

Food capture kinematics of the suction feeding horn shark, *Heterodontus francisci*

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Received 16 August 2000

Accepted 22 March 2001

Key words: elasmobranchs, prey capture, modulation, diet

Synopsis

The goal of this study was to examine the feeding kinematics of the horn shark, *Heterodontus francisci*, a member of the most basal clade of galeomorph sharks, the Heterodontiformes. The accessibility of the food was manipulated to determine if the horn shark modulated capture. Three different methods of presenting food were used to mimic the different positions of prey items found in the natural diet of the horn shark. Food was presented unattached to the substrate, securely attached, or fitted snugly in a tube. Using high-speed video kinematic analysis, capture events were examined. *Heterodontus francisci* uses inertial suction facilitated by rapid mandible depression and labial cartilage protrusion to capture food. The horn shark conforms to a capture kinematic profile characteristic of both basal and derived inertial suction feeding sharks. Unusual post-capture behaviors include body leveraging, use of the mouth to form a seal over food, and chisel-like palatoquadrate protrusion. When presented with food of different accessibility, *Heterodontus francisci* used one consistent kinematic pattern for capture that was not modulated. Only post-capture behaviors varied according to food accessibility.

Introduction

The horn shark, *Heterodontus francisci*, is a small, common inshore species of the eastern Pacific Ocean that feeds on a wide variety of benthic sessile and infaunal invertebrates including peanut worms, anemones, sea urchins, and crabs (Strong 1989, Segura-Zarzosa et al. 1997). Horn sharks belong to the most basal clade of galeomorph sharks, the Heterodontiformes (Figure 1), of which there is very little known of their feeding behavior and mechanisms (Nobiling 1977, Strong 1989). Captive feeding consists of lunging at and grasping food, however field observation suggests that *H. francisci* uses inertial suction to capture prey (Strong 1989). Inertial suction feeding is employed by other shark species such as the orectolobiform nurse shark, *Ginglymostoma cirratum*, the squaliform spiny dogfish, *Squalus acanthias*, and the carcharhiniform leopard shark, *Triakis semifasciata*

(Tanaka 1973, Ferry-Graham 1998, Wilga & Motta 1998a, Motta & Wilga 2001).

Heterodontus francisci may conform to a kinematic profile seen in such bottom dwelling, inertial suction feeding sharks, yet differ from sharks that ram or over-swim their elusive prey (Tricas & McCosker 1984, Wu 1994, Motta et al. 1997, Ferry-Graham 1998, Robinson 1999, Wilga & Motta 1998a). This profile begins with rapid mandible depression coupled with labial cartilage extension (expansive phase of capture), resulting in a laterally enclosed and round mouth for suction generation. Substantial cranial elevation is typical of sharks that ram feed, but appears to be mostly lacking in specialized inertial suction feeding sharks (Motta et al. unpublished). The compressive phase that follows is characterized by mandible elevation, labial retraction, and concomitant protrusion of the palatoquadrate cartilage. In many carcharhiniform and lamniform sharks the toothed palatoquadrate is protruded

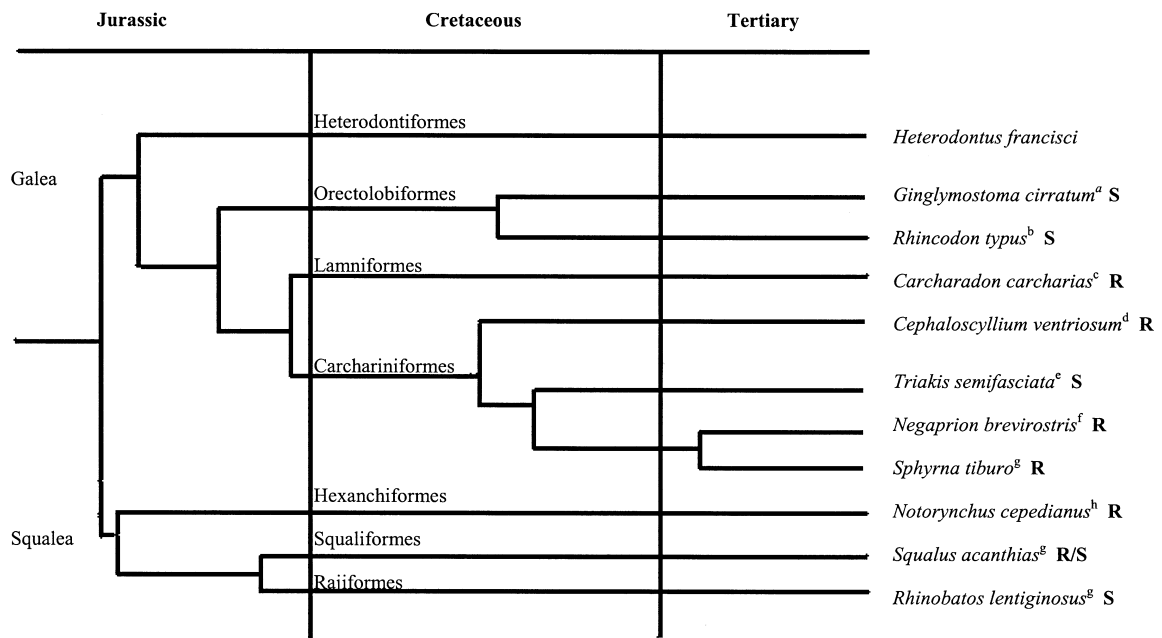


Figure 1. Phylogeny of neoselachians according to Shirai (1996) incorporating feeding types (R= ram feeding; S= inertial suction feeding) based on kinematic data. The character states of inertial suction (S) and ram (R) were assigned to each species according to the following studies: ^aTanaka 1973; ^bClark & Nelson 1997; ^cTricas & McCosker 1984; ^dFerry-Graham 1997; ^eFerry-Graham 1998; ^fMotta et al. 1997; ^gWilga 1997, Wilga & Motta 1998b; ^hunpublished data PJM.

to bite through or gouge its prey (Tricas & McCosker 1984, Frazzetta 1994). The extent or function of upper jaw protrusion in benthic feeding sharks such as *Heterodontus francisci* remains unclear. Finally, in most sharks retraction of the palatoquadrate follows in the recovery phase after the gape is closed by mandible elevation.

