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# Relative importance of growth and behaviour to elasmobranch suction-feeding performance over early ontogeny

Dayv Lowry<sup>1,\*</sup> and Philip J. Motta<sup>2</sup>

<sup>1</sup> Washington Department of Fish and Wildlife, Point Whitney Shellfish Laboratory,  
1000 Point Whitney Road, Brinnon, WA 98320-9707, USA

<sup>2</sup>Department of Biology, University of South Florida, SCA 110, 4202 East Fowler Avenue,  
Tampa, FL 33620-5200, USA

Development of the ability to capture prey is crucial to predator survival. Trends in food-capture performance over early ontogeny were quantified for leopard sharks *Triakis semifasciata* and whitespotted bamboo sharks *Chiloscyllium plagiosum* by measuring suction pressure and flow in front of the mouth during feeding. At any size, *C. plagiosum* produce greater subambient pressure and ingest more rounded water parcels. Maximum subambient pressure scaled with negative allometry in *T. semifasciata* and was accompanied by an increase in the time to reach maximum gape. Despite a similar trend in buccal expansion timing, maximum pressure in *C. plagiosum* scaled with isometry and was accompanied by an earlier onset of hyoid depression and a positive allometric increase in buccal reserve volume. Growth was the primary factor responsible for developmental trends in both species, with size-independent behavioural changes contributing little to overall performance variability. Ontogenetic dietary shifts are predicted for both species as a consequence of size-dependent changes in performance. *Chiloscyllium plagiosum* becomes anatomically and behaviourally canalized towards suction feeding, limiting the effective range of prey capture and possibly necessitating stalking. *Triakis semifasciata*, by contrast, retains the flexibility to employ both ram and suction and therefore captures more elusive prey with age.

**Keywords:** inertial suction feeding; kinematics; pressure catheter; water parcel ingestion

## 1. INTRODUCTION

In aquatic vertebrates, feeding performance is influenced by both anatomical structure and spatial organization and the coordinated timing of movement during feeding (Ferry-Graham *et al.* 2001; Carroll *et al.* 2004; Wainwright & Day 2007; Wilga *et al.* 2007). Changes in the mechanical properties, shape and scaling of structural elements of the jaws, hyoid and head have all been shown to affect feeding performance (Summers 2000; Adriaens *et al.* 2001; Robinson & Motta 2002; Carroll *et al.* 2004; Herrel *et al.* 2005). While structural changes that influence performance take time to develop, behavioural variability is nearly universal in aquatically feeding vertebrates during every stage of development (Wainwright & Lauder 1986; Sanderson 1990). Additionally, distinct and consistent changes in feeding behaviour in response to prey attributes or particular conditions (modulation) are thoroughly documented in aquatic vertebrates (Deban 1997; Ferry-Graham *et al.* 2001; Motta & Wilga 2001) and

have been shown to enhance feeding performance (Norton 1991; Wainwright *et al.* 2001a; Day *et al.* 2005; Higham *et al.* 2005).

Several specific morphological and behavioural correlates that enhance suction-feeding performance have been identified in aquatically feeding vertebrates (Liem 1993; Carroll *et al.* 2004; Gibb & Ferry-Graham 2005; van Wassenbergh *et al.* 2005). These include a small oral opening that is laterally enclosed, reduced oral dentition, a deep head profile, rapid cranial rotation and a rapidly expandable buccal cavity controlled by powerful expansive muscles (Muller & Osse 1984; Liem 1993; Svanback *et al.* 2002; Carroll *et al.* 2004; Gibb & Ferry-Graham 2005; van Wassenbergh *et al.* 2005; Carroll & Wainwright 2006). While the precise relationships among these attributes are complex and vary by species, in essence they interact to produce a brief, high-magnitude pressure differential in the oral cavity of the predator that generates a focused, rapid influx of water through the mouth to displace the prey. Gradual changes may occur over ontogeny in these morphological and behavioural traits that influence suction, producing the potential for substantial changes in feeding capacity and performance with age (Galis *et al.* 1994; Koehl 1996).

\*Author for correspondence (lowrydcl@dfw.wa.gov).

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Though prey capture in teleost fishes over ontogeny has been studied in some detail (Cook 1996; Hernandez 2000; Krebs & Turingan 2003; van Wassenbergh *et al.* 2005), few studies have focused on elasmobranchs (Ferry-Graham 1998a,b; Robinson & Motta 2002; Summers *et al.* 2004; Huber *et al.* 2006; Lowry & Motta 2007; Lowry *et al.* 2007). Ontogenetic dietary changes are well documented in elasmobranchs (Lowe *et al.* 1996; Cortes 1999; Kao 2000; Ebert 2002) and are typically attributed to changes in habitat and/or growth. However, it is probable that developmental changes in morphology and behaviour affect performance and diet by changing how prey are captured or allowing the exploitation of novel prey (Galis *et al.* 1994; Hernandez 2000; Ferry-Graham *et al.* 2001). Therefore, the goals of this study were to (i) quantify developmental changes in food-capture performance from birth/hatching through the first year of life for two species of sharks with differing prey-capture mechanisms, (ii) determine the contribution of organism size and behavioural development to performance changes over ontogeny, and (iii) integrate knowledge of morphology, behaviour and performance to explain developmental trends in the feeding behaviour of young sharks that impact prey-capture capacity and survival. The study was limited to the first year of life because juvenile mortality is high in many elasmobranchs, in part due to high energy requirements and foraging inexperience (Duncan 2006), but declines with age (Heupel & Simpfendorfer 2002), making this a critical developmental period.

## 2. MATERIAL AND METHODS

### 2.1. Experimental animals

The leopard shark *Triakis semifasciata* (Girard 1854) is a primarily benthic species found along the west coast of North America and northern Central America (Compagno 1984a). Pups are born at approximately 20–26 cm total length (TL) and grow between 2 and 4 cm yr<sup>-1</sup> (Compagno 1984a; Kusher *et al.* 1992). *Triakis semifasciata* is an opportunistic generalist that feeds on diverse prey, including benthic invertebrates and fishes, throughout ontogeny (Talent 1976; Kao 2000). Despite having morphological attributes typical of suction feeders, previous study has shown that *T. semifasciata* generally ram feeds (Ferry-Graham 1998a). However, this species is capable of modulating its feeding behaviour in response to food size and elusivity to employ suction (Lowry *et al.* 2007).

The whitespotted bamboo shark *Chiloscyllium plagiosum* (Bennett 1830) is a benthic species found in the Indo-West Pacific and along the southeast Asian coast (Compagno 1984b). Hatchlings emerge at approximately 12–20 cm TL (Tullis & Peterson 2000). *Chiloscyllium plagiosum* is an opportunistic generalist, feeding primarily on benthic invertebrates and fishes. Previous study has shown that *C. plagiosum* displays characteristic suction-feeding morphology and uses behaviourally conservative, suction-dominated capture behaviour (Wu 1993; Lowry & Motta 2007; Wilga *et al.* 2007).

