and (5) cranial elevation angles = angles formed from the ventral margin of the first gill slit, through the pupil, to the anterior tip of the mandible and snout, respectively.

*Statistical analysis.*—Normality and equality of variances of each of the nine kinematic data sets were tested with the Kolmogorov-Smirnov test and the Levene Median test, respectively. Duration of each of the nine kinematic variables (e.g., mandibular depression) was then separately analyzed with a one-way ANOVA for differences among sharks (Table 1). Head elevation occurred so infrequently as to preclude its analysis. If a difference was detected by ANOVA, a Tukey test was used to test all pair wise comparisons. When normality or equality of variances could not be achieved by transformation, a Kruskal-Wallis one-way ANOVA on ranks was used. If this indicated significant differences among sharks, a Dunn's multiple comparisons procedure tested all pair wise comparisons ( $P < 0.05$ ). Because many of these variables are correlated, a sequential Bonferroni correction was applied to the ANOVA or Kruskal-Wallis analyses (Rice, 1989).

To test whether duration of capture kinematics changes with satiation, duration of mandibular depression, mandibular elevation, labial protrusion, and labial retraction were linearly regressed against bite number independently for two sharks that took numerous bites per feeding (males, TL 79 and 80 cm). In the case where the shark took a piece of food but a clear video image of those particular bites was lacking, the regression analysis, which requires a balanced design, was performed without those data points (represented by gaps on the figures). ANOVA was performed on the regressions after normality and equality of variances was demonstrated. The duration of mandibular elevation and labial retraction for Nurse 4 failed normality but passed equality of variances regardless of transformation. Therefore, in addition to ANOVA, a Model II geometric mean (GM) regression on these data was calculated (Teissier, 1948), confirming the results of the linear regression.

To test whether any change in duration of mandibular depression or labial cartilage protrusion was a result of the shark changing the extent of mouth opening with satiation, the distance from the eye to the anterior edge of fully protracted medial labial cartilage was regressed against bite number. As labial cartilage protrusion is mechanically linked to mandibular depression (Motta and Wilga, 1999), and the mandible tip was not as clearly defined in the video, labial cartilage protrusion was also used as a proxy for the extent of mandibular depression. Select video images were captured from video and measured with Sigma Scan Pro (SPSS Science).

To compare the durations of the eight kinematic variables with and without food, paired *t*-tests were conducted for each kinematic variable independently for each of the two sharks with a sequential Bonferroni correction (Rice, 1989). Statistical tests were performed with Sigma Stat (Jandell Scientific Inc., vers. 2.0), with the exception of the Bonferroni correction and GM regression, which were calculated independently.

## RESULTS

*Food capture.*—Sharks were quickly conditioned to feed when the filming lights were turned on. In trials with the feeding platform, there were two patterns of food capture. In most feeding trials, the shark would swim to the platform, stop before the food, raise itself on its pectoral fins, and suck the food item into its mouth. In other trials, the shark used an apparent che-

mosensory-mediated search to find the food. It would swim slowly by the food, swinging its head from side to side, turn sharply, and suck it in. All food capture was by inertial suction in that the shark rapidly opened its mouth, and the velocity of the food toward the mouth greatly exceeded the velocity of the shark approaching the food, if the shark was moving at all. When conditioned to feed through a hole in the feeding platform, the shark would immediately swim onto the platform when the lights were turned on, cease swimming, and in many cases begin numerous suction attempts through the hole even before food was presented. Some suction attempts that appeared more vigorous were accompanied by loud and audible popping sounds perhaps indicating cavitation. The small pieces of food offered in this experiment were usually captured and swallowed in one suction event without being grasped by the teeth. In some cases, the food was captured by inertial suction, grasped by the teeth, and transported from the buccal cavity into the esophagus by a second suction event. Some pieces of food were held in the teeth or mouth after inertial suction capture, and repeatedly blown out of the mouth and sucked in again, reorienting the food or reducing it in size.

Food capture began with an expansive phase, which involved mandibular depression, labial cartilage protrusion, and occasionally cranial elevation. The sequence began with mandibular depression averaging 26 msec in duration (Figs. 2–4, Table 1). Cranial elevation (29 msec) and depression (29 msec) were uncommon and generally very slight, occurring in only 15% of the bites. In some cases, the head was actually lowered prior to the bite as it was positioned toward the food. The labial cartilages began to protrude anteriorly eight msec after the beginning of mandibular depression. Maximum labial cartilage protrusion (27 msec) occurred slightly after maximum gape (32 msec), shortly after which the food was usually sucked into the buccal cavity (36 msec) and no longer visible. The external gill slits closed during the expansive phase. The compressive phase began with mandibular elevation that took an average of 66 msec. Palatoquadrate protrusion, obscured by labial cartilage protrusion in perfectly lateral bites, began during the compressive phase and reached a maximum at approximately the same time mandibular elevation ceased (Fig. 2). Labial cartilage retraction (65 msec) then followed the beginning of mandibular elevation. As the compressive phase proceeded, the hyoid complex (basihyal and distal ceratohyal) was observed to bulge ventrally, then become ob-

