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An Electromyographic Analysis of the Biting Mechanism of the Lemon Shark, *Negaprion brevirostris:* Functional and Evolutionary Implications

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ABSTRACT The kinetics of the head and function of select jaw muscles were studied during biting behavior in the lemon shark, *Negaprion brevirostris.* High speed cinematography and electromyography of seven cranial muscles were recorded during bites elicited by a probe to the oral cavity. In weak bites mandible depression was followed by mandible elevation and jaw closure without cranial elevation. In strong bites cranial elevation always preceded lower jaw depression, lower jaw elevation, and cranial depression. The average duration of the strong bites was rapid (176 msec), considering the size of the animal relative to other fishes. Different electromyographic patterns distinguished the two forms of bite, primarily in activity of the epaxial muscles, which effect cranial elevation. A composite reconstruction of the activity of seven cranial muscles during biting revealed that epaxial muscle activity and consequently cranial elevation preceded all other muscle activity. Mandible depression was primarily effected by contraction of the common coracoarcual and coracomandibularis, with assistance by the coracohyoideus. Simultaneous activity of the levator hyomandibulae is believed to increase the width of the orobranchial chamber. The adductor mandibulae dorsal was the primary jaw adductor assisted by the adductor mandibulae ventral. This biomechanically conservative mechanism for jaw opening in aquatic vertebrates is conserved, with the exception of the coracomandibularis, which is homologous to prehyoid muscles of salamanders.

Aquatic vertebrates, particularly fishes, incorporate some of the most diverse and versatile feeding morphologies and behaviors within the Vertebrata. Studies on their feeding apparatus have attempted to describe the mechanisms and versatility of feeding in these vertebrates to gain a better understanding of their functional morphology and the evolution of the vertebrate feeding mechanism. Consequently, functional studies on the feeding structures of bony fishes have centered on the mechanics of prey capture, prey processing, and feeding performance (Osse, '69; Anker, '74; Dutta, '79; Liem, '80; Barel, '83; Lauder, '83a; Wainwright, '87; Motta, '88; Sanderson, '88; Kotrschal, '89; Sanford and Lauder, '89). To better understand the evolution of feeding mechanisms, phylogenetic interpretations of bony fish feeding structures have been forwarded (Lauder, '80, '82; Schaefer and Lauder, '86; Huey, '87; Kotrschal, '88; Motta, '89) and related to aquatic feeding in salamanders (Lauder and Shaffer, '85, '86; Wainwright et al., '89). However, an understanding of the mechanics and evolution of aquatic feeding suffers from a profound lack of information on elasmobranch feeding (Lauder and Shaffer, '85).

The elasmobranchs incorporate a diverse group of aquatic feeders that have radiated from a grasping ancestor to include cutting, suction-crushing, gouging, crushing, and filter feeding forms (Moss, '77). Many studies provide valuable data on the anatomy of the head and jaws of sharks (Gegenbauer, 1865; Allis, '23; Daniel, '34; Harris, '38; Holmgren, '40, '41; Gohar and Mazhar, '64; Nobiling, '77; Compagno, '88), and include descriptive studies of the feeding structures (Vetter, 1874; Allis, '14; Holmgren, '40, '41, '43; Lightoller, '39) (see Moss, '77 for a review).

There have been few synthetic studies on shark feeding mechanisms. Early studies provided valuable observational data (Springer, '61; Gilbert, '62; Budker, '71; Tricas, '79) and later studies have centered on their functional anatomy based on manipulative or photographic studies (Moss, '72, '77; Tanaka, '73; Tricas and McCosker, '84; Tricas, '85; Frazzetta and Prange, '87; Frazzetta, '88; Wu, '88). Despite all the anatomical and descriptive studies on shark feeding, there are no studies incorporating motion analysis and electromyography of any elasmobranch biting or feeding. The paucity of knowledge on the group may stem from (a) the typological comparison with other vertebrates, in which they are considered "primitive," when in fact the elasmobranchs have evolved a diversity of feeding mechanisms which is probably unparalleled by other groups containing so few extant species (Moss, '77), and (b) the inherent difficulty in maintaining and studying active, predaceous sharks.

The purpose of this study is to investigate the biting mechanism of a representative galeoid shark, the lemon shark *Negaprion brevirostris,* an abundant carcharhinid distributed in the Western Atlantic coastal waters from New Jersey to Brazil (Compagno, '84). The galeoid sharks are the dominant predaceous sharks of modern seas, comprising 73% of living sharks, including the lamnoids, carcharhinoids, orectoloboids, and heterodontoids (Compagno, '77, '88; Carroll, '88). This study investigates the muscle activity patterns associated with biting in the lemon shark and compares the mechanics and evolution of the jaw opening mechanism in this shark with those of other aquatic vertebrates.

MATERIALS AND METHODS

Electromyography

Two juvenile male lemon sharks *N. brevirostris* (79 and 85 cm TL) were collected in the Florida Keys and held in a large seminatural outdoor pond at Mote Marine Laboratory, Sarasota, Florida. Sharks were first anesthetized by immersion in a bath of tricaine methanesulfonate (MS 222, 1g/l) and maintained under running seawater containing the anesthetic (0.1g/l) for the duration of the surgery.

Bipolar EMG electrodes were constructed from pairs of multi-strand teflon-coated stainless steel wire (0.0045 in. dia.) with 2 mm exposed tips and separated by a 2 mm gap. Electrode pairs were threaded through a 27G hypodermic needle and implanted in the anesthetized animal through a 5 mm incision in the skin (Loeb and Gans, '86). The electrodes were inserted into seven muscles on the head at a 45° angle so that electrode wires were positioned parallel to the muscle fiber tracts (the optimal orientation for each muscle was determined from previous dissections on preserved material). The incision was then closed with cyanoacrylate cement and 2 cm of the wire bonded to the skin posterior to the insertion. All pairs of electrode wires from each muscle were then collectively bonded together and attached to a plastic tag on the dorsal fin. Fish were then revived within 5 min with fresh seawater to an alert and active state and placed in the experimental tank.

Each EMG wire pair was differentially amplified (1,000–10,000 ×) and filtered (60 Hz) at a bandpass of 100–3,000 Hz with an A-M Systems, Inc. Model 1700 AC differential amplifier. Signals were monitored with a Tektronix 502 oscilloscope and audio equipment and recorded on either an eight channel A.R. Vetter Co. model 3000A pulse code modulator or a four channel Sony TC 277-4 reel-to-reel tape recorder at speeds of 15⅞ ips. In most experiments a calibration signal was also recorded on one track. Analog data from the reel-to-reel recorder were played at 1⅞ ips speed into a pen (Grass H 25-60) chart recorder at 25 mm/sec and 50 mm/sec, and those from the pulse code modulator onto a thermal (Gould TA 2000) chart recorder at a speed of 100 cm/sec.

