

FEEDING KINEMATICS OF JUVENILE SWELLSHARKS, *CEPHALOSCYLLIUM VENTRIOSUM*

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Summary

To investigate how feeding behaviors change with prey size, high-speed video recording was used to examine the kinematics of prey capture and transport in 1-year-old swellsharks *Cephaloscyllium ventriosum* (Scyliorhinidae: Carchariformes) feeding on two differently sized prey items. Prey capture in these sharks generally consisted of an initially ram-dominated capture bite, one or more manipulation bites, a holding phase during which the food was held in the teeth of the shark, and then suction-dominated prey transport. During initial capture and transport, most of the water taken in is forced back out of the mouth anteriorly rather than continuing posteriorly out through the gill openings. Dye experiments in which dye-perfused prey items were ingested by the sharks confirm this observation; distinct jets of colored water were video-taped as they were ejected from the mouth. Very late in prey transport, a bolus of water is ejected through the

gill slits; however, by this time, the majority of water appears already to have exited the buccal cavity through the mouth. Such patterns were observed for sharks feeding on both small and large prey items. Although a basic pattern of prey capture and transport was regularly repeated among strikes, kinematic patterns during prey capture and transport were variable both within and among individuals, indicating that prey acquisition is not tightly controlled. However, the amount of variability was similar among prey sizes. In addition, there were no detectable changes in behavior due to prey item size. Ram-suction index values confirmed that similar capture modes were being utilized for both prey sizes.

Key words: kinematics, behavior, prey capture, prey transport, bidirectional flow, prey item size, suction feeding, *Cephaloscyllium ventriosum*, swellshark.

Introduction

As comparative studies become more prominent in the field of functional morphology, one of the striking conclusions is that even taxa that differ markedly in their morphology use remarkably similar kinematic patterns for performing certain behaviors (Lauder and Prendergast, 1992). These behaviors include feeding in an aquatic medium, which has been studied and compared in fishes, salamanders and turtles, among others (see, for example, Lauder and Prendergast, 1992; Reilly and Lauder, 1992). It has been suggested that the density and viscosity of the aquatic medium impose certain constraints on feeding that may result in similarities among feeding behaviors across even distantly related taxa. Thus, as we compare several different aquatic taxa, we are likely to observe general behavioral patterns that are utilized by all species in question.

In most laboratory studies of feeding behavior, similar prey items (in size or type) are offered to potential predators, as the range of prey items that can be used experimentally is often limited. For video-taping and analyzing the resulting data with precision, presentation of highly active or very small prey items is often avoided. Further, for the purpose of comparative studies, the use of similar prey items is highly desirable in

order to avoid the confounding factor of prey type on subsequent behavioral comparisons. However, several papers have illustrated not only that prey-capture behaviors in teleost fishes are plastic (see, for example, Liem, 1978, 1979; Wainwright and Lauder, 1986; Norton and Brainerd, 1993), but also that a given predator may utilize different behaviors for different feeding situations (Norton, 1991; Nemeth, 1995). An organism may regularly utilize the entire range of behaviors at its disposal, thus *really* using only a single, highly variable behavior (variability in prey capture, Fig. 1A). Conversely, the predator may utilize distinct portions of its behavioral repertoire in response to particular challenges, thereby using one of two or more statistically distinct behaviors (modulation of prey capture, Fig. 1B). Such a distinction between simple within-individual variation and actual modulation of behavior has not always been made clear in the literature. However, recent work suggests that modulation should be a term reserved for actual transitions from one distinct behavior to another in response to a stimulus (see Wainwright and Lauder, 1986; Nemeth, 1995).

Frazzetta and Prange (1987) have proposed a series of

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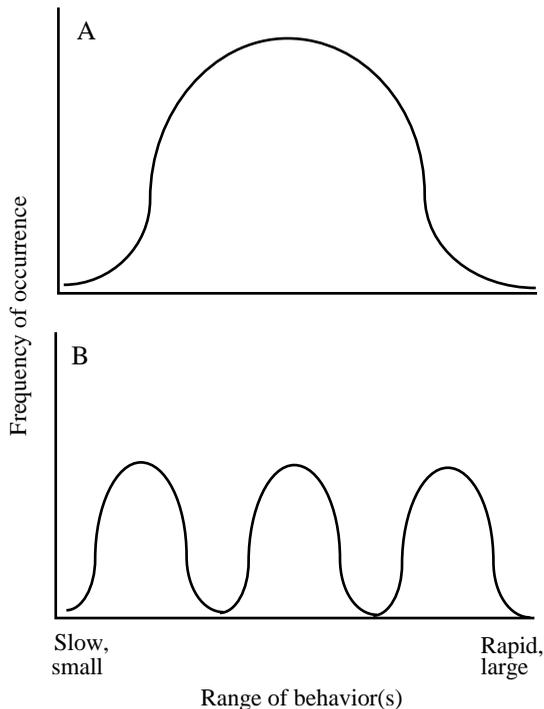


Fig. 1. Theoretical representation of variability in prey-capture behavior (A) and modulation of prey-capture behavior (B). The x -axis in both graphs represents predator behavior; either a single behavior, such as displacement of a kinematic variable, or a collection of behaviors. The examples shown could be movements that range from small to large amplitude, or slow to rapid. In A, the predator uses the entire range of movements with fairly high frequency; thus, the movements utilized form a distribution of use (a normal distribution in this example) that describes a behavior that is highly variable, but possesses a single mean behavior. In B, distinct portions of the range of movements are utilized for particular situations; thus, a multimodal situation arises in which each distributional peak can be thought of as distinct and as describing a different behavior. The primary distinction to be made between variability in behavior and actual modulation of behavior is that modulation occurs *in response* to the feeding situation. Portions of a variable behavior are used at random; thus, over several feeding trials, no clear separation within the range of movements occurs.

hypotheses regarding how prey capture should change with prey item size. Smaller prey items should be captured using suction (where the prey is drawn to the predator by suction created by the predator in opening and expanding the oral cavity) or ram-feeding (in which the predator physically overtakes the prey by locomotion). Larger prey items (although still smaller than the maximum mouth size of the predator) should be bitten, perhaps to ensure the best grip on the prey item. Even larger items still may require multiple bites to capture and then reposition (manipulation bites) the prey for successful transport, or may require head shaking to cut appropriately sized pieces for transport. Accordingly, prey-capture kinematics might change to accommodate the transition from a suction-dominated to a ram-dominated attack, or even a biting attack, as required for successful capture of a

prey item of a particular size. It is unknown whether and how prey transport might be altered by prey item size, as this has not been addressed in previous studies.

The swellshark *Cephaloscyllium ventriosum* (Scyliorhinidae) was chosen to investigate questions related to modification of feeding behaviors by sharks. As a member of the Carchariniiformes, it is a member of the most derived and possibly biologically the most well understood order of sharks (see Moss, 1972; Compagno, 1984; Motta *et al.* 1991; Waller and Baranes, 1991; Motta and Wilga, 1995). Swellsharks are found in shallow temperate waters throughout the eastern Pacific and are thought to be both active predators and scavengers of fish and crustaceans (Compagno, 1984). Egg cases from this species can be collected (or produced by captive breeding colonies as they are extremely fecund for an elasmobranch) and reared with great success in captivity such that animals of known age can be used for experiments. Juveniles are generally amenable to laboratory manipulation. A preliminary analysis of prey capture and transport in this species was presented by Ferry (1996), who first observed that unusual water flow patterns appeared to occur in the buccal cavity during prey transport and occasionally during prey capture. Thus, this species may also exhibit a novel feeding behavior not previously described for any shark species.

The aim of this paper is to describe the basic pattern of prey capture and transport in the swellshark. I will test the hypothesis that these two behaviors are statistically different from one another. I will also determine whether a unique pattern of water flow occurs during prey capture and transport. Finally, I will test the hypothesis that the basic patterns of prey capture and transport, including the prey-capture mode, are modified by the swellshark in response to prey items of different sizes.

Materials and methods

Animals

Swellsharks *Cephaloscyllium ventriosum* (Garman) of known ages were obtained from local public aquaria where the egg cases had been maintained prior to and during hatching. Prior to experiments, sharks were housed together in a 4001 tank in the laboratory, maintained at a temperature of 18 ± 2 °C, and fed the same prey as used in the experiments.