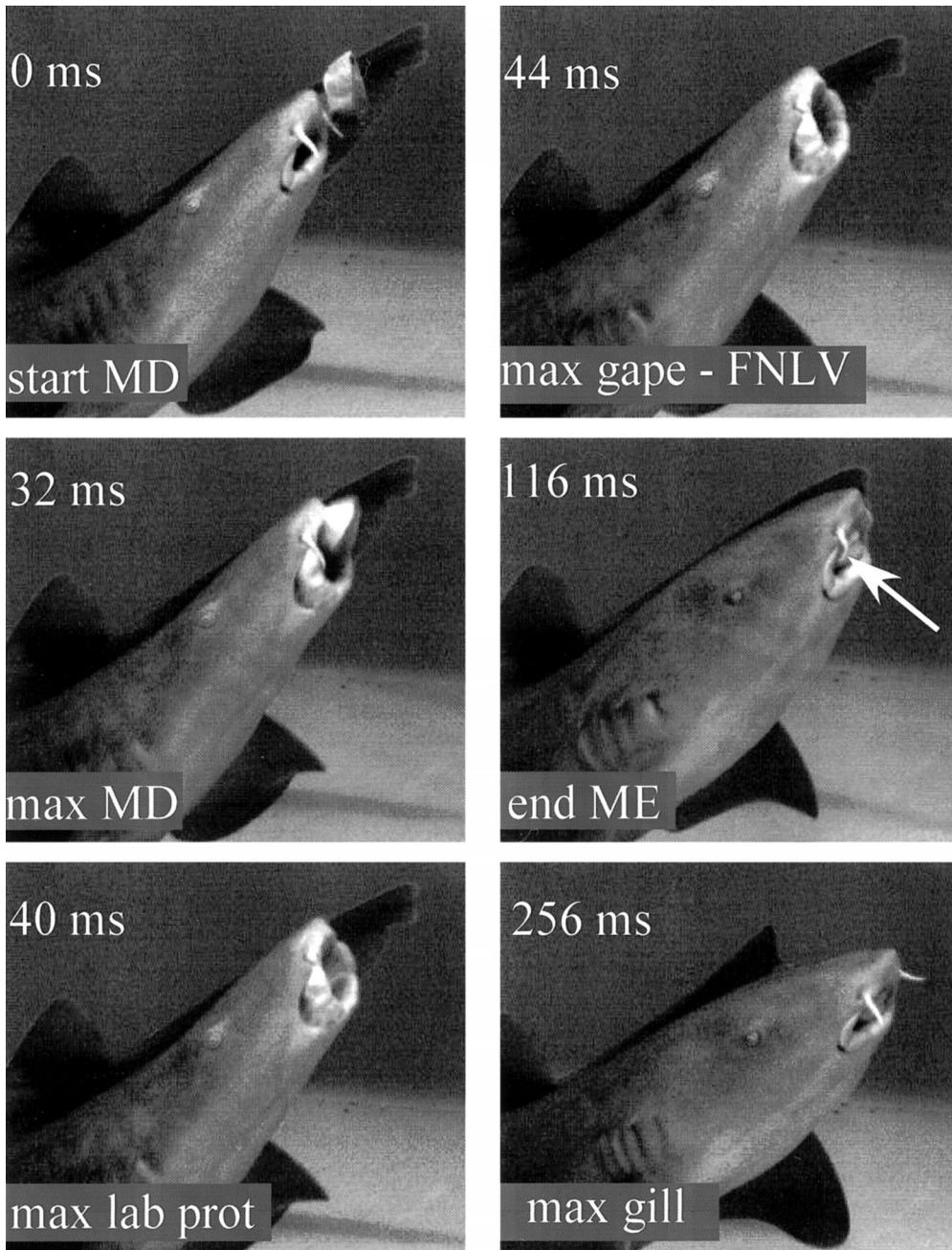


Fig. 2. Food capture sequence of a 85 cm TL female *Ginglymostoma cirratum* suction feeding on food item. Start MD = start of mandibular depression as the food is visible anterior to the mouth; the caudal fin is visible behind the food; max MD = maximum mandibular depression occurs as the food is entering the mouth; max lab prot = maximum labial protrusion; max gape—FNLV = maximum gape and when the food is sucked into the mouth and no longer visible; end ME = the end of mandibular elevation; the protruded upper jaw (arrow), which appears white, is clearly visible in the mouth; max gill = maximum opening of the gill slits as the water rushes posteriorly out of the branchial cavity. Numbers indicate msec elapsed from the beginning of mandibular depression.

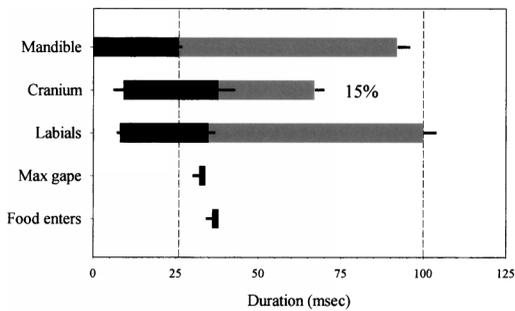


Fig. 3. Composite diagram of means of kinematic events for food capture ( $n = 5$  sharks, 53 bites) in *Ginglymostoma cirratum*. Events (black bars) indicate start to peak activity followed by peak to end of activity (grey bars), with 1 SE bars. Error bars on the left of head movement, labial cartilage movement, maximum gape, and time until food enters the mouth indicate the SE of the onset time from the beginning of mandibular depression until initiation of that event. The dashed vertical line on left indicates the end of mandibular depression, and the dashed line on the right indicates the cessation of the bite marked by retraction of the labial cartilages. Cranial elevation only occurred in 15% of recorded bites and is not included in the statistical analysis.

scured by a general swelling of the entire pharyngeal cavity as the water preceded posteriorly, with the water eventually exiting through the open external gill slits. The compressive phase terminated with labial cartilage retraction at which time the protruded palatoquadrate was still clearly visible. The entire capture sequence from the beginning of mandibular depression until retraction of the labial cartilages had an average duration of 100 msec. Palatoquadrate retraction continued into the recovery phase.

*Individual variability.*—There was considerable combined within and among individual variability in the timing of most kinematic events for the five sharks (Fig. 5). Eight of the kinematic variables involving mandibular depression and elevation, labial cartilage protrusion and retraction, and time to maximum gape exhibited interindividual variability based on the ANOVA results, but there was no difference in the time it took the food to enter the mouth (Table 1).

*Effects of satiation on bite duration.*—For one of the two sharks with multiple recorded bites (Nurse 4, male, TL 80 cm) the duration of labial cartilage protrusion (slope =  $-0.37$ ,  $F = 5.11$ ,  $P = 0.031$ ) and mandibular depression (slope =  $-0.45$ ,  $F = 14.59$ ,  $P = 0.001$ ) decreased as the shark consumed more than 40 pieces of food to satiation, that is, the shark

opened its mouth quicker with successive captures (Fig. 6). However, the distance that the labial cartilage extended anteriorly did not change with increasing number of bites ( $F = 1.65$ ,  $P = 0.208$ ; therefore the quicker mouth opening was not reflective of the mouth simply opening less. This shark did not change the time to close the mouth as it became satiated, because there was no relationship between bite number and duration of mandibular elevation ( $F = 1.61$ ,  $P = 0.29$ ) or labial cartilage retraction ( $F = 0.43$ ,  $P = 0.515$ ). For the other shark (Nurse 5), there was no change in the duration of mandibular depression and elevation or labial cartilage protrusion and retraction with increasing satiation (mandibular depression  $F = 1.45$ ,  $P = 0.240$ ; mandibular elevation  $F = 1.03$ ,  $P = 0.321$ ; labial cartilage protrusion  $F = 2.86$ ,  $P = 0.101$ ; labial cartilage retraction  $F = 3.58$ ,  $P = 0.069$ ).

*Effects of food on bite durations.*—For one shark (Nurse 4), there was essentially no difference in the duration of the various kinematic events in the presence or absence of food, except for the time to elevate the mandible and the related total time to depress and elevate the mandible (Table 2). However, the other shark (Nurse 5) was consistently slower in the absence of food, with the exception of the time to depress the mandible and the time for onset of labial cartilage protrusion relative to the initiation of mandibular depression (Table 2).

