

Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks

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Synopsis

Sharks as a group have a long history as highly successful predatory fishes. Although, the number of recent studies on their diet, feeding behavior, feeding mechanism, and mechanics have increased, many areas still require additional investigation. Dietary studies of sharks are generally more abundant than those on feeding activity patterns, and most of the studies are confined to relatively few species, many being carcharhiniform sharks. These studies reveal that sharks are generally asynchronous opportunistic feeders on the most abundant prey item, which are primarily other fishes. Studies of natural feeding behavior are few and many observations of feeding behavior are based on anecdotal reports. To capture their prey sharks either ram, suction, bite, filter, or use a combination of these behaviors. Foraging may be solitary or aggregate, and while cooperative foraging has been hypothesized it has not been conclusively demonstrated. Studies on the anatomy of the feeding mechanism are abundant and thorough, and far exceed the number of functional studies. Many of these studies have investigated the functional role of morphological features such as the protrusible upper jaw, but only recently have we begun to interpret the mechanics of the feeding apparatus and how it affects feeding behavior. Teeth are represented in the fossil record and are readily available in extant sharks. Therefore much is known about their morphology but again functional studies are primarily theoretical and await experimental analysis. Recent mechanistic approaches to the study of prey capture have revealed that kinematic and motor patterns are conserved in many species and that the ability to modulate feeding behavior varies greatly among taxa. In addition, the relationship of jaw suspension to feeding behavior is not as clear as was once believed, and contrary to previous interpretations upper jaw protrusibility appears to be related to the morphology of the upper jaw-chondrocranial articulation rather than the type of jaw suspension. Finally, we propose a set of specific hypotheses including: (1) *The functional specialization for suction feeding hypothesis* that morphological and functional specialization for suction feeding has repeatedly arisen in numerous elasmobranch lineages, (2) *The aquatic suction feeding functional convergence hypothesis* that similar hydrodynamic constraints in bony fishes and sharks result in convergent morphological and functional specializations for suction feeding in both groups, (3) *The feeding modulation hypothesis* that suction capture events in sharks are more stereotyped and therefore less modulated compared to ram and bite capture events, and (4) *The independence of jaw suspension and feeding behavior hypothesis* whereby the traditional categorization of jaw suspension types in sharks is not a good predictor of jaw mobility and prey capture behavior. Together with a set of questions these hypotheses help to guide future research on the feeding biology of sharks.

Introduction

The feeding behaviors, mechanisms, and mechanics of sharks are of interest to biologists for a variety of reasons. From an evolutionary and functional standpoint chondrichthyan fishes represent a basal group of jawed fishes that share a common ancestor with bony fishes (Schaeffer & Williams 1977, Carroll 1988, Long 1995). As such, studying the feeding behavior of sharks has the potential to teach us a great deal about the function and evolution of vertebrate feeding systems (Wilga et al. 2000). In addition, extant sharks number about 467 (R. Martin personal communication) species inhabiting a wide range of marine and fresh water environments and possess great morphological diversity. Interestingly, no sharks are herbivorous, but their prey spans a variety of trophic levels ranging from zooplankton to the largest marine mammals. Although sharks feed opportunistically, they typically consume relatively small amounts of food (Pratt et al. 1982, Compagno 1984, Cortes 2000). Furthermore, compared to bony fishes, sharks retain a relatively simple feeding apparatus composed of a fused chondrocranium, jaws consisting of a palatoquadrate and Meckel's cartilage, and a hyoid arch composed of only three elements: a hyomandibula, ceratohyal, and basihyal. Despite this simple mechanism sharks utilize a variety of prey capture modes that include suction, ram, bite, bite and gouge, and filter feeding (Moss 1972, 1977, Frazzetta 1994). The rich fossil history that we have of shark teeth means that we have one of the most extensive indicators of vertebrate feeding mechanisms. Although much is known about tooth replacement and growth patterns, we still have an incomplete understanding of their function during feeding beyond that of grasping prey. A tremendous increase in our knowledge of feeding mechanics of bony fishes has taken place within the last three decades (Alexander 1967, Liem 1978, Lauder 1985), yet such studies on sharks are advancing at a much slower rate (Moss 1972, 1977, Nobiling 1977, Shirai & Nakaya 1992). A key finding in bony fishes is that most have the ability to modulate feeding behavior in response to differing prey sizes and types (Liem 1978, Sanderson 1988, Nemeth 1997). Early studies indicated that feeding behavior of sharks is a highly predictable sequence of events (Gilbert¹). This has raised the question as to whether

sharks have similar modulatory abilities as bony fishes, or is the ability to vary capture behavior in sharks related to different types of capture mechanisms (ram, suction, bite, filter). Furthermore, the size of sharks span a tremendous range, from the largest fishes in the oceans to diminutive deepwater species. How the scaling of feeding structures affects their feeding mechanics and behavior remains relatively unknown. And despite what every student of comparative anatomy learns about jaw suspension types and the relationship to jaw mobility and feeding in sharks, new evidence challenges some of these assumptions and we are beginning to understand the relationship between jaw suspension types and feeding mechanics.

The goal of this paper is to review past work on the feeding behaviors, mechanisms, and mechanics of sharks and to begin to integrate these topics in order to interpret relationships between feeding behavior and morphology. By posing a set of hypotheses and questions we hope to guide research into the next millennium. To clarify the use of various terms we offer the following definitions. The term mechanism refers to the anatomical parts of the feeding apparatus such as teeth, cartilages, muscles and connective tissue structures. Mechanics refers to the functioning of the feeding mechanism and deals with the motions of the various parts and the forces acting upon them. Kinematics simply deals with motion without reference to forces. Prey refers here to dietary items captured by natural feeding, and food refers to pieces of or whole food items offered under experimental conditions. The term feeding behavior is used in a more general ethological sense and also interchangeably with prey or food capture behavior. In this review we do not specifically cover batoids although we do occasionally discuss them. It is not our goal to review feeding ecology or diet per se, although we relate diet to feeding mechanisms and behavior. The reader is referred to dietary studies and reviews listed in the text. Lastly, the sensory system as it relates to feeding has been reviewed by Hodgson & Mathewson (1978), Hueter & Gilbert (1990), Bleckmann & Hofmann (1999) and elsewhere in this volume.

Discussion

Evolution of the feeding mechanism

The earliest fossil evidence of sharks consists of scales dating back to the Silurian Period and perhaps as early as the late Ordovician Period some 455 million years

¹ Gilbert, P.W. 1970. Studies on the anatomy, physiology, and behavior of sharks. Final report, Office of Naval Research, Contract Nonr-401(33): Project NR 104-471. 45 pp

ago (Schaeffer & Williams 1977, Carroll 1988, Long 1995, Monastersky 1996, Sansom et al. 1996). The earliest sharks, the Cladoselachida (extinct), had an amphistylic jaw suspension characterized by a long palatoquadrate cartilage with otic and orbital processes articulating with the neurocranium, a long mandible, a long and presumably non-suspensory hyomandibula, a large and mostly terminal mouth with multi-cuspid teeth, relatively small labial cartilages, and a body and caudal fin form similar to modern fast-swimming pelagic sharks (Figure 1). These predators had a dentition suited for seizing and tearing prey rather than shearing or sawing, and it is speculated that they captured prey by overtaking and engulfing it, although suction probably played a role in their feeding (Shaeffer 1967, Moy-Thomas & Miles 1971, Carroll 1988, Lund & Grogan 1997).

