

RESEARCH ARTICLE

Turning performance of brief squid *Lolliguncula brevis* during attacks on shrimp and fish

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ABSTRACT

Although squid are generally considered to be effective predators, little is currently known of how squid maneuver and position themselves during prey strikes. In this study, high-speed video and kinematic analyses were used to study attacks by the brief squid *Lolliguncula brevis* on both shrimp and fish. Squid attack success was high (>80%) and three behavioral phases were identified: (1) approach, (2) strike and (3) recoil. *Lolliguncula brevis* demonstrated greater maneuverability (i.e. a smaller length-specific turning radius) and employed more body adjustments (i.e. mantle angle posturing) during approaches toward shrimp versus fish. Squid exhibited higher linear approach/strike velocities and accelerations with faster-swimming fish prey compared with slower shrimp prey. Agility (i.e. turning rate) during prey encounters was comparable to performance extremes observed during non-predatory turns, and did not differ according to prey type or distance. Despite having the ability to modulate tentacle extension velocity, squid instead increased their own swimming velocity rather than increasing tentacle velocity when targeting faster fish prey during the strike phase, but this was not the case for shrimp prey. Irrespective of prey type, *L. brevis* consistently positioned themselves above the prey target prior to the tentacle strike, possibly to facilitate a more advantageous downward projection of the tentacles. During the recoil, *L. brevis* demonstrated length-specific turning radii similar to those recorded during the approach despite vigorous escape attempts by some prey. Clearly, turning performance is integral to prey attacks in squid, with differences in attack strategy varying depending on the prey target.

KEY WORDS: Predator–prey, Maneuverability, Agility, Turning, Squid, Kinematics

INTRODUCTION

High proficiency in unsteady maneuvers is important for many aquatic predators that target evasive prey, as they often need to accelerate and turn within relatively short time periods for capture success (Domenici, 2001; Domenici and Blake, 1997; Webb, 1984; Weihs and Webb, 1984). Performance in some key unsteady parameters, such as length-specific turning radius and turning speed, decrease with size in many aquatic vertebrates, leading larger vertebrates to adopt strategies to account for performance limitations, such as filter feeding, hunting in groups, tail-slapping and production of bubble curtains (Domenici, 2001). Smaller and intermediate-sized fishes will often employ S-starts that involve rapid linear acceleration towards prey (Webb and Skadsen, 1980;

Rand and Lauder, 1981; Harper and Blake, 1991; Domenici and Blake, 1997). The flow associated with these rapid approaches and/or the pressure field of suction feeding strikes trigger sensory structures in prey that can induce early escape responses (Visser, 2001; Holzman and Wainwright, 2009; Stewart et al., 2013). Thus, predators that employ sub-maximal attack velocities (Webb, 1984; Harper and Blake, 1991), have narrow body depths (Webb, 1984) or delay mouth openings (Rand and Lauder, 1981) can reduce their hydrodynamic footprint and experience greater success in prey capture.

Squids (cephalopod molluscs) are predators that differ considerably from the vertebrate aquatic predators considered to date in predator–prey biomechanical studies. Indeed, they have different body architectures, physiology and attack behaviors than fishes and marine mammals, and therefore represent a unique taxon for comparative study. Unlike vertebrate predators, many squid need to swim continuously using a combination of jet propulsion and fin movements to oxygenate their gills and offset negative buoyancy (Bartol et al., 2001a; O’Dor and Webber, 1991). Most coastal, inshore squids are active visual predators and have very limited energy reserves, requiring them to feed frequently on small crustaceans and fishes (Messenger, 1968; O’Dor and Webber, 1991). Attacks on mobile prey are always performed in an arms-first orientation, with the tentacles being the primary means of capture (Kier and Van Leeuwen, 1997; Messenger, 1968; Nicol and O’Dor, 1985), setting them apart from the mouth-based attacks of many aquatic vertebrate predators. The arms and tentacles of squid lack hardened elements and operate as muscular hydrostats, with the musculature of the arms and tentacles acting as both the effectors of movement and the support system (Kier, 1982; Kier and Smith, 1985).

In addition to the arms and tentacles, the paired fins and pulsed jet, which constitute the locomotory system of cephalopods, are powered and supported by muscular hydrostats (Kier et al., 1989). This system is very flexible; the fins are capable of undulating and oscillating independent of each other, and the pulsed jet is produced by mantle contraction and ejection of fluid through a bendable funnel that can be oriented in any direction below the body (Anderson and DeMont, 2000; Bartol et al., 2001b, 2009; Foyle and O’Dor, 1988; O’Dor and Webber, 1991). Tail-first swimming appears to be the preferred orientation for sustained, economical locomotion over a wide range of speeds (Bartol et al., 2016, 2001b). However, squid always orient arms-first for attacks on prey. Arms-first attacks by squid and cuttlefish on prey have been well documented (Foyle and O’Dor, 1988; Kier and Van Leeuwen, 1997; Messenger, 1968; Nicol and O’Dor, 1985) and allow the squid to position the tentacles and arms toward the prey so that they can be used to strike, manipulate and deliver prey to the mouth (Foyle and O’Dor, 1988; Messenger, 1968; Nicol and O’Dor, 1985).

Tentacle strikes and body movements have been examined during prey attacks in cuttlefish *Sepia officinalis* (Messenger, 1968, 1977)

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List of symbols and abbreviations

A_{avg}	mean acceleration
A_{max}	peak acceleration
COR	center of rotation
DML	dorsal mantle length
L	total body length
R	radius of the center of rotation
$(R/L)_{\text{mean}}$	mean length specific turning radius
$(R/L)_{\text{min}}$	minimum length specific turning radius using a 90% cut-off
V_{avg}	mean swimming velocity
V_{max}	peak swimming velocity
θ_{la}	lateral angle between the arms and mantle at the start of the approach
θ_{ls}	lateral angle between the arms and mantle at the start of the strike
θ_{total}	total angular displacement
θ_{v}	ventral angle between the arms and mantle
θ_{va}	ventral angle between the arms and mantle at the start of the approach
θ_{vs}	ventral angle between the arms and mantle at the start of the strike
ω_{max}	maximum angular velocity
ω_{mean}	mean angular velocity

and squid *Doryteuthis pealeii* (Kier, 1982; Kier and Van Leeuwen, 1997). Messenger (1968) described prey attacks by *S. officinalis* as falling into three phases: attention, positioning and strike. The attention phase starts with the cuttlefish tracking the prey with its eyes and turning its head so that the arms and tentacles are projected towards the target and the angle between the body axis and the prey axis is near or at zero (Messenger, 1968). During positioning, the cuttlefish swims either forwards or backwards to create the optimal attacking distance (Messenger, 1977), and then the arms and tentacles extend outward towards the prey during the strike phase (Messenger, 1968). Tentacle strikes are thought to be all-or-none responses with limited neuromuscular variability (Messenger, 1968). In the squid *D. pealeii*, the tentacles begin to extend outward slightly when they are ~4–6 cm from the prey. The arms then separate outward from the tentacles and the tentacles extend rapidly in a straight trajectory toward the prey (Kier, 1982; Kier and Van Leeuwen, 1997; Messenger, 1968).

Foyle and O'Dor (1988) studied attack behavior of the squid *Illex illecebrosus* on large and small fish and divided attacks into similar phases as those reported by Messenger (1968): (1) rotation, where the squid changes from tail-first to arms-first swimming; (2) approach, which involves rapid acceleration towards the prey; (3) tracking, where the squid slowly follows the prey; and (4) capture, where the prey is subdued. For larger fish prey, *I. illecebrosus* employs a prolonged tracking phase at low speed before the strike. This longer tracking phase is thought to be important for extensive behavioral assessment of fast prey (Foyle and O'Dor, 1988). Maximum arms-first body acceleration rates for *I. illecebrosus* were 12 m s^{-2} during these interactions (Foyle and O'Dor, 1988), which is low relative to fish that exhibit maximum acceleration rates of $30\text{--}50 \text{ m s}^{-2}$ (Webb, 1978; Domenici and Blake, 1991, 1997; Domenici, 2001). In addition to relatively low body accelerations, low rotation rates ($\sim 90 \text{ deg s}^{-1}$) and large turning radii (0.5 body lengths) were also observed. However, these may be underestimates given that a detailed kinematic analysis was not performed.

Although the studies above have provided valuable insight into attack behavior in cephalopods, few studies have examined the kinematic parameters of attacks in detail, particularly with regard to

quantitative turning performance metrics. Clearly, the tentacles are effective high-velocity tools for capturing prey, but it is unclear how unsteady movements are employed during turns. Previous research on vertebrate systems has revealed the importance of turning performance in predator–prey interactions (Domenici, 2001; Domenici and Blake, 1997; Webb, 1984; Weihs and Webb, 1984), and we also expect this to be the case with squid. In this study, we focus on measuring the kinematics of approach and attack behavior of the brief squid *Lolliguncula brevis* during encounters with both shrimp and fish prey. This squid is an excellent test subject for predator–prey trials because recent studies have shown that it can achieve intermediate/high turning rates and low turning radii during routine swimming (Jastrebsky et al., 2016) relative to other aquatic taxa measured to date (Blake et al., 1995; Domenici and Blake, 1991; Fish, 2002; Fish and Nicastro, 2003; Parson et al., 2011; Rivera et al., 2006; Walker, 2000). The objectives are: (1) to document turning behaviors during prey encounters, (2) to determine if squid exhibit high levels of maneuverability and agility during prey encounters, and (3) to determine if turning performance and attack strategies in squid changes with prey type. For consistency with previous studies, we use ‘maneuverability’ to refer to the animal’s ability to turn in a confined space, defined as the radius (R) of the turning path divided by the body length (L) and ‘agility’ to refer to the angular velocity of the turn (ω) (Norberg and Rayner, 1987; Webb, 1994; Walker, 2000; Rivera et al., 2006; Jastrebsky et al., 2016).

