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Cheryl D. Wilga
University of Rhode Island, cwilga@uri.edu

Philip J. Motta

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CONSERVATION AND VARIATION IN THE FEEDING MECHANISM OF THE SPINY DOGFISH *SQUALUS ACANTHIAS*

CHERYL D. WILGA* AND PHILIP J. MOTTA
Department of Biology, University of South Florida, 4202 East Fowler Avenue, Tampa, FL 33620, USA
*Present address: Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA 92697-2525, USA
(e-mail: cwilga@uci.edu)

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Summary

Changes in the feeding mechanism with feeding behavior were investigated using high-speed video and electromyography to examine the kinematics and motor pattern of prey capture, manipulation and transport in the spiny dogfish *Squalus acanthias* (Squalidae: Squaliformes). In this study, *Squalus acanthias* used both suction and ram behaviors to capture and manipulate prey, while only suction was used to transport prey. The basic kinematic feeding sequence observed in other aquatic-feeding lower vertebrates is conserved in the spiny dogfish. Prey capture, bite manipulation and suction transport events are characterized by a common pattern of head movements and motor activity, but are distinguishable by differences in duration and relative timing. In general, capture events are longer in duration than manipulation and transport events, as found in other aquatic-feeding lower vertebrates. Numerous individual effects were found, indicating that individual sharks are capable of varying head movements and motor activity among successful feeding events. Upper jaw protrusion in the spiny dogfish is not restricted by its orbitostylic jaw suspension; rather, the upper jaw is protruded by 30 % of its head length, considerably more than in the lemon shark *Negaprion brevirostris* (Carcharhinidae: Carcharhiniformes) (18 %) with its hyostylic jaw suspension. One function of upper jaw protrusion is to assist in jaw closure by protruding the upper jaw as well as elevating the lower jaw to close the gape, thus decreasing the time to jaw closure. The mechanism of upper jaw protrusion was found to differ between squaliform and carcharhiniform sharks. Whereas the levator palatoquadrati muscle assists in retracting the upper jaw in the spiny dogfish, it assists in protruding the upper jaw in the lemon shark. This study represents the first comprehensive electromyographic and kinematic analysis of the feeding mechanism in a squaliform shark.

Key words: spiny dogfish, *Squalus acanthias*, kinematics, electromyography, feeding, behavior, elasmobranch, jaw protrusion.

Introduction

Major concepts regarding the evolution of feeding mechanisms have been advanced from comparative studies of bony fishes, lungfishes, salamanders and turtles (Lauder and Shaffer, 1993). However, our understanding of aquatic vertebrate feeding mechanisms is limited by the lack of studies on a group as large and diverse as the chondrichthyans (Lauder and Shaffer, 1993). Two major groups comprise the Chondrichthyes, the Holocephali (chimeras) and the Elasmobranchii (sharks and rays). Sharks comprise the majority of elasmobranch orders (Shirai, 1996; de Carvalho, 1996; McEachran *et al.* 1996), yet the few functional studies of feeding behavior in live sharks have concentrated on only two of these groups. These include the white shark *Carcharodon carcharias* (Lamniformes) and several carcharhiniform sharks, the lemon shark *Negaprion brevirostris*, blacknose shark *Carcharhinus acronotus*, blacktip shark *Carcharhinus limbatus* and swellshark *Cephaloscyllium ventriosum* (Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Ferry-Graham, 1997). Only one study has investigated muscle function during feeding in a chondrichthyan, the lemon shark (Motta *et al.* 1991, 1997). These studies indicate that the basic kinematic sequence of the head and jaw movements appears to be conserved during feeding in carcharhiniform and lamniform sharks.

The earliest neoselachians possessed a cladodont dentition (one large conical cusp, multiple smaller lateral cusps, disc-like base), long jaws, an immobile upper jaw and a wide gape, which suggests a grasping type of feeding mechanism (Schaeffer, 1967; Moy-Thomas and Miles, 1971; Carroll, 1988). Subsequent evolution involved shortening of the jaws and modification of the suspensorium to form a more maneuverable feeding apparatus in which the upper jaw moved freely (Moss, 1977; Carroll, 1988). Several different jaw suspension types conferring varying degrees of mobility have evolved within the Chondrichthyes (Gregory, 1904; Maisey, 1980). Galeoid sharks (Carcharhiniformes, Lamniformes, Orectolobiformes and Heterodontiformes) possess a hyostylic type of jaw suspension in which the orbital process of the upper jaw articulates with the ethmoid region of the cranium. In contrast, squaloid sharks (Squaliformes, Hexanchiformes, Squatiniformes and Pristiophoriformes) have an orbitostylic type of jaw suspension in which the orbital process of the upper jaw articulates with the orbital wall of the cranium. In addition, the elongated orbital process of orbitostylic sharks is thought to limit the degree of upper jaw protrusion compared with that in hyostylic sharks, which have a relatively shorter orbital process (Gregory, 1904; Maisey, 1980; Compagno, 1988).

The ability to protrude the upper jaw towards the prey may have many functions during feeding. Some proposed advantages of upper jaw protrusion include more efficient biting and manipulation of the prey, gouging of the upper jaw into large prey, providing a versatile yet hydrodynamic subterminal mouth, orienting the teeth for increased grasping ability, providing for nearly simultaneous closure of the upper and lower jaws, and decreasing the time to jaw closure (Springer, 1961; Alexander, 1967; Moss, 1972, 1977; Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Frazzetta, 1994; Motta *et al.* 1997).

In addition to upper jaw protrusion, many sharks have been observed to shake their head from side to side during feeding (Springer, 1961; Moss, 1972, 1977; Frazzetta and Prange, 1987; Frazzetta, 1988, 1994; Motta *et al.* 1997; C. D. Wilga and P. J. Motta, in preparation). This head-shaking behavior is thought to be a mechanism for gouging pieces from large prey, cutting prey into smaller pieces and subduing the prey (Springer, 1961; Hobson, 1963; Gilbert, 1970; Moss, 1972; Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Frazzetta, 1994; Powlik, 1995).

Several hypotheses related to the conservation of feeding mechanisms and the function of jaw suspension in the spiny dogfish *Squalus acanthias* (Squalidae: Squaliformes) are tested in the present study using high-speed video and electromyography. Prey-capture, manipulation and transport behaviors are characterized by a common pattern of kinematic and motor activity, but are distinguishable by differences in duration and relative timing. Upper jaw protrusion is effected by contraction of the preorbitalis and quadratomandibularis muscles and is not limited by the orbitostylic jaw suspension. Head shaking is used to reduce large prey to smaller, more easily consumable, pieces.

Materials and methods

Specimens

Specimens of spiny dogfish *Squalus acanthias* (L.) were collected by otter trawl in East Sound and Upright Head off Orcas Island in the San Juan Islands, Washington, USA. The sharks were maintained in 2.4 m diameter circular holding tanks with an open seawater circulating system at 11 °C. The sharks were fed Pacific herring *Clupea pallasii* (2 cm×3 cm pieces and 16 cm whole fish) every other day, a common natural prey item (Jensen, 1965; Jones and Geen, 1977). Eight subadult and adult spiny dogfish (range 46–65 cm total length, TL) were used in the experimental analyses. All experiments were conducted within 11–23 days after capture of the sharks.

Myology

A thorough knowledge of the morphology of the muscles is necessary for electromyographic analyses; therefore, the muscles of the head and hypobranchial region were dissected and described in order to construct a stereotactic map to ensure consistent electrode placement (Marion, 1905; Haller, 1926; Holmgren, 1941; Marinelli and Strenger, 1959; Shirai, 1992). Eight muscles that have previously been shown to function, or are suspected of functioning, during feeding were implanted with electrodes: the epaxialis, coracomandibularis, coracoarcualis, coracohyoideus, levator palatoquadrati, levator hyomandibularis, quadratomandibularis and preorbitalis (Moss, 1972, 1977; Frazzetta, 1994; Walker and Homberger, 1992; Motta *et al.* 1991, 1997; Motta and Wilga, 1995). Eight fresh dead specimens were dissected for the anatomical analysis (50–100 cm TL).

