Feeding behavior and kinematics of the lesser electric ray, *Narcine brasiliensis* (Elasmobranchii: Batoidea)

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Abstract

Jaw protrusion is a major functional motif in fish feeding and can occur during mouth opening or closing. This temporal variation impacts the role that jaw protrusion plays in prey apprehension and processing. The lesser electric ray *Narcine brasiliensis* is a benthic elasmobranch (Batoidea: Torpediniformes) with an extreme and unique method of prey capture. The feeding kinematics of this species were investigated using high-speed videography and pressure transduction. The ray captures its food by protruding its jaws up to 100% of head length ($\sim 20\%$ of disc width) beneath the substrate and generating negative oral pressures ($\leqslant 31$ kPa) to suck worms into its mouth. Food is further winnowed from ingested sediment by repeated, often asymmetrical protrusions of the jaws ($> 70°$ deviation from the midline) while sand is expelled from the spiracles, gills and mouth. The pronounced ram contribution of capture (jaw protrusion) brings the mouth close enough to the food to allow suction feeding. Due to the anatomical coupling of the jaws, upper jaw protrusion occurs in the expansive phase (unlike most elasmobranchs and similar to bony fishes), and also exhibits a biphasic (slow-open, fast-open) movement similar to tetrapod feeding. The morphological restrictions that permit this unique protrusion mechanism, including coupled jaws and a narrow gape, may increase suction performance, but also likely strongly constrain dietary breadth.
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Introduction

Upper jaw protrusion is unique to aquatic feeding vertebrates and likely serves many roles, even within a single species. Although the basic kinematic sequence of prey capture is conserved among fishes, the upper jaw can protrude either during mouth opening (expansive phase protrusion) or closing (compressive phase protrusion; Lauder, 1985; Wainwright and Lauder, 1986; Motta and Wilga, 2001; Wilga et al., 2001).

Temporal variation in upper jaw protrusion has functional consequences and has proved a fairly reliable distinguishing character of feeding behaviors between elasmobranchs and other fishes (but see Carroll and Wainwright, 2003). The majority of elasmobranchs are compressive phase protruders; this may allow quick reduction of gape, orient the teeth for greater functionality, permit effective gouging, chiseling, or grasping of prey (Moss, 1977; Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Frazzetta, 1994; Wu, 1994; Edmonds et al., 2001; Motta and Wilga, 2001; Wilga et al., 2001). In contrast, in most bony fishes mouth opening drives protrusion of the upper jaw (Liem, 1980, 1991; Motta, 1984). This expansive phase protrusion may provide a small and laterally occluded gape, increase the velocity component of the strike, decrease the predator–prey distance, increase subambient pressure generation for suction-feeding, and/or allow

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procurement of otherwise unreachable prey (Alexander, 1967a, b; Motta, 1984; Ferry-Graham et al., 2001; Waltzek and Wainwright, 2003).

The disparity in relative timing of upper jaw protrusion is determined morphologically through interactions of the palatoquadrate (upper jaw), mandibular (lower jaw) and hyoid (suspensorial) cartilages. Phylogenetically, the Elasmobranchii show a gradual loosening or removal of the more rostral connections of the upper jaw to the cranium (Wilga, 2002). Conversely, adaptive radiation in teleost feeding mechanisms came about through restructuring and reorientation of the jaws, suspensorium and palate (Schaeffer and Rosen, 1961). The freedom of motion available to the palatoquadrate in the majority of elasmobranchs can be considered the result of a relatively uncoupled interaction between the upper and lower jaws (Wilga et al., 2001), in stark contrast to teleosts where the protrusion of one is often dictated by the other (Motta, 1984).

The lesser electric ray, *Narcine brasiliensis* (Batoidea: Torpediniformes) is unique compared to the majority of elasmobranchs in that the jaw arch (upper and lower jaws) functions as a unit (Dean and Motta, 2004). This species is a benthic suction feeder with highly protrusible jaws. In addition to the stabilizing joints between the upper and lower jaws, the jaws are further restricted by an enlarged caudal series of overlapping flanges and several intrinsic ligaments (Fig. 1). As a result, appreciable motion of the jaws relative to one another is only possible in the sagittal plane (opening and closing of the mouth).

This coupling is reflected in the unique protrusion mechanism of this species, involving an extreme reorientation of the jaw arch. Protrusion is effected by medioventral rotation of the hyomandibulae. This motion is transmitted to the mandibles and, due to the coupled jaws and exceptionally loose symphyses, results in medial compression of the entire jaw arch. This reduces the distance between the left and right sides of the jaw arch and extends the jaws as an oral tube (Dean and Motta, 2004).

In both elasmobranchs and teleosts, structural modifications have led to subsequent increases in kinesis and disassociation of the hyoid (suspensorium) and jaw arches, releasing constraints on jaw protrusion capability. This decoupling of the mandibular and hyoid arches is most pronounced in the jaw suspension of batoid elasmobranchs (skates, rays, guitarfishes and sawfishes) in which only the most dorsal suspensorial element (hyomandibula) suspends the jaws from the cranium. The remaining hyoid elements are reduced or lost. This separation and the lack of rostral ligaments between the upper jaw and cranium allow batoids to have more protractile jaws than many sharks (Compagno, 1999; Wilga et al., 2001).
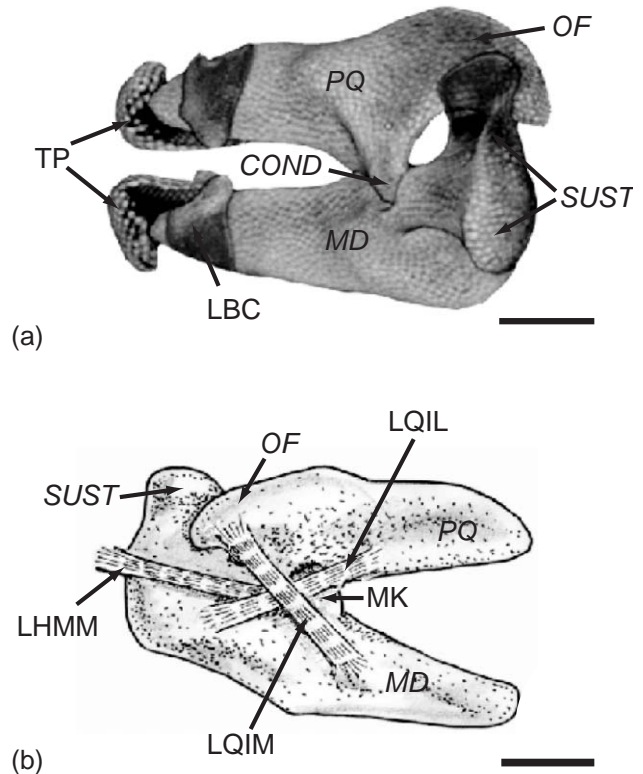

Fig. 1. Jaw arch (palatoquadrate, PQ and mandible, MD) of *N. brasiliensis* in (a) lateral and (b) left lingual views. The jaws are stabilized by dual joints between the palatoquadrate condyle (COND) and the mandibular knob (MK), as well as by the overlapping medial (LQIM) and lateral (LQIL) internal quadratomandibularis ligaments. The caudally expanded otic flange of the palatoquadrate (OF) and mandibular sustentaculum (SUST) further restrict jaw mobility to rotation in the coronal plane (opening and closing). Labial cartilages, LBC; hyomandibular-mandibular ligament, LHMM; tooth pads, TP; Scale bars = 1 cm. Modified from Dean and Motta (2004). Reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

We propose that the increased kinesis of the batoid jaw arch and the morphological coupling of the upper and lower jaws in *N. brasiliensis* are what allow the highly protrusible and versatile tubular jaw apparatus, capable of adjustment in position to capture benthic invertebrates (Rudloe, 1989a; Rudloe and Rudloe, 1993). Based on the apomorphic coupling of jaw elements in *N. brasiliensis*, it is expected that the relative timing of upper jaw protrusion in prey capture will be similar to the generalized sequence of teleost fishes in which the upper and lower jaws protrude in the expansive phase of capture. The goals of this study are to (1) characterize the feeding kinematics and behaviors of *N. brasiliensis*, (2) compare the relative timings of upper jaw protrusion with those of other elasmobranchs and bony fishes, and (3) examine the use of its unique jaw protrusion mechanism in food capture and processing.

Materials and methods

Animal collection and conditioning

N. brasiliensis is found in western Atlantic waters from North Carolina to Brazil and in the Caribbean (Bigelow and Schroeder, 1953; De Carvalho, 1999). This species rarely exceeds 40 cm in length (∼20 cm disc width), and feeds primarily on polychaete annelids (Funicelli, 1975; Rudloe, 1989b; Goitein et al., 1998; De Carvalho, 1999). Six subadult *N. brasiliensis* (20.0 ± 2.9 cm total length, TL; 10.5 ± 1.8 cm disc width, DW) were obtained near Cape Canaveral on the eastern coast of Florida between July and September of 2000 and 2001. *Narcine* 1–3 were housed together in a 300 l tank, while the remaining individuals were maintained individually in 100 l tanks. All aquaria were equipped with under-gravel and accessory mechanical filtration.

Rays were maintained on a 12L:12D light cycle at 21–24°C and 29–32 ppt salinity, and fed a diet of bloodworms (*Glycera dibranchiata*), nightcrawlers (*Lumbricus terrestris*), and glass- and ghost-shrimp (*Natania* sp.) with carapaces crushed to disable elusive movement. This maintenance diet was offered once every other day.