MATERIALS AND METHODS**Animals**

This study was conducted in accordance with Old Dominion University’s Institutional Animal Care and Use Committee (IACUC) protocol 692436-2. *Lolliguncula brevis* Blainville 1823 [2.8–6.3 cm dorsal mantle length (DML)] were caught by trawl net at the Virginia Institute of Marine Science Eastern Shore Lab (VIMS ESL), Wachapreague, VA, USA and were transported back to Old Dominion University’s Marine Aquatics Facility (ODU MAF) in aerated livewells. The squid were maintained in a 450 gallon (~1700 liters) recirculating seawater system (salinity, 25–30 ppt; temperature, 15–21°C; pH 8.0–8.2; ammonia <0.2 ppm). A moderate current was maintained in the holding tank to facilitate active swimming of squid, and squid were fed a diet of live grass shrimp *Palaemonetes pugio* and small fish *Pimephales promelas*. The *P. pugio* that were used for this study (mean \pm s.d. total length, $2.3 \pm 0.7 \text{ cm}$) were also collected at the VIMS ESL by dip net. At the ODU MAF, the shrimp were maintained in aerated aquaria filled with seawater matching the conditions described above and fed fish flake food. The *P. promelas* (mean total length = $3.4 \pm 0.5 \text{ cm}$) were purchased from Animal Adventure (Chesapeake, VA, USA) and maintained in separate aerated aquaria at ambient temperature (19–22°C) and also fed flake food.

Experimental setup

The experimental setup is described in detail in Jastrebsky et al. (2016). It included two synchronized high-speed Dalsa Falcon video cameras (1400×1200 pixel resolution; 100 frames per second; DALSA, Waterloo, ON, Canada) positioned beside and below a $30.5 \times 30.5 \times 25.4 \text{ cm}$ Plexiglass viewing chamber. Video frame triggering and acquisition were achieved using CLSAS capture cards and Streams 5 software (IO Industries, London, ON, Canada).

For each trial, squid were placed in the viewing chamber and allowed to acclimate for at least 5 min prior to recording. Several

squid were often placed in the chamber at one time to increase the probability of an attack. The prey *P. pugio* and *P. promelas* were dropped into the chamber at random locations, and the squid only had the choice of one type of prey at a time. The fish or shrimp were placed in the experimental chamber for ~30 s and trials were terminated if the fish/shrimp or squid were unresponsive during that time period. A total of 58 attacks from 49 *L. brevis* individuals were recorded, with 40 attacks on shrimp by 34 individuals and 18 attacks on fish by 15 individuals. One squid in shrimp trials and one squid in fish trials did not strike and recoil after approaching the prey, lowering the sample sizes to 33 and 14 individuals, respectively, for these phases. The mean±s.d. size of brief squid was 4.1±0.9 cm DML ($N=34$) for shrimp trials and 3.5±0.3 cm DML ($N=15$) for fish trials.

Attack analysis

Successful attack sequences were classified into three phases: approach, strike and recoil. The approach was defined as the interval from when the squid head began to rotate toward the prey to when the arms started to spread in preparation for the tentacle strike; the strike was the period from the start of tentacle extension to contact with the prey; and the recoil was the period from prey contact to

wrapping the prey in the arms close to the mouth (determined visually). In contrast to previous studies, distinct sub-phases of approach behavior were not observed, and thus behaviors prior to the strike were all considered part of the approach phase. Unsuccessful attack sequences were separated into two categories: approach without a strike, where the squid rapidly approached the prey but did not extend the tentacles and approach with a strike but where the strike missed the prey.

Frame-by-frame position tracking of cephalopod body features was accomplished using MATLAB-based image tracking code (see Hedrick, 2008). Ten points were tracked in the ventral view (Fig. 1A), and seven points were tracked in the lateral view (Fig. 1B). The tracked points in the ventral view were used to determine center of rotation (COR) radius, angular velocity (ω), total angular displacement (θ_{total}), mantle diameter, and distance between the predator and prey during the approach and strike phases. We refer the reader to Jastrebsky et al. (2016) for a detailed description of calculations of COR, the point in the ventral view that moved the least during the turn, and ω (Fig. 1G). In brief, the procedures involved (1) smoothing data using the cross-validation criterion (CVC), (2) finding the COR, and (3) determining the radius of curvature (R) of the COR path using analytical geometry

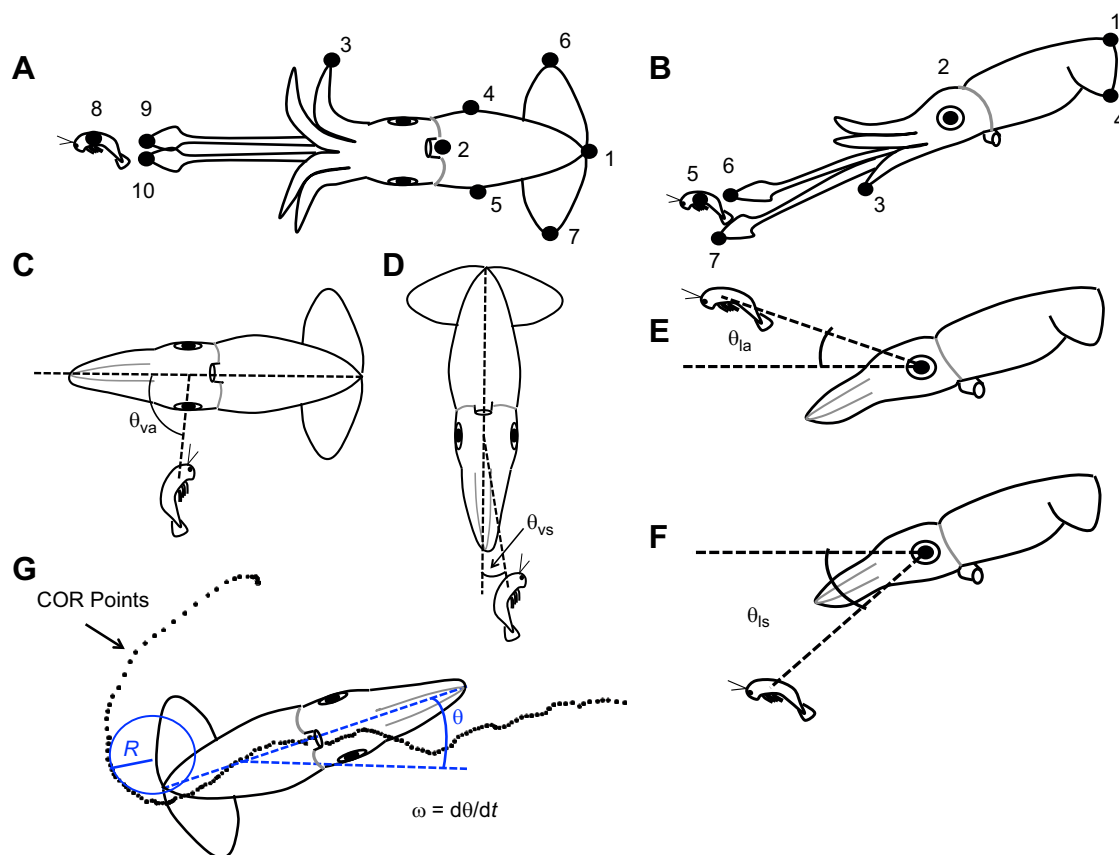


Fig. 1. Points and angles tracked in lateral and ventral views in the brief squid *Lolliguncula brevis*. (A) The tracked ventral points were: (1) tail tip, (2) base of the funnel, (3) tip of arm pair IV, (4) right side of the mantle midway down the length, (5) left side of the mantle midway down the length, (6) right fin tip (max chord), (7) left fin tip (max chord), (8) prey (midway along the prey body), (9) tentacle tip I, and (10) tentacle tip II. (B) The tracked lateral points were: (1) tail tip, (2) eye, (3) tip of ventral arm pair, (4) fin tip, (5) midpoint along prey body, (6) tentacle tip I, and (7) tentacle tip II. (C, D) The ventral angle was the angle between the longitudinal axis of the squid and a line drawn from a point equidistant between the squid eyes to the midpoint of the prey body at the start of the approach (θ_{va}) and at the start of the strike (θ_{vs}). (E, F) The lateral angle was the angle between the horizontal and a line connecting the squid eye with the midpoint of the prey at the start of the approach (θ_{la}) and the start of the strike (θ_{ls}). (G) Example of center of rotation (COR) points for a squid turning counterclockwise during the approach phase (COR points are displayed per 0.1 s). The radius (R) of the COR path is measured throughout the turn and divided by the total length of the animal (L) to calculate length-specific radii of the turns (R/L). The numerical derivative of the animal (θ) versus time was determined using a fourth-order finite difference formula to compute angular velocities (ω).

and the equation:

$$\frac{1}{R} = \frac{y''}{[1 + (y')^2]^{3/2}}, \quad (1)$$

where $y' = dy/dx$, x and y are the coordinates of the COR in the ventral view and the derivatives were evaluated using fourth-order accurate finite difference equations. These steps were accomplished using custom in-house MATLAB routines developed by our team. The smoothing method used the CVC where the level of smoothing is determined such that the root-mean-squared error of the smoothed splines determined with points from the data individually excluded is minimized (Walker, 1998). In the present implementation, the minimization is determined to within 0.1% of the actual minimum to speed convergence of the method (Jastrebsky et al., 2016). $(R/L)_{\text{mean}}$ is the average of all the center of rotation radii throughout a turn divided by the length of the animal (Fig. 1G). $(R/L)_{\text{min}}$ is the minimum center of rotation turning radius during a turn, using a 90th percentile cut-off value to account for frame digitization error as described in Jastrebsky et al. (2016). The 90th percentile was used because it was a reliable cut-off between outliers and more typical values. ω_{avg} and ω_{max} are the mean and maximum angular velocity throughout a turn, respectively.