Electromyography

Electromyograms (EMGs) and kinematics were analyzed from eight individuals for 44 prey capture events (3–10 per individual), 35 bite manipulation events (4–6 per individual) and 27 suction transport events (3–7 per individual). Electromyograms were analyzed from six sharks for 13 lateral headshakes (two per individual). Two days before the experiment, the shark was moved from the holding tank to a 280 l rectangular glass experimental tank. Electromyographic recordings with simultaneous video recordings were used to document the sequence of muscle activation relative to kinematic pattern. Electromyograms were recorded using bipolar electrodes constructed from 3.8 m lengths of 0.0057 cm diameter insulated alloy wire. Approximately 1 mm at the end of each wire was stripped of insulation and bent backwards to form a hook. A third 3 cm long piece of hooked insulated wire was placed alongside each bipolar electrode to verify the position of electrode placement in case the electrode was inadvertently pulled out. The electrodes were implanted using 24 gauge hypodermic needles into eight cranial muscles using the stereotactic map to ensure consistent placement. Sharks were anesthetized for surgery using $0.05\,\mathrm{g\,l^{-1}}$ of tricaine methanesulfonate (MS-222). The sharks were maintained on this dosage of anesthetic during surgery using a recirculating system with intubation such that the treated sea water was pumped continuously across the gills. Following electrode implantation, the electrode wires were glued together and sutured to a loop of suture in the skin anterior to the first dorsal fin. The surgical procedure took approximately 30 min.

The shark was returned to the experimental tank after surgery and its gills flushed with fresh sea water until it had recovered enough to commence swimming (5–15 min). Electrodes were connected to a Grass P5 signal amplifier, set at a gain of 500–5000, bandpass at 100–3000 Hz with a 60 Hz notch filter. Signals were recorded on a TEAC MR-30 tape recorder and played back on a Graphtec Mark 11 chart recorder. Feeding trials began after normal swimming behavior had been observed for at least 1 h post-recovery and continued until the shark was satiated. Pieces of herring (2 cm×3 cm) were dropped into the tank to facilitate lateral video recordings. Whole fish (16 cm) were also offered in order to induce head shaking and prey cutting behavior.

Electromyograms were recorded from eight muscles as follows: the epaxialis (eight individuals), levator hyomandibularis (eight individuals), quadratomandibularis dorsal (eight individuals), preorbitalis (eight individuals), levator palatoquadrati (five individuals), coracomandibularis (four individuals), coracohyoideus (three individuals) and coracoarcualis (one individual). Since recordings could be made from only six muscles during an experiment, only one of the hypobranchial muscles (coracomandibularis, coracohyoideus and coracoarcualis) was implanted per individual in addition to the remaining muscles for any given experiment.

The onset and duration of motor activity during each feeding event were measured from chart recordings played back at one-quarter real time at a chart speed of $25\,\mathrm{mm\,s^{-1}}$ to the nearest 0.5 mm. The onset of lower jaw depression, as identified by the pattern of synchronization marks on the video images and EMG tracing, was used as the reference from which the onset of muscle activity was measured.

At the termination of each experiment, the shark was killed with an overdose of MS-222 according to the University of Washington and University of South Florida Animal Care and Use Committee guidelines. The positions of the electrodes were verified by dissection, and standard measurements were taken to the nearest millimeter.

Video recording

A NAC HSV-200 high-speed video (200 fields $\mathrm{s^{-1}}$) or a Sony Hi-8 video (60 fields $\mathrm{s^{-1}}$) system was used to record video images during the electromyography experiments. To synchronize the video and electromyograms, a synchronizer unit was used that emitted an electrical signal to a light-emitting diode strobe recorded by the video camera and to one channel of the tape recorder. A Panasonic AG1730 VCR, with a FOR-A time base corrector, Quick-Capture video capture board and NIH Image digitizing software or a Panasonic AG1970 VCR, Video Blaster video capture board and Sigma Scan digitizing software was used to play back video sequences, capture them into a computer and digitize the video images. The time of the following kinematic events (in ms) was calculated from video images by digitizing or by counting field-by-field (1 field=5 ms): start of head lift, time of peak head lift, end of head depression, start of lower jaw depression, time of peak lower jaw depression, time of complete jaw closure, start of upper jaw protrusion, time of peak upper jaw protrusion, end of upper jaw retraction, start of hyoid depression, time of peak hyoid depression, time of peak hypobranchial depression, start of labial extension, peak labial extension, start and end of prey movement. In addition, the following five durations were calculated from the kinematic events digitized above: head lift, head depression, lower jaw elevation, upper jaw protrusion and upper jaw retraction. Kinematic variables (in ms) were measured relative to the reference point of the start of lower jaw depression because this usually initiated the feeding sequence. Peak gape and peak upper jaw protrusion were calculated by digitizing the anterior tip of the upper jaw and the anterior tip of the lower jaw.

The ram–suction index (RSI) was calculated for 31 capture events from four individuals (mean six per shark) in order to analyze predator and prey kinematics during feeding. $\mathrm{RSI}=(D_{\mathrm{predator}}-D_{\mathrm{prey}})/(D_{\mathrm{predator}}+D_{\mathrm{prey}})$, where D is the distance moved by the predator or prey (Norton and Brainerd, 1993). In a pure ram-feeding event, the predator moves and the prey does not, resulting in an RSI of +1. In a pure suction-feeding event, the prey moves and the predator does not, resulting in an RSI of −1. Thus, the ram–suction index is a continuum that ranges from +1 to −1. It is a simple method that is used to quantify the relative contributions of ram and suction prey-capture mechanisms to shortening the predator–prey distance during the strike. The RSI was calculated using the positions of the eye of the predator and the anterior tip of the prey in the video images containing the start of lower jaw depression and the end of prey movement.

Statistical analyses

A mixed-model two-way analysis of variance (ANOVA) was performed on the electromyographic (EMG) and kinematic variables. Behavior (capture, manipulation and transport) is a fixed main effect and was tested by the individual×behavior term. The variables tested were the time of onset and the duration of EMG activity and the time of start, peak and end and the duration of kinematic activity relative to the onset of lower jaw depression. If a difference was detected by ANOVA ($P<0.05$), a Student–Newman–Keuls multiple-comparison test ($P<0.05$) was applied. A Student’s *t*-test ($P<0.05$) was used to test peak gape distance *versus* peak gape minus peak upper jaw protrusion distance in order to determine whether upper jaw protrusion contributed to reducing the gape. Analysis of variance, multiple comparison and Student’s *t*-test were performed using SAS (version 6.12) statistical software. Assumptions of parametric statistics were tested using SigmaStat (Jandell Scientific Inc., version 2.0) statistical software: homogeneous variances using the Levene Median test ($P<0.05$) and normal distribution using the Kolmogorov–Smirnov test ($P<0.05$). Some of the variables were log-transformed in order to meet the assumptions of parametric statistics.

Results

Jaw suspension

Squaloids have an orbitostylic type of jaw suspension in which the hyomandibula suspends the jaws from the cranium, the palatoquadrate articulates with the orbital wall of the cranium by a relatively long orbital process, and the ceratohyal–basihyal complex articulates with the distal hyomandibula (Fig. 1) (Gregory, 1904; Maisey, 1980). In the resting position, the long orbital process of the upper jaw lies in a vertically oriented ethmopalatine groove in the orbital

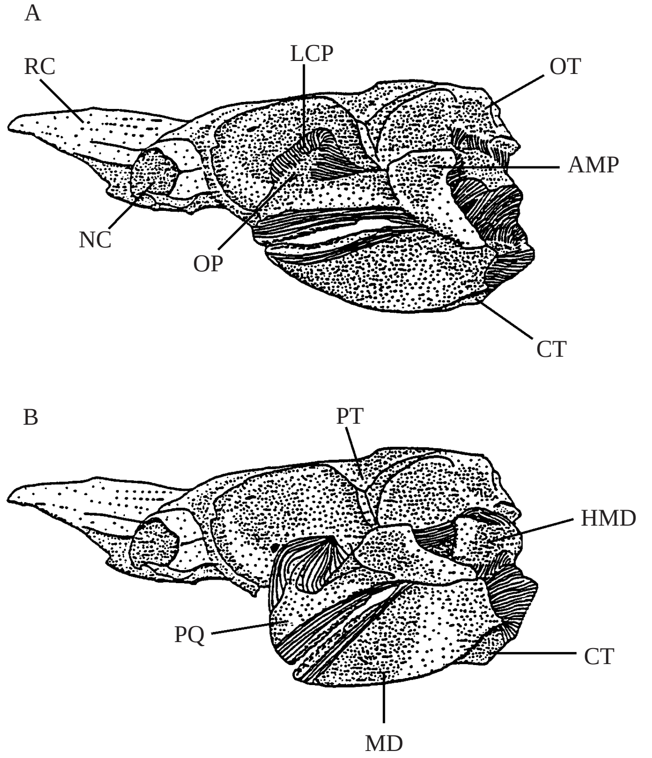

Fig. 1. Left lateral view of the cranium, jaws and hyoid arch of a 74.5 cm total length female *Squalus acanthias* with the skin and muscles removed. (A) Resting position; (B) peak upper jaw protrusion. See text for details. AMP, adductor mandibulae process of palatoquadrate; CT, ceratohyal; HMD, hyomandibula; LCP, ethmopalatine ligament; MD, mandible or lower jaw; NC, nasal capsule; OP, orbital process of palatoquadrate; OT, otic capsule of cranium; PQ, palatoquadrate cartilage or upper jaw; PT, postorbital process of cranium; RC, rostral cartilage.

wall. The sheet-like ethmopalatine ligament extends from the edges of the ethmopalatine groove to the base of the orbital process and ensheathes the orbital process. In the retracted position, the ethmopalatine ligament folds back on itself. The orbital process in the ethmopalatine groove, the ectethmoid condyles and the hyomandibula restrict anteroposterior movement of the upper jaw. During manual manipulation, the orbital process does not leave the ethmopalatine groove even at peak upper jaw protrusion. Therefore, the orbital processes in the ethmopalatine grooves restrict lateral and anteroposterior movement of the upper jaw. Ventral movement of the upper jaw is restricted up to the length of the unfolded ethmopalatine ligament and by the surrounding skin and muscles between the upper jaw and chondrocranium.