## DISCUSSION

*Conservation of kinematic sequence.*—The inertial suction feeding *G. cirratum* captures food with an abbreviated kinematic feeding sequence compared to that of squaliform, carcharhiniform and lamniform sharks (Tricas and McCosker, 1984; Motta et al., 1991, 1997; Wilga and Motta, 1998a). The feeding sequence of *G. cirratum* is composed of expansive, compressive and recovery phases, with no evidence of an initial mouth closing preparatory phase as has been noted for some aquatic feeding vertebrates (Liem, 1978; Lauder, 1985; Lauder and Prendergast, 1992), although lacking buccal pressure profiles it is not possible to ascertain definitively the lack of a preparatory phase. The sequence is further abbreviated by the lack of head lifting during the expansive phase.

The expansive phase of *G. cirratum* is characterized by mandibular depression and labial cartilage protrusion. As in the inertial suction feeding *H. francisci* and *T. semifasciata* (Ferry-Graham, 1998; Pretlow-Edmonds, 1999; Table

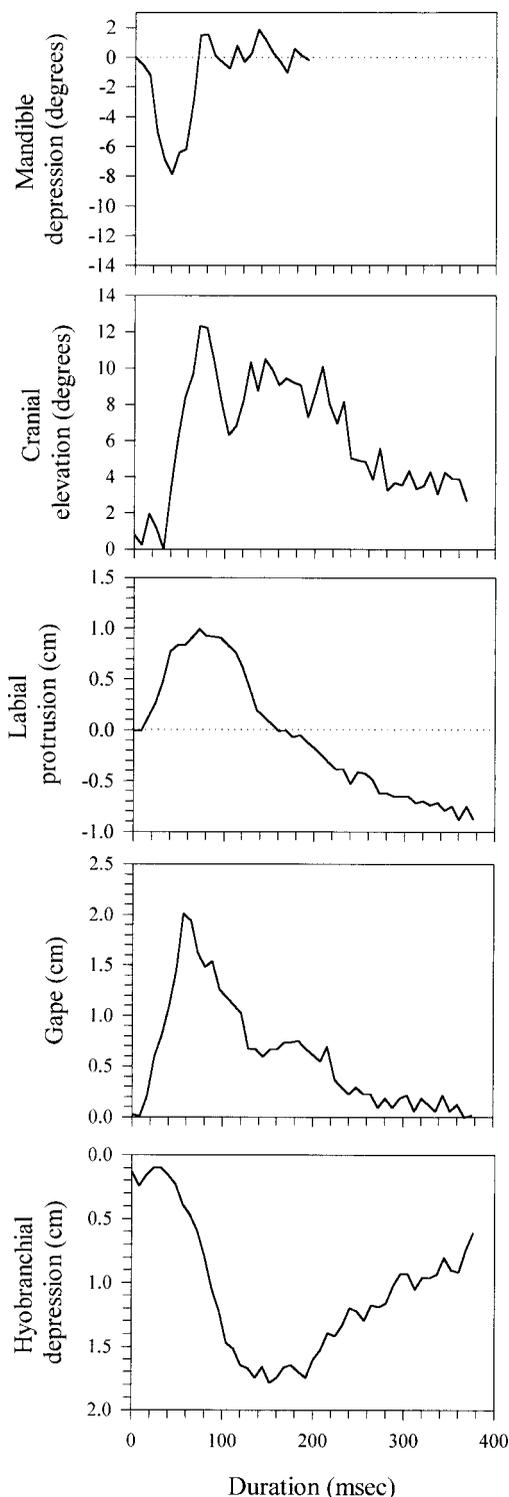


Fig. 4. Kinematic profile of an 85 cm TL female *Ginglymostoma cirratum* suction feeding on a food item. Although this bite was longer in duration than the average bite, the shark was lateral to the camera facilitating digitization. Zero msec indicates the begin-

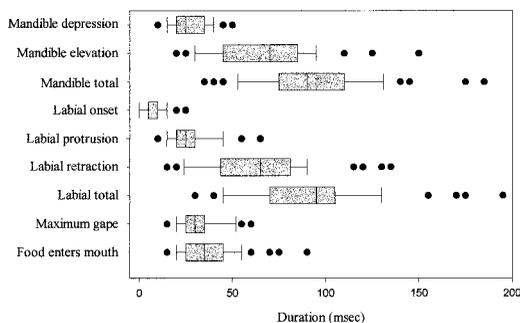


Fig. 5. Box plot of kinematic variables for all *Ginglymostoma cirratum* combined ( $n = 5$  sharks and 53 bites total per variable) showing median, 10th, 25th, 75th, 90th percentiles, and outliers that exceed the 90th percentile.

3), the expansive phase of *G. cirratum* lacks cranial elevation during the majority of bites, and when it does occur it is of small magnitude. Using compensatory suction and ram, lamniform and carcharhiniform sharks often consume large prey items with their ventrally located mouth. In these sharks cranial elevation is coupled with mandibular depression to open the mouth as much as possible and direct the gape more anteriorly toward the prey. However, *G. cirratum* and *H. francisci* primarily capture relatively small fishes and benthic invertebrates (Bigelow and Schroeder, 1948; Compagno, 1984; Castro, 2000) with a mouth that is almost terminal when maximally open (Edmonds et al., 2001). Lifting of the cranium to orient the open mouth is not necessary. Conversely, when feeding on small benthic food items, *T. semifasciata* swims over them protruding its tubular

←

ing of mandibular depression. Rapid mandibular depression is followed by labial cartilage protrusion and peak gape. The mandibular depression trace ceases after 200 msec as the tip of the mandible is obscured because of the shark turning slightly away from the camera. The labial cartilages which were slightly protruded at the beginning of the capture consequently return to a more retracted position. Although cranial elevation only occurs in approximately 15% of suction captures (Fig. 3), it is evident in this feeding event as the head is elevated and slowly returns to its original position. Peak hyobranchial depression occurs toward the end of the capture as the water rushes posteriorly through the mouth and pharynx and out the gill slits. The longer duration of this capture is primarily a result of lengthening of the compressive and recovery phases as mandibular depression occurs within approximately 40 msec. The smaller scale oscillations in the traces are a result of measurement error.