Attack angle, velocity and acceleration calculations

Using ImageJ software (National Institute of Health, USA; available at <http://imagej.nih.gov/ij/index.html>) the following angles were determined: (1) lateral angle of the mantle relative to the horizontal during approach and recoil; (2) lateral angle of the arms relative to the mantle during approach and recoil; (3) the ventral angle between the longitudinal axis of the squid and a line drawn from a point equidistant between the squid eyes to the midpoint of the prey body at the start of the approach (θ_{va}) and at the start of the strike (θ_{vs}); and (4) lateral angle between the horizontal and a line connecting the squid eye with the midpoint of the prey at the start of the approach (θ_{la}) and the start of the strike (θ_{ls}) (Fig. 1). The lateral and ventral distances between squid and prey at the start of the approach and start of the strike were determined using ImageJ software. Both lateral and ventral points were used together, via calculations in Excel, to determine squid and prey swimming velocities (V), distances traveled during the approach by both squid and prey, distances to the prey at the start of the approach and strike, tentacle extension velocity during the strike (averaged from both tentacles) and distance traveled during the strike by the squid. All velocities and mantle diameter data were smoothed using a fourth order Butterworth filter within an in-house MATLAB routine. Mantle contraction rate and all accelerations (A) were calculated from the smoothed data for each sequence by evaluating the derivatives using fourth order finite difference equations using in-house MATLAB code.

When multiple attacks were recorded for an individual squid, average values for kinematic variables per squid were used in statistical analyses. Mean and peak velocities (V_{avg} and V_{peak}) and accelerations (A_{avg} and A_{peak}) were calculated for squid during each of the three attack phases. In addition, V_{avg} and A_{avg} were computed for the prey during the approach and V_{avg} and V_{peak} were calculated for the tentacles during the strike. However, because the temporal window was too short to use proper smoothing methods, R , ω , θ_{total} , A , mantle contraction rate, and fin beat frequency were not determined for the strike.

Statistical methods

For each phase, i.e. approach, strike and recoil, differences in kinematic variables for attacks on shrimp versus fish were determined using one-way MANOVAs (SPSS v.18). Two additional one-way MANOVAs (one for shrimp encounters, one for fish encounters) were performed to examine differences in agility and maneuverability during the approach, recoil and non-predatory turns. Data for non-predatory turns derive from Jastrebsky et al. (2016) and were recorded using identical measurement approaches to those described here, with the only difference being that non-predatory turns did not involve prey. MANOVAs were used to account for possible relationships among kinematic variables and control for experiment-wise error that may arise from running multiple ANOVAs or t -tests. The Wilks' Lambda test statistic was used for MANOVAs and the least significant difference *post hoc* test was used for multiple comparisons. The ventral angles and distances between predator and prey from the start of the approach and start of the strike were compared using paired t -tests (SPSS). To account for percentage data, a non-parametric Kruskal–Wallis one-way ANOVA (SPSS) was used to evaluate potential differences in squid–prey distance and angle. The mantle and arm angles for posture were compared using one-way ANOVAs (SPSS). To determine if squid V_{avg} and V_{peak} differed during the approach, strike and recoil for attacks on shrimp and fish, repeated measures ANOVAs (SPSS) were performed, as the same individuals were considered across the three phases. If the data did not meet assumptions for normality, either a log10 or square root transformation was performed.

RESULTS

Attacks on shrimp

When attacks on shrimp were considered, squid $(R/L)_{\text{min}}$ and squid $(R/L)_{\text{mean}}$ were significantly lower for non-predatory turns than for the approach phase, with squid $(R/L)_{\text{mean}}$ also being significantly lower for non-predatory turns than for the recoil phase (Table 1). Squid demonstrated greater maximum agility (ω_{max}) during the recoil phase than for the approach phase and non-predatory turns, but ω_{mean} was highest for non-predatory turns followed by the recoil and approach phases of predator–prey interactions (Table 1). Squid decreased the ventral angle (θ_{v}), ventral distance and three-dimensional distance (using both lateral and ventral views) between themselves and shrimp prey from the start of the approach [mean $\theta_{\text{va}} = 52.3 \pm 7.6$ deg (mean \pm s.e.m. convention used here and throughout Results), mean ventral distance = 9.3 ± 0.9 cm and mean distance = 14.9 ± 2.0 cm] to the start of the strike (mean $\theta_{\text{vs}} = 5.7 \pm 0.6$ deg, mean ventral distance = 3.6 ± 0.3 cm and mean distance = 4.4 ± 0.4 cm) (paired t -test ventral angle: $t = 9.0$, df_{33} , $P < 0.001$; paired t -test ventral distance: $t = 8.8$, df_{33} , $P < 0.001$; paired t -test three-dimensional distance: $t = 8.9$, df_{32} , $P < 0.001$). Out of 40 attacks on shrimp, there were 33 successful captures, 4 strikes with no capture and 3 approaches with no strike. Therefore, capture success rate when strikes were initiated was 89.2%.

Attacks on fish

When attacks on fish were considered, squid demonstrated significantly higher $(R/L)_{\text{min}}$ for both the approach and recoil phases than for non-predatory turns. Squid $(R/L)_{\text{mean}}$ was significantly greater during the recoil phase than for non-predatory turns, but there was no significant difference between the approach and recoil phases (Table 1). The squid ω_{max} in the recoil phase was significantly higher than both the approach phase and non-predatory turns. The squid ω_{mean} was significantly lower for both the approach and recoil phases than for non-predatory turns

Table 1. MANOVA results for kinematic variables in attacks on either shrimp or fish between the approach phase, recoil phase and non-predatory turns

	Approach	Recoil	Non-predatory turns	MANOVA
Attacks on shrimp				
(R/L) _{min}	^a 0.007±0.001	^{a,b} 0.007±0.001	^b 0.004±0.0006	$F=2.02$, $df_{10,138}$ * $P=0.049$ (Ap versus Np)
(R/L) _{mean}	^a 0.3±0.04	^a 0.3±0.07	^b 0.009±0.004	$F=7.0$, $df_{10,138}$ ** $P=0.001$ (Ap versus Np) ** $P=0.002$ (Re versus Np)
ω_{max}	^b 288.3±33.4 deg s ⁻¹	^a 425.6±39.6 deg s ⁻¹	^b 268.4±32.9 deg s ⁻¹	$F=4.4$, $df_{10,138}$ * $P=0.016$ (Ap versus Re) * $P=0.016$ (Re versus Np)
ω_{mean}	^a 36.2±3.8 deg s ⁻¹	^b 60.0±9.3 deg s ⁻¹	^c 110.3±14.6 deg s ⁻¹	$F=13.5$, $df_{10,138}$ * $P=0.047$ (Ap versus Re) ** $P<0.001$ (Ap versus Np) ** $P=0.001$ (Re versus Np)
Attacks on fish				
(R/L) _{min}	^a 0.01±0.002	^a 0.01±0.002	^b 0.004±0.0006	$F=8.3$, $df_{10,70}$ ** $P=0.001$ (Ap versus Np) ** $P=0.001$ (Re versus Np)
(R/L) _{mean}	^{a,b} 0.6±0.1	^a 1.0±0.4	^b 0.009±0.004	$F=4.8$, $df_{10,70}$ ** $P=0.004$ (Re versus Np)
ω_{max}	^b 302.6±50.7 deg s ⁻¹	^a 444.0±55.6 deg s ⁻¹	^b 268.4±32.9 deg s ⁻¹	$F=3.7$, $df_{10,70}$ * $P=0.041$ (Ap versus Re) * $P=0.014$ (Re versus Np)
ω_{mean}	^b 50.3±12.8 deg s ⁻¹	^b 71.2±12.9 deg s ⁻¹	^a 110.3±14.6 deg s ⁻¹	$F=5.3$, $df_{10,70}$ ** $P=0.003$ (Ap versus Np) * $P=0.05$ (Re versus Np)

All values are reported as means ±s.e.m. Attacks on shrimp: $N_{approach}=34$, $N_{recoil}=33$, $N_{non-pred}=14$; attacks on fish: $N_{approach}=15$, $N_{recoil}=14$, $N_{non-pred}=14$. Same letters within a row indicate no significant difference. * $P<0.05$, ** $P<0.005$. Ap, approach; Re, recoil; Np, Non-predatory turns. Data for non-predatory turns are from Jastrebsky et al. (2016).