Myology

The epaxialis inserts on the posterodorsal surface of the chondrocranium (Fig. 2). The levator palatoquadrati originates on the cranium and extends ventrally to insert on the palatoquadrate. The levator hyomandibularis originates on the epaxialis and cranium and extends ventrally to insert on the hyomandibula. The adductor mandibulae complex is considered to be a functional unit consisting of the preorbitalis and quadratomandibularis muscles (Lightoller, 1939). The quadratomandibularis dorsal is composed of four distinct divisions that extend from the palatoquadrate to the mandible: anterior (implanted in this study), superficial, posterior and deep (Wilga, 1997). The quadratomandibularis ventral originates from the mandible and extends dorsally to merge with the preorbitalis. The preorbitalis muscle originates on the nasal capsule and extends posteriorly to merge with the quadratomandibularis ventral. The coracoarcualis originates on the coracoid bar and extends anteriorly to insert on the coracohyoideus (Fig. 3). The coracohyoideus originates on the coracoarcualis and extends anteriorly to insert on the basihyal. The coracomandibularis originates on the coracoid bar and coracoarcualis and extends anteriorly to insert on the mandible.

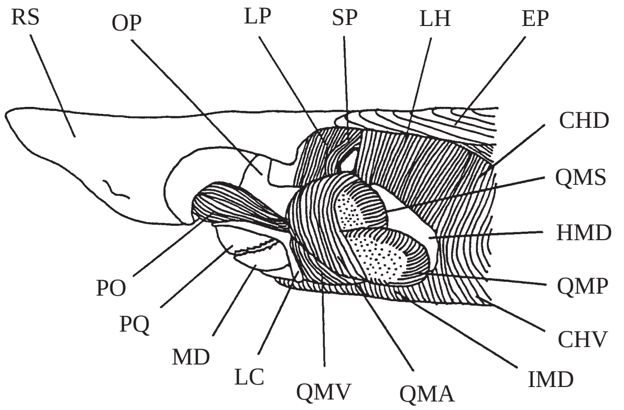

Fig. 2. Left lateral view of the head of a 74.5 cm total length female *Squalus acanthias* with the skin and eye removed and muscle fiber direction indicated. Skin over the rostrum and cranium is left intact. Myosepta only of the epaxialis muscle are indicated. Raphes overlying quadratomandibularis are indicated by stippling. CHD, constrictor hyoideus dorsalis; CHV, constrictor hyoideus ventralis; EP, epaxialis; HMD, hyomandibula of suspensorium; IMD, intermandibularis; LC, labial cartilages; LH, levator hyomandibularis; LP, levator palatoquadrati; MD, mandible or lower jaw; OP, orbital process of palatoquadrate; PO, preorbitalis; PQ, palatoquadrate or upper jaw; QMA, quadratomandibularis anterior; QMS, quadratomandibularis superficial; QMP, quadratomandibularis posterior; QMV, quadratomandibularis ventral; RS, rostrum; SP, spiracularis.

Labial cartilages

The dorsal and ventral labial cartilages lie along the upper and lower jaws, respectively (Fig. 2). Ligaments attach the labial cartilages at their distal ends to the upper and lower jaws and also at their proximal ends to each other at the angle of the mouth. When the jaws are closed, the labial cartilages lie in the folds of skin against the upper and lower jaws with their proximal ends at the angle of the mouth.

Kinematics of feeding behavior

Prey capture is the initial acquisition of the prey. The expansive phase begins with mouth opening by nearly simultaneous depression of the lower jaw and elevation of the cranium (Figs 4A, 5; Table 1). The labial cartilages are extended as the lower jaw is depressed. The orobranchial chamber is rapidly expanded, and the prey may be drawn by suction into the mouth shortly before peak labial cartilage extension and peak lower jaw depression. The compressive phase begins at peak gape, which is followed by upper jaw protrusion and elevation of the lower jaw. Peak head lift occurs shortly before the jaws close completely. Peak upper jaw protrusion (mean 1.2 cm) is attained just prior to complete elevation of the lower jaw and reduces peak gape (mean 2.4 cm) by 51 % ($P<0.001$), leaving the remainder of the gape for elevation of the lower jaw to close. Peak hyoid depression occurs as the upper and lower jaws are completely closed. The recovery phase begins at complete jaw closure and consists of depression of the cranium and retraction of the upper jaw and hyoid. The recovery phase ends when the cranial elements are returned to their resting positions. The total duration of prey-capture events from the start of snout lift or lower jaw depression to the end of upper jaw retraction ranged from 135 to 510 ms with a mean of 280 ms. Prey movement was analyzed for calculation of RSI values for capture events only.

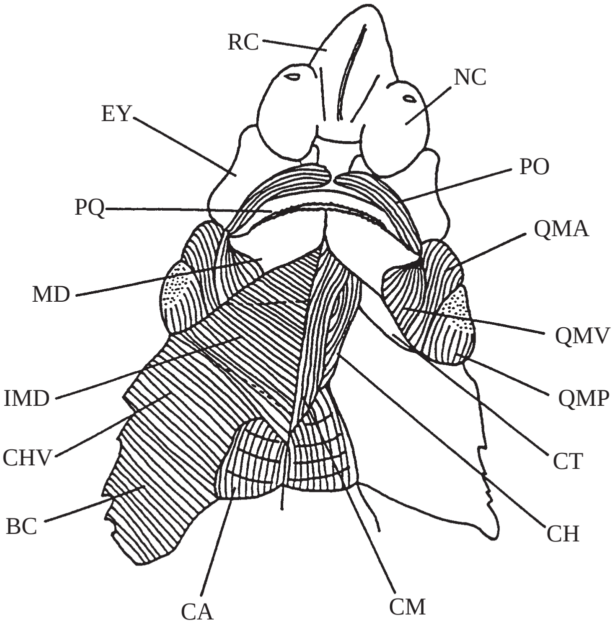

Fig. 3. Ventral view of the head of a 60 cm total length female *Squalus acanthias* with the skin removed and muscle fiber direction indicated. Raphes over quadratomandibularis are indicated by stippling. Anterior and posterior margins of the interhyoideus (deep to IMD) are indicated by dotted lines. Left side shows deep muscles, right side shows superficial muscles. BC, branchial constrictors; CA, coracoarcualis; CH, coracohyoideus; CHV, constrictor hyoideus ventralis; CT, ceratohyal; CM, coracomandibularis; EY, eye; IMD, intermandibularis; MD, mandible or lower jaw; NC, nasal capsule; PO, preorbitalis; PQ, palatoquadrate or upper jaw; QMA, quadratomandibularis anterior; QMP, quadratomandibularis posterior; QMV, quadratomandibularis ventral; RC, rostral cartilage.

Primarily suction (69 % of all captures) but also ram mechanisms are used to capture herring pieces. The mean RSI for prey capture by suction is −0.23 and by ram is 0.31. During capture by suction, the prey may be transported directly past the teeth and into the buccal cavity. Alternatively, the prey is grasped between the jaws as they are completely closed, as during ram captures.

The kinematics during manipulation (Figs 4B, 6) and transport (Figs 4C, 7) events are similar to those during capture events except that the prey is already grasped between the jaws at the beginning of the event. Labial excursion was usually obscured by the prey and was not analyzed for transport events. Prey manipulation occurs after capture and prior to transport. In manipulation events, the jaws are opened then closed back onto the prey. The total duration of prey manipulation events from the start of head lift or lower jaw depression to the end of upper jaw retraction ranges from 175 to 420 ms with a mean of 236 ms. Prey transport is movement of the prey from the jaws through the pharynx and into the esophagus for swallowing. In transport events, the jaws are opened and the prey is moved rapidly from between the jaws to the esophagus, presumably by suction. The total duration of prey transport events from the start of head lift or lower jaw depression to the end of upper jaw retraction ranges from 200 to 280 ms with a mean of 227 ms.

