

Fluid dynamics of feeding behaviour in white-spotted bamboo sharks

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SUMMARY

Although the motor control of feeding is presumed to be generally conserved, some fishes are capable of modulating the feeding behaviour in response to prey type and or prey size. This led to the ‘feeding modulation hypothesis’, which states that rapid suction strikes are pre-programmed stereotyped events that proceed to completion once initiated regardless of sensory input. If this hypothesis holds true, successful strikes should be indistinguishable from unsuccessful strikes owing to a lack of feedback control in specialized suction feeding fishes. The hydrodynamics of suction feeding in white-spotted bamboo sharks (*Chiloscyllium plagiosum*) was studied in three behaviours: successful strikes, intraoral transports of prey and unsuccessful strikes. The area of the fluid velocity region around the head of feeding sharks was quantified using time-resolved digital particle image velocimetry (DPIV). The maximal size of the fluid velocity region is 56% larger in successful strikes than unsuccessful strikes (10.79 cm² vs 6.90 cm²), but they do not differ in duration, indicating that strikes are modulated based on some aspect of the prey or simply as a result of decreased effort on the part of the predator. The hydrodynamic profiles of successful and unsuccessful strikes differ after 21 ms, a period probably too short to provide time to react through feedback control. The predator-to-prey distance is larger in missed strikes compared with successful strikes, indicating that insufficient suction is generated to compensate for the increased distance. An accuracy index distinguishes unsuccessful strikes (−0.26) from successful strikes (0.45 to 0.61). Successful strikes occur primarily between the horizontal axis of the mouth and the dorsal boundary of the ingested parcel of water, and missed prey are closer to the boundary or beyond. Suction transports are shorter in duration than suction strikes but have similar maximal fluid velocity areas to move the prey through the oropharyngeal cavity into the oesophagus (54 ms vs 67 ms).

Key words: hydrodynamics, DPIV, accuracy, behaviour, feeding, shark.

INTRODUCTION

Motor control of the feeding mechanism is typically regarded as phylogenetically conserved in fishes as neuromuscular patterns are similar among diverse species (Wainwright et al., 1989; Friel and Wainwright, 1998; Lauder and Shaffer, 1993; Wilga and Motta, 1998a; Wilga and Motta, 1998b; Wilga and Motta, 2000; Wilga et al., 2000; Grubich, 2001; Wainwright, 2002) (see also Wilga et al., 2001). In spite of this conservatism, most of these fishes are capable of modulating the kinematics of the feeding behaviour in response to prey type, prey size or stage (strike, process, transport, swallow) (Moss, 1972; Liem, 1978; Lauder, 1981; Frazzetta and Prange, 1987; Motta et al., 1997; Nemeth, 1997a; Nemeth, 1997b; Ferry-Graham, 1998; Wilga and Motta, 1998a; Wilga and Motta, 1998b; Wilga and Motta, 2000; Friel and Wainwright, 1998; Pretlow-Edmonds, 1999; Ferry-Graham et al., 2001). In particular, suction strikes are typically shorter in duration than bite strikes, and suction transports are shorter than suction strikes (Gillis and Lauder, 1995; Wilga and Motta, 1998a; Wilga and Motta, 1998b; Wilga and Motta, 2000; Motta et al., 1997; Westneat, 2006; Motta, 2004). Technological advances in measuring fluid flow have resulted in a recent upsurge of studies on the hydrodynamics of suction feeding in fishes (Higham et al., 2006a; Higham et al., 2006b; Nauwelaerts et al., 2007). Thus, the effect of kinematic modulation on the resulting fluid-flow pattern around the head of a feeding fish can now be tested.

Specialized suction or ram feeding shark species exhibit shorter durations and less modulatory ability than more generalized taxa that use a combination of these behaviours (Motta and Wilga, 2001). These observations led to the ‘feeding modulation hypothesis’, which states that rapid suction strikes are pre-programmed and stereotyped events that proceed to completion once initiated regardless of sensory input (Motta and Wilga, 2001). If this hypothesis holds true, then, once initiated, the hydrodynamics of successful strikes should be indistinguishable from those of unsuccessful strikes owing to a lack of feedback control.

Another essential component of the feeding mechanism is transport of the prey (Lauder, 1985; Lauder and Shaffer, 1993; Gillis and Lauder, 1994; Gillis and Lauder, 1995). If the prey is not swallowed as part of the strike event, the food must be transported through the oropharyngeal cavity into the oesophagus. The kinematics of aquatic prey transport are distinct from those of the strike in larval tiger salamanders, *Ambystoma tigrinum* (Gillis and Lauder, 1994), bluegill sunfish, *Lepomis macrochirus* (Gillis and Lauder, 1995), and elasmobranchs (Motta et al., 1997; Wilga and Motta, 1998a; Wilga and Motta, 1998b; Wilga and Motta, 2000; Dean and Motta, 2004). The duration of prey transport is typically shorter than the strike, and this trend is remarkably consistent among phylogenetically divergent basal vertebrate taxa. The hydrodynamics of suction transports might also be abbreviated as the prey is already contained within the jaws, indicating modulation by feeding stage.

However, the hydrodynamics of suction transports might be indistinguishable from suction strikes, supporting the feeding modulation hypothesis.

In this study, the hydrodynamic characteristics of the feeding behaviour are used to test two hypotheses regarding feeding in a suction feeding specialist – the white-spotted bamboo shark *Chiloscyllium plagiosum*. First, the hydrodynamics of successful prey strikes are compared with those of unsuccessful strikes (misses) to test whether strike behaviour is a pre-programmed stereotypical event that runs to completion once initiated – i.e. testing the ‘feeding modulation hypothesis’. If the hypothesis is true, then the hydrodynamics of successful and unsuccessful strikes should be indistinguishable owing to a lack of feedback control. We calculate an accuracy index to determine whether prey position or proximity affects success rate. Second, the hydrodynamics of suction strike and suction transport behaviours are compared to test whether suction behaviours in general conform to the feeding modulation hypothesis or whether they are modulated depending on feeding stage. Our findings will be discussed in the framework of both feed-forward and feedback control theory.