For cinematography, individual rays were offered bloodworms sectioned to lengths three times the width of each animal's mouth. Food items larger than this were not utilized as they elicited longer processing events in which rays would typically swim off the bottom and leave the camera's field of view. No more than ten capture events were recorded for an individual in a single day to avoid satiation effects (Sass and Motta, 2002). Food was withheld from each animal for two days prior to each experiment in order to encourage active feeding during filming. Animal care and handling procedures were approved by the Institutional Animal Care and Use Committee of the University of South Florida (IACUC♯1719).

Terminology

Unless referring to prey capture under natural or semi-natural conditions (i.e., buried, intact polychaetes), the term "food" is used to refer to items ingested during experimental procedures. Feeding sequences can be divided into several distinct events: food capture is the initial acquisition of a food item (Gillis and Lauder, 1994), beginning with jaw opening (Wilga and Motta, 1998b). Winnowing (the separation of food items from sediment) and food processing (reduction, manipulation or reorientation of food items) follow capture. Individual jaw protrusion events during food/prey processing (i.e., separate from a winnowing cycle) are referred to as processing protrusions, as opposed to the capture protrusions used in initial food/prey acquisition. Food/prey transport involves rostrocaudal motion of the food item from the orobranchial cavity to the esophagus for swallowing. The terms palatoquadrate and Meckel's cartilage will be used interchangeably with upper jaw and lower jaw, respectively.

Cinematography

Food capture kinematics

Fifteen food capture events per individual (13 for *Narcine* 2 due to its death) were recorded with two synchronized Redlake (PCI-1000 and PCI-500) video cameras at 250–500 fields/s. Cameras were positioned orthogonally to grant simultaneous anterior and lateral views. Rays were filmed under quartz-halogen lighting at 1000 W intensity and a 60 W standard soft-white light bulb, used to illuminate the ventral surface of the animals.

Although *N. brasiliensis* is described anecdotally to capture buried prey items (Rudloe, 1989a), for all trials, food was positioned on the surface of the substrate. This facilitated anterior viewing of the protruded jaws (protrusion was visibly occluded by the pectoral fins in lateral view). With this presentation, rays would lift their rostra prior to food capture.

Twenty-four kinematic, displacement, and velocity variables were analyzed for each capture sequence. Kinematic variables were measured relative to the initiation of mouth opening/lower jaw depression (time zero). Duration of kinematic variables were assessed by counting the number of frames (2–4 ms/frame) from onset to offset of a given behavior: (1) time to onset of rostral lifting; (2) time to peak rostral lifting (frame in which the ray's rostrum reached its highest point above the substrate); (3) time to onset of body lunge (anterior rostral movement); (4) time to peak lunge (peak anterior excursion of the rostrum); (5) time to onset of palatoquadrate protrusion; (6) time to peak jaw protrusion; (7) time to food contact; (8) time to onset of food movement toward the ray; (9) time to ingestion of the food item (movement of the food item past the plane of the oral gape or cessation of movement); (10) time to onset of eye retraction (ventral retraction of the eye closest to the lateral camera); (11) time until eye returns to its resting position; (12) time to onset of labial flaring (lateral flaring of labial cartilages, resulting in the jaws forming an inverted T; Fig. 2); (13) time to mouth closure; (14) time to onset of jaw retraction; and (15) time to end of jaw retraction (when the jaws end their dorsal movement; this was not always a complete return to resting jaw position, as processing often began directly from a partially protruded state). Displacement variables relate to both cranial kinematics and body posture: (16) capture initiation distance at time zero (measured from the mandibular symphysis to the point
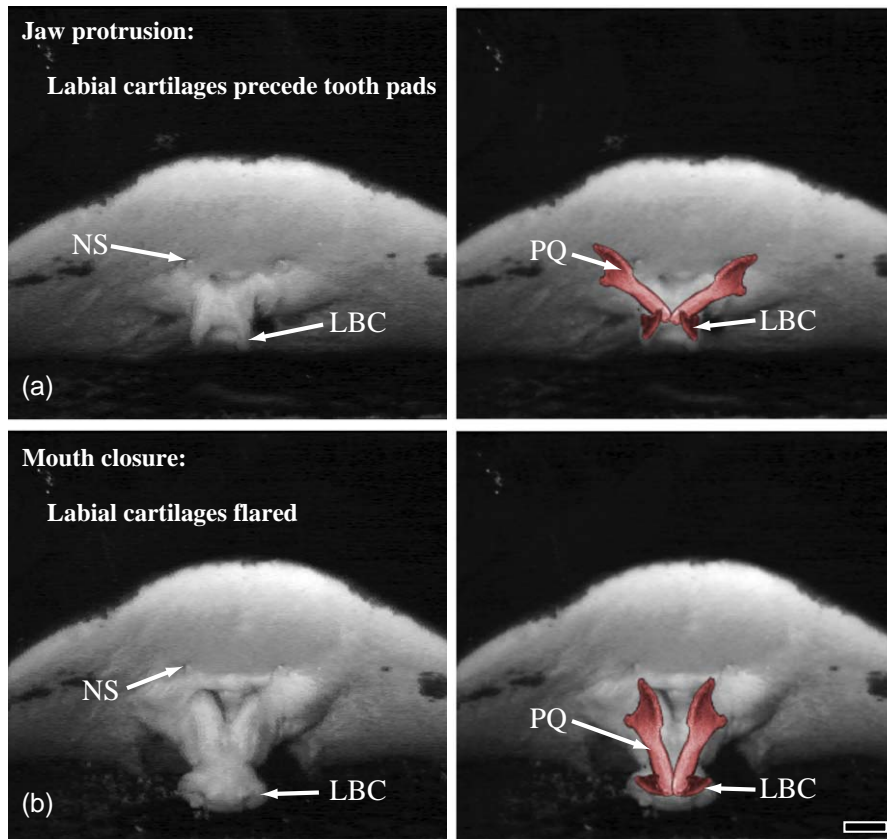
Fig. 2. Anteroventral view of labial cartilage movement during food capture in *N. brasiliensis*. The high-speed video images in (a) and (b) are duplicated to the right and overlain with red representations of skeletal elements to indicate the relative positions of the palatoquadrates (PQ) and labial cartilages (LBC). The nares (NS) are indicated in the left-hand images for reference. Prior to food contact (a), the labial cartilages are the most ventral structures of the protruding jaws. Following ingestion of the food by suction (b), the jaws close, flaring the labial cartilages dorsolaterally. Scale bar = 1 cm. Figure modified from Dean and Motta (2004). Reprinted with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

of first contact on the food item); (17) protrusion distance at food contact; and (18) peak jaw protrusion distance. Velocities of displacement were calculated from measured distances and duration of behaviors: (19) lunge velocity; (20) velocity of mandibular depression; (21) velocity of palatoquadrate protrusion (from time zero to the point of food contact for variables 20 and 21); (22) velocity of mandibular protrusion; (23) velocity of palatoquadrate protrusion (from time zero to peak protrusion for variables 22 and 23); and (24) velocity of jaw retraction.

Normality and equality of variance for kinematic variables were tested using the Kolmogorov-Smirnov test ($p \leqslant 0.05$) and the Levene Median test ($p \leqslant 0.05$), respectively; if the parametric assumptions were not met, data were transformed.

A principal components analysis (PCA) was used to reduce the dimensionality of the capture data set. The PCA provides an indication of the relative contribution of variables to the overall variation and groups variables with similar influence. The resultant combinatorial variables delimit a multidimensional behavioral/kinematic space for each individual. A multivariate analysis of variance (MANOVA) was applied to the PCA scores to look for differences among these individual clusters according to their distribution in multivariate space. Axes exhibiting significant differences were further investigated with one-way ANOVAs of the axis variables to localize variables contributing significantly to variation among individuals. All statistical tests were completed using Sigma Stat (version 2.03, SPSS Science, Inc.) and SYSTAT (version 10, SYSTAT Software, Inc.) statistical programs.

Winnowing and asymmetrical jaw protrusion

Winnowing and food processing behaviors were extremely variable and complex, often exceeding the recording time of the camera. Due to this partial data set, only 2 s following the onset of winnowing were analyzed from haphazard random subsets of six bites per individual.

Winnowing and food processing involved cycles of repeated jaw protrusion and retraction. A winnowing cycle starts with the cessation of jaw retraction of the previous cycle and ends when the jaws reach the maximum extent of their retraction toward the ventral body wall following peak protrusion. The following variables were measured for each cycle: (1) cycle duration; (2) rostral height at cycle onset; (3) distance of peak winnowing protrusion; and (4) velocity of winnowing protrusion. The wide variability of these measurements and small sample size resulted in low power of test (<0.20), precluding statistical analysis.

Asymmetrical jaw protrusions (deviating laterally from the animal's mid-sagittal axis) occurred both between and during winnowing cycles. In these cases, the following variables were measured: (1) direction of protrusion relative to the animal; (2) distance of protrusion from the center of the nasal curtain; and (3) angle of excursion from the mid-sagittal axis. To investigate potential "handedness" (preference for a particular side), a χ^2 test was performed on the number of right-hand and left-hand asymmetrical protrusions for each individual and all rays. Also, the distance of processing (including asymmetrical) protrusion was compared graphically with capture protrusion distance to examine differences in protrusion behavior between capture and processing.

In addition, the following variables were measured for the entire processing event: (1) time to onset of winnowing relative to the end of jaw retraction during capture; (2) duration of the entire winnowing event (when the endpoint was able to be recorded); and (3) cycle frequency (the number of winnowing cycles per second). Incomplete winnowing cycles (e.g., cycles with incomplete retractions, cycles including a processing protrusion) were excluded from calculations of cycle frequency. A one-way ANOVA compared winnowing frequencies among individuals ($p \leqslant 0.05$).