Statistical analysis of the kinematics of capture, manipulation and transport events revealed only two differences among behaviors (Table 1). Peak hyoid depression occurs later and the duration of head lift is longer in capture events than in manipulation or transport events. The range of duration in capture events from lower jaw depression or head lift to the end of upper jaw retraction (135–510 ms) encompasses the entire range of variation in manipulation (175–420 ms) as well as transport (200–280 ms) events. Individual effects were found in most of the kinematic variables (Table 1).

Thirteen lateral head-shaking sequences were observed, four of which ended with cutting of the prey. During lateral headshakes, the shark rapidly throws its head and anterior body from one side to the other (Fig. 4D). This activity continues until the prey is either cut into two pieces or the shark stops shaking and swallows the prey intact. After transport of the cut piece of prey grasped between the teeth, the shark then returns to engulf the severed piece.

Motor activity patterns

Representative EMG recordings from a suction capture event in the spiny dogfish are shown in Fig. 8A (mean motor patterns are given in Fig. 5). The coracomandibularis and coracoarcualis muscles begin activity shortly before lower jaw depression and end activity just after and at peak lower jaw depression, respectively. The coracohyoideus muscle begins activity just prior to lower jaw depression and ends activity well before peak lower jaw depression. A second burst of activity may occur in the coracohyoideus just before the compressive phase. The epaxialis muscle begins activity just

Table 1. *Statistical variables and results of two-way ANOVA on kinematics of capture, manipulation and transport behaviors in* Squalus acanthias

Kinematic variable	Capture	Manipulation	Transport	*P*-value	SNK
Head lift start	4±10	9±16	23±19	0.555	
Head lift duration	150±11	112±17	103±15	0.029†,*	C>M,T
Head lift peak	155±12	138±15	111±14	0.365†	
Head depression duration	150±9	116±36	78±18	0.054	
Head depression end	304±14	235±40	187±29	0.082†	
Lower jaw depression peak	100±11	100±10	87±11	0.630†	
Lower jaw elevation duration	90±7	94±10	69±17	0.835†	
Jaw closure complete	192±16	194±16	156±14	0.333†	
Upper jaw protrusion start	106±10	101±7	93±7	0.883†	
Upper jaw protrusion duration	60±6	70±14	62±5	0.734	
Upper jaw protrusion peak	164±13	181±12	152±8	0.386†	
Upper jaw retraction duration	117±12	52±6	75±9	0.429†	
Upper jaw retraction end	280±14	236±15	227±8	0.221†	
Hyoid depression start	13±7	37±17	33±3	0.143	
Hyoid depression peak	178±13	101±30	115±14	0.026†,*	C>M,T
Hypobranchial depression peak	139±10				
Labial extension start	35±6	5±7		0.316	
Labial extension peak	110±11	60±8		0.316†	
Prey movement start	69±10				
Prey movement end	97±17				

Values are means ± S.E.M. (in ms; *N*=8).

SNK, results of Student–Newman–Keuls multiple-comparisons test; *significant behavior effect at *P*<0.05; †significant individual effect at *P*<0.05. C, capture; M, manipulation; T, transport.

Table 2. *Statistical variables and results of two-way ANOVA on motor activity of capture, manipulation and transport behaviors in* Squalus acanthias

Muscle	Capture	Manipulation	Transport	*P*-value	SNK
Coracomandibularis onset	–22±8	–5±2	–8±6	0.016*	M,T>C
Coracomandibularis duration	154±11	98±18	88±8	0.016*	C>M,T
Coracohyoideus onset	–10±7	19±8	27±5	0.242†	
Coracohyoideus duration	57±5	55±6	67±30	0.873†	
Coracoarcualis onset	–17±22	38±6	17±18	0.227	
Coracoarcualis duration	115±23	47±22	87±9	0.039*	C,T>M
Epaxialis onset	–28±10	6±8	9±20	0.115	
Epaxialis duration	133±9	118±14	90±11	0.0004†,*	C>M,T
Quadratomandibularis anterior onset	85±8	100±7	83±3	0.242†	
Quadratomandibularis anterior duration	98±9	118±12	64±6	0.009†,*	M,C>T
Preorbitalis onset	103±13	101±10	92±8	0.865	
Preorbitalis duration	109±16	81±12	82±6	0.195†	
Levator palatoquadrati 1 onset	25±20	10±20	12±7	0.825†	
Levator palatoquadrati 1 duration	19±4	70±13	25±15	0.055†	
Levator palatoquadrati 2 onset	182±26		165±27	0.654	
Levator palatoquadrati 2 duration	76±25		40±10	0.714	
Levator hyomandibularis 1 onset		–16±25	–74±41	0.072	
Levator hyomandibularis 1 duration		77±11	87±10	0.782	
Levator hyomandibularis 2 onset	192±18		133±15	0.130†	
Levator hyomandibularis 2 duration	76±11		75±7	0.600	

Values are means ± S.E.M. (in ms; *N*=8).

SNK, results of Student–Newman–Keuls multiple-comparisons test; *significant behavior effect at *P*<0.05; †significant individual effect at *P*<0.05. C, capture; M, manipulation; T, transport.

1, 2 following a muscle name indicates results for the first and second periods of activity.

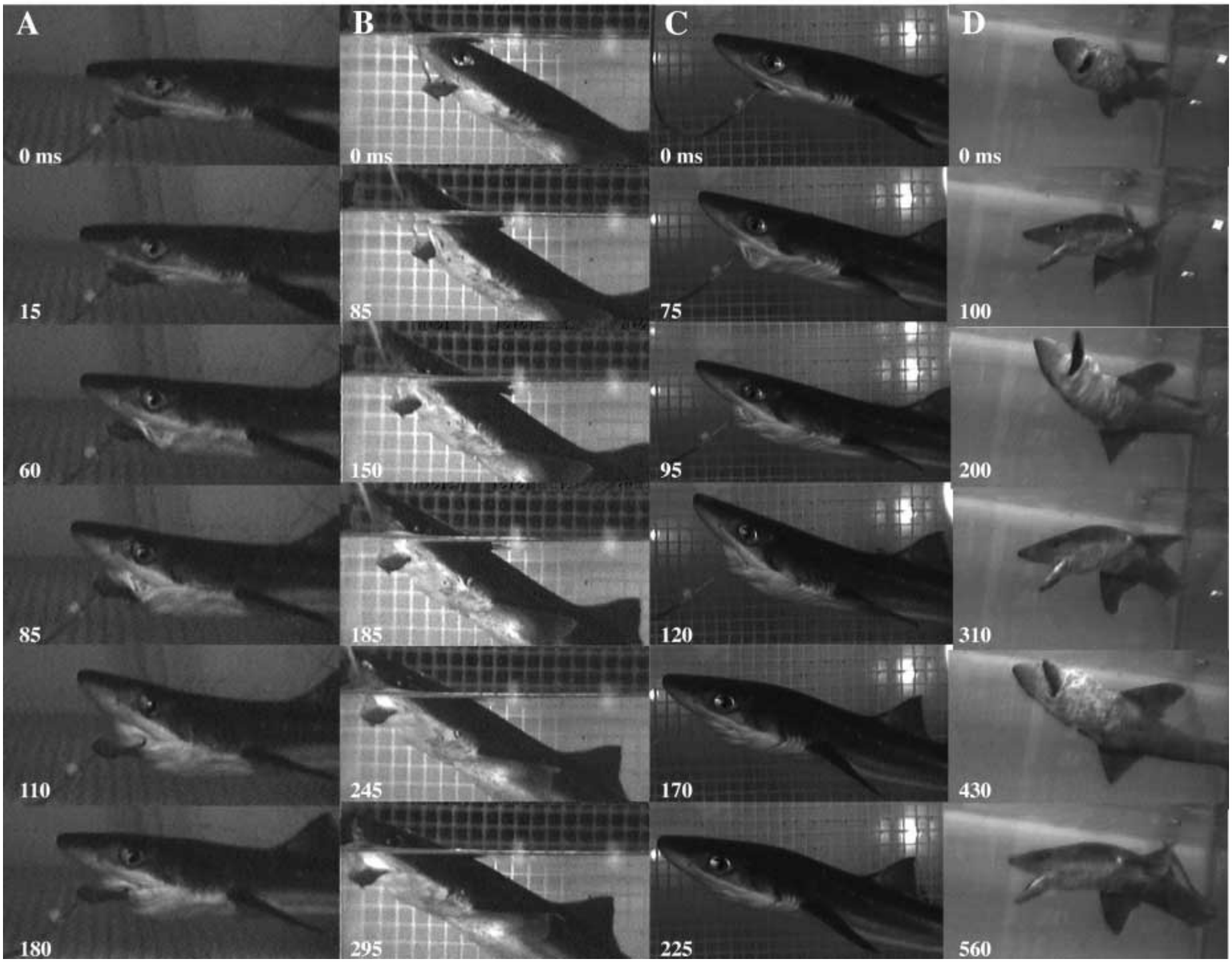

Fig. 4. Video images of representative suction prey-capture (A), bite manipulation (B), suction transport (C) and headshake (D) events in *Squalus acanthias*. Times are in milliseconds, with 0 indicating the start of lower jaw depression in A–C. (A) 15 ms, labial cartilage extension starts; 60 ms, peak lower jaw depression; 85 ms, midway through capture; 110 ms, peak upper jaw protrusion; 180 ms, complete jaw closure and peak hyoid depression. (B) 85 ms, peak lower jaw depression; 150 ms, jaw closure; 185 ms, still biting on prey; 245 ms, peak hyoid depression; 295 ms, end of upper jaw retraction. (C) 75 ms, peak lower jaw depression; 95 ms, jaw closure; 120 ms, peak hyoid depression; 170 ms, end of snout drop; 225 ms, end of upper jaw retraction. (D) Headshake event showing peak lateral excursions of the head for three consecutive headshakes.