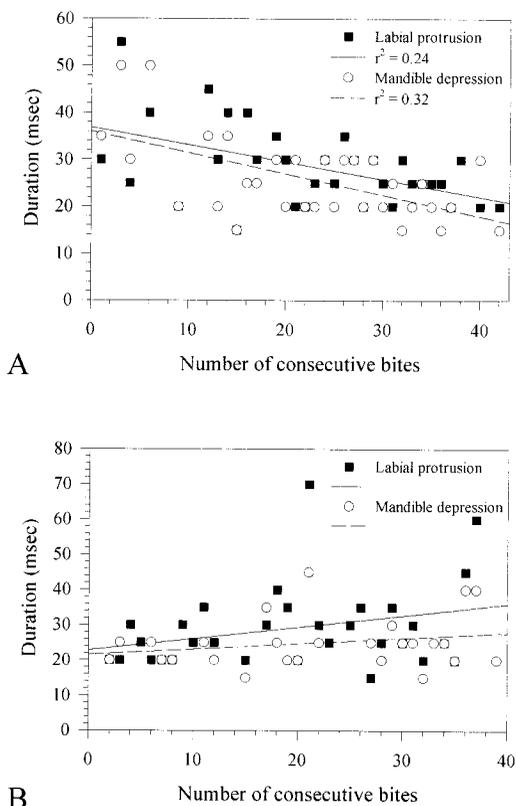


Fig. 6. Linear regressions of labial cartilage protrusion, and mandibular depression as a function of number of consecutive bites for (A) nurse 4, a 80 cm TL male fed up to 42 pieces of food during one experiment, and (B) nurse 5, a 79 cm TL male *Ginglymostoma cirratum* fed up to 39 pieces of food during one experiment. For the first shark the time for the mandible to depress ( $P = 0.001$ ) and the time for the labial cartilage to protrude ( $P = 0.031$ ) both decreased with satiation. Because the distance these elements moved did not change, the velocity of jaw opening increased with satiation.

mouth anteroventrally to capture them, resulting in little if any cranial elevation (Ferry-Graham, 1998).

During the compressive phase the mandible is elevated, the palatoquadrate protruded, the hyoid depressed and the labial cartilages retracted. Not only is mandibular depression in *G. cirratum* the fastest recorded for any shark, but in contrast to nearly all sharks examined so far, the expansive phase in *G. cirratum* is considerably faster than the compressive phase (Table 1). Therefore, similar to some other bony fishes, aquatic amphibians, and some aquatic feeding amniotes, *G. cirratum* has a fast opening phase during the expansive phase (Lauder,

1985; Lauder and Reilly, 1994; Summers et al., 1998).

The recovery phase in carcharhiniform and squaliform sharks includes retraction of the palatoquadrate, hyoid, and branchial apparatus into their resting position (Motta et al., 1997; Wilga and Motta, 1998a). In *G. cirratum* the palatoquadrate is retracted; however, the general bulging of the buccal and branchial cavities resulting from water inflow masks movements of the hyoid and branchial apparatus in the video images. Presumably the hyoid is retracted to its resting position. This awaits confirmation by our electromyographic experiments.

Water flow during inertial suction feeding in *G. cirratum* is apparently unidirectional, in the mouth and out of the gill slits, as evidenced by the posteriorly traveling bulge in the head as the mouth closes and the gill slits open during the compressive phase, and the position of the buccal valves at the anterior end of the mouth (Motta and Wilga, 1995). This contrasts with water flow in juvenile swell sharks *Cephaloscyllium ventriosum*, during ram-dominated feeding in which water taken in the mouth is later forced out the mouth rather than continuing posteriorly through the gill slits (Ferry-Graham, 1997). The reverse flow of water out the mouth of *G. cirratum* is hindered by two passive connective tissue oral valves at the anterior end of the mouth. These valves, which are lacking in the carcharhinid *N. brevirostris*, are extensions of the mandibulohyoid connective tissue sheath (Motta and Wilga, 1995, 1999).

Most sharks capture their prey by inertial suction, compensatory suction, ram or a combination of these, or by biting a piece off a prey item. After capture there is often one or more manipulation bites in which the prey is reduced in size by cutting with the teeth, followed by transport of the bolus of food from the mouth into the esophagus (Motta and Wilga, 2001). In all sharks examined to date, transport is always by suction (Ferry-Graham, 1997; Motta et al., 1997; Wilga and Motta, 1998a). Under the experimental conditions reported here, and through observation of juvenile *G. cirratum* feeding on small pieces of food in the field (PJM, pers. obs.), the food is usually captured and transported by one initial inertial suction event. However, in some cases, pieces of food are captured by inertial suction and held in the teeth, whereupon larger pieces may be repeatedly blown out of the mouth and sucked in, dismembering them, and then subsequently transported by suction from the mouth into the esophagus.

Lauder (1980b, 1983) proposed a model of

TABLE 2. KINEMATIC VARIABLES WITH AND WITHOUT FOOD FOR TWO *Ginglymostoma cirratum* AND RESULTS OF THE PAIRED *t* TESTS. \* indicates values considered significant at  $P = 0.05$ , \*\* at  $P = 0.01$ , NS = not significant after sequential Bonferroni correction.

Nurse 4 Factor	Duration with food $\pm$ SE (msec)	Duration w/o food $\pm$ SE (msec)	df	<i>t</i> value	<i>P</i>
Mandibular depression	29 $\pm$ 3	40 $\pm$ 5	11	-1.418	0.184 NS
Mandibular elevation	83 $\pm$ 6	128 $\pm$ 5	11	-4.885	<0.001**
Mandibular total	113 $\pm$ 9	167 $\pm$ 9	11	-3.659	0.004*
Labial onset	6 $\pm$ 1	10 $\pm$ 2	11	-1.295	0.222 NS
Labial protrusion	30 $\pm$ 3	38 $\pm$ 3	11	-1.743	0.109 NS
Labial retraction	82 $\pm$ 8	115 $\pm$ 4	11	-2.910	0.014 NS
Labial total	113 $\pm$ 9	154 $\pm$ 6	11	-2.979	0.013 NS
Maximum gape	35 $\pm$ 3	48 $\pm$ 5	11	-1.951	0.077 NS
Nurse 5 Factor	Duration with food $\pm$ SE (msec)	Duration w/o food $\pm$ SE (msec)	df	<i>t</i> value	<i>P</i>
Mandibular depression	22 $\pm$ 2	30 $\pm$ 3	11	-2.246	0.046 NS
Mandibular elevation	77 $\pm$ 3	102 $\pm$ 4	11	-5.702	<0.001**
Mandibular total	98 $\pm$ 3	132 $\pm$ 5	11	-5.875	<0.001**
Labial onset	2 $\pm$ 0	4 $\pm$ 1	11	-0.713	0.491 NS
Labial protrusion	25 $\pm$ 2	34 $\pm$ 3	11	-4.158	0.002**
Labial retraction	78 $\pm$ 2	109 $\pm$ 5	11	-6.423	<0.001**
Labial total	103 $\pm$ 2	143 $\pm$ 6	11	-7.407	<0.001**
Maximum gape	25 $\pm$ 2	39 $\pm$ 3	11	-3.484	0.005*

