

FEEDING MECHANISM AND FUNCTIONAL MORPHOLOGY OF THE JAWS OF THE LEMON SHARK *NEGAPRION BREVIROSTRIS* (CHONDRICHTHYES, CARCHARHINIDAE)

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Summary

This study tests the hypothesis that preparatory, expansive, compressive and recovery phases of biting behavior known for aquatically feeding anamniotes are conserved among extant elasmobranch fishes. The feeding mechanism of the lemon shark *Negaprion brevirostris* is examined by anatomical dissection, electromyography and high-speed video analysis. Three types of feeding events are differentiated during feeding: (1) food ingestion primarily by ram feeding; (2) food manipulation; and (3) hydraulic transport of the food by suction. All feeding events are composed of the expansive, compressive and recovery phases common to aquatically feeding teleost fishes, salamanders and turtles. A preparatory phase is occasionally observed during ingestion bites, and there is no fast opening phase characteristic of some aquatically feeding vertebrates. During the compressive phase, palatoquadrate protrusion accounts for 26% of the gape

distance during jaw closure and is concurrent with muscle activity in the dorsal and ventral preorbitals and the levator palatoquadrati. Hydraulic transport events are shorter in duration than ram ingestion bites. Prey ingestion, manipulation and hydraulic transport events are all found to have a common series of kinematic and motor components. Individual sharks are capable of varying the duration and to a lesser extent the onset of muscle activity and, consequently, can vary their biting behavior. We propose a model for the feeding mechanism in carcharhinid sharks, including upper jaw protrusion. This study represents the first electromyographic and kinematic analysis of the feeding mechanism and behavior of an elasmobranch.

Key words: elasmobranch, electromyography, kinematics, variability, jaw protrusion, feeding, lemon shark, *Negaprion brevirostris*.

Introduction

To understand the function and evolution of feeding mechanisms in vertebrates, we must have a thorough understanding of the anatomy and functional morphology of the feeding apparatus of fishes. Our knowledge of the evolution of aquatic feeding mechanisms, however, is limited by a lack of studies on cartilaginous fishes. The Chondrichthyes diverged from a common ancestor with the Teleostomi before the Devonian period and have retained the same major skeletal features for over 400 million years (Schaeffer and Williams, 1977; Long, 1995). Elasmobranchs have undergone two major episodes of adaptive radiation, one of these being in the ctenacanthid lineage that gave rise to neoselachians (modern sharks, skates and rays) (Carroll, 1988). Within the neoselachians, the most speciose group is the Galeomorpha, which includes the Lamniformes, Carcharhiniformes,

Orectolobiformes and Heterodontiformes, the dominant predaceous sharks of modern seas (Compagno, 1988; Shirai, 1996). From the earliest cladodont ancestor that grasped and possibly swallowed its prey whole or tore pieces from it (Schaeffer, 1967; Moy-Thomas and Miles, 1971), sharks have radiated to cover a variety of prey ingestion mechanisms including biting, gouging and biting, ram-feeding, suction-feeding and filter-feeding.

The transition from an amphistylic jaw suspension in the earliest sharks to hyostyly in modern sharks (galeoids and squaloids) (see Compagno, 1977; Maisey, 1980, regarding jaw suspension terminology) presumably resulted in the exploitation of new feeding niches. Associated with this change in jaw suspension was a shortening of the jaws, palatoquadrate or upper jaw protrusion, a dentition suited for shearing and

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sawing, and presumably greater bite force (Schaeffer, 1967; Moy-Thomas and Miles, 1971). The evolution of a highly kinetic upper jaw and upper jaw protrusibility in elasmobranchs is convergent with these same features in bony fishes (Schaeffer and Rosen, 1961; Schaeffer, 1967).

Compared with studies on teleosts, there have been fewer anatomical studies on elasmobranch feeding structures (reviewed in Motta and Wilga, 1995). There are even fewer data on the natural feeding behavior of sharks (Springer, 1961; Gilbert, 1962; Tricas, 1985; Frazzetta, 1994), and the only studies on the functional morphology and kinematics of the feeding apparatus have been based either on manual manipulation of dead specimens or on cine analyses of live feeding sharks (Moss, 1977; Tricas and McCosker, 1984; Tricas, 1985; Frazzetta and Prange, 1987; Wu, 1994).

In contrast to our relatively limited knowledge of feeding in sharks, extensive studies on aquatic feeding in teleosts, salamanders and turtles have revealed common patterns. Four distinct phases occur during suction or ram prey capture: the preparatory, expansive, compressive and recovery phases (Liem, 1978; Lauder, 1985; Lauder and Shaffer, 1985; Lauder and Prendergast, 1992; Lauder and Reilly, 1994; Reilly, 1995). In bony fishes, the kinematic patterns involved in hydraulic prey transport towards the esophagus are very similar to those of initial prey capture by suction feeding (Lauder and Reilly, 1994).

There are many sources of intra- and inter-individual variation in muscle activity patterns during feeding in teleost fishes. Most teleosts appear to be capable of modulating the timing and activity patterns of the jaw muscles in response to different prey (Liem, 1980; Lauder, 1981; Wainwright and Lauder, 1986). By comparison, the feeding behavior of sharks has been considered to be a series of stereotyped movements (Gilbert, 1970; Tricas, 1985), although there is preliminary evidence of inter-individual variation in prey capture kinematics and modulation of the biting behavior (Frazzetta and Prange, 1987; Motta *et al.* 1991).

The elasmobranch mechanism of jaw protrusion is very different from that of teleosts owing to a different anatomy. This raises the possibility that the biological role of protrusion is also different (see Motta, 1984, for a review of protrusion in teleost fishes). The mechanism and biological role of jaw protrusion in sharks have been speculative, and a variety of conflicting mechanisms involving muscles such as the preorbitalis, levator palatoquadrati, levator hyomandibuli and quadratomandibularis have been proposed (Luther, 1909; Moss, 1972, 1977; Frazzetta, 1994; Wu, 1994).

In this paper, we provide the first electromyographic and high-speed video analyses of the feeding mechanism of a chondrichthyan under semi-natural feeding conditions. The lemon shark *Negaprion brevirostris* (Carcharhinidae) was chosen as a study animal because, compared with other carcharhinid species (1) its anatomy is well documented (Compagno, 1988; Motta and Wilga, 1995), (2) its diet (primarily small teleosts swallowed whole or larger teleosts bitten into pieces) and feeding behavior are well studied (Gruber, 1984; Wetherbee *et al.* 1990; Morrissey and Gruber,

1993a,b; Cortés and Gruber, 1990), (3) preliminary functional data exist on its biting behavior (Motta *et al.* 1991) and (4) it is readily available and thrives in captivity.

The goal of this study was to investigate the feeding mechanism of a carcharhinid shark, *N. brevirostris*, under semi-natural conditions. We tested the following hypotheses: (1) the kinematic pattern of preparatory, expansive, compressive and recovery phases common to other aquatically feeding vertebrates is conserved in *N. brevirostris* during the three feeding events of prey ingestion, manipulation and hydraulic transport; (2) there is inter-individual variability of kinematic and motor patterns in the feeding events, such that muscle activity and kinematic events vary only in duration, not in relative timing; (3) the three feeding events have a common series of kinematic and motor patterns but are distinguishable by their duration and relative timing; and (4) upper jaw protrusion is effected by contraction of the preorbitalis, levator palatoquadrati, levator hyomandibuli and quadratomandibularis muscles. From the analysis of our results, we propose a quantitative functional model of the feeding apparatus of *N. brevirostris*.

Materials and methods

High-speed video recording

Specimens of juvenile *Negaprion brevirostris* (Poey, 1868) were collected in Florida Bay north of the Florida Keys, USA, and held in 5 m diameter circular holding tanks in natural sea water at Mote Marine Laboratory, Sarasota, Florida. Specimens ranged from 66.5 to 78 cm in total length, corresponding to ages of approximately 1–2 years old (Brown and Gruber, 1988). Approximately 2 weeks prior to the experiments, each animal was transferred to a 2.4 m diameter, 1400 l semicircular tank with a 0.5 m×1.7 m acrylic window and was fed cut pieces of fish three times a week. Pieces of fillets of Atlantic thread herring (*Opisthonema oglinum*) and crevalle jack (*Caranx hippos*) were presented to the shark as it swam past the window. In most cases, the shark took the food from plastic tongs or a plastic rod, which were used to position the food in the vicinity of the shark's mouth as the animal continued to swim forward. We offered approximately 2 cm×7 cm×1 cm pieces of fish for most bites. Towards satiation, usually after 12–20 bites, we occasionally offered larger pieces of fish, approximately 7 cm×7 cm×2 cm.

All sharks were filmed during feeding with two high-speed video cameras (NAC HSV-200, 200 fields s⁻¹) positioned beside each other to capture a wide horizontal view. A mirror placed at 45° below the transparent floor of the tank provided a simultaneous ventral view of the shark. Illumination was provided by approximately 3000 W of quartz-halogen lights. To synchronize the electromyographic (EMG) signals with the video recordings, a repeating light-emitting diode stroboscopic light was simultaneously recorded by one of the cameras and a voltage spike was recorded on one channel of the EMG analysis record.

The following durations were determined for six sharks by counting the number of fields (1 field=5 ms) occupied by each

kinematic event: (1) time from start of mandible depression to maximum mandible depression (mandible depression); (2) time from maximum mandible depression to end of mandible elevation (mandible elevation); (3) total time for mandible depression and elevation; (4) time from beginning of lower jaw depression to beginning of head elevation; (5) time from start of head elevation to maximum head elevation (head elevation); (6) time from maximum head elevation to end of head depression (head depression); (7) total time of head elevation and depression; (8) time from start of mandible depression to start of jaw protrusion; (9) time from start of palatoquadrate protrusion to maximum jaw protrusion (palatoquadrate protrusion); (10) time from maximum palatoquadrate protrusion to end of jaw retraction (palatoquadrate retraction); (11) total time of palatoquadrate protrusion and retraction; (12) time from start of mandible depression to maximum gape; (13) time from start of mandible depression to maximum hyobranchial depression; and (14) time from start of mandible depression to end of palatoquadrate retraction (usually the duration of the entire bite).

