Food capture kinematics in the deep-water chain catshark *Scyliorhinus retifer*

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The chain catshark (*Scyliorhinus retifer*) is a member of one of the most well studied groups of elasmobranchs (Order: Carcharhiniformes), yet its feeding strategy is unknown due to the inaccessible deep water environment in which it lives (greater than 200 m). To investigate the feeding biology of captive *S. retifer*, high-speed videography was used to document the kinematic events during capture of two differently sized fish pieces, 'large' (scaled to the mouth width), and 'small' (scaled to one-half the mouth width). Despite a significant delay in the timing of select kinematic variables for large food captures, a multivariate analysis of the feeding behaviour indicated that overall, food capture kinematics and strike behaviour in *S. retifer* were not statistically different between large and small items (MANOVA, Wilks' Lambda P =0.598, df=4,24). Food capture in *S. retifer* was suction-dominant, with items being drawn into the mouth about twice the distance that the predator moved. While suction-dominant food capture appears to be an advantage to benthic predators, it contrasts sharply with the phylogenetic position of *S. retifer* among several ram-feeding carcharinoid sharks including *Cephaloscyllium ventriosum*, a member of the same family (Scyliorhinidae). Thus, feeding mode in carcharinoid sharks seems to reflect their ecology and does not appear to have been phylogenetically constrained.

INTRODUCTION

Despite the dramatic rise of feeding kinematics studies in sharks and rays in the past few decades (Tricas & McCosker, 1984; Frazzetta & Prange, 1987; Ferry-Graham, 1997; Motta et al., 1997; Wilga & Motta, 2000; Edmonds et al., 2001; Dean & Motta, 2004; Matott et al., 2005; Sasko et al., 2006), research has focused primarily on species common to inshore and shallow habitats. Specifically, investigations of feeding kinematics have examined coastal species, commonly found at depths less than 200 m, or within the confines of the continental shelf (Table 1). Nonetheless, a large component of elasmobranch diversity is found in the deeper ocean regions (Musick et al., 2004), yet feeding behaviour in these taxa still remains largely unknown.

Table 1. *Habitat, distribution and feeding mode of sharks used in previous feeding kinematics studies. Habitat and distribution adapted from Musick et al., 2004. Feeding modes and kinematic studies are superscripted; 1, Wilga, 1997; 2, Edmonds et al., 2001; 3, Wu, 1994; 4, Robinson & Motta, 2002; Motta et al., 2002; 5, Tricas & McCosker, 1984; 6, Ferry-Graham, 1997; 7, Ferry-Graham, 1998b; 8, Frazzetta & Prange, 1987.*

Order	Family	Species	Benthic, benthopelagic, pelagic	Coastal, oceanic, bathyal	Suction, ram, bite	Phylogenetic position
Squaliformes	Squalidae	*Squalus acanthias*	Benthopelagic	Coastal	Suction/Ram[1]	BASAL
Heterodontiformes	Heterodontidae	*Heterodontus francisci*	Benthic	Coastal	Suction[2]	
Orectolobiformes	Orectolobidae	*Orectolobus maculatus*	Benthic	Coastal/Bathyal	Suction[3]	
	Ginglymostomidae	*Ginglymostoma cirratum*	Benthic	Coastal	Suction[4]	
Lamniformes	Lamnidae	*Carcharadon carcharias*	Benthopelagic	Coastal/Oceanic	Ram/Bite[5]	
Carcarhiniformes	Scyliorhinidae	*Cephaloscyllium ventriosum*	Benthic	Coastal/Bathyal	Ram[6]	
	Triakidae	*Triakis semifasciata*	Benthopelagic	Coastal	Suction/Ram[7]	
	Carcharhinidae	*Carcharhinus perezi*	Benthopelagic	Coastal	Ram[8]	
		Carcharhinus acronotus	Benthopelagic	Coastal	Ram[8]	
		Negaprion brevirostris	Benthopelagic	Coastal	Ram[8]	
	Sphyrnidae	*Sphyrna tiburo*	Benthopelagic	Coastal	Ram[1]	DERIVED

The Scyliorhinidae represent the largest family of extant sharks (within the largest order, Carcharhiniformes), and include more than 15 genera and over 100 species (Compagno, 1999). Within the Carchariniformes, scyliorhinids occupy a relatively basal phylogenetic position (Shirai, 1996). Scyliorhinid sharks inhabit tropical and temperate seas, ranging from the intertidal zone to depths below 2000 m (Compagno, 1984). With such a variety of species and habitats, it is difficult to identify the dominant feeding mode (ram, suction, bite, or filter) of this diverse family. Various species of the family Carcharhinidae utilize ram feeding as their dominant food capture mode (Frazzetta & Prange, 1987; Motta et al., 1997; Wilga & Motta, 2000; Motta & Wilga, 2001), but the results remain less clear in the Scyliorhinidae as only one species has been studied. The juvenile swellshark *Cephaloscyllium ventriosum*, an inshore Pacific species, has already been described as a ram-dominant feeder (Ferry-Graham, 1997, 1998a). In order to determine potential feeding modes and capture behaviours present among the highly diverse scyliorhinids we investigated food capture in a deep-water offshore representative, *Scyliorhinus retifer* (Garman, 1881).