MATERIALS AND METHODS

Animals

Four white-spotted bamboo sharks, *Chiloscyllium plagiosum* (Bennett 1830) (total length 68–72 cm), were donated by SeaWorld of San Diego, CA, USA. The sharks were housed in 3028 l aquaria at 24°C and maintained on a diet of squid and silverside fish. The sharks were individually trained to feed on squid in a 151 l experimental glass tank before experiments. An egg-crate wall with an 8×10 cm rectangular opening was placed across the width of the tank and positioned 20 cm from the side of the experimental tank to allow only the head of the shark to pass through. Further forward movement of the shark was restricted by the presence of the pectoral fins against the egg-crate. Pieces of squid mantle ~1 cm² were offered to the shark on the other side of the egg-crate wall to induce capture behaviour (Fig. 1).

Digital particle image velocimetry

The area of the fluid flow generated by the feeding shark was visualized and quantified using digital particle image velocimetry (DPIV). Water in the experimental tank was seeded with silver-coated, near neutrally buoyant, reflective particles at a density of 6.6 mg l⁻¹ (Potter, 12–14 µm diameter). A light beam from a continuous argon-ion laser was focused into a vertical sheet 1–2 mm thick and 10 cm wide to illuminate the plane near the prey and shark head (Fig. 1). As only the head fitted through the egg-crate gate, it was possible to position the laser sheet in the middle of the gate and hence the middle of the head of the shark, ensuring the detection of maximal speed and hence the maximal information that can be provided by a two-dimensional view of a three-dimensional phenomenon. A high-speed, high-resolution (1024×1024 pixels) Photron APX camera was placed perpendicular to the laser sheet to record shark and particle movement at 500 frames s⁻¹.

The fluid-flow pattern around the head of the sharks was recorded for three behaviours for each individual. Strikes are the behaviour whereby the prey was moved towards and into the mouth by suction. Transports are behaviours in which the prey was previously captured and started with the prey held between the jaws and then transported towards the oesophagus using suction. A behaviour was categorized as an unsuccessful strike when a suction event did not result in the prey reaching the jaws at the end of jaw closure.

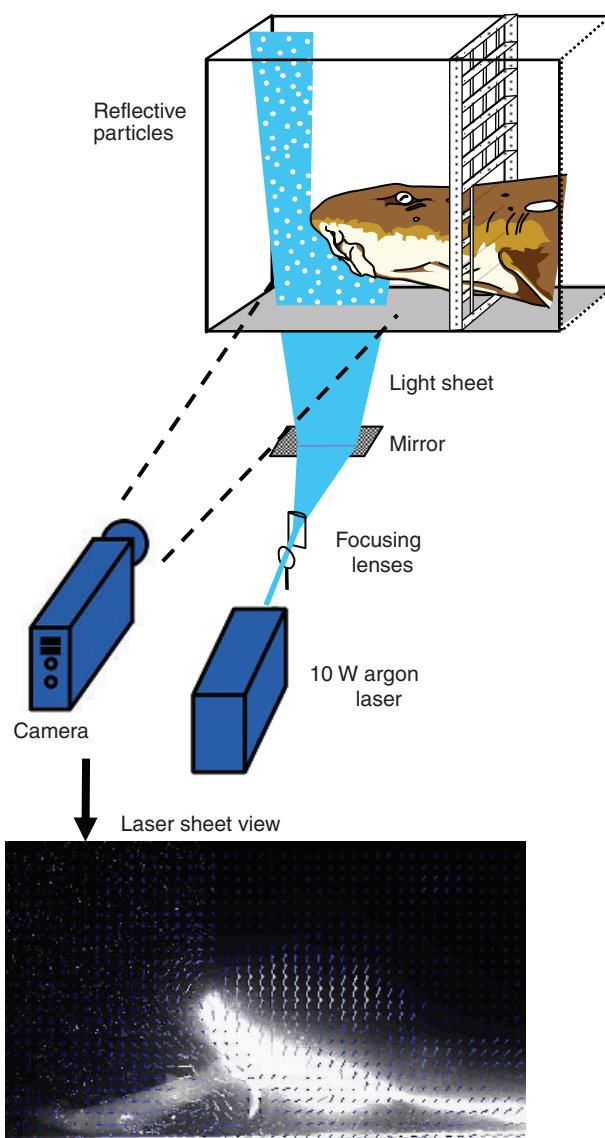


Fig. 1. Schematic of the experimental set-up. The experimental tank was filled with seeded sea water, a 10 W laser was used at 5 W with an optics and mirror system to create a vertical laser sheet, a laterally placed high-speed camera recorded video, and an egg-crate divider ensured an appropriate feeding posture of the shark during experiments. Pieces of squid were presented to the shark using a long blackened skewer.

Images were processed using DaVis 6.2.4 software (LaVision) using a sequential cross-correlation without pre-processing. An initial correlation window of 64×64 pixels was selected with multi-pass with decreasing size to a final interrogation window of 32×32 pixels with 50% overlap. Vector validation was performed, rejecting any vectors with a magnitude greater than two standard deviations from the mean. Vectors interpolated from surrounding vectors replaced rejected vectors. The resulting vector plots representing fluid flow are displayed using the corresponding video image for background and colour-coded vectors indicating velocity. All vectors above the threshold of 5 cm s⁻¹ are considered to be significant flow due to feeding (relative to background flow) (Nauwelaerts et al., 2007). This threshold velocity was chosen at ~5–10% of the peak fluid speed (Muller and Osse, 1984; Day et al., 2005).

Four sequences for each of the three behaviours (successful strikes, transports, unsuccessful strikes) for each of the four individuals were analysed as vector magnitude plot sequences. Time was set to zero at the first image in which vectors above the threshold velocity were calculated. The hydrodynamic cycle measured from the onset of fluid movement into the mouth to the end of fluid movement into the mouth is used synonymously with feeding sequence: note that the hydrodynamic cycle might differ slightly from the gape cycle that is typically used in feeding studies. The area of significant flow is the area comprising all flow vectors with a velocity higher than the threshold velocity. This fluid velocity area was measured throughout the sequence using SigmaScan Pro 4.01. Profiles of fluid velocity area through time were plotted. The time when the prey begins to enter the mouth and when engulfed fully into the mouth cavity was determined from video recordings and plotted onto the fluid velocity area profiles. The initial distance between mouth and the middle of the prey was measured for successful and unsuccessful strikes using SigmaScan Pro 4.