inertial suction feeding in bony fishes that approach their food slowly or remain stationary before food capture. The gill arches effectively separate the buccal and parabranchial/opercular cavities such that a large pressure differential is set up between the two cavities during which the food is sucked into the mouth. Abduction of the operculum has a negligible role in generating subambient mouth cavity pressures. After peak subambient buccal pressure is reached, the abducting opercula result in an anteroposterior flow of water from the buccal cavity through the gills into the opercular cavity, after which it exits through the opercular slit. This mechanism is contingent on a rigid operculum that is forcibly abducted. This mechanism cannot function during inertial suction feeding in sharks as they lack a rigid operculum. Subambient pressures generated external to the gill filaments in the parabranchial chamber of sharks during respiration are apparently a result of elastic recoil of the visceral skeleton and not active expansion of this cavity (Hughes and Balintijn, 1965; Ferry-Graham, 1999). Therefore, the suction mechanism of *G. cirratum* is best modeled by an expanding single buccopharyngeal/orobranchial cavity resulting from depression of the mandible, depression of the floor of the mouth (hyoid apparatus) and depression of the branchial region. This is followed by reduction of the cavities resulting from mandibular

elevation and subsequent hyoid and branchial elevation that results in the anteroposterior flow of water from the mouth out of the parabranchial chambers.

*Variability.*—Many bony fishes exhibit interindividual variability of motor and kinematic patterns within food types and can modulate their feeding mechanisms in response to different prey/food types and positions (Liem, 1978; Sanderson, 1988; Nemeth, 1997). To date, the results on modulatory abilities of elasmobranch fishes are conflicting, but interindividual variability in food capture kinematics appears to be widespread in sharks (reviewed in Motta and Wilga, 2001). There was interindividual variability in all of the kinematic variables in *G. cirratum* with the exception of the time required for the food to enter the mouth, which averaged 36 msec. Despite the variability, the kinematic sequence during food capture was very consistent and stereotyped. Even in the absence of food, one shark displayed no difference in the majority of kinematic durations as compared to bites with food, and both sharks did not differ in the time to depress the mandible with or without food present. Rapid mandibular depression is an important parameter in the generation of inertial suction forces (Lauder, 1980a; Muller et al., 1982; Liem, 1993). A study of feeding kinematics in *G. cirratum* ranging in

TABLE 3. MEAN CAPTURE BITE DURATIONS (MSEC) FOR SELECT KINEMATIC VARIABLES FOR A VARIETY OF SHARKS. Predominant food capture behavior (ram vs inertial suction) indicated below each species. Incomplete values indicate those data are not available (N/A).

	<i>G. arctatum</i> (suction)	<i>H. francisci</i> (suction) <sup>a</sup>	<i>T. semifasciata</i> (suction-ram) <sup>b</sup>	<i>S. acanthias</i> (suction-ram) <sup>c</sup>	<i>S. tiburo</i> (ram) <sup>d</sup>	<i>N. brevirostris</i> (ram) <sup>e</sup>	<i>C. berzi</i> (ram) <sup>f</sup>	<i>C. ventriosum</i> (ram) <sup>g</sup>	<i>C. archaicas</i> (ram) <sup>h</sup>
Head elevation	rare	rare	none or slight	89–165	111	66	84	none	171
Head depression	rare	rare	none or slight	129–150	113	62	83	226–334 <sup>i</sup>	405
Mandibular depression	26	47–64	90–110	65–111	162	75	115	305–354	140
Mandibular elevation <sup>j</sup>	66	66–84	60–70	58–137	86	77	105	N/A <sup>k</sup>	220
Maximum protrusion <sup>l</sup>	N/A	21–25	80–110	46–69	57	59	53	none or slight	83
Maximum gape	32	47–64	90–110	100	162	81	120	236–347	167
Total bite time	100	113–148	150–180	266–280	302	309	383	367–419	405

<sup>a</sup> Pretlow-Edmonds (1999) for three food presentations.

<sup>b</sup> Ferry-Graham (1998) for two food types and two food sizes.

<sup>c</sup> Wilga (1997) for three food sizes

<sup>d</sup> Wilga (1997).

<sup>e</sup> Motta et al. (1997).

<sup>f</sup> Motta and Wilga (2001).

<sup>g</sup> Ferry-Graham (1997) for two food sizes.

<sup>h</sup> Tricas and McCosker (1984), Tricas (1985).

<sup>i</sup> Time to maximum negative head angle.

<sup>j</sup> From peak depression.

<sup>k</sup> During capture food was held with the teeth resulting in no jaw closure.

<sup>l</sup> Duration from start of upper jaw protrusion until maximum protrusion.

size from 33–268 cm TL similarly found that the prey capture sequence did not change ontogenetically, the angular and linear kinematic excursions of the jaw elements were isometric, and the use of inertial suction feeding as judged by the Ram Suction Index (Norton and Brainerd, 1993) did not change with size (Robinson and Motta, 2002).

As *G. cirratum* became satiated, the time to open the mouth was very consistent for one of the sharks but decreased for the second. The fact that the labial cartilages extended the same distance for the latter shark indicated that this was not simply an artifact of the shark opening the mouth less, but rather the velocity of mandibular depression increased. This contrasts with *Lepomis* sp. (Perciformes: Centrarchidae) that decrease buccal pressure magnitude with satiation (Lauder, 1980b), and largemouth bass *Micropterus salmoides* (Centrarchidae) that decrease the speed of mouth opening and also open the mouth less as they become satiated (Sass, 1999). The ecological implications of the interindividual variability in kinematic events and the effects of satiation on bite speed are probably minimal in *G. cirratum* as the suction events are so rapid and powerful that the food enters the mouth in the same time regardless of the variability, and the time to mandibular depression in one of the satiated *G. cirratum* only changed by approximately 20 msec. However, how such differences in kinematic events may affect capture success of whole prey remain to be tested.

The conservative feeding kinematics under these experimental conditions in which the size and type of food are held constant indicate that inertial suction food capture in *G. cirratum* is a stereotyped modal action pattern (sensu Barlow 1968, 1977). This implies that the bites are very stereotyped, involve central nervous system integration (not a simple reflex), are independent from feedback once initiated, involve greater variability in the taxic component than in the kinetic component, and the behavior is widely distributed among individuals of a population (i.e., heritable). Other orectolobiform sharks (*O. maculatus* and *Hemiscyllium ocellatum*) are also apparently stereotyped in their food capture kinematics (Wu, 1994). *Heterodontus francisci* (Heterodontiformes) showed stereotyped suction feeding when presented food of differing accessibility (Edmonds et al., 2001). Similarly, *C. ventriosum* and *T. semifasciata* (Carcharhiniformes) do not appear to modulate capture kinematics when presented with food of different sizes (Ferry-Graham, 1997, 1998). Even though *S. californica* vary their attack ap-

proach based on position of the food in the water column, a stereotyped kinematic sequence was used for capture. The bites of *S. californica* are believed to represent a modal action pattern (Fouts and Nelson, 1999), as Tricas (1985) proposed for *C. carcharias* feeding on surface food.

