

EFFECTS OF PREY SIZE AND MOBILITY ON PREY-CAPTURE KINEMATICS IN LEOPARD SHARKS *TRIAKIS SEMIFASCIATA*

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Summary

Recent work on teleosts suggests that attack behaviors or kinematics may be modified by a predator on the basis of the size of the prey or the ability of the prey to sense predators and escape capture (elusivity). Sharks are generally presumed to be highly visual predators; thus, it is reasonable to expect that they might also be capable of such behavioral modulation. In this study, I investigated the effect of prey item size and type on prey-capture behavior in leopard sharks (*Triakis semifasciata*) that had been acclimated to feeding in the laboratory. Using high-speed video, sharks were filmed feeding on two sizes of the same prey item (thawed shrimp pieces) and two potentially more elusive prey items (live earthworms and live mud shrimp). In leopard sharks, little effect of prey elusivity was found for kinematic variables during prey capture. However, the large proportion of successful captures of the

live prey suggests that they did not prove to be truly elusive prey items for the leopard shark. There were significant size effects on prey-capture kinematics, with the larger non-elusive items inducing greater head expansion during prey capture. Ram-suction index values also indicated that strikes on large, non-elusive prey had a significantly larger suction component than strikes on similar small prey items. This finding is interesting given that the two sizes of non-elusive prey item offered no differential challenge in terms of a performance consequence (reduced capture success).

Key words: feeding kinematics, behaviour, prey capture, elusivity, suction feeding, morphology, elasmobranch, leopard shark, *Triakis semifasciata*.

Introduction

Predicting ecological interactions has been a long-standing goal of ecomorphologists (Motta *et al.* 1995). However, it is generally recognized that the ecomorphological paradigm, a popular theory in the past which stated that the ecological role of an organism can be accurately predicted given a quantification of its morphology, no longer holds true for a wide variety of cases (Liem, 1993). It is clear that morphology may limit ecological interactions or, to use a classic example, limit the items from a given habitat that an organism is capable of utilizing. Morphology alone, however, is not sufficient for determining which items will actually be utilized (Liem, 1993).

Thus, a goal of ecomorphologists has recently been refined to determining which morphological variables might be predictors of ecological interactions such as predator-prey relationships (Wainwright and Reilly, 1993). The terms 'morphology' and 'ecology' in this context are rather imprecise and often encompass measures of physiology, biochemistry and behavior (Motta *et al.* 1995). Recent work on prey capture in teleost fishes suggests that behavior may be just such a predictor (see, for example, Nemeth, 1997).

Quantification of the behaviors elicited during feeding

includes an understanding of the different kinds of behaviors that might be used in different feeding situations. The literature on teleost fishes predicts that large-mouthed predators should use behaviors that maximize the effect of mouth size, namely ram-feeding behaviors in which the predator takes the prey item into the oral cavity by opening the jaws and overtaking the item (Norton and Brainerd, 1993). In contrast, small-mouthed predators should be better at generating suction during feeding, since the gape in these species is generally much smaller than the region expanded posterior to the mouth (Norton and Brainerd, 1993; Cook, 1996). For those fishes that have been studied, small-mouthed species have a lower success rate than large-mouthed species when attempting to capture elusive prey (Norton, 1991), and their diets reflect this (Norton, 1995). Interestingly, at least one small-mouthed teleost species will switch to ram-feeding in response to elusive prey, thereby increasing the number of successful attacks, although not to the degree of success found in large-mouthed ram-feeders (Norton, 1991). Nemeth (1997) recently proposed an addition to these generalizations: predators with intermediate mouth sizes are less likely to employ one particular feeding method over

another because their lack of specialization, in terms of mouth size, does not constrain them to a certain mode of attack. The ability to utilize different behaviors given a distinct ecological challenge is termed modulation (see Liem, 1978). As predicted, Nemeth (1997) found that increasing prey elusivity induced an increased use of ram-feeding behaviors by the teleost species studied.

Whether such predictions hold true for the other major clade of fishes, elasmobranchs, remains to be tested. Sharks, in general, are highly visual predators when feeding on prey at close range. They can distinguish between shape and brightness at least as well as teleosts (Gruber and Cohen, 1978) and, thus, it is reasonable to assume that different sizes or types of prey might elicit different prey-capture behaviors, as has been documented in teleosts, or modulation of prey-capture behaviors. In addition, sharks possess a very different cranial morphology compared with the ray-finned fishes. The jaw movements that result are complex and are probably most well understood in sharks of the order Carcharhiniformes. These sharks have been the focus of work by Moss (1972, 1977) and Motta *et al.* (1991, 1997). The degree to which the described patterns of jaw movement can be modified by carcharhiniform sharks in response to the prey has been only briefly investigated by Frazzetta and Prange (1987) and Ferry-Graham (1997).

The present study was undertaken to investigate prey-capture behaviors in juvenile leopard sharks (*Triakis semifasciata* Girard) and to determine the degree to which modulation is present in this carcharhiniform shark. In this study, both prey size and prey type effects were investigated to determine the range of potential modulation. Different prey types were offered to present potentially differing degrees of prey elusivity to the sharks. Thus, in addition to describing the basic kinematic patterns of prey capture in the leopard shark, the specific questions addressed were: (1) do leopard sharks modulate prey-capture behaviors in response to prey items of different sizes, and (2) do leopard sharks modulate prey-capture behaviors in response to differing prey types?

Materials and methods

Specimens

The four leopard sharks (*Triakis semifasciata* Girard) (mean total length, TL 38.1 cm; range 36.4–39.6 cm) used in this study were collected using hook and line from the surf zone off the Santa Monica Pier, Santa Monica, California, USA. Leopard sharks were chosen for this study for several reasons. First, they are members of the Carcharhiniformes; thus, this study may yield important evolutionary information when added to recent studies on other members of the order (see Motta *et al.* 1991, 1997; Motta and Wilga, 1995; Ferry-Graham, 1997, 1998; Wilga, 1997). Leopard sharks survive extremely well in captivity and feed reliably. In contrast to other shark species, their diet has been studied directly and it is known that they consume a diverse range of prey items in the wild (Russo, 1975; Talent, 1976). Leopard sharks readily accepted both the dead and live items used in this experiment.

Multiple sizes of dead and live prey were presented to the sharks to determine the potential for modulation of prey-capture behavior. Pieces of thawed shrimp (Caridea) were chosen as non-elusive prey items because they could be cut into precise sizes and so that feeding behaviors might be compared directly with those described in other studies (Ferry-Graham, 1997). Pieces approximately equal to the mouth diameter (range 2.4–2.5 cm for all individuals) and half the mouth diameter were fed to the sharks. Shrimp pieces represent items that might naturally be scavenged by feeding leopard sharks (Russo, 1975). Sections of live earthworms, *Lumbricus terrestris* (Annelida), 1–2 cm in length were offered as a prey item that was slightly more difficult to capture because of their mobility and to mimic clam siphons, since small clams regularly occur in the diet of the leopard shark (Talent, 1976). Sections were freshly cut prior to presentation and, if they stopped wriggling during the experiment, they were replaced. Mud shrimp, *Callinassa pacifica* (Thalassinidea), also occur in the natural diet of the leopard shark and were offered live to provide a more elusive prey item for comparison (Russo, 1975). Mud shrimp were approximately 1 cm in carapace diameter and 4 cm from the anterior margin of the carapace to the tip of the tailfan when stretched.