Accuracy index

An accuracy index was calculated for each successful and unsuccessful strike sequence, following the protocol described by Higham and colleagues (Higham et al., 2006a). The boundary of the ingested volume was determined by tracking individual ingested particles during each sequence reversed in time. The length of the long axis and the perpendicular axis at the centre of the long axis was measured and the aspect ratio of the volume calculated as an indicator of the shape of the parcel of ingested water. Strike accuracy was defined as 1 minus the distance from the intersection of both axes (COP) to the centre of mass of the prey (COM), divided by the distance between the COP and the boundary of the ingested volume that intersects the COM of the prey (Higham et al., 2006a). The vertical (A_y) and horizontal (A_x) components of accuracy were determined by projecting prey position onto the coordinate system defined by the two axes, with the COP being the origin, and left and below the origin being negative. These distances were normalized by dividing them by the total lengths of the axes, with the sign of the projection preserved. Thirty-three sequences were analysed here: 16 strikes in the water column, 11 unsuccessful strikes and six strikes on the substrate.

Statistics

The maximal area, duration of the slow mouth-opening phase, total duration of feeding event and prey distance were tested for significant differences among group means of successful strikes, transports and unsuccessful strikes using a MANOVA in STATISTICA 6.1. All data passed the Shapiro–Wilk W test for normality without transformation. Tukey's honestly significant difference (HSD) tests were used as *post hoc* tests. Prey distance was used as the covariate in additional ANCOVAs to test whether the position of the prey confounded the differences between the behaviours. A correlation matrix run in STATISTICA 6.1 was used to test for an association between movement of the prey into the mouth and the time of maximal fluid velocity area.

The aspect ratio of the ingested parcel of water, accuracy index and normalized vertical and horizontal components of accuracy were tested for significant differences in group means among strikes in open water, strikes on substrate and unsuccessful strikes using a MANOVA in STATISTICA 6.1. All data passed the Shapiro–Wilk W test for normality without transformation. Tukey's HSD tests were used as *post hoc* tests. For all the above analyses, behaviour was treated as a fixed effect, and individual as a random effect.

Unless stated otherwise, results are given as means \pm s.d.

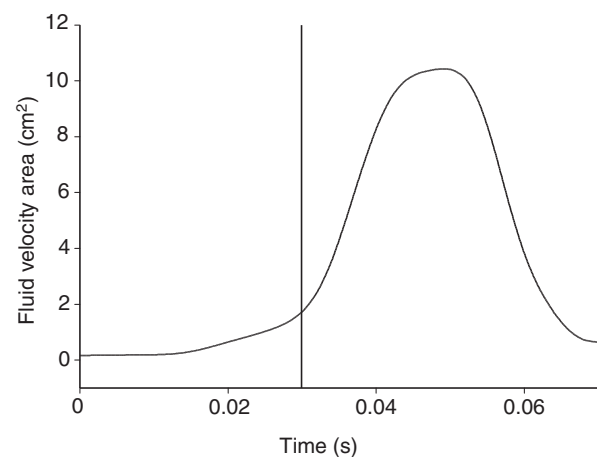


Fig. 2. Fluid velocity area profile showing a representative example of a sequence with a slow fluid-flow phase followed by a fast fluid-flow phase. The vertical line shows the transition from a slow change in area to a phase with more rapidly changing area, as visible from the change in slope of the profile.

RESULTS

Successful strikes

Some strike sequences have a slow opening phase in which slower development of the flow precedes a more rapid development of the flow in a fast opening phase (Fig. 2). A representative sequence showing the general fluid field associated with a suction strike in *C. plagiosum* is illustrated in Fig. 3A. The sequence spans 52 ms and shows three vector magnitude plots superimposed over the image from a strike sequence. The fluid velocity field increases to a mean maximal area of $10.79 \pm 0.86 \text{ cm}^2$ (s.d.; Fig. 4) halfway through the gape cycle (mean $53\% \pm 9\%$). The fluid velocity field begins to decrease when the prey enters the mouth (54% of the events) or when the prey is fully contained within the mouth (27% of the events). The time of maximal fluid velocity area is correlated with the time that the prey enters the mouth ($r^2=0.42$, $P<0.05$) as well as with the time that the prey is fully contained inside the mouth ($r^2=0.46$, $P<0.05$). The mean duration of strike sequences is 67 ± 4 ms. The mean initial prey distance is 13.3 ± 0.8 mm (Fig. 4).

Unsuccessful strikes

A representative sequence of the general fluid field associated with an unsuccessful strike in *C. plagiosum* is illustrated in Fig. 3B. The sequence spans 62 ms and shows three vector magnitude plots superimposed on the image from an unsuccessful strike sequence. The fluid velocity field increases to a mean maximal area of $6.90 \pm 1.04 \text{ cm}^2$ halfway through the gape cycle (mean $59\% \pm 10\%$) (Fig. 5). As in captures and transports, a slow fluid-flow phase sometimes precedes the fast fluid-flow phase. A plateau in velocity halfway through the profile characterizes the fluid velocity areas of unsuccessful strikes, rather than being a distinct peak as in captures. The mean duration of unsuccessful strikes is 76 ± 4 ms. The average initial prey distance is 18.8 ± 1.8 mm.

Prey transport

A representative sequence of the general fluid field associated with a suction prey transport in *C. plagiosum* is illustrated in Fig. 3C. The sequence spans 52 ms and shows three vector magnitude plots superimposed on the image from a prey transport sequence. Suction