Semi-natural excavation and prey capture

Semi-natural prey capture trials were performed in a shallow 1351 tank to provide a more ecologically relevant supplement to food capture experiments. Live bloodworms (*G. dibranchiata*) of varying size were allowed to bury in the sediment (approximately 7.5 cm deep rinsed ♯3 blasting sand, ∼1.5 mm particle size) and on two separate occasions, *Narcine* 4–6 were introduced individually into the system and allowed to hunt for ∼60 min, until cessation of apparent hunting behaviors. Rays were withheld food for two days prior to filming. Individuals were filmed continuously during each trial using a handheld JVC GR-DVL9800 camcorder (125 fields/s) on a tripod. Video was dubbed to VHS tape at 30 frames/s and behaviors were qualitatively analyzed at 60 fields/s using a Panasonic AG 1980 desktop video editor.

Pressure recording

Subambient pressures generated on the surface of food items were recorded using a Millar Mikro-tip pressure transducer (Model TCB-500) sheathed in hard plastic tubing. Pressure traces were amplified through a Millar TCB-500 transducer control unit and recorded as voltages directly to a Dell Inspiron notebook computer using LabView 6 software (National Instruments, Inc.). To calibrate the pressure sensor, four trials each for four calibration pressures (generated with a syringe; mmHg) were recorded in a closed system and a best-fit line calculated ($r^2 = 0.996$) as a base-line for transducer voltage data.

The pressure catheter was threaded through the body cavity of a sectioned bloodworm such that the tip of the tubing was flush with the extreme end of the worm. The food was presented just above the substrate. A handheld JVC GR-DVL9800 camcorder (125 fields/s) was used to record food capture kinematics and the output screen of the laptop simultaneously to provide approximate correlation between cranial movements and pressure generation. A total of 11 food capture events were filmed from *Narcine* 5 and due to the animal's inadvertent grasping of the pressure catheter in its protective housing, five processing protrusions and four apparent compression transports (see Results) were also recorded. Due to the limited sample size, only descriptive statistics were performed.

Results

Cinematography

Food capture kinematics

Several distinct feeding behaviors were observed in *N. brasiliensis*: food location and orientation, food capture, winnowing (processing) and compression transports. When food was introduced into tanks, rays began an exploratory behavior, "walking" along the substrate using alternating unilateral or coordinated bilateral thrusts of the pelvic fins, swinging the rostrum from side to side in slow arcs.

Upon locating food or prey (intact, living worms), exposed or buried, *N. brasiliensis* typically oriented with the rostrum (anterior to the nasal flap) over the potential food item. In trials where food was presented on the surface of the sediment, orientation included slow lifting of the rostrum, which continued well into the capture event (Table 1, Fig. 3). The lateral tips of the pectoral fins were kept in contact with the substrate such that the raised rostrum formed an enclosure around the food. Onset of rostral lifting was highly variable and began from 30 ms to more than 250 ms before time zero (lower

Table 1. Means and principal components analysis (PCA) scores for 88 food-capture events by six sub-adult *Narcine brasiliensis*

Variable	Mean ± S.E. (N = 6 subadults)	PC1 'Timing and velocity'	PC2 'Distance and velocity'	PC3 'Protrusion and retraction'
KINEMATIC VARIABLES (MS)				
Onset of rostral lifting	−252 ± 18	—	—	—
Peak rostral lifting	55 ± 2	—	—	—
Onset of body lunge	−96 ± 5	—	—	—
Time to peak lunge	88 ± 6	—	—	—
Onset of upper jaw protrusion	22 ± 1	**0.82**	0.23	0.10
Time to food contact	31 ± 1	**0.92**	0.33	−0.02
Onset of food movement	34 ± 1	**0.92**	0.32	−0.01
Time to food ingestion	44 ± 1	**0.93**	0.21	−0.06
Time to peak protrusion	53 ± 1	**0.95**	0.15	−0.03
Onset of eye retraction	26 ± 1	**0.93**	0.17	0.05
Return to resting position	144 ± 3	**0.60**	0.06	−0.23
Onset of labial flaring	52 ± 1	**0.91**	0.18	−0.01
Time to mouth closure	58 ± 1	**0.92**	0.11	0.01
Onset of jaw retraction	63 ± 1	**0.92**	0.05	−0.01
End jaw retraction	237 ± 5	**0.48**	**−0.41**	**0.61**
Winnowing onset	276 ± 6	**0.68**	−0.14	**0.46**
DISPLACEMENT VARIABLES (CM)				
Capture initiation distance	0.53 ± 0.02	0.09	**0.74**	−0.22
Protrusion distance (at food contact)	0.81 ± 0.03	0.25	**0.84**	−0.08
Protrusion distance (at peak protrusion)	1.44 ± 0.03	−0.14	**0.63**	**0.63**
VELOCITY VARIABLES (CM/S)				
Lunge velocity	6.57 ± 0.25	—	—	—
Velocity of lower jaw protrusion (to food contact)	27.58 ± 0.92	**−0.71**	**0.49**	−0.05
Velocity of upper jaw protrusion (to food contact)	86.84 ± 3.19	**−0.64**	**0.40**	0.12
Velocity of lower jaw protrusion (to peak protrusion)	27.58 ± 0.92	**−0.78**	0.34	**0.45**
Velocity of upper jaw protrusion (to peak protrusion)	49.16 ± 1.36	**−0.64**	**0.43**	**0.48**
Velocity of jaw retraction	7.44 ± 0.23	−0.22	**0.72**	−0.15
% Total variance explained		49.68	15.95	7.46

The first three PCs described 73.08% of the variance in prey capture variables. Bolded PC scores indicate axis assignment and functional implications of loading combinations are noted for each PC axis. Lunge and rostral lifting variables were excluded from PCA.

jaw depression). After the onset of rostral lifting, but prior to lower jaw depression, the animal lunged forward with bilateral thrusts of the pelvic fins.

Variable lifting of the body resulted in great variation in the mandible-to-food distances from which capture began. Initial depression of the lower jaw was almost imperceptible in many cases due to anteroventral deflection of the nasal flap concomitant with any ventral motion of the jaws. Onset of upper jaw protrusion began 22 ms after lower jaw depression onset and was initiated with the mouth slightly open in most cases.

The upper and lower jaws were simultaneously extended ventrally or anteroventrally with the symphy-

seal angle (the angle between the two moieties of the palatoquadrate in anterior view) becoming more acute with increasing protrusion distance (Fig. 3). In addition, after palatoquadrate protraction onset, the eyes began to retract ventrally.

The rate of lower jaw depression was similar to the rate of rostral lifting until the onset of palatoquadrate protrusion. The upper jaw began to protrude past the nasal flap approximately 67.5% of the way through the time taken for the lower jaw to depress and contact the food item. In this way, the velocity of upper jaw protrusion from onset to food contact (86.8 ± 3.19 cm/s) was more than double that of the lower jaw
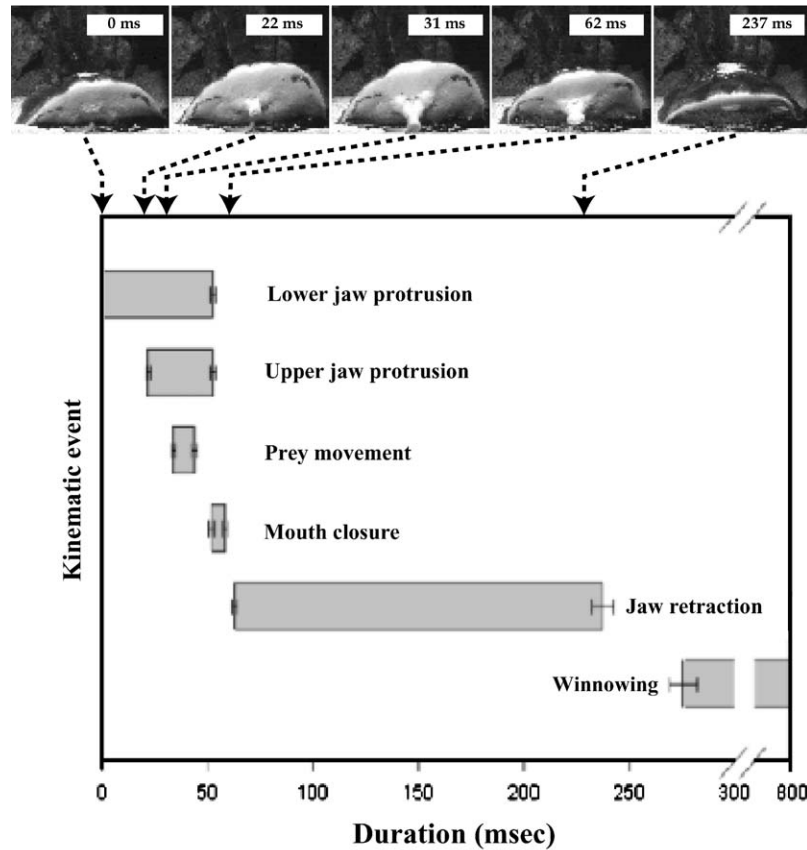
Fig. 3. Synchronized means of kinematic events during 88 food captures in six subadult *N. brasiliensis*, with time zero as the onset of mandibular depression. Images are from high-speed video recordings of a representative capture sequence and arrows indicate their relative positions in the kinematic sequence. Note that the food item, a bloodworm, is visible for the first three frames of the image sequence. Error bars at the left- and right-hand side of each kinematic event represent standard error of onset and offset times, respectively. Winnowing can continue for more than 60 s and is not displayed in entirety.

$(27.6 \pm 0.92 \, \text{cm/s})$ (Table 1). Therefore, the majority of the distance covered by the protruding oral tube occurred after palatoquadrate protrusion began (Fig. 4).