Data collection

In the laboratory, sharks were housed together in 400 l saltwater aquaria at $20 \pm 2^\circ\text{C}$ on a 12 h:12 h light:dark photoperiod. The filming chamber used in this study was a 28 cm \times 28 cm \times 104 cm acrylic aquarium maintained at $20 \pm 0.5^\circ\text{C}$. One end of the chamber was made dark with heavy paper to provide a refuge for the sharks and to provide a 'runway' for them to initiate attacks. Sharks were allowed to acclimate to the aquaria prior to beginning any experiments. Stressed sharks will not feed (L. A. Ferry-Graham, personal observation); thus, resumption of feeding was used as an indication that acclimation was complete. Acclimation took between 6 and 48 h depending on the individual shark.

Leopard sharks were filmed at $250 \text{ fields s}^{-1}$ feeding on each of the four prey items; large shrimp pieces, small shrimp pieces, live mud shrimp and live worm sections. Prey item order was randomized, and individual items were offered consecutively by placing them on the floor of the filming chamber and allowing the shark to approach and subsequently capture the item. Live mud shrimp and worm sections that moved out of the camera's view prior to prey capture were trapped by lowering a polyvinylchloride pipe around the prey item and slid gently back into position. Sufficient time between presentations was allowed such that the sharks retreated to the darkened end of the chamber between feeding events. Presentation of prey items ended when the sharks approached satiation, as indicated by reduced patrolling of the filming chamber, and was resumed 48–72 h later. No more than five prey were consumed by any shark on any day. Two cameras, aimed at a lateral and ventral view respectively, were used to record the feeding events so that movements could be visualized in three dimensions and the actual angle of the

sharks with respect to the cameras could be determined. Four feeding events, in which the head and jaws were clearly visible, were subsequently analyzed from each shark for each prey item; this resulted in a total of sixteen sequences from each shark. In total, 145 successful feeding events were filmed from the four sharks in order to obtain the 64 acceptable sequences.

Video sequences were digitized using a custom-designed digitizing program. Points on one side of the head, jaws, hyoid and buccal cavity, as well as several reference points on the body and chamber background were digitized. Only the lateral camera image was needed for digitizing, although the ventral image was useful for helping to pinpoint the position of relevant morphological features. A zoom lens was used to focus quite closely on the feeding shark so that small movements of the upper jaw and hyoid could be measured; thus, only the head of the shark was visible when it was feeding (see Fig. 1). At least 20 fields were digitized per feeding event. Digitizing always began when the shark's first gill was visible on screen, and fields were digitized every 48ms until the onset of rapid mouth opening.

The onset of rapid mouth opening was designated as 'time zero' and signified the initiation of the strike, a subset of the attack. Fields digitized before rapid mouth opening are expressed here using negative time values to indicate time prior to strike initiation. At the onset of the strike and throughout the gape cycle, fields were digitized every 12 ms. Approximately 12 ms before and after peak gape, the digitizing rate was increased to every 4 ms, equivalent to the maximum sampling rate of the high-speed video system, to ensure that maximum gape was measured. Throughout mouth closure, fields were digitized at 12 ms intervals. Following mouth closure, digitizing continued until the hyoid returned to a relaxed or pre-feeding position or until the shark disappeared off the screen. Generally, the latter occurred first.

The kinematic variables quantified were selected to be consistent with those analyzed by Ferry-Graham (1997) and also by Wilga (1997). These were: (1) gape angle (degrees), the angle between the upper and lower jaw; (2) head angle (degrees), the angle of the head with respect to the midline of the body; (3) gape distance (cm), the distance between the upper and lower jaw tips; (4) labial cartilage displacement (cm), the anterior displacement of the labial cartilage away from the jaw articulation; (5) upper jaw protrusion (cm), the anteroventral displacement of the upper jaw away from the neurocranium; (6) hyoid depression (cm), the ventral and posterior displacement of the hyoid elements; and (7) head depth (cm), an indicator of total head expansion during feeding, the distance from the dorsal to the ventral surface at the first gill arch and at the pectoral fin insertion. The maximum value and the time of the respective maxima for each variable were also recorded. Gape cycle time, defined as the time from mouth opening to mouth closure, was also used as a measure of the total duration of a feeding event.

In addition to the above kinematic variables, several specific strike variables were also quantified. These included: (1) strike distance (cm), the distance from the tip of the lower jaw of the shark to the leading edge of the prey item with respect to the shark at the onset of the strike; and (2) the ram-suction index

$[RSI=(D_{pred}-D_{prey})/(D_{pred}+D_{prey})]$, a dimensionless index which serves as an indicator of the relative contribution of ram or suction to the strike. D_{pred} , or predator distance (cm), is the forward distance moved by the predator from the onset of the strike to the time at which the prey item first enters the mouth. D_{prey} is the movement of the prey item from the onset of the strike until the time it first enters the mouth. RSI values between 0 and 1 indicate a ram-dominated strike while values between -1 and 0 indicate a suction-dominated strike (Norton and Brainerd, 1993).

Statistics

Principal components analysis (PCA) was used to reduce the many kinematic variables to a few, non-correlated linear variables that could be used to describe the feeding event. In this PCA, data from all individuals and all prey items are combined to calculate the principal components (PCs). Kinematic trends among individual sharks and their responses to different prey items are tested in subsequent analyses on the component loading scores or PC scores. Feeding events among the four individuals and the four prey items were compared using a two-factor, mixed-model multivariate analysis of variance (MANOVA) (Systat 5.2.1). In the MANOVA, individual was a random factor, and prey item was a fixed factor tested over the interaction term. The multiple, dependent variables compared using this analysis were the PCs, representing a combination of variables, rather than single kinematic variables. Given a significant MANOVA result for a PC, univariate ANOVAs were performed to determine the nature of the differences detected. Planned comparisons were then performed within the main effect of prey item to determine the degree of modulation exhibited by the feeding sharks in response to each prey item.

A brief discussion of confounding factors is required at this point to explain how pairwise comparisons were selected *a priori* for analysis. The prey items used in this set of experiments were chosen to create a crossed design for analysis of prey-capture behaviors. Large and small shrimp pieces could be compared directly to test the effects of prey item size without the confounding effects of elusivity. The mud shrimp were the largest of the prey items offered but they tended to maintain a slightly curled posture in the tank (reducing their effective length); they were therefore most comparable to the large shrimp pieces in size for testing the effect of elusivity. Worm pieces were most directly comparable to the small shrimp pieces. Additionally, taken together with the results from previous comparisons, worm captures can be compared with mud shrimp captures to begin to tease out the potential effects of prey mobility; wriggling *versus* swimming. Thus, four comparisons were selected *a priori* for analysis: large shrimp pieces *versus* small shrimp pieces, mud shrimp *versus* large shrimp pieces, worm sections *versus* small shrimp pieces, and mud shrimp *versus* worm sections.