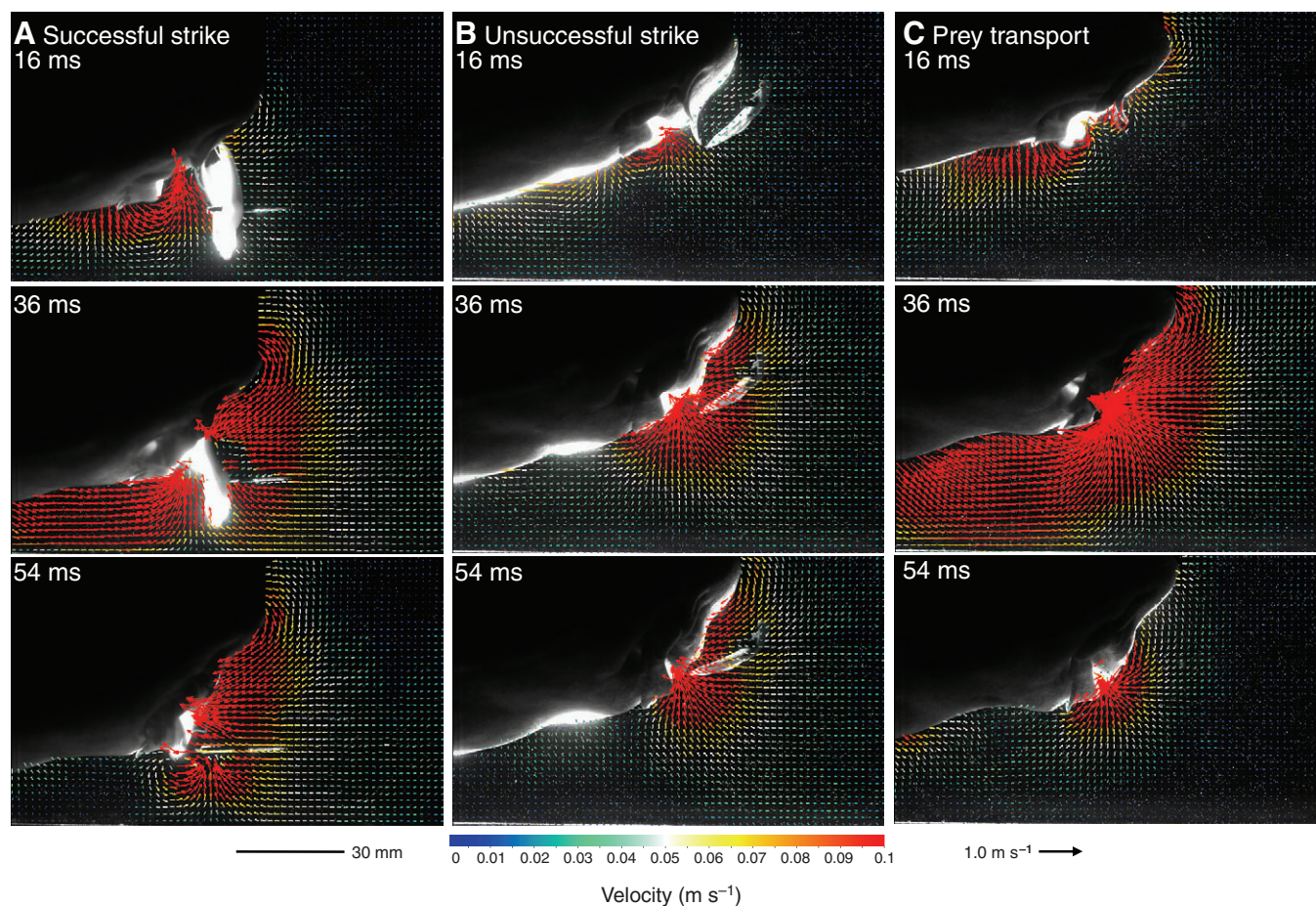


Fig. 3. Representative sequences of the general fluid field at key moments of the feeding cycle associated with three feeding behaviours in *C. plagiosum*. (A) Successful strike. (B) Unsuccessful strike. (C) Transport event. Vector magnitude is colour coded between zero (blue) and 1.0 m s^{-1} (red) fluid speed. The maximal areas of the fluid velocity field are similar for successful strikes and transports (note more red) but were significantly smaller for unsuccessful strikes.

is always used to move the prey from the jaws further into the oropharyngeal cavity. The fluid velocity field increases to a mean maximal area of $11.06 \pm 1.24 \text{ cm}^2$ halfway through the gape cycle (mean $55 \pm 9\%$) (Fig. 5). As in the suction strikes, a slow fluid-flow phase sometimes precedes the fast fluid-flow phase. The mean duration of suction transport events is $54 \pm 4 \text{ ms}$.

Behaviour comparisons

The mean maximal area of the fluid velocity region is 1.6-fold larger in successful strikes compared with unsuccessful strikes ($F=3.67$; $P=0.03$) (Figs 3, 4, 6). No individual effect is found on the maximal size of the fluid velocity region ($F=0.18$; $P=0.91$) or interactions ($F=0.11$; $P=0.99$) (Fig. 6). In successful and unsuccessful strikes, the mean maximal area of the fluid velocity region increases with initial prey distance ($F=0.001$; $P=0.02$) (Fig. 4) at the same slope (test of parallelism, $P=0.64$). Successful and unsuccessful strikes have similar durations ($F=2.51$; $P=0.08$) (Fig. 7). The same results are found in the ANCOVA test using prey distance as a covariable (Fig. 4). There is a strong individual effect on duration ($F=4.07$; $P=0.01$) (Fig. 7); however, individuals respond in the same way to the different behaviours ($F=1.39$; $P=0.74$). Initial prey distance was 30% longer in unsuccessful strikes than in successful strikes ($F=6.45$; $P=0.018$). No individual effects were found on prey distance ($F=1.27$; $P=0.31$).

The mean maximal area of the fluid velocity region is similar in suction strikes and suction transports ($F=0.05$; $P=0.95$) (Figs 3 and 4). The duration of the hydrodynamic cycle of suction transports is 20% shorter than that of suction strikes ($F=9.34$; $P=0.001$) (Fig. 7).

Accuracy index

A MANOVA was used to test for differences in accuracy index, aspect ratio of the volume and the normalized horizontal and vertical components of accuracy among successful strikes in the water column, unsuccessful strikes and successful strikes on the substrate. The accuracy index was lower for unsuccessful strikes than for successful strikes (water column or substrate) ($F=7.62$; $P<0.05$) (see Table 1). There was a tendency for the accuracy index to be higher in the successful strikes on the substrate, but, owing to the large variation, this was not significant ($F=0.45$; $P=0.64$). It was also not possible to distinguish between the successful and unsuccessful strikes on the basis of the horizontal and vertical components of accuracy, although on average A_x ($F=1.37$; $P=0.27$) was larger for the unsuccessful strikes and A_y was smaller for the substrate strikes ($F=1.06$; $P=0.36$). The aspect ratio of the ingested parcel of water was significantly lower for the substrate sequences ($F=5.42$; $P<0.05$). A polar plot of all strikes shows that unsuccessful strikes tended to be higher in the water column and further from the mouth compared with successful strikes (Fig. 8).