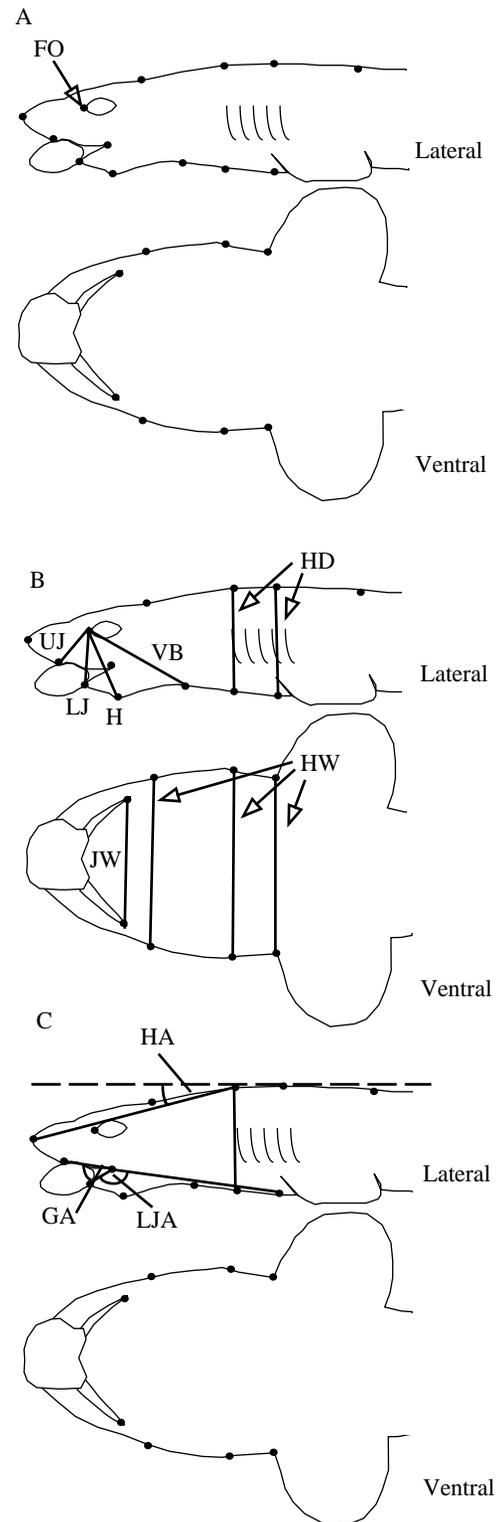
Data acquisition

Five individuals with a mean total length of 30.0 cm (range 23.6–37.0 cm) were video-taped feeding on prey items (pieces of fish, described below) in filming tanks (801 aquaria) maintained at the same mean temperature as the holding tanks (18 ± 0.5 °C). The apparatus used was described previously by Gibb (1995), who provides further details. Data were collected by video-taping sharks capturing and transporting prey items at $250 \text{ fields s}^{-1}$ using an NAC HSV-500 high-speed video system. Two video cameras were used simultaneously to record two views, lateral and ventral, in order to observe and measure the movement of selected points on the head and

Fig. 2. Schematic representation of a shark biting a prey item as recorded using the two-camera system used to video-tape shark feeding. In each panel, both the lateral and ventral views are shown. In A, only the digitized points on the shark's head and body are shown. The anterior margin (most rostral point) of the eye orbit is labeled FO. In B, the distances calculated between the digitized points are indicated (distances from the eye were expressed relative to a starting value of zero by subtracting the resting orbit-to-point distance, body heights and widths were absolute). The two head depth measurements (HD, see also Fig. 5) are indicated, and the distances from the front of the orbit to the ventral surface of the buccal region (VB), the hyoid element (H), the lower jaw tip (LJ) and the upper jaw tip (UJ) are also shown. In the ventral view, the multiple head width (HW, see also Fig. 5) measurements, as well as the jaw width (JW) measurement are shown. In C, the three angles calculated from the digitized points are drawn. They are head angle (HA), gape angle (GA) and lower jaw angle (LJA). Note that GA and LJA are complementary.

body. The ventral view was obtained by aiming a camera at a front-surface mirror angled at 45° beneath the tank. The lateral and ventral images were scaled equivalently using marked grids and a reference scale placed in the tank at the location of an individual shark's head (prior to beginning experiments). Output from the two cameras was combined on a split screen. The tank was lit from the side by a high-intensity 600 W tungsten lamp.

The prey items used were pieces of smelt (Atherinidae) or shrimp (Caridea). These non-elusive prey items were chosen to reflect natural prey types and because they could easily be cut into exact sizes. To account for differently sized sharks, the prey sizes offered to each individual were scaled to the diameter of the shark's mouth. One of two prey sizes was offered to the sharks in a random order (determined by random number generation): (1) equal to half the mouth diameter, and (2) equal to the mouth diameter. Sizes larger than the mouth were not offered as this is known to induce novel behaviors associated with cutting the prey item (e.g. head shaking). Pieces were cut such that they were approximately cuboid. Prey items were offered by placing them on the base of the filming tank using forceps, which were then removed as quickly as possible. The generally stationary shark then accelerated to approach the prey and subsequently capture it. Only video sequences in which the head and jaws were clearly visible in both the lateral and ventral views were used. For measurement consistency, only sequences in which the shark remained approximately perpendicular to the cameras were used. Four captures (the first bite that contacted the prey item if bites were used, also referred to as the strike) and their subsequent transports were analyzed for each of the prey item sizes for each individual. Manipulation bites did occur following the strike, but will be treated elsewhere. Care was taken to allow each shark sufficient time between feeding events such that a subsequent feeding event would not be influenced by the previous event; this was necessary for statistical independence among samples. The time between consecutive feeding events was determined by the shark's



behavior; when a shark had returned to a stationary position and respiration had slowed (indicated by regular but faint flaring of the gills), it was assumed that a sufficient period had passed.

Video sequences were analyzed frame by frame using a custom-designed digitizing program. Frames were downloaded at 0.024 s intervals starting at 'time zero', defined as three

intervals (0.072 s) prior to the onset of rapid mouth opening (this was meant to catch slow movements of the jaws and other cephalic components that are sometimes nearly imperceptible). The download rate was increased in frequency to 0.012 s intervals just prior to maximal mouth opening (maximum gape); this rate was maintained throughout prey capture, transport and complete mouth closure. The holding phase (described later) served to separate the capture and transport temporally into discrete units of activity for analysis. Kinematic traces were used to determine the time of mouth reopening following the holding phase (any detectable movement), and that time was designated as time zero for prey transport. Landmarks on the shark's head and jaws (determined by skeletal elements, whose position could be determined through the skin, and by external morphological features) were digitized in order to calculate cephalic displacements, distances and angles (Fig. 2). The most rostral portion of the orbit was always the most reliably digitized point and was therefore used to determine the relative movement of several other variables (see Fig. 2B, lateral view). Distances from the front of the orbit to the upper jaw tip, the lower jaw tip, the hyoid and the ventral surface of the buccal region were calculated. These lengths were set to a starting value of zero by subtracting the resting orbit-to-point distance (prior to the beginning of prey capture); thus, absolute movements or displacements of each point were determined. Head thickness or depth was measured at the first gill arch and at the pectoral fin insertion (see Fig. 2B). Body height off the tank bottom (distance from the ventral body surface to the tank bottom) was also determined, as these sharks often rise vertically off the bottom (from a nearly stationary position), particularly during prey transport. From the ventral view (Fig. 2B), head width was measured at the following positions: across the posterior edge of the Meckel's cartilages (lower jaw), at the first gill arch and at the pectoral fin insertion. Jaw width was also determined by measuring from the distance between the right and left jaw articulations (quadratomandibular joint). Head angle (measured as a positive or negative angle relative to the dorsal surface of the body), gape angle (the angle between the upper and lower jaws) and lower jaw angle (the complementary angle to gape angle; a lower jaw angle of 180° indicates that the mouth is closed) were also calculated (see Fig. 2C). Predator-prey distance was also determined.

Statistics and other analyses

Comparisons (capture *versus* transport, small prey *versus* large prey, and among individuals) were performed for kinematic variables of interest using multiple three-factor, mixed-model analysis of variance (ANOVA). Feeding phase and prey item size were fixed factors; individual was a random factor. Significance levels were corrected accordingly (Bonferroni correction) for conducting separate tests on multiple dependent variables. *F*-ratios were calculated according to Zar (1984) for this type of ANOVA. The dependent variables were maximum upper jaw protrusion, maximum hyoid depression, maximum buccal expansion, maximum negative head angle, maximum gape angle,

minimum lower jaw angle, starting head angle (at time zero), time to maximum upper jaw protrusion (from time zero), time to maximum hyoid depression, time to maximum buccal expansion, time to maximum negative head angle, time to maximum gape angle and time to minimum lower jaw angle. Prior to conducting any analyses, Cochran's tests (Winer, 1971) were used to check for heterogeneity of variances within these variables at the smallest level tested (the level of prey item size \times phase \times individual interaction). Cochran's tests were used because they are thought to be the most robust test without being overly sensitive. It was assumed that if the variances were homogeneous then the data were also normally distributed, as there is rarely a problem with deviations from normality if variances are homogeneous, and ANOVA is robust to slight deviations from normality (Underwood, 1981). The statistical software package SuperANOVA was used for this and all subsequent *t*-test, ANOVA or analysis of covariance (ANCOVA) analyses.

The potential problem of independence among samples was addressed by a graphical analysis of the data. In particular, potential trends in the kinematic data (timing of an event, maximum or minimum displacements) that could be attributed to the time of the feeding event (strikes 1–8) were sought (e.g. if maximum hyoid depression decreased or increased with strike number). Kinematic variables that showed even a slight trend over time were analyzed using repeated-measures ANOVA. As no significant trends were detected by repeated-measures ANOVA, the ANOVA described above was utilized because of the many assumptions associated with repeated-measures analyses and the difficulty in meeting them inherent in most data sets.

Because of the size range of sharks used, ANCOVA was used to test the above variables for possible covariation with head length (measured from the tip of the snout to the first gill arch). In cases where the effect of the covariate (head length) was significant, the residuals from the resulting regressions were used in all subsequent analyses, thus removing the confounding effect of head size (the variables that covaried with head length were maximum hyoid depression, maximum buccal expansion, maximum negative head angle, maximum gape angle and minimum lower jaw angle).