An early period of chondrichthyan radiation in the Paleozoic was followed by a period of elasmobranch radiation in the Mesozoic and Cenozoic. A ctenacanthid ancestor then gave rise to the neoselachians, which

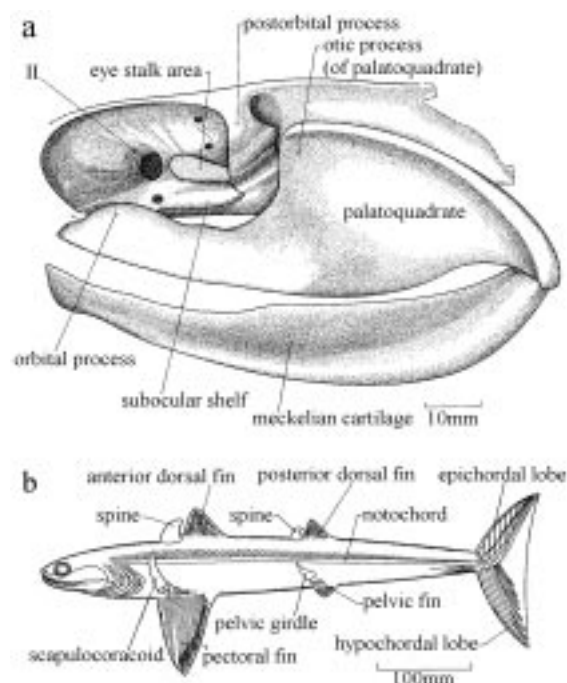


Figure 1. a – Restoration of the neurocranium and jaws of *Cladodus*, b – restoration of *Cladoselache fylei*. The cladodont palatoquadrate shown in (a) had a large otic process which is not well represented in the whole animal reconstruction (b). The narrow suborbital ramus also extends anteriorly to the rostrum (Schaeffer 1967) (reproduced with permission from Moy-Thomas & Miles 1971).

includes all modern sharks, skates and rays. Three major groups comprise the neoselachians, the galeoids, squaloids, and batoids (but see Compagno 1973, Carroll 1988, Shirai 1996). The feeding apparatus in modern sharks has changed primarily in the proportions of the skeletal elements and in the mechanism of jaw suspension. Modern sharks have a sub-terminal mouth that opens ventrally, shorter jaws, more moveable hyomandibula that suspends the jaws, more protrusible palatoquadrate cartilage with a smaller otic process and a dentition better suited for sawing and shearing compared to ancestral sharks (Shaeffer 1967, Carroll 1988).

Diet and feeding activity

The diet of sharks is perhaps one of the most thoroughly investigated areas related to feeding, yet many studies are confined to relatively few species. Most of the work on shark diet is on carcharhiniform sharks. Sharks are generally asynchronous opportunistic feeders on the most abundant prey item, which are primarily other fishes. Feeding occurs in short bursts followed by longer periods of digestion when feeding is reduced (Wetherbee et al.²). Sharks in general eat only about 3–14% of their body weight per week (Budker 1971). Mean weight of recently ingested prey items as a percent of body weight is generally low: 2.25% for the Australian sharpnose shark, *Rhizoprionodon taylori* (Simpfendorfer 1998); 2.68% for lemon shark, *Negaprion brevirostris* (Cortes & Gruber 1990); and 4.23% for juvenile sandbar shark, *Carcharhinus plumbeus* (Medved et al. 1988). Examining 148 species representing 22 families, Cortes (2000) found that sharks are tertiary consumers, with significant differences in diet occurring among the six orders examined. Trophic level and body size is positively correlated, especially within the carcharhinid sharks, and within the Carcharhiniformes teleost fishes are the dominant prey item.

The diet of young lemon sharks, *N. brevirostris*, has been extensively studied, revealing that their diet is dominated by teleosts. Feeding is asynchronous, intermittent and stomach contents are evacuated in

² Wetherbee, B.M., S.H. Gruber & E. Cortes. 1990. Diet, feeding habits and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. pp. 29–48. In: H.L. Pratt Jr., S.H. Gruber & T. Taniuchi (ed.) Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries, NOAA Tech. Rep. NMFS 90.

25–41 h. Daily ration is estimated at 1.5–2.1% of body weight per day (Cortes & Gruber 1990, Wetherbee et al.²). In southwest Florida, the bonnethead shark *Sphyrna tiburo* has a very homogeneous diet dominated by crustaceans, particularly blue crabs *Callinectes sapidus* (Cortes et al. 1996). On the contrary, the tiger shark *Galeocerdo cuvieri* is an opportunistic feeder in Hawaiian waters, undergoing ontogenetic dietary shifts from a diet dominated by teleosts and cephalopods, to a broader diet that includes elasmobranchs, turtles, land mammals, crustaceans, and indigestible items. The ontogenetic shifts in this species may be attributable to increased size, expanded range, and improved hunting skills (Lowe et al. 1996). Leopard sharks, *Triakis semifasciata*, undergo dietary shifts in Monterey Bay, California. Sharks less than 130–140 cm total length feed primarily on benthic invertebrates, whereas fishes were the most important items in larger sharks (see Lowe et al. 1996 for a summary of ontogenetic dietary shifts). However, the vast majority of dietary data in sharks is confined to stomach content analyses which vary greatly in the number of stomachs analyzed (Bigelow & Schroeder 1948, Budker 1971, Compagno 1984, Cortes 2000).

In general less is known about feeding activity patterns of sharks, and many of these studies are confined to easily observable or captive species, many of which are coastal. In addition to ontogenetic feeding shifts many sharks undergo seasonal or diel changes in diet and feeding activity patterns. Most white sharks, *Carcharodon carcharias*, at the South Farallon Islands, California are transient visitors, but a few sharks are short-term residents. The sharks apparently regulate the timing of their movements so they arrive at the Farallon Islands during the time of year that coincides with previously successful foraging on pinniped prey (Klimley & Anderson 1996). In contrast to young lemon sharks that show no diel feeding activity (Cortes & Gruber 1990), large tiger sharks *G. cuvieri*, which have large home ranges, feed near the bottom at night, but also feed at the surface during the day (Lowe et al. 1996, Holland et al.³). At French Frigate Shoal in the Hawaiian Islands, a tagged tiger shark showed a diurnal activity pattern. The shark spent most of its daytime

activity on the outer reef where it swam close to the bottom. The shark occasionally swam to the surface to investigate prey and perhaps feed. At night, most of the shark's activity was centered above or beyond the drop-off (Tricas et al. 1981). Telemetric and digestive rate studies on blue shark *Prionace glauca* off Santa Catalina Island, California, indicate that these sharks forage in waters near the surface from around midnight through dawn, feeding on dispersed schools of anchovies and mackerel (Tricas 1979). Swell sharks *Cephaloscyllium ventriosum*, are nocturnal feeders that detect the bioelectric fields of their individual prey items (Tricas 1982). Horn sharks *Heterodontus francisci* off Santa Catalina Island, California, exhibit diel activity patterns of increased activity at night, particularly at 18:00 h. Few sharks are exposed in the day, instead seeking shelter among rocks, whereas sharks are frequently found in exposed locations at night, coinciding with their increased feeding on nocturnally active prey (Nelson & Johnson 1970, Finstad & Nelson 1975, Strong 1989). Large diurnal aggregations of scalloped hammerhead *Sphyrna lewini* occur at seamounts in the Gulf of California. These sites may serve as a refuge point at the center of foraging paths. During the day the sharks swim slowly back and forth over the seamount and do not forage. At night the sharks leave either as solitary animals or in small groups to forage in the pelagic environment (Klimley & Nelson 1981, 1984, Klimley et al. 1988, Klimley 1995). Small numbers of whitetip reef sharks *Triaenodon obesus* aggregate in caves during the day. At night they disperse and feed within and about the reefs, although some feeding during the day evidently occurs (Randall 1977).

Apparently many shark species segregate by sex, resulting in dietary differences that in turn result in different growth rates, with females growing to a larger size. This is attributed to differing reproductive pressures on sexes. The scalloped hammerhead, *S. lewini*, is a case in point. Females of this species move offshore at a smaller size than males, consequently females feed more on pelagic prey than males and with greater predatory success. Females therefore grow to reproductive size more rapidly than males (reviewed by Klimley 1987).

Feeding behavior – capture and approach

Sharks capture their prey in a variety of ways. During ram capture the shark swims over the relatively stationary prey, engulfs it whole or seizes it in its jaws

³ Holland, K.N., S.M. Kajiura, A. Bush, B.M. Wetherbee, C.G. Lowe & C. Meyer. 1997. Movement patterns of tiger sharks in Hawaiian waters. Abstracts, American Society of Ichthyologists and Herpetologists 77th Annual Meeting, 26 June–2 July 1997, University of Washington, Seattle. p. 166.

and may use manipulation bites to reduce it in size. The food is then transported by hydraulic suction from the mouth through the pharyngeal cavity into the esophagus. Many species of carcharhinid and lamnid sharks primarily rely on ram feeding. Ram feeding sharks generally have a large gape in comparison to suction feeders (see below). Bonnethead sharks, *S. tiburo*, ram feed benthic food by depressing the mandible and scooping the food up as they swim over it (Wilga 1997, Wilga & Motta 2000). White sharks, *C. carcharias*, primarily ram capture their food sometimes approaching the food at great speeds (Tricas & McCosker 1984, Tricas 1985, Klimley 1994, Klimley et al. 1996). Oceanic whitetip sharks, *Carcharhinus longimanus*, employ a feeding behavior similar to ram capture. These sharks have been observed to swim slowly through schools of tuna with their mouth open at the surface, without snapping or chasing, simply engulfing prey that enters its mouth (Bullis 1961, Compagno 1984). During ram feeding, particularly at high swimming speeds, the predator might displace a wave of water anterior to the mouth in effect pushing the prey away from the open mouth. In this case they might incorporate what has been termed compensatory suction to overcome the inertia of water being displaced anteriorly to the moving head (Van Damme & Aerts 1997).