Four to seven cranial muscles were simultaneously monitored for each experiment: the adductor mandibulae dorsal head (AMD), adductor mandibulae ventral head (AMV), common coracoarcual (CC) (arcualis communis), coracomandibularis (CM), coracohyoideus (CH), epaxial muscle (EP), levator hyomandibulae (LH). (Moss ('72, '77) has described the dorsal and lateral cranial muscles. A distinct common coracoarcual in *N. brevirostris* comprises five myomeres; the anteriorly attached coracohyoideus comprises three myomeres). The levator palatoquadratii and preorbitalis were not monitored in this study as palatoquadrate protrusion was either absent or only weakly present in the bites. By maintaining one particular electrode in a reference muscle (usually the epaxial), but changing the electrode pairs input into the available recording equipment, it was possible to obtain simultaneous activity of various combinations of up to six separate muscles on one shark. All muscles were implanted unilaterally on the right side or in the centerline in the case of the coracomandibularis. A total of 172 bites from five trials on two sharks were analyzed. The analyzed bites ranged in intensity from weak to strong (see Results).

Experiments to determine muscle activity during a bite were performed in a small aquarium (91 × 25 × 25 cm) supplied with fresh running seawater at 24°C. The small experimental aquarium was necessary to reduce entanglement of the multiple electrode wires by a free-swimming animal. Sharks generally remained motionless as they respired and were easy to manipulate in experiments. Because sharks will not normally feed under these constrained conditions, each subject was induced to bite by gently probing the oral or pharyngeal cavity with an insulated copper wire probe or plastic probe. There was no apparent difference in response between the two stimuli. Probing the mouth usually resulted in bites of mild or moderate intensity (termed weak bites), although avoidance behavior that involved jaw opening also occurred. Avoidance behavior is characterized by mandible depression, and in some cases cranial elevation, but no jaw closure. Avoidance behavior was not included in the photographic or electromyographic analysis. Pharyngeal stimulation through the gill slits evoked the most forceful bites (termed strong bites). Although the difference between a weak and strong bite were obvious to the observer, the gradation between them was not readily quantified due to (a) the fine gradation of head movements between weak and strong bites, and (b) the difficulty and cost of high speed cine photography of 172 bites. Therefore, although some analyses involved data pooled from all bites, representative EMGs of various bite intensities were also illustrated. At the termination of experiments the sharks were euthanized by anesthetic overdose and recording sites were marked by electrolytic deposition of iron from each electrode. Recording sites were verified histologically on preserved tissue after reacting with potassium ferrocyanide (Loeb and Gans, '86). Synchronized EMG and photographic records were not possible with this equipment.

From these data the duration of activity of individual muscles and relative timing of the different muscle activations were recorded. The mean onset of the epaxial muscle was used as the primary onset mark for a bite because of its consistent contraction, its well-defined activity, and because it usually was the first muscle to fire. The mean duration from the onset of EP to onset of CC, CH, CM, and LH was calculated. Because EP activity was not always measured during activity of the following muscles, the mean duration from the onset of CM to AMD, AMV, and LH was similarly calculated.

Photography

High speed cinematography (Kodak Tri-X reversal film, 320 ASA) was conducted on four juvenile male sharks (80–87 cm TL) by means of a Photosonics 1PL 16 mm camera at 150 frames per second with 1,500 watts of light. Calibration of the camera by means of LED timing light indicated actual speed at 146 fps. Sharks were induced to bite similar to the procedure outlined above. The film was subsequently analyzed frame by frame with a LW Athena photoanalyzer. Duration of the bites and relative timing and excursion of the cranial elements were determined from 17 strong bites elicited by pharyngeal stimulation.

In addition, a juvenile male shark (87 cm TL) was anesthetized and 1.5 cm reflective plastic tabs glued to the skin anterior to the eye, posterior to the angle of the jaw, and on the anterior end of the lower jaw. A strong bite was induced as described above and filmed with a NAC V-14B video camera at 60 fps with 2,500 watts of illumination. An Interlink 174 force sensing resistor was placed in the mouth to record contact of the teeth during jaw closure. These data were stored in a PDP 11-73 computer with VICON camera interface, video and analog data capture software, and photogrammetry software (Oxford Metrics Inc.). This permitted temporal analysis of head movements and force during a bite.

RESULTS

Photographic analysis

Analysis of the high speed film reveals that elicited bites range in intensity from weak to strong. Weak bites are characterized by no head elevation or upper jaw protrusion and are most commonly evoked by probing the

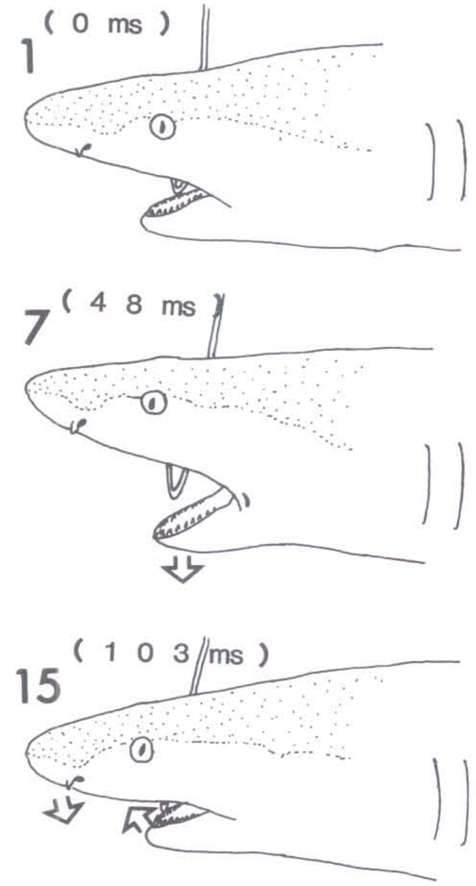

Fig. 1. A weak bite by *N. brevirostris* following tactile stimulation of the oral cavity. Time sequence from stop frame analysis taken at 146 frames/sec. Frame number and duration indicated for three frames. Lower jaw depression (middle) followed by cranial depression and lower jaw elevation (bottom).

oral cavity. In some weak bites the lower jaw or mandible is depressed and then raised against the object, such that there is no change in the longitudinal axis of the head. In the other type of weak bite the mandible is first depressed, then raised as the head is depressed, such that the longitudinal axis of the head is lowered below the resting position (Fig. 1).