(Table 1). Squid decreased the ventral angle, ventral distance and three-dimensional distance between the squid and the fish prey from the start of the approach (mean=42.1±9.4 deg, 14.0±3.1 cm and 24.4±6.3 cm) to the start of the strike (mean=3.3±0.4 deg, 4.6±0.6 cm and 5.3±0.6 cm) (paired t -test ventral angle: $t=8.1$, df_{14} , $P<0.001$; paired t -test ventral distance: $t=3.9$, df_{14} , $P=0.002$; and paired t -test three-dimensional distance: $t=4.05$, df_{13} , $P=0.001$, respectively). Out of 18 attacks there were 13 successful captures, 3 strikes with no capture and 2 approaches with no strike. Thus, capture success rate when strikes were initiated was 81.3%.

Approach kinematics

The distance traveled by the squid during the approach did not significantly differ between attacks on shrimp and fish. However, the distance traveled by prey during the approach did differ significantly between shrimp and fish encounters, with fish traveling about twice as far (Table 2). The squid swam and accelerated significantly faster in the approach during attacks on fish than attacks on shrimp, as indicated by higher V_{avg} , V_{peak} , A_{avg} and A_{peak} . This is consistent with higher V_{avg} and A_{avg} values recorded for fish prey relative to shrimp prey (Table 2). The squid traveled significantly faster than the prey on average during the approach for attacks on shrimp (t -test: $t=4.5$, df_{33} , $P<0.001$) but not for attacks on fish ($t=0.8$, df_{14} , $P=0.4$). As prey V_{avg} for both shrimp and fish increased during the approach, so did squid V_{avg} (Fig. 2A).

Squid were significantly more maneuverable [lower (R/L)_{min} and (R/L)_{mean}] in the approach for attacks on shrimp than attacks on fish (Table 2). However, no significant differences in ω_{max} , ω_{mean} or

θ_{total} were found for squid approaching shrimp relative to fish. No significant difference in ventral angle (θ_{va}) for attacks on shrimp and fish was found, and ω_{max} and ω_{mean} increased with increasing θ_{va} for both shrimp and fish (Fig. 2B,C). As total angular displacement (θ_{total}) during the approach increased, ω_{max} and ω_{mean} also increased for encounters with both shrimp and fish (Fig. 3A,B).

Mantle contraction rate largely correlated well with acceleration, indicating that the pulsed jet had a large impact on speed during the approach, with many sequences correlating strongly (Pearson correlation: $r>0.5$, $P<0.005$). Generally, there were two peaks in velocity during the approach, with the first peak occurring at the beginning of the approach and the second occurring at the end of the approach, just before the strike was initiated (Fig. 4). The first peak in velocity corresponded with a peak in angular velocity, as the squid made a rapid turn toward the prey, and the second peak in velocity occurred during the final arms-first lunge towards the prey, following a largely linear trajectory toward the prey (Fig. 5A,B,E,F). In cases where the prey was moving quickly during the approach, additional corrective turns were often necessary to realign with the prey (Fig. 5C,D,G,H). However, even in these corrective cases, the initial turn toward the prey was still associated with the greatest angular velocities.

Strike kinematics

During the strike phase, the squid V_{avg} and V_{peak} were significantly higher for fish encounters than shrimp encounters (Table 3). The highest individual squid swimming velocity was 47.5 cm s⁻¹ (8.2 DML s⁻¹) for attacks on shrimp and 56.4 cm s⁻¹

Table 2. MANOVA results for approach kinematic comparisons between attacks on shrimp and attacks on fish

	Attacks on shrimp	Attacks on fish	MANOVA
Distance traveled by squid during approach	8.4±1.0 cm	10.5±2.4 cm	$F=0.9$, $df_{20,28}$, $P=0.3$
Distance traveled by prey during approach	4.6±0.7 cm	8.9±1.6 cm	$F=8.2$, $df_{20,28}$, * $P=0.006$
Squid V_{avg}	2.1±0.2 DML s ⁻¹	3.7±0.4 DML s ⁻¹	$F=20.6$, $df_{20,28}$, ** $P<0.001$
Squid V_{peak}	4.1±0.3 DML s ⁻¹	8.5±1.1 DML s ⁻¹	$F=27.9$, $df_{20,28}$, ** $P<0.001$
Prey V_{avg}	3.5±0.5 cm s ⁻¹	8.9±1.5 cm s ⁻¹	$F=18.5$, $df_{20,28}$, ** $P<0.001$
Squid A_{avg}	6.1±0.5 DML s ⁻²	12.7±1.3 DML s ⁻²	$F=33.8$, $df_{20,28}$, ** $P<0.001$
Squid A_{peak}	24.5±2.6 DML s ⁻²	44.3±5.0 DML s ⁻²	$F=15.7$, $df_{20,28}$, ** $P<0.001$
Prey A_{avg}	25.9±3.7 cm s ⁻²	43.5±7.3 cm s ⁻²	$F=5.8$, $df_{20,28}$, * $P=0.02$
Squid (R/L) _{min}	0.007±0.0009	0.01±0.002	$F=7.8$, $df_{20,28}$, * $P=0.007$
Squid (R/L) _{mean}	0.3±0.04	0.6±0.1	$F=6.4$, $df_{20,28}$, * $P=0.02$
Squid ω_{max}	288.3±33.4 deg s ⁻¹	302.6±50.7 deg s ⁻¹	$F=0.06$, $df_{20,28}$, $P=0.8$
Squid ω_{mean}	36.2±3.8 deg s ⁻¹	50.3±12.8 deg s ⁻¹	$F=2.02$; $df_{20,28}$, $P=0.2$
Squid θ_{total}	46.9±6.6 deg	44.9±9.6 deg	$F=0.03$, $df_{20,28}$, $P=0.9$

All values are reported as means ±s.e.m. Attacks on shrimp: $N=34$; attacks on fish: $N=15$. * $P<0.05$, ** $P<0.005$. DML, dorsal mantle length.

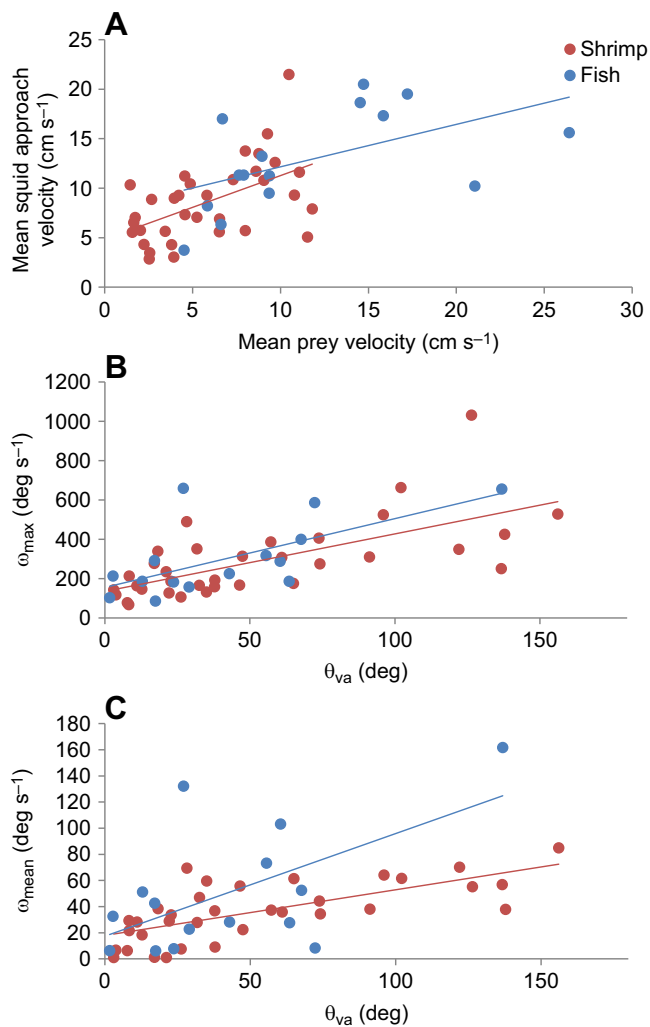


Fig. 2. Kinematic measurements recorded as squid approached shrimp and fish. (A) Mean squid approach velocity increased with increased mean shrimp velocity (linear regression: $y=0.6x+4.8$, $R^2=0.3$, $P=0.001$) and mean fish velocity (linear regression: $y=0.4x+7.9$, $R^2=0.3$, $P=0.04$). (B) Squid maximum and (C) mean angular velocity (ω_{\max} and ω_{mean} , respectively) increased with greater ventral angles (θ_{va}) at the start of approach (squid ω_{\max} for shrimp interactions: linear regression, $y=2.9x+135.6$, $R^2=0.4$, $P<0.001$; squid ω_{\max} for fish interactions: linear regression, $y=3.5x+155.8$, $R^2=0.4$, $P=0.009$; squid ω_{mean} for shrimp interactions: linear regression, $y=0.3x+17.9$, $R^2=0.5$, $P<0.001$; squid ω_{mean} for fish interactions: linear regression, $y=0.8x+17.3$, $R^2=0.3$, $P=0.02$).