Twelve neonatal *T. semifasciata* (approx. three weeks old) were obtained from Mote Marine Laboratory, Sarasota, Florida and six hatchlings *C. plagiosum* (approximately one week old) were obtained from SeaWorld, Orlando, Florida. *Triakis semifasciata* were maintained in a 2.4 m diameter, 1400 l semicircular communal holding tank at 27±1°C and 32±2 ppt salinity, while *C. plagiosum* were maintained in a 340 l holding tank at 26±1°C and 33±2 ppt salinity. Individuals were isolated into a 90×45×30 cm filming tank containing 55 l of water from their respective holding tank during experimental sessions.

Animals were fed twice weekly with diverse live and dead food types totalling 3–4% of their body weight. For feedings preceding experimental sessions, the ration was cut to 2%. During experimental sessions, animal were fed pieces of Atlantic threadfin herring *Opisthonema oglinum* (for *T. semifasciata*) or the clam *Mercinaria mercinaria* (for *C. plagiosum*) that were scaled to mouth width. These food types were selected from a subset for which the behavioural response of these species is known and suction is employed to a greater degree than with other types tested (Lowry & Motta 2007; Lowry *et al.* 2007). Though an experimental session often consisted of 10 or more food captures per individual, only the first five were considered for analysis to avoid satiation effects (Sass & Motta 2002).

### 2.2. Experimental techniques

The 1-year experimental period post-birth/hatching was divided into four discrete time intervals for analysis to facilitate statistical comparison with the data of Lowry & Motta (2007) and Lowry *et al.* (2007) (see below). Experimental sessions occurred during the middle four weeks of each 13-week interval, providing a sample of feeding performance at distinct times. Experiments could not be conducted immediately after birth/hatching because sharks had to be quarantined and conditioned to feed under experimental lighting. Feeding performance was measured using two independent techniques (suction pressure and particle motion), both of which were accompanied by high-speed recordings. The recordings were made with a Redlake PCI 1000 high-speed digital camera (Redlake, San Diego, CA, USA) placed perpendicular to the aquarium to provide a lateral view. An angled mirror placed beneath the shark provided a ventral view. The recordings were made at 250 fps with a shutter speed of 1/1000 ms and illumination was provided by two 500 W quartz-halogen lights. Animals were acclimated for 30 min prior to each feeding session. A rule beside the shark provided distance measure and only perpendicular views were retained for analysis. Kinematic data were measured from recordings using REDLAKE MOTIONSCOPE PCI software v. 2.21.1 (Redlake, Inc., Tucson, AZ, USA) and SIGMASCAN PRO v. 4 (SPSS, Inc., Chicago, IL, USA). The variables selected have been shown to be functionally relevant in prior studies of elasmobranch feeding (Motta *et al.* 1997; Ferry-Graham 1998a; Wilga & Motta 1998). From the onset of lower jaw depression (time 0 ms), the following variables were quantified: (i) strike distance, from the closest point on the food to the lower

jaw of the shark (cm and as a percentage of head length), (ii) maximum gape (cm), (iii) time to maximum gape (ms), (iv) time to jaw closure (ms), (v) maximum cranial elevation (degrees), (vi) time to maximum cranial elevation (ms), (vii) time to onset of cranial elevation (ms), (viii) time to offset of cranial elevation (ms), (ix) duration of cranial elevation (ms), (x) time to onset of hyoid depression (ms), (xi) maximum hyoid depression (cm), (xii) time to maximum hyoid depression (ms), (xiii) time to hyoid retraction (ms), (xiv) duration of hyoid depression (ms), (xv) time gills start to open (ms), (xvi) total strike duration (ms), (xvii) duration of food movement during strike (ms), (xviii) distance food moves during strike (cm), (xix) velocity of food throughout strike ( $\text{cm s}^{-1}$ ), (xx) distance predator moves during strike (cm), and (xxi) velocity of predator throughout strike ( $\text{cm s}^{-1}$ ). Variables (xviii) and (xx) were used to calculate the ram-suction index (RSI; Norton & Brainerd 1993). The RSI is calculated as  $(D_{\text{PREDATOR}} - D_{\text{PREY}}) / (D_{\text{PREDATOR}} + D_{\text{PREY}})$ , where  $D$  is distance, and indicates the relative contribution of forward motion of the predator and motion of the prey to a given capture event. Owing to inherent problems with the RSI (Van Damme & Aerts 1997), including the rapidly decreasing effect of suction with increasing distance from the mouth of the predator (Lauder & Clark 1984; Muller & Osse 1984; Wainwright *et al.* 2001a,b), the RSI is used here for comparison with other studies and as a general indicator of feeding modality. Both the distance moved by and velocity of the food were used as indicators of performance in subsequent analyses (see below). No measures were made of jaw protrusion because it was not present during all bites.

Simultaneous with the recordings described above, food-capture performance was measured by quantifying subambient suction pressure at the position of the food during feeding. A 5-French Millar MPC-500 Mikro-tip catheter (Millar Instruments, Inc., Houston, TX, USA) was inserted through a Plexiglas false bottom that divided the filming tank vertically. Food items were notched and wrapped around the catheter so that the pressure transducer at the tip was exposed directly to flow generated by the shark. The catheter was placed in the food because the pressure generating food displacement was the performance variable of interest. The pressure gradient acting on food/prey has been identified as the most important force affecting its motion during suction feeding (Wainwright & Day 2007). A catheter was not placed inside the buccal cavity of the shark because long-term effects of cannula implantation or permanent catheterization on elasmobranch growth remain unknown. The catheter was connected to a Millar TCB-500 transducer control unit (Millar Instruments, Inc., Houston, TX, USA) that was calibrated and zeroed to measure pressure differential. The output was recorded with a Yokogawa DL 716 digital oscilloscope (Yokogawa Corporation of America, Newnan, GA, USA) and exported to a computer for analysis with LABVIEW v. 6.0 (National Instruments Corp., Austin, TX, USA). Recordings from the camera and oscilloscope were synchronized via a cyclically repeating electronic pulse. Performance variables measured from the recordings were: (i) duration of

the subambient pressure pulse (pulse duration, ms), (ii) area under the curve of the subambient pressure pulse (pulse magnitude, kPa ms), (iii) maximum subambient pressure (kPa), i.e. the peak absolute value of pressure, (iv) time to reach maximum subambient pressure from onset lower jaw depression (ms), (v) time to reach maximum subambient pressure from onset hyoid depression (ms), and (vi) rate of pressure drop from onset subambient pressure until maximum subambient pressure ( $\text{kPa ms}^{-1}$ ). Twenty suction pulses with synchronized video of successful food capture were recorded from each time interval for both species, resulting in the analysis of 160 captures. While the greatest subambient pressure generated by an individual on a given day was typically used, the goal was to obtain a biologically meaningful range of pressures that result in successful food capture. No more than three captures per individual during a time interval were included in the analysis to avoid pseudoreplication.