Scyliorhinus retifer (Cacharhiniformes: Scyliorhinidae), the chain catshark, is a small (<1 m total length (TL)) demersal shark found as deep as 754 m and no shallower than 74 m (Bigelow & Schroeder, 1948; Springer, 1979; Compagno, 1984). These sharks inhabit upper slope regions of the north-west Atlantic Ocean, ranging as far north as the Georges Bank off Massachusetts and as far south as Nicaragua, in water temperatures from 8.5 to 14°C (Springer, 1979; Compagno, 1984; Able & Flescher, 1991). Submersible observations indicate that this species prefers to lie against upright structures dispersed about a rough substrate (Able & Flescher, 1991), which appears to be essential to the oviparous behaviour of mature females (Castro et al., 1988). Limited dietary data on *S. retifer* reveal that the diet is broad and includes nematodes, cephalopods, polychaetes, crustaceans, and unidentified teleost fish (Bowman et al., 2000). However, it is not known where *S. retifer* feeds (i.e. water column, bottom), or how it captures prey. In this study we specifically tested the prediction that *S. retifer* utilizes a ram-dominant feeding strategy, given its phylogenetic proximity to the ram feeder *Cephaloscyllium ventriosum*.

A second goal of this study was to investigate modulation of food capture kinematics in *S. retifer*. Modulation is defined as the ability of an organism or species to change its behaviour repetitively and consistently in response to different stimuli (Liem, 1978; Nemeth, 1997b; Frost & Sanford, 1999). Studies encompassing a wide variety of vertebrate taxa have demonstrated modulation of feeding behaviour at many physiological levels. These have included changes in kinematics (timing and magnitude) of head movements, muscle activity, or buccal pressure with the presentation of prey of differing shape and texture (Deban, 1997; Frost & Sanford, 1999; Van Wassenbergh et al., 2006), size (Frazzetta & Prange, 1987; Wilga, 1997; Ferry-Graham, 1998b) or elusiveness (Norton, 1991; Wainwright & Turingan, 1993; Anderson, 1993; Nemeth, 1997a,b). Despite prominent individual variation in some species, past studies of feeding kinematics in suction-dominated sharks have shown that

food capture is generally a conservative process (Edmonds et al., 2001; Motta & Wilga, 2001; Motta et al., 2002; Matott et al., 2005), whereas ram-dominant feeders appear capable of modulating the contribution of ram and suction, at least with respect to food size (Frazzetta & Prange, 1987; Wilga, 1997; Motta & Wilga, 2001).

In order to evaluate the ability of *S. retifer* to modulate behaviour in response to differences in food size we specifically tested the prey-size hypothesis (Frazzetta & Prange, 1987): that in *S. retifer* larger food items would elicit ram feeding and biting behaviours, whereas smaller items elicit greater suction. We also investigated the effects of food size on distinct kinematic and strike variables, predicting that because *S. retifer* lives under such environmentally challenging conditions (i.e. low light and scarce prey) and consumes a wide variety of prey, it will modulate prey capture to increase performance.

MATERIALS AND METHODS

Specimens

Four chain catsharks (*Scyliorhinus retifer*) were obtained from Atlantis Marine World (Riverhead, NY) and housed in the Hofstra University Animal Laboratory. Animals were maintained in a 568-l rectangular aquarium at a temperature of 12±1°C. The sharks ranged in size from 40.3 to 42.2 cm total length (TL) (mean=41.2 cm; SE=0.47), which is indicative of both mature male and female adults (Sminkey & Tabit, 1992). Mouth width (MW) ranged from 2.27 to 2.74 cm (mean=2.56 cm, SE=0.115). The sharks were fed a steady diet of mostly chopped silversides (*Menidia menidia*) and shrimp (Caridae), two to three times a week. Occasionally, additional food items were offered, which included squid (*Loligo* sp.), chopped clams (*Mercenaria* sp.), crabs (*Hemigrapsus* sp.) and worms (*Nereis* sp.) in that order of abundance and frequency. These items were presented in an effort to avoid acclimation to a particular diet and represented the types of prey naturally encountered (Bowman et al., 2000).

Videography

When a shark was observed eating regularly it was transferred to a 208-l rectangular tank for filming. This tank was connected to the same circulation/filtration unit as the stock tank to minimize the stress individuals might have experienced in a new environment. However, this required feedings in the stock tank and experimental tank to be synchronized since the scent of food infiltrated both tanks. A clear Plexiglas® sheet was inserted in the experimental tank to create an elevated floor, which served as a platform for the shark to feed on. This insert also provided sufficient area for a 45° angled-mirror to be placed below, facilitating a ventral view of the shark. A plastic barricade at the back of the tank kept sharks feeding in a narrow area towards the front.

Acclimation to filming conditions in the experimental tank ranged from a few hours to three days. Following acclimation (when the shark was ready to feed), food items were placed on top of the false-bottom and situated directly over the 45° angled-mirror. Although a variety of food items were offered randomly to the sharks in the stock tank, pieces
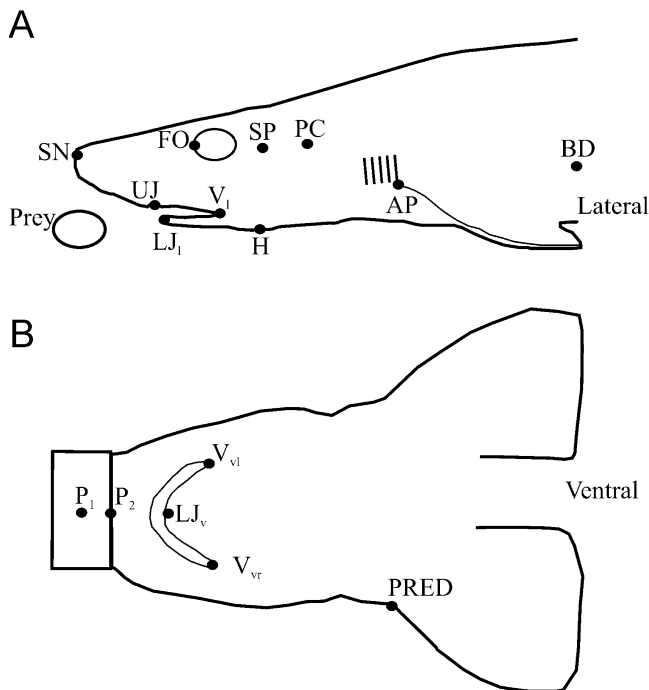
Figure 1. Diagram of the points digitized on the head of *Scyliorhinus retifer* for frame by frame analysis. (A) Digitized lateral points: AP, anterior pectoral fin origin; BD, body landmark; FO, front of orbit; H, most ventral portion of hyoid; LJ_l, dorsal and most anterior tip of the lower jaw; PC, posterior margin of the chondrocranium; SN, anterior tip of the snout; UJ, anterior and most ventral tip of the upper jaw; V_l, vertex of upper and lower jaws. (B) Digitized ventral points: LJ_v, most anterior tip of the lower jaw; P_1, centre of mass of the food item; P_2, point on margin of food item closest to the mouth of the shark; PRED, pectoral fin origin; V_{vl}, left ventral vertex of upper and lower jaw; V_{vr}, right ventral jaw vertex.