During ram feeding by white sharks, Tricas & McCosker (1984) and McCosker (1985) noted that the sharks often bite such prey as elephant seals, and then retreat until the prey lapses into shock or bleeds to death. The shark then returns to feed on the prey. Tricas & McCosker (op. cit.) referred to this as the 'bite and spit' strategy. However, Klimley (1994) and Klimley et al. (1996) proposed that white sharks hold the pinniped prey tightly in their mouth and drag it below the surface, often removing a bite from the prey in the process. The prey may be released underwater upon which it floats or swims to the surface and dies by exsanguination. Meanwhile, the shark follows the prey to the surface to begin feeding after it dies.

Inertial suction feeding involves a decrease in the pressure of the buccopharyngeal chamber such that the prey or food is pulled into the mouth. This is commonly referred to as suction feeding. There is a functional continuum from pure ram to pure inertial suction and sharks can use a combination of both (Norton & Brainerd 1993, Van Damme & Aerts 1997, Wilga & Motta 1998a). Although the vast majority of shark feeding behaviors have not been studied, morphological specialization for suction

feeding is found in many shark lineages including the Squaliformes, Heterodontiformes, Carcharhiniformes, Orectolobiformes, Squatiniformes and the Batoidea, while suction feeding appears to be the predominant food capture behavior in the Orectolobiformes (Tanaka 1973, Moss 1977, Wu 1994, Fouts 1995, Clark & Nelson 1997, Wilga 1997, Ferry-Graham 1998b, Heupel & Bennett 1998, Wilga & Motta 1998a,b, Fouts & Nelson 1999, Pretlow-Edmonds 1999, Robinson 1999).

Specializations for suction feeding in sharks can include a relatively small mouth as compared to ram feeding sharks, small teeth, a laterally enclosed mouth such as by large labial cartilages, hypertrophied abductor muscles and rapid buccal expansion (Motta & Wilga 1999). The nurse shark, *Ginglymostoma cirratum*, is apparently an obligate suction feeder. When it approaches its food, the shark usually ceases swimming and initiates a very stereotyped food capture behavior. The mandible is rapidly depressed as the robust labial cartilages move anteriorly to laterally occlude the mouth and there is often no cranial elevation. It takes approximately 32 msec to open its mouth, one of the fastest food capture sequences of any shark recorded. Even in the absence of food when animals were conditioned to feed, the entire sequence occurred with little variation. This explosive suction action can generate sub-ambient pressures as low as -1 atm, and large nurse sharks can even dismember their food in this manner (Tanaka 1973, Motta & Wilga 1999, Robinson 1999, Motta personal observation). Specializations for suction prey capture in *G. cirratum* and other specialized suction feeding sharks are apparently functionally convergent with those of high speed inertial suction feeding bony fishes. Bony fishes that are suited for inertial suction feeding usually have a small, laterally enclosed mouth, reduced dentition, strongly developed abductor muscles, buccal expansion is large and rapid, the expansive phase is shorter in duration than the compressive phase, and peak hyoid depression occurs after peak gape. In contrast to *G. cirratum*, upper jaw protrusion in bony fishes may contribute significantly to buccal expansion (Lauder 1980, 1985, Muller et al. 1982, Liem 1993, Motta & Wilga 1999).

Biting, which may accompany ram feeding, may also occur when a shark approaches its prey or food, ceases swimming, and simply bites the prey or pieces off the prey. The negative buoyancy of sharks does not facilitate this behavior in mid-water, and the shark may try to swim in-place to maintain its position in the water

column. The cookiecutter shark, *Isistius brasiliensis*, shows a unique biting behavior in which it employs its modified pharyngeal muscles, upper jaw, hyoid and branchial arches to suck onto its prey of pelagic fishes or marine mammals. Forming a seal with its fleshy lips, it then sinks its hook-like upper teeth and saw-like modified lower teeth into the prey, twists about its longitudinal axis to gouge out a plug of flesh, leaving a crater-like wound (Jones 1971, Compagno 1984, LeBoeuf et al. 1987, Shirai & Nakaya 1992).

Continuous ram filter feeding, such as in basking sharks, *Cetorhinus maximus*, occurs when the shark continuously swims forward with the mouth open. In this manner these sharks will actively seek and locate zooplankton patches on the surface (Sims et al. 1997, Sims & Merrett 1997). The megamouth shark, *Megachasma pelagios*, and perhaps the whale shark, *Rhincodon typus*, can employ intermittent suction filter feeding, generating suction with aperiodic pulses (Taylor et al. 1983, Diamond 1985, Compagno⁴, Sanderson & Wassersug 1993, Clark & Nelson 1997, Martin & Naylor 1997). Whale sharks can also use continuous ram filter feeding, or hang vertically in the water column. In the latter case they will suck prey into the mouth, or rise vertically out of the water and sink back under water, creating an inflow of water and prey into their open mouths (Gudger 1941b, Springer 1957, Budker 1971, Colman 1997).

It often has been speculated that mouth position and body form in sharks is related to where they feed and how they approach the prey (Budker 1971). The subterminal mouth of modern sharks does not preclude them from feeding on prey in front of or above them. Sharks will approach surface or underwater food either with a direct head-on approach or roll on their side to bite at the food (Budker 1971). White sharks, *C. carcharias*, have been observed to approach and feed on underwater bait or a floating whale carcass either in their normal orientation, by rolling on their side, or rolling completely over so their ventral side is up (Pratt et al. 1982, Tricas & McCosker 1984). Surface feeding blue shark, *P. glauca*, approach schools of squid on the surface with an underwater approach or a surface charge. Small anchovies

are captured from a normal swimming posture, but when capturing larger whole mackerel from behind blue sharks may roll on their side (Tricas 1979). Surface feeding blacknose, *Carcharhinus acronotus*, oceanic white tip sharks, *C. longimanus*, and white sharks, *C. carcharias*, have been observed to raise the head just prior to capture (Bullis 1961, Tricas & McCosker 1984, Frazzetta & Prange 1987). This might place the open mouth in line with food as the shark approaches (Frazzetta & Prange 1987).

Feeding on or in the benthos is not uncommon. Gray reef sharks, *Carcharhinus amblyrhynchos*, in Hawaii primarily feed near the bottom on reef associated teleosts and supplement their diet with invertebrates (Wetherbee et al. 1997). Rays are often taken by sharks, particularly hammerhead sharks (Gudger 1907, Budker 1971). Great hammerhead sharks, *Sphyrna mokarran*, have been observed to use their head to deliver powerful blows and to restrain rays on the substrate prior to biting pieces off the ray (Strong 1990). Leopard sharks, *T. semifasciata*, can apparently suck worms out of their burrows in addition to biting pieces off their benthic prey (Talent 1976, Compagno 1984). Small bonnethead sharks, *S. tiburo*, ram capture their food by depressing the mandible considerably as they swim over the food, catching the food either within the mouth or with the anterior mandibular teeth. Occasionally they swim in tight circles biting at benthic food (Wilga 1997, Wilga & Motta 2000). The epaulette shark, *Hemiscyllium ocellatum*, and the whitespotted bamboo shark, *Chiloscyllium plagiosum*, employ a feeding behavior uncommon among sharks. These sharks occasionally thrust their head into the sediment up to the level of the first gill slit, apparently using suction to capture their benthic prey of worms and crabs. They then winnow the prey from the sand in the buccopharyngeal cavity and eject the sand through the first gill slit (Heupel & Bennett 1998, Wilga personal observation).