In addition to measuring subambient pressure, performance was quantified during independent sessions by describing the flow patterns into the mouth during feeding. *Artemia* sp. cysts (4.1 g) were soaked for 1–3 hours in seawater until neutrally buoyant and added to the filming tank, producing a final seeding density of approximately  $3 \text{ g l}^{-1}$  (Lauder & Clark 1984). *Artemia* sp. cysts were selected in lieu of artificial spheres (Muller & Osse 1984; Ferry-Graham *et al.* 2003; Day *et al.* 2005; Higham *et al.* 2005) because they are biodegradable and repeated exposure over ontogeny is not detrimental to fishes. The filming tank was enclosed within a photo-opaque, non-reflective box that admitted light through two 3 mm wide slits on the top and one side of the box. This created a sheet of light perpendicular to the camera that ran through the midsagittal plane of the shark and permitted discrimination of particles directly in-line with the shark. Particles that entered the mouth during feeding were tracked backward field by field from ingestion to their initial position at the onset of lower jaw depression. Connecting the initial positions of the distal-most particles in each direction allowed delineation of the parcel of water ingested by the shark during feeding (figure 1; Day *et al.* 2005; Higham *et al.* 2005). A minimum of 20 particle trajectories were described per capture and more particles were tracked until additional trajectories did not alter the shape of the ingested parcel. Flow was described in a planar rather than three-dimensional fashion because both species have prominent labial cartilages that anecdotal observations from head-on bites suggest greatly restrict lateral flow (D. Lowry 2003, unpublished data). Additionally, manual quantification of particle motion in three dimensions is labour-intensive and complex, and the food moved primarily anteroposteriorly. The following attributes of the ingested parcel were quantified as indicators of performance using SIGMASCAN Pro v. 4 (SPSS, Inc., Chicago, IL, USA): (i) maximum parcel length (cm and relative to mouth width (MW)), (ii) maximum parcel height (cm and MW), and (iii) parcel area ( $\text{cm}^2$ ). Parcel height was then divided by parcel length to obtain an aspect ratio that described the relative shape of the ingested parcel

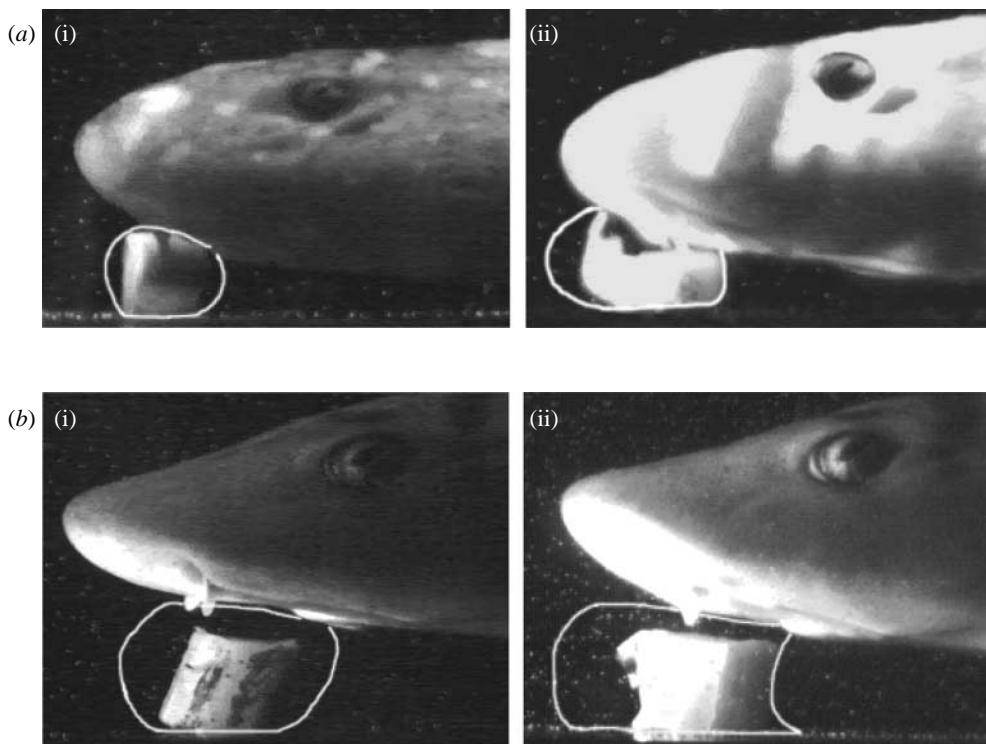


Figure 1. Illustrative examples showing the range of water parcel shape and size (outlined area) ingested by (a) *C. plagiostomum* and (b) *T. semifasciata* during feeding. Images are scaled so that head length is equal in all cases. Parcels are truncated ventrally by the Plexiglas bottom and dorsally by the rostrum. Images (a(i), b(i)) depict relatively rounded, high-aspect-ratio parcels, while (a(ii), b(ii)) depict more elongated, low-aspect-ratio parcels. Overall, high-aspect-ratio parcels ( $0.80 \pm 0.21$ ) are typical of *C. plagiostomum* (a(i)) while low-aspect-ratio parcels ( $0.57 \pm 0.11$ ) are typical of *T. semifasciata* (b(ii)).

(Day *et al.* 2005; Higham *et al.* 2005). Ten flow patterns were recorded for each time interval for both species, resulting in a total of 80 bites. Ten samples were used rather than the 20 used for the catheter experiments because sharks often veered out of the light plane before closing their mouth, making complete analysis of these videos impossible. No more than two captures per individual during a time interval were included in the analysis to avoid pseudoreplication.

### 2.3. Statistical analyses

To determine whether the catheter or particles influenced feeding behaviour, kinematic data were compared against data for the same species feeding on the same food type when neither performance quantifying method was used (Lowry & Motta 2007; Lowry *et al.* 2007). All kinematic data were log transformed and checked for normality and homogeneity of variance. Data for each variable were then compared against TL using model II linear regression and the studentized residuals obtained (Quinn & Keough 2002). Model II regressions were appropriate because both of the variables used in these comparisons contained measurement error (McGowan 1988). Size-corrected, studentized residuals for all variables were then used in a principal components analysis (PCA; Quinn & Keough 2002). An equimax rotation was applied and variables that loaded above  $|0.5|$  were identified as contributing to the respective principal component (PC). PCs with eigenvalues greater than 1.0 were retained for further analysis. Scores for each

bite on each PC were then used in a series of one-way MANOVAs to identify the differences between clusters of bites in multivariate space. Bites from each time interval using each technique to quantify performance were independently compared against captures during the same time interval in which neither technique was employed (Lowry & Motta 2007; Lowry *et al.* 2007). Significance was assessed using Pillai's trace. Regressions were performed with SIGMASTAT PRO v. 3.1 (SPSS, Inc., Chicago, IL, USA), while PCA and MANOVA tests were performed with SYSTAT v. 11 (SPSS, Inc., Chicago, IL, USA).