To determine whether certain kinematic events lagged significantly behind others, paired, one-tailed *t*-tests were used to compare the timing of those events. For each test, the null hypothesis was that the difference between the timing of two events was not greater than zero (or no difference). Kinematic events were selected *post-hoc* for comparison based on the outcomes of previous analyses.

ANCOVA was used to determine whether there was a relationship between the duration of prey capture (clearly dependent on the number of capture and manipulation bites used in prey capture) and the duration of the holding phase between prey capture and transport (described below). A two-factor ANCOVA was used in which the continuous random factor, prey capture duration, and the fixed factor, prey item size, were tested against the dependent variable, duration of the

holding phase. A full ANCOVA model indicated that there was no interaction among factors to be tested.

The ram-suction index (RSI; Norton and Brainerd, 1993) was used to determine the contributions of ram and suction to a feeding event. By calculating $(D_{\text{predator}} - D_{\text{prey}}) / (D_{\text{predator}} + D_{\text{prey}})$, where D is the distance moved by the predator or the prey, a single value is obtained that characterizes the strike. The resulting ratio ranges between 1 (purely ram) and -1 (purely suction). Values between 1 and -1 reflect strikes that contain a combination of these behaviors. Swellsharks often had to be encouraged to eat by placing the prey quite close to their snouts. Because of possible experimental artifacts, sequences that began with the predator less than 1 cm from the prey item were analyzed separately from those in which the predator was farther away (meant to simulate a strike under more natural conditions). Starting positions of both the predator and the prey were determined at time zero (as defined for prey capture), and the change in position or distance traveled (D) by each was noted when the prey item first entered the mouth. Two-factor ANOVA was used to compare RSI values among prey item sizes (fixed factor) and strike distances (fixed factor) during prey capture.

Results

Prey capture

Prey capture in swellsharks generally consisted of a ram-

dominated capture bite in which the prey item remained relatively stationary during prey capture while the shark moved forward to overtake it (Fig. 3). In most cases, a stationary shark initiated a locomotory undulatory wave and accelerated its body along the bottom of the tank towards the prey item. As described above, food sometimes had to be presented quite close to the snout of the shark in order to initiate a feeding response (see 'starting distance' in Table 1), although even prey presented at close range (less than 1 cm) resulted in some forward locomotion by the sharks. Even for captures that were initiated from a distance greater than 1 cm, mouth opening did not begin until the shark was close to the prey item (Table 1) and was coupled with a reduced head angle (head depression). At this point, the shark often swam with its mouth opened maximally (gape angle sometimes exceeding 90° ; Table 1) until the upper jaw was positioned directly over the prey item. As a result of this movement, in some feeding events the lower jaw actually contacted the prey item before mouth closure was initiated. In most prey-capture events, particularly those with the prey item placed very close to the shark's snout, a small amount of suction was detected late in the gape cycle (after mouth closure had been initiated), which lifted the prey item very slightly off the base of the filming tank.

Mouth closure was followed by subsequent biting events (manipulation bites) or by a 'holding phase' prior to prey transport. As might be expected with non-elusive prey, sharks

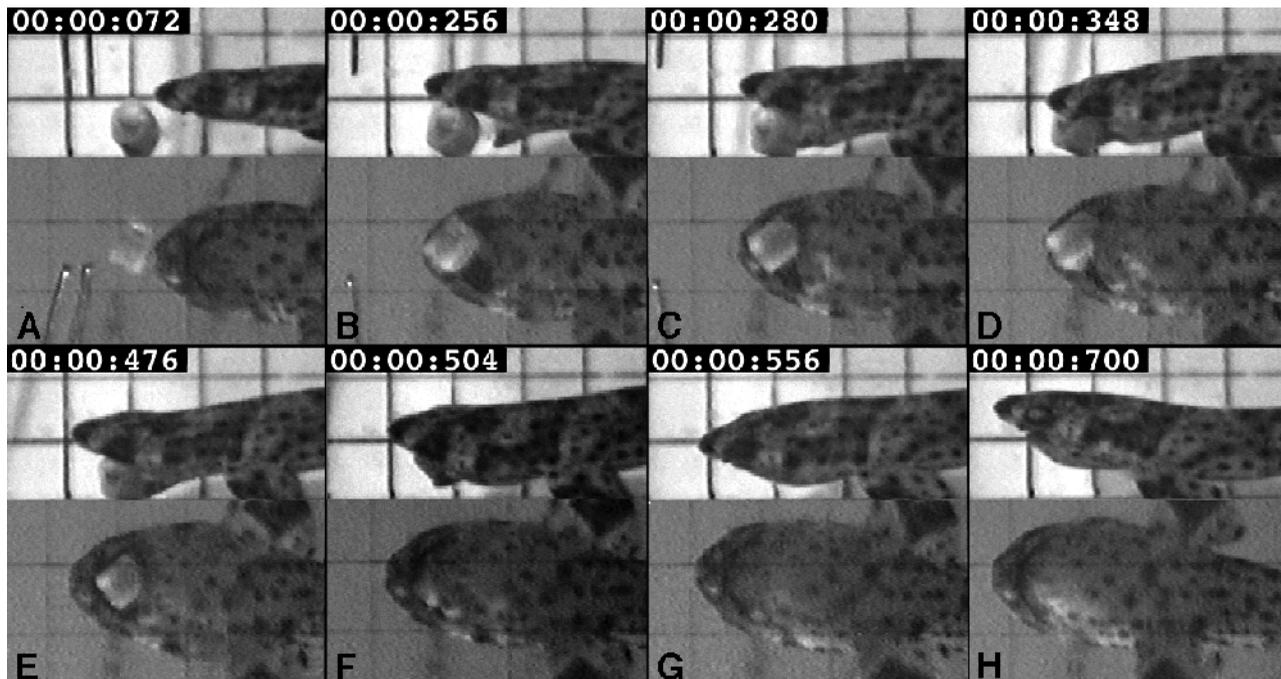


Fig. 3. Composite of video images comprising a successful strike by a swellshark. Numbers in the upper left corner of each image depict a time code (min:s:ms) standardized to time zero (onset of rapid mouth opening) for this sequence, providing an indication of the relative speed of this feeding event. The grid in the background has 2 cm \times 2 cm squares. Frames A–D represent prey capture; mouth opening begins in A, maximum gape angle is reached in B, and hyoid protrusion is evident by C. Notice that the prey item maintains the same position, whereas the shark changes its position to overtake the prey. The bite is complete in D, and the shark has entered the holding phase described in the text. In E, transport is initiated, the mouth opens again and the prey is taken into the mouth (F). In G, the mouth is closed, and the ventral surface of the shark's branchial region is expanded by the water taken in during prey transport (buccal expansion). This bulge has moved anteriorly and has started to exit the mouth in H.

Table 1. Grand means of the 13 variables analyzed for prey capture and transport for all strikes (separated according to prey size) across all individuals, plus four additional variables pertaining only to prey capture

Variable	Capture		Transport	
	Small prey	Large prey	Small prey	Large prey
Maximum upper jaw protrusion (cm)	0.242 (0.074)	0.282 (0.094)	0.400 (0.132)	0.362 (0.158)
Maximum hyoid depression (cm)	1.069 (0.271)	1.178 (0.476)	1.123 (0.281)	1.186 (0.344)
Maximum buccal expansion (cm)	1.099 (0.205)	1.164 (0.458)	1.494 (0.336)	1.498 (0.272)
Starting head angle (degrees)	-13.488 (4.681)	-13.514 (3.572)	-8.162 (3.922)	-5.470 (4.328)
Maximum negative head angle (degrees)	-16.761 (4.294)	-17.893 (3.752)	-16.339 (3.412)	-11.324 (5.850)
Maximum gape angle (degrees)	85.486 (19.578)	83.774 (27.441)	81.792 (13.667)	75.690 (11.557)
Minimum lower jaw angle (degrees)	111.941 (15.147)	112.654 (23.056)	107.395 (11.868)	107.339 (10.544)
Time to maximum negative head angle (s)	0.226 ¹ (0.078)	0.334 ¹ (0.104)	0.148 ⁶ (0.077)	0.140 ⁶ (0.049)
Time to maximum upper jaw protrusion (s)	0.236 ² (0.029)	0.347 ² (0.093)	0.110 ⁵ (0.042)	0.071 ⁵ (0.171)
Time to maximum gape angle (s)	0.306 ³ (0.081)	0.348 ³ (0.095)	0.031 ² (0.007)	0.025 ² (0.006)
Time to maximum negative lower jaw angle (s)	0.305 ⁴ (0.086)	0.353 ⁴ (0.098)	0.027 ¹ (0.005)	0.025 ¹ (0.007)
Time to maximum hyoid depression (s)	0.310 ⁵ (0.063)	0.370 ⁵ (0.094)	0.038 ³ (0.015)	0.035 ³ (0.010)
Time to maximum buccal expansion (s)	0.350 ⁶ (0.078)	0.366 ⁶ (0.086)	0.067 ⁴ (0.013)	0.062 ⁴ (0.013)
Time to bite (s)	0.367 ⁷ (0.076)	0.419 ⁷ (0.114)	–	–
Total number of bites	1.200 (0.694)	1.650 (0.379)	–	–
Hold time (s)	0.293 (0.067)	0.507 (0.144)	–	–
Starting predator-prey distance (cm)*				
Strikes originating from >1 cm	1.627 (0.489)	2.266 (0.923)	–	–
Strikes originating from <1 cm	0.424 (0.205)	0.471 (0.104)	–	–

Standard deviations are given in parentheses. Numbered superscripts indicate the order of occurrence of the timing variables.