In contrast, ram feeding carcharhinid sharks including the Caribbean reef shark *Carcharhinus perezi*, blacknose *Carcharhinus acronotus*, blacktip *Carcharhinus limbatus*, and *N. brevirostris* show considerable variation in the timing and extent of upper jaw protrusion during food capture (Frazzetta and Prange, 1987; Motta et al., 1997; Motta and Wilga, 2001). *Squalus acanthias* (Squaliformes) is capable of using a wide variety of food capture strategies on a single food type, and there is extensive modulation between capture and transport events (Wilga and Motta, 1998a). This ability is properly referred to as variability rather than modulation though, because there is a continuous range of behaviors in the face of a single stimulus (Ferry-Graham, 1997). Despite the apparent lack of modulatory ability in some sharks, individual variability is common during feeding in all sharks examined so far (Motta et al., 1997; Ferry-Graham, 1998; Wilga and Motta, 1998a).

These preliminary findings must be viewed with caution as most of these studies were confined to laboratory conditions and a diverse range of food types, sizes, or prey mobilities were not tested. However, the emerging pattern suggests a continuum from more stereotyped and faster food capture bites in morphologically specialized, and benthic inertial suction feeding sharks such as *G. cirratum*, to less stereotyped, and generally slower bites in larger ram feeding sharks (Table 3).

*Specialization for inertial suction prey capture.*—Suction feeding is the ancestral dominant mode of prey capture in bony fishes (Lauder, 1985). Bony fishes that are suited for inertial suction feeding usually have a small, laterally enclosed mouth, protrusible upper jaw, reduced dentition, strongly developed abductor muscles, and buccal expansion is large and rapid (Lauder, 1980a; Muller et al., 1982; Liem, 1993). The parcel of water sucked into the mouth is usually small and particles move toward the center line of the mouth from each side of the head, although most of the water entering the mouth passes through the area anterior to the gape (Lauder and Clark, 1984).

Specializations for inertial suction prey capture in *G. cirratum* and inertial suction feeding bony fishes are functionally convergent. The open mouth of this shark is small (less than one-

third head length), anteriorly directed and close to the tip of the snout. The functionally terminal mouth is a derived character of orectoloboids (Bigelow and Schroeder, 1948; Compagno, 1984, 1988). The open mouth is approximately round when open and laterally occluded by three prominent labial cartilages and the palatoquadratomandibular connective tissue sheath. A medially directed cartilaginous process of the medial cartilage abuts the upper jaw, holding the labial cartilages away from the jaw and preventing their collapse during the powerful sub-ambient suction forces, which can reach  $-760$  mm Hg. Two buccal valves inhibit back-flow of water out of the mouth (Tanaka, 1973; Motta and Wilga, 1999). Labial cartilages that laterally occlude the gape and form a roughly circular mouth are also found in the inertial suction feeding *H. francisci* (Pretlow-Edmonds, 1999), *T. semifasciata* (Ferry-Graham, 1998), and *S. acanthias* (Wilga and Motta, 1998a). Mandibular depression in *G. cirratum* is extremely rapid (26 msec) and the fastest recorded for an elasmobranch (Table 3). The depressor muscles of the hyoid and branchial arches, most notably the coracohyoideus and the coracobranchiales, are apparently hypertrophied compared to carcharhinid sharks (Moss 1965, 1977). *Ginglymostoma cirratum* comes close to functionally replicating the feeding mechanism of an inertial suction feeding bony fish (Lauder, 1980b; Liem, 1980b), and it does it with a similar suite of modifications to the prey capture apparatus.

Fossil evidence and observation of morphologically similar but extant sharks indicate the ancestral prey capture behavior in elasmobranchs might have involved grasping the prey whole or tearing pieces from it (Schaeffer, 1967; Moy-Thomas and Miles, 1971; Maisey, 1980). Specialization for inertial suction prey capture has apparently arisen repeatedly in sharks and rays, often nested within clades of ram feeders (Fig. 1). Therefore, specialization for inertial suction feeding including rapid jaw opening, formation of a round, somewhat terminal mouth, prominent labial cartilages, a dentition reduced in size, and generation of large sub-ambient suction pressures has apparently evolved independently in conjunction with a benthic lifestyle in several elasmobranch lineages. These sharks and rays feed on both elusive and non elusive prey that lives in or on the substrate, are attached to it, or are benthic-associated (Compagno, 1984). *Rhincodon typus* is a notable exception. This shark has a relatively large terminal mouth and slow jaw kinematics, and utilizes a pulsatile suction and filtering mecha-

nism to feed on a wide variety of planktonic and nektonic prey that is generally aggregated in space and much smaller relative to its body size (Taylor et al., 1983; Clark and Nelson, 1997; Colman, 1997).

In summary, the inertial suction feeding *G. cirratum* captures its food with a conservative but abbreviated kinematic sequence of cranial movements. Water flow during inertial suction feeding is unidirectional, and the suction mechanism is driven by the expanding buccopharyngeal cavity. Despite interindividual variability in the feeding kinematics, inertial suction food capture in this shark is apparently a stereotyped, modal action pattern. Specializations for inertial suction feeding include a small, terminal and laterally occluded mouth, small teeth, modified labial cartilages, oral valves to prevent back-flow of water out of the mouth, hypertrophied abductor muscles of the hyoid and branchial arches, and extremely fast buccal expansion. These functional and morphological specializations make *G. cirratum* the cartilaginous fish equivalent of the bony fish inertial suction specialist. These specializations are shared to various degrees with other shark species, including members of several other families. This specialization for inertial suction feeding in sharks and bony fishes represents an important example of functional convergence.

#### ACKNOWLEDGMENTS

We gratefully acknowledge the contributions of time and material made by many persons and institutions. S. Barker, R. Carr, N. Edwards, S. Gold, A. Griffith, E. Minor, T. Pietrzak, L. Riley, C. Wilga and C. Wood provided technical assistance. E. Sander, J. Bonnel, C. Luer, Keys Marine Laboratory and Mote Marine Laboratory donated specimens. Mote Marine Laboratory and the University of South Florida provided facilities and expertise. Animals were treated according to the University of South Florida and Mote Marine Laboratory Institutional Animal Care and Use Committee guidelines, Certificate 510. The project was supported by grants from the National Science Foundation to PJM and REH (DEB 9117371 and IBN 9807863).