Once the effects of catheter and particle presence were assessed, log-transformed data for each performance variable were regressed against log-transformed TL data using model II linear regressions to describe ontogenetic changes in performance. Significance was assessed via ANOVA. In addition to testing for performance trends over ontogeny, the nature of these trends was determined. The predicted isometric scaling coefficient for each performance variable was determined either by the dimensionality of the variable or based on existing kinematic and anatomical scaling data for these species (Lowry & Motta 2007; Lowry *et al.* 2007). Linear variables, such as velocity of the food, were predicted to scale with a coefficient of 1. Planar variables, such as pulse magnitude, were predicted to scale with a coefficient of 2. Maximum parcel height and length relative to mouth width (i.e. with size accounted for), as well as parcel aspect ratio, were predicted to scale with a coefficient of zero. As strike duration did not scale with size in either species (Lowry & Motta 2007;

Lowry *et al.* 2007), the duration of the pressure pulse and the time of its onset relative to the onset of lower jaw depression were predicted to scale with coefficients of zero. The onset of hyoid depression does not scale with size in *T. semifasciata* (Lowry *et al.* 2007), but scales with a coefficient of  $-0.3$  in *C. plagiostomum* (Lowry & Motta 2007). Thus, the time of maximum subambient pressure relative to the onset of hyoid depression was expected to scale with coefficients of  $0$  and  $-0.3$ , respectively. Maximum subambient pressure, though influenced by behavioural deviation in the rate and duration of buccal expansion (Muller & Osse 1984; Carroll *et al.* 2004), correlated strongly with volume change in the buccal cavity during feeding (Svanback *et al.* 2002; Carroll *et al.* 2004). The volume difference of the buccal cavity between closed and maximally expanded (buccal reserve volume) had been shown to scale with a coefficient of  $3.0$  in *T. semifasciata* (Lowry *et al.* 2007) and  $3.3$  in *C. plagiostomum* (Lowry & Motta 2007), so maximum subambient pressure was predicted to scale similarly. Deviation from isometry was tested for each variable using a modified Student's *t*-test (Zar 1999). Differences between regressions at the species level for a given variable were also assessed using a modified Student's *t*-test (Zar 1999).

To determine whether changes in performance variables occurred over ontogeny irrespective of size, studentized residuals were obtained from the regressions of each variable against TL and regressed against log-transformed age data (in days). Deviation from a coefficient of zero, tested using ANOVA, indicated performance differences over ontogeny that could not be accounted for simply by growth. For each performance variable that displayed a trend over ontogeny after accounting for size, a backward stepwise multiple regression was used to elucidate the contribution of specific kinematic variables to this relationship ( $F$ -to-Enter =  $2.0$ ,  $F$ -to-Remove =  $1.9$ , 20 steps; Quinn & Keough 2002). Only the variables that directly related to the timing, duration and extent of motion of cranial features were retained for this analysis (i.e. strike distance, duration of food movement and RSI were not included). Stepwise regressions were performed with SIGMASTAT PRO v. 4 (SPSS, Inc., Chicago, IL, USA).

### 3. RESULTS

Sharks of both species generally swam slowly in circles or rested on the bottom until food was introduced. On average, strikes were faster in *C. plagiostomum* (strike duration =  $69 \pm 17$  ms) than in *T. semifasciata* ( $96 \pm 16$  ms), involved relatively less excursion of anatomical structures and were characterized by substantially less variability (Lowry & Motta 2007; Lowry *et al.* 2007). Strike distance, both absolute and relative to head length, did not change significantly over ontogeny in *T. semifasciata* but increased with negative allometry (slope =  $0.87$ ,  $p = 0.003$ ) in *C. plagiostomum* (Lowry & Motta 2007; Lowry *et al.* 2007).

Statistical differences were not detected in multi-dimensional space during any time interval between capture events with and without catheterized food or between capture events with and without particles

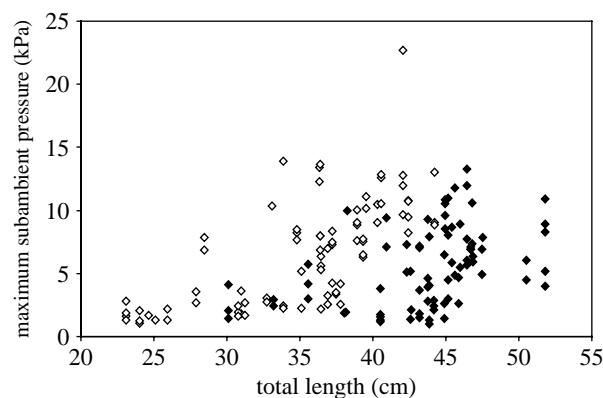


Figure 2. Values of maximum subambient pressure at the position of the food generated during food-capture events in *C. plagiostomum* (open diamonds) and *T. semifasciata* (filled diamonds) relative to TL. At any given TL, values are generally higher (i.e. greater pressure drop) in *C. plagiostomum*.

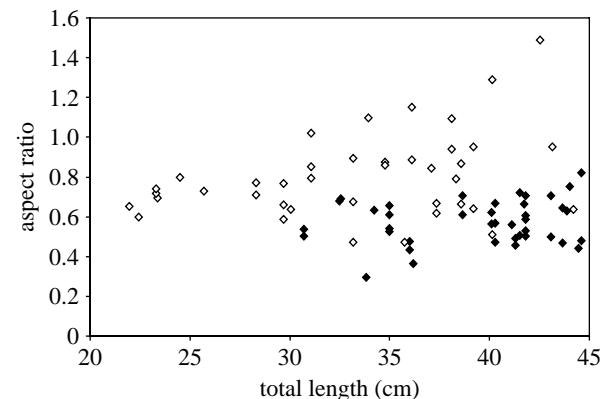


Figure 3. Aspect ratio values for parcels of water ingested during food-capture events in *C. plagiostomum* (open diamonds) and *T. semifasciata* (filled diamonds) relative to TL. At any given TL, values tend to be higher (i.e. more rounded) in *C. plagiostomum*.

present (see appendix 1 in the electronic supplementary material). At any given TL, the maximum subambient pressure produced by *C. plagiostomum* was generally greater than that produced by *T. semifasciata*, though considerable overlap existed (figure 2). The greatest subambient pressure recorded for *C. plagiostomum* was  $22.67$  kPa (42.1 cm TL) while the greatest subambient pressure recorded for *T. semifasciata* was  $11.77$  kPa (45.6 cm TL). At any given TL, the aspect ratio of the parcel ingested was generally higher (i.e. more rounded) in *C. plagiostomum* and lower (i.e. more elliptical) in *T. semifasciata* (figures 1 and 3). A summary of performance data by species during each time interval is provided in table 1.