Results

Composite video images have been constructed to illustrate the general sequence of events that occurred during a

successful prey-capture event (Fig. 1). A single individual is shown performing prey captures on all four prey items. Generally, the shark swam slowly around the tank prior to feeding. Prey items were detected by the shark as it passed by. If the snout was lifted as the prey item was approached, it was lifted only slightly. Mouth opening began very close to the prey item (see frames marked B in Fig. 1) and often occurred after the prey item had actually been passed by the shark, forcing the shark to turn sharply or to brake rapidly to capture the prey item. As mouth opening, or gape angle, increased, the labial cartilages swung anteriorly (see frames marked C in Fig. 1),

presumably blocking any potential prey escape routes out of the sides of the open mouth, and the hyoid began to be depressed, further expanding the buccal cavity (see also Table 1). During the period of buccal cavity expansion, the prey item began to move noticeably towards and into the open mouth. In Fig. 1, the very short time intervals between successive frames indicates the rapid entry of the prey item into the buccal cavity. As the mouth began to close, the upper jaw was protruded and assisted in bringing the two jaws together quickly (see frames marked D in Fig. 1). The hyoid tended to remain depressed throughout mouth closure and prey transport,

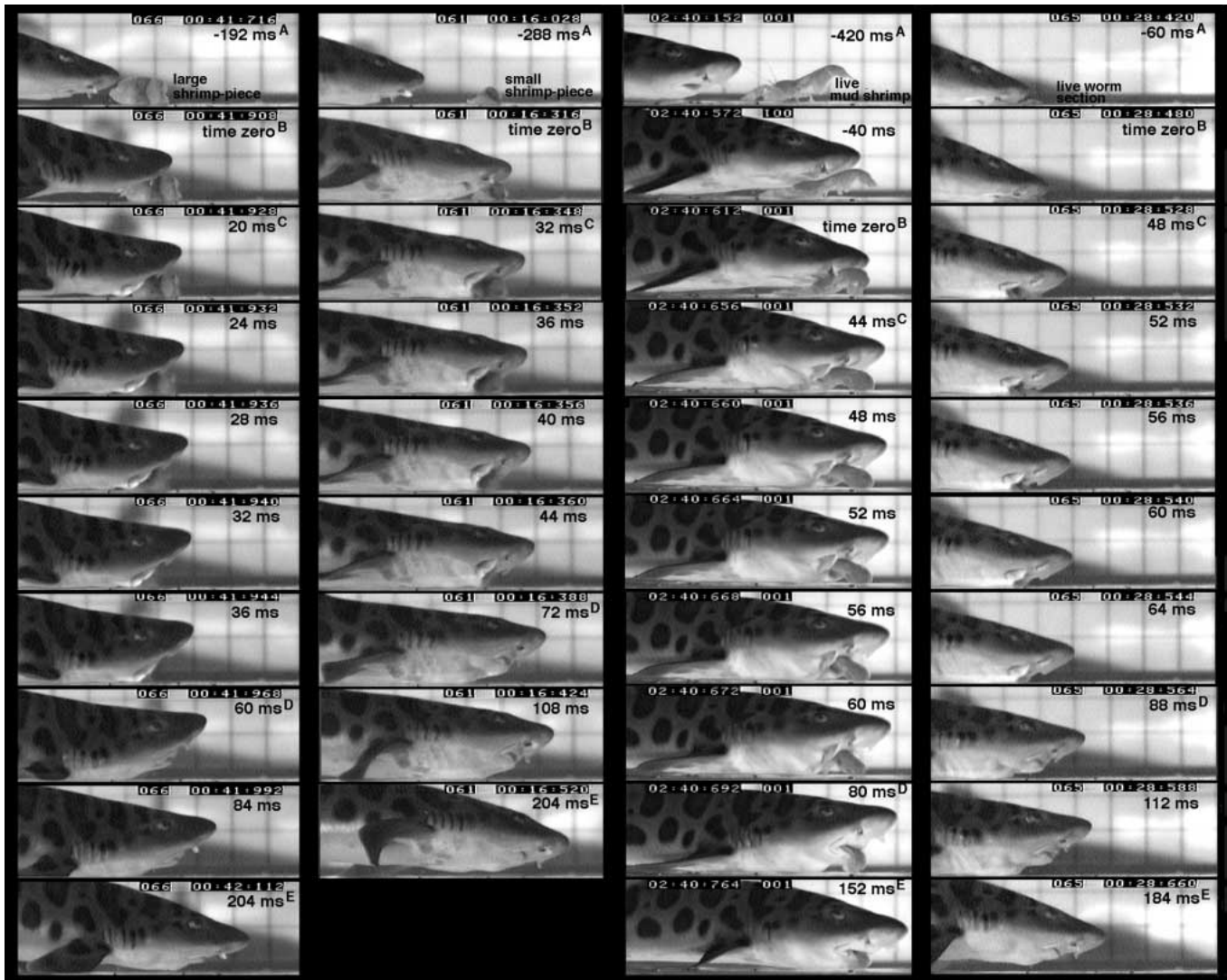


Fig. 1. Composite video image of a representative individual feeding on each of the four prey items (labeled). Individual sequences progress from top to bottom. In each frame, the time is indicated in the black box and is expressed as min:s.ms. Also included is a standardized time, with time zero as the initiation of mouth opening, in ms. Frames occurring before the strike have negative times, indicating the amount of time before time zero. In each sequence, analogous kinematic events are noted. Frame A in each sequence corresponds to the moment the shark first appeared on screen and is part of the attack portion of the feeding event. Frame B in each sequence is time zero, or the onset of mouth opening. An extra frame is included between A and B in the live mud shrimp feeding event to illustrate a rare tail-flip behavior being initiated by the shrimp. Frame C indicates maximum gape angle and also corresponds to the point in time when the prey item began to enter the buccal cavity rapidly. Successive frames after frame C are generally only 4 ms apart. Frame D indicates mouth closure or minimum gape angle; note the visibly protruded upper jaw contributing to closure. Frame E is the time at which the upper jaw returned to its position against the chondrocranium; note that the hyoid remains visibly depressed at this time.

Table 1. Selected kinematic displacement variables measured for four strikes on each prey item by each of the four individuals

	Prey item			
	Large shrimp piece	Small shrimp piece	Live mud shrimp	Worm section
Maximum labial cartilage protrusion (cm)	0.78±0.06	0.78±0.04	0.76±0.09	0.59±0.13
Maximum gape distance (cm)	2.13±0.04	1.76±0.04	1.69±0.11	1.34±0.21
Maximum gape angle (degrees)	92.36±1.84	86.65±3.59	82.94±5.56	68.48±10.22
Maximum hyoid depression (cm)	1.44±0.07	1.26±0.07	1.28±0.06	1.24±0.14
Maximum upper jaw protrusion (cm)	0.70±0.03	0.58±0.01	0.54±0.08	0.59±0.06
Bite (= minimum gape angle) (cm)	0.40±0.16	0.28±0.06	0.72±0.14	0.18±0.02
Time to maximum labial cartilage protrusion (s)	0.10±0.02	0.09±0.01	0.09±0.01	0.09±0.02
Time to maximum gape (s)	0.10±0.02	0.09±0.02	0.11±0.01	0.09±0.02
Time to maximum hyoid depression (s)	0.14±0.01	0.13±0.02	0.15±0.02	0.12±0.02
Time to maximum upper jaw protrusion (s)	0.16±0.02	0.16±0.02	0.15±0.01	0.16±0.02
Time to bite (= gape cycle time) (s)	0.17±0.02	0.16±0.02	0.18±0.01	0.15±0.02

Values are means ± S.E.M. of individual means (N=4).

which continued off screen. Head depth tended to increase with hyoid depression and remained similarly expanded at the end of prey capture, after mouth closure or minimum gape angle had been reached.