The benthic invertebrates that *H. francisci* feeds on are most likely found clinging to rocks, burrowed in the substrate, or hiding in crevices. With such a wide range of prey items that could occupy a variety of locations, the horn shark may modulate prey capture. Modulation refers to the ability to alter motor patterns or kinematic feeding sequences according to changing feeding situations (Liem 1978, Chu 1989, Nemeth 1997). There is evidence to suggest that modulation in the feeding repertoire of bony fishes is linked to increased dietary diversity (Chu 1989, Liem & Kaufman 1984, McKaye & Marsh 1983, Nemeth 1997). Broad diets and a diversity of feeding behaviors are also associated with sharks, yet the full extent of feeding flexibility in sharks remains to be investigated (Motta & Wilga 2001).

Despite the range of feeding behaviors and prey, modulation of food capture has been documented experimentally in only two shark species: the leopard shark, *Triakis semifasciata*, which exhibits greater buccal cavity expansion when feeding on larger food items (Ferry-Graham 1998), and the spiny dogfish, *Squalus acanthias*, which exhibits shorter capture durations with smaller food items (Wilga 1997). Other studies of shark feeding have detected a great deal of variability in the duration of kinematic events both within and among individuals (Motta et al. 1991, 1997, Ferry-Graham 1997, 1998, Wilga 1997, Wilga & Motta 1998a). These wide ranges in values for kinematic events for one prey type (individual variability), however, are not the same as consistent differences in the kinematics among prey types (modulation) (Chu 1989). Previous studies on modulation have determined that prey elusivity (Liem 1978, 1979, Sanderson 1988, 1990, Wainwright 1986) and size (Ferry-Graham 1998) influence capture kinematics. Both of these factors relate to physical prey characteristics and therefore should not be considered the sole influences on capture behavior. Other factors such as the location or accessibility of the prey could

also significantly influence the predator's behavior. The effect of prey accessibility may be most apparent in benthic habitats, where the prey can be found attached to rocks, hidden in crevices, or buried in the substrate. When capturing these types of prey, size and elusivity may not be as important as the accessibility of the prey, particularly if the prey is hidden or clinging tightly to the substrate. In order for a bottom-dwelling predator such as a shark to successfully capture all of these organisms, it may need to alter or modulate its prey capture.

The present study examines the feeding kinematics of the horn shark *Heterodontus francisci*. Three main questions are addressed: (1) How does *H. francisci* capture food? (2) Does the food capture kinematic profile of *H. francisci* match what is known for other sharks, or are there variations unique to this species? and (3) In view of the trophic spectrum of *H. francisci*, does it modulate its capture kinematics when capturing food of differing accessibility?

Materials and methods

Specimens

Five *H. francisci* ranging in size from 55 to 70 cm total length were used in this study (Table 1). Sharks 1–3 had lived in captivity for 3 years, shark 4 for 6 months, and shark 5 was collected near the Channel Islands, California, two weeks before the experiment. Sharks 1–3 were housed and studied at the Florida Aquarium, Tampa, in a 500 000 l public exhibit aquarium maintained at 20°C. Their diet consisted of frozen squid (*Loligo* sp. and *Illex* sp.) and frozen shrimp (*Penaeus* sp.) offered three times a week. Sharks 4 and 5 were housed at Mote Marine Laboratory (MML), Sarasota, Florida in an insulated 1400 l semicircular tank with an acrylic window. The tank was maintained

at 20°C and had a closed, natural seawater system equipped with a biological filter. The MML sharks were fed a mixed diet of frozen squid, shrimp, and Atlantic thread herring, *Opisthonema oglinum*, once a week.

Food items

During preliminary feeding trials, sharks were offered a variety of benthic invertebrates, including live blue crabs (*Callinectes* sp.), live shrimp (*Penaeus* sp.), live sea urchin (*Lytechinus* sp.), and frozen squid (*Loligo* sp. and *Illex* sp.). Squid was selected as the experimental food item because the sharks refused all other items. Three methods of food presentation were designed to mimic natural differences in prey accessibility. Food was presented unattached to the substrate (unattached), securely attached to a small feeding platform (attached), or fitted snugly in a tube (burrowed) (Figure 2). This design controlled for all other potential food factors (e.g., size, shape, elusivity, etc.) leaving only the effect of accessibility to be tested.

Squid (head, arms, and pen removed) were cut into 4 cm² pieces for all feeding trials. When using *Illex* sp., the viscera also were removed because the cut viscera clouded tank water. To present unattached food, squid was placed onto a 9 cm² acrylic platform that was anchored to the bottom of the aquarium (Figure 2a). In this way the food was completely accessible to the shark. For presenting attached food, an identical acrylic platform was used with a slit (6.0 cm × 0.5 cm) cut into one side (Figure 2b). A piece of squid was wedged into the slit and secured under the platform with a clip. Most of the squid extended above the platform. The clip held the squid firmly enough so that only a forceful pull could remove the squid from the platform, in order to mimic prey clinging to the substrate.

To mimic prey burrowed in a crevice, an acrylic box (28 cm h × 28 cm w × 37 cm l) was used in which a plastic tube (1.5 cm diameter, 4 cm long) was

Table 1. Data on individual *Heterodontus francisci* used in kinematic study of food capture.