#### 3.1. Scaling of performance

When trends associated with growth were compared to isometry, only five out of the 14 performance variables exhibited the same pattern of development for both species (SL<sub>exp</sub> and *t* columns, table 2). Both pulse magnitude and maximum parcel height scaled with positive allometry, velocity of the food scaled with negative allometry and both maximum relative parcel length and parcel aspect ratio scaled isometrically

Table 1. Average values of performance variables during each time interval for *T. semifasciata* and *C. plágiosum*. (Each time interval is 13 weeks long and experimental sessions occurred during the middle of each interval. Sample size (*N*) for each time interval for each species is 20 for all pressure variables and 10 for all flow variables.)

	<i>Triakis semifasciata</i>				<i>Chiloscyllium plágiosum</i>			
	time 1	time 2	time 3	time 4	time 1	time 2	time 3	time 4
pressure variables								
RSI	0.12	-0.04	-0.10	-0.18	-0.33	-0.48	-0.55	-0.57
distance, lower jaw to catheter (cm)	0.71	1.00	1.15	1.19	0.51	0.67	0.81	0.75
pulse duration (ms)	38.75	51.15	73.50	56.75	31.15	34.10	19.35	18.45
peak subambient pressure (kPa)	3.02	4.50	7.48	6.85	2.02	4.62	8.63	10.96
pulse magnitude (kPa ms)	29.95	23.86	75.98	88.69	78.85	363.07	1659.91	3181.72
time of peak subambient pressure relative to	—	—	—	—	—	—	—	—
onset lower jaw depression (ms)	41.75	42.25	50.65	47.30	34.35	33.15	21.55	21.75
onset hyoid depression (ms)	17.15	19.85	27.25	22.50	25.15	21.15	12.55	12.15
rate of pressure drop (kPa ms <sup>-1</sup> )	0.19	0.22	0.25	0.23	0.16	0.28	0.88	1.19
flow variables								
RSI	0.00	-0.10	-0.21	-0.15	-0.31	-0.67	-0.62	-0.63
distance, lower jaw to food (cm)	0.56	0.82	0.61	0.87	0.37	0.32	0.25	0.44
parcel area (cm <sup>2</sup> )	2.33	3.15	4.65	5.32	0.74	0.78	0.94	1.47
maximum parcel length (cm)	2.58	2.75	3.06	3.62	0.99	1.19	1.20	1.59
maximum parcel length (MW)	1.14	1.12	1.15	1.36	1.02	0.96	0.82	1.00
maximum parcel height (cm)	1.26	1.64	1.85	2.05	0.69	0.89	1.03	1.30
maximum parcel height (MW)	0.56	0.67	0.69	0.77	0.72	0.72	0.70	0.81
parcel aspect ratio	0.49	0.61	0.62	0.58	0.70	0.78	0.87	0.85

( $SL_{exp}$  and  $t$  columns, table 2). Pulse magnitude increased markedly faster in *C. plágiosum* (slope = 6.55) than in *T. semifasciata* (slope = 3.93;  $p < 0.001$ ). For *T. semifasciata*, pulse duration increased allometrically and the rate of pressure drop decreased allometrically (table 2), causing maximum subambient suction pressure to increase with negative allometry (slope = 2.45) from an average of  $3.02 \pm 1.84$  kPa (37.9 cm TL) to  $6.85 \pm 2.58$  kPa (47.7 cm TL). By contrast, pulse duration decreased allometrically in *C. plágiosum*, while the rate of pressure drop increased allometrically (table 2). This facilitated an isometric increase in the maximum subambient pressure generated by *C. plágiosum* from an average of  $2.02 \pm 0.73$  kPa (26.9 cm TL) to an average of  $10.96 \pm 3.39$  kPa (40.9 cm TL). The difference in these trends between species was significant ( $p < 0.001$ ). The absolute length, height and area of the water parcel ingested by *T. semifasciata* scaled with a greater allometric coefficient than for *C. plágiosum* ( $p = 0.002$ ), indicating that over ontogeny a relatively more elongate, deeper, higher-volume parcel of water was ingested by *T. semifasciata* (figure 1 and table 2). In fact, both absolute parcel length and parcel area increased with positive allometry in *T. semifasciata*, indicating that relatively more water was being ingested with growth, whereas they scaled with negative allometry in *C. plágiosum* signifying a relative decrease in the amount of water ingested with growth (table 2).

### 3.2. Behavioural effects on performance

Regression of performance data against TL indicated that growth was the primary factor accounting for changes in these variables over ontogeny. However,

regression of studentized residuals of these analyses against time indicated that a number of significant trends remained which were not explained by growth (table 3). For *T. semifasciata*, pulse duration, pulse magnitude, distance moved by the food, maximum parcel height and parcel area exhibited weakly increasing trends over time (table 3). Backward stepwise multiple regressions indicated that numerous kinematic variables contributed to these trends (table 4). The extent of maximum gape contributed to trends in all of these performance variables except pulse magnitude, which was primarily related to strike duration (table 4). In addition to maximum gape, a mixture of kinematic variables partially accounted for trends in the remaining performance variables, with no single variable clearly predicting performance (table 4). Two notable exceptions to this generalization were the time to hyoid retraction and the duration of hyoid depression, which exhibited strong relationships with distance moved by the food during a strike (table 4).

For *C. plágiosum*, only pulse duration and maximum subambient pressure displayed increasing trends over time irrespective of growth (table 3). Backward stepwise multiple regression revealed that for pulse duration these trends could be accounted for primarily by variables measuring the timing and extent of maximum cranial elevation. However, strike duration explained the trend in maximum subambient pressure (table 5).