To test whether the electrode wires modified the kinematics of feeding, the timing of the above cranial movements was compared statistically for four sharks with implanted wires *versus* two sharks without implanted wires. Ingestion bites were analyzed separately from hydraulic transport events. For subsequent analyses, kinematic data from implanted and non-implanted sharks were pooled, and the variables compared for ingestion bites and hydraulic transport (there were insufficient manipulation bites for analysis). Of the 30 bites used for the kinematic analysis, only 15 had accompanying EMG data (see Table 1 for total number of sharks and bites used).

In addition to the timing variables, protrusion was characterized by analysis of eight ingestion bites from four sharks. Sequential video fields were captured with a Video Blaster video capture board (Creative Labs, Inc.) and stored on computer. To measure the distance that palatoquadrate protrusion decreases the gape during jaw closure, two measurements were taken: maximum vertical height of the gape, and maximum vertical distance that the palatoquadrate protrudes below the upper labium. Protrusion distance was then expressed as a percentage of maximum gape. Measurements were made using Sigma Scan software (Jandel Scientific Software).

Electromyography

Prior to these experiments, bipolar electrodes were prepared by gluing together two strands of single-strand, 0.06 mm diameter alloy wire (Evanohm R ML enamel, 200 Ω per foot, Carpenter Technology Corp.) with cyanoacrylate adhesive. Approximately 5 mm of the insertion end was left unglued, with 2 mm bent to produce a small barb. The most distal 1 mm portion of the wire was stripped of insulation. Sharks were then anesthetized with 0.133 g l⁻¹ tricaine methanesulfonate (MS 222) in a recirculating seawater/anesthetic ventilation system. Electrodes were implanted with 23 gauge hypodermic needles in 11 cranial muscles per animal. A stereotactic map of the head and musculature was used to ensure that the electrodes for each

Table 1. Sample sizes and statistical tests used for analysis of kinematics on food ingestion and hydraulic transport in *Negaprion brevirostris*

Kinematic event	Feeding event	Sharks
Mandible depression	^{1,2} N=7, 30	¹ N=7, 30
Mandible elevation	³ N=7, 30	³ N=7, 30
Total time of mandible depression and elevation	^{1,2} N=7, 30	¹ N=7, 30
Lag of head elevation from start of mandible depression	¹ N=7, 30	¹ N=7, 30
Head elevation	^{1,2} N=7, 30	³ N=7, 30
Head depression	¹ N=7, 30	¹ N=7, 30
Total time of head elevation and depression	^{2,3} N=7, 30	¹ N=7, 30
Lag of jaw protrusion from start of mandible depression	^{1,2} N=7, 28	¹ N=7, 28
Palatoquadrate protrusion	¹ N=7, 28	^{1,2} N=7, 28
Palatoquadrate retraction	¹ N=7, 28	¹ N=7, 28
Total time of palatoquadrate protrusion and retraction	¹ N=7, 28	¹ N=7, 28
Start of mandible depression to maximum gape	^{1,2} N=7, 30	¹ N=7, 30
Start of mandible depression to maximum hyobranchial depression	^{1,2} N=7, 30	¹ N=7, 30
Start of mandible depression to end of palatoquadrate protrusion	^{1,2} N=7, 28	³ N=7, 28

¹One-way ANOVA; ²SNK multiple-comparisons test by ranks, $P < 0.05$; ³Kruskal–Wallis one-way ANOVA on ranks.

Analysis is by feeding event (ingestion, hydraulic transport) and by individual shark.

Upper left superscript indicates statistical test, N indicates number of sharks and bites, respectively.

Seven juvenile sharks, three male 66.5–76.5 cm in total length (TL) and four female 61–78.1 cm TL were used.

muscle were placed at a similar location and depth in all sharks. Implanted muscles included: the levator palatoquadrati, dorsal preorbitalis, ventral preorbitalis, quadratomandibularis dorsal, quadratomandibularis ventral, levator hyomandibularis, coracobranchialis, coracoarcualis, coracomandibularis, coracohyoideus and epaxialis (Figs 1, 2). These muscles are suspected of being or have been shown to be directly involved with feeding in sharks (Luther, 1909; Edgeworth, 1935; Moss, 1972, 1977; Frazzetta, 1994; Motta *et al.* 1991). The anatomy and nomenclature of these muscles are discussed by Motta and Wilga (1995). To verify the position of the electrodes, we placed a third 2–3 cm piece of insulated, barbed electrode wire alongside the bipolar leads. If the bipolar leads pulled out, the ‘tell-tale’ wire usually remained embedded in the muscle, protruding slightly from the insertion hole.

All pairs of electrode wire were glued together using polystyrene cement and attached by a loop of suture to the first dorsal fin. Each electrode pair (approximately 2 m length) was connected to a 3 m cable, differential amplified at 1000 \times (AM Systems Inc., model 1700) and bandpass- (100–3000 Hz) and notch- (60 Hz) filtered. Six muscles (channels) were monitored

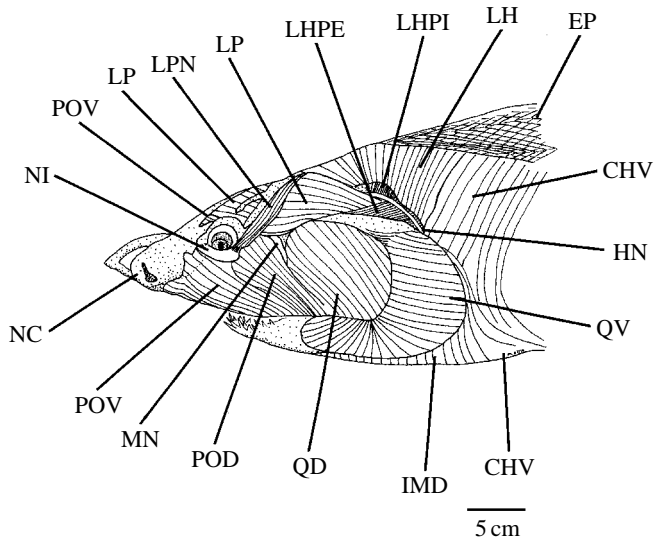


Fig. 1. Left lateral view of the head of a 229 cm total length *Negaprion brevirostris* with the skin removed and muscle fiber direction indicated. Myosepta of the epaxialis muscle (W-shape) are indicated in addition to the muscle fiber direction. Nerves and blood vessels are not indicated, with the exception of the hyomandibular nerve and the mandibular branch of the trigeminal nerve. CHD, constrictor hyoideus dorsalis; CHV, constrictor hyoideus ventralis; EP, epaxialis; HN, hyomandibular nerve; IMD, intermandibularis; LH, levator hyomandibularis; LHPE, external hyomandibula-palatoquadrate ligament; LHPI, internal hyomandibula-palatoquadrate ligament; LP, levator palatoquadrati; LPN, levator palpebrae nictitantis; MN, mandibular branch of trigeminal nerve; NC, nasal capsule; NI, nictitating membrane; POD, dorsal preorbitalis; POV, ventral preorbitalis; QD, quadratomandibularis dorsal; QV, quadratomandibularis ventral (reprinted with permission from Motta and Wilga, 1995).

simultaneously. Signals were displayed simultaneously on a four-channel oscilloscope (Tektronix, model 2214) and recorded on an eight-channel thermal array recorder (Western Graphtec, Mark-11) and pulse-code modulator (A. R. Vetter Co., model 3000A). The seventh channel of the pulse-code modulator recorded a digital electronic pulse signal that was synchronized with the high-speed camera.

The surgical procedure took approximately 45 min. Following surgery, the shark recovered from the anesthesia within 5 min and was then allowed to acclimate for approximately 1 h in the experimental tank prior to the experiment. During the latter part of recovery and throughout the experiment, the shark generally swam at a slow rate around the perimeter of the tank. During the experiment, the temperature of the tank sea water ranged from 22 to 28 °C. Food was presented as outlined in the kinematics section. At the termination of the experiment, the position of the electrodes was surgically verified after the shark had been killed with an overdose of MS 222 according to the University of South Florida and Mote Marine Laboratory Institutional Animal Care and Use Committee guidelines.

Analog EMG data for individual bites were digitized using

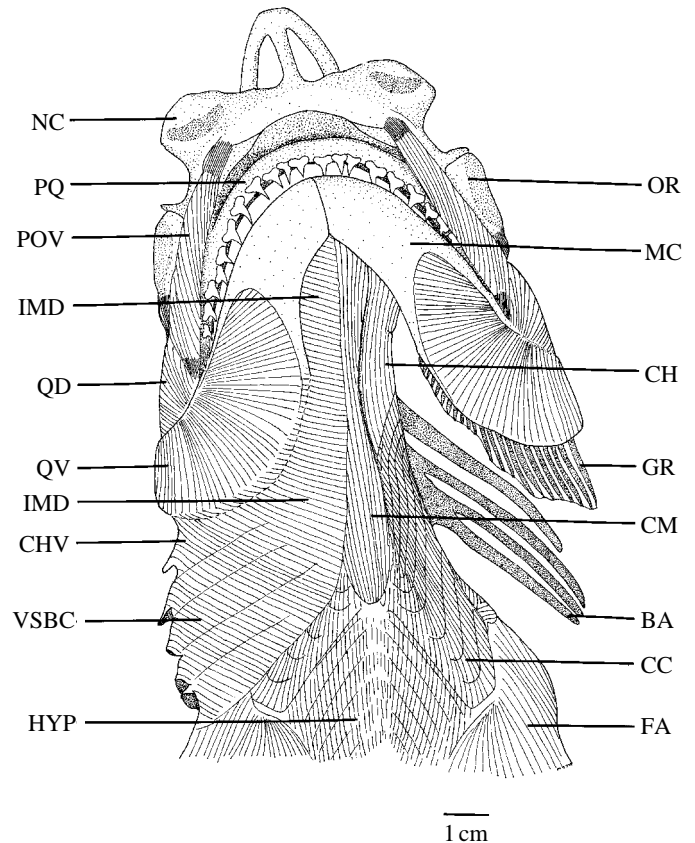


Fig. 2. Ventral view of the head of a 78 cm total length *Negaprion brevirostris* with the skin removed and muscle fiber direction indicated. The superficial musculature is removed on the left side to expose the deeper musculature. The head is slightly flexed to the right to expose the position of the branchial arches, which are not detailed. Nerves and blood vessels are not indicated. BA, branchial arches; CC, coracoarcualis; CH, coracochoyoides; CHV, constrictor hyoideus ventralis; CM, coracomandibularis; FA, fin adductor; GR, gill rays; HYP, hypaxial; IMD, intermandibularis; MC, Meckel's cartilage; NC, nasal capsule; OR, orbit; POV, ventral preorbitalis; PQ, palatoquadrate; QD, quadratomandibularis dorsal; QV, quadratomandibularis ventral; VSBC, ventral superficial branchial constrictor (reprinted with permission from Motta and Wilga, 1995).

an analog-to-digital converter (Cambridge Electronics Design, Ltd, model 1401plus controlled by Spike 2 software) and stored digitally. A sampling rate of 8333 Hz was used (Jayne *et al.* 1990). Electromyograms for each muscle for each bite were analyzed for burst duration, sequence and timing relative to the activity of the coracoarcualis muscle. We used this reference because it was a large and easy muscle to implant and because, during most bites, lower jaw depression was the first kinematic event and, consequently, the coracoarcualis was usually one of the first muscles to fire.