This order of events was consistent among strikes on the different prey items (see timing variables in Table 1), although qualitative differences in the magnitude of displacement of the kinematic variables were observed. Most apparent was a difference in the magnitude of maximum gape angle achieved during the capture event. A striking progression is apparent when comparing maximum gape angle (Fig. 2A–D). The degree to which the labial cartilages were protruded anteriorly during the period of increased gape angle also showed variation among prey items. As gape angle decreases, the contribution of upper jaw protrusion is most prominent and is seen most clearly in Fig. 2B, the strikes on live mud shrimp. Similarly, the magnitude of head depth was variable among

prey items and appears largest in Fig. 2B,D, the strikes on live mud shrimp and large shrimp pieces, respectively.

PCA indicated that 71.2% of the variance in the data set could be described by the first three PCs generated (Table 2). Variables tended to load highly on only one PC, and the combinations of variables that loaded highest on each of the three PCs suggests a functional connotation to the loadings. All the timing variables loaded highly on the first PC, and this PC alone described 39.7% of the variance in the data set (Table 2). The second PC contained variables related to head expansion: maximum gape distance, maximum gape angle, maximum labial cartilage protrusion and maximum hyoid depression. This PC explained 19.4% of the variance in the data set. The third PC consisted of two variables related to mouth closure: maximum upper jaw protrusion and minimum gape angle, and explained 12.1% of the variance in the data set.

The MANOVA did not detect a prey item effect; however,

Table 2. Principal component scores resulting from the principal components analysis performed on the kinematic variables

Kinematic variable	PC1 'Timing'	PC2 'Head expansion'	PC3 'Mouth closure'
Maximum labial cartilage protrusion (cm)	-0.15	0.58	-0.22
Maximum gape distance (cm)	0.05	0.87	0.15
Maximum gape angle (degrees)	0.15	0.65	0.51
Maximum hyoid depression (cm)	0.01	0.74	-0.01
Maximum upper jaw protrusion (cm)	-0.18	0.42	-0.67
Bite (= minimum gape angle) (cm)	0.40	-0.06	0.72
Time to maximum labial cartilage protrusion (s)	0.88	0.02	-0.34
Time to maximum gape (s)	0.92	-0.06	-0.03
Time to maximum hyoid depression (s)	0.82	-0.04	0.04
Time to maximum upper jaw protrusion (s)	0.74	0.24	-0.12
Time to bite (= gape cycle time) (s)	0.90	0.02	-0.02

The values presented are loadings.

The correlation matrix was used to generate component loading scores.

Values in bold type are considered to be the highest or most interpretable loadings. The resulting functional implication of the loading combinations is given for each principal component.

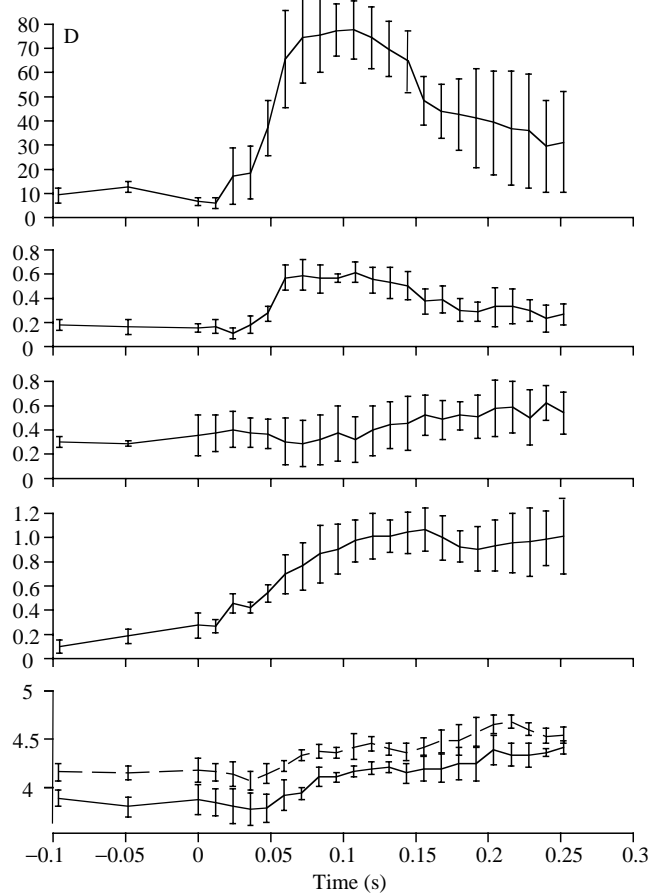
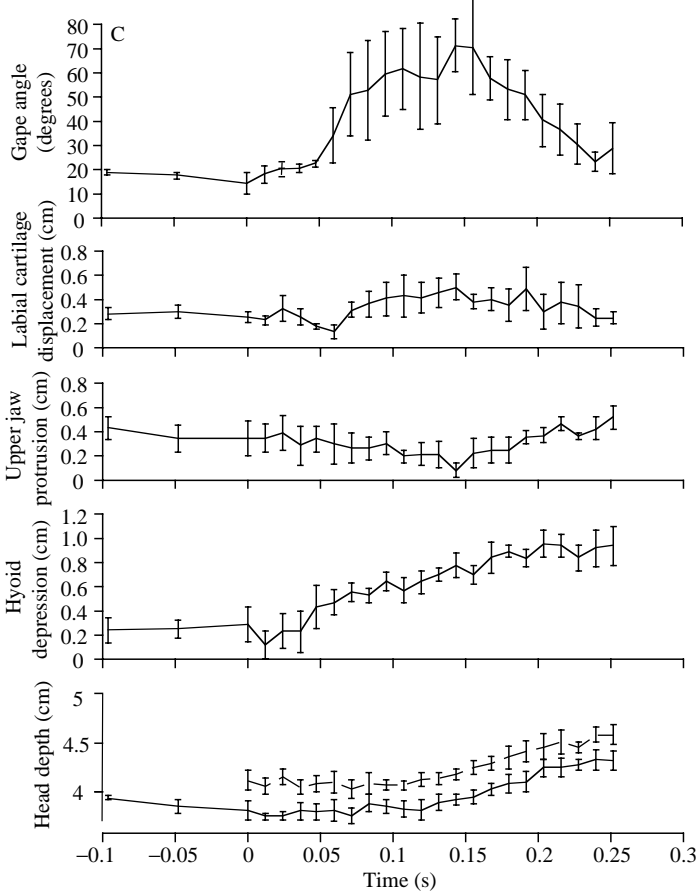
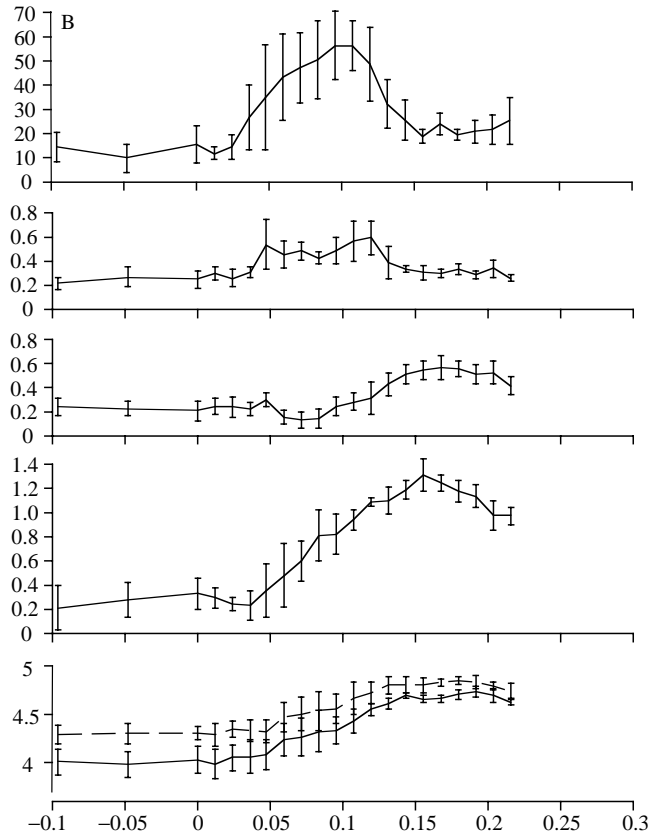
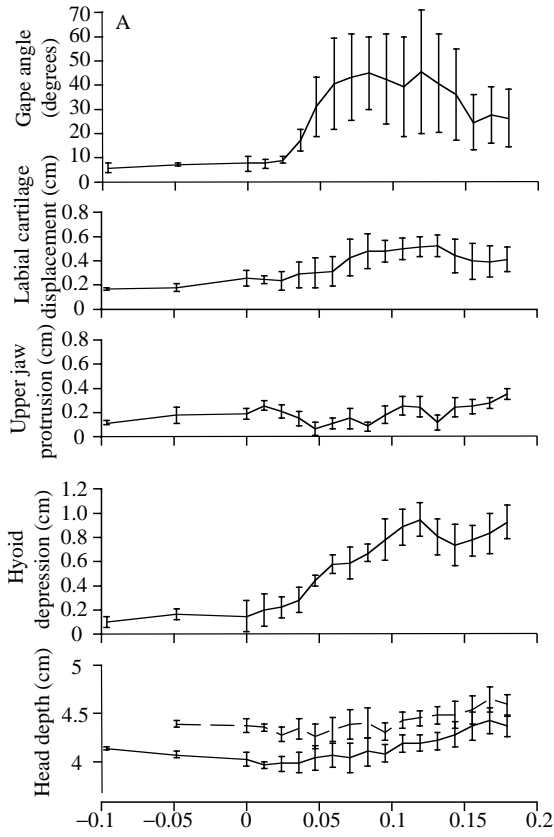