(16.5 DML s^{-1}) for attacks on fish. The V_{avg} and V_{peak} of the tentacles did not differ significantly for attacks on shrimp and fish (Table 3). The fastest tentacle V_{peak} (averaged from both tentacles) observed from an individual was 123.7 cm s^{-1} for shrimp and 102.4 cm s^{-1} for fish. The tentacle V_{avg} during the strike was significantly faster than both the shrimp swimming V_{avg} (t -test: $t=10.4$, df_{32} , $P<0.001$) and fish swimming V_{avg} (t -test: $t=4.3$, df_{13} , $P=0.001$). No significant differences in squid/prey angles or distances at the start of the strikes were detected for attacks on shrimp and fish. As squid/prey distance at the start of the strike increased, squid V_{peak} and tentacle V_{peak} increased for attacks on shrimp and fish (Fig. 3C,D). For attacks on shrimp, tentacle V_{avg} and V_{peak} increased with squid V_{avg} and V_{peak} , respectively (regression V_{avg} : $R^2=0.3$, $P=0.001$; regression V_{peak} : $R^2=0.2$, $F=7.8$, $P=0.009$). However, no such relationship was detected for attacks on fish.

There was no significant difference in capture success for attacks on shrimp versus attacks on fish.

Recoil kinematics

During the recoil phase, the squid switched from arms-first swimming to tail-first swimming, reversing swimming direction from the approach and strike. Squid V_{avg} , V_{peak} , A_{avg} and A_{peak} were all significantly higher for attacks on fish than shrimp (Table 4). Squid $(R/L)_{\text{min}}$ and $(R/L)_{\text{mean}}$ were both significantly lower for shrimp recoils than for fish recoils (Table 4). There were no significant differences in ω_{\max} , ω_{mean} or θ_{total} between shrimp and fish recoils (Table 4). ω_{mean} and ω_{\max} increased with greater θ_{total} for attacks on both shrimp and fish (Fig. 3E,F).

Predator–prey angles and squid posture

At the beginning of the squid approach, shrimp prey were positioned equally above and below the squid. However, at the beginning of the strike, significantly more shrimp were located below than above the squid (ANOVA: $F=11.6$, $df_{3,156}$, $P=0.02$). This was also the case for fish–squid interactions (ANOVA: $F=4.3$, $df_{3,68}$, $P=0.03$) (Fig. 6A,B). Mantle orientation played a role during shrimp attacks, with the percentage of tail-up strikes (mean=88.2±6.0%) being significantly greater than tail-down strikes (mean=11.8±2.7%) and tail-down approaches (mean=42.7±5.0%) (ANOVA: $F=10.1$, $df_{3,316}$, $P<0.001$ and $P=0.01$, respectively) (Fig. 6C). There was also a significantly greater percentage of tail-up approaches than tail-down strikes (ANOVA: $F=10.1$, $df_{3,316}$, $P=0.004$) (Fig. 6C). In contrast, there were no differences in percentage of attacks in tail-up or -down orientations for attacks on fish (Fig. 6D).

DISCUSSION

This study represents the first comprehensive quantitative kinematic analysis of squid and prey in unrestrained predator–prey encounters. The results presented here demonstrate that agility, maneuverability, and swimming speed/acceleration are all important for prey capture in *L. brevis*. During fish and shrimp prey interactions, squid exhibited ω_{\max} values for the approach and recoil phases comparable to, or even higher than, those observed at the performance extremes of non-predatory turning. During shrimp encounters, squid exhibited R/L values more similar to those reported for non-predatory turning than in fish encounters, and R/L values for approaches on shrimp were lower than those for approaches on fish. While squid did not turn as tightly when chasing fish, they achieved higher swimming velocities and accelerations than those during shrimp encounters, which is consistent with the higher swimming speeds/accelerations observed for fish prey. The different *Lolliguncula brevis* attack strategies for the two prey seem to be very effective given the high capture success rates observed for both fish (81%) and shrimp (89%) in the present study. Indeed, the capture success rates recorded here are very similar to those for cuttlefish *Sepia officinalis* attacking prawns (91%) (Messenger, 1977).

Like many nekton, squid located prey positioned laterally to their bodies, turned and attacked head first (and eyes first). The greatest ventral angle that an individual *L. brevis* noticed prey in this study was 156.1 deg, indicating that *L. brevis* is capable of detecting prey at high angles within their visual field. Irrespective of prey type, squid reduced their ventral angle relative to the prey from the beginning of the approach, when the target was first identified, to the beginning of the strike, thereby quickly aligning the tentacles with the prey in preparation for the strike. This is supported by higher squid angular velocities occurring with larger ventral angles and larger total

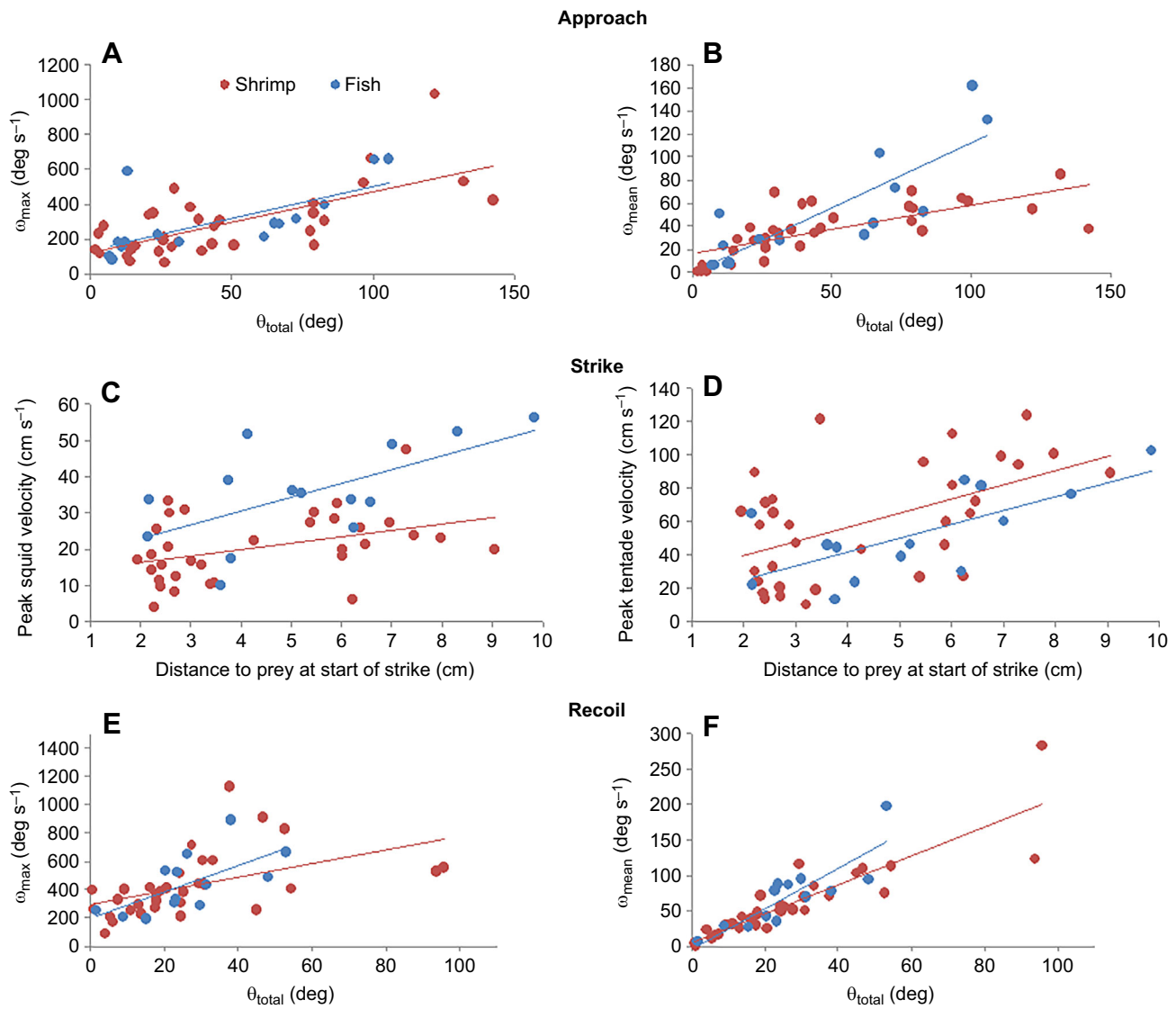


Fig. 3. Kinematic measurements for the approach, strike and recoil phases for squid pursuing shrimp and fish. (A,B) As total angular displacement (θ_{total}) of the squid increased during the approach, maximum and mean angular velocity of the squid (ω_{max} and ω_{mean} , respectively) increased both for interactions with shrimp (ω_{max} linear regression, $y=3.5x+125.1$, $R^2=0.5$, $P<0.001$; ω_{mean} linear regression, $y=0.4x+16.5$, $R^2=0.5$, $P<0.001$) and fish (ω_{max} regression, $y=3.7x+138.8$, $R^2=0.5$, $P=0.004$; ω_{mean} linear regression, $y=1.1x-0.1$, $R^2=0.7$, $P<0.001$). (C,D) As distance to the prey at the start of the strike increased, peak squid velocity (linear regression for shrimp encounters: $y=1.8x+12.8$, $R^2=0.2$, $P=0.02$; linear regression for fish encounters: $y=3.8x+15.3$, $R^2=0.4$, $P=0.02$) and peak tentacle velocity (linear regression for shrimp encounters, $y=8.5x+22.5$, $R^2=0.3$, $P=0.002$; linear regressions for fish encounters, $y=8.3x+8.5$, $R^2=0.5$, $P=0.006$) also increased. (E,F) As total angular displacement (θ_{total}) of the squid increased during the recoil, maximum and mean angular velocity of the squid (ω_{max} and ω_{mean} , respectively) increased both for interactions with shrimp (ω_{max} linear regression, $y=4.8x+295.7$, $R^2=0.2$, $P=0.004$; ω_{mean} linear regression, $y=2.0x+5.1$, $R^2=0.8$, $P<0.001$) and fish (ω_{max} linear regression, $y=9.4x+196.5$, $R^2=0.4$, $P=0.02$; ω_{mean} linear regression, $y=2.8x-4.3$, $R^2=0.7$, $F=29.4$, $df_{1,11}$, $P<0.001$).

angular displacements during the approach for both shrimp and fish prey encounters (Figs 2 and 3). In contrast, there was no relationship between angular velocity and total angular displacement for non-predatory turns where prey strikes were not the end point (Jastrebsky et al., 2016). This difference between non-predatory and predatory turns suggests that squid actively increase turning speed when targeting prey positioned at high ventral angles, allowing for rapid positional adjustment upon initial detection of prey.