Electromyographs were categorized by shark and by feeding events. Feeding events included the following: ingestion bites; manipulation bites, which immediately followed ingestion bites and during which the food was usually repositioned or cut by the teeth; and hydraulic transport events in which the

Table 2. Sample sizes and statistical tests used for analysis of electromyographic data on duration and onset of muscle activity for eleven cranial muscles in *Negaprion brevirostris*

Muscle	Feeding event	Duration		Onset	
		Shark	Event × Shark	Feeding event	Shark
Epaxialis	¹ N=6, 60	^{1,3} N=6, 60		⁴ N=5, 47	⁴ N=5, 47
Coracoarcualis	¹ N=5, 85	¹ N=5, 85	⁵ N=5, 85		
Coracomandibularis	^{1,3} N=5, 39	¹ N=5, 39		⁴ N=4, 26	⁴ N=4, 26
Coracohyoideus	¹ N=4, 36	^{1,3} N=4, 36		⁴ N=3, 22	⁴ N=3, 22
Coracobranchialis	¹ N=4, 27	^{1,3} N=4, 27		¹ N=4, 25	^{1,3} N=4, 25
Levator palatoquadrati	¹ N=2, 47	¹ N=2, 47		^{1,3} N=2, 44	¹ N=2, 44
Ventral preorbitalis	^{1,3} N=4, 45	¹ N=4, 45		^{1,3} N=3, 42	¹ N=3, 42
Dorsal preorbitalis	¹ N=2, 9	¹ N=2, 9		¹ N=2, 8	no data
Levator hyomandibularis	no data	² N=2, 8		no data	no data
Quadratomandibularis ventral	¹ N=5, 32	¹ N=5, 32		¹ N=4, 18	¹ N=4, 18
Quadratomandibularis dorsal	¹ N=3, 15	¹ N=3, 15		no data	no data

¹One-way ANOVA; ²Mann–Whitney rank sum test; ³SNK multiple-comparisons test by ranks, $P<0.05$; ⁴Kruskal–Wallis one-way ANOVA on ranks; ⁵two-way mixed-model ANOVA GLM procedure.

Analysis is by feeding event (ingestion, manipulation, hydraulic transport), by individual shark or by feeding event × shark.

Upper left superscript indicates statistical test, N indicates number of sharks and bites, respectively.

Seven juvenile sharks, four male 66.5–76.5 cm total length (TL) and three female 70–78 cm TL were used.

food was moved rapidly from between the teeth through the pharynx into the esophagus. Hydraulic transport may be preceded by multiple manipulation bites. However, only the first manipulation bite of a sequence was analyzed. Because of the inherent difficulties of recording from these constantly swimming sharks, not all muscles were successfully recorded in every shark for every feeding event (Table 2).

Statistical analyses of electromyographic data

For each muscle, burst durations and onset times (relative to the coracoarcualis muscle onset) for all bites were tested separately for normality using the Kolmogorov–Smirnov test ($P<0.05$), and equality of variances was tested using the Levene median test ($P<0.05$). If the data did not meet these assumptions of parametric statistics, data were square-root-transformed or \log_e -transformed. When normality or equality of variances could not be achieved either way, nonparametric statistics were used. All tests were performed using Sigma Stat Software (Jandell Scientific Inc., version 1.01).

For burst duration of each muscle, a one-way analysis of variance (ANOVA) was performed first on feeding events (sharks combined) and then on sharks (feeding events combined) for each of the 11 cranial muscles. Similar analyses were performed on the time of onset of activity data for each muscle separately. Data from numerous individual bites of each shark were used in the calculations (not means from each shark) (see Table 2). In one case involving the duration of coracoarcualis activity, both a significant bite type and shark effect were detected. To test for interactions between feeding events and sharks, a two-way mixed-model ANOVA was used, with feeding event as the fixed factor and individual shark as the random factor. We divided the bite type mean square by the bite type by shark mean square to correct for the mixed-model ANOVA. We did not use two-way ANOVA throughout

because it would severely reduce our data set owing to the requirement for a balanced design in which all cells (sharks × feeding events) must have data.

If differences were detected by ANOVA, a Student–Newman–Keuls (SNK) multiple-range test by ranks was used to test all pairwise comparisons ($P<0.05$) (Zar, 1984). In a few cases, the parametric assumptions of the one-way ANOVA could not be met. In these cases, data were analyzed using the Kruskal–Wallis test, or the Mann–Whitney U -test in the case of two comparisons ($P<0.05$).

Statistical analyses of kinematic data

The durations of each of the 14 kinematic variables for four sharks implanted with EMG wires were compared with those for two sharks without implants. Because of the small and unequal sample sizes, means for each variable were computed for each shark to avoid pooling data. Mann–Whitney ($P<0.05$) tests were used to compare ingestion bites with and without EMG leads implanted, and hydraulic transport events with and without leads implanted. Since there was no significant difference in kinematics for either bite type, all subsequent analyses combined data from implanted and non-implanted animals.

Normality and equality of variances were tested on the combined data sets using the Kolmogorov–Smirnov test ($P<0.05$) and the Levene median test ($P<0.05$), respectively. The duration of each of the 14 kinematic events (e.g. mandible depression) was separately analyzed using a one-way ANOVA first for ingestion bites *versus* hydraulic transport (sharks combined) and then by sharks (feeding events combined). Data from numerous individual bites of each shark were used in these calculations (not means from each shark) (see Table 1). When normality or equality of variances could not be achieved by \log_e -transformation, a Kruskal–Wallis one-way ANOVA on ranks was used. If a difference was detected by ANOVA,

a Student–Newman–Keuls multiple-range test by ranks was used to test all pairwise comparisons ($P < 0.05$). To test whether upper jaw protrusion contributes to gape closure, the vertical gape distance remaining after jaw protrusion (maximum gape distance minus maximum protrusion distance) was compared with maximum gape distance using a paired t -test.

Results

Kinematics

In our analysis, we distinguished between three separate feeding events: (1) prey ingestion bites; (2) manipulation bites;

and (3) hydraulic transport of the food through the pharynx (Fig. 3). In a typical ingestion event, the shark captured the food item by ram feeding, that is, by swimming over the food and grasping it in its jaws. In a few cases, suction of the food occurred during ingestion bites (Norton and Brainerd, 1993). In these cases, the food was transported rapidly past the jaws and through the pharynx in one motion with relatively little forward movement of the shark. After capturing the food, the shark used one or more manipulation bites in rapid succession to reduce the size of the food and reposition it for swallowing. When large pieces of food were offered, the shark shook its head vigorously with the food clasped in its jaws, resulting in