prior to the start of head elevation and ends activity shortly before peak head lift. Activity in the quadratomandibularis muscle begins shortly before lower jaw elevation and ends shortly before complete jaw closure. The preorbitalis muscle begins activity just before upper jaw protrusion begins and does not end until well after peak upper jaw protrusion at jaw closure. Activity in the levator palatoquadrati muscle may occur in the middle of the expansive phase or during upper jaw retraction in the recovery phase. The levator hyomandibularis muscle begins activity at complete jaw closure during retraction of the upper jaw and ends the prey-capture event.

Representative EMGs from a bite manipulation event (Fig. 8B; see Fig. 6 for mean motor patterns) and a suction transport event (Fig. 8C; see Fig. 7 for mean motor patterns) show that activity in the jaw opening and closing muscles is similar to that in capture events. However, the activity in the jaw retractor muscles has a different pattern in each event (see Figs 5–7): in capture events, the levator hyomandibularis is always active and the levator palatoquadrati is usually active during the recovery phase; in manipulation events, they are both active during the expansive phase; and in transport events, they are both active during both the expansive and the recovery phases.

Statistical analysis of the motor patterns during capture, manipulation and transport events reveals several differences among the behaviors (Table 2). In general, the differences are due to the longer duration of capture events than manipulation and transport events. In capture events, the mouth opening muscles (coracomandibularis and epaxialis) are active earlier and active longer than in manipulation and transport events. The duration of coracoarcualis activity is also longer in capture and transport events than in manipulation events. Activity in the jaw adductor, the quadratomandibularis, is longer in duration during capture and manipulation events than in

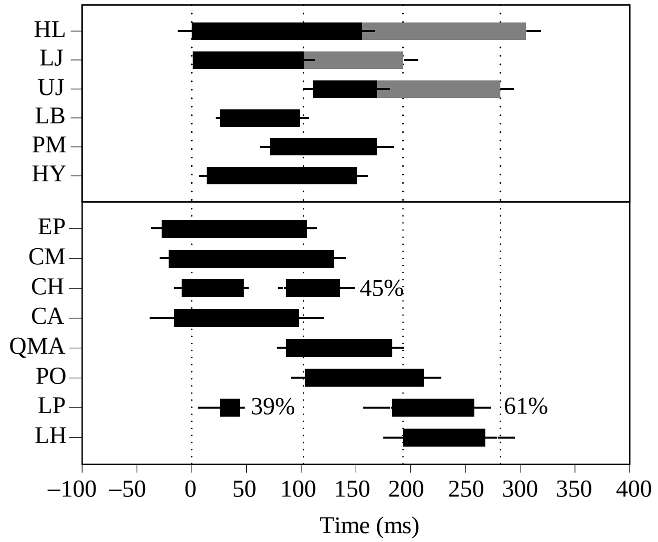

Fig. 5. Composite diagram of synchronized means of kinematic (top) and motor (bottom) patterns during all prey-capture events (*N*=8) in *Squalus acanthias.* Kinematic events are represented by black bars indicating start to peak activity followed by grey bars representing peak to end of activity, with error bars indicating 1 S.E.M. Motor events are shown by black bars representing the onset and duration of motor activity, with error bars indicating 1 S.E.M. The dotted vertical lines indicate, from left to right, the start of the expansive, compressive and recovery phases and the end of the recovery phase. EP, epaxialis; CA, coracoarcualis; CH, coracohyoideus; CM, coracomandibularis; HL, head lift; HY, peak hyoid depression; LB, labial extension; LH, levator hyomandibularis; LJ, lower jaw; LP, levator palatoquadrati; PM, prey movement; PO, preorbitalis; QMA, quadratomandibularis anterior; UJ, upper jaw. The percentage values indicate the proportion of the total activity in which that burst was active, if less than 100 %.

transport events. Individual effects were found in many of the motor pattern variables (Table 2).

Muscle activity during lateral headshakes and cutting of the prey consists of nearly simultaneous repeated bursts of activity in all of the muscles of the head (Fig. 8D). Nearly simultaneous bursts of activity occurred in the muscles of the adductor mandibulae complex in five separate headshake events in one individual (Fig. 9). These bursts of activity were observed during each sideways shake of the head; for example, Fig. 9 illustrates an average of four shakes to one side and five shakes to the contralateral side, with the last burst occurring as the prey is severed.

Discussion

Variation in prey-capture mode

Squalus acanthias is a jack-of-all-trades and uses suction, ram and bite mechanisms variably while feeding on herring. In capturing prey, suction is used twice as often as ram. In all of the suction capture events and even some of the ram feeding events, the prey can be clearly seen to move towards the mouth of the shark. This is supported by the large range in RSI values (–0.32 to 0.74, mean –0.23 for suction and 0.31 for ram capture events) indicating the variation in relative contributions of ram and suction components during prey capture. The ram-feeding swell shark *Cephaloscyllium ventriosum* has a much larger ram than suction component during prey capture, as shown by an RSI of 0.60 (Ferry-Graham, 1997). Suction and ram are used exclusively or cooperatively to manipulate prey during processing events. Biting is used to sever large prey into smaller more manageable pieces. Not all capture events were followed by manipulation: in some feeding events, transport of the prey immediately followed prey capture, as also noted for carcharhinid sharks (Frazzetta and Prange, 1987; Motta *et al.* 1997; Wilga, 1997). Transport of the prey for swallowing was always accomplished by suction.

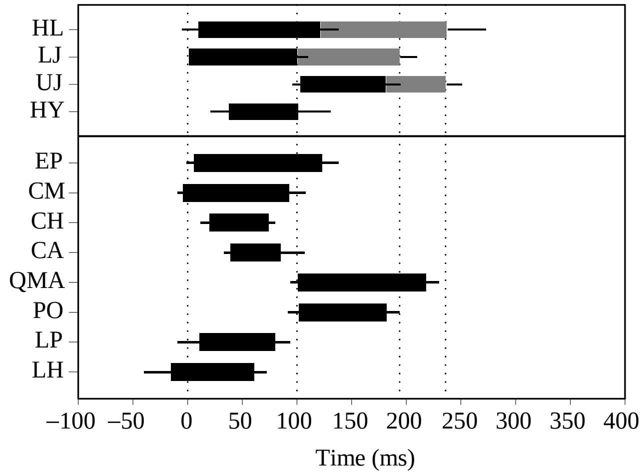

Fig. 6. Composite diagram of synchronized means of kinematic (top) and motor (bottom) patterns during all bite manipulation events (*N*=8) in *Squalus acanthias.* Kinematic events are represented by black bars indicating start to peak activity followed by grey bars representing peak to end of activity, with error bars indicating 1 S.E.M. Motor events are represented by black bars representing the onset and duration of motor activity, with error bars indicating 1 S.E.M. The dotted vertical lines indicate, from left to right, the start of the expansive, compressive and recovery phases and the end of the recovery phase. EP, epaxialis; CA, coracoarcualis; CH, coracohyoideus; CM, coracomandibularis; HL, head lift; HY, hyoid depression; LH, levator hyomandibularis; LJ, lower jaw; LP, levator palatoquadrati; PO, preorbitalis; QMA, quadratomandibularis anterior; UJ, upper jaw.