During jaw protrusion, the labial cartilages were clearly visible forming ventrally directed ridges to the advancing tooth pads. As a result, the labial cartilages were the most ventral structures of the protruding jaws and the first to contact the food (Figs. 2, 3 and 5).

The food began to be drawn into the oral cavity 34 ms after the onset of mandible depression (Figs. 3 and 5). Food items of this size (length $= 3 \times$ mouth width) were completely ingested (no longer visible) in 10 ms or less as the jaws continued to protrude. Depression of the hyoid/branchial region was typically obscured anteriorly by the jaws and laterally by the pectoral fins, however on many occasions, ventral expansion of this region was visible prior to food movement. Due to continued body lifting (Fig. 4), the distance of protrusion at food contact $(0.81 \pm 0.026 \, \text{cm}; \, 7.08\% \, \text{DW})$ is greater than the distance of the jaws from the food item at time zero $(0.53 \pm 0.025 \, \text{cm}; \, 4.64\% \, \text{DW})$ (Table 1).

Peak protrusion of the jaws after complete food ingestion (53 ms) was simultaneous with complete retraction of the eyes and peak rostral lifting (Fig. 3). The mean distance of peak jaw protrusion was 1.44 cm (12.56% DW) with a maximum of 2.07 cm (approximately 18% DW or 10% TL). From onset to peak protrusion, the velocity of the upper jaw protrusion $(49.16 \pm 1.36 \, \text{cm/s})$ was also greater than lower jaw protrusion $(27.58 \pm 0.92 \, \text{cm/s})$, but to a lesser degree than from onset to food contact (Table 1). This was due to deceleration of both upper and lower jaws following food contact. Simultaneous with the jaws reaching the extent of their ventral protraction, the labial cartilages began to flare dorsolaterally, such that when the mouth closed, the labial cartilages were nearly perpendicular to the axis of protrusion in anterior view (Fig. 2).

After mouth closure, the jaws began to slowly retract in an anterodorsal arc, with the retraction phase (175 ms) more than 100 ms longer in duration than the capture phase to that point (63 ms) (Fig. 3). The velocity of jaw retraction $(7.44 \pm 0.23 \, \text{cm/s}$; upper and lower jaws
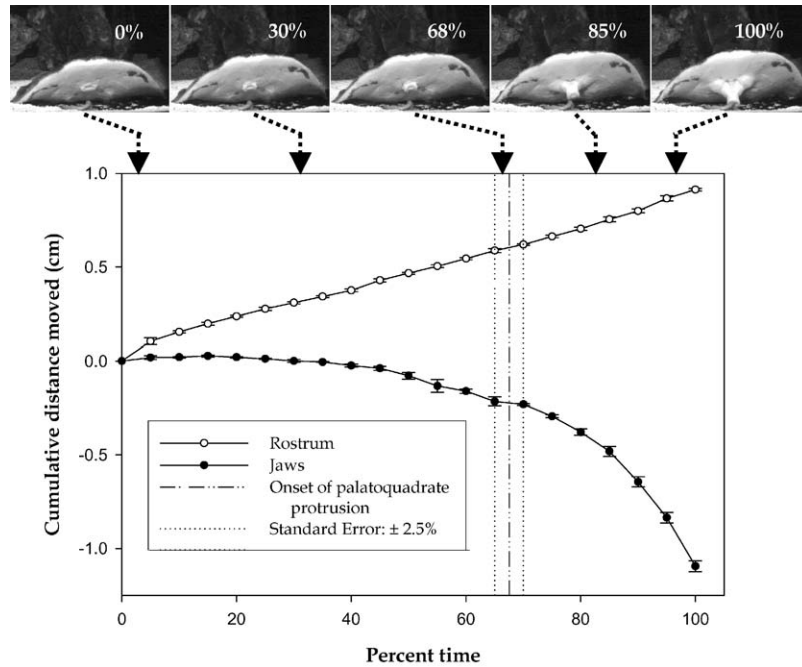
Fig. 4. Cumulative distance change for rostrum lifting and lower jaw protrusion during food capture in *N. brasiliensis* ($N = 6$). Upper images are from high-speed video recordings of a representative capture sequence and arrows indicate their relative positions in the kinematic sequence. To standardize between captures of varying duration, time is measured in percent from the onset of mandibular depression (0%) to food contact (100%). Food items begin to enter the mouth through suction immediately after food contact (see Fig. 5). Velocity of jaw protrusion shows marked increase with onset of palatoquadrate protrusion, occurring on average at $67.54 \pm 2.5\%$ of the capture process.

retracted as a single unit) was considerably slower than any of the jaw protrusion velocities (Table 1). The animal reached the anterior extent of the body lunge (less than 10% TL, 18% DW) and began to slowly move backwards onto laterally splayed pelvic fins and the dorsolateral margins of the pectoral fins. The eyes
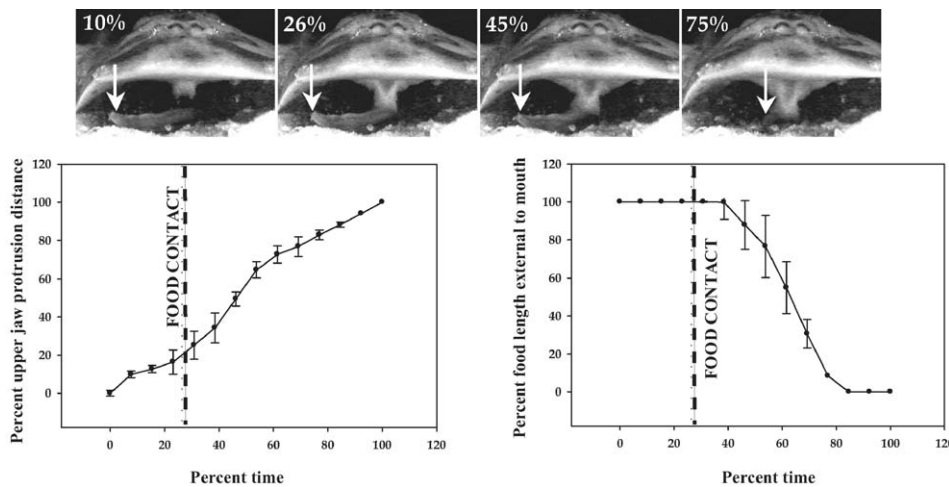

Fig. 5. Food movement by inertial suction relative to upper jaw protrusion in a subset of *N. brasiliensis* food capture events ($N = 10$). To standardize between individual events, jaw protrusion distance (left graph) and food movement (right graph) are presented as percent. For example, 100% jaw protrusion distance is peak jaw protrusion and 100% food length indicates that the entire food item is outside of the mouth. Time 0% is the frame prior to the onset of palatoquadrate protrusion (the fast-open phase) and time 100% is peak protrusion. The onset of food movement (~ 40–50% time) occurs after the jaws contact the food item (mean = 26.4% time, indicated by a vertical dashed line in both plots). The upper four frames from high-speed video footage show representative food movement at a given percentage time. The white arrows mark the distal end of the food item as it moves into the buccal cavity.
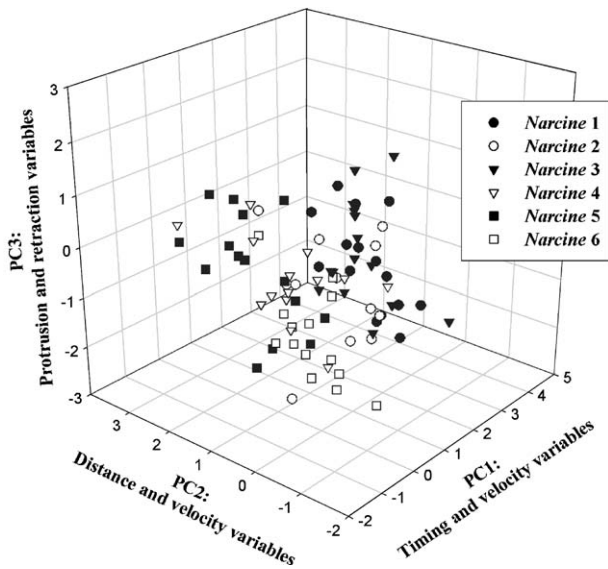
Fig. 6. Principal component (PC) plots comparing PC1, PC2 and PC3 for 88 food-capture events by six subadult *N. brasiliensis*. Capture variables are highly correlated and load on multiple axes with all principal components exhibiting significant interindividual variation. Individual animals are designated by unique data symbols.

returned to resting position, and capture ended with complete retraction of the jaws, 237 ms after the onset of lower jaw depression (Fig. 3).

PCA indicated that 73.08% of the variance in the data set could be described by the first three principle

component axes generated (Table 1). All kinematic variables and jaw protrusion velocity variables loaded highly on the first PC axis (Table 1; Fig. 6). The second axis consisted of jaw protrusion and retraction velocities, all displacement variables and the end of jaw retraction. The third axis contained jaw protrusion velocity variables, protrusion distance, the end of jaw retraction, and onset of winnowing. These axes have functional and temporal connotations, with variables describing the early, middle and late portions of capture loading on axes one, two and three, respectively. However, several variables loaded on more than one PC, indicating significant correlation between all portions of capture.

MANOVA detected significant individual effects (Wilk's $\lambda = 0.264$; d.f $= 15$, 218; $F = 9.025$; $p < 0.001$) with all axes contributing significantly (*p*-values: PC1 < 0.001; PC2 < 0.001; PC3 < 0.001). Post hoc tests showed no individual consistently caused the individual effect to be significant in the univariate ANOVA results.