*Predator-prey distance at time of mouth opening for strikes in which prey could be offered from farther than 1 cm away from the shark and for those in which the prey had to be brought closer.

rarely failed to capture the prey item, although manipulation bites were frequently observed (Table 1; Fig. 4), presumably functioning to reposition the prey item. On rare occasions, a shark approached a prey item already performing rapid mouth opening and closing. These missed strikes were not analyzed. However, they appeared to be unsuccessful only because of the distance to the prey item.

Additional information can be obtained by examining the kinematic profiles of several of these variables (Fig. 5). During prey capture, the onset of mouth opening (increased gape angle) appeared to precede slightly the start of hyoid depression (Fig. 5). Head angle was highly variable within and among strikes and among individuals; however, the head was generally more elevated during mouth opening and depressed during mouth closure (decreased gape angle; Fig. 5). Maximum hyoid depression appeared to coincide with maximum gape angle; however, across individuals, it occurred significantly later (no individual effect detected by ANOVA, see Table 2; paired one-tailed *t*-test, d.f.=39, *t*=2.159,

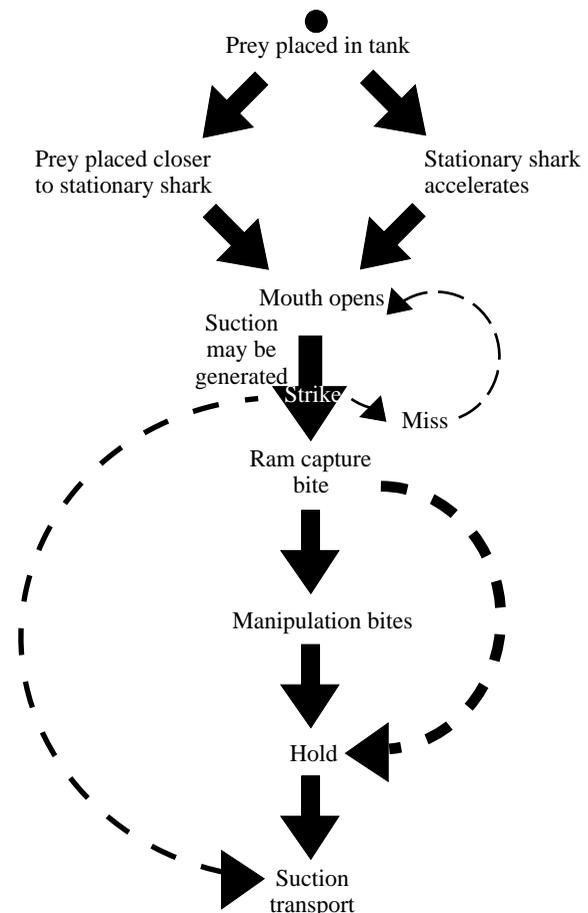


Fig. 4. Schematic flow chart of the behaviors observed during prey capture in swellsharks in response to a food stimulus. The heavy arrows connecting the behaviors represent the most common scenario utilized by the feeding sharks. Dashed lines represent the alternative behaviors observed, the thickness of the line giving an indication of the frequency of occurrence of that particular behavior in the behavioral series. Note that a small proportion of strikes were recorded in which the prey item was taken directly into the mouth without a capture bite.

$P=0.0399$). Maximum buccal expansion, replicating the pattern of movement of the hyoid, occurred later than maximum hyoid depression (no individual effect detected by ANOVA, see Table 2; paired one-tailed t -test, $d.f.=39$, $t=2.159$, $P=0.0371$). The hyoid and the buccal (branchial basket) region could be seen both depressing and retracting (moving posteriorly) in video footage. The kinematic values plotted in Fig. 5 encompass both of these movements. Examination of data on dorsoventral hyoid and buccal movement alone indicated that both depression and retraction are important components of hyoid movement and buccal expansion, with retraction occurring slightly after depression (Fig. 6). Results from a single strike are presented in Fig. 6 as they identify subtle differences in timing that are lost in a mean kinematic profile. Generally, movement of the hyoid and buccal region appeared to be strongly linked to the occurrence of suction generated late into the gape cycle.

Upper jaw protrusion, although small, was directed primarily ventrally (relative to the snout; Fig. 6). This ventrally directed movement has been referred to previously as both protraction and depression in the literature, but will be referred to only as depression here. Little anterior movement (more properly termed protraction) of the jaw away from the skull was detected (Fig. 6). Jaw depression is more evident in the kinematic profile for a single strike (Fig. 6), as the subtle movements of the upper jaw are masked by a mean kinematic profile (see Fig. 5).

Head depth at both the first gill arch and the pectoral fin insertion increased at approximately the same time as head angle began to decrease (albeit slightly) again. Hyoid depression and buccal expansion remained relatively constant throughout this period of increased head depth until gape angle reached a minimum (this was greater than zero as the prey item was held in the teeth). Although this pattern was sometimes repeated during subsequent bites (manipulation bites) on the prey item, a minimum gape angle was eventually reached and held constant for a period. This minimum marked the beginning of the holding phase.

All sharks eventually entered a holding phase if a bite was

used to capture the prey item. During the holding phase, sharks remained relatively motionless except that the snout was lifted such that the entire anterior portion of the body lifted and rotated posteriorly, and the sharks sat propped up on their pectoral fins (not visible in Fig. 3). Often, the hyoid remained depressed throughout this phase. Although the holding phase is not included in Figs 5 and 6, the final positions of each of the variables (with the obvious exception of head angle) are similar to their starting position in the prey-transport phase

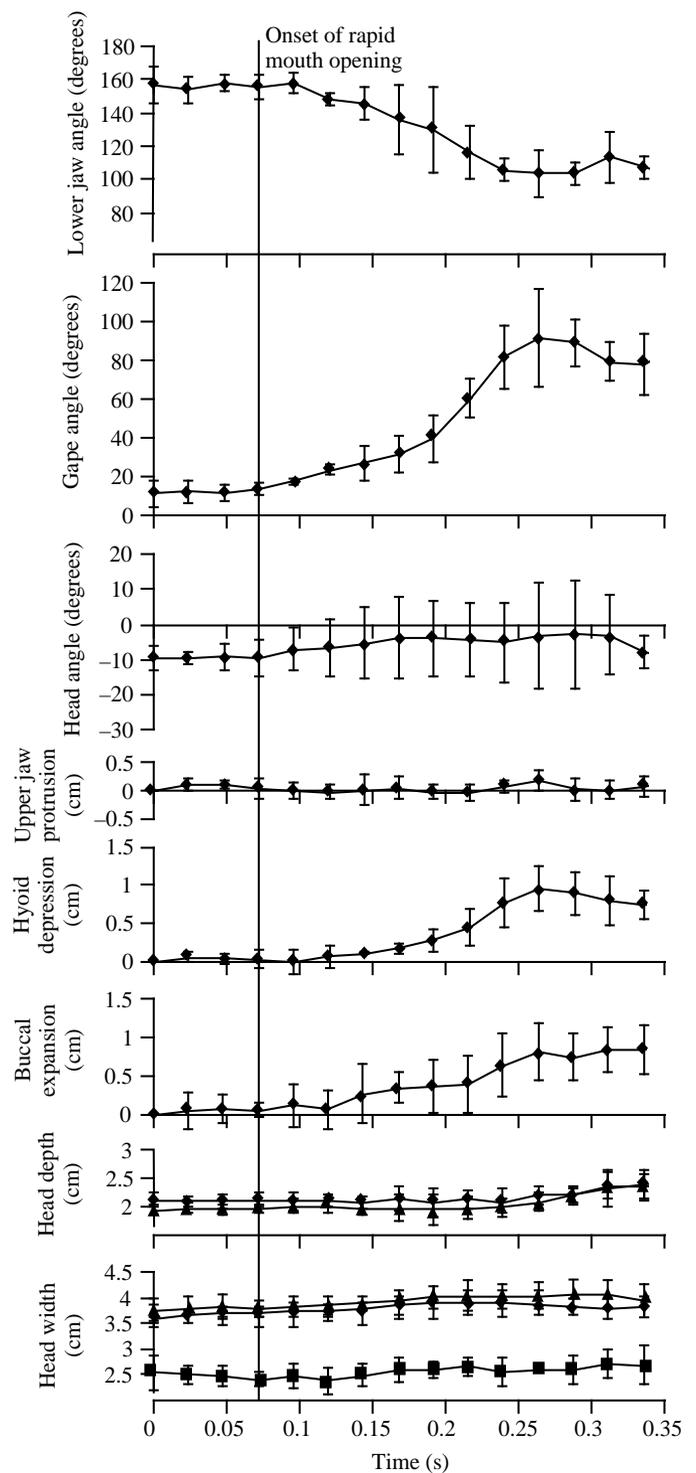


Fig. 5. Kinematic plots of selected variables from those digitized for a single representative individual (23.6 cm, female) capturing small prey items. Values are means \pm s.d. for four strikes (first bite). For clarity, sampling rate has been reduced to 24 ms. The onset of rapid mouth opening is indicated by the vertical line (frame A in Fig. 3), time zero is three increments (0.072 s) prior to the onset of rapid mouth opening. Notice that changes do occur in several of the kinematic variables prior to the onset of rapid mouth opening. In the plot of head depth, triangles (\blacktriangle) represent the depth measured at the first gill, and diamonds (\blacklozenge) are the depth measured at the point of pectoral fin insertion (see Fig. 2B). Similarly, in the plot of head width, squares (\blacksquare) are the jaw width, diamonds (\blacklozenge) are the width measured at the Meckel's cartilages and triangles (\blacktriangle) represent the width measured at the first gill. Head width at the fin insertion point is not shown, as these values could not be distinguished visually from those measured at the first gill (\blacktriangle). Note that additional bites followed for some strikes.