#### LITERATURE CITED

- BARLOW, G. W. 1968. Ethological units of behavior. p. 217-232. *In*: The central nervous system and fish behavior. D. Ingle (ed.). Univ. of Chicago Press, Chicago.
- . 1977. Modal action patterns. p. 98-134. *In*: How animals communicate. T. A. Sebeok (ed.). Indiana Univ. Press, Bloomington.

- BIGELOW, H. B., AND W. C. SCHROEDER. 1948. Fishes of the western North Atlantic. Lancelets, cyclostomes, sharks. Mem. Sears Found. Mar. Res. 1(part1):1-576.
- CARRIER, J. C., AND C. A. LUER. 1990. Growth rates in the nurse shark, *Ginglymostoma cirratum*. *Copeia* 1990:686-692.
- CASTRO, J. I. 2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. *Environ. Biol. Fish.* 58:1-22.
- CHU, C. T. 1989. Functional design and prey capture dynamics in an ecologically generalized surfperch (Embiotocidae). *J. Zool.* 217:417-440.
- CLARK, E., AND D. R. NELSON. 1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environ. Biol. Fish.* 50: 63-73.
- COLMAN, J. G. 1997. A review of the biology and ecology of the whale shark. *J. Fish Biol.* 51:1219-1234.
- COMPAGNO, L. J. V. 1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Species Catalogue. Vol. 4. Part 1. Hexanchiformes to Lamniformes. U.N. Dev. Prog., FAO, Rome.
- . 1988. Sharks of the order Carcharhiniformes. Princeton Univ. Press, Princeton, NJ.
- DIAMOND, J. M. 1985. Filter-feeding on a grand scale. *Nature* 316:679-680.
- EDMONDS, M. A., P. J. MOTTA, AND R. E. HUETER. 2001. Prey capture kinematics of the suction feeding horn shark, *Heterodontus francisci*. *Environ. Biol. Fish.* 62:415-427.
- FERRY-GRAHAM, L. A. 1997. Feeding kinematics of juvenile swellsharks, *Cephaloscyllium ventriosum*. *J. Exp. Biol.* 200:1255-1269.
- . 1998. Effects of prey size and mobility on prey-capture kinematics in leopard sharks, *Triakis semifasciata*. *Ibid.* 201:2433-2444.
- . 1999. Mechanics of ventilation in swellsharks, *Cephaloscyllium ventriosum* (Scyliorhinidae). *Ibid.* 202:1501-1510.
- FOUTS, W. R., AND D. R. NELSON. 1999. Prey capture by the Pacific angel shark, *Squatina californica*: visually mediated strikes and ambush-site characteristics. *Copeia* 1999:304-312.
- FRAZZETTA, T. H., AND C. D. PRANGE. 1987. Movements of cephalic components during feeding in some requiem sharks (Carcharhiniformes: Carcharhinidae). *Ibid.* 1987:979-993.
- HUGHES, G. M., AND C. M. BALLINTIJN. 1965. The muscular basis of the respiratory pumps in the dogfish (*Scyliorhinus canicula*). *J. Exp. Biol.* 43:363-383.
- LAUDER, G. V. 1980a. Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *J. Morphol.* 163:283-317.
- . 1980b. The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. Exp. Biol.* 88:49-72.
- . 1983. Prey capture hydrodynamics in fishes: experimental tests of two models. *Ibid.* 104:1-13.
- . 1985. Aquatic feeding in lower vertebrates, p. 210-229. *In: Functional vertebrate morphology*. M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake (eds.). Belknap Press, Cambridge.
- . 1990. Functional Morphology and systematics: Studying functional patterns in an historical context. *Ann. Rev. Ecol. Sys.* 21:317-340.
- , AND B. D. CLARK. 1984. Water flow patterns during prey capture by teleost fishes. *J. Exp. Biol.* 113:143-150.
- , AND T. PRENDERGAST. 1992. Kinematics of aquatic prey capture in the snapping turtle *Chelydra serpentina*. *Ibid.* 164:55-78.
- , AND S. M. REILLY. 1994. Amphibian feeding behavior: Comparative biomechanics and evolution, p. 163-195. *In: Biomechanics of feeding in vertebrates*. V. Bels, M. Chardon, and P. Vandewalle (eds.). Springer-Verlag, Berlin, Germany.
- LEBOEUF, B. J., J. E. MCCOSKER, AND J. HEWITT. 1987. Crater wounds on northern elephant seals: the cookiecutter shark strikes again. *U.S. Fish. Bull.* 85: 387-392.
- LIEM, K. F. 1978. Modulatory multiplicity in the functional repertoire of the feeding mechanisms in cichlid fishes. I. Piscivores. *J. Morphol.* 158:323-360.
- . 1980a. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* 20:295-314.
- . 1980b. Acquisition of energy by teleosts: adaptive mechanisms and evolutionary patterns, p. 299-334. *In: Environmental physiology of fishes*. M.A. Ali (ed.). Plenum Publishing Corporation, New York.
- . 1993. Ecomorphology of the teleostean skull, p. 422-452. *In: The skull. Functional and evolutionary mechanisms*. J. Hanken, and B. K. Hall (eds.). Vol. 3. Univ. of Chicago Press, Chicago.
- MAISEY, J. G. 1980. An evaluation of jaw suspension in sharks. *Am. Mus. Novit.* 2706:1-17.
- MOSS, S. A. 1965. The feeding mechanisms of three sharks: *Galeocerdo cuvieri* (Peron & Le Sueur), *Negaprion brevirostris* (Poey), and *Ginglymostoma cirratum* (Bonnatere). Unpubl. Ph.D. diss., Cornell Univ., Ithaca, NY.
- . 1977. Feeding mechanisms in sharks. *Am. Zool.* 17:355-364.
- MOTTA, P. J., AND C. D. WILGA. 1995. Anatomy of the feeding apparatus of the lemon shark, *Negaprion brevirostris*. *J. Morphol.* 226:309-329.
- , AND ———. 1999. Anatomy of the feeding apparatus of the nurse shark, *Ginglymostoma cirratum*. *Ibid.* 241:33-60.
- , AND ———. 2001. Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. *Environ. Biol. Fish.* 60:131-156.
- , R. E. HUETER, AND T. C. TRICAS. 1991. An electromyographic analysis of the biting mechanism of the lemon shark, *Negaprion brevirostris*: functional and evolutionary implications. *J. Morphol.* 210:55-69.
- , T. C. TRICAS, R. E. HUETER, AND A. P. SUMMERS. 1997. Feeding mechanism and functional morphology of the jaws of the lemon shark *Negaprion brevirostris* (Chondrichthyes, Carcharhinidae). *J. Exp. Biol.* 200:2765-2780.
- MOY-THOMAS, J. A., AND R. S. MILES. 1971. Paleozoic fishes. Chapman and Hall, London.
- MULLER, M., J. W. M. OSSE, AND J. H. G. VERHAGEN. 1982. A quantitative hydrodynamic model of suction feeding in fish. *J. Theor. Biol.* 95:49-79.
- NEMETH, D. H. 1997. Modulation of attack behavior