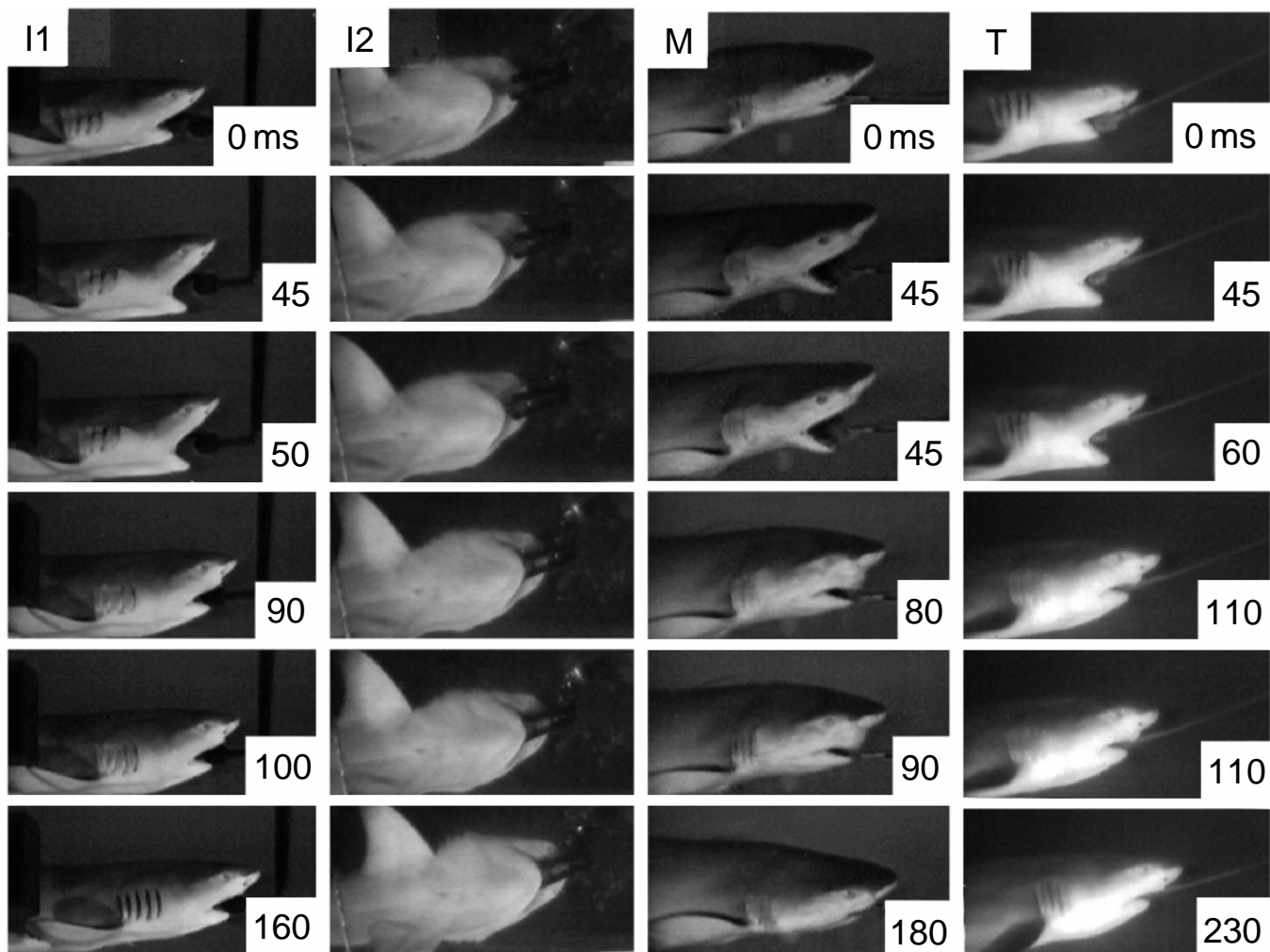


Fig. 3. Video fields of three feeding events for *Negaprion brevirostris*: I1, lateral view and I2, ventral view of food ingestion bite; M, food manipulation bite; T, hydraulic transport of food. The top fields show the start of lower jaw depression ($t=0$ ms); the second field, maximum lower jaw depression; the third field, maximum cranial elevation; the fourth field, maximum palatoquadrate protrusion; the fifth field, the end of cranial depression; and the sixth or bottom field, the end of palatoquadrate protrusion. If two of these events occur during the same frame (M and T) they are both indicated by the same time. The food consists of pieces of fish held with plastic tongs or a rod. In I, the shark ingests the food with ram feeding, swimming over the food and grasping it in its jaws. Manipulation bites, M, consist of one or more bites after food ingestion in which the shark bites the food and often cuts it into two pieces. During hydraulic transport, T, the food is rapidly sucked from between the jaws into the esophagus. In this particular series, the plastic rod holding the food has not been removed from the shark's mouth, although in many of the analyzed sequences the tongs or rod are moved away from its mouth before hydraulic transport. This particular hydraulic transport offered a clear video image, although it was uncharacteristically long in duration. Hydraulic transport events are shorter in duration than ingestion bites (see text). I and T, 76.5 cm TL male; M, 78.1 cm TL female. TL, total length.

the cutting of the food into two or more pieces. In a few cases, there were no manipulation bites and the feeding sequence proceeded directly to transport. This was a rapid hydraulic suction transport of the food from between the teeth to the pharynx and into the esophagus. During this transport event, the shark continued to move forward, but slowly relative to the movement of the food into the pharynx. After this event, there were no further swallowing events evident in either the video recordings or the electromyograms.

Ingestion bites were composed of a series of cranial movements that varied both within and among sharks. Most bites began with the initiation of mandible depression, although the initiation of cranial elevation occasionally constituted the first movement (Fig. 4). Cranial elevation usually began shortly after the beginning of mandible depression, such that the gape was widening as the shark swam over the food, and maximum mandible depression usually occurred just before maximum head elevation. Maximum gape occurred between these two

maxima. Elevation of the mandible was followed closely by depression of the head. Palatoquadrate protrusion began shortly after the beginning of mouth closure in the majority of bites. Maximum palatoquadrate protrusion, which contributed to 26% of the gape distance ($P < 0.0001$), usually occurred at the end of head depression and mandible elevation as the food was pierced by the upper and lower teeth. Maximum depression of the hyobranchial area occurred at the end of the bite as the mouth was closed on the food. The total time for protrusion and retraction of the upper jaw was highly variable, as indicated by the relatively large standard errors in Fig. 4 and Table 3, and, together, both were longer than the entire preceding sequence. Mean palatoquadrate retraction time was approximately three times longer than protrusion. However, palatoquadrate protrusion was entirely lacking in some food ingestion bites, as was cranial elevation. The total duration for food ingestion bites with palatoquadrate protrusion, from the beginning of mandible depression to complete palatoquadrate retraction, ranged from

Fig. 4. Activity of jaw and head muscles and associated kinematics during an ingestion bite in *Negaprion brevirostris*. (A) Composite block diagram of electromyographic activity in the cranial muscles during a food ingestion bite with palatoquadrate protrusion. The mean onset (left edge) and offset (right edge) of the blocks indicate the duration of muscle activity in seconds. Time 0 s marks the onset of the coracoarcualis (CC) muscle activity. A mean for each shark was calculated, and a grand mean was used to calculate the onset and duration for each muscle. Error bars represent the standard error of the grand mean. The bar on the leading edge of each block is one standard error of the onset, the bar on the trailing edge is one standard error for duration of muscle activity. In cases where there were data from a single shark, there is no error bar. When a second burst of activity occurred more than 25% of the time, it is shown with the percentage of occurrence and without error bars. CB, coracobranchialis; CC, coracoarcualis; CH, coracohyoideus; CM, coracomandibularis; EP, epaxialis; LH, levator hyomandibularis; LP, levator palatoquadrati; POD, dorsal preorbitalis; POV, ventral preorbitalis; QD, quadratomandibularis dorsal; QV, quadratomandibularis ventral. (B) Composite block diagram of kinematics during a food ingestion bite with palatoquadrate protrusion. A mean for each shark was calculated, and a grand mean used to calculate the onset and duration for each kinematic event. Error bars represent the standard error of the grand mean. Only a subset of the bites used for the EMG analysis above are used for the kinematic analysis. The heavy vertical bars represent maxima with associated standard error bars. Line drawings below indicate the approximate positions of the head relative to a food item for select kinematic events indicated by fine dotted lines. Cran. mov., cranial movement; Man. mov., mandibular movement; PQ prot., palatoquadrate protrusion; Pk. gp., peak gape; Max. hy., maximum hyobranchial depression.

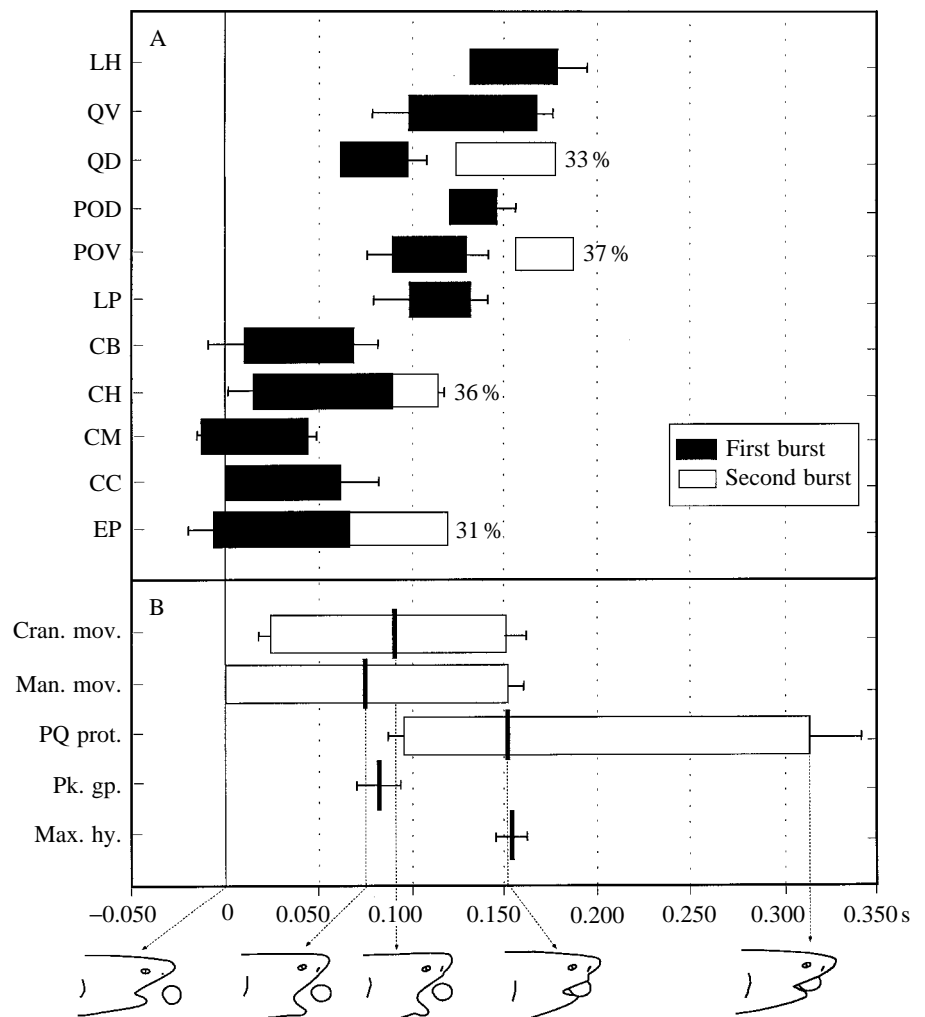


Table 3. Mean durations of cranial movements during food ingestion and hydraulic transport events in *Negaprion brevirostris*

	Ingestion	Hydraulic transport
Cranial elevation (ms)	66±10	48±6
Cranial depression (ms)	62±7	53±3
Mandible depression (ms)	75±8	52±3
Mandible elevation (ms)	77±6	63±4
Palatoquadrate protrusion (ms)	59±10	46±4
Palatoquadrate retraction (ms)	159±31	93±17
Time to peak gape (ms)	81±7	58±3
Time to maximum hyobranchial depression (ms)	155±10	106±8
Total time of feeding event (ms)	309±41	207±20

The values are represented graphically in the lower parts of Figs 4 and 5.