Winnowing

Winnowing (cyclic protrusion and retraction of the jaws with expulsion of inedible material) is typically initiated from a body posture where the animal's rostrum is raised and the body supported by laterally splayed pelvic fins and the dorsolateral margins of the pectoral fins (Fig. 7). The duration of the winnowing behavior is extremely variable, lasting from 1410 ms to more than 60 s. Mean cycle frequency for the winnowing
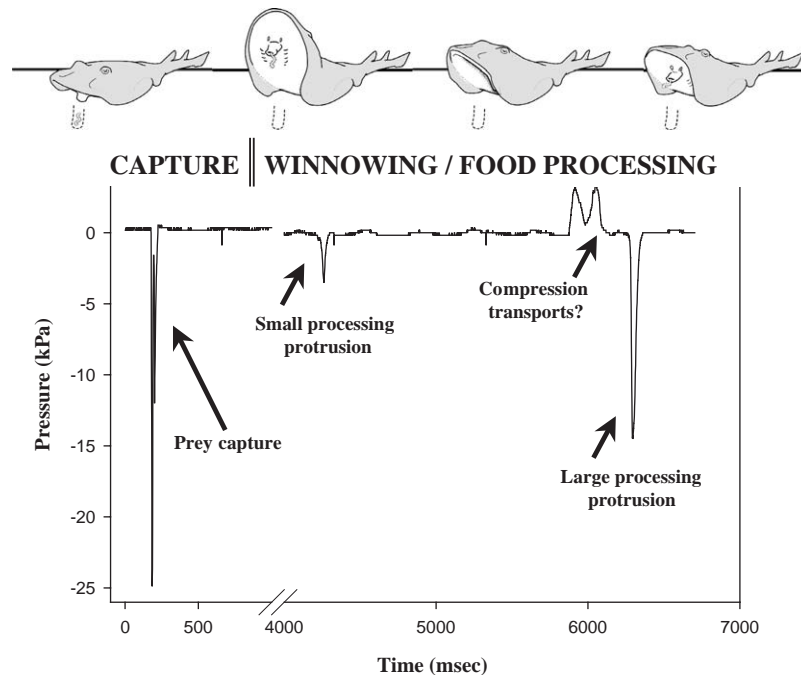

Fig. 7. Representative food capture sequence compiled from extra- and intraoral pressure recordings ($N = 11$) and semi-natural food capture events ($N = 6$) in *N. brasiliensis*. Whole-body sketches at the top of the figure indicate typical body position during capture and processing, with corresponding pressure peaks below each image.
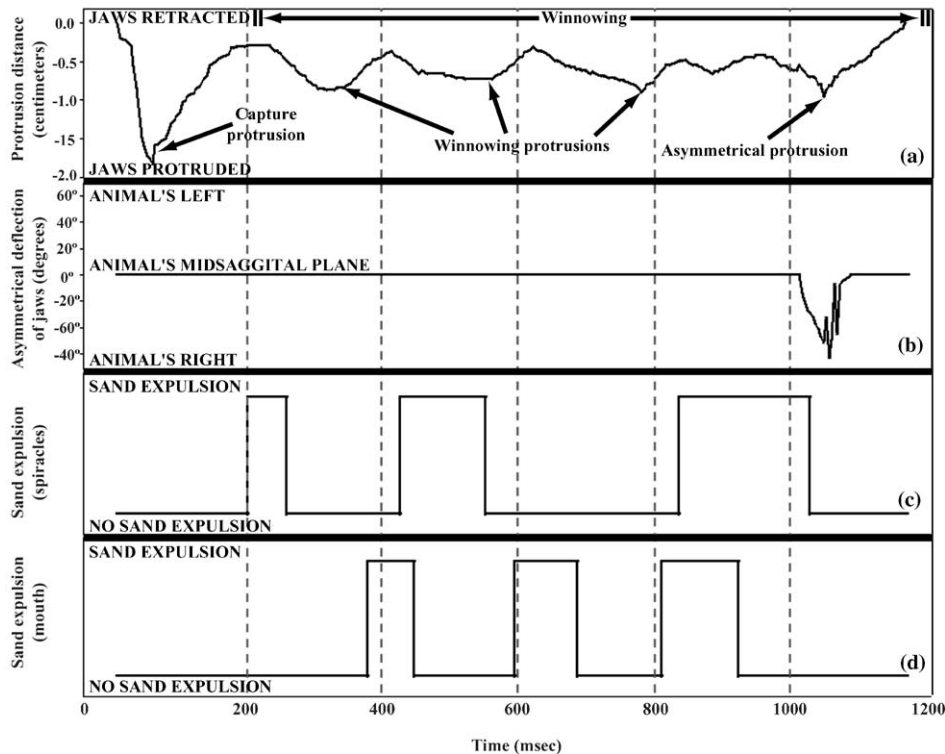
Fig. 8. Representative jaw motion and sand expulsion in one food capture event for an individual subadult *N. brasiliensis*. Each row (a–d) represents a behavior or position of the jaws, with changes in that condition occurring on the *y*-axis. Jaw protrusion distance (a) is typically greater during capture (~0–200 ms) than during winnowing (~200–1200 ms), with the majority of asymmetrical jaw protrusion events (a, 1050 ms; b) occurring during processing. Sand expulsion from the spiracles (c) and mouth (d) usually occurs as the jaws are retracted during winnowing.

event is 4.5 ± 0.1 Hz, with no significant interindividual variation ($p = 0.671$). The rostrum is raised and lowered from this position throughout the winnowing period, with no apparent pattern. Sediment is expelled from the mouth, spiracles and gills as the jaws are retracted (Fig. 8).

Food may also be repeatedly expelled through the mouth, either completely or into the grasp of the tooth pads, and reingested. In cases where food is held externally between the tips of the jaws, it does not appear to be repeatedly raked over the teeth. Rather, the food item is sucked into the mouth during a single, apparently more vigorous, protrusion of the jaws (see description of asymmetrical protrusion).

Asymmetrical protrusion

Although asymmetrical processing protrusions were common (occurring in over 95% of feeding events analyzed), only a single asymmetrical capture protrusion was observed in the entire study (Fig. 9). However, food items were always placed directly below feeding rays. Protrusions of the jaws during processing were interspersed, either between or within winnowing cycles with no apparent regularity, but often coinciding with suction events to ingest food items held between the jaws.

Individuals exhibited no significant differences between the numbers of left- and right-hand protrusions ($\chi_1^2, N = 268 = 3.841$, $p < 0.001$). Protrusion distance decreased with increased lateral deviation from the mid-sagittal axis (Fig. 9) with a maximum lateral
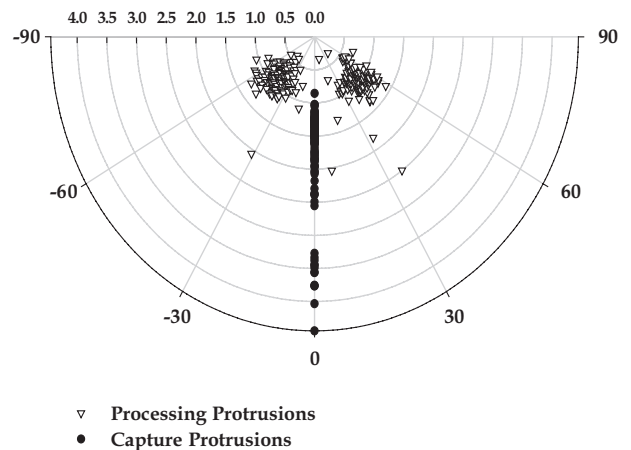