Strong bites involve cranial elevation followed by lower jaw depression, lower jaw elevation and cranial depression (Figs. 2, 3). Strong bites are elicited most frequently by stimulation of the pharyngeal cavity through the gills. Mandible depression begins an average 36 msec (± 10 msec SD) after head elevation (Table 1). The average duration from the

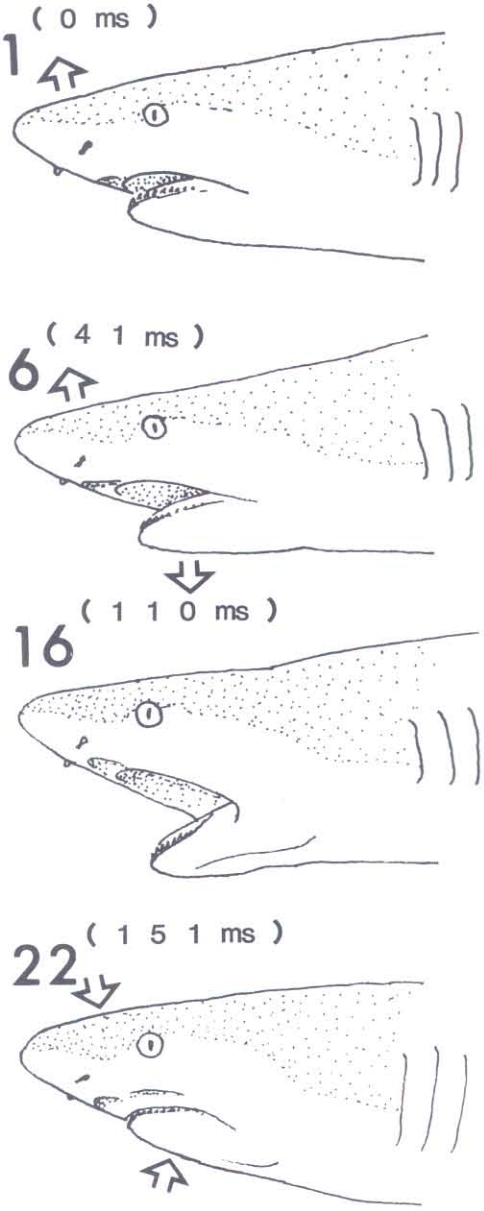

Fig. 2. A strong bite with head elevation by *N. brevirostris* elicited by pharyngeal stimulation. Time sequence from stop frame analysis of film taken at 146 frames/sec. Frame number and duration indicated for four frames. Bite composed of cranial elevation (top), initiation of mandible depression during cranial elevation (second from top), maximum gape (third from top), and termination of bite by lower jaw elevation and head depression (bottom).

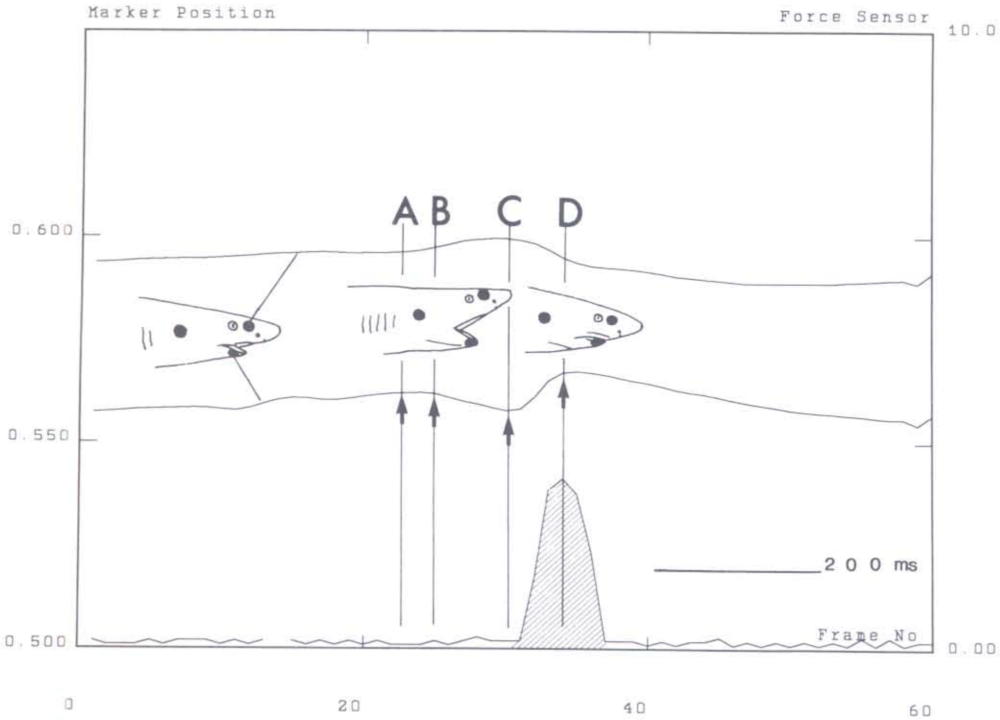

Fig. 3. Concurrent tracing of kinesis of the upper and lower jaws and force of a strong bite by *N. brevirostris*. Upper line indicates relative height of the tab on snout and lower line relative height of tab on lower jaw. Left Y axis indicates height of tabs on shark relative to a focal point below graph. Right Y axis indicates relative force on an uncalibrated scale of 1 to 10. X axis indicates 60 photographic frames, with 200 msec indicated on graph. **A:** Cranial elevation begins on upper line. **B:** Lower jaw depression begins on lower line as cranial elevation continues on upper line. **C:** Peak cranial elevation (upper line) and lower jaw depression (lower line) occur simultaneously. **D:** Jaw closure coincides with peak force as measured by force sensor in the oral cavity.

beginning of lower jaw depression to the beginning of lower jaw elevation is 97 msec (± 36 msec SD). Therefore, the mandible begins elevation 133 msec after the initiation of head elevation. Similarly, the head begins depression an average 134 msec (± 42 msec SD) after initiation of head elevation, and therefore, the upper and lower jaws begin closure approximately simultaneously. Duration of a complete bite (from the beginning of head elevation until closure of the upper and lower jaws) takes an average 176 msec (± 42 msec SD) (Table 1). There is little (Fig. 2) or no protrusion of the upper jaw during the strong bite in these experiments. Maximum force of the bite is concurrent with simultaneous head depression and mandible elevation (Fig. 3).

TABLE 1. Relative duration of head movements during strong bites (N = 17) induced by pharyngeal stimulation in Negaprion brevirostris *(146 frames/second)*

	Start head elevation to start jaw drop	Start jaw drop to start jaw close	Start head elevation to start head drop	Start head elevation to jaw close
Mean (msec)	36	97	134	176
SD (msec)	10	36	42	42

Electromyography

The intensity and duration of activation of the epaxial muscle varies according to the intensity of the bite. Weak bites most commonly do not include cranial elevation, resulting in no epaxial muscle activity (Fig. 4). In some weak bites slight EP activity may be coupled with minimal cranial elevation (Fig. 5). However, there exists a continuum in epaxial muscle activity depending on the degree of head elevation (Fig. 6). Strong epaxial activity and, therefore, vigorous cranial elevation may occur for example, as the shark forcibly raises its head (and simultaneously