Table 3. Multivariate analysis of variance results from the statistical comparison of the principal components analysis results

Effect	Wilks' λ	d.f.	F	P
Individual	0.498	9, 109	4.040	<0.0001*
Prey item type	0.217	9, 17	1.668	0.1732
Prey item \times individual	0.349	27, 132	2.120	0.0029*

PC1–PC3 (see Table 2) were used as multiple dependent variables in the MANOVA analysis. The fixed effect of prey item was tested over the interaction term.

Significant effects are marked with an asterisk.

it did indicate a significant prey item \times individual interaction effect on prey-capture kinematics (Table 3). Investigation of this significant effect is required for making inferences regarding the main effects in the model (see Sokal and Rohlf, 1995; Underwood, 1997). Univariate ANOVA suggested that PC2 was the only dependent variable contributing significantly to the interaction term and to a potential prey item effect (Table 4). Because there was a significant prey item \times individual interaction, planned comparisons were performed for PC2 that incorporated pairwise comparisons among prey items for each individual (Table 5). Small differences in mean displacements were difficult to detect with the statistical model used here; however, within individuals, a few differences existed in PC2 in response to different prey items (Table 5). Interestingly, the data in Table 5 appear to suggest that individuals responded differently in terms of the prey that elicited modulation of prey-capture kinematics, with individual 4 showing the least modulation.

Table 1, however, shows that, within the kinematic variables that comprise PC2, there is an apparent rank order among individuals in mean magnitude of displacement, with strikes on large shrimp pieces eliciting the largest mean displacement, followed by strikes on small shrimp pieces, then strikes on mud shrimp, and strikes on worm sections eliciting the smallest mean displacement. A graphical presentation of PC2 illustrates this gradient of responses to each prey item (Fig. 3). For each individual, this trend in maxima and minima was consistent; however, the ranked position of strikes on small shrimp pieces and live mud shrimp seemed to be interchangeable, thus causing the prey item \times individual interaction in the MANOVA. This pattern can be seen more clearly in Fig. 4, where the responses of each individual to each prey item are

Fig. 2. Averages of four feeding events on (A) worm sections, (B) live mud shrimp, (C) small shrimp pieces and (D) large shrimp pieces. The mean displacements of selected kinematic variables are shown for the same representative individual depicted in Fig. 1. Values are means \pm S.E.M. from four strikes on the prey item. Axes have been scaled for each variable so that each graph is directly comparable with other kinematic plots of the same variable. In the plot of head depth, the solid line indicates depth at the first gill opening and the broken line indicates depth at the fin insertion.