Sharks will ambush, stalk, or lure their prey, perhaps forage cooperatively, and in some cases feed in large aggregations resulting in what is termed 'feeding frenzies'. By partially burying themselves in the soft substrate, Pacific angel sharks, *Squatina californica*, ambush demersal fishes. These sharks appear to actively select ambush sites within localized areas adjacent to reefs (Fouts 1995, Fouts & Nelson 1999). White sharks *C. carcharias*, will stalk prey downstream in oceanic or tidal currents (Pyle et al. 1996), while other sharks may lure prey to them. Luminescent tissue on the upper jaw of the megamouth

⁴ Compagno, L.J.V. 1990. Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits. pp. 357–379. In: H.L. Pratt, Jr., S.H. Gruber & T. Taniuchi (ed.) Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries, NOAA Tech. Rep. NMFS 90.

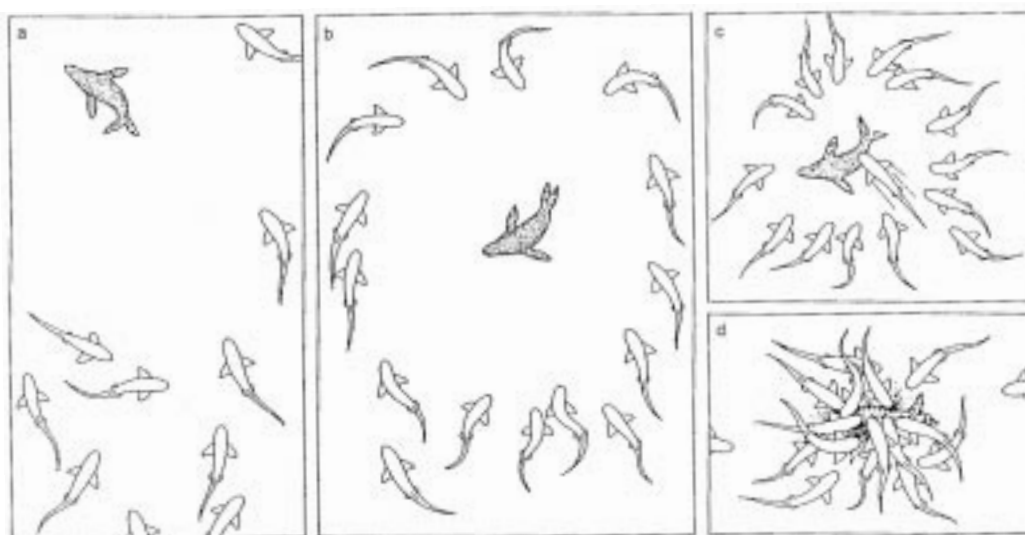


Figure 2. Illustration of sevengill shark, *Notorynchus cepedianus*, feeding by social facilitation: a – typical attack pattern begins when a group of sharks forms a loose circle around its intended victim, b – attempts to escape are prevented by the pack, which gradually tightens its circle around the prey, c – eventually, one or more sharks bite the prey, which stimulates the rest of the pack to converge on it, d – once the attack has been initiated, the rest of the pack quickly joins in to obtain its share of the food (reproduced with permission from Ebert 1991).

shark, *M. pelagios*, might attract euphausiid shrimp and other prey into its mouth (Compagno⁴), the white tips on the pectoral fins of oceanic whitetip sharks, *C. longimanus*, might act as visual lures to aid in the capture of its rapid moving prey (Myrberg 1991), and bioluminescence in the cookiecutter shark, *I. brasiliensis*, might serve to lure pelagic predators from which it gouges chunks of flesh (Jones 1971, Widder 1998).

Although many species of sharks forage solitarily, in some cases aggregations of sharks will come together to feed. Cooperative foraging by sharks has been suggested repeatedly. Blacktip reef sharks, *Carcharhinus melanopterus*, and lemon sharks, *N. brevirostris*, were observed to apparently herd schools of fish against the shoreline and then feed on them (Eibl-Eibesfeldt & Hass 1959, Morrissey 1991) and oceanic whitetip sharks, *C. longimanus*, were observed to herd squid at night (Strasburg 1958). In one instance more than a hundred sandtiger sharks, *Carcharias taurus*, were observed to surround blue fish (Pomatomidae), force them into a school and then all dashed in to feed on the prey at the same instant (Coles 1915). Thresher sharks (*Alopias*) are reported to apparently work in groups to capture fish, using their long caudal fins to herd and stun fishes (Coles 1915, Budker 1971, Castro 1996). When hunting seals sevengill sharks,

Notorynchus cepedianus, will circle the seal and prevent its escape (Figure 2). The circle is tightened and eventually one shark initiates the attack that stimulates the others to begin feeding (Ebert 1991). However, in many of these cases of supposed cooperative foraging it is not clear if the sharks are actually cooperating or the behavior (e.g. circling the prey) represents an aggregation of sharks to one prey item.

Feeding frenzies also resemble cooperative foraging behavior. Feeding frenzies involve aggregations of sharks attacking prey or food items indiscriminately. These sharks move at an accelerated speed, disregarding any injuries they may receive in the attack. Injured or hooked sharks are often attacked and consumed by the other sharks. These feeding bouts, which can involve as few as six sharks to hundreds of sharks, can end abruptly as they begin (Gilbert 1962, Vorenberg 1962, Springer 1967, Nelson 1969, Hobson 1963).

Feeding mechanisms and mechanics

The feeding apparatus and cranial anatomy of sharks have been extensively reviewed (e.g. Daniel 1934, Marinelli & Strenger 1959, Gohar & Mazhar 1964, Moss 1972, 1977, Nobiling 1977, Compagno 1988,

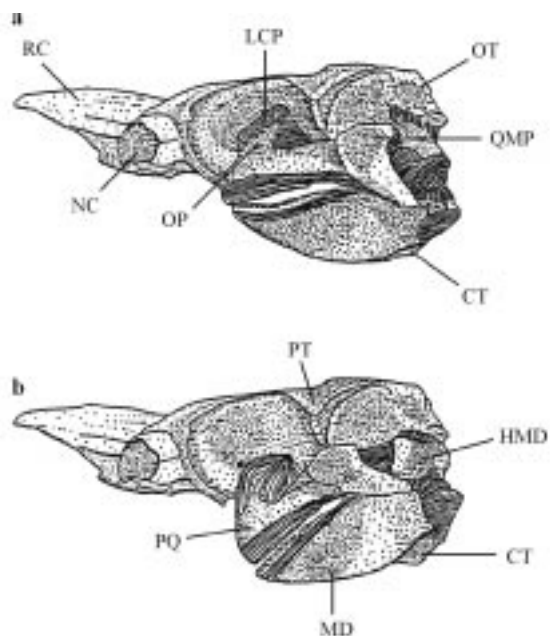


Figure 3. Left lateral view of the neurocranium, jaws and hyoid arch of a 74.5 cm TL spiny dogfish, *Squalus acanthias*, with the skin and muscles removed: a – at resting position, b – at peak upper jaw protrusion. QMP = quadratomandibularis process of palatoquadrate, CT = ceratohyal, HMD = hyomandibula, LCP = ethmopalatine ligament, MD = mandible or lower jaw, NC = nasal capsule, OP = orbital process of palatoquadrate, OT = otic capsule of cranium, PQ = palatoquadrate cartilage or upper jaw, PT = postorbital process, RC = rostral cartilage (reproduced with permission from Wilga & Motta 1998a).

Waller & Baranes 1991, Shirai & Okamura 1992, Frazzetta 1994, Wu 1994, Motta & Wilga 1995, 1999). The majority of the studies have been on the hard parts of the carcharhiniform cranial skeleton, although some have reviewed the joints, ligaments and muscles (Gadow 1888, Luther 1909, Goodey 1910, Daniel 1915, 1934, Allis 1923, Edgeworth 1935, Lightoller 1939, Marinelli & Strenger 1959, Moss 1972, Nobiling 1977, Motta & Wilga 1995, 1999).