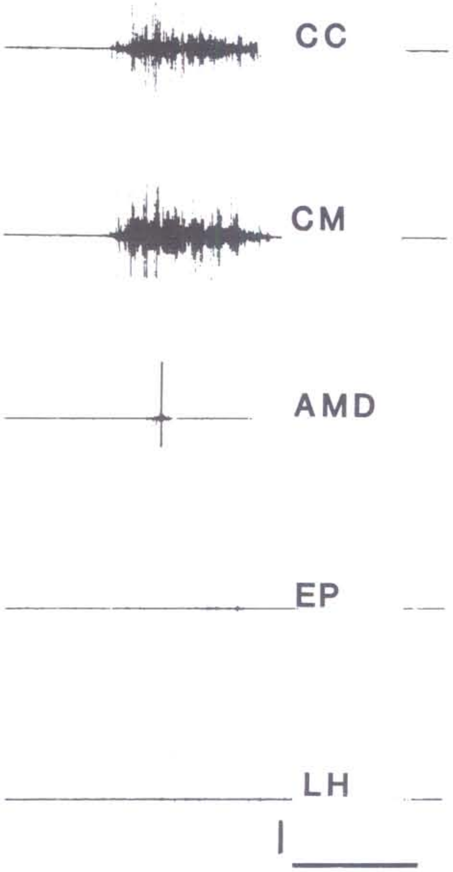

Fig. 4. Electromyograph of a weak bite involving no cranial elevation in *N. brevirostris*. Activity in CC and CM precedes brief activity in AMD. There is no activity in EP or LH. Horizontal bar represents 200 msec, vertical bar 200 μv. Abbreviations: AMD, adductor mandibulae dorsal; CC, common coracoarcual; CM, coracomandibularis; EP, epaxial; LH, levator hyomandibulae.

lowers the mandible) during avoidance behavior (Fig. 6B). During weak bites mandible depression is mediated by contraction of the hypobranchial muscles CC, CM, and CH. Jaw elevation is primarily represented by weak activity in AMD. There is little or no activity in LH (Figs. 4, 5).

Strong bites that include cranial elevation may be characterized by multiple bursts in EP activity during head elevation. Epaxial activity is followed by activity in the hypobranchial muscles, primarily CC and CM as the mandible is depressed. Strong simultaneous activity in AMD and AMV occurs as the jaws are closed. There is abbreviated

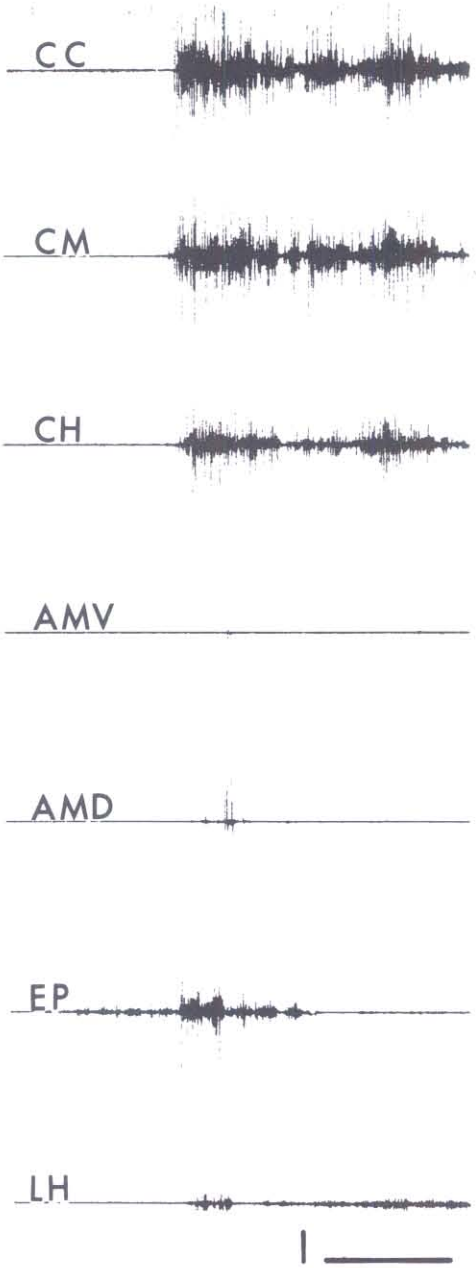

Fig. 5. Electromyograph of a weak bite with slight cranial elevation in *N. brevirostris*. Weak activity in EP precedes strong and simultaneous activity in CC, CM, and CH, followed by brief activity in AMD, but not in AMV. Weak activity in LH occurs. Horizontal bar represents 200 msec, vertical bar 200 μv. Abbreviations: AMD, adductor mandibulae dorsal; AMV, adductor mandibulae ventral; CC, common coracoarcual; CH, coracohyoideus; CM, coracomandibularis; EP, epaxial; LH, levator hyomandibulae.

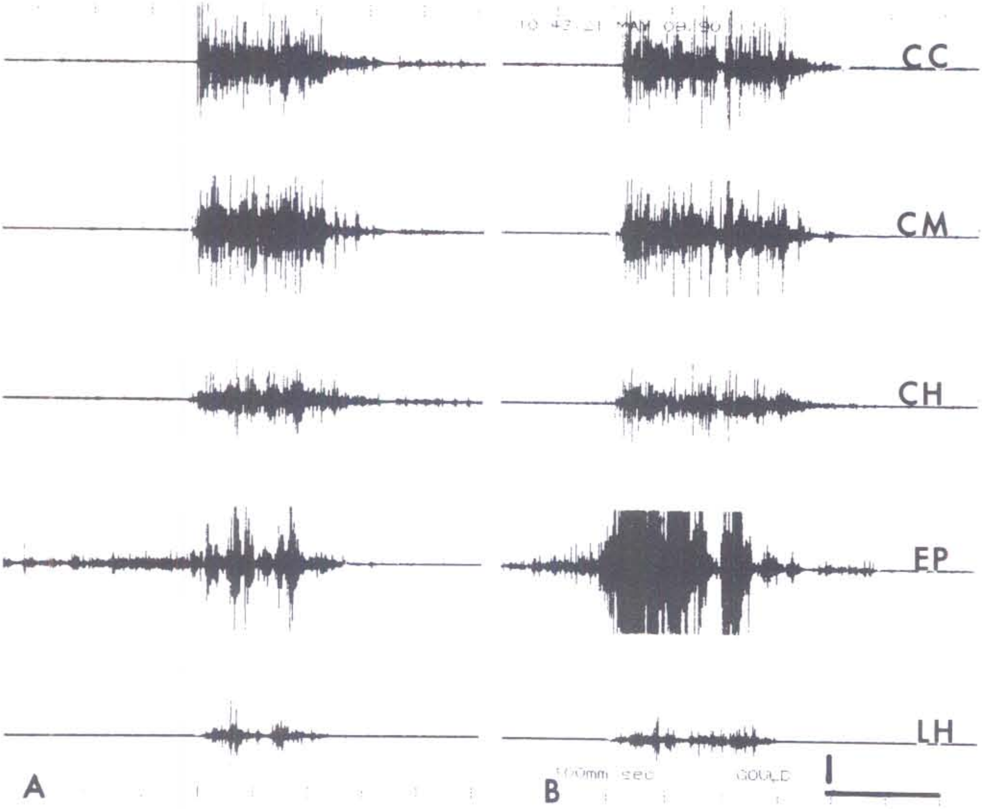

Fig. 6. Electromyograph of muscles involved in head elevation and lower jaw depression in *N. brevirostris.* **A:** moderate activity in EP precedes activity in CC, CM, and CH during a bite. Moderate activity in LH overlaps that of the other muscles. This bite characterized by slight cranial elevation followed by lower jaw depression; **B:** Strong activity in EP precedes activity in CC, CM, and CH, with concurrent activity in LH. Strong cranial elevation preceded lower jaw depression when shark attempted to avoid probe placed in mouth. Horizontal bar represents 200 msec, vertical bar 200 μv. Abbreviations: CC, common coracoarcual; CH, coracohyoideus; CM, coracomandibularis; EP, epaxial; LH, levator hyomandibulae.

activity in CH and LH as the jaws are closed (Fig. 7).