Shark	Total length (cm)	Sex	No. trials used to calculate kinematic durations			No. trials used to calculate kinematic displacements		
			Unattached	Attached	Burrowed	Unattached	Attached	Burrowed
1	70	F	15	13	11	11	11	11
2	60	M	16	15	13	11	11	11
3	66	M	17	23	12	11	11	11
4	64	M	25	21	14	11	11	11
5	55	M	31	18	20	11	11	11

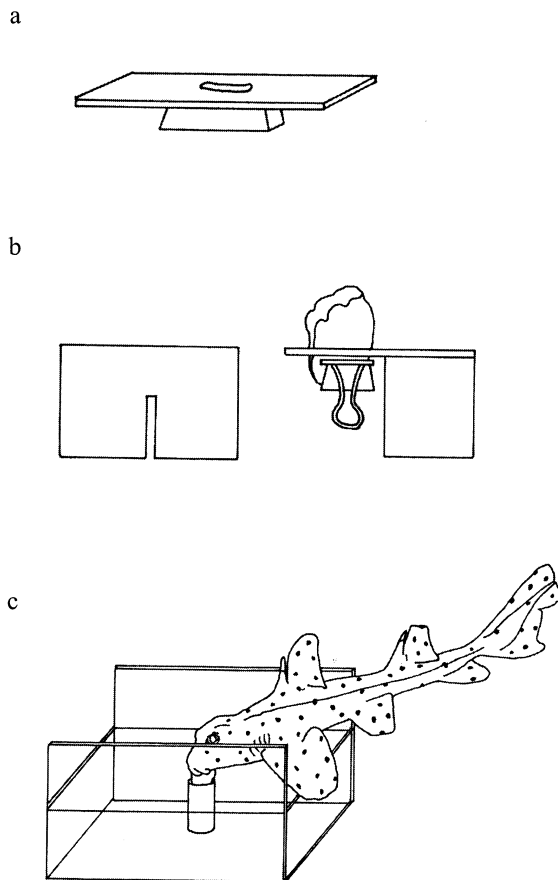


Figure 2. Schematic diagram of each food presentation apparatus (a, b, c) used during feeding trials. In a and c, camera views are shown. In b, dorsal view is depicted on the left, and lateral view on the right. For presenting unattached food (a), squid was placed on the top of the platform. For presenting attached food (b), squid was wedged into slit (see left diagram) and secured with a clip beneath the platform (right diagram). The third apparatus (c) was designed for burrowed feeding trials, where squid was inserted firmly into a tube suspended from the center of a platform.

suspended down from the center of a horizontal platform (Figure 2c). A squid piece was inserted into the tube from above using a 5 cc syringe, so that the squid fit snugly within the tube and extended slightly above the tube opening.

Data collection

At MML, sharks were videotaped during feeding with a high-speed video camera (NAC HSV-200, 200 fields sec^{-1}). Illumination was provided by 3000 W of tungsten-halogen light. To ensure a lateral view of

the shark while feeding, two parallel acrylic walls were placed 30 cm apart on the aquarium bottom parallel to the viewing window. A feeding apparatus could then be placed in between the walls, allowing the shark to orient laterally to the camera when feeding. This structure was not used when presenting burrowed food, since that apparatus already oriented the shark in this manner (Figure 2c).

At the Florida Aquarium, sharks also were recorded with high-speed video through the acrylic window of the exhibit tank. Illumination from outside the tank ranged from 1000 to 3000 W of tungsten-halogen light. Sharks were fed directly in front of the window by a diver who remained in the tank throughout the experiment. The diver ensured that the sharks were oriented laterally to the camera while feeding, and was in charge of assembling each feeding apparatus. At both the Florida Aquarium and MML sharks were videotaped in their holding tanks during daytime hours.

Experiments were conducted once a week for eleven weeks at MML, and once a week for twelve weeks at the Florida Aquarium. During experiments, trials were run until the shark stopped feeding. A feeding trial consisted of presenting one piece of squid to the shark using one of the three food presentation methods at a time. The logistical problems of food presentations within the Florida Aquarium necessitated these sharks be presented food one presentation method at a time, not randomly presented. Therefore, all sharks were presented food in the same manner. Initially all sharks were presented unattached food and experiments continued until at least ten bites had been recorded for each shark. Following this each shark was presented with attached food and videotaped until at least fifteen bites were recorded. Preliminary analyses of the data revealed that an adequate sample size for statistical analyses had not been reached, and therefore additional unattached and attached food trials were conducted. On those days each shark was offered either unattached or attached food, but never both on the same day. After sufficient data were collected, trials using burrowed food were conducted. Adequate sample size was determined using the Bros & Cowell (1987) method (Table 1).

Capture events were recorded on VHS tape and trials were later analyzed field by field at 5 millisecond intervals using a Panasonic AG1970 video editor. In addition, images were selected using a Video Blaster video capture board (Creative Labs, Inc.) and then digitized using Sigma Scan Image (Jandel Scientific Software). The following kinematic events were quantified (time in milliseconds, distance in centimeters): (1) mandible

depression, the time from beginning of mandible depression to maximum gape; (2) mandible elevation, the time from beginning of mandible elevation to jaw closure; (3) start of palatoquadrate protrusion, the time from beginning of mandible depression to start of palatoquadrate protrusion; (4) protrusion, the time from beginning of palatoquadrate protrusion to maximum protrusion; (5) retraction, the time from maximum protrusion to complete retraction of the upper jaw; (6) total bite duration, the time from beginning of mandible depression to the closing of the jaws on the squid; (7) maximum gape, the distance from the tip of the mandible at maximum depression to the most anterodorsal point of the upper labial cartilage (the upper labial cartilage forms the anterior border of the gape); and (8) maximum palatoquadrate protrusion, the distance of a line drawn from the distal tip of the palatoquadrate through its center to the upper labial cartilage. No discernible cranial elevation was observed, and therefore cranial elevation was not selected as a kinematic variable.