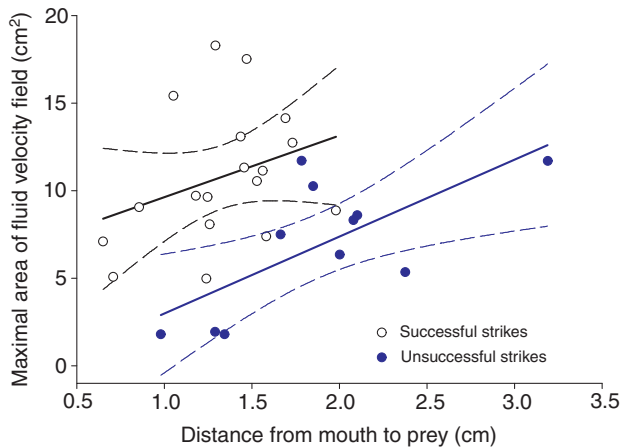


Fig. 4. Scatter plot of maximal area of the fluid velocity region against initial prey distance for successful strikes (unfilled black circles) and unsuccessful strikes (filled blue circles), together with regression lines (solid lines) and 95% confidence interval (dashed lines). Note the lower maximal area for the same prey distance and the longer mean initial prey distance for unsuccessful compared with successful strikes.

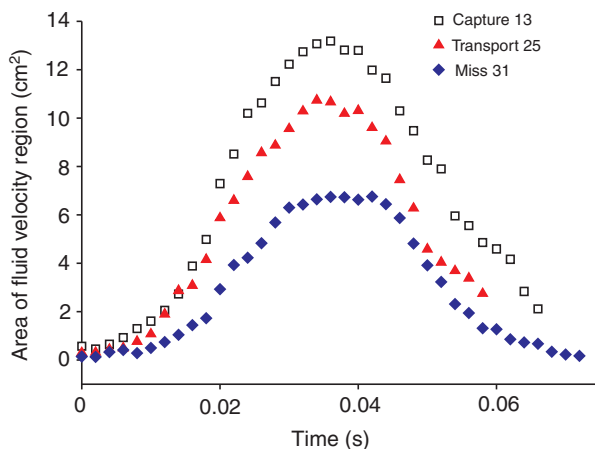


Fig. 5. Representative fluid velocity area profiles through time. Successful strikes are shown in white, transports in red and unsuccessful strikes in blue. Note the shorter duration for transports and the smaller maximal area and plateau in maximal area for unsuccessful captures. $N=4$ for each behaviour for each animal.

DISCUSSION

Prey capture in *C. plagiosum*

White-spotted bamboo sharks are specialized suction feeders, capturing prey in 67 ms (mean duration). By contrast, other specialized suction feeders of similar size – nurse sharks (*Ginglymostoma cirratum*) – have a gape cycle twice as long (133 ms mean duration) as that of bamboo sharks when feeding on squid (Matott et al., 2005). By comparison, generalist feeding elasmobranchs take two-and-a-half to three times as long to capture prey: juvenile leopard sharks (160–170 ms), the spiny dogfish *Squalus acanthias* (192 ms) and the Atlantic guitarfish *Rhinobatos lentiginosus* (200 ms) (Ferry-Graham, 1998; Wilga and Motta, 1998a; Wilga and Motta, 1998b). Thus, *C. plagiosum* is capable of capturing prey using suction in a shorter time compared with that of bite-feeding shark species of comparable size. Because of this

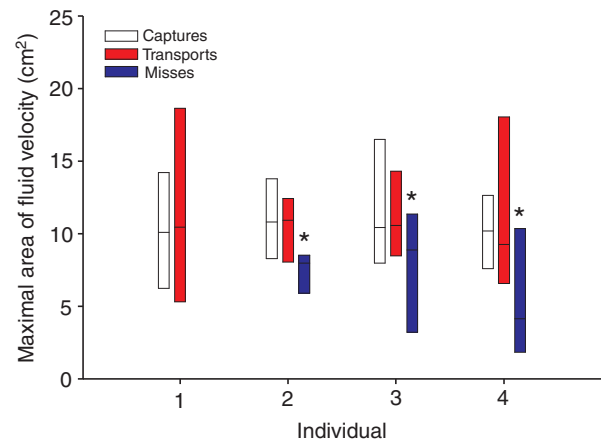


Fig. 6. Bar chart of the median and standard deviation of the maximal area of fluid velocity region for each individual for three behavioural categories. Successful strikes are shown in white, transports in red and unsuccessful strikes in blue. Asterisks indicate smaller maximal area for unsuccessful captures. $N=4$ for each behaviour for each animal.

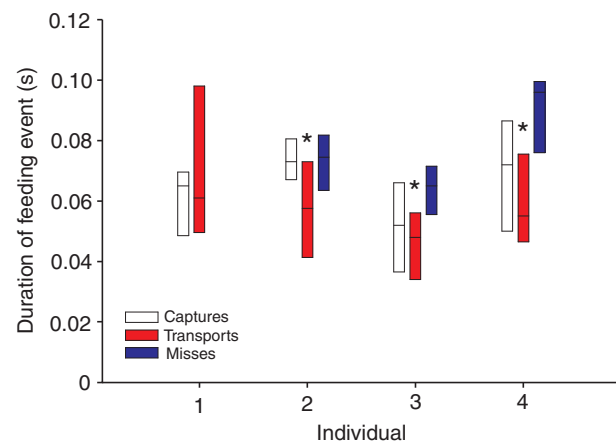


Fig. 7. Bar chart of the median and standard deviation of the maximal area of fluid velocity duration for each individual for three behavioural categories. Successful strikes are shown in white, transports in red and unsuccessful strikes in blue. Asterisks indicate the shorter duration of transports.

remarkably short feeding duration, white-spotted bamboo sharks are an excellent species to test the feeding modulation hypothesis.

Feeding modulation hypothesis – successful vs missed strikes

Traditionally, rapid events combined with stereotyped motor output to muscles have been interpreted as being the result of pre-programmed muscle activity (Motta and Wilga, 2001) governed by a pattern generator at the level of the central nervous system (Nyberg, 1971; Aerts, 1990; Ross et al., 2007). Modulation – *in sensu* consistent changes in feeding behaviour according to prey type or prey size (Frazzetta and Prange, 1987; Ferry-Graham, 1998) – is often observed in fish feeding studies, but the key point of pre-programming is that the appropriate behaviour is selected *prior* to the physical onset of the behaviour. Similar conditions should therefore result in a similar response. Unsuccessful strikes are initiated, albeit failed, attempts to capture prey. Therefore,

Table 1. Distinguishing features of successful vs unsuccessful strikes

	Successful strike in water column	Unsuccessful strike	Successful strike on substrate
Accuracy index	0.45±0.07	-0.26±0.09	0.61±0.12
Normalized A_x	0.24±0.08	0.43±0.09	0.21±0.13
Normalized A_y	0.24±0.06	0.36±0.08	0.06±0.10
Aspect ratio	0.75±0.15	0.74±0.14	0.23±0.07
N	16	11	6