Table 2. Results of univariate analyses (ANOVA) of 13 variables associated with both prey capture and transport (phase) and prey item size

Variable	Individual effect		Prey item size effect		Phase effect	
	$F_{4,55}$	P	$F_{1,4}$	P	$F_{1,4}$	P
Maximum upper jaw protrusion (cm)	3.306	0.0169	0.171	0.7001	5.788	0.0739
Maximum hyoid depression (cm)	42.698	<0.0001*	0.065	0.8115	0.064	0.8130
Maximum buccal expansion (cm)	47.270	<0.0001*	0.075	0.7975	0.027	0.8784
Starting head angle (degrees)	1.526	0.2074	3.514	0.1341	67.569	0.0012*
Maximum negative head angle (degrees)	2.573	0.0477	0.019	0.8971	0.959	0.3829
Maximum gape angle (degrees)	3.069	0.0236	0.939	0.3873	0.011	0.9214
Minimum lower jaw angle (degrees)†	3.962	0.0068	0.111	0.7554	0.024	0.8836
Time to maximum negative head angle (s)	0.294	0.8806	0.629	0.4722	0.190	0.6856
Time to maximum upper jaw protrusion (s)	0.458	0.7661	0.064	0.8132	11.772	0.0265
Time to maximum gape angle (s)	1.488	0.2183	0.933	0.3887	117.204	0.0004*
Time to maximum negative lower jaw angle (s)	1.607	0.1856	1.337	0.3119	105.888	0.0005*
Time to maximum hyoid depression (s)	1.124	0.3548	0.890	0.3988	138.894	0.0003*
Time to maximum buccal expansion (s)	1.879	0.1272	0.048	0.8366	86.597	0.0007*

F -ratios and P -values are given. According to the Bonferroni correction method, P -values of less than 0.0038 are considered significant at the 0.05 probability level and are marked by asterisks.

†Variable for which a significant interaction was detected: individual \times phase interaction; $F_{4,55}=4.432$, $P=0.0035$.

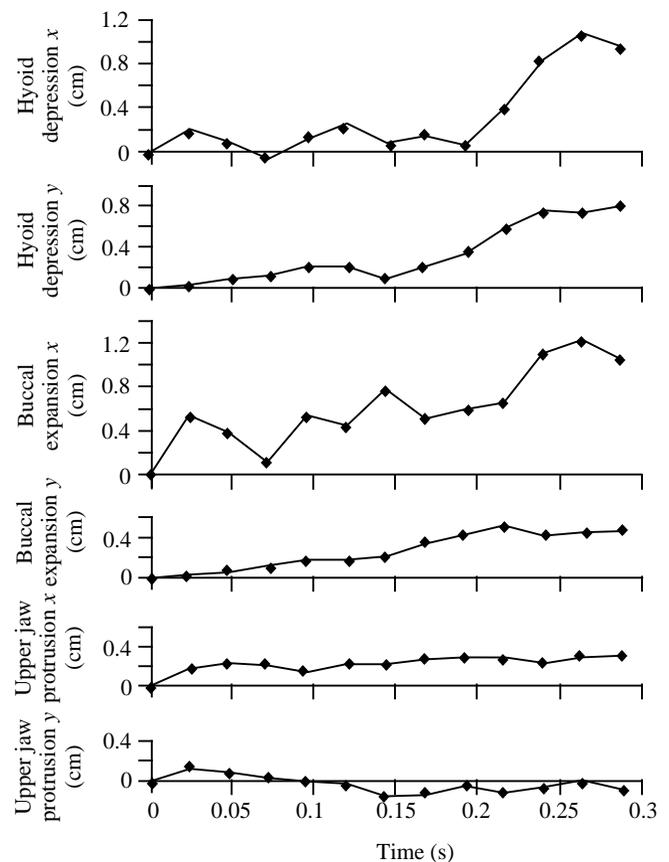
(Fig. 7). Re-opening of the mouth signified the initiation of prey transport. ANCOVA indicated that the duration of the holding phase covaried with the total time for prey capture and manipulation ($F_{1,32}=4.218$, $P=0.0482$; Fig. 8).

Prey transport

Following the holding phase, the prey item was taken into the pharynx by suction, although in some feeding events sharks were still moving forward due to the momentum of the ram capture event (see Fig. 3). For all strikes combined, the mouth opened significantly more quickly during transport than during prey capture (see Tables 1, 2). Maximum upper jaw protrusion did not occur significantly earlier during transport in an absolute sense, but it occurred after maximum gape angle rather than before it as during capture (Table 1). Gape angle increased only slightly to allow passage of the prey item into the oral cavity (see Fig. 7; 0–0.025 ms) as the prey item was already being held in the teeth. During this transition, however, the lower jaw angle also increased (as it moved towards the upper jaw); a movement apparently compensated for by the slightly increased angle of the head from its already elevated

starting position. Maximum gape angle occurred at the same time as maximum hyoid depression (see Table 1; paired one-tailed t -test, d.f.=39, $t=5.918$, $P<0.0526$). Maximum buccal expansion was observed after maximum hyoid depression (paired one-tailed t -test, d.f.=39, $t=5.918$, $P<0.0001$) during

Fig. 6. Kinematic plots of selected variables for a single strike from the same representative individual as shown in Fig. 5 capturing a small prey item. The displacements of the variables in two dimensions are shown; thus, protraction/retraction (x -dimension; anteroposterior movement) and depression (y -dimension; dorsoventral movement) are depicted as separate kinematic events. Note the small amount of upper jaw protrusion in the x -dimension (protraction), and the more prominent movement of the upper jaw in the y -dimension (depression). This particular sequence began with the jaw already depressed slightly; thus, the negative values for upper jaw protrusion occur later into the strike. The maximum depression of the upper jaw is approximately 0.4 cm.



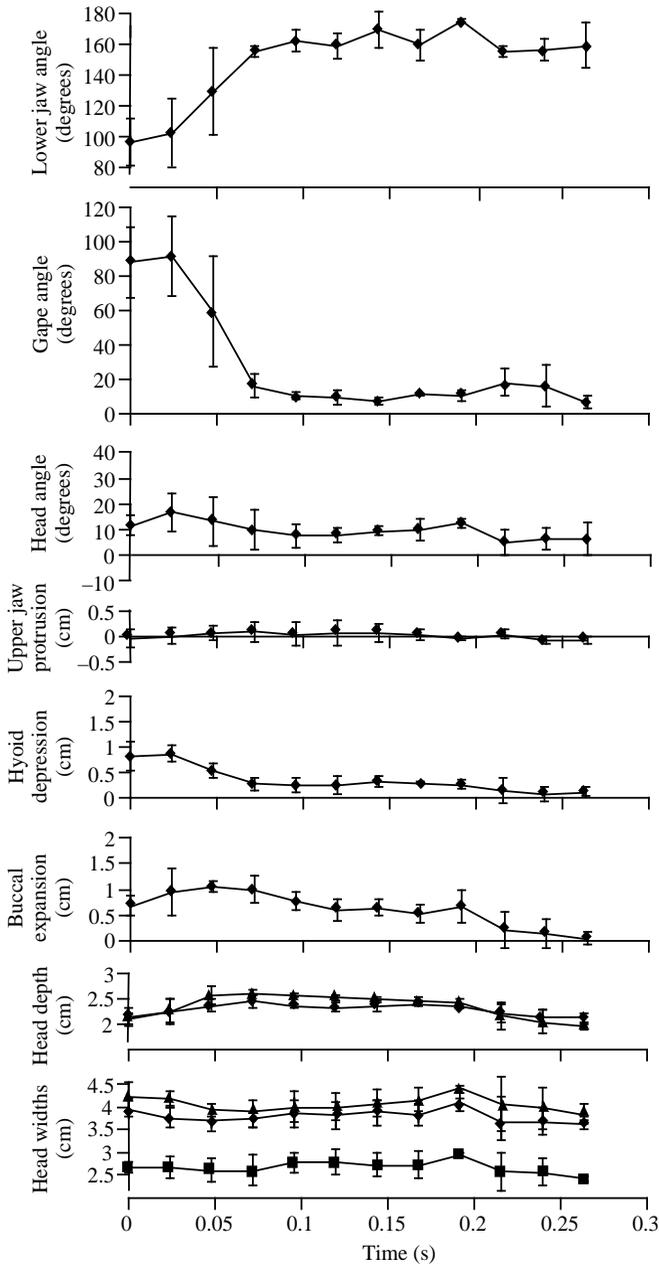


Fig. 7. Kinematic plots of selected variables for the same representative individual shown in Fig. 5 transporting small prey items. Plots have been standardized to begin at time zero for prey transport, a time that occurs slightly before frame E in Fig. 3. Values are means \pm S.D. for four transport events. For clarity, sampling rate has been reduced to 24 ms (0.024 s). In the plot of head depth, triangles (\blacktriangle) represent the depth at the first gill and diamonds (\blacklozenge) are the depth measured at the point of pectoral fin insertion. In the plot of head width, squares (\blacksquare) are the jaw width, diamonds (\blacklozenge) are the width at the Meckel's cartilages, and triangles (\blacktriangle) are the width at the first gill. As in Fig. 5, head width at the point of fin insertion has been omitted for clarity.