Figure 8 presents a composite diagram of mean duration of activity for 171 EP, 172 CM, 133 CC, 102 CH, 58 AMD, 58 LH, and 22 AMV activity from bites ranging in intensity from weak to strong. Epaxial muscle activity is used as the reference muscle to time onset of most of the other muscles. The variation in duration of epaxial muscle activity is presented (Fig. 9). The mean duration of the first EP burst is 329 msec. In 33% of bites involving epaxial activity, there is an additional second burst of activity that follows an average 112 msec later (Fig. 8). Overlapping and almost simultaneous activity of the CC, CM, and CH occurs between 78 to 120 msec after initiation of epaxial contraction. In nearly all cases only one burst of activity occurs in each of these three muscles (339, 338, 315 msec respectively). In 5% of the bites involving CH activity, there is a second period of activity that overlaps the average duration of the first burst.

A relatively short period of activity (221 msec) of LH begins on average 207 msec after onset of EP activity and overlaps activity of the hypobranchial muscles (CC, CM, CH) (Fig. 8). In all bites in which adductor mandibulae activity was recorded (N = 58 bites), there is at least one brief period (51 msec) of activity of AMD (Figs. 4, 5, 7, 10). Onset of activity of the first burst of AMD is 220 msec after initiation of EP activity. The AMD contracts in up to five bursts, with a large percentage of the second and third bursts occur-

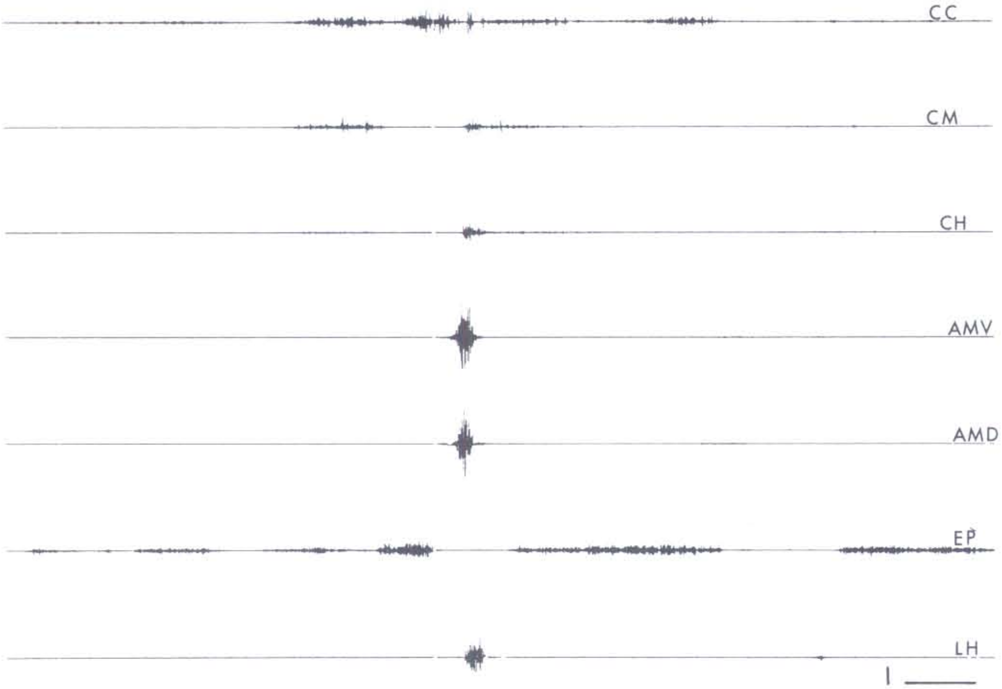

Fig. 7. Electromyograph of a strong bite with cranial elevation and jaw depression in *N. brevirostris*. Prolonged activity of EP precedes that of CC and CM, with only brief activity of CH. Strong activity of AMD and AMV slightly precede activity of LH. Horizontal bar represents 200 msec, vertical bar 200 μv. Abbreviations: AMD, adductor mandibulae dorsal; AMV, adductor mandibulae ventral; CC, common coracoarcual; CH, coracohyoideus; CM, coracomandibularis; EP, epaxial; LH, levator hyomandibulae.

ring after activity of EP and hypobranchial muscles (Figs. 8, 10). The AMV division contracts in only 39% of cases in which any adductor mandibulae activity is recorded. Multiple bursts occur in a few cases (Figs. 8, 10). Activity of AMV follows the first burst of AMD, but slightly precedes activity of the repeated bursts of the AMD.

DISCUSSION AND CONCLUSIONS

Kinetics of the biting mechanism

The observational and electromyographic sequence recorded here for biting in the lemon shark, *N. brevirostris,* is in general agreement with the high speed cinematographic studies of Tricas and McCosker ('84) and Frazzetta and Prange ('87). The latter authors recorded cranial elevation 50 msec prior to and during mandible depression during the majority of *N. brevirostris* bites on dead prey. Our study reveals that weak bites include no cranial elevation, while in strong bites it is pronounced. In strong bites cranial elevation precedes lower jaw depression by an average of 36 msec. The white shark *Carcharodon carcharias* initiates snout lift simultaneously with lower jaw depression in 36 feeding bouts (Tricas and McCosker, '84). Cranial elevation appears to function in keeping the biting axis in the same line of the body (Frazzetta and Prange, '87). Head elevation and lower jaw depression during feeding also occurs in primitive (Lauder, '80) and advanced (Liem, '80) actinopterygian fishes and serves to open the mouth.

Clearly, less forceful bites on smaller objects, such as demonstrated here, may not involve cranial elevation as reported in other studies (Tricas, '79, '85; Tricas and McCosker, '84). In some weak bites the head is lowered below the longitudinal axis of the shark. Maintaining the axis of the body and attaining maximum gape may not be as important for stationary bites on smaller objects. The use of such bites needs to be verified with further studies on prey handling.