Statistics

Differences in capture kinematics among the three food presentation methods from all five sharks were assessed using analyses of variance (ANOVA). Normality was tested using the Kolmogorov–Smirnov test, and the assumption of equal variances was tested using the Levene median test (Sigma Stat v.2.0). Data were transformed using natural log or square root transformations if needed. If assumptions for parametric statistics were met, then two-way, mixed model ANOVAs were performed on the kinematic variables (Systat 5.0). In the mixed model, individual shark was the random factor and feeding type was the fixed factor. The random factor was tested over the error mean square, while the fixed factor was tested over the interaction (feeding type \times individual) mean square (Zar 1984). After measurement of maximum palatoquadrate protrusion, assumptions for parametric statistics could not be met even after transformations, so a Kruskal–Wallis one-way ANOVA was performed. One ANOVA was performed on the kinematic data to detect differences among sharks with all feeding types combined, and then a separate ANOVA was used for differences among feeding types with all sharks combined. Since a total of eight ANOVA tests (7 two-way + 1 one-way) were used on these related variables, p -value significance was adjusted using a sequential Bonferroni

correction to control for the group-wide Type I error rate (Rice 1989). Significance was tested at table-wide values of $\alpha = 0.05$ for $k = 8$ tests. Data from all five sharks were used for testing each kinematic event in both the one- and two-way ANOVAs, except for the three timing events associated with movement of the palatoquadrate (start of protrusion, protrusion, and retraction). For these three events, data from only three sharks were used to form a balanced design for the two-way, mixed model ANOVA.

In those cases where a significant effect was found with the parametric tests, the Tukey–Kramer post hoc test (Systat 5.0) was used to determine where the differences occurred. If a significant effect was found with a Kruskal–Wallis ANOVA, then a Student–Newman–Keuls post hoc test (Sigma Stat 2.0) was used in the same manner.

Thirty linear regressions of sequential bite number against duration of mandible depression and total bite duration were performed to ascertain if there was a satiation effect on bite kinematics. Analyses of variance were run on each linear regression ($p = 0.05$) (Excel 97).

A ram-suction index (RSI; Norton & Brainerd 1993) was calculated to determine the degree to which compensatory suction/ram or inertial suction was used during capture: $(D_{\text{predator}} - D_{\text{prey}}) / (D_{\text{predator}} + D_{\text{prey}})$, where D is the distance moved¹. Index values range from +1 (ram with possible compensatory suction) to -1 (pure inertial suction strike), with intermediate values representing combinations of the two behaviors. Data from three trials on each of four individuals feeding on unattached food were used to calculate an index for food capture by *H. francisci*.

Results

Description of capture

All captures, regardless of presentation method, began with an initial suction strike. Average total bite duration during an initial strike on unattached food was 113 ± 4 ms (SE), 132 ± 4 ms on attached food, and 148 ± 8 ms for burrowed food (Table 2). The average RSI during feeding on unattached food was -0.57 ± 0.06

¹ Compensatory suction involves sucking in just enough water to keep the prey from escaping or being forced away from the mouth of the predator as the predator swims over it (Van Damme & Aerts 1997).

Table 2. Average values and standard errors of the eight kinematic events associated with initial food capture strikes of all *Heterodontus francisci* individuals feeding on unattached, attached, or burrowed food.

Kinematic event	Presentation method		
	Unattached	Attached	Burrowed
Duration of mandible depression (ms)	46.8 (2.3)	52.1 (2.4)	63.6 (4.6)
Duration of mandible elevation (ms)	66.4 (2.9)	79.8 (3.3)	84.4 (5.3)
Start of palatoquadrate protrusion (ms)	85.2 (6.3)	79.4 (3.8)	105.1 (7.8)
Duration of palatoquadrate protrusion (ms)	20.7 (0.9)	25.3 (0.9)	21.3 (0.7)
Duration of palatoquadrate retraction (ms)	74.4 (5.1)	99.0 (5.1)	100.5 (8.6)
Total bite duration (ms)	113.2 (3.6)	131.8 (4.3)	148.0 (8.0)
Maximum gape (cm)	1.8 (0.1)	1.9 (0.1)	1.9 (0.1)
Maximum palatoquadrate protrusion (cm)	0.7 (0.04)	0.8 (0.1)	0.7 (0.03)

and ranged from -0.96 to 0.10 , although 0.10 was the only positive RSI calculated. The average RSI value of -0.57 indicates a relatively greater contribution of suction than ram used during such a strike.

Capture of unattached food was composed of an initial suction strike made up of a common sequence of kinematic events (Figures 3a and 4). Before initiating capture, a shark first swam up to the platform until its snout touched the squid (Figure 4a). It then rested on the bottom propped up on its pectoral fins in a tripod fashion in front of the platform. The expansive phase began with mandible depression, and was accompanied by extension of the labial cartilages (Figures 4b,c). As gape distance increased, extension of the labials increased. No cranial elevation was observed. While mandible depression ensued, expansion of the pharyngeal region near the ventral hyoid area was observed, and this expansion continued until after the jaws had closed (Figures 4c–f). Pharyngeal expansion made it difficult to observe and quantify peak hyoid depression, and therefore hyoid depression was not quantified. During the period of buccal cavity expansion, the food moved toward and into the buccal cavity until it was no longer visible (Figures 4b,c). After reaching maximum gape, the compressive phase began with elevation of the mandible. As mandible elevation occurred,