of silversides were the only experimental food type used. We varied food item size as this is the most likely variable to elicit feeding modulation in sharks based on previous studies (Frazzetta & Prange, 1987; Wilga, 1997; Ferry-Graham, 1998b). Silverside pieces were randomly offered at two different size categories: 'large'—where the length of the fish piece equalled the mouth diameter of the shark (approximately 2.6×1.0 cm), and 'small'—where the length of the fish piece equalled one-half of the mouth diameter of the shark (1.3×1.0 cm). Recordings were performed with a NAC HSV-500 video system at 250 frames s⁻¹ (fps) with the camera situated perpendicularly to the front of the tank. Illumination was provided by two 600 watt halogen lights, which did not visibly alter individual feeding behaviour. Recordings lasted until the shark had consumed the entire food item, or once the shark left the camera view. Filming of capture events ended after consumption of four food items for each session (even though the shark would readily feed on more than this quantity) in order to minimize satiation effects (Sass & Motta, 2002). Finally, when the shark ceased feeding (or reached the allotted number of feedings) a 10 cm ruler was inserted in the tank for calibration. All experiments were approved by Hofstra University's Animal Care Committee (Protocol no. 05/06-7).
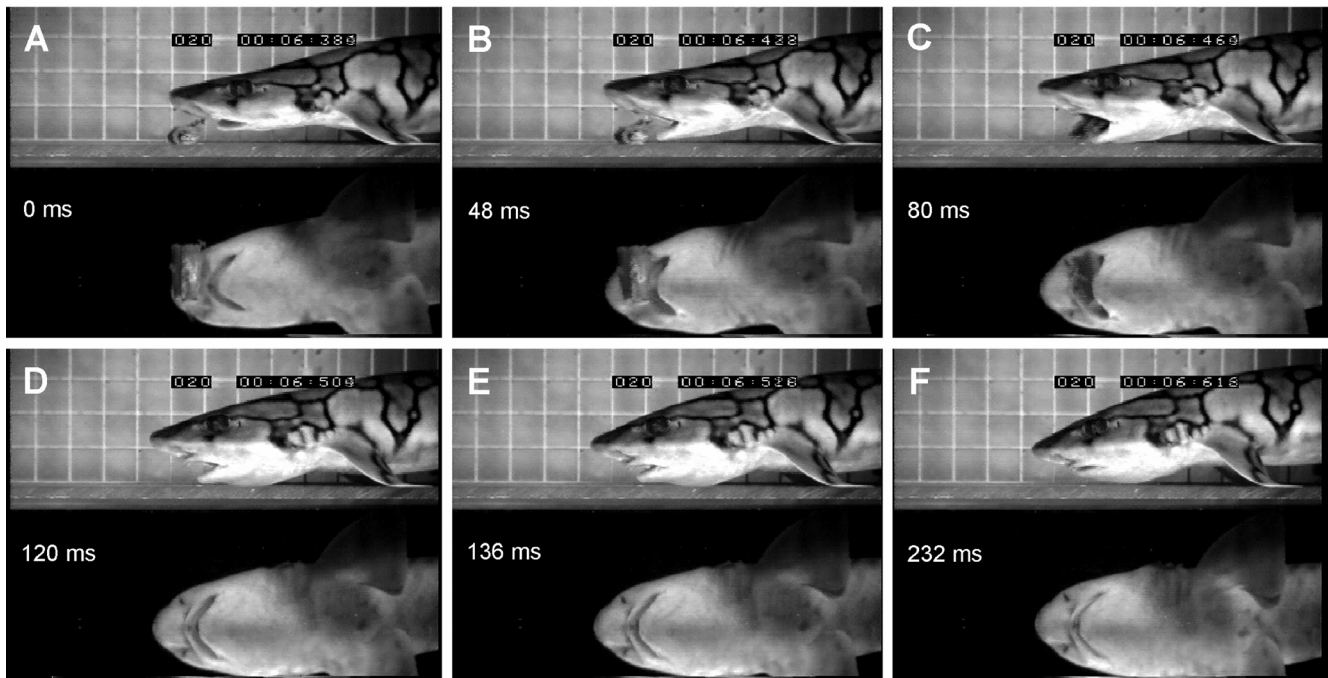
Digitizing kinematic variables