Our study reveals lower jaw elevation begins approximately simultaneously with initi-

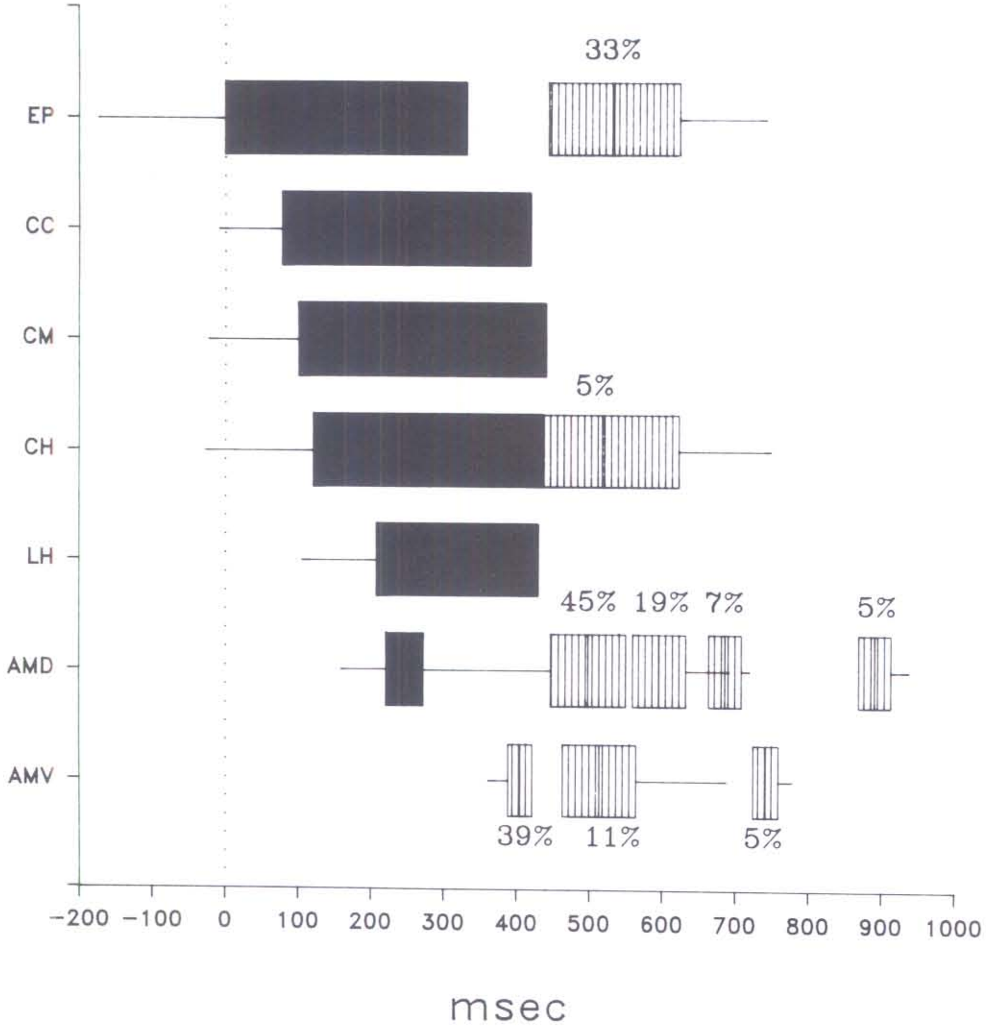

Fig. 8. Composite block diagram of muscle activity during a representative bite involving cranial elevation, lower jaw depression, and mouth closure in *N. brevirostris.* Data from 172 bites of varying intensity in five trials are included. The mean onset (left edge) and offset (right edge) of the blocks indicates the duration of muscle activity. The horizontal lines indicate one standard deviation of that mean. Dark blocks indicate activity in that particular muscle during all bites recorded, hatched blocks indicate the percentage of times that particular muscle was active (e.g., in 33% of bites involving EP activity there is an additional second burst of activity; AMV contracts in only 39% of cases in which any adductor mandibulae activity is recorded (AMD and AMV); in 11% of these cases there is a second burst of activity; and in 5% there is a third burst of activity). Multiple activity in some muscles indicated by multiple blocks. Dotted vertical line indicates mean onset of epaxial muscle. EP activity precedes activity of CC, CM, and CH. LH activity follows that of the hypobranchial muscles CC, CM, and CH. Brief activity in AMD coincides with LH activity, with up to five bursts occurring in some bites. AMV is only active in 39% of the bites in which it was recorded, with up to three bursts of activity occurring. Abbreviations: AMD, adductor mandibulae dorsal; AMV, adductor mandibulae ventral; CC, common coracoarcual; CH, coracohyoideus; CM, coracomandibularis; EP, epaxial; LH, levator hyomandibulae.

ation of head depression (134 msec). Frazzetta and Prange ('87) similarly found that head lowering and lower jaw elevation are strongly related within a brief time period. Head depression begins approximately equally before and simultaneously with mouth elevation in *N. brevirostris*. Lower jaw elevation precedes snout drop (head depression) in the white shark feeding at the surface (Tricas and McCosker, '84).

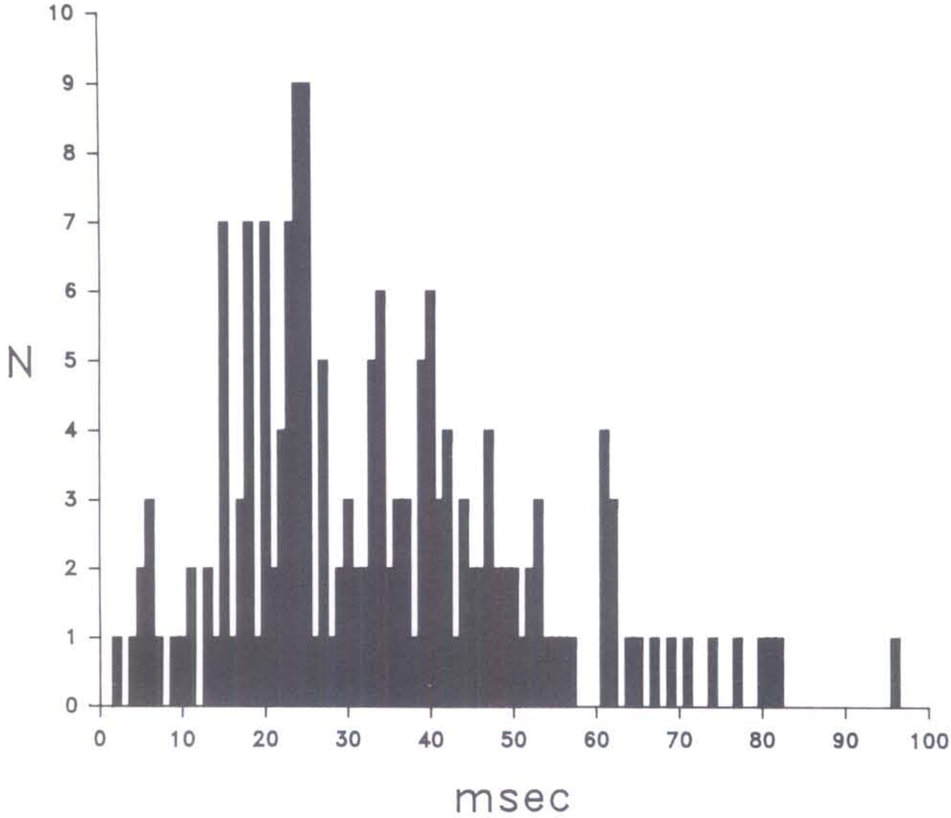

Fig. 9. Histogram to illustrate the variability in burst duration in the epaxial muscle in two individuals of *N. brevirostris* for 172 bites. This muscle was usually the first to contract in a bite sequence, and thus it is utilized as a reference muscle for the timing of most of the other muscles.