transport. Hyoid depression occurred rapidly, followed by rapid buccal expansion (Tables 1, 2). Although these events occur significantly earlier relative to time zero during transport

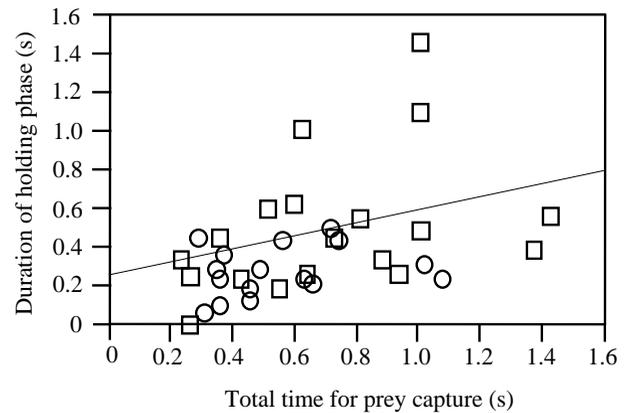


Fig. 8. The relationship between the duration of the holding phase and the total time for prey capture (directly dependent on the number of capture plus manipulation bites in any given feeding event). In each plot, open circles (\circ) represent small prey items and open squares (\square) represent large prey items. A prey item size effect was not detected; therefore, a single regression line is shown ($y=0.16+0.382x$, $r^2=0.166$, $P=0.0152$).

than during capture (see Table 2), the difference in mouth opening time (time to maximum gape angle) offsets the absolute time difference, i.e. the time between maximum gape and maximum hyoid depression is nearly identical for both capture and transport (see Table 1). Ventral buccal expansion could be observed to move posteriorly, rebound anteriorly and then disappear as the mouth began to open again (Fig. 7). Dye experiments confirmed that this expansion was an accurate indicator of the presence and movement of water in the oral cavity (see below). This expansion was more prominent during transport than during prey capture (see Figs 5, 7) and appears to be related to an additional increase (beyond the maximum seen in prey capture) in head depth that occurred during transport mouth closure (see Figs 5, 7). These changes suggest that buccal expansion may be linked to the generation of a strong suction event. Changes in head depth during transport parallel the changes in head angle during this phase (Fig. 7).

A curious behavior commonly observed in swellsharks during prey transport was repeated vertical lunging off the tank bottom. Measurements of the height of the center of the pectoral fins off the tank bottom indicated that sharks regularly achieved vertical distances of 2 cm off the bottom. This measurement was different from the simple lifting of the ventral region off the bottom during snout lifting (described above), which rarely lifted the ventral body surface at the center of the pectoral fins more than 0.5 cm off the tank bottom. Scrutiny of the video tapes indicated that this lunging behavior appeared to be the result of pushing exclusively with the pectoral fins while the body was kept horizontal. It is not known what role this behavior plays during prey transport.

Bidirectional flow

Video images of swellsharks feeding on dye-perfused prey items confirmed that the pattern of buccal expansion reflected

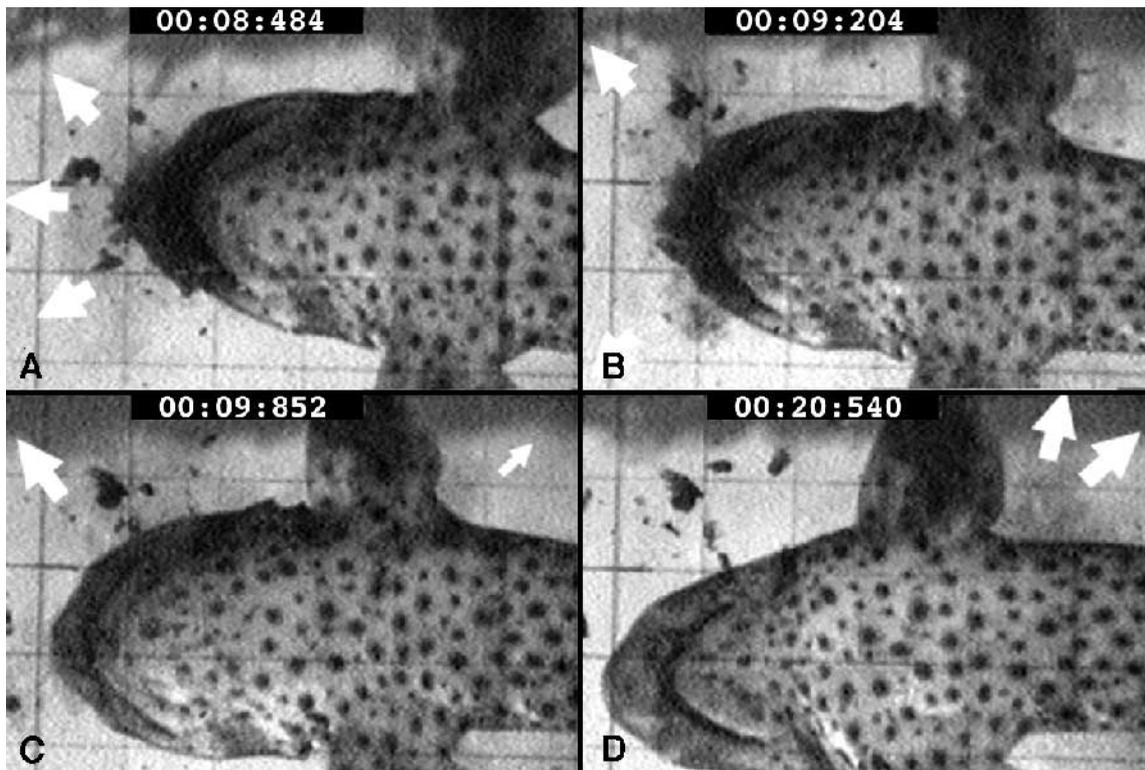


Fig. 9. Composite of images from a successful strike on a piece of fish soaked with food coloring. The time code (min:s:ms) has not been standardized since the times shown do not correspond directly with those in previous figures. In A, mouth closure is nearly complete, and dye can be seen exiting the mouth. In B, the shark has just completed a second bite and is entering the holding phase. At this time, the largest quantity of dye exits the mouth. In C, just prior to the initiation of prey transport, a small amount of dye can be seen exiting the gills. The majority of the dye that exits the gills is not seen until D, well after the completion of prey transport and more than 10 s later than C.

the net movement of water into and out of the mouth (Fig. 9) and that bidirectional flow occurs in swellsharks. During both capture and transport, as buccal volume decreased, a prominent stream of dye was ejected from the mouth, often as two distinct jets at an angle of 45° to the midline of the shark. Distinct dye streams were not observed exiting the gills until several seconds (Fig. 9) after the mouth had closed following prey transport.

During mouth closure in prey transport, a shark sometimes rotated its head ventrally to give a head angle smaller than that at the start of prey capture and resulting in apparent compression of the gills (see Fig. 9D, this position is still evident even at this time in the strike). The presence of this compression appears to be correlated with the ability to pass water out of the gills unidirectionally; however, the mechanism by which this is achieved and the actual function of this apparent gill compression are unknown.

Careful examination of the video sequences revealed that, even when such compression was absent during a transport event, the gills did not open to any noticeable degree until after the mouth had re-opened and the water had exited anteriorly (as indicated by a large dye stream). During gill opening, little dye was seen exiting the gills, further indicating that a majority of the water taken in during feeding had already been expelled from the open mouth.

Prey-size effect

The general kinematic patterns described above for prey capture were found for both prey sizes offered to the sharks. ANOVAs performed on capture and transport variables detected significant individual and phase effects (see Table 2); however, the effect of prey size was never significant. Such results indicate that the variation among and even within individuals is greater than any variation in prey capture or transport kinematics specifically caused by changing prey item size.

ANCOVA indicated that, although the duration of the holding phase covaried with the total time for prey capture ($F_{1,32}=4.218$, $P=0.0482$; see Fig. 8), there was no significant effect of prey size ($F_{1,1}=0.021$, $P=0.9079$).

Prey capture mode also did not change with prey item size, as indicated by the RSI values calculated for both predator-prey distances ($F_{1,23}=1.216$, $P=0.2815$; Fig. 10). However, significant decreases were detected in the contribution of suction with increasing strike distance ($F_{1,23}=36.336$, $P<0.0001$).