Analogue NAC recordings of the feeding events were converted to digital movie files (.avi format, Microsoft) using Adobe Premiere v. 6.0 video editing program. Feeding events where the whole shark head was clearly visible and perpendicular to the view of the camera were the only sequences analysed. These digital feeding sequences were imported into a Trackeye Motion Analysis program (TEMA bio v. 2.2, Image Systems AB, Sweden) to track the movement of head landmarks during food capture. A total of ten landmarks were digitized frame by frame (every 4 ms) from the lateral (l) view of the shark throughout the feeding event: the front of the orbit (FO), the ventral prominence of the hyoid (H), anterior margin of the pectoral fin (AP), the tip of the snout (SN), the posterior margin of the chondrocranium (PC), the most anterior point of the upper jaw (UJ), the anterior tip of the lower jaw (LJ_l), the vertex (articulation) between the upper and lower jaw (V_l), a body landmark along vertebral axis of the body (BD) and the spiracle (SP) (Figure 1A). Using these points as landmarks, the following displacements were determined: maximum gape distance (the change in distance between the anterior tip of the upper jaw and the most anterior tip of the lower jaw; UJ–LJ_l), maximum upper jaw protrusion (the change in distance between the anterior orbit and most anterior tip of the upper jaw; FO–UJ) and maximum hyoid depression (the change in distance between the spiracle and base of the hyoid; SP–H) (Figure 1A). In addition to these distances, three angles were derived: maximum gape angle (the change in angle between the upper and lower jaws using the articulation as the vertex; UJ–V_l–LJ_l), maximum cranial elevation (the change in angle between the snout and body using the posterior portion of the cranium as the vertex; SN–PC–BD), and minimum lower jaw angle (the change in angle between the tip of the lower jaw and anterior origin of the pectoral fin using the jaw articulation as the vertex; LJ_l–V_l–AP; which represents maximum depression of the lower jaw) (Figure 1A). All linear distances are measured in cm and angles in degrees.

In order to understand the behaviour of these movements over a temporal scale, tracking of kinematic variables began 72 ms prior to the beginning of the strike until 32 ms after jaw closure (or the end of the gape cycle). The onset of rapid mouth opening (a sudden increase in gape) was designated as 'time-zero' (t_0) and represented the beginning of the strike. For each kinematic variable above, we obtained the time of onset, the time of maximum displacement, and the magnitude of maximum displacement (i.e. change in distance or angle) relative to t_0. The duration of food capture, from t_0 to jaw closure, was termed the 'gape cycle time'. A total of 18 derived kinematic variables were calculated using TEMA.

Strike variables

In addition to kinematic variables, which assessed different movements of the predator, a number of strike variables were measured to assess the interaction between the predator and the food item during the feeding event. Strike variables were measured by digitizing the following points from the ventral (v) view: the estimated centre of mass of food item (P_1), the point on the margin of food item closest

Figure 2. High-speed video sequence of individual *Scyliorhinus retifer* feeding on a large fish piece (i.e. scaled to one mouth width). Upper case letters indicate distinct events in the sequence at times specific to this food capture event (not averages). (A) t_0 (0 ms); (B) maximum head elevation (48 ms); (C) maximum gape (80 ms); (D) maximum hyoid depression (120 ms); (E) maximum upper jaw protrusion (136 ms); (F) jaw closure (232 ms). Frames A–C represent the expansive phase of capture, while D–F represent compression.

to the lower jaw tip of the shark (P_2), the most anterior tip of the lower jaw (LJ_v), the pectoral fin origin (PRED), the left vertex (articulation) of the upper and lower jaws (V_{vl}), and the right vertex (articulation) of the upper and lower jaws (V_{vr}) (Figure 1B).

The first strike variable, ram-suction index (RSI) (Norton & Brainerd, 1993), was calculated to test the degree of ram or suction used to capture differently sized food-items.

$$RSI = (D_{pred} - D_{prey})/(D_{pred} + D_{prey}) \qquad (1)$$

where D_{pred} = the distance moved by the predator and D_{prey} = the distance moved by the prey (food).

An RSI value of '−1' would represent an event in which the food was moving, but the predator did not (i.e. pure suction). A value of '+1' would represent an event where the predator moved to overtake the food item, which remained stationary (i.e. pure ram).

Tracking for D_{pred} and D_{prey} was performed in TEMA using the ventral view of the feeding sequence. The predator was tracked using the anterior margin of the pectoral fin (Figure 1B). Past studies have used various regions of the mouth for the predator (to assess D_{pred}) landmark (Ferry-Graham, 1997, 1998a,b). However, we found this landmark to be unreliable because, during the strike, the lower jaw moved posteroventrally due to an increase in gape. The pectoral fin origin (PRED) was not affected by any head movements and was therefore a more reliable indicator of the predator's overall forward movement. The food (P_1) was tracked using the centre of mass of the food item, which was calculated using the intersection between the long and short axes of the rectangular fish piece. The distances moved by both the predator (D_{pred}) and food (D_{prey}) were calculated by tracking

the overall movement of these two landmarks beginning from t_0 to the time at which P_1 first passed the plane of the predator's gape ($T_{capture}$). The absolute distances travelled by these two landmarks were used to compute the RSI for each feeding event. A scatterplot was also generated of D_{pred} vs D_{prey} to visually examine the variation in each of these variables. Finally, the initial predator–food distance ($LJ_v - P_2$, at t_0) and the average predator velocity ($D_{pred}/T_{capture}$) and mean food velocity ($D_{prey}/T_{capture}$) were also calculated to gauge the approach parameters of the predator and movements of the food during the strike. We used the estimated centre of mass of the food item (P_2) rather than P_1 to calculate the initial predator–food distance to account for differences in initial orientation of the food item among feedings. In all, a total of five strike variables were analysed for each food capture event: D_{pred}, D_{prey}, $T_{capture}$, RSI, and initial predator–food distance.