Pronounced protrusion of the upper jaw is not observed in this study, presumably because the bites are of either very low intensity or because these bites are elicited by artificial means and not by feeding. Slight palatoquadrate protrusion is apparent in some of the strong bites (Fig. 2, Frame 22). Frazzetta and Prange ('87) observed it not to occur in three out of ten bites on prey, and to occur in the other seven bites by the lemon shark.

Total duration of a bite involving cranial elevation averages 176 msec, which is considerably faster than that of the larger white shark ($\bar{x}$ = 985 msec, Tricas and McCosker, '84), most likely due to the smaller mass and rotational moments of juvenile lemon sharks, and perhaps due to the fact that biting on inanimate objects and not feeding was elicited in our sharks. However, our results are similar to that of three species of carcharhinid sharks, the lemon shark, blacknose (*Carcharhinus acronotus*), and blacktip shark (*Carcharhinus limbatus*), which were found to have an average bite duration of 120 msec when feeding on pieces of fish (Frazzetta and Prange, '87). Compared with other aquatic feeding fishes, however, lemon shark bites are relatively rapid: large largemouth bass (*Micropterus salmoides*) approximately 110 msec (Nyberg, '71); non-piscivorous cichlids, 400 msec; the perch (*Perca flavescens*) 230 msec (Osse, '69; Liem and Osse, '75); the piscivorous cichlid *Haplochromis compressiceps* feeding on elusive prey with an expansive and compressive phase of 75 msec (Liem, '78). However, the lemon shark is considerably slower than predators on highly elusive, small prey, such as the gar *Lepisosteus* (20 msec, Lauder, '80), the longnose butterflyfish *Forcipiger longirostris* (40 msec, Motta, '88), or the ultrafast gape and suck

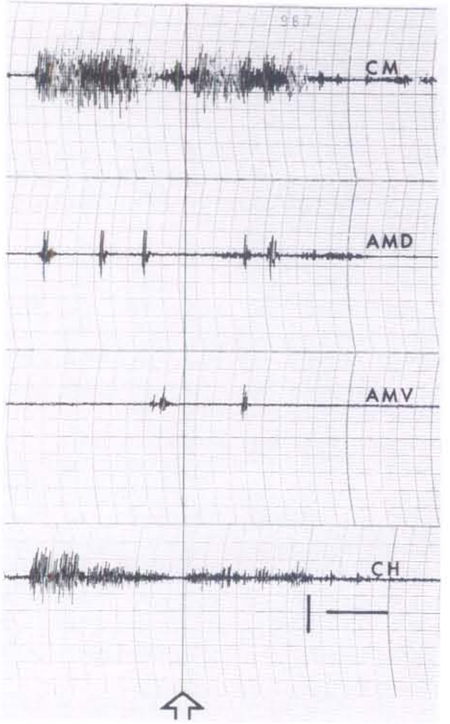

Fig. 10. Electromyograph of two bites in rapid succession in *N. brevirostris.* Arrow and vertical line indicate onset of second bite. Activity of CM and CH precede brief activity of the AMV and repetitive bursts of AMD. Horizontal bar represents 200 msec, vertical bar 200 μv. Abbreviations: AMD, adductor mandibulae dorsal; AMV, adductor mandibulae ventral; CH, coracohyoideus; CM, coracomandibularis.

feeder *Antennarius hispidus,* which attains *maximum gape* in 4 msec (Grobecker and Pietsch, '79).

The composite electromyographic sequence of a bite is of greater duration (900 msec) than the average duration of a bite (176 msec) as recorded photographically, and individual kinetic events, such as cranial elevation, which take an average of 134 msec, are characterized by an average muscle activity pattern of over 300 msec. In the lemon shark this is most apparent in muscles that control abduction of the head and jaws (EP, CC, CM, CH). Lauder ('80, Fig. 10) recorded peak gape in *Lepisosteus oculatus* to occur within approximately 10–15 msec of initiation of a bite with epaxial muscle activity occurring for over 50 msec. Prolonged muscle activity patterns may be a function of overcoming the inertia in moving cranial elements and overcoming the series of elastic components in muscle and connective tissue. Furthermore, information used to characterize the duration of muscle activity (e.g., Fig. 8) does not only reflect peaks of muscle activity (e.g., Fig. 6), which more accurately reflect kinetic events. Rather, the composite figure incorporates low to high amplitude EMG signals. Unfortunately, synchronization of kinetic events recorded on film with EMG discharge patterns was not possible in this study.

In this and other studies synchronous activity of antagonistic jaw muscles occurs. During weak bites the AMD, a jaw adductor, fires briefly and partially overlaps high amplitude activity of the jaw abductors CC, CM, and CH. During strong bites activity of the jaw adductors AMV and AMD is of greater duration and also overlaps relatively weaker activity of the jaw abductors CC, CM, and CH. Liem ('78) also found this in high velocity ambush hunting cichlids. He found it paradoxical that the greater the overlap of firing sequence of jaw opening and closing muscles, the greater the velocity of jaw movements. Coactivation of agonist-antagonist muscle pairs may occur instead of reciprocal inhibition. This centrally or peripherally mediated reciprocal coactivation results in high stiffness (force/length) and low torque of the joint, and is poorly understood (Basmaijian and DeLuca, '85). Such antagonistic activity during ballistic movements of jaw opening and closing may help to regulate the speed and degree of jaw movements, reducing potential damage to joints and muscles. The larger mass of the adductor mandibulae compared with that of the combined jaw abductors (CC, CM, CH) results in jaw closure despite coactivation of agonist-antagonist muscle groups.