Fig. 9. Upper jaw protrusion distance (cm) and protrusion angle for *N. brasiliensis* ($N = 6$) during capture and food processing. Dots indicate the position of the mandibular tooth pad at peak protrusion. Angle measurements are relative to the animals' mid-sagittal plane.
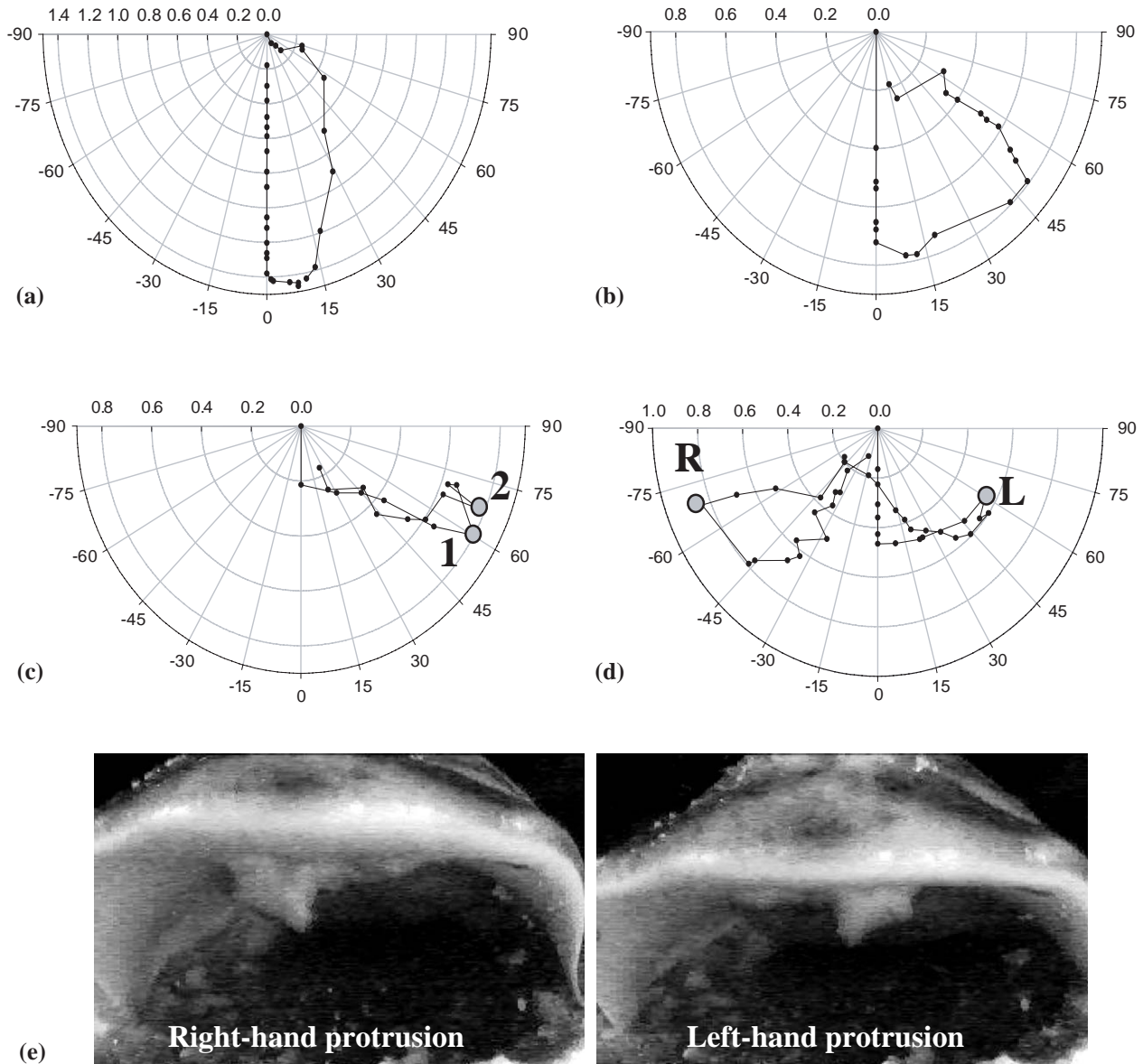
Fig. 10. Representative traces of asymmetrical processing protrusion events ($N = 4$ individual bites) for *N. brasiliensis* from high-speed video sequences. Dots indicate the position of the mandibular tooth pad. The linear axis is distance in centimeters, and angular data represent angular deviation of the jaws from the mid-sagittal axis. Traces begin at the origin (the jaws in retracted state), with each data point 8 ms apart. Asymmetrical protrusion can (a) be asymmetrical from the retracted state, (b) deviate from the midline upon reaching the protruded state, or (c) deviate from the midline partway through mid-sagittal protrusion. Asymmetrical protrusions can involve a series of short protrusions and incomplete retractions in series, either (c) unilaterally (1 and 2) or (d) bilaterally (R and L). The high-speed video sequences shown in (e) are anterior views of the peak asymmetrical frames (L and R) from the sequence shown in (d).

deviation of $70.84°$. Motion of the jaws in processing events could follow several patterns: asymmetrical protrusion directly from a retracted state (e.g., Fig. 10a), lateral deflection of the jaws at peak protrusion (e.g., Fig. 10b), or asymmetrical deviation from a ventrally directed protrusion (e.g., Fig. 10c). Asymmetrical protrusion may also involve a brief, incomplete retraction and a second protrusion (e.g., Figs. 10c and d).

Compression transport

Completion of the feeding event is marked by compression transport behavior in which *N. brasiliensis* depresses its rostrum and retracts its jaws dorsally (from the anatomically retracted position, with the upper and lower jaws flush with the ventral body wall). Rostral depression appears as a flexing of the anteromedial rostral cartilages rather than a depression of the whole body or head.

Compression transport may be present before the end of winnowing (e.g., between winnowing cycles); however, the end of the feeding event is always marked by this behavior, with one to several compression transports of the jaw arch (Fig. 7). The animal then settles to the sediment and often exhibits a coughing behavior lasting 10–20 ms in which the labial cartilages are extended ventrally as the mouth is opened and water expelled.

Semi-natural excavation and prey capture

Accurate duration measurements for semi-natural feeding behaviors were not possible with the handheld camera, but were apparently similar to those recorded with high-speed video. Capture of buried bloodworms involved similar exploratory behavior to capture of unburied food. Pre-strike pauses, presumably directly over prey items, lasted from approximately 30 s to over 10 min, with rays repeatedly adjusting and reorienting their rostra or body positions.

Capture began with a short, anteroventrally directed lunge in which the rostrum was pressed against the sediment and the eyes retracted as the jaws were protruded beneath the sand to extract prey (Fig. 7). Columns of sand were often expelled from the spiracles as the eyes reached peak retraction. Worms were typically grasped immediately caudal to their everted pharynx and oral hooks as the ray levered its body dorsocaudally on its pelvic fins to extract the entire prey item. Winnowing always began from this posture, with the worm held away from the sediment. In these experiments, individual *N. brasiliensis* commonly excavated and ingested polychaetes as long or longer than their total lengths.

With prey longer than approximately five mouth widths, *N. brasiliensis* swam off the bottom during the winnowing phase of capture, circling the tank while the worm remained hanging from the jaws. The prey item was then drawn incrementally into the oropharyngeal cavity through repeated processing protrusions, with the ray often expelling clouds of blood from the spiracles during compression transport.

Pressure recording

Suction amplitude during strikes showed wide variation (mean -21.68 kPa ± 2.72 S.E., maximum -30.89 kPa) with onset of suction generation appearing to correlate with food contact (Fig. 7). Likewise, there was large variation in suction amplitude during processing (mean -20.66 kPa ± 4.52 S.E., maximum -34.25 kPa), with suction generation apparently correlating with peaks in processing protrusions. Retraction of the jaws during compression transport exhibited positive spikes in pressure (4.03 kPa ± 0.93 S.E., maximum 6.88 kPa),

occurring in both recorded events as peaks in quick succession (143–246 ms apart).

Discussion

Prey/food capture phases

Narcine brasiliensis employs a food capture behavior characterized by extreme jaw protrusion that, although conforming to the basic rostrocaudal sequence of cranial and hyoid expansions characteristic of aquatic vertebrate feeding, exhibits several notable alterations. Some suction-feeding elasmobranchs, including those batoids previously examined, exhibit a preparatory phase of buccal volume reduction prior to mouth opening as a means of maximizing generation of subambient pressures (Wilga and Motta, 1998b; Sasko, 2000; Motta et al., 2002). In *N. brasiliensis*, brief jaw retraction immediately prior to protrusion was visible in cinefluoroscopic study and may represent a preparatory phase (Dean and Motta, 2004).

The expansive phase in elasmobranchs typically involves depression of the lower jaw at a relatively constant and high velocity (Motta and Wilga, 2001; Motta et al., 2002). In *N. brasiliensis*, the initial phase of mouth opening involves slow depression of the mandible similar to the slow opening phase of tetrapods (Bramble and Wake, 1985) and some bony fishes (Wainwright et al., 2001). This is followed by the fast opening phase, marked by a sharp increase in jaw protrusion/depression velocity at the onset of palatoquadrate protrusion.