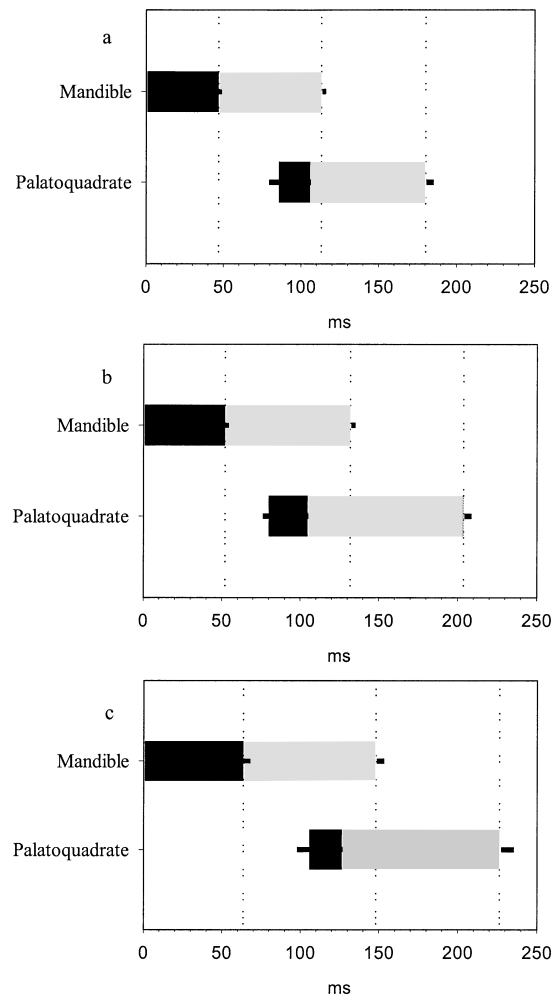


Figure 3. Composite block diagrams of movements of the mandible and palatoquadrate during initial strikes on unattached (a), attached (b), and burrowed (c) food. A grand mean was used from all five sharks to calculate the onset and duration of both kinematic events. For mandible movement, black blocks represent duration of mandible depression, gray blocks represent duration of mandible elevation. For palatoquadrate movement, black blocks represent duration of palatoquadrate protrusion, gray blocks represent duration of palatoquadrate retraction. Dotted lines indicate (from left to right) end of mandible depression, end of mandible elevation, and end of palatoquadrate retraction. Error bars represent the standard error of the grand mean. The bar on the trailing edge of each block is one standard error of the duration of the kinematic event; the bar on the leading edge of the black blocks is one standard error of the onset.

movement of the palatoquadrate in an anteroventral direction was observed (Figure 4d). Average velocity of mandible elevation was 24.7 cm sec^{-1} , and average velocity of palatoquadrate protrusion was

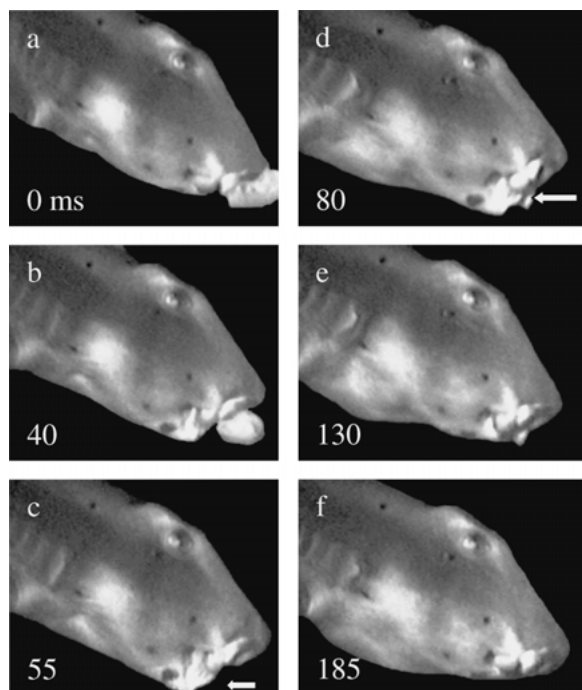


Figure 4. Sequence of food capture events taken from actual video images of shark 3 feeding on unattached food. Numbers in bottom left corner of each image represent time in milliseconds. Before initiating capture, the shark first swims up to the platform until its snout touches the food (a). Mandible depression begins in b, reaches a maximum in c, and starts to elevate in d. Note that the food apparent in b has disappeared by frame c, and extension of the labial cartilages has occurred (indicated by arrow). The upper jaw begins to protrude in d (indicated by arrow), and continues protruding to a maximum (e). The lower jaw has stopped elevating by e. Finally, in f, the upper jaw returns to its original position. Note expansion of the pharyngeal region beginning in c and continuing through to f.

31.3 cm sec^{-1} . The palatoquadrate continued to protrude even after the mandible returned to its elevated position. During the recovery phase, the palatoquadrate was retracted until the jaw was no longer visible (Figure 4f).

Capture of attached and burrowed food began with the initial suction strike already described (Figures 3b,c), but was followed by post-capture strikes and body movements to remove the food fully from the substrate. For both attached and burrowed trials, the initial suction strike generally resulted in only a portion of the food clasped within the jaws at the end of the recovery phase. The rest of the food either remained tethered to the platform or stuck in the tube. Figure 5 depicts the various body movements and post-capture strikes

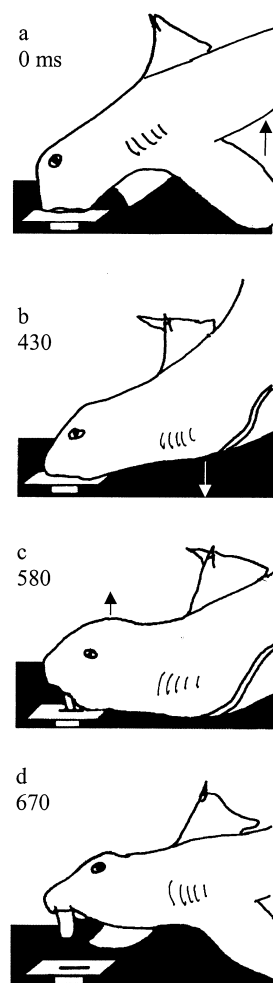


Figure 5. Video tracings depicting the post-capture strikes and leveraging behavior associated with capture of attached and burrowed food. A representative sequence is shown for feeding on attached food. Time (in milliseconds) is given in top left corner. Movement of the body into a vertical headstand position begins in a, accompanied by a suction strike. Then body arches (b), pressing pectoral fins and head down onto platform, with tail still overhead. Next (c), tail moves ventrally and head is forced dorsally, pulling on squid. In d, the squid has been removed from the platform.