The feeding apparatus is perhaps best known in the spiny dogfish, *Squalus acanthias*, and the lemon shark, *N. brevirostris*. The jaw suspension differs somewhat between the two. Squaloids have an orbitostylic type of jaw suspension in which the hyomandibula suspends the jaws from the cranium, and the palatoquadrate articulates with the orbital wall of the cranium by a relatively long orbital process (Marinelli & Strenger 1959, Maisey 1980, Wilga & Motta 1998a) (Figures 3, 4, 5, 6). The lemon shark has the jaws

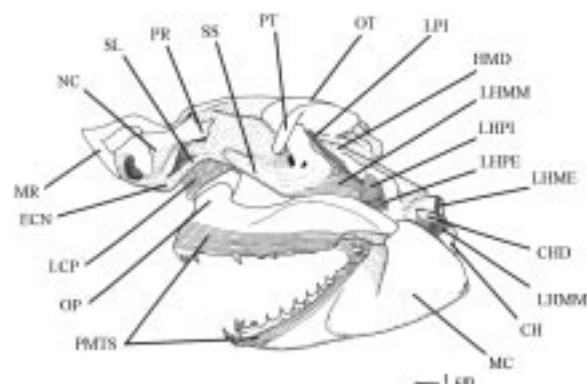


Figure 4. Left lateral view of the neurocranium, jaws and hyoid arch of a 122 cm TL lemon shark, *Negaprion brevirostris*, with the skin and muscles removed. Tendons and ligaments are indicated. CH = ceratohyal, CHD = constrictor hyoideus dorsalis tendon, ECN = ectethmoid condyle, HMD = hyomandibula, LCP = ethmopalatine ligament, LHME = external hyomandibular ligament, LHMM = medial hyoid-mandibular ligament, LHPE = external hyomandibula-palatoquadrate ligament, LHPI = internal hyomandibula-palatoquadrate ligament, LPI = postspiracularis ligament, MC = Meckel's cartilage or lower jaw, MR = medial rostral cartilage, NC = nasal capsule, OP = orbital process of palatoquadrate, OT = otic capsule, PMTS = palatoquadrate-mandibular connective tissue sheath, PR = preorbital process, PT = postorbital process, SL = suborbital ledge, SS = suborbital shelf (reproduced with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc. from Motta & Wilga 1995).

suspended from a more posteroventrally oriented hyomandibula, in contrast to the more laterally directed hyomandibula of the dogfish. The distal hyomandibula is braced against the mandibular knob of the mandible, and the ceratohyal is ligamentously bound to the distal hyomandibula and the mandible. The smaller orbital process of the lemon shark palatoquadrate is attached to the chondrocranial wall by the ethmopalatine ligament as it does in the dogfish (Moss 1965, 1972, 1977, Motta & Wilga 1995). In both species, the hyomandibula is ligamentously bound to the ceratohyal and in turn to the ventral basihyal which rests somewhat dorsal to the mandibular symphysis.

Electromyographic analyses reveal that during jaw opening a relatively conservative series of events occur in both species. Similar to the expansive phase described for teleost fishes (Liem 1978, Lauder 1985), the cranium is elevated by contraction of the epaxialis muscle, although cranial elevation need not occur (see pp. 134–137) (Motta et al. 1991, 1997, Wilga & Motta 1998a) (Figures 7, 8). Almost

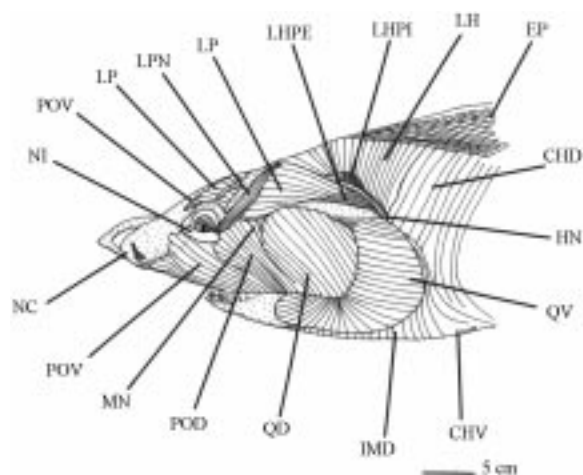


Figure 5. Left lateral view of the head and muscles of a 229 cm TL lemon shark, *Negaprion brevirostris*, with the skin removed and muscle fiber direction indicated. Myosepta of the epaxialis muscle (W-shape) are indicated in addition to the muscle fiber direction. The chondrocranial-palatoquadrate connective tissue sheath is removed. 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 palatoquadrate, 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 (reproduced with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc. from Motta & Wilga 1995).

simultaneously, the mandible is depressed primarily by the action of the coracomandibularis muscle, and the basihyal-ceratohyal apparatus begins to depress due to contraction of the coracoarcualis and coracohyoideus muscles. The branchial apparatus is depressed by action of the coracobranchiales muscles. In the dogfish in particular, the labial cartilages are extended as the mandible is depressed and laterally occlude the mouth (Motta et al. 1991, 1997, Wilga & Motta 1998a). The compressive phase begins at peak gape as the mouth is maximally open, which is followed by the beginning of upper jaw protrusion and elevation of the mandible. Jaw adduction in both species is accomplished by contraction of the quadratomandibularis muscle. Various combinations of the preorbitalis and levator palatoquadrate muscles that are particular to each taxon protrude the upper jaw (see pp. 146–149). As the upper jaw protrudes, the folded and elastic ethmopalatine ligament

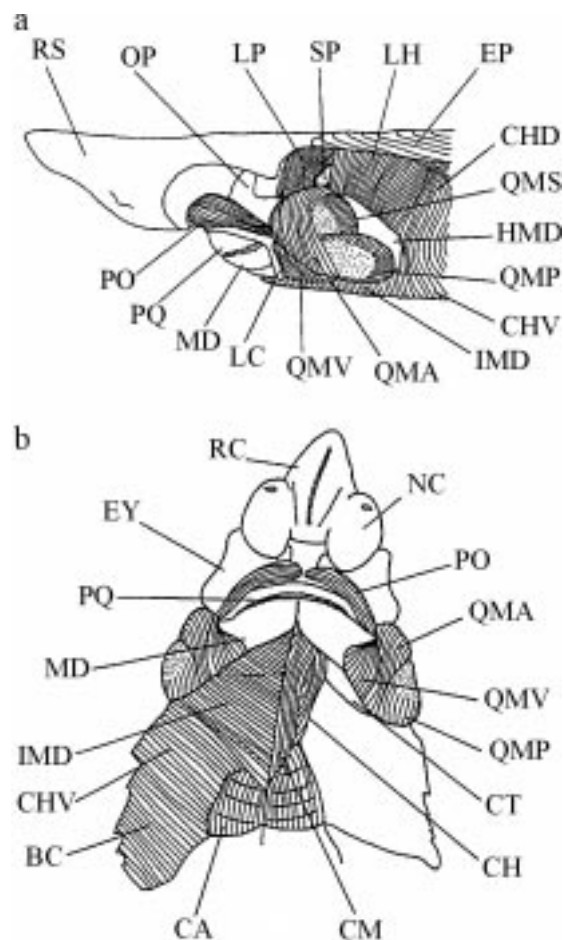


Figure 6. a – Left lateral view (74.5 cm TL), and b – ventral view (60 cm TL) of the head of the spiny dogfish, *Squalus acanthias*, with the skin and eye removed and muscle fiber direction indicated. Skin over the rostrum and cranium is left intact. Myosepta only of the epaxialis muscle are indicated. Raphe overlying quadratomandibularis is indicated by stippling. Anterior and posterior margins of the interhyoideus (deep to IMD) is indicated by dotted lines. BC = branchial constrictors, CA = coracoarcualis, CH = coracohyoideus, CHD = constrictor hyoideus dorsalis, CHV = constrictor hyoideus ventralis, CM = coracomandibularis, CT = ceratohyal, EP = epaxialis, EY = eye, HMD = hyomandibula, IMD = intermandibularis, LC = labial cartilages, LH = levator hyomandibularis, LP = levator palatoquadrate, MD = mandible or lower jaw, NC = nasal capsule, OP = orbital process of palatoquadrate, PO = preorbitalis, PQ = palatoquadrate or upper jaw, QMA = quadratomandibularis anterior, QMS = quadratomandibularis superficial, QMP = quadratomandibularis posterior, QMV = quadratomandibularis ventral, RC = rostral cartilage, RS = rostrum, SP = spiracularis (reproduced with permission from Wilga & Motta 1998a).