Values are means ± 1 S.E.M.

160 to 730 ms, with an average duration of 309 ms (Table 3). The majority of this variation was attributable to variation in the duration of palatoquadrate protrusion and particularly retraction.

Manipulation bites (Fig. 3) were not quantified owing to lack of video data, but were composed of essentially the same cranial movements as food ingestion bites. Palatoquadrate protrusion was present in most of the bites, even when there were repeated manipulation bites. Hydraulic transport events were also composed of the same cranial movement events as food ingestion bites (Fig. 5). However, maximum hyobranchial depression generally occurred before maximum palatoquadrate protrusion. The total duration of hydraulic transport events ranged from 135 to 350 ms, with an average duration of 207 ms (Table 3). Palatoquadrate protrusion and cranial elevation were absent in a few hydraulic transport events.

Kinematic analyses

When ingestion bites and hydraulic transport event data were pooled, only one kinematic event, the duration of palatoquadrate protrusion, was different among individual sharks. However, the SNK multiple-comparisons test failed to find a significant difference (Table 4). When results for individual shark data were pooled, differences between ingestion bites and hydraulic transport events were found. Ingestion bites had longer durations than hydraulic transport events for the following variables: mandible depression; total

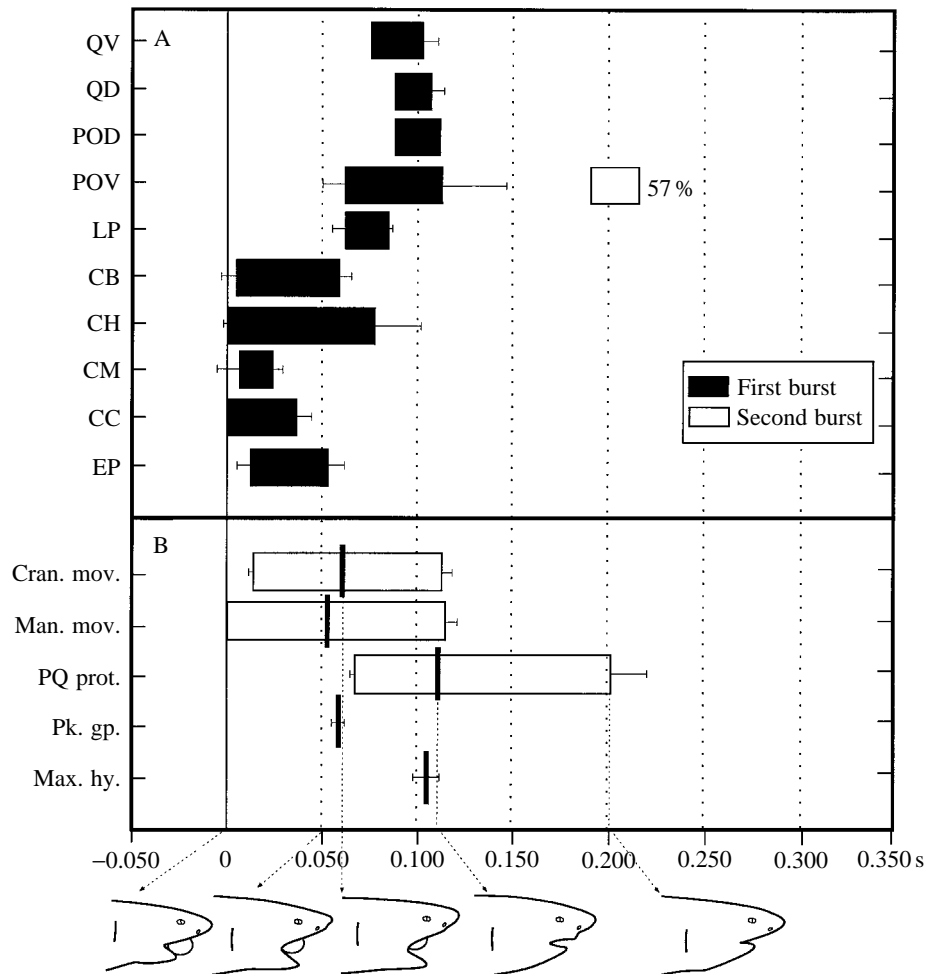


Fig. 5. Activity of jaw and head muscles and associated kinematics during hydraulic transport in *Negaprion brevirostris*. (A) Composite block diagram of electromyographic activity in the cranial muscles during hydraulic transport with palatoquadrate protrusion. (B) Composite block diagram of kinematics during hydraulic transport with palatoquadrate protrusion. See Fig. 4 for details.

Table 4. ANOVA of duration of kinematic events involved with the feeding events of food ingestion (I) and hydraulic transport (T) in *Negaprion brevirostris*

Kinematic event	Feeding events, I, T	Sharks
Mandible depression	*** (18.05, 1) I > T	NS
Mandible elevation	NS	NS
Total time of mandible depression and elevation	***(15.01, 1) I > T	NS
Lag of head elevation from start of mandible depression	NS	NS
Head elevation	** (7.35, 1) I > T	NS
Head depression	NS	NS
Total time of head elevation and depression	** (7.49, 1) I > T	NS
Lag of jaw protrusion from start of mandible depression	** (7.57, 1) I > T	NS
Palatoquadrate protrusion	NS	** (3.83, 6) ¹
Palatoquadrate retraction	NS	NS
Total time of palatoquadrate protrusion and retraction	NS	NS
Start mandible depression to maximum gape	*** (14.8, 1) I > T	NS
Start mandible depression to maximum hyobranchial depression	*** (15.69, 1) I > T	NS
Start mandible depression to end of palatoquadrate protrusion	** (6.98, 1) I > T	NS

¹SNK test indicates no significant difference among all pairwise comparisons; NS, not significant.

** $P < 0.01$; *** $P < 0.001$.

F-statistic and degrees of freedom are given in parentheses.

Tests were performed separately on each kinematic event first for feeding events with sharks pooled, and then for individual sharks with feeding events pooled.

time of mandible depression and elevation; head elevation; total time of head elevation and depression; time lag from the start of jaw protrusion to the start of mandible depression; time

from the start of mandible depression to maximum gape; time from the start of mandible depression to maximum hyobranchial depression; and time from the start of mandible depression to the end of palatoquadrate protrusion (the total time of the bite) (Table 4).

Motor patterns

The muscles of mandible abduction or depression were usually the first muscles activated during food ingestion, processing and hydraulic transport. The coracoarcualis, coracomandibularis and coracohyoideus muscles were active during mandible and hyoid depression. Cranial elevation was concomitant with epaxialis muscle activity (Figs 4–6). In 31 % of the ingestion bites, there was a second burst of activity in the epaxialis muscle, as well as in 36 % of the bites for the coracohyoideus muscle (Fig. 4). For ingestion bites and hydraulic transport events, maximum mandible depression was approximately coincident with the cessation of firing of the mandible depressors, and maximum cranial elevation occurred slightly after the cessation of epaxialis muscle activity (Figs 4, 5). The coracobranchiales muscles usually fired during the activity period of the mandible depressors, presumably abducting the branchial arches. However, maximum hyobranchial depression occurred much later, towards the termination of jaw elevation (Figs 4, 5).

Adduction of the jaws occurred during activity of the quadratomandibularis dorsal and ventral. The initiation of their muscle activity generally began before the cessation of activity of the mandible and hyoid depressors during ingestion and manipulation bites, but after cessation of activity in hydraulic transport events (but see statistics below). In 33 % of the ingestion bites, there was a second burst of activity in the quadratomandibularis dorsal; in 50 % of the manipulation bites, there was a second burst of activity of the quadratomandibularis ventral (Figs 4–6).

Coincident with activity in the quadratomandibularis muscles, the dorsal and ventral preorbitalis and the levator

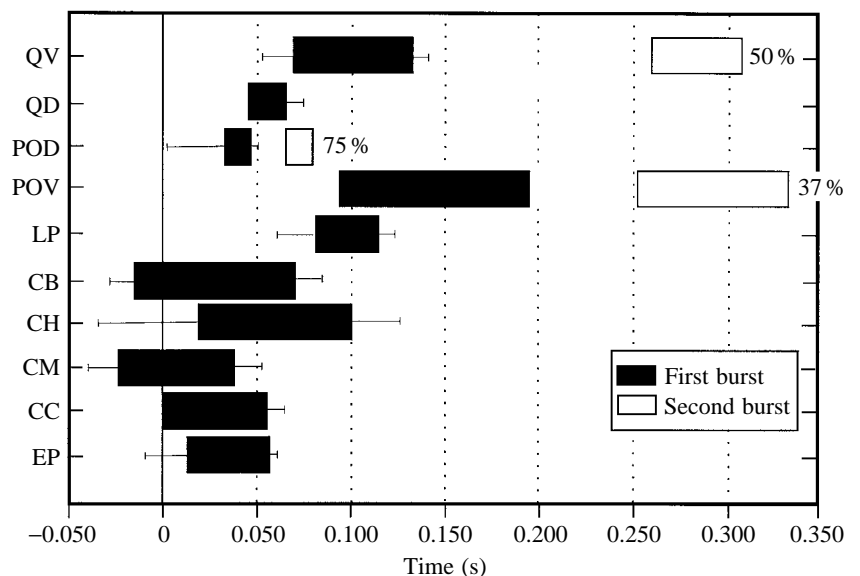


Fig. 6. Composite block diagram of electromyographic activity in the cranial muscles of *Negaprion brevirostris* during a manipulation bite with palatoquadrate protrusion. See Fig. 4 for details.

palatoquadrati muscles fired during palatoquadrate protrusion. Maximum palatoquadrate protrusion occurred at approximately the cessation of activity of the latter three muscles. The ventral preorbitalis muscle had second bursts of activity, some quite lengthy, in 37% of the ingestion bites, 37% of the manipulation bites and 57% of the hydraulic transport events. In manipulation bites, the dorsal preorbitalis had second bursts of activity in 75% of the bites. Finally, the levator hyomandibularis muscle was the last muscle to initiate activity in the food ingestion bites (no data were available for this muscle for the other feeding events) (Figs 4–6).