the sharks used to loosen or fully remove the squid. Body movements suggested that all five sharks were using their bodies as a lever to loosen the squid from the substrate. With the jaws still clasped onto the food, sharks shifted their bodies vertically (snout down) until they assumed a headstand-like position (Figure 5a). In this position, the animals often initiated another suction strike at the squid. In 29% of burrowed trials, the labial

Table 3. Results of ANOVAs for the eight kinematic events associated with initial food capture strikes compared among five *Heterodontus francisci*.

Kinematic event	Shark d.f. = 4,249		Presentation method d.f. = 2,8		Shark × presentation method d.f. = 8,249		Post hoc tests ^d
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	
Duration of mandible depression (ms)	9.629	<0.001*	4.307	0.054	1.610	0.122	5 > 1, 2, 3, 4***
Duration of mandible elevation (ms)	25.313	<0.001*	1.238	0.340	5.703	<0.001*	1, 5 > 2, 3, 4***
Start of palatoquadrate protrusion (ms) ^a	8.95	<0.001*	2.940	0.164	0.333	0.855	1 > 3, 4**
Duration of palatoquadrate protrusion (ms) ^a	0.31	0.734	1.661	0.298	2.673	0.036	
Duration of palatoquadrate retraction (ms) ^a	22.757	<0.001*	7.925	0.041	1.420	0.233	4 > 3 > 1**
Total bite duration (ms)	33.852	<0.001*	2.553	0.139	5.157	<0.001*	5 > 1 > 2, 3, 4**
Maximum gape (cm) ^b	4.321	0.002*	0.382	0.683	1.495	0.163	3 > 1, 2**
Maximum palatoquadrate protrusion (cm) ^c	57.201	<0.001*	0.717	0.699	—	—	3, 4 > 1, 2, 5**

*After sequential Bonferroni correction, *p*-values of <0.0071 are considered significant at the 0.05 probability level.

Significant at *p* < 0.05. *Significant at *p* < 0.001. ^a*N* = 3 sharks, Shark d.f. = 2,101; Presentation method d.f. = 2,4; Interaction d.f. = 4,101. ^bShark d.f. = 4,150; Presentation method d.f. = 2,150; Interaction d.f. = 8,150.

^cKruskal–Wallis one-way ANOVA performed on each main effect. H-values given. Shark d.f. = 4; Presentation method d.f. = 2. ^dTukey–Kramer or SNK tests. 1, 2, 3, 4, 5 refers to individual shark.

cartilages were extended and pressed against the platform to surround the tube opening, forming a seal. If the food was not removed during the expansive phase of the post-capture strike, then at the end of the recovery phase the squid would remain clasped within the jaws. The sharks then arched their bodies, pressing the head and pectoral region flat against the platform, tail overhead (Figure 5b). As the tail was moved ventrally, the head was forced dorsally, the jaws pulling the squid up with them (Figures 5c,d). Such a pull often resulted in the food tearing off the platform near the clip, rather than cutting of the food at the jaws. If the squid was not removed from the feeding apparatus, then sharks employed additional suction strikes and/or leveraging pulls. No thrashing of the head from side to side occurred in any feeding event.

Although capture of attached and burrowed food was characterized by post-capture strikes and pulls, there were trials where no such behaviors were observed. In one attached feeding trial, shark 1 captured the squid with simply an initial suction strike. In a total of nine attached feeding trials, sharks 2–4 were able to capture the food with an initial suction strike and one

subsequent pull. This combination of one initial strike and one pull to remove food was not as common during burrowed feeding trials, for it was only observed in a total of four trials by two individuals. All five individuals were able to capture burrowed food at least once using only an initial suction strike.

The other 136 feeding trials on attached and burrowed food consisted of an initial suction strike followed by post-capture suction strikes and pulls. The average number of post-capture suction strikes per trial for attached food was 1.6 ± 0.1 , and for burrowed food was 1.8 ± 0.2 , although the actual number per trial ranged from 0 to 8. The number of pulls that were observed per trial also ranged from 0 to 8, but there was a significantly greater number of pulls that occurred during attached trials (1.6 ± 0.1) than burrowed trials (0.8 ± 0.1) (Mann–Whitney Rank Sum test, $p < 0.001$).

Palatoquadrate protrusion was observed during trials of all five individuals with all three food presentation methods, and was observed in 53% of initial suction strikes and 43% of post-capture suction strikes. Among food presentation methods, protrusion occurred during

initial strikes in 43.3% of unattached trials, 52.2% of attached trials, and 68.6% of burrowed trials. Protrusion also was observed in 38.5% of post-capture strikes on attached food, and 49.2% of post-capture strikes on burrowed food. The average distance for the upper jaw to protrude during initial strikes overall was 0.73 ± 0.02 cm, which amounts to approximately 7% of average head length (distance from first gill slit to tip of snout) and contributes to 39% of gape distance. Average duration of protrusion during initial strikes was 22 ± 0.5 ms overall.

Kinematic analyses

No modulation of the kinematic events associated with initial strikes was detected with food of the three different accessibilities presented to *H. francisci* (Table 3). On the other hand, seven of the eight kinematic events differed significantly among individual sharks. Post hoc tests indicated that these individual differences were independent of where the sharks were filmed (i.e., MML versus Florida Aquarium).