Approach phase

The maximum angular velocity during the approach phase for squid encounters with shrimp and fish was comparable to non-predatory turns, but mean angular velocity was actually less than in non-predatory turns (Table 1). The lower mean angular velocity for the

approach phase in the present study is most likely due to the approach phase not being entirely rotational, i.e. when tracking prey, translation is required to keep pace with the prey as opposed to exclusive turning. This higher level of translation is also likely to have impacted R/L , which tended to be higher for approaches toward prey [$(R/L)_{\text{mean}}=0.3-0.6$] than during non-predatory turns [$(R/L)_{\text{mean}}=0.009$]. Although squid clearly are capable of exhibiting high agility (turning speed) during the approach, agility did not consistently increase for faster prey (i.e. no difference in squid ω was detected between shrimp and fish, Table 2), suggesting that other factors besides prey speed impact agility performance during the approach toward the prey.

Clear differences were observed in how squid behave in encounters with shrimp versus fish. Fish prey swam and accelerated significantly faster than the shrimp prey during the squid approach, and the

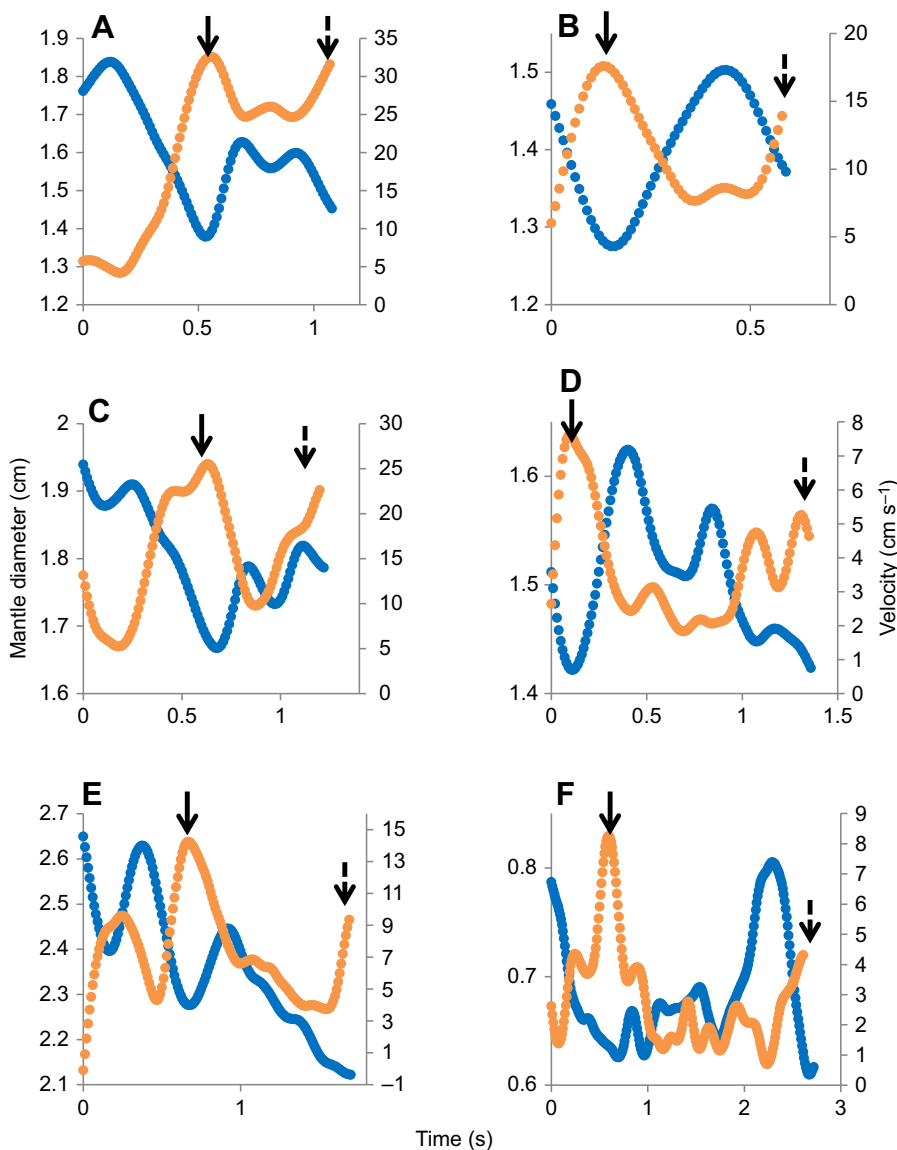


Fig. 4. Mantle diameter and swimming velocity for squid during six approach sequences. Mantle diameter (blue circles) and swimming velocity (orange circles) for attacks on shrimp (A,C,E) and fish (B,D,F). Note the peak in velocity at the beginning of the approach (solid black arrow) and near the end of approach (broken black arrow) generally correlated with mantle contraction.

fast-swimming fish also elicited higher squid approach velocities and accelerations (Table 2). Fish probably had a greater capacity for escape than shrimp during the approach because of their faster swimming speeds and the presence of a lateral line for sensing predator wakes (Coombs et al., 1989; Stewart et al., 2014), and thus the squid may have increased its approach speed to limit the opportunity for the fish to initiate a fast escape. Fish prey that are approached by a fish predator moving at a higher speed respond and escape at greater distances than fish prey approached by predators moving at slower speeds (Domenici and Blake, 1991, 1997; Stewart et al., 2013, 2014). The improved escape response at higher predator approach speeds is due to the formation of larger bow waves from faster predators, which can be more readily sensed by the lateral line system of fish prey (Stewart et al., 2014). Although squid also produce bow waves as predators, the correlation between approach speed and prey escape success was not obvious in this study. This may be simply a product of limited successful prey escape sequences, or perhaps it is related to the production of smaller bow wakes by squid. Unlike fish that strike prey targets with their jaws, often with an associated suction wake (Visser, 2001; Holzman and Wainwright, 2009; Stewart et al., 2013, 2014), squid impact their prey targets with

streamlined, fast-moving tentacles that likely have a reduced bow flow profile. This intriguing hypothesis merits further study.

Based on the lower $(R/L)_{\min}$ and $(R/L)_{\text{mean}}$ observed in this study for squid approaching shrimp versus fish, squid exhibited a higher degree of maneuverability when targeting shrimp. Since shrimp move much slower than the fish prey, the squid have more time during the approach to perform controlled tight turns to get into an optimal position for striking. Squid presumably did not have the luxury of precise turning during encounters with faster swimming fishes. Instead, the squid relied more heavily on fast swimming speed and acceleration to approach the fish.

The arms-first approaches toward fish in the present study were performed at relatively high speeds, reaching average velocities of up to 5 DML s^{-1} (60 cm s^{-1}). This result differs from observations in other squids. Foyle and O'Dor (1988) found that *I. illecebrosus* slowly stalk faster and larger fish prey, similar to cuttlefish (Messenger, 1968, 1977). This strategy was thought to be due to swimming limitations in the arms-first orientation (Foyle and O'Dor, 1988). Although there are funnel aperture constraints during arms-first swimming that potentially limit steady rectilinear swimming speeds (Bartol et al., 2001b), the high arms-first