During both ingestion and manipulation bites, simultaneous video images and electromyographs showed that palatoquadrate protrusion was coincident with activity in the dorsal and ventral preorbitalis and the levator palatoquadrati muscles, with strong activity in the latter two (Figs 7, 8). The ventral preorbitalis muscle showed prolonged activity, either in one or more bursts, compared with the dorsal preorbitalis or levator palatoquadrati muscles (Figs 4–7). Prolonged activity of the ventral preorbitalis was coincident with prolonged protrusion of the upper jaw, thus supporting its control over palatoquadrate protrusion.

Motor pattern analyses

For all feeding events combined, there were differences among sharks for the onset of the coracobranchiales muscles and for the duration of muscle activity of the epaxialis, coracoarcualis, coracohyoideus, coracobranchiales and levator palatoquadrati muscles (Table 5). For all sharks combined, differences among ingestion bites, manipulation bites and

hydraulic transport were confined to the muscles of mandible depression and palatoquadrate protrusion. The duration of activity of the mandible depressors, that is, the coracoarcualis and coracomandibularis, was shortest for hydraulic transport. For the coracoarcualis, hydraulic transport events were shorter in duration than ingestion bites, but not manipulation bites. The duration of activity of the coracomandibularis did not differ for ingestion or manipulation bites, but both of these feeding events were longer in duration than hydraulic transport events.

The duration of muscle activity of the ventral preorbitalis was shorter for ingestion bites and did not differ for manipulation bites or hydraulic transport. The onset of the levator palatoquadrati was shorter for hydraulic transport compared with those of the other two feeding events, which were the same. Similarly, the onset for the ventral preorbitalis was longer for the ingestion bites compared with hydraulic transport, whereas the manipulation bites did not differ from either the ingestion bites or hydraulic transport. The duration of activity in the coracoarcualis muscle, which was different for both feeding events and among sharks, had no interaction among sharks and feeding events. The other muscle of palatoquadrate protrusion, the dorsal preorbitalis, was only comparable for ingestion and manipulation bites because of lack of data for hydraulic transport events (Table 5). The composite block diagrams of electromyographic activity (Figs 4, 5) indicate that the quadratomandibularis dorsal and ventral fired after the cessation of activity in the muscles of jaw depression in hydraulic transport but before the cessation of activity in ingestion bites. However, insufficient data existed to test this (Table 5).

Table 5. ANOVA for the burst duration and onset from the initial firing of the coracoarcualis muscle for eleven cranial muscles controlling three feeding events [food ingestion (I), manipulation (M) and hydraulic transport (T)] in *Negaprion brevirostris*

Muscle	Feeding events, I, M, T	Duration		CC onset	
		Shark	Bite × Shark	Feeding events, I, M, T	Shark
EP	NS	** (3.52, 5)		NS	NS
CC	** (4.59, 2) <u>I M T</u>	** (4.42, 4)	NS		
CM	** (4.78, 2) <u>I M T</u>	NS		NS	NS
CH	NS	*** (19.2, 3)		NS	NS
CB	NS	* (3.25, 3)		NS	** (6.71, 3)
LP	NS	* (4.37, 1)		* (4.15, 2) <u>I M T</u>	NS
POV	** (7.17, 2) <u>M T I</u>	NS		** (5.41, 2) <u>I M T</u>	NS
POD	NS	NS		NS	No data
	(Only types I, M)			(Only types I, M)	
LH	No data	NS		No data	No data
QV	NS	NS		NS	NS
				(Only types I, M)	
QD	NS	NS		No data	No data

NS, not significant.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

F -statistic and degrees of freedom are given in parentheses. Tests were performed separately on each muscle first for feeding events with sharks pooled, and then for individual sharks with feeding events pooled, for both duration and onset data.

Lines below feeding events indicate values that do not differ.

CB, coracobranchialis; CC, coracoarcualis; CH, coracohyoideus; CM, coracomandibularis; EP, epaxialis; LH, levator hyomandibularis; LP, levator palatoquadrati; POD, dorsal preorbitalis; POV, ventral preorbitalis; QD, quadratomandibularis dorsal; QV, quadratomandibularis ventral.

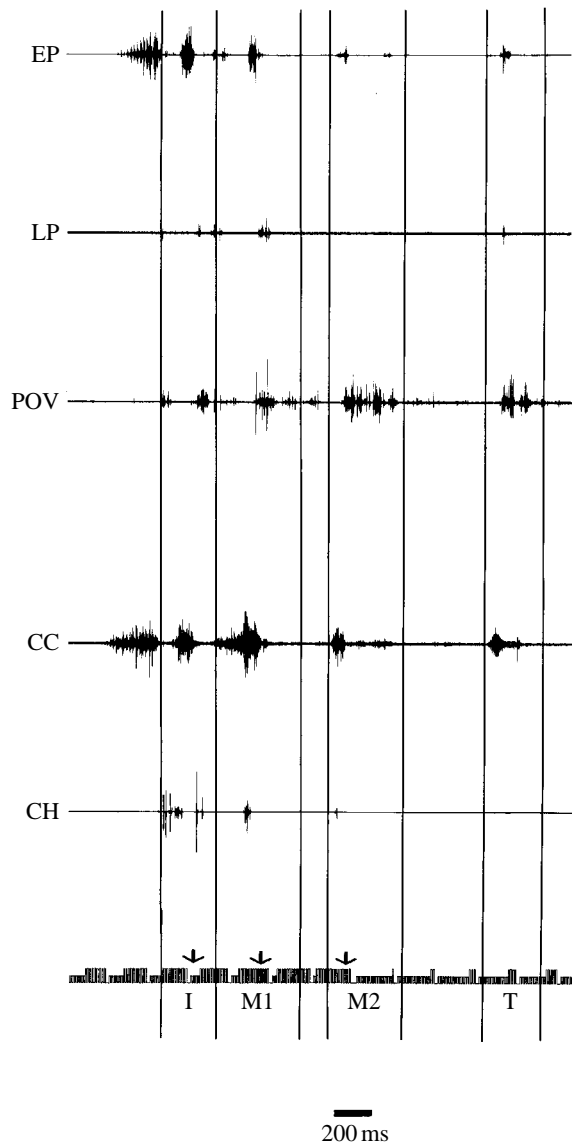


Fig. 7. Electromyograms of five muscles during a food ingestion bite (I), two manipulation bites, (M1, M2) and hydraulic transport of the food (T) in a 78 cm total length female *Negaprion brevirostris* feeding on a piece of fish. Prior to the food ingestion bite (I), the shark opened its mouth and lifted its head slightly, as indicated by activity in CC and EP, respectively. Palatoquadrate protrusion was visible on the video approximately at the points indicated by small black arrows. The lower signal indicates the synchronization pulse for the video camera. CC, coracoarcualis; CH, coracohyoideus; EP, epaxialis; LP, levator palatoquadrate; POV, ventral preorbitalis.

Discussion

Functional conservation of kinematic pattern

Negaprion brevirostris primarily uses ram feeding to ingest food under our experimental conditions. The kinematic pattern of expansive, compressive and recovery phases known for other aquatic anamniotes is conserved during ingestion bites, manipulation bites and hydraulic transport events in this shark. We occasionally observe preparatory phases of ingestion bites during which the mouth is closed prior to the bite. These phases

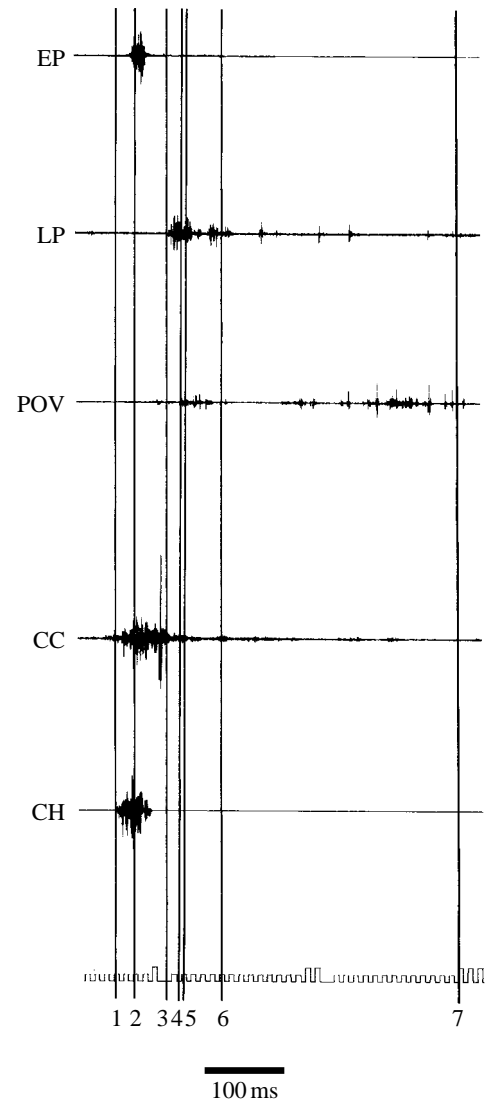


Fig. 8. Electromyograms of five muscles during a food manipulation bite in a 78 cm total length female *Negaprion brevirostris* feeding on a piece of fish. Select kinematic events from the simultaneous video images are marked by vertical lines and numbers along the bottom as follows: 1, start of mandible depression; 2, start of cranial elevation; 3, maximum gape; 4, start of cranial depression; 5, start of palatoquadrate protrusion and simultaneous mandible elevation; 6, mandible elevated and biting food with palatoquadrate still protruded; 7, palatoquadrate still slightly protruded as it ends this manipulation bite and begins another (not shown). The lower signal indicates the synchronization pulse for the video camera. CC, coracoarcualis; CH, coracohyoideus; EP, epaxialis; LP, levator palatoquadrate; POV, ventral preorbitalis.

have also been observed in kinematic and motor pattern analyses of suction prey capture in teleost fishes and aquatic salamanders, and ram feeding in turtles. Many fishes lack a preparatory phase, particularly during hydraulic prey transport (Liem, 1978; Lauder, 1985; Lauder and Shaffer, 1985; Reilly and Lauder, 1990; Lauder and Prendergast, 1992; Lauder and Reilly, 1994; Reilly, 1995). The expansion phase in *N. brevirostris* begins with either mandible depression or cranial

elevation and terminates with maximum gape. The compressive phase generally begins with elevation of the mandible and the head is depressed shortly thereafter. Palatoquadrate protrusion occurs during the compressive phase, although protrusion (and cranial elevation) is lacking in some bites, as was also noted for carcharhinid sharks by Frazzetta and Prange (1987). The compressive phase ends with the jaws closed on the food. The expansive phase is not faster than the compressive or closing phase in *N. brevirostris* or *Squalus acanthias* (C. A. D. Wilga and P. J. Motta, unpublished data). From this, we conclude that there is no fast opening phase characteristic of some bony fishes, aquatic amphibians and some aquatically feeding amniotes (Lauder and Prendergast, 1992; Lauder, 1985; Lauder and Reilly, 1994). The recovery phase involves retraction of the palatoquadrate and the hyoid and branchial apparatus.