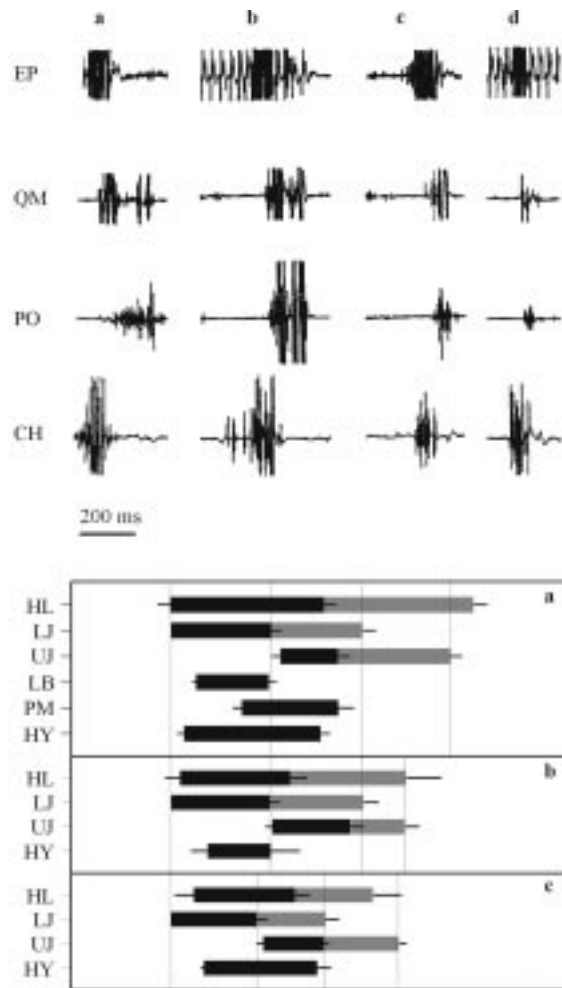


Figure 7. Motor activity and kinematic patterns for: a – suction capture, b – bite manipulation, c – suction transport, and motor activity for d – one head shake to one side in the spiny dogfish, *Squalus acanthias*. Motor activity is from four muscles: epaxialis, quadratomandibularis, preorbitalis, and coracohyoideus. Kinematic events are represented by black bars indicating start to maximum movement followed by gray bars indicating maximum to end of movement, with error bars indicating 1 standard error of the mean (SEM). Vertical lines indicate, from left to right, the start of the mouth opening, mouth closing, and jaw retraction phase, and end of the jaw retraction phase respectively. CH = coracohyoideus, EP = epaxialis, HL = head lift, HY = hyoid depression, LB = labial cartilage extension, LJ = lower jaw depression, PM = prey movement, PO = preorbitalis, QM = quadratomandibularis, UJ = upper jaw protrusion (reproduced with permission from Wilga & Motta 1998a).

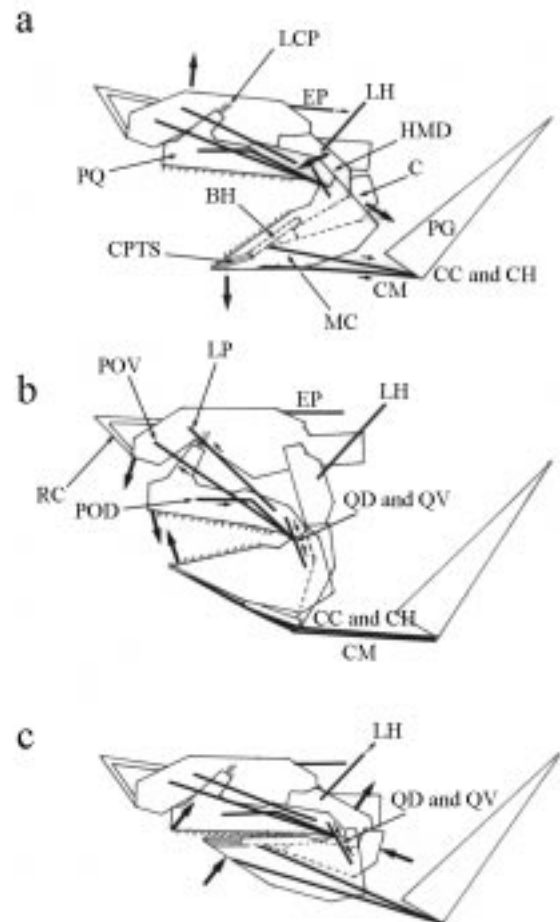


Figure 8. A model of chondrocranial, mandibular and hyoid arch kinetics during feeding in the lemon shark, *Negaprion brevirostris*: a – expansive phase, characterized by depression of the mandible and elevation of the cranium, b – compressive phase, characterized by elevation of the mandible, cranial 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 direction of muscle contraction. BH = basihyal, C = ceratohyal, CC = coracocarcualis, CH = coracohyoideus, CM = coracomandibularis, CPTS = chondrocranial-palatoquadrate connective tissue sheath, EP = epaxialis, HMD = hyomandibula, LCP = ethmopalatine ligament, LH = levator hyomandibularis, LP = levator palatoquadrate, MC = Meckel's cartilage or lower jaw, OP = orbital process of palatoquadrate, PG = pectoral girdle, POD = dorsal preorbitalis, POV = ventral preorbitalis, PQ = palatoquadrate cartilage or upper jaw, QD = quadratomandibularis dorsal, QV = quadratomandibularis ventral, RC = rostral cartilage (modified and reproduced with permission from Motta et al. 1997).

between the orbital process of the upper jaw and the chondrocranium unfolds and stretches, and the distal end of the hyomandibula swings anteroventrally as the distal ceratohyal and basihyal complex continues to pivot posteroventrally. Consequently, peak hyoid depression occurs in the latter half of the compressive phase. In both species the mandible meets the maximally protruded upper jaw either with the food grasped between the teeth or after the food has been engulfed and passes through the buccal cavity. Finally, the recovery phase occurs as the palatoquadrate is retracted into its cranial seat. In the dogfish the dorsoventrally oriented levator palatoquadrati assists in its retraction, whereas in the carcharhinids the elastic ethmopalatine ligament assists. It is not known if the ethmopalatine ligament of squaloids is elastic. In both species however, the levator hyomandibularis retracts the hyomandibula helping to elevate the entire jaw apparatus (Motta et al. 1997, Wilga & Motta 1998a).

This kinematic sequence is similar to that reported for carcharhiniform sharks such as the blacknose *C. acronotus*, blacktip *Carcharhinus limbatus*, swell *C. ventriosum*, bonnethead *S. tiburo*, and Caribbean reef *Carcharhinus perezii* sharks although cranial elevation and upper jaw protrusion may be lacking in some bites (Frazzetta & Prange 1987, Ferry-Graham 1997a, 1998a, Wilga 1997, Wilga & Motta 2000, Motta personal observation) (Figure 9). This differs somewhat for the lamnid white shark, *C. carcharias*, in that peak upper jaw protrusion occurs well before the lower jaw is completely elevated, and cranial depression does not occur until the recovery phase rather than during the compressive phase (Tricas & McCosker 1984, Tricas 1985) (Figure 10). Prey capture, manipulation, and transport events in lemon *N. brevirostris*, spiny dogfish *S. acanthias*, and bonnethead *S. tiburo* sharks have a common kinematic and motor pattern sequence, but are distinguishable from each other by their duration and relative timing of individual kinematic events. Manipulation and transport events are typically shorter than capture events, although crushing manipulation events may be extensive in some species (Motta et al. 1997, Wilga 1997, Wilga & Motta 1998a,b, 2000).

In contrast to these ram-feeding sharks, suction feeding sharks from a variety of families such as the nurse shark, *G. cirratum* (Ginglymostomatidae), leopard shark, *T. semifasciata* (Triakidae), and horn shark, *H. francisci* (Heterodontidae), appear to exhibit an abbreviated kinematic sequence in which cranial elevation is reduced or lacking. In these sharks as well