Values are means ± s.e.m. for total accuracy index, one-dimensional accuracy indices (A_x and A_y) and aspect ratio of the ingested volume for three behaviours: successful strikes in the water column, unsuccessful strikes and successful strikes on the substrate. All variables are dimensionless. N , the sample size in each group.

comparison of unsuccessful or missed strikes with successful strikes might reveal whether the behaviour is pre-programmed and stereotypical or modulated. If pre-programmed, the hydrodynamics of unsuccessful strikes should not differ from those of successful strikes, once initiated. In *C. plagiosum*, the mean maximal size of the fluid velocity region is 56% larger in successful strikes compared with that of unsuccessful strikes, thus contradicting the hypothesis. However, the larger area of significant fluid velocity in successful strikes can be explained in two ways: either the behaviour is modulated based on some aspect of the prey (although this was standardized in our study) or simply a result of decreased effort on the part of the predator because of an error in processing the information necessary for accurate execution of a feed-forward-controlled behaviour. The key element, however, is that the hydrodynamic profiles differ from each other *after* initiation (and thus again contradicting the feeding modulation hypothesis). The fluid velocity region reaches a plateau in size in unsuccessful strikes, whereas a more rapid increase in area leads to a pronounced peak and greater maximal area in successful strikes (Fig. 5). We interpret the longer plateau in missed strikes as a stall in the magnitude of maximal fluid velocity. This stalling does not cause unsuccessful strikes to be significantly longer in duration than successful strikes, mainly because of the large variation in duration among unsuccessful strikes; it only appears as a lack of maximal area, as if the top of the profile is cut off. This is in contrast with the study of Aerts (Aerts, 1990), who found a longer duration in the kinematics of feeding for missed strikes in a cichlid.

The lower mean maximal area of significant fluid velocity of missed strikes compared with that of successful strikes might also

be explained as diminished suction effort over the duration of the feeding event because of the absence of a trigger necessary to initiate maximal suction effort (defined as how much mechanical work the shark is putting into the feeding event) or, again, a judgement error in feed-forward control. Missed strikes are unlikely to be caused by lack of motivation (defined as how incited the shark is to strike, a more psychological term) by the sharks as missed strikes were nearly always immediately followed by a successful strike.

However, a larger mean predator-to-prey distance occurs in missed strikes compared with successful strikes. This indicates that the shark is not generating sufficient fluid velocity to compensate for the increased distance to the prey, probably owing to small errors in control.

Feeding modulation hypothesis – strikes vs transports

The prey passes into the mouth just before or at peak fluid speed during the strike in *C. plagiosum*, similar to results found for *Lepomis macrochirus* (Day et al., 2005). Accordingly, variation in the timing of the maximal fluid velocity region is correlated with the timing of the prey passing the jaws. This partially explains why suction transports are shorter in duration than suction strikes but have similar maximal fluid velocity areas. The prey has already been captured. If the prey is the necessary signal to trigger maximal suction effort, this would fit the theory of feedback control (but see feedback control section). The mouth opens to allow the suction inflow to move the prey further into the oropharyngeal cavity. Suction effort during transports is just as strong as that during strikes not only to prevent prey escape but to move the prey into the oesophagus, a relatively longer distance than during a strike.

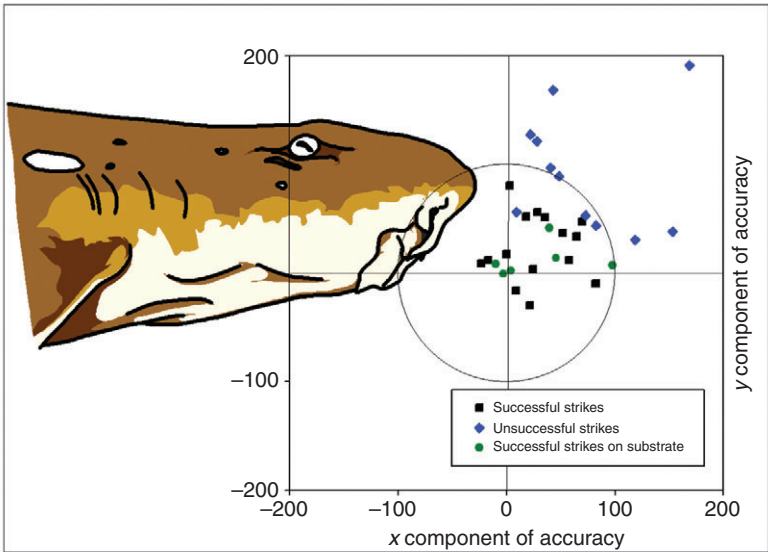


Fig. 8. Polar plot of the x and y components of the accuracy index normalized to total size of the ingested parcel of water. Note that most strikes occur in the upper, far quarter of the parcel.

Feedback control

Comparison of unsuccessful strikes with successful strikes might reveal the presence of a feedback system (Aerts, 1990; Gray and Nishikawa, 1995). The fluid velocity field is the net result of motor activation of muscles controlling mouth opening and closing combined with the inherent inertial properties of the musculoskeletal system interacting with the surrounding medium. If the fluid velocity field generated is controlled by feedback, then the onset of the suction sequence should be similar during the two behaviours. On average, the profiles of successful and unsuccessful strikes differ after 21 ms (± 3 ms). Although the profiles are similar at onset but differ later, there does not appear to be enough time to process feedback information and react accordingly. The processing time from perception of the signal to stimulating the trigger directing a change in activity of the motor neurons to the muscles can be very short. However, muscle activation time is constrained by the inertia of the system and the physiological capacity and anatomical spring elements of the associated muscles. In vertebrate muscle, activation time ranges from 20 to 80 ms (Carroll, 2004; Marsh, 1999; Nelson and Roberts, 2008; Roberts et al., 2007), whereas the relaxation time of muscles can take even longer. If feedback controls from the sensory and central nervous systems activate the muscular response to a trigger signal, then the signal has to be initiated at least 30 ms before the point at which missed and successful strikes differ in effort. While this is just within the range of vertebrate muscle, the difference in suction effort is detected well before 30 ms in *C. plagiosum*. One way to overcome this problem would be to possess a power amplification mechanism that relies on a catch-and-release system (Van Wassenbergh et al., 2008). However, even if such a mechanism is present, the benefits of a feedback-controlled mechanism remain unclear.