It has been proposed that maximum hyoid depression occurs after maximum gape during prey capture by aquatic suction feeders (Reilly and Lauder, 1992). We have demonstrated that maximum hyobranchial depression also occurs after maximum gape during ram bites and hydraulic transports in *N. brevirostris*. Therefore, this appears to be a general property of aquatic feeding in this animal, not just of suction feeding. If recovery of the hyobranchial apparatus occurred before closure of the mouth in either ram or suction feeding, it would produce a reverse water current that would tend to force the prey back out of the mouth.

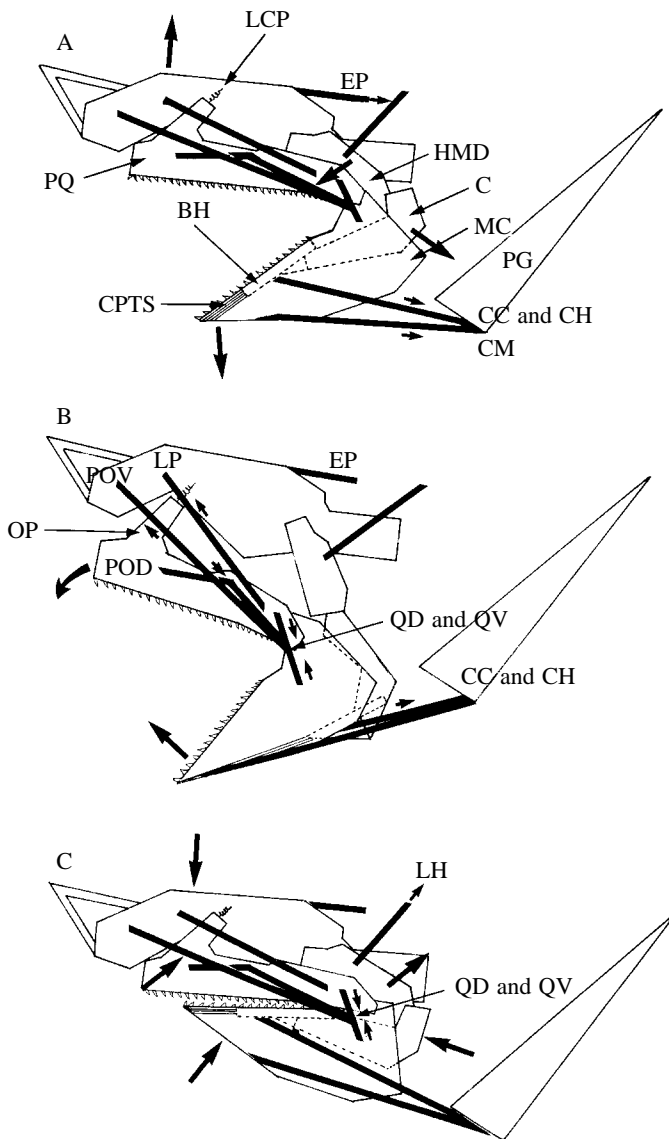
The sequence of expansive, compressive and recovery phases and its variability are similar to those found previously in *N. brevirostris* and in two other carcharhinids, the blacknose (*Carcharhinus acronotus*) and blacktip (*Carcharhinus limbatus*) sharks (Frazzetta and Prange, 1987). The diet of *N. brevirostris* and most other carcharhinid sharks consists primarily of bony fishes (Wetherbee *et al.* 1990; E. Cortés, personal communication). Natural feeding on fish prey by carcharhinid sharks usually involves a brief period of pursuit followed by capture of the prey below the snout. In *N. brevirostris*, the closure of the mouth is coincident with the peak protrusion of the palatoquadrate, which can be sustained for a prolonged period. One result of upper jaw protrusion is the anteroventral movement of the upper jaw and attached teeth, which enhances grasping and retention of the prey in the jaws.

The position of the teeth during the compressive phase of the ingestion bite also facilitates the processing of teleost prey. When offered large pieces of food, *N. brevirostris* often grasps the prey between the lower jaw and the protruded upper jaw. This is usually followed by vigorous shaking of the body and head in a side-to-side motion, such that the upper jaw cuts the food into two or more pieces. Similar head-shaking behavior occurs in numerous other carcharhinid sharks (Springer, 1961; Moss, 1972, 1977; Frazzetta and Prange, 1987; Frazzetta, 1988, 1994). The behavior of slashing the exposed teeth of the protruded upper jaw through the prey, propelled by lateral movements of the head, presents an efficient cutting mechanism that reduces the prey to a consumable size.

In contrast, kinematic analysis of the white shark *Carcharodon carcharias*, feeding on large bait near the surface, shows that this lamnid exhibits a different sequence of upper jaw movements during feeding. Like *N. brevirostris*, the bite action of *C. carcharias* begins with the nearly coincident lifting of the head and depression of the mandible, which together produce the maximum gape. However, unlike *N. brevirostris*, extension of the palatoquadrate in *C. carcharias* is maximal well before full elevation of the lower jaw and depression of the cranium. Furthermore, the palatoquadrate can retract to its subcranial resting position while the snout is lifted, but normally does not remain protruded after the snout is lowered. We suggest that this difference in jaw kinematics reflects the contrasting feeding behavior of these two species of sharks which normally feed on different-sized prey. Unlike juvenile *N. brevirostris*, adult *C. carcharias* commonly use a feeding strategy in which they attack a large pinniped at or near the surface, inflicting a massive, usually singular, wound (Tricas and McCosker, 1984; McCosker, 1985; Klimley *et al.* 1996). The prey is often released after this bite and is usually not consumed further until a subsequent attack. In this case, the early protrusion of the upper jaw relative to the elevation of the lower jaw may maximize the penetration of the upper jaw into the large mammalian prey. In addition, the prolonged elevation of the cranium in *C. carcharias* permits the delivery of a rapid series of multiple bites by sequential protrusions and retractions of the palatoquadrate, a feeding behavior sometimes used for excision of large pieces of flesh from whale carcasses (Pratt *et al.* 1982).

The mean duration of the complete feeding bout (which included ingestion and manipulation bites) in adult *C. carcharias* is 985 ms, with a range of 750–1708 ms (Tricas and McCosker, 1984). In contrast, we measured a mean duration of an ingestion bite in juvenile *N. brevirostris* of 309 ms, ranging from 160 to 730 ms. The longer duration in adult *C. carcharias* may be due to the greater inertia required to move the larger mass of the head and jaws. Alternatively, the data for *N. brevirostris* and *C. carcharias* are consistent with the findings of Richard and Wainwright (1995), who observed a relative slowing of muscle shortening rate with increasing size in largemouth bass *Micropterus salmoides*. The shark gape cycle data are congruent when fitted to the scaling regression for the bass (A. P. Summers, unpublished data).

Ingestion and manipulation bites as well as hydraulic transport events in *N. brevirostris* have similar motor and kinematic patterns. A preparatory phase during ingestion bites is occasionally present and involves activity of the quadratomandibularis muscles as the jaws are closed prior to the expansive phase. The expansive phase is characterized by mandible depression coincident with activity in the coracoarcualis, coracomandibularis and coracohyoideus muscles, hyobranchial depression during activity of the coracohyoideus and coracobranchiales, and head elevation during firing of the epaxialis muscle (Fig. 9A). During the expansive phase, the distal end of the hyomandibula pivots anteroventrally, while the distal end of the ceratohyal pivots



posteroventrally owing to its ligamentous attachments (Motta and Wilga, 1995). The compressive phase is characterized by elevation of the mandible and depression of the head, coinciding with contraction of the quadratomandibularis dorsal and ventral, although the stored elastic energy from the bending of the anterior part of the axial skeleton and stretching of the ligaments, skin and other tissues probably also contributes (Fig. 9B). Palatoquadrate protrusion occurs during the compressive phase.

Maximum depression of the hyobranchial apparatus occurs at the termination of the compressive phase when the mouth has closed on the food. This is after the cessation of the first and second bursts of activity in the mandibular and hyoid abductors. Computer axial tomography (CAT scans) of dead, manipulated sharks indicates that this ventral bulge is due to the movement of the basihyal from its anterior position just posterior to the mandibular symphysis to a more posteroventral position (Motta and Wilga, 1995). Undoubtedly, the branchial arches contribute to the depression of the pharyngeal floor, but

Fig. 9. A model of chondrocranial, mandibular and hyoid arch kinetics during feeding in *Negaprion brevirostris* based on dissection, computer axial tomography, electromyography and video analysis. (A) Expansive phase, characterized by depression of the mandible and elevation of the cranium; (B) compressive phase, characterized by elevation of the mandible, cranial depression and palatoquadrate protrusion; (C) recovery phase, characterized by hyomandibular and palatoquadrate retraction. Only the major components of the chondrocranium, mandibular and hyoid arch are represented; the branchial arches are not included. Thick dark lines indicate muscles, large arrows indicate the movement of specific elements, and small arrows indicate the direction of muscle contraction. See Discussion for a description of the specific phases, contractile events and kinesis of the cranial elements. BH, basihyal; C, ceratohyal; CC, coracoarcualis; CH, coracohyoideus; CM, coracomandibularis; CPTS, chondrocranial–palatoquadrate connective tissue sheath (oral mucous membrane); EP, epaxialis; HMD, hyomandibula; LCP, ethmopalatine ligament; LH, levator hyomandibularis; LP, levator palatoquadrate; MC, Meckel's cartilage; OP, orbital process; PG, pectoral girdle; POD, dorsal preorbitalis; POV, ventral preorbitalis; PQ, palatoquadrate; QD, quadratomandibularis dorsal; QV, quadratomandibularis ventral.

our methods in the present study did not allow visualization of their movement. The hyoid arch and the branchial apparatus remain in the abducted state until the onset of activity of the levator hyomandibuli in the recovery phase.