Discussion

Prey capture

The prey-capture behaviors described here for the

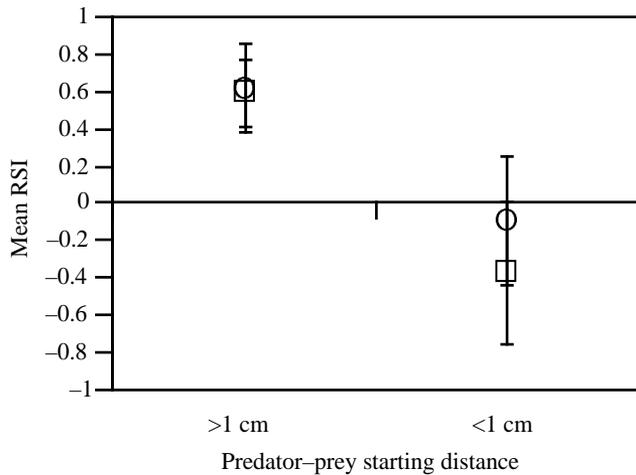


Fig. 10. Ram-suction index (RSI) values for strikes initiated at a distance greater than 1 cm from the prey item ($N=15$; 10 for small prey, 5 for large prey) and those starting closer than 1 cm ($N=12$; 7 for small prey, 5 for large prey). In addition, there were 13 strikes (not shown) which happened too quickly to ensure that the prey item was released from the forceps in time to prevent interference with prey movements (D_{prey}) used in calculating RSI values. Values are means \pm s.d. for all strikes. Open circles (○) represent small prey items and open squares (□) represent large prey items.

swellshark can be qualitatively contrasted with what appears to be a standard carchariform feeding pattern in terms of the basic kinematic pattern used (Frazzetta and Prange, 1987; Motta *et al.* 1991; Frazzetta, 1994). Mouth opening is achieved by head angle elevation and lower jaw depression (jaw depression may follow head elevation by up to 0.050; Frazzetta and Prange, 1987). Motta *et al.* (1991) noted that, in weaker bites, head angle elevation can be absent. Mouth closure is initiated by lower jaw elevation and then supplemented by head angle depression and upper jaw protrusion (although upper jaw protrusion may also be observed during lower jaw depression on occasion; Frazzetta, 1994). Mouth closure is generally completed with the added contribution of maximum upper jaw protrusion. Tricas and McCosker (1984) noted that this pattern was also used by the white shark (*Carcharodon carcharias*), although the head angle was generally not depressed until the feeding bout had ended (often after all manipulation bites had occurred). Mouth closure therefore occurs in the white shark by lower jaw elevation and by upper jaw protrusion only. In swellsharks, as a prey item is approached, the head may be rotated dorsally while the lower jaw is depressed. The capture bite is achieved primarily through lower jaw elevation, although simultaneous head angle depression does sometimes occur. Upper jaw protrusion (either depression or protraction) does not appear to contribute to prey capture.

Theories about the benefits of upper jaw protrusion are widespread in the literature. Jaw protrusion may assist in producing a forceful bite, possibly even increasing the rate of jaw closure (Moss, 1972; Tricas and McCosker, 1984; Frazzetta and Prange, 1987). Protrusion may assist in directing

currents into the mouth in suction feeding (Moss, 1972) or may assist in performing precise biting or picking behaviors (Moss, 1972). Protrusion, along with head depression, may even assist in aligning the teeth precisely (see also Frazzetta, 1994; Wu, 1995).

It is reasonable to assume that protrusion is more prominent in the larger sharks studied previously. Protrusion appears to be correlated with the movement of the distal end of the hyomandibula antero-ventrally (Frazzetta, 1994). This hyomandibular movement is thought to control displacement of the jaws at their articulation point. However, obvious expansion (rotation outwards) of the jaw cartilages, which should occur during the bite, partially as a result of this hyomandibular movement, was not observed for any individual in the present study. Frazzetta and Prange (1987) noted that protrusion was not always observed even in larger individuals (*Carcharinus acronotus*, *C. limbatus* and *Negaprion brevirostris*), and they attribute the lack of such activity in successful strikes to prey item size (smaller prey). Motta and Wilga (1995) note that in a freshly killed carchariform (*N. brevirostris*) jaw opening without upper jaw protrusion or protraction is accomplished by depression of the lower jaw and hyoid elements without hyomandibular kinesis.

Protrusion, and specifically protraction, may not be as useful to the swellshark as is postulated for other elasmobranchs. Tooth alignment may not be necessary as the teeth are arranged in rows on the lower jaw such that they protrude slightly out of the mouth; thus, they are at an angle to meet precisely the inwardly inclined teeth on the upper jaw. Picking-type feeding behaviors have not been observed in this species. Swellsharks in captivity have been observed to use suction to pull prey items out of otherwise inaccessible corners and crevices (L. A. Ferry-Graham, personal observation), although unfortunately this behavior was not recorded in the present experiments or others meant specifically to induce it. It is possible that jaw protraction has a more prominent role during suction feeding in the swellshark. Suction made only a small contribution to feeding in the present set of experiments.

The generation of a small amount of suction during capture as a separate kinematic event from the ram prey-capture event, as implied by the significantly delayed occurrence of buccal expansion, is a unique finding. Frazzetta and Prange (1987) note specifically that, in their feeding experiments in which fish (prey) were suspended in the water column, the prey item was not taken into the mouth by suction. They do suggest, however, that suction may be more important when feeding on the bottom. This suggestion is supported by the present study, as portions of the strike were characteristic of a suction feeding event. RSI values of approximately 0.60 were calculated for both small and large prey items, indicating the presence of a large ram component to the strike, but also suggesting a contribution from suction. The negative values calculated for closer strikes appear to indicate an even larger contribution of suction; however, these results do not indicate that more absolute suction is produced. The shark does not have to move as far to obtain the prey item (D_{predator} is lower); thus, the RSI

is lower if D_{prey} remains the same. It is likely that a similar amount of suction is generated in strikes that originate from both distances, but this is masked by the movement of the predator in the calculation of the former RSI ratio (RSI=0.60). The data from closer strikes are useful because they show that the contribution of suction to prey capture, although real, is actually quite small. If swellsharks were strong suction feeders, they theoretically would not have to move at all to capture a prey item offered at close range. Yet, during strikes at close range, their movements still nearly equal the prey's total movement during capture, as indicated by RSI ratios near zero.

The kinematic pattern of expansion and depression described here for swellsharks suggests that there is a wave of enlargement of the head and oral cavity that moves posteriorly over time and which may possibly facilitate the generation of suction late in prey capture. Evidence for this comes from the increase in head thickness over time during transport and from the significantly delayed generation of buccal expansion relative to hyoid depression and maximum gape. This is further supported by the observation that the gills do not open to allow dye to escape prior to mouth reopening during the dye trials, thus allowing for head expansion.

Tricas (1982) provided a preliminary description of swellsharks feeding in the wild and cited two types of prey-capture behavior: gulping and yawning. In the gulping behavior, in response to a prey fish (the blacksmith *Chromis punctipinnis*: Pomacentridae) that approached within 1–5 cm of the mouth, the shark rapidly performed head elevation while depressing the lower jaw, presumably taking the prey item into the mouth by suction. This behavior was extremely rapid, relative to the more passive second behavior pattern (yawning; Tricas, 1982). As the prey fish approaches the shark, the gape angle of the shark is increased (if the fish reverses direction, the gape angle is reduced) until the fish is ultimately captured because it swims or drifts into the open mouth. Although suction has been observed in captive animals (L. A. Ferry-Graham, personal observation), yawning behavior was never observed, even when live prey were offered and a more natural environment was created (small rock caves and tunnels). Tricas (1982) does not describe a behavior similar to the ram-dominated, biting capture events described for the swellsharks used in this study, although this is probably due to the differences between the prey offered (live, tethered blacksmith *versus* pieces of fish). It is probable that swellsharks utilize biting behaviors for less mobile prey and scavenging in the wild, as has been observed for other closely related shark species in the wild or in large (i.e. public aquaria) captive settings (see Tricas and McCosker, 1984; Frazzetta and Prange, 1987).

Prey transport

Prey transport as a separate feature of feeding is poorly described for charchariform sharks. As found previously for teleosts (Gillis and Lauder, 1995), there were distinct kinematic differences between prey capture and transport in the swellsharks studied here. Interestingly, in the swellshark, differences were not found in the maximum displacements or angles of the kinematic variables measured. Maximum gape

angle was statistically similar between capture and transport, as were maximum hyoid depression and maximum negative head angle. Additionally, although transport was a suction-dominated event, and buccal expansion is thought to be related to the generation of suction, maximum buccal expansion was no greater during transport than during ram-dominated prey capture. Maximum upper jaw protrusion showed a tendency to be greater during transport than during capture (although this was not significant), as seen in teleosts (Gillis and Lauder, 1995).

The timing of various kinematic events differs significantly between capture and transport in the swellshark. The mouth was opened more rapidly during prey transport than during prey capture, a pattern also seen in teleost fishes (Gillis and Lauder, 1995) and supported by the limited observations of Frazzetta and Prange (1987). In swellsharks, although occurring at the same absolute time, upper jaw protrusion occurred after maximum gape angle during transport, but before it during capture. As opposed to capture, maximum hyoid depression was not significantly later than maximum gape angle. Gibb (1995), using a suction-feeding teleost fish, found that maximum hyoid depression does not necessarily need to occur later than maximum gape angle for the effective generation of suction as was previously thought (see Reilly and Lauder, 1992, for further discussion). Buccal expansion occurred significantly later relative to maximum hyoid depression in transport, which may be a consequence of reversing the direction of flow of a bolus of water taken in by a suction event.