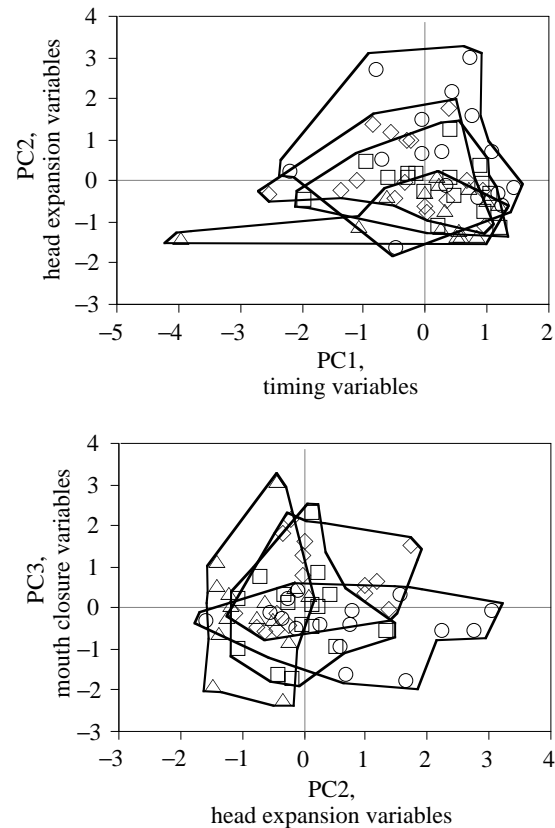


Fig. 3. Principal component (PC) plots comparing PC1, PC2 and PC3. Axes have been scaled identically in both plots for direct comparison of the morphospace encompassed by each prey item and of the descriptive value of each PC. In each plot, the prey items shown are as follows: large shrimp pieces (triangles), small shrimp pieces (squares), live mud shrimp (diamonds) and worm sections (circles).

plotted. Although large shrimp pieces always elicited a larger displacement than strikes on small shrimp pieces, small shrimp pieces did not always elicit a larger displacement than live mud shrimp. Interestingly, if the aforementioned analysis is conducted using only the data for small and large shrimp pieces, a highly significant effect of prey size is detected for PC2 ($F=12.071$; $d.f.=1,3$; $P=0.0311$), without an interaction between the prey effect and the non-significant individual effect. The results for PC1 and PC3 are unchanged.

The ram-suction index (RSI) further suggested that prey-capture behaviors varied in response to prey item variation. When comparing strikes on live mud shrimp with strikes on small shrimp pieces (a potentially relevant comparison, as suggested by the previous paragraph) across all individuals, the RSI values suggested a stronger suction component for the more mobile prey item, live mud shrimp (Table 6). This was true in spite of the fact that strikes on live mud shrimp also had the highest D_{pred} measurement or distance moved by the predator to overtake the prey item. However, a graphical presentation of the data by individual suggested that the live mud shrimp did not consistently elicit a larger suction response

Table 4. Univariate analysis of variance results for the three dependent variables, PC1–PC3

Effect	d.f.	PC1		PC2		PC3	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Individual*	3, 47	5.324	0.0031	3.627	0.0198	2.732	0.0543
Prey item type	3, 9	0.800	0.5243	3.199	0.0768	2.095	0.1711
Prey item × individual*	9, 47	1.271	0.2779	3.990	0.0009†	1.335	0.2455

Effects that were significant in the full MANOVA model (Table 3) and are of interest in this analysis are indicated by asterisks (all ANOVA factors have been included for reference).

Note that PC2 is primarily responsible for the prey item × individual interaction term significant in the MANOVA (marked by a dagger).

(Fig. 5). This suggests that the position of the mud shrimp in the ranked order of RSI response was variable (see Fig. 5B) and often interchangeable (see Fig. 5D) with the ranked position of small shrimp pieces. Interestingly, when comparing strikes on small *versus* large shrimp pieces, RSI values always suggested a stronger suction component for the larger prey item (Table 6). If an ANOVA such as that mentioned above is performed on the RSI data from strikes on the large and small shrimp pieces only, the suction contribution to strikes on large shrimp pieces is significantly different from the contribution to strikes on small shrimp pieces ($F=17.617$; d.f.=1,3; $P=0.0245$; prey item × individual, $P=0.9067$). Large shrimp pieces had the second highest mean D_{pred} (Table 6).

In all cases, the mean D_{pred} was actually greater than the mean strike initiation distance, or the distance between the predator and prey at the onset of mouth opening (Table 6). This

is an artifact of the behavior described previously in which sharks actually swam past the prey item and were then forced to backtrack in order to bring the prey item into the mouth. During this time, stationary prey items were sometimes brushed or actually pushed, effectively causing the strike distance to be increased, and also often causing the prey item to be moved away from the mouth at an angle to the midline of the shark's body. Mud shrimp that attempted to escape predation also moved away from the oncoming shark with a similar trajectory. Such interference with, or changes in, the path of the prey item will affect the calculation of RSI values, probably causing the suction contribution to be underestimated.

Among individuals, capture success was nearly 100% for each of the four prey items. Seven misses were recorded out of the original 145 video sequences collected. Of these, one was on a worm section, one on a small piece of shrimp, two

Table 5. Results of a priori Bonferroni–Dunn planned comparisons within the interaction effect of prey item type × individual from the multivariate analysis of variance and corresponding univariate analysis of variance on PC2 (see Table 4)

Individual	Prey elusivity effect		Prey size effect	
	Mud shrimp <i>versus</i> large shrimp pieces	Worm section <i>versus</i> small shrimp pieces	Large <i>versus</i> small shrimp pieces	Mud shrimp <i>versus</i> worm section
	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
1	0.0200*	>0.9999	>0.9999	>0.9999
2	0.1446	0.0010*	0.6049	0.0058*
3	>0.9999	>0.9999	>0.9999	0.0319*
4	>0.9999	>0.9999	>0.9999	>0.9999

P-values reported have been adjusted for 16 planned comparisons.

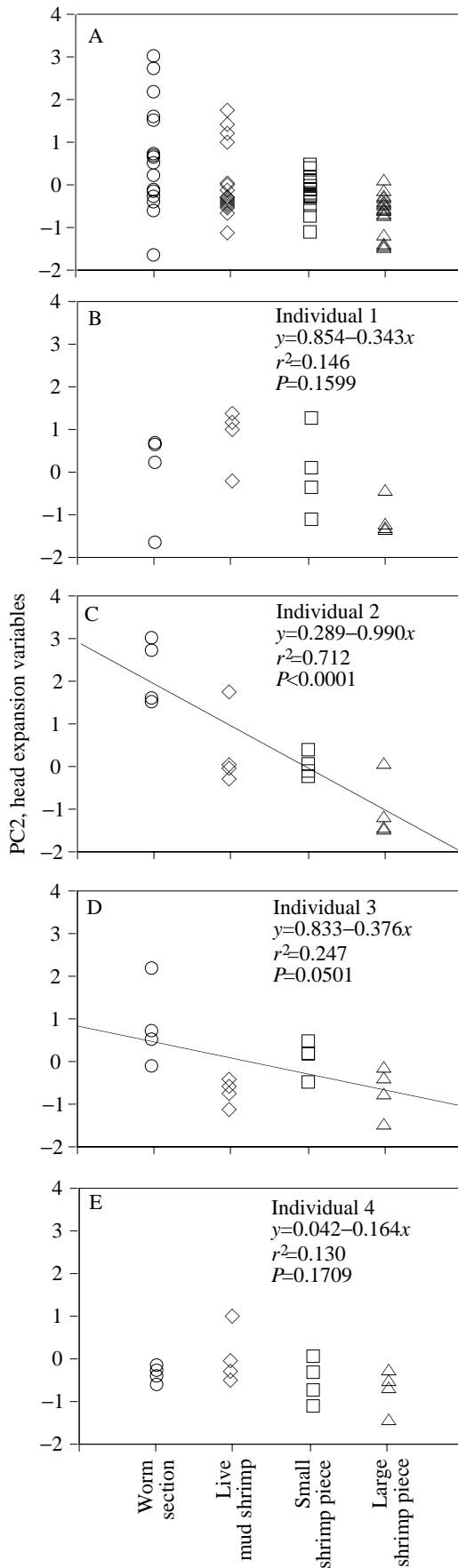
Significant comparisons are marked with an asterisk.