## 4. DISCUSSION

Trends exist in several measures of food-capture performance for both *T. semifasciata* and *C. plágiosum* over ontogeny that can be accounted for by predator

Table 2. Regression parameters for performance variables versus TL and tests of isometry for both species. (The observed slope (slope) and expected slope ( $SL_{exp}$ ) are given. StErr, standard error;  $y$ -int,  $y$ -intercept of regression line. Standard error and  $p$  values are from ANOVA tests for relationships between each variable and TL. The expected slope for isometry is given in the column  $SL_{exp}$ . Where the expected slope was not zero, a modified Student's  $t$ -test was used to assess isometry. Where the expected slope was zero (n.a.), the results of the ANOVA were used. For variables quantified with catheterized food,  $t_{0.05(1),78} = 1.665$ . For variables quantified with particles present,  $t_{0.05(1),38} = 1.686$ .)

variable	slope	$y$ -int	$r^2$	StErr	$p$	$SL_{exp}$	$t$
<i>Triakis semifasciata</i>							
pulse duration	1.08	-0.06	0.10	0.37	0.005	0.0	n.a.
pulse magnitude	3.93	-4.86	0.24	0.79	<0.001	2.0	79.85
maximum subambient pressure	2.45	-3.35	0.18	0.59	<0.001	3.0	-30.26
time of maximum pressure relative to onset of lower jaw depression	—	—	—	—	—	—	—
onset of hyoid depression	0.21	1.29	0.01	0.30	0.481	0.0	n.a.
rate of pressure decrease	0.13	1.36	0.00	0.53	0.812	0.0	n.a.
distance food moves	0.95	-2.30	0.03	0.63	0.134	1.0	-2.70
velocity of the food	1.45	-2.15	0.25	0.41	0.001	1.0	37.57
maximum parcel length (cm)	0.94	-0.10	0.06	0.58	0.115	1.0	-3.77
maximum parcel length (MW)	1.05	-1.21	0.34	0.24	<0.001	1.0	7.67
maximum parcel height (cm)	0.25	-0.33	0.03	0.24	0.292	0.0	n.a.
maximum parcel height (MW)	1.40	-2.00	0.39	0.28	<0.001	1.0	47.69
maximum parcel height (MW)	0.60	-1.13	0.10	0.28	0.042	0.0	n.a.
parcel area	2.74	-3.81	0.56	0.40	<0.001	2.0	63.72
parcel aspect ratio	0.34	-0.80	0.03	0.30	0.262	0.0	n.a.
<i>Chiloscyllium plagiosum</i>							
pulse duration	-1.38	3.49	0.28	0.25	<0.001	0.0	n.a.
pulse magnitude	6.55	-8.21	0.62	0.58	<0.001	2.0	154.91
maximum subambient pressure	3.26	-4.31	0.59	0.31	<0.001	3.3	-1.63
time of maximum pressure relative to onset of lower jaw depression	—	—	—	—	—	—	—
onset of hyoid depression	-1.11	3.12	0.26	0.21	<0.001	0.0	n.a.
rate of pressure decrease	-1.53	3.61	0.15	0.42	<0.001	-0.3	-57.90
distance food moves	4.42	-7.20	0.58	0.42	<0.001	1.0	160.16
velocity of the food	0.66	-1.03	0.13	0.28	0.026	1.0	-21.82
maximum parcel length (cm)	-0.06	1.53	0.00	0.37	0.876	1.0	-52.26
maximum parcel length (MW)	0.73	-1.03	0.37	0.16	<0.001	1.0	-31.35
maximum parcel height (cm)	-0.30	0.42	0.09	0.16	0.065	0.0	n.a.
maximum parcel height (MW)	1.12	-1.72	0.53	0.17	<0.001	1.0	12.40
maximum parcel height (MW)	0.08	-0.27	0.01	0.17	0.622	0.0	n.a.
parcel area	1.16	-1.80	0.37	0.25	<0.001	2.0	-61.95
parcel aspect ratio	0.38	-0.69	0.09	0.20	0.067	0.0	n.a.

growth and, to a lesser degree, behavioural variation. Size effects are prevalent in most studies of biomechanical performance (Losos 1990; Elsworth *et al.* 2003; Herrel *et al.* 2005) and have led to the development of numerous models to predict kinematic scaling coefficients (Richard & Wainwright 1995; Deban & O'Reilly 2005). Explanatory mechanisms for size-related trends typically assume isometric growth and range from changes in muscle contraction rate to the disparity between the scaling coefficient of muscular force production (slope = 2) and the mass of skeletal elements (slope = 3). The model used here was based on knowledge of the scaling of kinematics in *T. semifasciata* and *C. plagiosum*, which primarily conform to the model of Richard & Wainwright (1995), but deviate owing to allometric growth in several anatomical features including head width, head depth at the location of the hyoid and buccal reserve volume (Lowry & Motta 2007; Lowry *et al.* 2007). Though requiring *a priori* knowledge of ontogenetic trends, integrating knowledge of anatomical scaling into predictive models of performance increases the accuracy and functional relevance of these models.

An increase in the suction pressure generated during feeding in bony fishes is correlated with increased power output of muscles that expand the buccal cavity, the rate of buccal and hyoid expansion and increased cranial elevation (Muller & Osse 1984; Norton & Brainerd 1993; Ferry-Graham *et al.* 2001; Sanford & Wainwright 2002). In both *T. semifasciata* and *C. plagiosum*, the absolute subambient suction pressure increases with size, but to a greater extent in *C. plagiosum*. In *T. semifasciata*, the times to reach maximum hyoid depression and maximum cranial elevation do not change with size. The time to reach maximum gape increases with positive allometry (slope = 0.35,  $p = 0.021$ ) despite positive allometric growth in the weight and cross-sectional area of jaw abducting muscles (Lowry *et al.* 2007). This suggests that in *T. semifasciata* maximum subambient pressure should scale with negative allometry as the rate of oral expansion decreases, and results indicate that this is the case. In *C. plagiosum*, the time to reach maximum gape, maximum hyoid depression and maximum cranial elevation all increase with positive allometry (slopes between 0.2 and 0.4) despite positive allometric

Table 3. Regression parameters for performance variables against age in days for both species irrespective of size (i.e. size effects accounted for via regression). (StErr, standard error; *y*-int, *y*-intercept of regression line. For variables quantified in the presence of the catheter,  $t_{0.05(1),19} = 1.729$ . For variables quantified with particles present,  $t_{0.05(1),9} = 1.833$ .)