- and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. J. Exp. Biol. 200:2155–2164.
- NORTON, S. F., AND E. L. BRAINERD. 1993. Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *Ibid.* 176:11–29.
- PRETLOW-EDMONDS, M. A. 1999. Prey capture kinematics in the horn shark, *Heterodontus francisci*. Unpubl. master's thesis, Univ. of South Florida, Tampa.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- ROBINSON, M. P., AND P. J. MOTTA. 2002. Patterns of growth and the effects of scale on the feeding kinematics of the nurse shark, *Ginglymostoma cirratum*. J. Zool. 256.
- RUSSO, R. A. 1975. Observations on the food habits of leopard sharks (*Triakis semifasciata*) and brown smooth-hounds (*Mustelus henlei*). Calif. Fish Game 61:95–103.
- SANDERSON, S. L. 1988. Variation in neuromuscular activity during prey capture by trophic specialists and generalists (Pisces: Labridae). *Brain Behav. Evol.* 32:257–268.
- SASS, G. G. 1999. The effects of satiation on prey capture kinematics in the largemouth bass, *Micropterus salmoides*. Unpubl. honors thesis, Univ. of South Florida, Tampa.
- SCHAEFFER, B. 1967. Comments on elasmobranch evolution. p. 3–35. *In: Sharks, skates and rays*. P. W. Gilbert, R. F. Mathewson, and D. P. Rall (eds.). Johns Hopkins Press, Baltimore, MD.
- SHIRAI, S. 1996. Phylogenetic interrelationships of neoselachians (Chondrichthyes: Euselachii), p. 9–34. *In: Interrelationships of fishes*. M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson (eds.). Academic Press, New York.
- SIMS, D. W. 2000. Filter-feeding and cruising swimming speeds of basking sharks compared with optimal models: they filter-feed slower than predicted for their size. J. Exp. Mar. Biol. Ecol. 249:65–76.
- STRONG JR., W. R. 1989. Behavioral ecology of horn sharks, *Heterodontus francisci*, at Santa Catalina Island, California, with emphasis on patterns of space utilization. Unpubl. master's thesis, California State Univ., Long Beach.
- SUMMERS, A. P., K. F. DAROUIAN, A. M. RICHMOND, AND E. L. BRAINERD. 1998. Kinematics of aquatic and terrestrial prey capture in *Terrapene carolina*, with implications for the evolution of feeding in cryptodire turtles. J. Exp. Zool. 281:280–287.
- TALENT, L. G. 1976. Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, Calif. Fish Game. 62:286–298.
- TANAKA, S. K. 1973. Suction feeding by the nurse shark. *Copeia* 1973:606–608.
- TAYLOR, L. R., L. J. V. COMPAGNO, AND P. J. STRUHSAKER. 1983. Megamouth—a new species, genus, and family of lamnoid shark (*Megachasma pelagios*, family Megachasmidae) from the Hawaiian Islands. *Proc. Calif. Acad. Sci.* 43:87–110.
- TEISSIER, G. 1948. La relation d'allometrie: sa signification statistique et biologique. *Biometrics* 4:14–43.
- TRICAS, T. C. 1985. Feeding ethology of the white shark, *Carcharodon carcharias*. *Mem. sth. Calif. Acad. Sci.* 9:81–91.
- , AND J. E. MCCOSKER. 1984. Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proc. Calif. Acad. Sci.* 43:221–238.
- VAN DAMME, J., AND AERTS, P. 1997. Kinematics and functional morphology of aquatic feeding Australian side necked turtles (Pleurodira: Chelodina). J. Morphol. 233:113–125.
- WAINWRIGHT, P. C., AND R. G. TURINGAN. 1993. Coupled versus uncoupled functional systems: motor plasticity in the queen triggerfish *Balistes vetula*. J. Exp. Biol. 180:209–227.
- WILGA, C. A. 1997. Evolution of feeding mechanisms in elasmobranchs: a functional morphological approach. Unpubl. Ph.D. diss., Univ. of South Florida, Tampa.
- WILGA, C. D., AND P. J. MOTTA. 1998a. Conservation and variation in the feeding mechanism of the spiny dogfish *Squalus acanthias*. J. Exp. Biol. 201:1345–1358.
- , AND ———. 1998b. Feeding mechanism of the Atlantic guitarfish *Rhinobatos lentiginosus*: modulation of kinematic and motor activity. *Ibid.* 201:3167–3184.
- , AND ———. 2000. Durophagy in sharks: feeding mechanics of the hammerhead *Sphyrna tiburo*. *Ibid.* 203:2781–2796.
- , P. C. WAINWRIGHT, AND P. J. MOTTA. 2000. Evolution of jaw mechanics in vertebrates: insights from Chondrichthyes. *Biol. J. Linn. Soc.* 71:165–185.
- WU, E. H. 1994. A kinematic analysis of jaw protrusion in orectolobiform sharks: a new mechanism for jaw protrusion in elasmobranchs. J. Morphol. 222:175–190.

(PJM) DEPARTMENT OF BIOLOGY, UNIVERSITY OF SOUTH FLORIDA, 4202 EAST FOWLER AVENUE, TAMPA, FLORIDA 33620; (REH) CENTER FOR SHARK RESEARCH, MOTE MARINE LABORATORY, 1600 KEN THOMPSON PARKWAY, SARASOTA, FLORIDA 34236; (TCT) DEPARTMENT OF BIOLOGICAL SCIENCES, FLORIDA INSTITUTE OF TECHNOLOGY, 150 WEST UNIVERSITY BOULEVARD, MELBOURNE, FLORIDA 32901; AND (APS) MUSEUM OF VERTEBRATE ZOOLOGY, DEPARTMENT OF INTEGRATIVE BIOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA 94720. PRESENT ADDRESSES: (TCT) DEPARTMENT OF ZOOLOGY, UNIVERSITY OF HAWAII AT MANOA, 2538 MCCARTHY HALL, HONOLULU, HAWAII 96822; AND (APS) DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY, UNIVERSITY OF CALIFORNIA, IRVINE, CALIFORNIA, 92697. E-mail: (PJM) motta@chumal.cas.usf.edu. Send reprint requests to PJM. Submitted: 23 May 2000. Accepted: 11 June 2001. Section editor: J. D. McEachran.