The recovery phase, therefore, is characterized by the retraction of the hyomandibula into its resting position concomitant with activity in the levator hyomandibuli, and the retraction of the palatoquadrate cartilage by the elastic ethmopalatine ligament (Motta and Wilga, 1995) (Fig. 9C). We did not investigate the role of other branchial muscles, such as the adductor arcuum branchialium and the arcualis dorsalis, in this or other phases (Vetter, 1874; Marion, 1905; Shirai, 1992).

As in our previous study on the biting mechanism of *N. brevirostris* (Motta *et al.* 1991), we recorded reciprocal co-activation of agonist–antagonist muscle pairs, such as the mandible adductor (quadratomandibularis dorsal) and the mandible depressors (coracoarcualis and coracohyoideus). Overlap of activity in antagonistic muscle complexes during feeding has also been noted in bony fishes and aquatic salamanders (Liem, 1980; Lauder, 1980; Lauder and Shaffer, 1985). During rapid movements (e.g. rapid jaw opening), such antagonistic activity may help to stiffen the joint and regulate the speed and degree of jaw movements, controlling movement around the joint and reducing potential damage to joints and muscle (Motta *et al.* 1991). Rapid multiple bursts of muscle activity often accompany strong sustained kinematic events, such as closure of the jaw on the food or sustained palatoquadrate protrusion (Fig. 8). These muscle activity bursts probably result in sustained contraction of the muscles, since elasmobranch fast glycolytic white muscle fibers produce fused tetani at multiple stimulation frequencies of 5–10 Hz and maximum isometric tensions at approximately 20 Hz (Johnston, 1980, 1981).

Variability in kinematic and motor patterns

We found no differences in the kinematic variables among individual sharks, although our small sample size requires caution. This lack of kinematic variation is interesting in that the durations of muscle activity do vary among sharks. There are differences among the sharks in the duration of firing of the head elevator (epaxialis), jaw depressors (coracoarcualis, coracohyoideus), branchial depressor (coracobranchiales) and at least one muscle effecting palatoquadrate protrusion (levator palatoquadrati). Further support for our hypothesis that relative timing does not vary is found in the activity onset data. The only difference in the muscle activity onset among individual sharks is in that of the coracobranchiales. So, while there are differences among sharks in the durations of the muscle activity bursts, the relative timing of the activity patterns appears to be quite consistent.

When ingestion bites are compared with manipulation bites and hydraulic transports, the muscle activity data are in general agreement with the kinematic analyses (although only ingestion bites and hydraulic transports were compared in the kinematic analysis), considering only 50% of the feeding events were used for both the electromyographic and kinematic analyses. Differences in muscle activity patterns among feeding events are confined to the muscles of mandible depression and palatoquadrate protrusion. Hydraulic transport events have shorter durations of muscle activity for the coracoarcualis and the coracomandibularis than ingestion bites. This corresponds with quicker mandible depression in hydraulic transport. Faster head elevation in hydraulic transports compared with ingestion bites is not reflected in the duration of epaxialis muscle activity. Palatoquadrate protrusion occurs earlier in hydraulic transports than in ingestion bites, since the onset for the levator palatoquadrati and the ventral preorbitalis are shorter for hydraulic transport events; the lack of data for the dorsal preorbitalis prevents its comparison with other muscles. In contrast, the duration of the first burst of the ventral preorbitalis (only first bursts were statistically analyzed) is shortest for the ingestion bites. However, this does not reflect the duration of subsequent bursts of activity of this muscle, which frequently occur during palatoquadrate protrusion. As a consequence, maximum gape and maximum hyobranchial depression occur earlier in hydraulic transport than in ingestion bites and, overall, hydraulic transport events are shorter in duration than ingestion bites. Manipulation bites appear to be somewhat intermediate in muscle activity duration and onset compared with ingestion bites or hydraulic transport events.

In comparing suction capture with suction transport in *Lepomis macrochirus* and *Ambystoma tigrinum*, Gillis and Lauder (1995) found that the time course for prey transport kinematics is often much faster than that of prey capture. They suggest that this difference may be widespread during aquatic feeding by anamniotes. Our findings with *N. brevirostris* provide support for this hypothesis.

Palatoquadrate protrusion

Palatoquadrate protrusion occurs during the compressive

phase of ingestion bites, manipulation bites or hydraulic transport events when the dorsal and ventral preorbitalis and the levator palatoquadrati muscles become active, as suspected by Luther (1909), Haller (1926), Zlabek (1931), Moss (1962, 1972) and Frazzetta (1994). There is no activity in the levator hyomandibularis during protrusion, refuting the hypothesis that it contributes to protrusion by pulling the hyomandibula anteriorly (Moss, 1972).

The dorsal preorbitalis originates on the quadratomandibularis muscle mass and inserts on the palatoquadrate at the base of the orbital process. It presumably acts to pull the palatoquadrate ventrally, such that the orbital process of the palatoquadrate is at least partially withdrawn from the orbital notch of the chondrocranium. This action requires co-activation by the quadratomandibularis muscles from which it originates.

The ventral preorbitalis originates on the nasal region of the chondrocranium and inserts on the quadratomandibularis complex. Together with the levator palatoquadrati, which originates on the orbital region and inserts on the palatoquadrate, the ventral preorbitalis pulls the palatoquadrate in an anterodorsal direction. In the retracted position, the upper jaw resists movement in an anterodorsal direction because the rounded orbital process sits in the orbital notch. Upper jaw protrusion occurs when the dorsal preorbitalis pulls the orbital process partially or totally out of the orbital notch. The ventral preorbitalis and levator palatoquadrati then pull the upper jaw anteriorly so that the orbital process is forced to glide on the anterior wall of the orbital notch, and the resultant force drives the upper jaw anteriorly and ventrally into the protruded position. Motion of the hyomandibula assists upper jaw protrusion by swinging anteroventrally. However, it moves passively because of its tight ligamentous connection to the jaws. Prolonged palatoquadrate protrusion appears to be primarily effected by the repeated contraction of the ventral preorbitalis, which shows multiple bursts of activity during this movement (Fig. 8). The ethmopalatine ligament and the chondrocranial–palatoquadrate connective tissue sheath limit palatoquadrate protrusion (Motta and Wilga, 1995).

Protrusible jaws and the array of tooth types that appear in the euselachian radiation of modern sharks are generally associated with increased ingestion and prey handling diversity (Schaeffer, 1967; Moss, 1977). However, the biological role of jaw protrusion in sharks is not clear (Moss, 1972, 1977; Tricas and McCosker, 1984; Frazzetta, 1994; Wu, 1994). Our study indicates that protrusion of the upper jaw in *N. brevirostris* probably decreases the time necessary for the teeth to impale the prey since protrusion accounts for an average of 26% of the gape distance during jaw closure in the majority of feeding events. During ingestion bites of *N. brevirostris*, anteroventral protrusion of the upper jaw, which can occur independently of cranial depression, begins as the cranium starts its descent and the lower jaw elevates. The food is initially impaled by the teeth when the upper jaw is maximally protruded, the cranium depressed and the mandible elevated. Thereafter, the upper jaw is retracted as the food remains impaled on the teeth. Without

upper jaw protrusion, the mandible would have to be elevated more to seize the food between both jaws.

Many teleost fishes can regulate the degree and velocity of jaw movements as well as modulate the timing and patterns of activity of the jaw muscles in response to different prey (Liem, 1978, 1979, 1980; Motta, 1988). Other work has found many sources of intra- and inter-individual variation in muscle activity patterns during feeding (Lauder, 1981; Wainwright and Lauder, 1986; Sanderson, 1988; Wainwright, 1989). Little is known about the ability of sharks to vary kinematic or muscle activity patterns during prey ingestion or whether prey ingestion is similar to prey manipulation or hydraulic transport. Earlier studies assumed that feeding behavior (implying prey ingestion) in any shark was composed of a series of stereotyped movements (Gilbert, 1970; Tricas, 1985). This study is significant because it is the first electromyographic and high-speed video analysis of the feeding mechanism of any chondrichthyan under semi-natural feeding conditions. Our hypothesis that the kinematic pattern of preparatory, expansive, compressive and recovery phases common to other aquatic feeding teleosts, salamanders and turtles is conserved in the carcharhinid shark *N. brevirostris* was largely supported, although a preparatory phase was often absent. Our second hypothesis proposing inter-individual variability of kinematic and motor patterns in the feeding events, where muscle activity and kinematic events vary only in duration but not in relative timing, was partly supported. Among individual sharks, there was variation in duration but little variation in the relative onset of muscle activity, resulting in no detectable kinematic variation. Our third hypothesis, that ingestion, manipulation and hydraulic transport all have a common series of kinematic and motor events but are distinguishable by their duration and relative timing, both kinematically and electromyographically, was supported. Finally, upper jaw protrusion is coincident with activity of the preorbitalis dorsal and ventral and the levator palatoquadrati, and not with activity of the levator hyomandibuli and quadratomandibularis. Further studies of elasmobranch feeding mechanisms should address the generality of these findings among the diversity of elasmobranch fishes and address the issue of behavioral and physiological modulation when feeding on different types of natural prey.

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