Statistical analyses

A total of 39 food capture sequences was analysed, consisting of ten sequences per individual (except individual II with nine sequences). Five feeding sequences per individual were analysed for each food size. Descriptive statistics (means and standard errors) were calculated for the 24 total variables (18 derived kinematic variables and six strike variables). Two-way mixed model univariate analyses of variance (ANOVA) were constructed to assess the significance of food size, individual, as well as the interaction effect of food size crossed with individual (food size×individual) for all kinematic and strike variables. The food size×individual term tested the effect that any differences observed in food type were consistent across all individuals. Because the
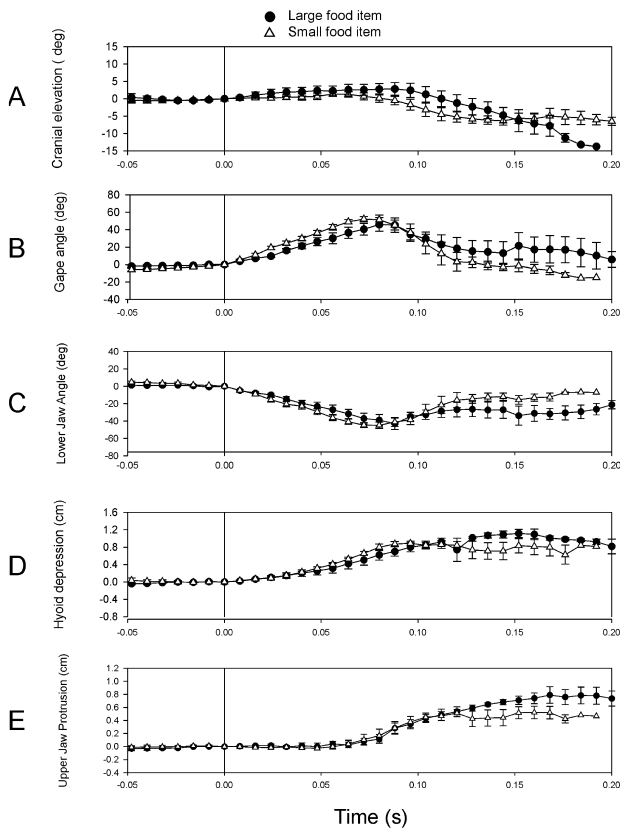
Figure 3. Kinematic plots of (A) cranial elevation; (B) gape angle; (C) lower jaw angle; (D) hyoid depression; and (E) upper jaw protrusion against time for one individual. For each variable, large food captures are indicated by black circles, while small food captures are indicated by open triangles. A vertical bar indicates t_0 (time zero), the onset of rapid mouth opening. There is very little cranial elevation and profiles are very similar for large and small food items. Points on the plot are means with standard error bars.

Figure 4. Horizontal bar plots of mean onset and peak times of kinematic variables during feeding in *Scyliorhinus retifer*. Large food item capture events are represented by solid bars. Small food item captures are indicated by open bars. Standard errors bars are shown. The vertical dashed lines are t_0 (time zero, the onset of rapid mouth opening), and the time of peak gape (the start of the compression). The overall temporal pattern is similar but time of peak lower jaw depression (A, A') and peak hyoid depression (B, B') are significantly longer for larger prey (ANOVA, $P < 0.05$).

'individual' was considered a random factor, the F-ratios for food size factor used the mean square error of the food size×individual as the denominator following Zar (1999). For tests in which the individual effect was significant, post-hoc tests (Bonferroni corrected) were performed to determine which of the individuals were responsible for the difference.

Due to the large number of variables used in this study, we also conducted a principal components analysis (PCA) to simplify interpreting the simultaneous comparison of several variables. In addition, gape distance and lower jaw angle variables were removed because they were highly correlated with gape angle. The PCA reduced the remaining 18 variables to four and was used to evaluate overall differences. The only components retained were those that had eigenvalues of at least 1.0. Because of the large number of variables used in our analysis we verified the stability of the overall PCA by repeating the analysis, removing each individual in turn from the model. Scatterplots of the factor scores resulting from the PCA were created to examine any effect of food size. To determine if there was an overall significant food-size effect, a multivariate analysis of variance (MANOVA) was conducted on the factor scores from the PCA. A significant difference in the MANOVA would mean that *S. retifer* is changing its overall capture behaviour in response to food
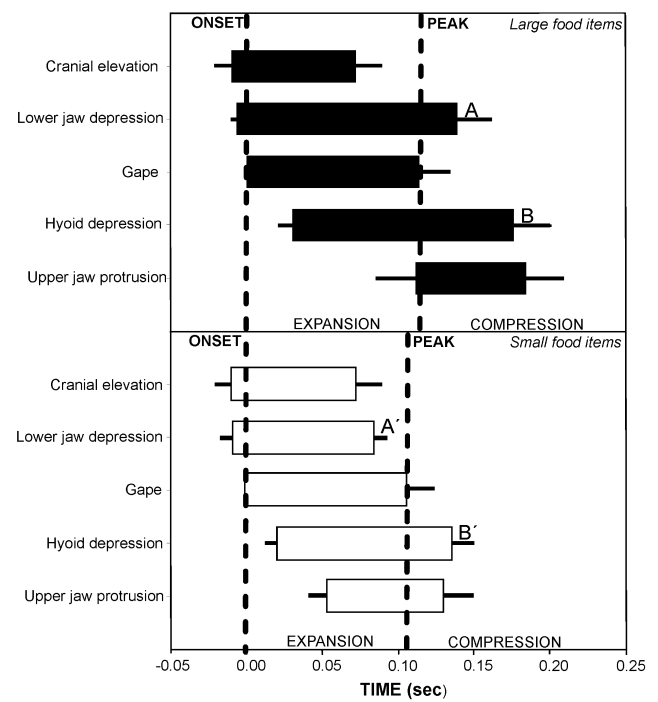
size when all variables are considered simultaneously. For all statistical analyses statistical significance was accepted if $P<0.05$. All statistical analyses were performed using SYSTAT v. 11.0 (SYSTAT Software, Inc.).