variable	slope	<i>y</i> -int	$r^2$	StErr	<i>p</i>
<i>Triakis semifasciata</i>					
pulse duration	0.13	−0.27	0.08	0.05	0.013
pulse magnitude	0.26	−0.54	0.07	0.11	0.020
maximum subambient pressure	0.22	−0.46	0.09	0.08	0.080
time of maximum pressure relative to onset of lower jaw depression	—	—	—	—	—
onset of hyoid depression	0.05	−0.10	0.01	0.04	0.286
rate of pressure decrease	0.04	−0.09	0.00	0.09	0.650
distance food moves	0.13	−0.28	0.13	0.05	0.022
velocity of the food	0.13	−0.28	0.06	0.08	0.119
maximum parcel length (cm)	0.04	−0.08	0.03	0.03	0.300
maximum parcel height (cm)	0.09	−0.20	0.14	0.04	0.016
parcel area	0.13	−0.27	0.13	0.05	0.023
parcel aspect ratio	0.06	−0.13	0.05	0.04	0.166
<i>Chiloscyllium plagiosum</i>					
pulse duration	0.43	−0.92	0.00	0.13	0.001
pulse magnitude	−0.01	0.03	0.13	0.06	0.808
maximum subambient pressure	0.17	−0.35	0.07	0.07	0.021
time of maximum pressure relative to onset of lower jaw depression	—	—	—	—	—
onset of hyoid depression	−0.01	0.02	0.00	0.05	0.832
rate of pressure decrease	0.16	−0.33	0.03	0.10	0.120
distance food moves	0.04	−0.08	0.00	0.07	0.597
velocity of the food	0.06	−0.13	0.01	0.09	0.508
maximum parcel length (cm)	0.01	−0.03	0.00	0.04	0.701
maximum parcel height (cm)	0.00	−0.01	0.00	0.04	0.918
parcel area	−0.02	0.05	0.00	0.06	0.725
parcel aspect ratio	−0.01	0.02	0.00	0.05	0.834

growth in abducting musculature (Lowry & Motta 2007). Taken together, this suggests that maximum subambient pressure should also scale with negative allometry. However, maximum subambient pressure scaled with isometry in *C. plagiosum*. This discrepancy may be due to the relationship between TL and the timing of initial hyoid depression. In *T. semifasciata*, the onset of hyoid depression shows no trend with growth (Lowry *et al.* 2007), but in *C. plagiosum* the hyoid begins to be depressed relatively earlier in the strike (slope = −0.32; Lowry & Motta 2007). Functionally, this means that flow is generated through a slowly expanding, smaller oral aperture earlier in the strike, which should increase the velocity of flow into the buccopharyngeal cavity and, consequently, maximum subambient pressure (Muller & Osse 1984; Svanback *et al.* 2002). Indeed, in *C. plagiosum*, the relative timing of maximum subambient pressure scales with negative allometry while the rate of pressure drop scales with positive allometry (slope = 4.42; table 2). Thus, despite the fact that several kinematic events occur later during a bite over ontogeny, the result is isometric rather than negatively allometric scaling of maximum subambient pressure. The timing of hyoid depression as the primary determinant of maximum subambient pressure has been hypothesized for orectolobid sharks (Motta 2004), and changes in the relative timing of hyoid depression appear to enhance pressure generation over ontogeny in *C. plagiosum*. However, it should be noted that strike

distance allometrically decreased in *C. plagiosum* over ontogeny and that the resultant variability in catheter position relative to the shark could influence pressure measurements. Assessing the degree of this influence requires surgically fixing the position of the catheter within the buccal cavity of the shark, a method not used here because its effect on growth was unknown.

Both *T. semifasciata* and *C. plagiosum* use inertial suction to capture food (Wu 1993; Ferry-Graham 1998a; Lowry & Motta 2007; Lowry *et al.* 2007; Nauwelaerts *et al.* 2007; Wilga *et al.* 2007), though the relative contribution of suction is greater in *C. plagiosum*. The viscosity and density of the aquatic medium dictate that suction is a relatively near-field phenomenon, as the effects of flow degrade as the cube of distance from the oral aperture (Muller & Osse 1984; Svanback *et al.* 2002; Ferry-Graham *et al.* 2003; Nauwelaerts *et al.* 2007; Wilga *et al.* 2007). The greatest parcel length of water sucked into the mouth by *T. semifasciata* was 4.45 cm (1.73 MW) and 2.15 cm (1.38 MW) for *C. plagiosum*. The absolute distance from which food was ingested scaled with slight positive allometry in *T. semifasciata* but with negative allometry in *C. plagiosum*. The relative distance from which food was ingested, scaled to mouth width, did not exhibit a trend with size in either species. These values correspond well with theoretical and empirical measures of suction distance (Lauder & Clark 1984; Muller & Osse 1984; Wainwright *et al.* 2001a) and

Table 4. Kinematic variables contributing to performance differences over time irrespective of size (i.e. size effects accounted for via regression) in *T. semifasciata*. (Only variables included in the final step of the backward stepwise multiple regressions are shown (e.g. those that contribute significantly). The total per cent variance explained is a measure of how well the multiple regression comprising the final kinematic variables describes the trend in the respective performance variable. Coeff, standardized partial regression coefficient; StErr, standard error; Max, maximum; Ret, retraction; Dep, depression; Pred, predator; Var, variance.)

variable	pulse duration				pulse magnitude				distance food moves				Max parcel height				parcel area					
	Coeff	StErr	p	Coeff	StErr	p	Coeff	StErr	p	Coeff	StErr	p	Coeff	StErr	p	Coeff	StErr	p	Coeff	StErr	p	
constant	0.00	0.02	—	0.00	0.04	—	0.00	0.02	—	0.00	0.01	—	0.00	0.00	—	0.00	0.01	—	0.00	0.25	<0.001	
Max gape	0.80	0.25	0.002	—	—	—	1.11	0.29	<0.001	0.59	0.20	0.006	1.11	0.25	—	—	—	—	—	—	—	
time to Max gape	0.58	0.26	0.031	—	—	—	—	—	—	-0.58	0.21	0.009	—	—	—	—	—	—	—	—	—	
time to jaw closure	0.47	0.13	<0.001	—	—	—	0.46	0.21	0.035	—	—	—	—	—	—	—	—	—	—	—	—	
time to onset hyoid Dep	—	—	—	—	—	—	—	—	—	—	—	—	0.30	0.13	0.031	—	—	—	—	—	—	—
Max hyoid Dep	—	—	—	—	—	—	—	—	—	-3.18	1.26	0.016	—	—	—	—	—	—	—	—	—	—
time to Max hyoid Dep	-0.78	0.31	0.015	—	—	—	2.50	1.02	0.019	—	—	—	0.42	0.20	0.048	—	—	—	—	—	—	—
time to hyoid Ret	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
duration of hyoid Dep	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
time gills start to open	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
total strike duration	—	—	—	—	—	—	1.48	0.55	0.008	—	—	—	—	—	—	—	—	—	—	—	—	—
distance Pred moves	—	—	—	—	—	—	—	—	—	14.6	—	—	—	—	—	—	—	—	—	—	—	—
total per cent Var explained	—	—	—	31.7	—	—	—	—	—	40.0	—	—	—	—	—	43.7	—	—	—	—	—	57.9

demonstrate the severe constraint imposed by the aquatic medium on the effective range of suction feeding. The ecological consequence of this relationship is that suction feeders must approach their prey closely before striking, potentially necessitating a stalking or ambushing predatory behaviour (Wainwright *et al.* 2001b; Motta 2004; Wilga *et al.* 2007).