Conservation of the feeding mechanism

A common pattern of kinematic and motor activity characterizes prey capture, manipulation and transport in the spiny dogfish *Squalus acanthias* as hypothesized. Occasionally, a preparatory phase was present in which the jaws were closed just prior to the expansive phase. The preparatory phase is characterized by activity in the quadratomandibularis, the levator palatoquadrati and the levator hyomandibularis. A preparatory phase is not always present during feeding in other sharks (Motta *et al.* 1997;

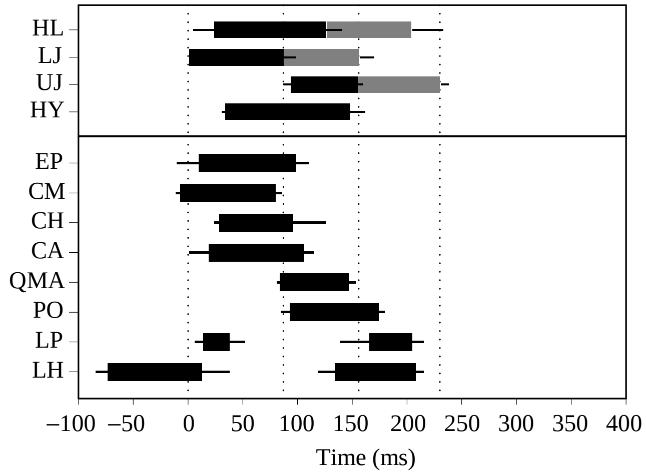

Fig. 7. Composite diagram of synchronized means of kinematic (top) and motor (bottom) patterns during all suction transport (*N*=8) events in *Squalus acanthias.* Kinematic events are represented by black bars indicating start to peak activity followed by grey bars representing peak to end of activity, with error bars indicating 1 S.E.M. Motor events are represented by black bars representing the onset and duration of motor activity, with error bars indicating 1 S.E.M. The dotted vertical lines indicate, from left to right, the start of the expansive, compressive and recovery phases and the end of the recovery phase. EP, epaxialis; CA, coracoarcualis; CH, coracohyoideus; CM, coracomandibularis; HL, head lift; HY, hyoid depression; LH, levator hyomandibularis; LJ, lower jaw; LP, levator palatoquadrati; PO, preorbitalis; QMA, quadratomandibularis anterior; UJ, upper jaw.

Wilga, 1997) or in bony fishes (Liem, 1978; Lauder, 1985; Gillis and Lauder, 1994, 1995).

The expansive phase (Fig. 10A–B) is characterized by activity in the mouth-opening muscles followed by activity in the hyoid depressor muscles. Mouth opening begins with posteroventral depression of the lower jaw, during coracomandibularis and coracoarcualis muscle activity, and simultaneous posterodorsal elevation of the cranium during epaxialis muscle activity. The labial cartilages are pivoted anteriorly as the lower jaw is depressed, pulling the folds of skin at the corner of the mouth forward to occlude the sides of the gape (see Fig. 4). Peak labial cartilage extension occurs shortly before peak gape. The anterior swinging of the labial cartilages occluding the lateral sides of the gape in the spiny dogfish functions in a similar manner to the anterior swinging of the maxilla and premaxilla in bony fishes (Alexander, 1967; Lauder, 1979, 1985). This prevents water inflow at the sides of the mouth and produces a tubular mouth opening which directs the suction inflow to the front of the mouth (Osse, 1969; Lauder, 1979, 1980, 1983; Muller and Osse, 1984).

Following the start of mouth opening, posteroventral depression of the basihyal (hyoid) occurs during coracohyoideus and coracoarcualis muscle activity. Expansion of the orobranchial cavity is mediated by depression of the basihyal and branchial, presumably by the coracohyoideus, coracoarcualis and coracobranchiales, as in the lemon shark (Motta *et al.* 1997). Depression of the lower jaw and hyoid pulls the distal end of the hyomandibula ventrally and slightly anteriorly through the mandibular–hyomandibular and ceratohyal–hyomandibular joints. This ventral pivoting of the hyomandibula allows the upper and lower jaws to protrude ventrally away from the chondrocranium, but does not appear to drive upper jaw protrusion in the spiny dogfish. Haller (1926) and Shirai and Okamura (1992) have proposed that the hyoid arch is crucial in protruding the upper and lower jaws from the chondrocranium in squaloids. This is partially true: ventral movement of the distal hyomandibula is crucial in allowing the jaw apparatus as a whole to move away from the cranium, but the hyomandibula apparently plays a passive role in being pulled by the jaws, not an active role in pushing the jaws. The hyomandibula allows some rotation of the jaws in the spiny dogfish, but to a lesser extent than in carcharhiniform and lamniform sharks (Moss, 1977; Motta *et al.* 1997).

The compressive phase is characterized by activity in the jaw adductor and upper jaw protrusion muscles (Fig. 10B–C). The lower jaw is elevated and the upper jaw is protruded during activity in the quadratomandibularis and preorbitalis muscles. Contraction of the preorbitalis muscle produces an anteriorly directed force near the posterior region of the jaws. This forces the orbital process of the upper jaw to slide ventrally along the ethmopalatine groove to protrude the upper jaw away from the chondrocranium. As the quadratomandibularis muscle adducts the jaws, it may assist upper jaw protrusion by depressing the upper jaw towards the lower jaw as the lower jaw is being elevated. Relaxation of the epaxialis muscle allows the head to drop passively towards its resting position. Elastic energy storage in the skeletal, integumental and other muscle tissue may also contribute to the recovery of the cranial elements to the resting position. Hyoid depression reaches its peak midway through this phase.

The recovery phase is characterized by activity in the jaw retractor muscles (Fig. 10C–A). Posterodorsal elevation of the upper jaw back under the chondrocranium occurs during activity in the levator palatoquadrati muscle. In addition, posterodorsal elevation of the hyomandibula elevates the entire jaw apparatus and occurs during activity in the levator hyomandibularis muscle. This supports the proposal of Shirai and Okamura (1992) that the levator palatoquadrati and levator hyomandibularis muscles restore the jaws and hyoid arch back to the resting position in squaloid sharks. The recovery phase is the longest of the three phases because of depression of the head to its resting position. The levator hyomandibularis muscle retracts the jaws in both the spiny dogfish and the lemon shark (Motta *et al.* 1997), supporting the proposal of Frazzetta (1994), and does not apparently assist in jaw protrusion as Moss (1972) proposed.

The kinematic sequence observed during feeding in the spiny dogfish is similar to that reported in carcharhiniform sharks, such as the lemon, blacknose, blacktip, swell and bonnethead (Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Ferry-Graham, 1997; Motta *et al.* 1997; Wilga,

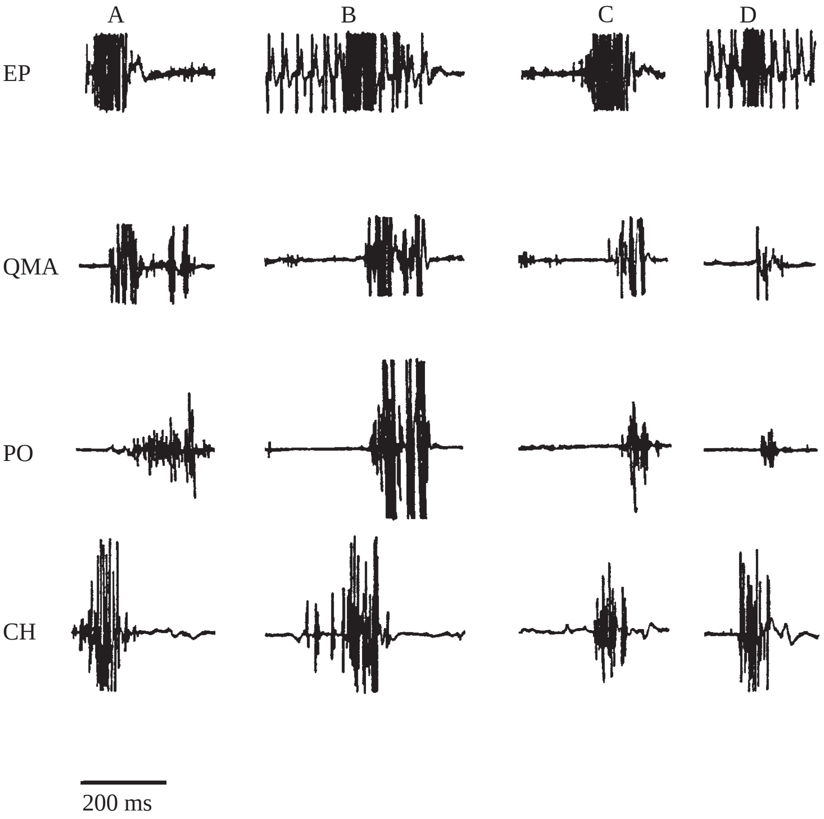

Fig. 8. Electromyographic recordings from four muscles during a representative suction capture (A), bite manipulation (B), suction transport (C) and head shake (D) in *Squalus acanthias*. EP, epaxialis; CH, coracohyoideus; PO, preorbitalis; QMA, quadratomandibularis anterior.