RESULTS

Scyliorhinus retifer responded to the introduction of food into the filming arena by increasing buccal pumping. The frequency and magnitude of pumping continued to increase until the otherwise stationary shark started to move in search of the food item. Search was usually characterized by frequent swaying of the rostrum from side to side across the Plexiglas® bottom. The shark continued this behaviour until it was positioned within a few centimetres of the food item, where it initiated food capture. The shark captured food items by lowering its head and simultaneously perching on its pectoral fins.

Kinematics of food capture

Food items were always taken from the substrate and the sharks would not feed in the water column. During food capture, the shark typically elevated its head slightly while substantially depressing the lower jaw and hyoid to draw in the food item (Figures 2A–C & 3A,C). The expansive phase of food capture lasted approximately 100 ms irrespective of food size (Figure 4). Maximum gape usually occurred when the food item first began to enter the mouth (Figure 2C). As

Table 2. *Means and standard errors (SE) for kinematic and strike variables in* Scyliorhinus retifer *feeding on large and small food items.*

	Large food	SE	Small food	SE
Kinematic variable				
Maximum cranial elevation (degrees)	2.236	0.688	2.679	1.099
Maximum gape angle (degrees)	29.156	4.089	31.443	4.263
Maximum gape distance (cm)	0.779	0.081	0.733	0.098
Minimum lower jaw angle (degrees)	28.227	3.721	28.250	4.346
Maximum hyoid depression (cm)	0.637	0.064	0.660	0.059
Maximum upper jaw protrusion (cm)	0.321	0.055	0.371	0.044
Onset of cranial elevation (s)	−0.017	0.015	−0.010	0.012
Onset of gape angle (s)	0.004	0.004	0.001	0.003
Onset of lower jaw angle depression (s)	−0.007	0.003	−0.009	0.011
Onset of hyoid depression (s)	0.030	0.010	0.020	0.008
Onset of upper jaw protrusion (s)	0.111	0.026	0.053	0.012
Time of maximum cranial elevation (s)	0.066	0.014	0.079	0.017
Time of maximum gape angle (s)	0.102	0.012	0.089	0.016
Time of maximum gape distance (s)	0.126	0.022	0.092	0.010
Time of minimum lower jaw angle (s)	0.140	0.023	0.096	0.016
Time of maximum hyoid depression (s)	0.176	0.024	0.135	0.015
Time of maximum upper jaw protrusion (s)	0.184	0.025	0.129	0.020
Gape cycle time (s)	0.280	0.031	0.195	0.021
Strike variable				
Average predator velocity (cm/s)	3.486	0.732	4.326	0.715
Time to capture (s)	0.128	0.026	0.079	0.008
Initial predator–prey distance (cm)	1.174	0.117	1.001	0.154
D_{pred} (cm)	0.382	0.089	0.349	0.070
D_{prey} (cm)	0.666	0.089	0.577	0.074
RSI	−0.315	0.135	−0.266	0.120

Table 3. *Table of principal component (PC) loadings for derived kinematic and strike variables. Loadings greater than 0.6 and lower than −0.6 are highlighted in bold.*

|	PC 1	PC 2	PC 3	PC 4
Kinematic variable				
Maximum gape angle	−0.115	**0.828**	−0.309	0.137
Maximum hyoid depression	−0.036	**0.849**	−0.285	0.028
Maximum neurocranial elevation	−0.228	0.500	0.367	0.402
Maximum upperjaw protrusion	−0.102	**0.833**	−0.148	−0.053
Onset of hyoid depression	**0.676**	0.236	−0.226	−0.275
Onset of neurocranial elevation	0.206	0.334	−0.440	**−0.653**
Onset of upper jaw protrusion	**0.917**	0.038	0.160	0.060
Time of maximum gape angle	**0.609**	0.038	0.326	0.171
Time of maximum hyoid depression	**0.941**	0.035	0.087	0.083
Time of maximum neurocranial elevation	0.383	0.083	−0.295	**−0.759**
Time of maximum upper jaw protrusion	**0.929**	0.182	0.151	−0.044
Gape cycle time	**0.827**	0.056	0.272	−0.053
Strike variable				
Average predator velocity	0.010	0.001	**−0.877**	0.411
Time to capture	**0.899**	0.002	0.232	0.192
Initial predator–prey distance	0.149	0.392	0.249	0.370
D_{pred}	0.456	−0.027	**−0.674**	0.472
D_{prey}	−0.147	**0.755**	0.255	0.047
RSI	0.434	−0.413	**−0.702**	0.285
Percent of total variance (%)	31.195	19.220	15.550	10.856
Eigenvalues	5.615	3.460	2.799	1.954
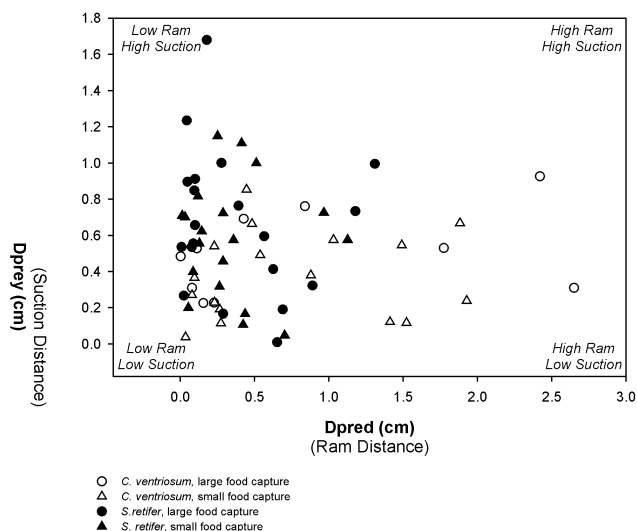
Figure 5. Scatterplot of D_{pred} vs D_{prey} superimposed on ram-suction space (Wainwright et al., 2001) of strikes on large (circles) and small (triangles) food items by *Scyliorhinus retifer* (black) and *Cephaloscyllium ventriosum* (white). Data for *C. ventriosum* acquired from L. Ferry-Graham, used with permission. Visual inspection shows strikes for *S. retifer* appear to cluster more closely in the suction space, whereas *C. ventriosum* appears to vary more along the D_{pred} (ram) axis.
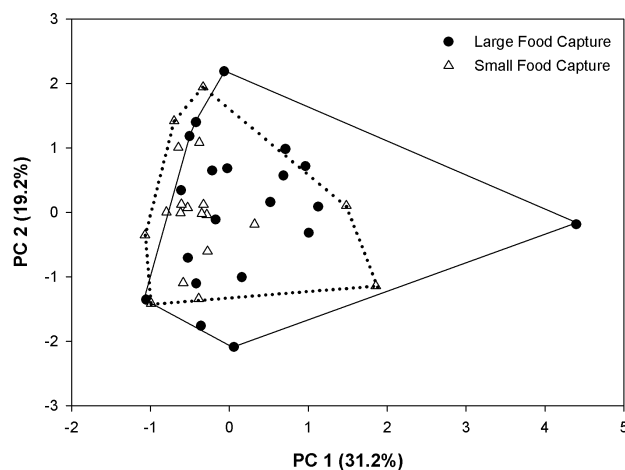