Although a feedback system provides an appealing and satisfactory explanation for the differences in successful versus unsuccessful strikes, the evidence does not overwhelmingly support the presence or absence of one. It has been proposed that inhibitory feedback control resulted in *prolonging* missed strikes during feeding in *Astatotilapia elegans* (Aerts, 1990). Sustained suction does not occur in *C. plagiosum* since missed strikes do not have longer durations than successful strikes (although there was individual variation in duration). In another study, missed strikes were not associated with changes in buccal pressure profiles in *Hexagrammos decagrammus* (Nemeth, 1997b). However, missed strikes in *C. plagiosum* have smaller areas of fluid velocity, thereby indicating lower buccal pressure. Mean predator-to-prey distance is also larger in missed strikes compared with successful strikes. However, we did not detect a clear signal that would trigger feedback control during suction feeding in *C. plagiosum*. Unsuccessful strikes appear to be due to inaccurate judgment of the position of the prey by the predator or they might be a first attempt to draw the prey closer in order for the next strike to be successful.

Accuracy

Proper timing of the strike is essential in successful feeding behaviour; thus, accuracy is probably an important aspect of suction feeding performance (Higham et al., 2006a). A metric for measuring accuracy based on the relative position of the prey to the centre of the ingested parcel of water drawn into the mouth by suction has been developed (Higham et al., 2006a). The accuracy index is capable of distinguishing unsuccessful strikes (mean -0.26) from successful strikes (mean water column 0.45 and substrate 0.61) (Table 1). *C. plagiosum* shows a bias for capturing prey in the upper far corner of the ingested area. Missed strikes are in the same quarter

but are either on the border or outside the ingested parcel of water. *Lepomis macrochirus* tends to capture prey closer to the centre of the ingested parcel of water and thus has a higher accuracy index (0.82) in the water column than either *Micropterus salmoides* (0.39) (Higham et al., 2006) or *C. plagiosum* (0.45), which is more accurate on the substrate (0.61). A negative accuracy index value reflects the position of the prey being further than the boundary, which is typical for unsuccessful strikes. Indeed, missed prey was nearly twice as far as successful strikes along the x axis. It appears that *C. plagiosum* successfully captures prey that are primarily between the horizontal axis of the mouth and the boundary of the fluid velocity region and misses prey that are well above the horizontal axis close to the boundary or that are further than the boundary of the ingested parcel (Fig. 8). This might be related to the position of the barbels, medial to the nostrils and dorsal to the mouth, which have a sensory function (Hueter et al., 2004).

The aspect ratio of the ingested parcel of water varies with movement of the predator and when feeding near a substrate. The aspect ratio of the ingested parcel of water is smaller for *C. plagiosum* (0.75 water column, 0.23 substrate) than for *Lepomis macrochirus* (1.09) and *Micropterus salmoides* (1.01) during relatively stationary feeding events (Day et al., 2005; Higham et al., 2006a). *C. plagiosum* typically stops swimming just before suction feeding, which makes the parcel of water engulfed less elongate when feeding in the water column and increases strike accuracy. By contrast, fish that swim forward through the water while suction feeding only ingest a volume of water that is directly in front of the mouth; thus, accuracy is more crucial with increased swimming speed (Day et al., 2005).

The proximity of a substrate has been hypothesized to have a positive effect on the accuracy of a strike (Nauwelaerts et al., 2007). As predicted, the shape of the ingested volume of water is changed by the substrate. The aspect ratio of the velocity field ingested during suction feeding in *C. plagiosum* is more than three times smaller when feeding near the substrate compared with that in the water column. Although the mean accuracy index tends to be higher for strikes on the substrate, they cluster tightly together above the horizontal completely within the larger cluster of water column strikes that can also occur below the horizontal and therefore are not statistically distinguishable.

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REFERENCES

- Aerts, P. (1990). Variability of the fast suction feeding process in *Astatotilapia elegans* (Teleostei: Cichlidae): a hypothesis of peripheral feedback control. *J. Zool., Lond.* **220**, 653–678.
- Carroll, A. M. (2004). Muscle activation and strain during suction feeding in the largemouth bass *Micropterus salmoides*. *J. Exp. Biol.* **207**, 983–991.
- Day, S. W., Higham, T. E., Cheer, A. Y. and Wainwright, P. C. (2005). Spatial and temporal patterns of water flow generated by suction-feeding bluegill sunfish *Lepomis macrochirus* resolved by particle image velocimetry. *J. Exp. Biol.* **208**, 2661–2671.
- Dean, M. N. and Motta, P. J. (2004). Anatomy and functional morphology of the feeding apparatus of the lesser electric ray, *Narcine brasiliensis* (Elasmobranchii: Batoidea). *J. Morphol.* **262**, 462–483.
- Ferry-Graham, L. A. (1998). Effects of prey size and mobility on prey-capture kinematics in leopard sharks *Triakis semifasciata*. *J. Exp. Biol.* **201**, 2433–2444.
- Ferry-Graham, L. A., Wainwright, P. C., Westneat, M. W. and Bellwood, D. R. (2001). Modulation of prey capture kinematics in the cheeklined wrasse *Oxycheilinus digrammus* (Teleostei: Labridae). *J. Exp. Zool.* **290**, 88–100.
- Frazzetta, T. H. and Prange, C. D. (1987). Movements of cephalic components during feeding in some requiem sharks (Carcharhiniformes: Carcharhinidae). *Copeia* **1987**, 979–993.
- Friel, J. P. and Wainwright, P. C. (1998). Evolution of motor patterns in tetraodontiform fishes: does muscle duplication lead to functional diversification? *Brain Behav. Evol.* **52**, 159–170.