1997). However, the white shark, a lamniform shark, differs in that upper jaw protrusion occurs well before peak lower jaw depression, and cranial depression does not occur until the recovery phase rather than during the compressive phase as in other sharks. Prolonged elevation of the cranium in the white shark is thought to allow the upper jaw time to protrude and retract rapidly multiple times during a bite cycle, a behavior that is sometimes used to excise pieces from large prey items (Pratt *et al.* 1982). The basic feeding sequence consisting of head lift and lower jaw depression, lower jaw elevation and peak hyoid depression after peak gape that has been observed in other aquatic-feeding vertebrates studied thus far, bony fishes and aquatic salamanders and turtles, is conserved in the spiny dogfish as well as in other sharks (Liem, 1980; Lauder, 1985; Lauder and Prendergast, 1992; Reilly and Lauder, 1992; Ferry-Graham, 1997; Motta *et al.* 1997; Wilga, 1997).

Variation in the feeding mechanism

Capture, manipulation and transport events are distinguished by several differences in the timing and duration of kinematic and motor pattern variables in the spiny dogfish. Most of the differences among behaviors are due to the earlier onset and longer duration of activity in the mouth-opening muscles (coracomandibularis and epaxialis) in capture events than in transport events. Other studies of feeding in sharks, bony fishes and aquatic salamanders have also found suction transport events to be shorter in duration than prey-capture events (Frazzetta and Prange, 1987; Gillis and Lauder, 1994, 1995; Ferry-Graham, 1997; Motta *et al.* 1997; Wilga, 1997), and this pattern may be widespread during aquatic feeding in lower vertebrates, as Gillis and Lauder (1995) suggest. One explanation for this is that, in transport events, the prey is already contained within the orobuccal cavity; therefore, the mouth does not need to be open for as long as it does in capture events to ensure apprehension of the prey. In manipulation events, activity in the quadratomandibularis muscle continues until well after the jaws have closed completely, indicating that the jaws are continuing to bite down onto the prey. In contrast, quadratomandibularis muscle activity ceases just prior to complete jaw closure in capture and transport events.

Variation among feeding behaviors (capture, manipulation and transport) may be masked by the great variation in individual prey-capture events that encompasses the entire variation in manipulation and transport events, resulting in few differences (Wilga, 1997). The numerous individual effects show that individuals are capable of varying their head movements and motor pattern from one successful feeding trial to the next. Individual effects in kinematics and motor activity patterns during feeding have been reported in other sharks (Ferry-Graham, 1997; Motta *et al.* 1997; Wilga, 1997); thus, individual variation appears to be an important component of the feeding mechanism. This shows that the feeding behavior of sharks is not a predictable sequence of events that is stereotypical among individuals, as has been thought previously (Gilbert, 1962, 1970; Tricas, 1985).

Modulation of activity in the levator palatoquadrati and levator hyomandibularis among the three behaviors was clearly observed, but was not detected by the present statistical

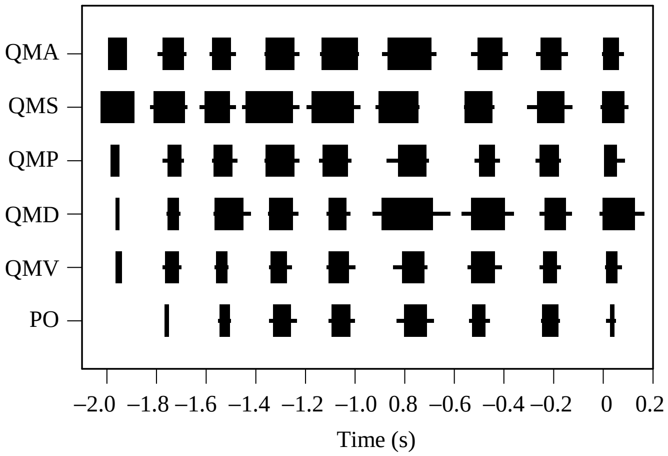

Fig. 9. Composite diagram of the mean motor pattern in the adductor mandibulae complex during five lateral headshake events in one *Squalus acanthias* individual. Electromyographic events are represented by black bars indicating the onset and duration of motor activity, with error bars indicating 1 s.e.m. Each column of bursts represents one movement of the head to one side, with the last column at time 0 including cutting of the prey. The *x*-axis represents time in seconds relative to the burst in which prey-cutting occurs. PO, preorbitalis; QMA, quadratomandibularis anterior; QMD quadratomandibularis deep; QMS, quadratomandibularis superficial; QMP, quadratomandibularis posterior; QMV, quadratomandibularis ventral.

methods. These two muscles elevate the upper jaw and mandibular arch, respectively, and act to retract the jaws during the recovery phase in capture and transport events. The reason for the lack of activity in the two muscles during the recovery phase in manipulation events, and thus the apparent absence of jaw retraction after the bite, is not clear. Activity in the two muscles during the expansive phase may be associated with events in which the prey is already contained in the mouth. If so, these muscles may act to elevate the upper jaw and dislodge the teeth from the prey prior to further processing. Activity in the levator palatoquadrati during the expansive phase may ensure that the upper jaw does not deflect the prey during capture.

Upper jaw protrusion

The spiny dogfish is capable of protruding the upper jaw up to 30 % of its head length, nearly 2 cm in one 53 cm TL individual. This is considerably more than the lemon shark, with its hyostylic jaw suspension, which has previously been thought to allow greater mobility of the upper jaw than in orbitostylic sharks (Gregory, 1904; Maisey, 1980; Compagno, 1988; Wilga, 1997). Substantial upper jaw protrusion was clearly evident in all of the feeding events recorded. Thus, its orbitostylic type of jaw suspension does not appear to limit upper jaw protrusion in this species, contrary to previous speculation (Schaeffer, 1967; Compagno, 1977).

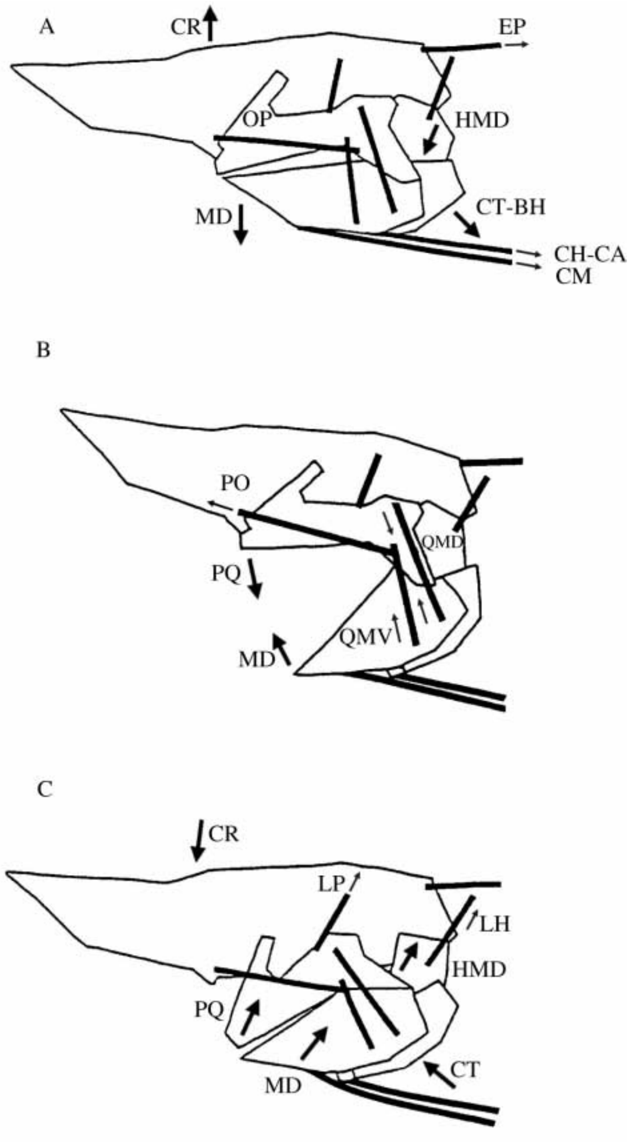

Fig. 10. Schematic diagram of the functional components of the cranium and jaws during feeding in *Squalus acanthias.* From the resting position (A), cranial elevation by the EP, lower jaw depression by the CM and hyoid depression by the CH and CA open the mouth to peak gape (B). Next, upper jaw protrusion and lower jaw elevation by the PO, QMV and QMD reduce the gape to peak upper jaw protrusion and complete jaw closure (C). Lastly, upper and lower jaw elevation by the LP and LH retracts the jaws back to the resting position. Thick black lines indicate muscles, with their direction of action indicated by small arrows, and open elements indicate cartilages, with their direction of movement indicated by large arrows. CH-CA, coracohyoideus and coracoarcualis; CM, coracomandibularis; CR, cranium; CT, ceratohyal; CT-BH, ceratohyal-basihyal; EP, epaxialis; HMD, hyomandibula; LH, levator hyomandibularis; LP, levator palatoquadrati; MD, mandible or lower jaw; OP, orbital process of palatoquadrate; PO, preorbitalis; PQ, palatoquadrate or upper jaw; QMD, quadratomandibularis dorsal (all divisions); QMV, quadratomandibularis ventral.