Cranial elevation in the lemon shark is effected by contraction of the epaxial muscle, followed by mandible depression by CC, CM, and CH. In 33% of the bites a second burst of the cranial elevator occurs briefly after the first burst, probably serving to maintain the head in the elevated position (see below). The common coracoarcual and coracomandibularis are the primary depressors of the mandible with the coracohyoideus playing a secondary depressor function, particularly in strong bites. On average, the most posterior muscle (CC) contracts first, although they generally contract simultaneously as a group, for approximately the same duration. These muscles are also active during mouth opening associated with active respiration in the dogfish *Scyliorhinus canicula* (Hughes and Ballintijn, '65). Hughes and Ballintijn similarly induced the dogfish to bite on a stick and found that the levator hyomandibulae is also active during the expansive phase prior to a bite. We found it to be active approximately 100 msec after initiation of the jaw depressors, terminating simultaneously with them. This muscle is believed by Moss ('72) to increase the width of the orobranchial chamber during feeding and to assist in upper jaw protrusion. However, during respiration in the dogfish it is clearly concerned with reduction of the oro-branchial cavity (Hughes and Ballintijn, '65). The confirmed function of this muscle still eludes us.

Lower jaw elevation and head depression are found to occur simultaneously or within 50 msec in three species of carcharhinid sharks, including the lemon shark (Frazzetta and Prange, '87). Dropping of the snout begins at the end of the lower jaw elevation in the white shark (Tricas and McCosker, '84). Our study shows that during more forceful bites involving cranial elevation, mandible elevation and head depression occur approximately simultaneously. Jaw closure during weak bites is effected by contraction of AMD primarily, but also by AMV. In all bites recorded, AMV is only active in 39% of the bites. Hughes and Ballintijn ('65) found a clear functional division in activity of different regions (including depths) of the adductor mandibulae in the dogfish.

Strong bites with cranial elevation are characterized by simultaneous and strong activity in both AMD and AMV. This is confirmed by independent stimulation of both divisions by means of the implanted electrodes, which results in lower jaw elevation. Rapid multiple bursts in AMD and AMV that occur in some cases (Fig. 8) most likely result in sustained contraction of those muscles. Upon multiple stimulation frequencies of 5 to 8 Hz, elasmobranch fast glycolytic (FG) white fibers produce fused tetani, and maximum isometric tensions at 10 to 20 Hz (Johnston, '80). Twitch-tetanus ratios of about 0.5 occur at 5 Hz and 10 Hz for dogfish red (S) and white fibers, respectively (Johnston, '81). Pink, or fast oxidative glycolytic (FOG), fibers (Johnston, '83) in elasmobranchs are innervated similar to white fast glycolytic (FG) fibers (Bone, '66). Therefore, multiple stimulation frequencies, such as that of AMD and AMV, most likely result in sustained muscle contraction and jaw closure.

Cranial depression or head drop (Tricas and McCosker, '84) constitutes an important part of the bite, but its mechanical basis is unknown. Depression of the cranium could come from: (a) gravity and/or stored elastic energy in the stretched muscles, ligaments, and tendons; or (b) contraction of the mandibular levators (AMD and AMV) (Moss, personal communication).

It is clear from the works of Tricas and McCosker ('84) and Frazzetta and Prange ('87) and from this study that the entire biting sequence in sharks such as the lemon and white shark is capable of significant modulation. Various muscles can have one or repeated bursts of activity, there is variation in the duration and timing of bursts, and certain cephalic movements, such as cranial elevation, jaw depression, and upper jaw protrusion, can vary. This study did not investigate variance in muscle activity patterns both within and between individuals, as has been found for certain teleost fishes (Shaffer and Lauder, '85; Wainwright and Lauder, '86). This remains an important area of investigation in sharks.

This study does not clarify the muscle activity patterns necessary for upper jaw protrusion nor upper jaw retraction. Luther ('09), Haller ('26), Zlabek ('31), and Moss ('62, '72) believe that the preorbitalis is involved in palatoquadrate protrusion, particularly the dorsal head (Moss, '72). Other muscles involved may be the anterior slips of the dorsal adductor mandibulae, the adductor mandibulae ventral, and perhaps the dorsal levators of the palatoquadrate and hyomandibular. The use of these muscles may depend on the contractile state of the lower jaw depressors or on other factors that restrict lower jaw mobility (Moss, '72).

Evolution of mandibular depression in sharks

Both feeding and respiration in fishes place important functional demands on the cranium, one being the existence of an efficient mechanism of mandibular depression. Mandibular depression in the primitive paleoniscoid fishes probably involved elevation of the neurocranium and retraction of the hyoid apparatus (Lauder, '80). The mouth was probably opened primarily through two couplings: the epaxial muscles-neurocranium-upper jaw coupling and the cleithrum-hyoid-mandible coupling (Lauder, '79). Primitive actinopterygian fishes, such as *Polypterus*, *Lepisosteus*, and *Amia*, retain two key features in the mouth opening mechanism: 1) neurocranial elevation during the expansive phase by the epaxial muscles; and 2) mandibular depression mediated by contraction of the sternohyoideus muscle (Lauder, '80). One conservative mechanism for mandible depression common to ray-finned fishes, coelacanths, lungfishes, and urodeles is the pathway involving the hypaxial muscles, rectus cervicis (sternohyoideus), hyoid apparatus, and the mandibulohyoid apparatus. This biomechanical pathway has existed in lower vertebrates for over 400 million years (Lauder and Shaffer, '85). Advanced teleosts developed a third mechanism of jaw opening that involved the levator operculi. This resulted in a great diversity of feeding structures (Lauder, '83b). Since the Osteichthyes and Chondrichthyes presumably share a bony jawed ancestor (Romer, '66; Schaeffer and Williams, '77; Zangerl, '81; Carroll, '88), the question remains as to whether or not the sharks have retained this primitive jaw opening mechanism, and if so, has it hindered their evolutionary feeding diversity.

In part, at least some sharks have retained this primitive jaw opening mechanism. Cranial elevation may occur during feeding in carcharhiniform and lamnoid sharks (Tricas and McCosker, '84; Frazzetta and Prange, '87) and most likely occurs in other sharks as well. This study demonstrates that this is mediated by epaxial muscle activity which generally precedes mandibular depression controlled by CC, CM, and CH. The kinetic mechanism of mandibular depression mediated by sternohyoideus/hypaxial muscle activity is conserved. The posthyoid rectus cervicis (= sternohyoideus) of bony fishes and aquatic salamanders is homologous to the coracohyoideus and common coracoarcual of sharks (Walker, '86, '87) and, therefore, is similarly used for lower jaw depression in all groups examined. However, one of the principal jaw abductors of sharks, the coracomandibularis, is a prehyoid muscle apparently homologous to the genioglossus and geniohyoid of salamanders (Walker, '86, '87), and, therefore, is not analogous. Utilization of this fundamentally conservative biomechanical pathway, coupled with upper jaw protrusion, has resulted in highly efficient feeding mechanisms in sharks, including suction feeding, gouging, cutting, filter feeding, and crushing.

This study provides the first quantitative electromyographic analysis of biting in any shark. Further studies of sharks feeding on natural prey are needed. They should include simultaneous EMG and photographic analysis of the cranial muscles studied here, as well as of other important muscles, in particular, the preorbitalis and levator palatoquadratii. These studies must also include a thorough kinetic analysis of cranial movements during biting and feeding and focus upon the functional flexibility of these feeding mechanisms.

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