Bidirectional flow

The most notable event during prey transport was the occurrence of bidirectional water movement into and out of the buccal cavity. Bidirectional flow has been described in several salamanders (Lauder and Shaffer, 1986; Reilly and Lauder, 1992) and turtles (Lauder and Prendergast, 1992). Its occurrence has been correlated with the absence of, or very reduced, gill opening, which prevents water from passing unidirectionally out through the gills. Swellsharks have relatively large gill openings and a well-developed system of buccal pumping during respiration (L. A. Ferry-Graham, personal observation). They can be seen methodically pumping water over the gills prior to a prey-capture event. This 'warm-up period' might allow the shark to taste the food and therefore to decide whether to strike (T. Tricas and D. Nelson, personal communication). Indeed, stationary sharks began actively pumping water over the gills within minutes of the prey being placed in the tank, and then either accelerated to strike or turned and swam away. In contrast, water flow during prey capture and transport was redirected out through the slightly open mouth (open as a result of the presence of the prey held in the teeth after capture, or reopened following transport) and did not pass posteriorly out through the gill openings until well after transport occurred. A key characteristic of a unidirectional flow pattern is the occurrence of water exiting out through the gills posteriorly *before* the mouth has closed (Reilly and Lauder, 1992).

Frazzetta and Prange (1987) cite the repeated flaring of the gill slits during feeding in other Carchariniformes as evidence for the unidirectional passage of water. However, they do note that the observed pattern of gill opening and closing may contribute to the generation of suction. The work of Hughes and Ballintijn (1965) on the dogfish *Scyliorhinus canicula* (Scyliorhinidae) suggests that the gills cannot be opened while food is held in the teeth. Expansion of the branchial basket during respiration is a passive event, mediated by contraction of the adductor mandibulae complex during mouth closure (Hughes and Ballintijn, 1965). Tonic contraction of the adductor mandibulae complex seems to hold the hyoid apparatus and lower jaw in a fixed position, the muscle itself serving as an 'anchor' that is pulled anteriorly to allow expansion of the branchial basket. During passive expansion, the gills are held closed. If contraction of the adductor mandibulae complex is necessary to hold a prey item in the teeth, then it would follow that the branchial basket is being expanded during this time and that the gills are not or cannot be opened during this period. Thus, during prey capture, the only possible route for water to exit the buccal cavity may be through the mouth. Hughes and Ballintijn (1965), however, also note that water is forced out of the gills during normal respiration because the main compressive phase occurs after the mouth has closed, thus preventing bidirectional flow. Why bidirectional flow also occurs during prey-transport events, when the mouth is allowed to close fully, is therefore unclear.

Several parallels can be drawn between the feeding kinematics of salamanders, turtles and swellsharks in which bidirectional flow is known to occur. In the salamanders *Amphiuma tigrinum* (Amphiumidae) and *Cryptobranchus allegheniensis* (Cryptobranchidae), rapid hyoid depression does not begin until near maximum gape. Head angle is strongly depressed (to below the starting value at the initiation of prey capture) during mouth closure, thereby contributing to gape closure. With the hyoid still depressed, the mouth reopens and water can be seen emerging from the mouth (Reilly and Lauder, 1992). In the snapping turtle *Chelydra serpentina*, rapid hyoid depression again does not begin until after the mouth starts to open. Head angle is reduced such that it is the primary contributor to jaw closure. The head begins to bend on the vertebral column ventrally while the lower jaw is still depressing; thus, gape distance is held constant for a period. When the lower jaw begins to reverse direction, it quickly meets the upper jaw, brought into position by the severely reduced head angle. The hyoid remains depressed while the mouth reopens slightly to let water out (Lauder and Prendergast, 1992). In swellsharks, the same patterns were observed: rapid hyoid movement beginning after mouth opening, and prolonged hyoid depression that persisted throughout mouth reopening.

The consequence(s) of these kinematic patterns for the bidirectional flow pattern in swellsharks is uncertain. Reduced head angle and upper jaw protrusion possibly help to close the mouth rapidly, preventing rebounding of the water from taking the prey item back out of the mouth again. Similarly, although maximum hyoid depression did not occur significantly later

than maximum gape angle during prey transport, continued hyoid depression as the mouth begins to close may serve to keep the majority of the water moving posteriorly, thus preventing premature flow-reversal of the bulk of the water mass. Although the expanded condition of the buccal cavity appears to be the relaxed state in terms of the activity of the musculature in that area, it is uncertain whether this expansion is merely a consequence of water being drawn into the mouth (possibly because of hyoid depression) or whether the branchial basket is intentionally expanded (by relaxing of the adductor mandibulae) to draw in water and assist in the production of suction. Reduction of the head angle may result in the compression of the gill arches, as was sometimes observed in feeding swellsharks. The timing of this compression appeared to be related to the ability to pass water out of the gills unidirectionally. Head bending, during which the gills appeared to be compressed, was often observed after mouth closure during prey transport. However, the mechanism and the function of this apparent gill compression are unknown. The timing of gill slit opening during feeding always appeared sporadic compared with the rhythmic pattern observed during respiration. The mechanism by which water is prevented from exiting the gills during feeding remains unclear.

Comparison of kinematic and muscle activity patterns during bidirectional water flow with those during respiration/buccal pumping in the swellshark would aid in understanding the bidirectional water movement pattern and why it might be utilized instead of the unidirectional flow pattern used in respiration. Swellsharks can inflate their body (thought to function as a defense mechanism by which they can wedge themselves into tight caves and crevices; Compagno, 1984) by gulping water into the stomach (L. A. Ferry-Graham, personal observation; Compagno, 1984). It is possible that the unusual water flow pattern during feeding is a consequence of morphological modifications in the Scyliorhinidae allowing for such a defense. Further comparative morphological studies are warranted.

Prey item size

Prey capture often involves multiple bites in Carchariniformes (P. Motta and C. D. Wilga, personal communication); however, captures that lack a bite whereby the prey is completely engulfed in a single event are also well documented (see Frazzetta and Prange, 1987). Frazzetta (1994), however, implies that multiple bites during capture, like those observed in this study, should only occur when the prey item is large, possibly only if the prey is larger than the mouth of the shark. The small items used in this study (half the mouth diameter) fall into the range described by Frazzetta (1994) for which a shark should swim over the item and engulf it either by ram or by suction. Similarly, the large items used in this study (equal to the mouth diameter) should require only one or two bites to secure them (equivalent to the medium prey items of Frazzetta, 1994) before transport into the mouth. Multiple bites (up to five), rather than a purely ram- or suction-dominated event, were observed in this study, and the average

number of bites used appears similar between prey sizes (1–2 bites; see Table 1). Similarly, the proportional contributions of ram and suction to the strikes were unaffected by prey size (see Fig. 10). Tricas (1982) and personal observations (L. A. Ferry-Graham) suggest that swellsharks are capable of modulating prey-capture mode; however, the lack of a prey size effect here implies that the sharks did not perceive the prey offered to them as different and thus requiring different prey-capture techniques.

The ram-suction index indicated that suction made a similar contribution to capture for both large and small prey items. The ram-suction index categorizes the mode of prey capture used by the predator on the basis of the effect of the predator upon the prey item. However, this ratio measures the *movements* of the prey item and the predator. Larger prey items will require the application of more suction to move them. RSI ratios indicated that the distance that the prey item moved relative to the distance moved by the sharks was the same between prey sizes, suggesting that the sharks might have had to generate a greater volume of suction to capture and transport large prey with the same resulting movement as small prey items (increased velocity of suction would be reflected in the distance moved by the prey item). It is not known whether the difference in the amount of force required to move a 1 cm piece of fish *versus* a 2 cm piece is significant to a feeding shark.

The similarity in the kinematic patterns between prey sizes (for both prey capture and transport) was unexpected, but implies that a greater amount of suction was not produced by the sharks in response to larger prey, as this should be reflected in the maximum displacements of the kinematic variables. There was variation in the timing and displacement of the kinematic variables investigated (see Table 1). However, systematic changes did not occur in response to increasing prey item size. Rather, a range of timing and displacements was recorded for sharks feeding on both sizes of prey items. It is therefore likely that the pattern observed was adequate for both sizes of prey offered and that no compensation or change in the kinematic pattern was necessary (see also Wainwright and Lauder, 1986, for similar findings for teleosts). The findings of Tricas (1982) suggest that changing prey item *type* might result in differences in the kinematic pattern used. While personal observations (L. A. Ferry-Graham) indicate that prey items larger than those used in this study induce a series of head shakes, as the shark tries to remove small pieces for transport (as occurs in other Carchariniformes, see Frazzetta and Prange, 1987; Frazzetta, 1994), the findings outlined in this paper suggest that the same kinematic patterns ultimately will be utilized to capture and transport a prey piece of a similar type to those used here.

In summary, a generalized pattern of feeding exists in swellsharks that typically consists of a ram-dominated capture bite, often followed by additional manipulation bites, a holding phase and rapid suction transport. The small amount of suction generated during prey capture and the suction generated during transport appear to be facilitated by a wave of expansion that passes posteriorly along the head. Suction transport and, to a

lesser degree, prey capture are unique among the other elasmobranchs studied in that water flow is bidirectional. Although the pattern of feeding was variable, there was no evidence for an influence of prey size on kinematics or prey-capture mode. This suggests that prey capture and transport are not modulated by the swellshark in response to prey-item size.

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