Movement of the lower jaw and its coupling to the upper jaw most likely mediates these two distinct episodes of the expansive phase. As the mandible begins to depress, there is a period of latency (slow open) before cartilaginous and ligamentous associations begin to pull the palatoquadrate ventrally (fast open). This may be further delineated by the paired coracohyomandibularis muscles (Fig. 11), which extend from the pectoral girdle to the hyomandibulae and likely aid in protrusion of the jaw arch (through medial rotation of the hyomandibulae; Dean and Motta, 2004). The coracohyomandibularis tendon turns anterolaterally at a sharp angle to run beneath the first hypobranchial at the anteroventral end of the branchial cavity. As the muscle contracts, the tendon appears to reach a critical angle that would decrease the work necessary to rotate the hyomandibulae and protrude the jaws (Dean and Motta, 2004). The arrival at this point of increased freedom of movement is likely represented by the fast open phase of jaw protrusion. This protrusion mechanism has potential to be "cocked" (pre-loaded) in a manner similar to jaw depression in the cichlid, *Astatotilapia elegans* (Aerts et al., 1987).
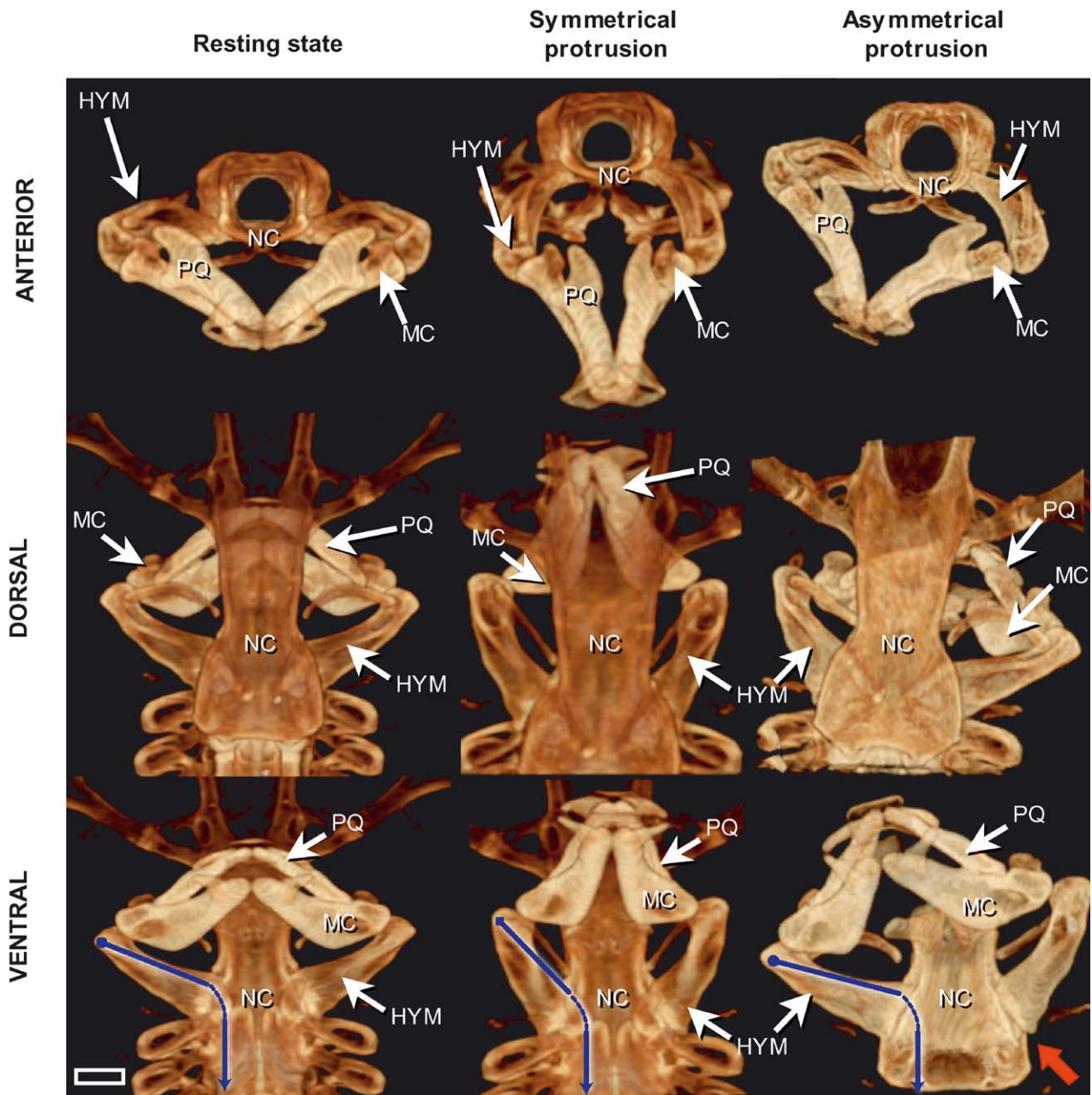
Fig. 11. Anterior, dorsal and ventral CT scans (top, middle and bottom rows) illustrating resting state (left column), symmetrical (middle column) and asymmetrical (right column) jaw protrusion in *N. brasiliensis* (female; 14.5 cm DW). The hyomandibulae (HYM) are the sole means of jaw suspension from the neurocranium (NC). In jaw protrusion, the hyomandibulae are rotated medioventrally, pushing Meckel's cartilage (MC; lower jaw) and the palatoquadrate (PQ; upper jaw) simultaneously. The hyomandibulae articulate with the cranium through dual facets arranged in rostral-caudal series. In asymmetrical protrusion, the jaws are pivoted laterally through differential rotation about these joints. The hyomandibula contralateral to mouth movement pivots into the rostral hyomandibular facet at the cranium, pulling away from the caudal facet (red arrow in asymmetrical protrusion state, ventral view). As a result, although the jaws flex symmetrically about the symphyses, the entire arch is displaced from the mid-sagittal plane. Jaw protrusion is largely mediated by the paired coracohyomandibularis muscles (only one shown; blue line in ventral views), which originate on the pectoral gridle, run beneath the first hypobranchial (dotted line) and insert on the hyomandibulae. The angle formed by the muscle at the hypobranchial becomes less acute as the jaw protrudes, orienting the muscle for more direct force transmission. Differential contraction of the coracohyomandibularis would result in asymmetrical jaw protrusion. Scale bar in resting state, ventral view = 1 cm. Figure modified from Dean and Motta (2004). Reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

Table 2. Relative timings of upper jaw protrusion compared with dominant feeding modes for all published kinematic studies of elasmobranch feeding behavior

Order	Species	Expansive/compressive	Ram (R) or suction (S)	Author
GALEA				
Heterodontiformes	*Heterodontus francisci*	C	S	Edmonds et al. (2001)
Orectolobiformes	*Ginglymostoma cirratum*	C (qualitative)	S	Wu (1994), Motta et al. (2002)
Orectolobiformes	*Orectolobus maculatus*	E	S	Wu (1994)
Lamniformes	*Carcharodon carcharias*	C	R	Tricas and McCosker (1984)
Carcharhiniformes	*Carcharhinus acronotus*	C (E rarely)	R (S rarely)	Frazzetta and Prange (1987), and Frazzetta (1994)
Carcharhiniformes	*Carcharhinus melanopterus*	C (E rarely)	R	Frazzetta and Prange (1987), and Frazzetta (1994)
Carcharhiniformes	*Carcharhinus perezi*	C (qualitative)	R	Motta and Wilga (2001)
Carcharhiniformes	*Cephaloscyllium ventriosum*	C	R = juv, S = adult	Ferry-Graham (1998b)
Carcharhiniformes	*Negaprion brevirostris*	C (E rarely)	R (S rarely)	Frazzetta and Prange (1987), Frazzetta (1994), and Motta et al. (1997)
Carcharhiniformes	*Triakis semifasciata*	C	S = juv, R = adult	Ferry-Graham (1998a)
Carcharhiniformes	*Sphyrna tiburo*	C	R	Wilga and Motta (2000)
SQUALEA				
Squaliformes	*Squalus acanthias*	C	R/S	Wilga and Motta (1998a)
Squatiniformes	*Squatina californica*	C (qualitative)	R? S? (anatomy = S)	Fouts (1995)
BATOIDEA				
Rhinobatiformes	*Rhinobatos lentiginosus*	C	S	Wilga and Motta (1998b)
Torpediniformes	*Narcine brasiliensis*	E	S	This study
Myliobatiformes	*Rhinoptera bonasus*	E	S	Sasko (2000)

Jaw protrusion in the expansive phase (E) indicates a protruding upper jaw as the mandible is depressing, while compressive phase protrusion (C) occurs when the jaw protrudes as the mouth is closing. Note that some carcharhiniform species are capable of protrusion in both phases. Those species where feeding mode is unsure or data are purely qualitative are indicated by a question mark or 'qualitative,' respectively. The feeding mode of the angel shark, *Squatina californica*, is not reported, however it possesses anatomical features typical of suction feeding elasmobranchs.

Oral tube formation in *N. brasiliensis* food capture is possible due to upper jaw protrusion in the expansive phase during lower jaw depression, similar to most bony fishes (Liem, 1980; Motta, 1984; Lauder, 1985; Wainwright et al., 2001). In contrast, the majority of elasmobranchs studied protrude the upper jaw during lower jaw elevation (compressive phase; Table 2). Expansive phase protrusion is exhibited consistently in the spotted wobbegong, *Orectolobus maculatus* (Galea; Wu, 1994) and cownose ray, *Rhinoptera bonasus* (Batoidea; Sasko, 2000) due to anatomical coupling of the upper and lower jaws. Some carcharhinid sharks (Galea) may variably exhibit this behavior, dependent upon prey presentation and presumably due to active muscular control (Frazzetta and Prange, 1987).

Temporal variation in upper jaw protrusion is thus found in numerous elasmobranch orders and jaw suspension types (Wilga, 2002) and apparently not correlated with feeding modality (Table 2). The horn shark, *Heterodontus francisci* (Galea; Edmonds et al., 2001), nurse shark, *Ginglymostoma cirratum* (Galea; Motta et al., 2002), spiny dogfish, *Squalus acanthias* (Squalea; Wilga and Motta, 1998a), and Atlantic guitarfish, *Rhinobatos lentiginosus* (Batoidea; Wilga and Motta, 1998b) are all suction-feeding elasmobranchs, yet exhibit compressive phase protrusion.

The compressive phase (lower jaw elevation and mouth closure) is notably brief in *N. brasiliensis* due to its small gape. The duration of jaw retraction in the recovery phase, however, is nearly 2.5 times longer than

the combined expansive and compressive phases, under-lining the rapidity of jaw protrusion in this species.

Processing

Upon retrieval of the food/prey item, processing in *N. brasiliensis* consists largely of the separation of edible and inedible items through repeated jaw protrusion and retraction. Similar buccal fluidization and selective retention of food items, involving cyclical movements of the jaws with reduced gape, has been exhibited in batoids (Gregory et al., 1979; Stokes and Holland, 1992; Sasko, 2000) as well as bony fishes (Sibbing et al., 1986; Sibbing, 1989; Drucker and Jensen, 1991). During this behavior the flow is bi-directional, beginning with protrusion of the closed jaws, such that particles are drawn anteriorly. This is followed by retraction of the jaws and creation of superambient orobranchial pressure to expel sediment and draw food toward the esophagus (Drucker and Jensen, 1991). Each cycle effectively further purifies the buccal contents through sifting.

Asymmetrical jaw protrusions (see below) and occasional reappearance of the food item between the oral jaws indicates that winnowing may also serve to hydraulically reorient the food item for swallowing (Bemis and Lauder, 1986). This would involve highly coordinated motion of the jaws and hyoid apparatus (Bemis and Lauder, 1986; Drucker and Jensen, 1991), made more kinetic in euhyostyly. High degree of muscular control and intra-individual variability are characteristic of processing behavior in Batoidea. Batoid species are capable of removing crustacean exoskeletons (this study), squid mantle (Sasko, 2000), bivalve shells (Coles, 1910; Gudger, 1914), and even medication embedded in pieces of food (T. Nietfeld, unpubl.) to ingest only edible portions. This fine muscular control may be possible due to the several novel jaw and hyoid depressors possessed by batoids relative to sharks (Miyake, 1988; Wilga and Motta, 1998b). The processing abilities of sharks are comparatively less dexterous, involving either repeated suction or biting for prey size-reductions/reorientation (Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Edmonds et al., 2001; Motta et al., 2002). The increased kinesis of the batoid jaw and hyoid depression mechanisms may therefore affect their dietary breadth as well.