There was no appreciable effect of sequential bite number and therefore satiation on the kinematic variables analyzed. Of the thirty regressions only one, total bite duration of attached food for shark 4, had a significant correlation with sequential bite number (slope = 5.87, $p = 0.01$, $r^2 = 0.58$).

Analyses of variance were performed on events associated with post-capture suction strikes, even though post-capture strikes were not always an integral component of attached and burrowed food capture, and the number of post-capture strikes per trial varied considerably among individuals². Two of the most informative post-capture kinematic events were selected to compare between attached and burrowed food capture: total bite duration, and duration of palatoquadrate protrusion. Results from a two-way ANOVA on total bite duration associated with post-capture strikes showed significant differences among sharks ($p < 0.001$), but again no differences among presentation methods. Post hoc tests revealed almost identical results among sharks as for total bite duration during initial strikes. Average total bite duration for post-capture strikes during attached trials was 107 ± 4 ms, and 124 ± 5 ms during burrowed trials. There was no difference between attached and burrowed trials for the

duration of palatoquadrate protrusion during post-capture strikes (attached = 21 ± 1 ms, burrowed = 19 ± 1 ms, $p = 0.218$).

Discussion

Method of food capture

The average RSI of -0.57 supports the observation that *H. francisci* uses inertial suction capture under these experimental conditions. This corroborates the findings of Strong (1989) who observed suction prey capture during feeding of *H. francisci* off Santa Catalina, California. This index value is nearly identical to that of the nurse shark *G. cirratum* (RSI -0.50), which is an obligate inertial suction-feeder (Robinson 1999). During compensatory suction the predator sucks in enough water to compensate for the anterior displacement of water resulting from its forward movement (Van Damme & Aerts 1997). Since the horn sharks remained stationary prior to food capture they were not using compensatory suction.

Kinematic profile

Food capture in this basal shark, *Heterodontus francisci*, conforms to the kinematic profile observed in a variety of inertial suction feeding sharks (Figure 1). The expansive phase of capture begins with rapid mandible depression, which is often accompanied by labial cartilage extension. Only the nurse shark *Ginglymostoma cirratum*, has a more rapid mandible depression (26 ms) than *H. francisci* (47–64 ms) of all sharks examined to date (Motta et al. unpublished data). Rapid mouth opening generally results in greater sub-ambient buccal pressures and is characteristic of specialized suction feeding fishes (Lauder 1980, Muller et al. 1982, Liem 1993). Anterior displacement of the labial cartilages in *H. francisci* produced a laterally enclosed mouth opening that prevents water inflow at the sides of the gape, and may even hinder prey escape as it moves into the buccal cavity (Muller & Osse 1984). Lateral enclosure of the mouth by labial cartilages has also been observed during feeding of the leopard shark, *Triakis semifasciata* (Ferry-Graham 1998), the spiny dogfish, *Squalus acanthias* (Wilga 1997), and the nurse shark, *Ginglymostoma cirratum* (Robinson 1999), which all utilize inertial suction feeding (Figure 1). During the compressive phase,

² Post-capture behavior did not occur during unattached trials.

palatoquadrate protrusion is frequently observed, and reaches a peak just before jaw closure on the food. The sequence is completed with the recovery phase, where the palatoquadrate is retracted into its original position. These morphological and kinematic specializations for suction feeding appear to be common to both basal and derived suction specialists alike.

The kinematic profile of *Heterodontus francisci* differs from that associated with ram feeding carcharhinid and lamnid sharks. The horn shark appears to lack cranial elevation during the expansive phase of initial suction strikes. Cranial elevation is an integral part of the feeding activity of the white shark, *Carcharodon carcharias* (Tricas & McCosker 1984), lemon shark, *Negaprion brevirostris* (Motta et al. 1997), Caribbean reef shark, *Carcharhinus perezi* (Motta & Wilga 2001), and swellshark, *Cephaloscyllium ventriosum* (Ferry-Graham 1997), which are ram feeders (Figure 1). Cranial elevation may position the mouth in line with the prey as the predator approaches, which would be particularly important for ram feeding sharks with inferior mouths (Frazzetta & Prange 1987). This may not be as important for inertial suction feeders, particularly the horn shark, which can position its mouth dorsally over its benthic invertebrate prey and whose open mouth is more anteriorly directed. Cranial elevation is also lacking in the inertial suction feeding leopard shark, *Triakis semifasciata* (Ferry-Graham 1998), and in the majority of the bites of the nurse shark, *Ginglymostoma cirratum* (Robinson 1999, Motta et al. unpublished data).

The horn shark protruded its upper jaw as much as 15% of head length in nearly half of the feeding trials of this study. Anatomical studies on the feeding apparatus of the horn shark report that the extensive ethmoidal articulation of the upper jaw should greatly restrict protrusion (Holmgren 1940, 1942, Schaeffer 1967, Taylor 1972, Maisey 1980). Extensive palatoquadrate protrusion in the horn shark is consistent with the findings of Wilga (1997) however, who found that the extent of upper jaw protrusion is not clearly related to the type of jaw suspension in sharks.

The biological role of upper jaw protrusion in sharks is unclear. Protrusion may be used for gouging pieces of prey items or for reorienting the teeth for increased grasping ability (Frazzetta & Prange 1987, Moss 1972, 1977, Tricas & McCosker 1984, see Motta & Wilga 2001 for a review). The horn shark feeds on invertebrates that cling tightly to the substrate, so protrusion could also assist in biting or picking at such prey items (Moss 1972). Protrusion of the upper jaw is so rapid (approximately 20 ms) that it may be functionally

analogous to the strike of a chisel. Such action is enhanced by the numerous cuspidate teeth along the anterior portion of the palatoquadrate (Taylor 1972), which most likely rasp and gouge prey during the chiseling protrusion action. Combining inertial suction with repetitive palatoquadrate protrusion, the upper jaw can strike the prey loose prior to it being sucked into the mouth.