Figure 6. Bivariate plot of principal components analysis Factors 1 and 2. Solid circles are *Scyliorhinus retifer* feeding on large food items and open triangles represent *S. retifer* feeding on small food items. Each symbol represents a single feeding event. Food-size polygons overlap extensively and are not significantly different (MANOVA Wilks' Lambda *P*=0.598).

the fish piece moved posteriorly towards the buccal cavity of the shark, closing of the upper and lower jaws commenced while the animal simultaneously perched up on its pectoral fins and depressed the head (Figure 2D–F). At this point, a substantial bulge (the hyoid) became apparent in the ventral region of the mouth and simultaneously depressed while the upper jaw protracted anteroventrally (Figures 2D & 3D,E). The hyoid apparatus and upper jaw reached peak displacement near jaw closure (Figures 2F & 3D). Once a food item was fully processed (by one or more manipulation bites and/or suction transport), the shark generally made a 180° turn and returned to the other side of the tank, facing away from the filming arena. A summary of mean kinematic data with standard errors is provided in Table 2.

Strike variables

On average, the onset of rapid mouth opening began with the food item located under the snout, 1.0–1.2 cm in front of the tip of the lower jaw. The mean distance moved by the predator after t_0 was 0.37 cm, approximately half the distance travelled by the food during capture for both small and large food items (Table 2). Although forward movement of the predator was present in most capture sequences, a few instances also occurred in which the shark paused within close proximity of the stationary food and subsequently drew it into the buccal cavity using only suction. These events were represented by RSI values near −1. Rarely, captures also involved the shark producing substantial forward movement used to overtake the food. These ram-dominated events were characterized by RSI values close to +1. However, the mean RSI was −0.315 (SE=0.135) for large food items and −0.266 (SE=0.120) for small food items. These values were not significantly different (ANOVA, *P*=0.253), but more importantly represented a greater component of suction

than ram. The lack of significant variation in RSI was supported by the scatterplot of D_{pred} and D_{prey}, which showed no overt visual trend as feedings were randomly scattered about the plot for both food sizes (Figure 5). However, when comparing D_{pred} vs D_{prey} between *S. retifer* and *Cephaloscyllium ventriosum* there appeared to be a slight separation of the two species. When superimposed onto ram-suction space *S. retifer* clustered more along the D_{prey} or suction distance axis, while *C. ventriosum* varied more greatly along the D_{pred} or ram axis (Figure 5).

Multivariate statistics

Factor loadings for the PCA are presented in Table 3. The majority (>50%) of the variance comes from PC 1 and PC 2 The plots of the factor scores for large and small food showed substantial overlap of polygons (Figure 6). The MANOVA of factor scores of the four principal components revealed that there was no significant difference when *S. retifer* was feeding on food of different sizes (Wilks' Lambda *P*=0.598, df=4,24). Thus, food size did not have a significant effect on food capture behaviour when all kinematic and strike variables were considered simultaneously.

DISCUSSION

We reject the hypothesis that *Scyliorhinus retifer* is a ram-dominant feeder because of its phylogenic proximity to *Cephaloscyllium ventriosum*; *S. retifer* utilized a suction-dominated mode (mean RSI=−0.3) for capture of both large and small food items (Table 2). This contrasts sharply with the only other studied catshark, *C. ventriosum*, which was reported as a ram-dominant feeder (mean RSI=+0.6) under similar experimental conditions (Ferry-Graham, 1997). Suction-dominant food capture does not appear to be prominent in any other examined carcharhinoid species, all of which predominantly capture items by ram (Frazzetta & Prange, 1987; Ferry-Graham, 1997, 1998b; Motta et al., 1997;

Wilga, 1997). However, the discovery of suction-dominant food capture (mean RSI<0) in *S. retifer* is not novel to the Elasmobranchii. Indeed, squaloid (Wilga & Motta, 1998a), heterodontoid (Edmonds et al., 2001), and orectoloboid sharks (Tanaka, 1973; Wu, 1994; Motta et al., 2002; Matott et al., 2005) and some batoids (Wilga & Motta, 1998b; Dean & Motta, 2004; Sasko et al., 2006) predominantly use suction to capture food. However, these groups are quite distant relatives of *S. retifer* (i.e. non-carcharhinoids), and therefore support the notion of the independent evolution of suction feeding in the elasmobranchs (Motta et al., 2002).