One function of upper jaw protrusion may be to assist in jaw closure by protruding the upper jaw as well as by elevating the lower jaw to close the gape. Protrusion of the upper jaw was found to reduce the gape by 51 %, leaving the remainder of the gape for elevation of the lower jaw to close. In the absence of upper jaw protrusion, the distance that the lower jaw would have to travel to close the gape would nearly double, assuming that velocity remains unchanged. Jaw closure may be achieved in a shorter time by protruding the relatively smaller mass of the upper jaw to close the gape rather than by depressing the greater mass of the entire head. It is important to note that cranial movements do not affect protrusion of the upper jaw. The upper jaw is connected to the cranium by long ethmopalatine ligaments anteriorly and by the hyomandibula posteriorly. As a result, movement of the upper jaw is independent of movement of the cranium, as shown by upper jaw protrusion occurring during cranial elevation as well as cranial depression.

Moss (1972) has proposed two mechanisms for upper jaw protrusion in sharks. The first mechanism involves contraction of the preorbitalis and levator palatoquadrati muscles in carcharhiniform sharks and contraction of the preorbitalis muscle in squaliform sharks. This first mechanism has been observed during feeding in two carcharhinid sharks (Motta *et al.* 1997; Wilga, 1997) as well as in the spiny dogfish. In the second mechanism, the lower jaw is held stationary against large prey while contraction of the quadratomandibularis muscle depresses the unobstructed upper jaw into the protruded state. This mechanism probably acts to protrude the upper jaw regardless of prey size, since the function of a jaw adductor is to bring the two skeletal elements together; thus, the upper jaw is moved ventrally as the lower jaw is moved dorsally. Both of these mechanisms probably act cooperatively to protrude the upper jaw in the spiny dogfish, and probably in other sharks as well, since nearly simultaneous activity in the quadratomandibularis and preorbitalis muscles occurs during upper jaw protrusion and lower jaw elevation, which are also nearly simultaneous.

Wu (1994) proposed a mechanism for upper jaw protrusion in orectolobiform sharks in which ventral rotation of the ceratohyal against the mandibular knob pushes the hyomandibula anteroventrally, thereby protruding the jaws. He showed that the articulation between the hyomandibula and mandibular knob is present in squalean and galean sharks and suggested that the ceratohyal mechanism occurs during jaw protrusion in many living sharks. The ceratohyal mechanism for upper jaw protrusion does not appear to be present during feeding in the spiny dogfish. Anterior movement of the relatively short hyomandibula is slight, and depression of the ceratohyal is not simultaneous with upper jaw protrusion in the spiny dogfish. In addition, hyomandibula depression appears to be passive in being pulled ventrally by ceratohyal depression.

The mechanism of upper jaw protrusion and retraction differs somewhat between squaliform and carcharhiniform sharks: the levator palatoquadrati assists in retraction of the upper jaw in squaliform sharks, while it assists in upper jaw protrusion in carcharhiniform sharks. Upper jaw protrusion in the spiny dogfish occurs during jaw closure, when the preorbitalis and quadratomandibularis muscles are active. In contrast, the levator palatoquadrati, preorbitalis and quadratomandibularis muscles are active during protrusion of the upper jaw in the lemon shark (Motta *et al.* 1997) and in the bonnethead shark *Sphyrna tiburo* (Wilga, 1997). In carcharhinid sharks, the levator palatoquadrati muscle is anteroposteriorly oriented (Compagno, 1988; Nakaya, 1975; Motta and Wilga, 1995); consequently, its contraction pulls the upper jaw anteriorly, as found in both the lemon (Motta *et al.* 1997) and bonnethead (Wilga, 1997) sharks. In contrast, the levator palatoquadrati muscle is dorsoventrally oriented in squalid sharks such as the spiny dogfish, where its contraction acts to elevate the upper jaw, as shown above. Interestingly, in the spotted catshark *Scyliorhinus canicula,* which is a carcharhiniform shark, the levator palatoquadrati muscle was found to be active simultaneously with the levator hyomandibularis muscle as the jaws became completely closed (Hughes and Ballintijn, 1965). However, the levator palatoquadrati muscle in the spotted catshark is vertically oriented, as in the spiny dogfish, not anteroposteriorly oriented, as in carcharhinid sharks, and appears to function similarly to retract the upper jaw.

Head shaking and the cutting mechanism

Lateral head shaking while grasping the prey between the jaws in *Squalus acanthias* is an effective means of cutting long prey into two pieces. Nearly simultaneous bursts of activity occur in the muscles of the head during each sideways shake of the head. If the shark is also actively biting onto the prey during each headshake, as suggested by the motor pattern of the adductor mandibulae complex, then severing of the prey may be enhanced. After cutting the prey, the shark swallows the piece of prey grasped within the jaws, then returns to engulf the severed piece. Head-shaking behavior has been observed during feeding in several species of sharks (Springer, 1961; Moss, 1972, 1977; Frazzetta and Prange, 1987; Frazzetta, 1988, 1994; Motta *et al.* 1997; Wilga, 1997) and is thought to be a mechanism for gouging pieces from large prey, cutting prey into smaller pieces or subduing the prey (Springer, 1961; Hobson, 1963; Gilbert, 1970; Moss, 1972; Tricas and McCosker, 1984; Frazzetta and Prange, 1987; Frazzetta, 1994; Powlik, 1995).

The morphology of the teeth is important in this head-shaking cutting behavior. The upper and lower teeth of the spiny dogfish are similar, with a large oblique cusp that is smooth (not serrated) and pointed laterally (Compagno, 1984). Smooth sharp blades, such as the teeth in spiny dogfish, cut by shearing the material through friction produced by drawing the edge of the blade against the material to be sliced (Frazzetta, 1988, 1994). Furthermore, if the blade or tooth is inclined towards the cutting direction, the shearing effect is increased and the tooth will dig deeper into the substratum as it is moved sideways (Frazzetta, 1988). Grasping or biting of the prey coupled with vigorous lateral headshakes cause the prey to shear across the teeth, resulting in an effective prey-cutting mechanism as Moss (1972) suggested.

Although the white shark and the spiny dogfish have different dentition patterns, they are both capable of effectively reducing large or long prey into smaller, more manageable, pieces. Powlik (1995) found that, during biting on prey, the sideways sliding of teeth between the upper and lower jaws increases the cutting area in the white shark. The teeth of the white shark are angled lingually and are effective at gouging pieces from large prey, holding prey or preventing the prey's escape from the mouth (Powlik, 1995). This is supported by its feeding strategy in which it attacks a large pinniped at the surface of the water, usually inflicting a massive singular wound (Tricas and McCosker, 1984; McCosker, 1985; Klimley *et al.* 1996). In contrast, the teeth of the spiny dogfish are inclined laterally and are effective at cutting long prey into two pieces. This is also supported by its diet (Jensen, 1965; Jones and Geen, 1977); it readily takes prey that are longer than the gape but in which the prey width does not exceed the gape (Wilga, 1997).

As the number of functional studies on the feeding mechanisms of sharks increase, it is becoming evident that feeding behavior in sharks is neither predictable nor stereotypical. Prey capture, bite manipulation and suction transport in the spiny dogfish, as well as in other shark species, have a common pattern of kinematic and motor activity but are distinguishable by their duration and relative timing. Furthermore, individual sharks are capable of varying head movements and motor pattern among feeding events, suggesting that the feeding mechanism is not a tightly controlled preprogrammed behavior. Rather than restricting upper jaw protrusion, the orbitostylic jaw suspension in the spiny dogfish allows relatively extensive upper jaw protrusion. One function of upper jaw protrusion may be to reduce the gape and decrease the time to jaw closure. The mechanism of upper jaw protrusion in the spiny dogfish differs from that described in carcharhinid sharks, with the levator palatoquadrati muscle assisting in upper jaw retraction rather than in upper jaw protrusion. Vigorous lateral head-shaking while grasping the prey tightly in the teeth is an effective means of cutting long prey into smaller, more easily swallowed, pieces. The basic kinematic feeding sequence observed in other aquatic-feeding lower vertebrates is conserved in the spiny dogfish.

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