Table 6. Strike variables measured for four strikes on each prey item by each of the four individuals

	Prey item			
	Worm section	Live mud shrimp	Small shrimp piece	Large shrimp piece
Strike initiation distance (cm)	0.65±0.14	0.72±0.17	0.65±0.20	0.53±0.26
D_{pred} (cm)	0.78±0.14	1.37±0.28	0.85±0.17	1.10±0.51
RSI	0.13±0.08	0.06±0.04	0.24±0.13	0.05±0.10

Values are means ± S.E.M. of individual means ($N=4$).

D_{pred} , distance moved by the predator; RSI, ram–suction index.



on large shrimp pieces and three on live mud shrimp. Only two misses occurred in full view of the camera. Misses, especially on the mud shrimp, occurred with far less frequency than anticipated and thus were not analyzed further.

Discussion

It appears that leopard sharks do not modulate their prey-capture behavior in a predictable (i.e. the same for all individuals) or distinctive (i.e. statistically significant) manner in response to prey with increased potential for elusivity. This finding is uncommon but not unique among aquatic organisms. Prey items as different as earthworms and live guppies (*Poecilia reticulata*) did not induce detectable modulation in the salamander *Ambystoma mexicanum* (Reilly and Lauder, 1989). As seen for leopard sharks, significant between-salamander variation existed such that behavior patterns between prey types (among individuals) did not differ statistically (Reilly and Lauder, 1989). Individual variation is present in nearly all studies, particularly in studies of shark feeding to date (Motta *et al.* 1997; Wilga and Motta, 1998), but rarely does it exist to the degree that is exhibited both in this study and in that of Reilly and Lauder (1989). Reilly and Lauder (1989) did find that the direction of change induced by elusive prey types was consistent among individuals, it was the magnitude of change that was much greater between individuals than among individuals feeding on different prey types. The pattern of change, however, suggested that even large increases in sample size would be unlikely to increase the statistical power sufficiently for behavioral modulation to be detected (Reilly and Lauder, 1989). The lack of modulation is probably a real, biologically relevant phenomenon.

The lack of modulation of prey-capture behavior in leopard sharks in response to prey with increased potential for elusivity is probably also real (i.e. not simply a result of the small sample sizes available when working with sharks) and is probably a result of the finding that none of the prey items proved to be truly elusive. One of the most striking observations in the present study was that the sharks rarely failed to capture any

Fig. 4. Plots of principal component 2 (PC2) against prey item for each individual to illustrate the graded response by individuals to changing prey items. The prey items have been arranged on the x-axis *post hoc* in the order of mean response to each prey item across all individuals (see A). Note that, in A, it appears that there is a trend of decreasing variance with prey type; however, when investigated among individuals, it is simply that each individual responds differently to the prey item. The response of each individual (B–E) is comparable in variation and, within an individual, the variation in response is quite consistent from prey item to prey item. Equations for the regression through each set of points (B–E), as well as the fit of the line and significance, are provided for comparison among individuals. Slopes significantly different from zero are shown. PC2 should be interpreted biologically as high values indicating less expansion and low or negative values indicating more expansion of the head because of the nature of the component loadings.

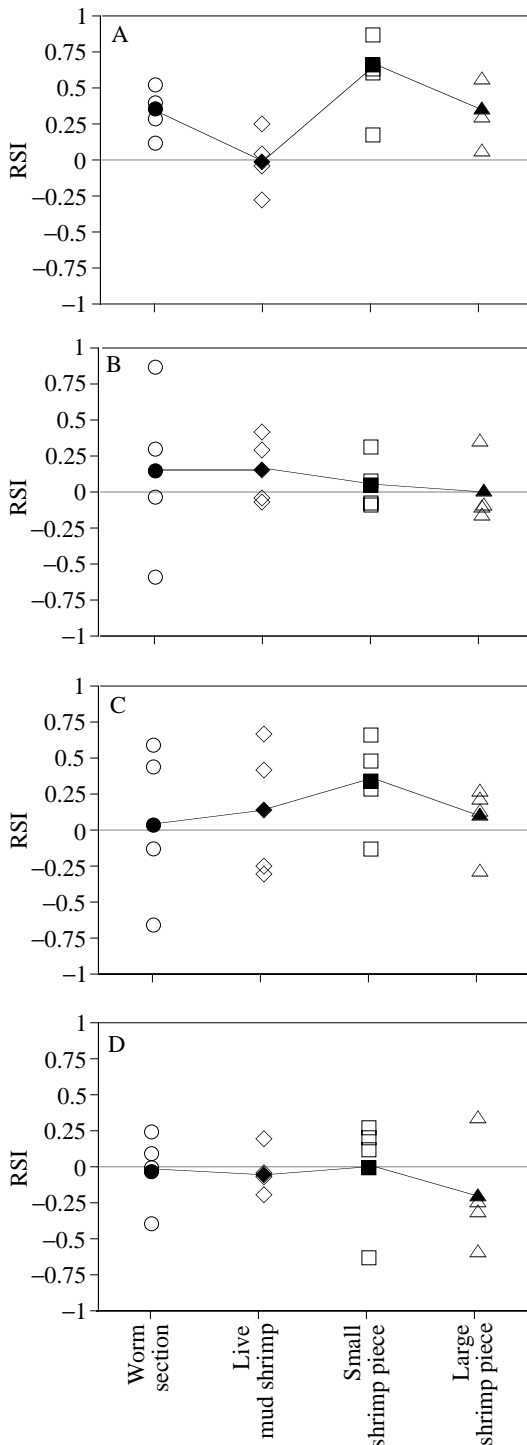


Fig. 5. Plots of ram-suction index (RSI) against prey item for each individual to illustrate the graded response by individuals to different prey types. The prey items have been arranged on the *x*-axis *post hoc* according to the order of mean response to each prey item identified in Fig. 4. The response of each individual (A–D) is shown with replicate measurements as open symbols, and the mean response is shown as a filled symbol. Mean RSI values for each prey item are connected to illustrate the general direction of modulation in response to each prey type. Positive values indicate a ram-dominated strike and negative values indicate a suction-dominated strike.

of the prey. Without a performance consequence, it can be argued that none of the prey used can be appropriately categorized as elusive, as elusivity is directly proportional to the prey's ability to escape predation. Even in response to what was presumably the most elusive prey item, the mud shrimp, strikes were almost always successful. A problem with defining elusivity is that the degree of elusivity of a prey item is not, in fact, an attribute of the prey item *per se* but of the predator and its response. Thus, elusivity cannot be determined *a priori*.