The combination of lever-like body movements with post-capture suction strikes has not been described for any other shark species. Movements of the head and body most likely augment the suction forces generated during post-capture strikes. By positioning the body in a headstand and then pulling its posterior end down, the horn shark may be able to generate torque about the pectoral fins that are positioned on the substrate, resulting in pulling up on the food. With the jaws clenched tightly on the food when the head elevates, the pieces of squid were effectively stretched and torn loose at the attachment site. The movements exhibited by the horn shark could be useful for capturing attached prey such as clinging sea urchins, anemone tentacles, or crabs wedged into crevices. Strong (1989) observed this species feeding off Santa Catalina, California, during which it raised up on its pectoral fins with the back arched, and moved the head up and down in a 'pecking' manner. He also reports juvenile *H. francisci* feeding on anemone tentacles this way.

Modulation of capture

Heterodontus francisci did not modulate the kinematic events of the initial suction strikes under these experimental conditions. There was no detectable difference in the maximum gape or palatoquadrate protrusion distances between the three food presentation methods, nor were there any differences in the durations of capture events among them. These results are not confounded by any effect of satiation, since there was no appreciable effect of sequential bite number on the kinematics. There was also no modulation evident in total bite duration or duration of palatoquadrate protrusion with post capture suction strikes for attached and burrowed food.

When the food is within the jaws yet still attached to or wedged in the substrate, *Heterodontus francisci* uses its relatively large flattened pectoral fins to lever itself if it can not remove the food with suction. This leveraging behavior was used for both attached and burrowed food, but significantly more head pulls were

used with attached food. This suggests that there was a greater resistance to removal with attached food, and an observable difference in accessibility of the food.

Another difference in the post-capture events between attached and burrowed trials was the use of the protruded labial cartilages and labia to form a seal over the food burrowed in the tube, while the shark hovered in a headstand position. With the mouth positioned directly over the tube opening, extension of the labial cartilages prevented water from entering the sides of the gape and interfering with the direction of suction. This behavior would be particularly effective for removing less accessible prey, such as crevice-dwelling or burrowed invertebrates.

Lack of modulation during feeding is not uncommon among aquatic vertebrates. The aquatic salamander, *Ambystoma mexicanum*, demonstrates a stereotyped motor feeding pattern that does not change with food type (Reilly & Lauder 1989). The swellshark, *Cephaloscyllium ventriosum*, does not appear to modulate its capture when presented with food of two different sizes (Ferry-Graham 1997). Even some teleosts, which frequently have been shown to modulate capture, display stereotyped motor patterns under certain conditions. For example, the rock bass, *Ambloplites rupestris*, lacks significant differences in muscle activity among three different food types (Wainwright & Lauder 1986). It is worth noting, however, that in many of these studies there may not have been a large enough detectable difference among the food offered to elicit behavioral modulation. In the present study it would appear that there was a large enough difference in the accessibility of food based on the post-capture behaviors described above, although we cannot discount the fact that utilization of one food type (squid) could elicit a similar initial food capture behavior due to a common odour. In addition, since all sharks were initially presented with unattached squid, the sharks could have been conditioned to associate squid with easy accessibility. This potential learning effect could have influenced the lack of modulation detected among subsequent food trials.

Our data indicate that *H. francisci* has one basic kinematic pattern for inertial suction food capture. This behavior, augmented by body movements, is effective at capturing unattached, attached, and burrowed food. If the texture, type, or size of the food were altered then perhaps *H. francisci* would modulate capture during the initial strike. The leopard shark, *Triakis semifasciata*, exhibits greater head expansion with larger food items (Ferry-Graham 1998), the spiny

dogfish, *Squalus acanthias*, exhibits longer duration of the entire capture event with larger food items (Wilga 1997), and the lemon, *Negaprion brevirostris*, and Caribbean reef shark, *Carcharhinus perezi*, both modulate the degree of cranial elevation and use of upper jaw protrusion depending on food presentation (Motta et al. 1997, Motta & Wilga 2001).

Although no consistent differences were detected in the kinematic variables between the three food presentation methods, there were significant differences found among individuals. Individual variability has been found in many studies of aquatic vertebrate feeding, such as during feeding of the lemon shark, *Negaprion brevirostris* (Motta et al. 1997), four species of sunfishes (Wainwright & Lauder 1986), and the aquatic salamander, *Ambystoma mexicanum* (Reilly & Lauder 1989).

In summary, *Heterodontus francisci* uses inertial suction facilitated by rapid mandible depression and labial cartilage protrusion to capture food. It also exhibits unusual post-capture behaviors that vary according to food accessibility. The kinematics of food capture are similar to other basal and derived suction feeding sharks, but differ from ram feeding sharks. The kinematics associated with these actions, as well as the lack of cranial elevation, place this shark among the specialized inertial suction feeders. With its chisel-like palatoquadrate protrusion, use of the mouth to form a seal over burrowed food, and unusual leveraging behavior, this shark exhibits some features that distinguish it from other elasmobranchs. When presented with food of different accessibility the horn shark uses one consistent kinematic pattern for capture that is not modulated, although individual sharks exhibit inter-individual variation in food capture kinematics.

Acknowledgements

We thank E. Hovland, D. Klemm, E. Lundy, and J. Tyminski for their research assistance, L. Ferry-Graham, S. Reilly, and A. Summers for their helpful comments on this manuscript, and F. Keller for her artistic contribution. This research was supported by the Mote Marine Laboratory and University of South Florida Graduate Fellowship in Elasmobranch Biology. Facilities were provided by the Center for Shark Research at Mote Marine Laboratory, and the Florida Aquarium. The project was supported by grants from the National Science Foundation to P.J.M. and R.E.H. (DEB 9117371 and IBN 9807863).

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