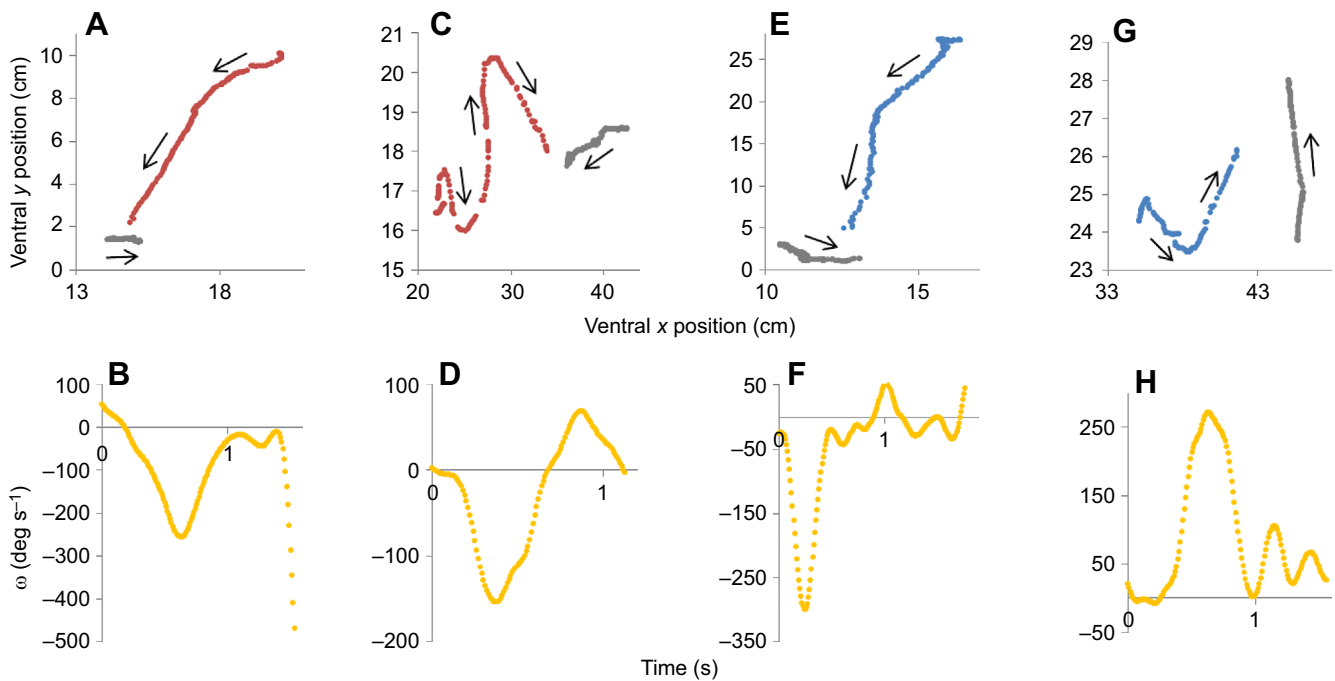


Fig. 5. Approach trajectories of squid and prey and angular velocity of squid. (A,C,E,G) Approach trajectories of squid and prey. Red circles represent attacks on shrimp, blue circles attacks on fish by the squid. Gray circles represent trajectories of shrimp (A,C) or fish (E,G). (B,D,F,H) Angular velocity (ω) of squid (orange circles; B,D: shrimp; F,H: fish). The squid trajectory was tracked using arm point 3 (see Fig. 1). The approach was complete when the arms began to splay to initiate the strike. Arrows indicate the direction of motion during the approach. The corresponding minimum length specific radius of the turn $[(R/L)_{\min}]$ for the squid approach angular velocity plots were: attacks on shrimp in A,B: 0.005 and C,D: 0.02; attacks on fish in E,F: 0.007 and G,H: 0.005. The corresponding squid maximum angular velocity (ω_{\max}) during the approach were: attacks on shrimp in B, 256.0 deg s⁻¹ and D, 153.7 deg s⁻¹; attacks on fish in F, 299.7 deg s⁻¹ and H, 270.8 deg s⁻¹. Intervals between points are 0.01 s.

speeds recorded here coupled with recent recorded *L. brevis* swimming speeds of 6.6 dorsal mantle lengths s⁻¹ in the arms-first orientation (Bartol et al., 2016) indicate that *L. brevis* is certainly capable of overcoming these constraints and producing short bursts of high-speed arms-first swimming when pursuing prey.

Some common behavioral patterns were observed for squid encounters with both fish and shrimp. For both prey, the squid approach began with a peak in angular velocity after a strong mantle contraction, indicating that the initial speed of the squid is mostly rotational. A second peak in linear velocity occurred at the end of the approach after a mantle contraction, moving into the strike. Thus, two jets are important for prey attacks: (1) an initial powerful jet to rotate the squid and orient it to the prey and (2) a secondary jet to accelerate the squid toward the prey for the attack. In some cases, additional corrective swimming movements were superimposed on these two principal jets to hone in on prey (Fig. 5).

Strike phase

The arms-first attack orientation observed in the present study has been well-documented in squid and cuttlefish (Messenger, 1968, 1977; Foyle and O'Dor, 1988; Nicol and O'Dor, 1985; Squires,

1966; Kier and Van Leeuwen, 1997), as the arms and tentacles are integral to prey capture. Somewhat unexpected, however, was the finding that squid were capable of controlling not only their own peak swimming velocity but also the tentacle peak extension velocity, depending on the squid–prey distance at the start of the strike. In addition to velocity modulation, torsional adjustments in the tentacles during strikes also probably aided strike success, as found in *D. pealeii* (Kier and Van Leeuwen, 1997). For both shrimp and fish encounters, the peak velocity of the squid and the tentacles increased with increased squid–prey distance at the start of the strike. This strategy probably improves strike success, as the squid needs to close the predator–prey gap more quickly with greater distances to reduce prey reaction times. The average and peak squid swimming velocity during the strike was higher for attacks on fish than shrimp (Table 3), most likely due to the fish's greater escape capacity. However, the average and peak tentacle extension velocity was no different for shrimp or fish prey, indicating that squid opt to increase swimming speed and not tentacle strike velocity when attacking faster prey. The cuttlefish *S. officinalis* maintains a distance of approximately one mantle length prior to the strike (Messenger, 1977) whereas *D. pealeii* attack prey at ~ 0.3 mantle lengths (Kier and Van Leeuwen, 1997).

Table 3. MANOVA results for strike kinematic comparisons between attacks on shrimp and attacks on fish

	Attacks on shrimp	Attacks on fish	MANOVA
Squid V_{avg}	3.3±0.3 DML s ⁻¹	6.8±0.8 DML s ⁻¹	$F=27.7$, $df_{10,36}$, $**P<0.001$
Squid V_{peak}	5.1±0.4 DML s ⁻¹	10.4±1.1 DML s ⁻¹	$F=30.9$, $df_{10,36}$, $**P<0.001$
Tentacle V_{avg}	21.6±1.7 cm s ⁻¹	23.9±3.1 cm s ⁻¹	$F=0.5$, $df_{10,36}$, $P=0.5$
	5.4±0.4 DML s ⁻¹	6.9±0.9 DML s ⁻¹	$F=3.0$, $df_{10,36}$, $P=0.09$
Tentacle V_{peak}	59.7±5.8 cm s ⁻¹	52.5±7.1 cm s ⁻¹	$F=0.5$, $df_{10,36}$, $P=0.5$
	14.6±1.4 DML s ⁻¹	15.1±2.0 DML s ⁻¹	$F=0.03$, $df_{10,36}$, $P=0.9$

All values are reported as means±s.e.m. Attacks on shrimp: $N=33$; attacks on fish: $N=14$. $**P<0.005$.

Table 4. MANOVA results for recoil kinematic comparisons between attacks on shrimp and attacks on fish

	Attacks on shrimp	Attacks on fish	MANOVA
Squid V_{avg}	2.9±0.2 DML s ⁻¹	4.4±0.4 DML s ⁻¹	$F=43.2$, $df_{15,29}$, $**P<0.001$
Squid V_{peak}	4.5±0.3 DML s ⁻¹	7.4±0.9 DML s ⁻¹	$F=11.8$, $df_{15,29}$, $**P=0.001$
Squid A_{avg}	12.0±1.0 DML s ⁻²	22.2±3.6 DML s ⁻²	$F=10.3$, $df_{15,29}$, $**P=0.002$
Squid A_{peak}	30.02±2.9 DML s ⁻²	52.0±0.9 DML s ⁻²	$F=6.2$, $df_{15,29}$, $*P=0.016$
Squid $(R/L)_{min}$	0.007±0.001	0.01±0.002	$F=7.6$, $df_{15,29}$, $*P=0.009$
Squid $(R/L)_{mean}$	0.3±0.07	1.0±0.4	$F=6.0$, $df_{15,29}$, $*P=0.019$
Squid ω_{max}	425.6±39.6 deg s ⁻¹	444.0±55.6 deg s ⁻¹	$F=0.06$, $df_{15,29}$, $P=0.8$
Squid ω_{mean}	60.0±9.3 deg s ⁻¹	71.2±12.9 deg s ⁻¹	$F=0.4$; $df_{15,29}$, $P=0.5$
Squid θ_{total}	26.9±4.02 deg	26.4±3.8 deg	$F=0.004$; $df_{15,29}$, $P=0.9$

All values are reported as means±s.e.m. Attacks on shrimp: $N=33$; attacks on fish: $N=14$. $*P<0.05$, $**P<0.005$.

In the present study, initiation of strikes occurred over similar distances (0.5–1.5 mantle lengths).

Sugimoto and Ikeda (2013) determined that the squid *Sepioteuthis lessoniana* only increased maximum swimming speed with greater distances to prey for the strike, while cuttlefish *Sepia pharaonis* only increased the maximum speed of the tentacles for greater distances to prey for the strike. Findings from the present study indicate that squid *L. brevis* use a combination of both approaches, increasing swimming speed and tentacle speed when necessary. Although squid swam faster during the strike for fish targets than shrimp targets, they still swam slower than the escaping fish. Conversely, squid consistently swam faster than shrimp targets during the strike. Irrespective of the prey target, tentacle speed was much faster than the swimming speed of the prey, with tentacle V_{peak} as high as 124 cm s⁻¹ for *L. brevis*. Larger squid (*D. pealeii*) exhibit even more impressive tentacle velocities of ~250 cm s⁻¹. Thus, clearly a combination of swimming and tentacle extension is essential for strike success, i.e. squid cannot capture faster-moving fish based on their swimming speed alone – they also require fast tentacle extension.