The high capture success rate on mud shrimp is probably explained by the behaviors utilized by the mud shrimp in the experiments as opposed to those predicted. Mud shrimp were chosen as a prey item primarily because they employed a standard decapod escape response and 'tail-flip' into the water column when disturbed in their holding tank. Thus, to avoid the oncoming predator, it was expected that they would tail-flip away from the shark's mouth. However, contrary to predictions, the tail-flip response was rarely actually utilized by the shrimp in the feeding experiments. The escape response more typically employed by the live mud shrimp was to turn and run away (on the tank floor rather than moving into the water column) from the oncoming shark. In seven of the sixteen captures analyzed, mud shrimp were bitten on their tail or side and then held in the teeth of the shark. In two additional captures, mud shrimp were bitten on the dorsal portion of the carapace. Mud shrimp run backwards quite effectively and this behavior was observed in four captures, resulting in the sharks biting the mud shrimp on the head. This escape tactic proved to be easily countered by the attacking shark. As mud shrimp are arguably still quite mobile relative to the other prey items that apparently offered no differential challenge to the feeding shark, it is interesting that modulation was not required.

Given that misses among all prey items were quite rare, it is unusual that repeatable patterns of differences in prey-capture kinematics should be observed at all. A significant size effect on prey-capture behaviors was detected. This is particularly interesting given that the two prey items being compared were both entirely non-elusive. Larger shrimp pieces consistently elicited more expansion of the head, while smaller shrimp pieces elicited less expansion. Further, larger shrimp pieces always elicited a larger contribution of suction to the strike, and Table 6 shows that strikes on large shrimp pieces were initiated from a distance greater than that for small shrimp pieces (generally indicating greater elusivity; see Nemeth, 1997).

Frazzetta and Prange (1987) introduced a hypothesis regarding size effects which stated that feeding sharks should engulf prey items smaller than the maximum diameter of the mouth by suction. Larger prey items, those roughly equivalent to the large shrimp pieces offered to the leopard sharks in this study, should require a bite, presumably to secure the prey item prior to prey transport (Frazzetta and Prange, 1987). Work on dogfish (*Squalus acanthias*; Squaliformes) using shrimp pieces scaled to half the mouth diameter and fish pieces equal to the mouth diameter would seem to support this idea (Wilga, 1997),

while Ferry-Graham (1997) found that swell sharks (*Cephaloscyllium ventriosum*; Carcharhiniformes) bit fish pieces irrespective of size and produced an equally large ram component in strikes on two prey sizes. The present work on leopard sharks seems to suggest that a third alternative might exist regarding how size should affect prey capture. For leopard sharks, strikes on larger prey items had a lower RSI value (stronger suction component). If the same amount of suction were generated for large and small prey items, strikes on larger prey items would presumably have a larger RSI value (stronger ram component), due to a larger mass and subsequently shorter distance moved towards the open jaw, or a reduced D_{prey} . If larger prey items have an equal or smaller RSI, then it can be assumed that an appropriately larger compensating force is being applied for the transfer of inertia to the item, resulting in the same or a greater distance moved by the prey towards the open jaw. The significantly smaller RSI values for strikes on larger prey items for the leopard sharks studied here suggest that the sharks are actually modulating the contribution of suction to the strike, and possibly even overcompensating.

Although feeding in these three shark species has not yet been compared quantitatively, some interesting trends can be discussed. Wilga (1997) found effects of prey item size on the timing of kinematic events in dogfish feeding on pieces of shrimp and herring (scaled to the mouth diameter in a manner analogous to that used in the present study). The duration of the capture event in dogfish was consistently shorter for small shrimp pieces than for large fish pieces. For the leopard sharks in the present study, effects on timing were not detected, but smaller prey items elicited a smaller magnitude of response in terms of maximum displacement of the kinematic variables. The swell shark, in contrast, did not appear to modify its prey-capture kinematics in response to prey items of different sizes (Ferry-Graham, 1997). The swell shark is a more strongly ram-dominated feeder; the RSI values measured for the swell shark feeding on both sizes of prey were very near 0.60 (Ferry-Graham, 1997). The maximum RSI value measured for the leopard shark was 0.24 for strikes on small shrimp pieces (Table 6). Although the leopard shark is more closely related phylogenetically to the swell shark (both are members of the Carcharhiniformes), morphologically, at least externally, it possesses many of the features prominent in the dogfish. Both the leopard shark and the dogfish possess a small- to intermediate-sized mouth (relative to the area of the buccal cavity) and labial cartilages that protrude forward to create a slightly more tube-like opening to the mouth, and both are capable of massive expansion of the buccal cavity. If such features were expressed to a more extreme degree, they would be considered stereotypical of suction feeders. Although also capable of substantial buccal cavity expansion, the swell shark has a very large gape relative to those of the leopard and dogfish sharks (Ferry-Graham, 1997; L. A. Ferry-Graham, personal observation). A detailed kinematic and morphological comparison has yet to be conducted. However, the possession of what appears to be a rather intermediate morphology may,

in part, be responsible for the potential for modulation of prey-capture behaviors in response to prey item size (see also Nemeth, 1997).

Given the results of this study, where an effect of prey size on prey-capture kinematics was detected, it may be appropriate to consider the results of previous studies on teleosts which purport to have detected an effect of elusivity on prey capture, but where interpretation of the results is confounded by the use of prey items of different sizes. Other researchers have used worms of various sorts and crustaceans or live fishes to represent degrees of elusivity in their analyses, generally in an attempt to use items that differ most from one another in their elusivity among those that the predator is able to utilize. Although the comparison may be ecologically relevant (if diet items are used), the ultimate cause of any modulation on the part of the predator in response to these stimuli remains in doubt because of the size differences among the prey. Elusivity probably still has an effect on prey capture, since Nemeth (1997), for example, used nearly size-matched prey items for measuring the effect. However, a careful design such as that of Nemeth (1997) and Norton (1995) is required to eliminate confounding factors such as size when determining the absolute effect of prey elusivity.

For the leopard sharks discussed in the present study, it would appear that prey item size shows potential for inducing some degree of behavioral modulation, while prey item mobility does not. The use of a more elusive prey item may, in the future, yield different results. The potential for modulation in response to prey item size is, in itself, an interesting finding since the presence and pattern of modulation are not consistent among the shark species that have been studied. Modulation also occurs regardless of a performance consequence. Leopard sharks appear to expand the buccal cavity more in response to larger prey items. Swell sharks, in contrast, use a maximally expanded buccal cavity regardless of the size of the prey, thus overexpanding the buccal cavity when faced with smaller prey items (Ferry-Graham, 1997). Dogfish appear to extend the duration of kinematic events during prey capture in response to a larger prey item (Wilga, 1997), in contrast to the leopard shark (this study) and swell shark (Ferry-Graham, 1997) in which there were no differences in timing of prey capture between prey sizes. An increased use of suction in response to increased prey item size has not previously been reported, but is probably not unique to the leopard shark. It was noted for the swell shark that strikes on larger prey did not subsequently result in a smaller suction component to the feeding event, indicating that a larger degree of suction was potentially being produced within the buccal cavity to counter the prey's larger size, and resulting in the same RSI value (i.e. suction contribution) for strikes on both prey sizes (Ferry-Graham, 1997). Further studies to determine the full extent to which feeding behaviors in sharks can be modulated in response to prey item size and type are warranted.

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