- Gillis, G. B. and Lauder, G. V. (1994). Aquatic prey transport and the comparative kinematics of *Ambystoma tigrinum* feeding behaviors. *J. Exp. Biol.* **187**, 159-179.
- Gillis, G. B. and Lauder, G. V. (1995). Kinematics of feeding in bluegill sunfish: is there a general distinction between aquatic capture and transport behaviors? *J. Exp. Biol.* **198**, 709-720.
- Gray, L. A. and Nishikawa, K. C. (1995). Feeding kinematics of Phyllomedusine tree frogs. *J. Exp. Biol.* **198**, 457-463.
- Grubich, J. R. (2001). Prey capture in actinopterygian fishes: a review of suction feeding motor patterns with new evidence from an elopomorph fish, *Megalops atlanticus*. *Amer. Zool.* **41**, 1258-1265.
- Higham, T. E., Day, S. W. and Wainwright, P. C. (2006a). Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *J. Exp. Biol.* **209**, 2713-2725.
- Higham, T. E., Day, S. W. and Wainwright, P. C. (2006b). The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in cantrachid fishes. *J. Exp. Biol.* **209**, 3281-3287.
- Hueter, R. E., Mann, D. A., Maruska, K. P., Sisneros, J. A. and Demski, L. S. (2004). Sensory biology of elasmobranchs. In *Biology of Sharks and Their Relatives*. (ed. J. Carrier, J. Musick and M. Heithaus). pp. 325-368. Boca Raton: CRC Press.
- Lauder, G. V. (1981). Intraspecific functional repertoires in the feeding mechanism of the characoid fishes *Lebiasina*, *Hoplias* and *Chalceus*. *Copeia* **1**, 154-168.
- Lauder, G. V. (1985). Aquatic feeding in lower vertebrates. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 210-229. Cambridge, MA: Harvard University Press.
- Lauder, G. V. and Shaffer, H. B. (1993). Design of feeding systems in aquatic vertebrates: major patterns and their evolutionary implications. In *The skull: Functional and Evolutionary Mechanisms*, vol. 3 (ed. J. Hanken and B. K. Hall), pp. 113-149. Chicago, IL: University of Chicago Press.
- Liem, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. *J. Morphol.* **158**, 323-360.
- Marsh, R. (1999). How muscles deal with real-world loads: the influence of length trajectory on muscle performance. *J. Exp. Biol.* **202**, 3377-3385.
- Matott, M. P., Motta, P. J. and Hueter, R. E. (2005). Modulation in feeding mechanics and motor pattern of the nurse shark *Ginglymostoma cirratum*. *Environ. Biol. Fishes* **74**, 163-174.
- Moss, S. A. (1972). The feeding mechanism of sharks of the family Carcharhinidae. *J. Zool., Lond.* **167**, 423-436.
- Motta, P. J. (2004). Prey capture behavior and feeding mechanics of elasmobranchs. In *Biology of Sharks and Their Relatives* (ed. J. Carrier, J. Musick and M. Heithaus), pp. 165-202. Boca Raton: CRC Press.
- Motta, P. J. and Wilga, C. D. (2001). Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. *Environ. Biol. Fishes* **60**, 131-156.
- Motta, P. J., Tricas, T. C., Hueter, R. E. and Summer, A. P. (1997). Feeding mechanism and functional morphology of the jaws of the lemon shark *Negaprion brevirostris* (Chondrichthyes, Carcharhinidae). *J. Exp. Biol.* **200**, 2765-2780.
- Muller, M. and Osse, J. W. M. (1984). Hydrodynamics of suction feeding in fish. *Trans. Zool. Soc. Lond.* **37**, 51-135.
- Nauwelaerts, S., Wilga, C., Sanford, C. and Lauder, G. (2007). Hydrodynamics of prey capture in sharks: effects of substrate. *J. R. Soc. Interface* **4**, 341-345.
- Nelson, F. E. and Roberts, T. J. (2008). Task-dependent force sharing between muscle synergists during locomotion in turkeys. *J. Exp. Biol.* **211**, 1211-1220.
- Nemeth, D. H. (1997a). Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *J. Exp. Biol.* **200**, 2155-2164.
- Nemeth, D. H. (1997b). Modulation of buccal pressure during prey capture in *Hexagrammos decagrammus* (Teleostei: Hexagrammidae). *J. Exp. Biol.* **200**, 2145-2154.
- Nyberg, D. (1971). Prey capture in the largemouth bass. *Am. Midl. Nat.* **86**, 128-144.
- Preteflow-Edmonds, M. A. (1999). Prey capture kinematics of the horn shark, *Heterodontus francisci*. MSc Thesis, University of South Florida, Tampa, FL, USA.
- Roberts, T. J., Higginson, B. K., Nelson, F. E. and Gabaldon, A. M. (2007). Muscle strain is modulated more with running slope than speed in wild turkey knee and hip extensors. *J. Exp. Biol.* **210**, 2510-2517.
- Ross, C. F., Eckhardt, A., Herrel, A., Hylander, W. L., Metzger, K. A., Schaerlaeken, V., Washington, R. L. and Williams, S. H. (2007). Modulation of intra-oral processing in mammals and lepidosaurs. *Integr. Comp. Biol.* **47**, 118-136.
- Van Wassenbergh, S., Aerts, P., Strother, J., Flammang, B. and Ferry-Graham, L. (2008). Evidence for mechanical power amplification in suction feeding pipefish. *Comp. Biochem. Phys.* **146**, S107.
- Wainwright, P. C. (2002). The evolution of feeding motor patterns in vertebrates. *Curr. Opin. Neurobiol.* **12**, 691-695.
- Wainwright, P. C., Sanford, C. J., Reilly, S. M. and Lauder, G. V. (1989). Evolution of motor patterns: aquatic feeding in salamanders and ray-finned fishes. *Brain Behav. Evol.* **34**, 329-341.
- Westneat, M. W. (2006). Skull biomechanics and suction feeding in fishes. In *Fish Biomechanics*, vol. 23 (ed. R. E. Shadwick and G. V. Lauder) In *Fish Physiology* (series ed. W. S. Hoar, D. R. Randall and A. P. Farrell). San Diego: Elsevier.
- Wilga, C. D. and Motta, P. J. (1998a). Conservation and variation in the feeding mechanism of the spiny dogfish *Squalus acanthias*. *J. Exp. Biol.* **201**, 1345-1358.
- Wilga, C. D. and Motta, P. J. (1998b). Feeding mechanism of the Atlantic guitarfish *Rhinobatos lentiginosus*: modulation of kinematic and motor activity. *J. Exp. Biol.* **201**, 3167-3183.
- Wilga, C. D. and Motta, P. J. (2000). Durophagy in sharks: feeding mechanics of hammerhead sharks, *Sphyrna tiburo*. *J. Exp. Biol.* **203**, 2781-2796.
- Wilga, C. D., Wainwright, P. C. and Motta, P. J. (2000). Evolution of jaw depression mechanics in aquatic vertebrates: Insights from Chondrichthyes. *Biol. J. Linn. Soc.* **71**, 165-185.
- Wilga, C. D., Hueter, R. E., Wainwright, P. C. and Motta, P. J. (2001). Evolution of upper jaw protrusion mechanisms in elasmobranchs. *Am. Zool.* **41**, 1248-1257.