Sharks and rays that feed by suction achieve negative intraoral pressure by rapid expansion of the buccal cavity via action of hypertrophied jaw depressor muscles, such as the coracohyoideus and the coracobranchiales (Wilga & Motta, 1999; Motta et al., 2002; Motta, 2004). Moreover, these taxa generally possess additional anatomical features that increase buccal volume, enhance water flow or position the mouth opening closer to the prey. For example, sharks from the families Orectolobidae and Triakidae take advantage of prominent labial cartilages that laterally occlude the mouth during expansion and make the buccal opening almost terminal for enhanced suction feeding (Wu, 1994; Ferry-Graham, 1998b; Motta et al., 2002). Batoids, on the other hand, have a euhyostylic feeding mechanism that permits extensive jaw protrusion towards benthic prey (Dean & Motta, 2004). However, neither robust jaw depressor muscles nor the aforementioned 'enhancements' to suction feeding are present in *S. retifer*, despite the demonstrated ability to produce substantial prey movement during strike (RSI values near −1). Though the myology of the feeding mechanism of *S. retifer* was not thoroughly investigated, the lack of anatomical characteristics associated with suction feeders may mean that these modifications are less important than previously thought. We hypothesize that strong hyoid movement may contribute to the suction draw, as demonstrated by Wilga & Sanford (2003), but a comparative investigation of the feeding mechanism of *S. retifer* and other suction feeding sharks is required in order to make any conclusive statements.

Scyliorhinus retifer does not modulate feeding behaviour based on food size (Figure 6). Instead, it appears that *S. retifer* performs a rather stereotypical set of movements when capturing both large and small food items, which could account for why there was no significant difference in RSI between food sizes (Table 2). While this lack of modulation in food capture behaviour conflicts with the 'prey-size hypothesis' (Frazzetta & Prange, 1987), it supports the 'feeding modulation hypothesis', which states that the kinematics of suction feeding sharks is stereotyped; relatively fast capture events reduce the likelihood of modulation (Motta & Wilga, 2001). The absence of modulation in *S. retifer* is consistent with the trend that modulation of capture behaviour in sharks has only been observed in ram-dominant feeders (Frazzetta & Prange, 1987; Wilga, 1997; Ferry-Graham, 1998b).

Though *S. retifer* may be expected to utilize a repertoire of strategies to capture the various prey which occur in its diet, dietary diversity does not appear to translate into the ability of a shark to modulate food capture (e.g. nurse sharks: Compagno, 2001; Matott et al., 2005), although the

relationship appears stronger in bony fish (Lauder 1983a,b; Sanderson, 1991; Ralston & Wainwright, 1997; Van Wassenbergh et al., 2006). Indeed, diverse stomach contents could reflect opportunism, and prey of various taxa could be still related in terms of behaviour and habit. Nonetheless, it is possible that when presented with prey of different types, *S. retifer* will modulate feeding kinematics. At present, food capture modulation in sharks has mostly been demonstrated for feeding on items differing in size (Wilga, 1997; Ferry-Graham, 1998b) and very few studies have offered truly elusive prey.

Some behaviours exhibited by *S. retifer* during food capture appear to be consistent with observations of other bottom-feeding sharks and rays. First, it utilizes a strong suction component to food capture, which has been reported in all kinematic studies of benthic elasmobranchs (Wu, 1994; Ferry-Graham, 1998b; Wilga & Motta, 1998b; Motta et al., 2002; Matott et al., 2005). Thus, suction appears to be more efficient than ram in capturing prey that may be attached, burrowed, fixed between crevices, or simply resting on substrate (Ferry-Graham & Wainwright, 2003; Nauwelaerts et al., 2007). A second line of support is provided by the characteristic anteroventral lowering of the chondrocranium while simultaneously perching on its pectoral fins. This behaviour, present in the majority of the recorded captures, may be important in providing enough space ventrally for the rapid lower jaw and hyoid depression associated with suction generation. Pectoral perching behaviour has also been observed in the horn shark, another benthic feeder (Edmonds et al., 2001). Although food items were placed on the bottom for all experiments, *S. retifer* did not appear to elevate its head even during capture of food items placed in the water column. A third finding consistent with bottom-feeding sharks is that the expansive phase of capture (mouth opening to maximum gape) is comparable to other benthic suction feeders (89–101 ms) and faster than most ram feeders (Robinson & Motta, 2002; Motta, 2004). Thus, the short duration of food capture coupled with the negative RSI would suggest a suction dominated capture event which is more effective when feeding off the substrate (Nauwelaerts et al., 2007). In colder, deep water, benthic predatory sharks are also less likely to encounter food regularly, and the short duration of capture might increase the likelihood of successful capture. Finally, additional evidence of bottom-feeding is provided by gut analyses of *S. retifer*, which report the presence of small pebbles in the otherwise empty stomachs (Springer, 1979; Compagno, 1984). Based on these lines of evidence we conclude that *S. retifer* feeds off the bottom and not in the water column.

Benthic sharks and rays employ suction feeding behaviour to capture prey on the bottom. Ram-feeders, in contrast, can more effectively capture prey in the water column or at the surface. These ecological differences between ram and suction feeders could explain the disparity in the dominant food capture mode between two closely related species, *Scyliorhinus retifer* and *Cephaloscyllium ventriosum*. Although members of the same family, *S. retifer* inhabits a deep, offshore habitat and feeds on a variety of prey items, while *C. ventriosum* is primarily a shallow coastal species that specializes in capturing small fish in the water column

(Tricas, 1982). The results of this study suggest that ecology (primarily feeding location and prey encountered), rather than phylogeny (taxonomic relationship), may have been the driving force behind the evolution of a suction dominant food capture mode in *S. retifer*. As this is the first study to provide a detailed analysis of food capture in a deep water elasmobranch (Table 1), it remains to be seen if suction dominated food capture represents a general pattern that is characteristic of deep-water benthic predators.

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