Asymmetry in cranial movements

The highly subdivided/duplicated cranial musculature of batoids (Miyake, 1988) likely allows the high degree of muscular control over fine jaw movements (Wainwright and Turingan, 1993; Wilga and Motta, 1998b; Friel and Wainwright, 1999). This is uniquely exhibited in the pronounced asymmetrical jaw protrusion in *N. brasiliensis*. Although asymmetrical motion of the jaws is reported in numerous vertebrate groups (Kardong, 1977; Lauder and Norton, 1980; Liem, 1980; Cundall et al., 1987; Lorenz-Elwood and Cundall, 1994; Lieberman and Crompton, 2000; Kley, 2001; Ferry-Graham et al., 2003), it is virtually unknown in the Chondrichthyes with no published examples in sharks (Summers, 2000). A single study illustrates asymmetrical quadratomandibularis contraction in the stingray *Dasyatis*, with increased asymmetry for items requiring more processing (shelled versus unshelled shrimp) (Summers, 1995).

The present study represents the first description of asymmetrical cranial kinesis in a basal batoid (i.e., non-myliobatid) and the only example in elasmobranchs of asymmetrical jaw protrusion. Movement of the jaw moieties relative to one another is limited. Rather, the asymmetry has its root in unequal pivoting of the hyomandibulae about their cranial joints (Fig. 11) (Dean and Motta, 2004). The high variability associated with this movement and lack of individual "handedness" indicates that the behavior is likely mediated by interoreceptive feedback of food position in the buccal cavity. Displacement of the jaws from the mid-sagittal plane may serve to readjust the hydraulic flows created during winnowing jaw protrusions, effectively managing buccal pressure gradients according to food position and allowing the fine separation of ingested materials.

Upper jaw protrusion

N. brasiliensis is capable of a degree of extreme upper jaw protrusion previously undescribed in the Elasmobranchii (Wilga et al., 2001). If represented as a percent of head length, measured from the most caudal aspect of the nasal capsules (disregarding rostral cartilages) to the otic region (as in Motta and Wilga, 2001), protrusion in *N. brasiliensis* is almost three times that reported for other highly protrusive elasmobranch species (Table 3). Extreme jaw protrusion (> 25% HL) in elasmobranchs appears to be determined by the presence of a long ethmopalatine ligament (as in the dogfish) or complete lack of such a ligament (as in batoids) and is not well predicted by jaw suspension type (Motta and Wilga, 2001; Wilga, 2002). However, in *N. brasiliensis* the medial folding of the jaw arch is likely also permitted by the disassociation of the jaws and hyoid and lack of ventral hyoid elements (Dean and Motta, 2004).

Suction feeding in fishes is a near-field phenomenon. The water velocities generated by subambient buccal pressures, and therefore the effectiveness of suction, decline rapidly with increasing distance from the mouth (Lauder and Clark, 1984; Ferry-Graham et al., 2001, 2003). Upper jaw protrusion in *N. brasiliensis* not only

Table 3. Jaw protrusion distance in elasmobranchs as a percentage of head length (as measured from the most caudal portion of the nasal capsule to the otic region of the cranium)

Order	Species	Maximum protrusive ability (percent head length) (%)
GALEA		
Heterodontiformes	*Heterodontus francisci*	7
Orectolobiformes	*Ginglymostoma cirratum*	12
Orectolobiformes	*Hemiscyllium ocellatum*	9
Orectolobiformes	*Orectolobus maculatus*	33*
Carcharhiniformes	*Sphyrna tiburo*	10
Carcharhiniformes	*Negaprion brevirostris*	18
SQUALEA		
Hexanchiformes	*Notorhynchus cepedianus*	9
Squaliformes	*Squalus acanthias*	29*
BATOIDEA		
Rhinobatiformes	*Rhinobatos lentiginosus*	26*
Torpediniformes	*Narcine brasiliensis*	96–100*

Percentages for species exhibiting extreme jaw protrusion (>25% HL) have asterisks; jaw protrusion in *Narcine brasiliensis* is nearly three times that of other highly protrusive elasmobranchs. Data from other studies compiled in Motta and Wilga (2001).

allows access to buried polychaetes, but positions the jaws in close enough proximity to the prey item to allow effective suction, as proposed for cichlid fishes (Wainwright et al., 2001). This method of reducing predator–prey distance is less prone to startle potential prey. Also, the resultant limited gape likely decreases the amount of sediment ingested during retrieval of buried worms. By reducing the surface area contacting the sediment (i.e., through protrusion of a reduced oral gape rather than the frontal surface of the entire jaw complex) the force per unit area, and therefore pressure, of initial sediment contact is increased, leading to a more efficient excavation tool.

Batoids excavate prey in a variety of ways. To remove bivalves, *R. bonasus* resuspends the sediment by protruding and retracting the jaw to expel water through the mouth and may also employ repeated dorsoventral bobbing of the head to clear a feeding pit (Gray et al., 1997; Sasko, 2000). *Myliobatis tenuicaudatus* also hydraulically mines invertebrate prey, yet is believed to use water forced from the anterior gill slits (Gregory et al., 1979). Additional myliobatid species have been considered to retrieve benthic infauna through flapping of the pectoral fins (MacGinitie and MacGinitie, 1968; Orth, 1975) or digging with their rostra (Gregory et al., 1979; Talent, 1982), while the round stingray *Urobatis jamaicensis* reportedly rotates in tight circles over buried prey items to create circular depressions (D. Fahy, unpubl.). The southern stingray *D. americana* will filter lancelets from the sediment by ingesting large amounts of sand and passing it through its gill slits, retaining only the larger food items (Stokes and Holland, 1992). Gudger (1914) hypothesized that the enlarged lower tooth plate of *Aetobatus* could be employed as a digging device.

Excavation of benthic prey by jaw protrusion necessitates an extremely protactile jaw and thus is most likely unique to the Narcinoidea (Torpediniformes: Narcinidae + Narkidae) within the Batoidea. Rudloe (1989a) and Rudloe and Rudloe (1993) first described this behavior for *N. brasiliensis*. Its closest reported behavioral analog in the chondrichthyes is exhibited by epaulette sharks, *Hemiscyllium ocellatum* and whitespotted bamboo sharks, *Chiloscyllium plagiosum* (Galea), which will bury their heads up to the first gill slit in pursuit of buried invertebrates (Heupel and Bennett, 1998).

Suction feeding and pressure recording

Feeding in *N. brasiliensis* involves a pronounced ram contribution followed by suction generation, as in turtles that powerfully extend their necks to ingest prey by suction (Lauder and Prendergast, 1992; Summers et al., 1998; Lemell et al., 2002). The largest subambient pressures recorded here (−31 kPa) are roughly a third of those recorded for nurse sharks, *G. cirratum* of 150–210 cm TL (∼101 kPa; Tanaka, 1973), however animal size/ontogeny (data here were taken from a single subadult *N. brasiliensis*) and diet (the nurse shark is piscivorous) are surely factors (Motta et al., 2002; Robinson and Motta, 2002).

Peak pressures recorded for *N. brasiliensis* are below the limits (100–200 kPa in <0.5 m of water) set by Merz and Woodin (2000) for suction-removal of three species

of tube-dwelling polychaetes with hooked setae actively engaged in their tube walls. However, the high velocity of jaw protrusion exhibited by this batoid may permit partial removal of tubiculous species before the remainder of the body can be anchored (Merz and Woodin, 2000). Peak suction pressures have been shown to occur prior to prey contact inside the buccal cavity of feeding fishes (Svanbäck et al., 2002; Ferry-Graham et al., 2003). Therefore, our estimates of suction pressure for *N. brasiliensis* are likely conservative.

Subambient pressure generation appears to correlate with jaw protraction, suggesting a further function for protrusion. Sagittal views of protruded jaws (from CT scans; Dean and Motta, 2004) indicate that the oral cavity becomes smoothly conical (narrower anteriorly than posteriorly) at peak protrusion. This may provide the mechanical conditions for maximally efficient water flow (Osse and Muller, 1980; Liem, 1993).

Compression (dorsoventral retraction) of the jaws from the resting state is similar to the compression transport seen at the end of capture sequences in *R. lentiginosus* (Wilga and Motta, 1998b). The positive pressure pulses associated with this behavior in *N. brasiliensis* and placement at the end of feeding events support Wilga and Motta's (1998b) hypothesis that this serves a swallowing function, forcing edible material into the esophagus. Cannulated pressure recordings are necessary to test this empirically.

Conclusions

Food/prey capture in *N. brasiliensis* involves a ram component (extreme jaw protrusion, $\sim 100\%$ HL) as well as inertial suction to retrieve fossorial prey items. The fine degree of adjustment during predatory strikes indicates that this behavior is mutable and likely highly dependent on exterofeedback. The behavioral flexibility of this novel method of excavation is the result of the complex cranial musculature and jaw suspension characteristic of the Batoidea. Asymmetrical motion of the jaws is a common aspect of processing behavior in *N. brasiliensis* and may also occur regularly in capture when prey is presented more naturally. This is the only reported case of an elasmobranch fish capable of asymmetrical jaw protrusion.

Although *N. brasiliensis* shares the basic anteroposterior sequence of cranial expansion characteristic of aquatic feeding, its expansive phase is both biphasic (as in tetrapods) and involves coupling of the upper and lower jaws. Simultaneous protrusion of both jaws distinguishes this species from most elasmobranchs and while the resultant gape limitation may impose dietary limitations, it may also increase suction performance.

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