Both empirical (Muller & Osse 1984; Higham *et al.* 2005) and theoretical work (Weihs 1980; Muller *et al.* 1982) have shown that mechanisms exist for overcoming physical constraints on suction distance. One of these is to increase predator velocity, generating a more focused, elongated region of effective suction. Though the aspect ratio of the ingested parcel did not exhibit a trend with growth in either species, it tended to be higher (i.e. more rounded) in *C. plagiosum* than in *T. semifasciata* at any given size. The strike velocity for *C. plagiosum* averaged only  $9.37 \pm 6.06 \text{ cm s}^{-1}$ , while for *T. semifasciata* it averaged  $19.10 \pm 6.75 \text{ cm s}^{-1}$ . This corroborates the tendency for increased forward motion of the predator during the strike to influence the shape and length of the parcel of water ingested. A second mechanism to overcome constraints on suction distance involves the use of the substrate to truncate and focus flow (Nauwelaerts *et al.* 2007). Food was presented on the bottom to both species in the current study and flow was clearly truncated ventrally by the substrate (figure 1). Additionally, the rostrum of both species appeared to limit the dorsal extent of the flow, an effect not previously noted in studies of teleost fishes with terminal mouths (Lauder & Clark 1984; Muller & Osse 1984; Day *et al.* 2005; Gibb & Ferry-Graham 2005), but noted recently for *C. plagiosum* (Nauwelaerts *et al.* 2007). Lateral extent of the flow was not considered here because both species possess prominent labial cartilages and manually measuring flow in three dimensions is problematic, but may also be affected by the substrate in some unquantified way. The additive effects of truncating flow into the mouth by feeding near the substrate and having a subterminal mouth may enhance suction capacity by extending the functional extend of the flow and almost certainly have consequences for prey-capture performance in the wild.

The variability in suction performance not accounted for by growth in this study could only partially be accounted for by behaviour. In *T. semifasciata*, combinations of several variables related to the timing and extent of jaw and hyoid motion, nearly all including the extent of maximum gape, were linked to performance variability. Variation in maximum gape can markedly affect the rate of flow at the oral aperture (Ferry-Graham & Lauder 2001; Day *et al.* 2005; Wainwright & Day 2007), affecting both the force available to move food and the volume of fluid ingested. Despite this clear functional relationship, neither maximum gape alone nor any combination of kinematic variables ever accounted for greater than 58% of the size-independent variability in performance. In *C. plagiosum*, variation in pulse duration was related to the timing and extent of cranial elevation, but no combination of kinematic variables ever predicted more than 18% of performance variability. Cranial

Table 5. Kinematic variables contributing to performance differences over time irrespective of size (i.e. size effects accounted for via regression) in *C. plagiostomum*. (Only variables included in the final step of the backward stepwise multiple regressions are shown. The total per cent variance explained is a measure of how well the multiple regression comprising the final kinematic variables describes the trend in the respective performance variable. Coeff, standardized partial regression coefficient; StErr, standard error; Max, maximum; Var, variance.)

variable	pulse duration			Max subambient pressure		
	Coeff	StErr	p	Coeff	StErr	p
constant	-0.02	0.39	—	1.59	0.42	—
Max cranial elevation	-0.17	0.08	0.045	—	—	—
time of Max cranial elevation	0.60	0.20	0.005	—	—	—
onset of cranial elevation	-0.10	0.05	0.037	—	—	—
total strike duration	—	—	—	-0.42	0.28	<0.001
total per cent Var explained			16.6			17.5

elevation is important in determining suction-feeding performance in teleost fishes (Carroll *et al.* 2004), and may be important to other aquatically feeding vertebrates. However, this relationship is only weakly supported here, perhaps because cranial elevation is minimal in suction-feeding sharks and is not mechanically linked to jaw protrusion and buccal expansion (Motta 2004; Matott *et al.* 2005; Wilga *et al.* 2007). Under the conditions tested here, size-independent behavioural variability contributes substantially less than growth to performance over ontogeny in young elasmobranchs and no single kinematic variable or combination of variables can be used as a predictor of suction performance. However, despite the apparent lack of importance attributed to behaviour, it is possible that what variability exists is enhanced in natural situations with diverse prey and becomes a crucial determinant of an individual's competitive ability.

#### 4.1. Ecological implications

Substantial changes in suction-feeding performance occur over ontogeny in both *T. semifasciata* and *C. plagiostomum* that are primarily attributable to growth and changes in behaviour that are correlated with growth. In *T. semifasciata*, these developmental trajectories generate an organism that is functionally adept at suction feeding, but less so than *C. plagiostomum*. Despite physical constraints imposed by the aquatic medium, the propensity to ram feed throughout ontogeny and produce greater absolute pressure with growth probably facilitates the known ontogenetic dietary shift in *T. semifasciata* towards more functionally diverse and elusive prey items (Talent 1976; Kao 2000). Ram feeding has been shown in several species of bony fishes to facilitate consumption of more elusive prey (Norton 1991; Ferry-Graham & Lauder 2001; Wainwright *et al.* 2001b). As increasingly diverse benthic prey types are taken over ontogeny, it is also possible that what suction *T. semifasciata* is able to generate is made more effective by feeding in close association with the substrate, which may substantially extend the effective suction distance (Nauwelaerts *et al.* 2007). As *C. plagiostomum* becomes functionally, anatomically and behaviourally canalized to feed via suction over ontogeny, it generates absolutely

greater suction but maintains a high aspect ratio, rounded parcel of ingested water. These developmental aspects constrain the distance from which *C. plagiostomum* can entrain prey, but provide for a more rapid, brief and forceful suction capture over ontogeny. Knowledge of the biological role for which this feeding mechanism is employed is crucial to making assertions about diet over ontogeny in this species. Orectolobiform sharks including *C. plagiostomum* and *Ginglymostoma cirratum* (P. Motta 2004, unpublished data) and the epaulette shark *Hemiscyllium ocellatum* (Heupel & Bennett 1998) are known to feed by thrusting their heads into soft sediment or crevices in rocky substrate. The capacity to capture prey via suction feeding may be augmented over ontogeny by the development of ambushing, stalking or excavating behaviours that make available crevice-dwelling or burrowing prey by positioning them close to the mouth. If such changes in foraging behaviour do occur over ontogeny, *C. plagiostomum* is anticipated to undergo an ontogenetic dietary shift towards increased utilization of benthic prey.

All animal maintenance and experimental handling procedures were approved by the University of South Florida Institutional Animal Care and Use Committee under protocol numbers 1709 and 2299.

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