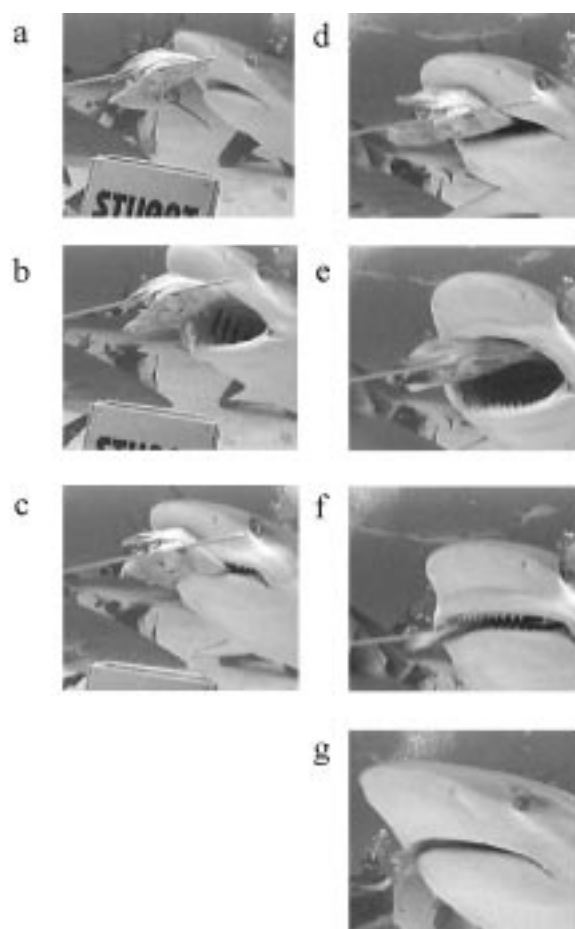
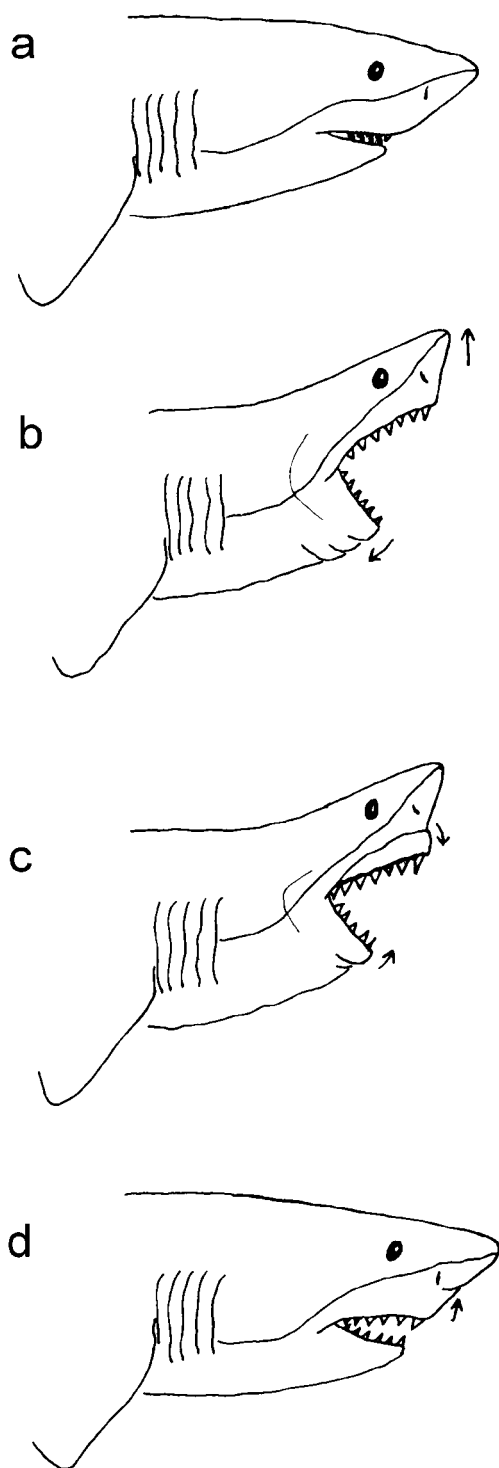


Figure 9. Food capture (a, b, c) and transport (d, e, f, g) sequence of a Caribbean reef shark, *Carcharhinus perezii*, feeding on a grouper (Serranidae) carcass offered on a pole near New Providence Island, Bahamas: a – beginning of the expansive phase marked by initiation of lower jaw depression, b – end of the expansive phase characterized by maximum gape with maximum mandible depression and cranium elevation (120 msec), c – end of the compressive phase when the cranium is depressed, the palatoquadrate protruded, and the mandible elevated as the food is seized (383 msec) (note exposed serrated upper teeth (also in f) during palatoquadrate protrusion), d – beginning of transport marked by mandible depression as the food is already grasped between the jaws, e – suction occurs as maximum gape is attained (note palatoquadrate is slightly protruded), f – the food has been sucked into the buccal cavity but is still attached to the feeding pole as the protruded upper jaw is closed against the elevated lower jaw, g – the palatoquadrate is finally retracted at the termination of the recovery phase. The horizontal width of the feeding box in (a) is 33 cm across for scale (from Pamela Christman personal communication).



as the predominantly suction feeding spiny dogfish, *S. acanthias*, the labial cartilages protrude anteriorly as the lower jaw is depressed to effectively form a lateral enclosure of the mouth. This not only directs the suction anteriorly but may also prevent the food escaping from the sides of the mouth (Ferry-Graham 1997b, 1998b, Wilga & Motta 1998a, Pretlow-Edmonds 1999, Motta & Wilga 1999).

The duration of the entire feeding sequence in these sharks is relatively rapid considering their size. Bite duration, from the beginning of mandible depression to retraction of the jaws to their resting position is shorter for the suction feeding sharks (nurse 92 msec, horn 148 msec, leopard 170 msec). Bite duration is 200 msec for suction and 280 msec for ram feeding sequences in the dogfish (Wilga 1997, Wilga & Motta 1998a). Ram feeding sharks have much longer bite durations, such as the bonnethead 302 msec, lemon 309 msec, and swell shark 367 msec, with the white shark having the longest recorded duration of 405 msec (Tricas & McCosker 1984, Tricas 1985, Ferry-Graham 1997a, Motta et al. 1997, Wilga 1997, Wilga & Motta 1998a, 2000, Pretlow-Edmonds 1999).

Dentition and feeding

The teeth of sharks are arranged in rows on the palatoquadrate and Meckel's cartilage, and are functionally related to feeding behavior and diet. A tooth in the functional position at the edge of the jaw and its replacement teeth constitute a tooth family. Teeth in neighboring families form diagonal rows (James 1953, Reif 1976). The rate of replacement has not been demonstrated to be related to damage such as during feeding or mating, but is species specific and affected by age of the animal, diet, seasonal changes and water temperature.

Figure 10. Food capture kinematics of the white shark, *Carcharodon carcharias*, feeding on surface bait: a – shark just prior to initiation to feeding action (snout and lower jaw are at normal resting position), b – snout lift and lower jaw depression result in maximum gape, c – palatoquadrate protrusion rotates upper jaw forward and downward exposing upper teeth (lower jaw moves forward and upward; these two components comprise the actual bite), d – snout drop entails retraction of the palatoquadrate cartilage to its normal position beneath cranium. Snout drop at the end of the feeding bout during the recovery phase. Arrows indicate direction of jaw movements (reproduced with permission of the California Academy of Sciences, from Tricas & McCosker 1984).

For most species only a few teeth are replaced at a time, although some sharks have different replacement rates for upper and lower jaws (Moss 1967). The cookiecutter shark, *I. brasiliensis*, is unusual in that its relatively large lower triangular teeth are shed together as a complete set (Strasburg 1963). Replacement rates, as measured by the rate of movement of a tooth from the row lingual to the functional row to that of the functional row, varies from 9 to 12 days for the leopard shark, *T. semifasciata* (Reif et al. 1978), 9 to 28 days for the nurse shark, *G. cirratum* (Reif et al. 1978, Luer et al. 1990), 8 to 10 days for the lemon shark, *N. brevirostris* (Moss 1967), and about 4 weeks for *Heterodontus* (Reif 1976).

True homodonty, where the teeth in a jaw are all the same shape and show no abrupt change in size, is rare in recent and fossil sharks, but apparently exists in *Rhincodon* and *Cetorhinus*. Heterodonty, the term applied to significant change in size and shape of the teeth in different parts of the jaw, is common in recent and fossil sharks but the term should not be applied to the normal reduction in tooth size from the front to the rear of the mouth (Applegate 1965, Compagno 1988). Heterodonty within the mouth can include blade-like teeth more suited for cutting to long, pointed teeth suited for grasping and piercing. Horn sharks (Heterodontidae) and bonnethead sharks (Sphyrnidae), two distant taxa, both have anterior cuspidate teeth for grasping and posterior molariform crushing teeth (Figure 11) (Smith 1942, Peyer 1968, Budker 1971, Taylor 1972, Reif 1976, Nobiling 1977, Compagno 1984). Carcharhinid sharks have more cuspidate lower jaw teeth lacking serrations, with more blade-like serrated upper teeth (Figure 12) (Bigelow & Schroeder 1948, Compagno 1984, 1988). The lower teeth may be used to grasp the prey and facilitate rapid penetration into the tissue. The mandible is then elevated and the prey grasped between the upper and lower jaw teeth. The serrated upper teeth saw through the prey, often facilitated by rapid head shaking (Springer 1961, Moss 1972, 1977, Frazzetta & Prange 1987, Frazzetta 1988, 1994, Motta et al. 1997). Serrated teeth cut compliant material such as skin and muscle with a grip-and-rip mechanism where serrations trap and cut sections of material (Abler 1992). Squaloid sharks have blade-like teeth in both jaws with a large laterally pointed oblique smooth cusp that functions similarly during lateral head shaking to cut food (Compagno 1984, Wilga & Motta 1998a). We believe that protrusion of the upper jaw exposes the serrated or blade-like upper teeth facilitating their unobstructed lateral movement through the prey.