Vertical positioning of the prey played a role in squid attack sequences. At the beginning of the approach phase, the shrimp or fish was equally likely to be above or below the squid. However, at the start of the strike both shrimp and fish were more likely to be positioned below the squid, as the squid repositioned itself so that it was above the prey before initiating the strike (Fig. 6). From this higher vantage point, the tentacles generally moved down and outward towards the prey during the strike. The base of the tentacles is located ventrally within the arm web (Young and Vecchione, 1996), and thus squid may select higher positions in the water column to facilitate easier tentacle elongation and more accurate strikes. Mantle positioning played a more important role in attack behavior for shrimp prey than fish prey, with tail-up orientations being preferred during shrimp strikes. As is the case for cuttlefish (Messenger, 1968, 1977), squid are likely to have significant anterior ocular convergence and the arms probably obscure the anterior visual field to some degree during prey strikes since they are often in-line with the prey strike zone. Thus, a tail-up posture during attacks, which elevates the eyes slightly above the arms, should provide a less obstructed view of the prey and allow the body to be

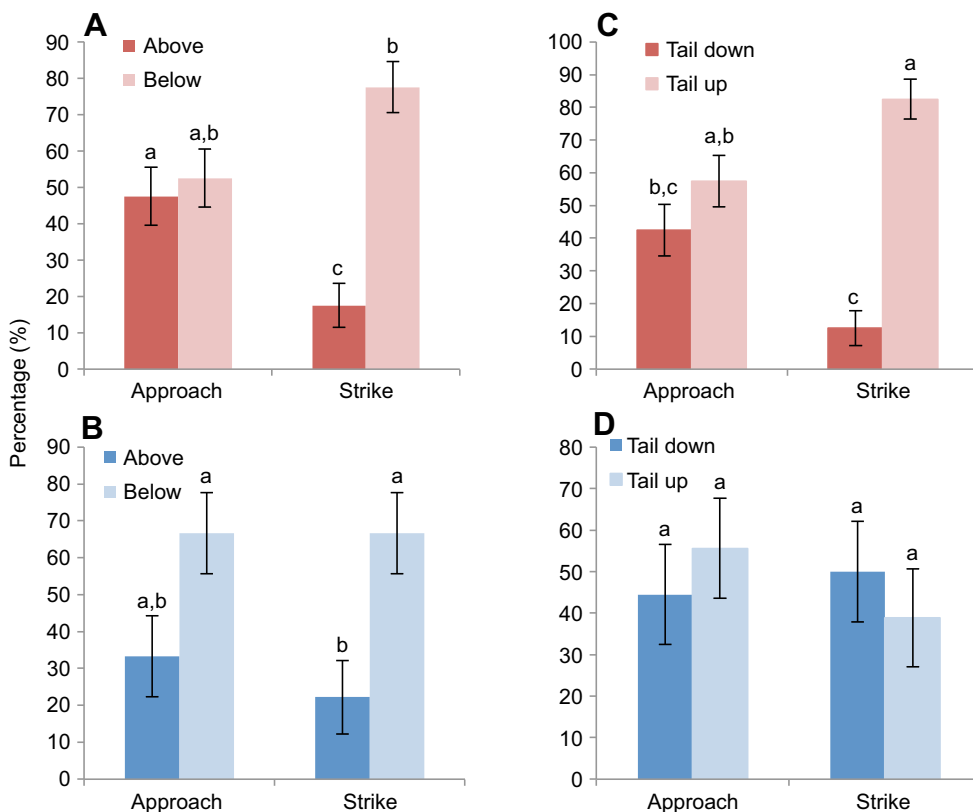


Fig. 6. Percentage of attacks by squid at different positions and orientations during interactions with shrimp and fish. The percentage of attacks is shown with the prey (A, shrimp; B, fish) above or below the squid and the percentage of attacks (C, shrimp; D, fish) with the squid in a tail-down or tail-up orientation at the start of the approach or start of the strike. Same letters indicate no significant difference; different letters indicate a significant difference. Values are means±s.e.m.

more in line with the prey located beneath it. This tail-up posturing was more prevalent during shrimp than fish encounters possibly because slower-swimming shrimp allowed for greater postural adjustments by the squid prior to attacks.

Recoil phase

During the recoil phase, the squid switched from swimming arms-first to swimming tail-first. This reversed motion, combined with simultaneous retraction of the tentacles that adhere to the prey via suckers on the club, mitigates prey escape success. The prey escape attempts are slowed by retraction forces created by the squid swimming in reverse and tentacle recoil. To escape, fish typically use C-starts that project the fish at a heading approximately 90 deg from their original trajectory in the direction opposite the side with initial lateral line hair cell stimulation (Domenici and Blake, 1997; Eaton and Emberley, 1991; Eaton et al., 1977; Gazzola et al., 2012). Shrimp are also capable of rapid escape responses using tail flips (Nicol and O'Dor, 1985). In the present study, tail-flipping escape behavior was not usually initiated until after the tentacles made contact with the shrimp, when capture success was 89%. In those few instances where the shrimp did initiate a tail-flip response prior to tentacle contact, the squid either abandoned the approach and did not deploy the tentacles, or deployed the tentacles but was unsuccessful at capturing the shrimp. In contrast, unsuccessful fish captures were characterized by inaccurate tentacle strikes, which often induced the fish to initiate a C-start escape response following the full deployment of the tentacles, as expected given the 'open loop' control reported in cuttlefish (Messenger, 1977). In successful fish captures, there was no evidence of C-start behavior before the strike, indicating that the fish had likely not sensed the approach of the squid. The observation that escapes were generally not initiated until full deployment of the tentacles provides support for the idea that squid are capable of keeping their body, fin and jet wakes away from the sensing structures of the prey (Arnott et al., 1998; Denton and Gray, 1989; Stewart et al., 2013; Wine, 1984) and maintaining a low tentacle bow wake signature.

During both the recoil and approach, squid exhibited agility measures (approach $\omega_{\max} > 280 \text{ deg s}^{-1}$; recoil $\omega_{\max} > 425 \text{ deg s}^{-1}$) greater than or similar to the performance extremes of turns when translation is not required to track prey targets ($\omega_{\max} = 268 \text{ deg s}^{-1}$). The observed angular velocities during the recoil phases were not driven by the escape attempts of the prey because angular velocity trajectories were smooth and unidirectional, implying that the squid was in control of the motions and no instances of prey escape were observed once the tentacles made contact with the prey. During the recoil phase, the speed and acceleration of the squid were higher for attacks on fish, while the minimum radius of the turn was lower for attacks on shrimp (Table 4). This finding indicates that squid rely more heavily on swimming speed than tight turning to obtain control of faster, stronger fish prey. Enhanced control of the smaller/slower shrimp allowed for more precise turning. The high ω_{\max} observed during recoil for both prey types ($> 425 \text{ deg s}^{-1}$) suggests that rapid spinning may also be important for subduing and possibly disorienting prey.

Comparisons with other taxa

Lolliguncula brevis exhibit high levels of maneuverability during predatory attacks [$(R/L)_{\min} \leq 0.01$] relative to most fishes and cetaceans [$(R/L)_{\min} = 0.06\text{--}0.47$] (Domenici and Blake, 1991, 1997; Webb, 1976, 1983; Webb and Keyes, 1981; Blake et al., 1995). However, they have lower agility ($\omega_{\max} < 500 \text{ deg s}^{-1}$) when compared with similar-sized flexible fish ($\omega_{\max} > 3000 \text{ deg s}^{-1}$) (Gerstner, 1999).

The peak velocities of *L. brevis* during prey strikes on fish (16.5 body lengths s^{-1}) are similar to those of many fishes, such as bluegill sunfish (15.8 body lengths s^{-1}), fathead minnows (14 body lengths s^{-1}), largemouth bass (18.8 body lengths s^{-1}), rainbow trout (15.9 body lengths s^{-1}), and angelfish (17.8 body lengths s^{-1}) (Webb, 1976, 1986; Domenici and Blake, 1991, 1997), but absolute accelerations (m s^{-2}) are lower in brief squid ($< 2.6 \text{ m s}^{-2}$) than in many fishes (10–50 m s^{-2}) (Domenici and Blake, 1991, 1997; Domenici, 2001), although *D. pealeii* can reach 30 m s^{-2} (Kier and Van Leeuwen, 1997). One key advantage that squid have over fish, however, is that they can rapidly extend appendages (tentacles) to capture prey, making them formidable predators.

Conclusions

This study demonstrates that both the tightness (maneuverability) and speed (agility) of turning play important roles throughout attack sequences. Peak agility was $> 280 \text{ deg s}^{-1}$ for the approach and $> 425 \text{ deg s}^{-1}$ for the recoil during both shrimp and fish encounters, and high maneuverability [$(R/L)_{\min} = 0.007$] was especially important for attacks on shrimp. Although maneuverability was also important for fish encounters, *L. brevis* relied more on maximizing linear attack velocities than minimizing turning radii when attacking fast swimming fish. Capture success rate in squid was high and did not differ significantly for shrimp (89%) or fish (81%), despite the ability of fish to swim much faster than shrimp. This result indicates that squid are very effective predators, irrespective of the prey target. This does not come as a surprise given their unique ability to swim readily in multiple orientations (Bartol et al., 2001a,b, 2016), their high maneuverability and agility (Jastrebsky et al., 2016), their capacity to rapidly extend their tentacles and manipulate their muscular arms (Kier and Van Leeuwen, 1997) and their high visual acuity (McCormick and Cohen, 2012; Watanuki et al., 2000).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

R.A.J. and I.K.B. collaborated on the experimental approach, data analysis and preparation of the manuscript. P.S.K. collaborated on the data analysis and preparation of the manuscript. R.A.J. performed the experiments and collected the data. All authors have approved the final version of this article.

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