Figure 11. Dorsal view of the lower jaw and teeth of the Port Jackson shark, *Heterodontus* sp. showing the grasping teeth in the front of the jaw and the molariform or grinding teeth behind. Rostral tip of jaw at top of picture (reproduced with permission from Budker 1971, Columbia University Press).

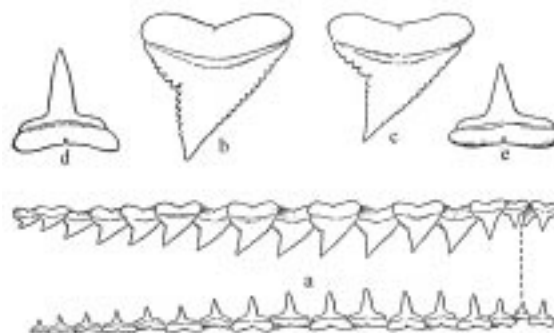


Figure 12. Teeth of silky shark, *Carcharhinus falciformis*: a – right-hand upper and lower teeth, b – fifth upper tooth, c – ninth upper tooth, d – second lower tooth, e – tenth lower tooth. Note serrations in upper teeth for cutting prey and smooth edges of lower teeth for impaling prey (Bigelow & Schroeder 1948, courtesy of the Sears Foundation for Marine Research, Yale University).

Frazzetta (1988, 1994) has proposed that the relatively loose fibrous connection of shark teeth to the jaw cartilage allows the teeth to conform to irregularities in soft tissue and guide around solid obstructions such as bone. Furthermore, he postulates that sharks can use

muscle contraction to voluntarily control the strength of tooth fixation onto the jaw (Frazzetta 1994), a finding we have not been able to substantiate (Motta & Wilga 1995, Motta et al. 1997), but certainly deserves further investigation.

In contrast to many carcharhinid sharks which have out-turned tooth tips probably more suitable for piercing small fish (Frazzetta 1988), the white shark *C. carcharias* has the tips of the front teeth angled inward perhaps making them more effective at gouging chunks of flesh, grasping prey items or preventing prey escape from the mouth. During mouth closure the tooth crown angle formed between the jaw and the center-most teeth increases by 8.7 degrees as the jaw closes through an angle of 20–35 degrees, and then decreases by 15.7 degrees as the jaw is adducted through 35 degrees or more. Although the mechanism isn't clear, this is believed to facilitate a plucking action during feeding (Powlik 1995).

Ontogenetic changes in diet may be associated with ontogenetic changes in dentition. The shape of the teeth and number of tooth cusps in horn sharks (Heterodontidae) change with ontogeny. Rear replacement teeth gradually lose cusps, broaden at the base, and flatten along the crown. The more anterior recurved teeth have larger central cusps and fewer overall cusps with age. Juvenile *H. portusjacksoni* with more pointed teeth apparently take more soft-bodied prey than the adults (Smith 1942, Peyer 1968, McLaughlin & O'Gower 1971, Taylor 1972, Reif 1976, Nobiling 1977, Compagno 1984). Tricas & McCosker (1984) found that white sharks less than 3 m (TL) with relatively long and narrow teeth fed primarily on fish prey, while larger animals with broader teeth preferred marine mammals, a finding they attributed in part to differences in tooth morphology. This change in tooth morphology with growth is termed ontogenetic heterodonty and may include the appearance of or increase in tooth serrations with age as occurs in the night shark, *Carcharhinus signatus*, scalloped hammerhead, *S. lewini*, and some *Rhizoprionodon* species. However, the ecological implications of this are unclear (Raschi et al. 1982, Compagno 1988).

Sexual heterodonty occurs in many species of sharks, and in many cases the teeth of adult males are different in shape from those of females and immature males. The dimorphism is often confined to the anterior teeth, and in the carcharhinoids it is confined to smaller sharks that are less than one meter in length. Sexual heterodonty in sharks and rays appears to be related

to courtship during which the males hold on to the females with their mouth, rather than feeding (Springer 1967, Compagno 1970, 1988, Ellis & Shackley 1995, Kajiura & Tricas 1996). Female sharks often have thicker skin than males due to a thicker stratum compactum layer of helically wound collagen fibers in the dermis. This might be related to the pre-copulatory biting behavior of male sharks (Motta 1977, Wainwright et al. 1978, Pratt 1979). The skin of female blue sharks, *P. glauca*, is more than twice the thickness of males, and exceeds the height of the male's dentition to reduce damage to the underlying muscle (Pratt 1979).

Seasonal change in feeding morphology occurs in basking sharks, *C. maximus*. Basking, and whale sharks, *R. typus*, are filter feeders that have specialized filamentous gill rakers that form a sieve used to filter feed. The rakers are formed from elongated and specialized mucous membrane denticles (Gudger 1941a, Peyer 1968). The sieve is apparently shed each year during winter, a period during which the sharks are believed not to feed (Parker & Boeseman 1954, Sims et al. 1997). Therefore, in many cases there appears to be a good ecomorphological relationship between diet, feeding behavior, and dental morphology in sharks. However, we still lack a good understanding of how teeth function during prey capture and manipulation.

Perhaps the least investigated aspect of teeth and their role in feeding involves the measurement of bite force. Bite force in large tiger sharks, *G. cuvieri*, can be so great as allow the shark to bite through the carapace and plastron of large chelonid sea turtles (Coles 1919, Springer 1961, Witzell 1987). Bite forces on the jaws and teeth have only been theoretically and experimentally verified for a few species (Nobiling 1977). Using an aluminum gnathodynamometer, Snodgrass & Gilbert (1967), Gilbert¹ and Evans & Gilbert (1971) estimated biting forces for a variety of sharks. Young silky sharks *Carcharhinus falciformis*, had biting forces ranging from 38 kg to 90.7 kg. In a series of experiments involving adult tiger sharks *G. cuvieri*, lemon sharks *N. brevirostris*, and dusky sharks *Carcharhinus obscurus*, they recorded a maximum force of 60 kg applied to a single tooth by a 2.5 m dusky shark. This was applied over an area of 2 square mm resulting in an estimated biting force of 30 kg per square mm. However, Frazzetta (1994) raises a cautionary note about such indirect measures of bite force. Clearly, direct measures of bite force remain an area of both theoretical and applied interest, as shark bites are

also implicated in damage to underwater cables (Marra 1989).

Modulation of feeding behavior

Early studies on the feeding behavior of sharks assumed that prey capture behavior was stereotyped and consisted of a predictable series of events that show only limited variation (Gilbert¹, Tricas & McCosker 1984, Tricas 1985). However, several recent studies have noted that individual sharks may exhibit extensive modulation and variation in head and jaw movements, some in motor pattern as well, in response to different feeding situations (Moss 1972, Frazzetta & Prange 1987, Motta et al. 1997, Wilga 1997, Wilga & Motta 1998a,b, Ferry-Graham 1998b, Pretlow-Edmonds 1999). Modulation is defined as consistent repeatable differences in feeding trials in response to different feeding situations while variation is random differences among feeding trials (Chu 1989, Liem 1978, Nemeth 1997). Modulation may be important to individual survival because the ability to modulate feeding behavior may enable a predator to increase its dietary diversity or increase its capture success (Nemeth 1997).

Several species of sharks have been observed to modulate their feeding behavior in response to food size or type. According to the prey size hypothesis, sharks should modulate their capture behavior in response to prey size (Frazzetta & Prange 1987). The prey size hypothesis states that inertial suction or ram feeding should be used to capture small prey (much smaller than the diameter of the mouth), whereas biting should be used to capture medium (closer to the diameter of the mouth, but not larger) and large prey (equal to or larger than the diameter of the mouth). Based on the ram-suction index (RSI) (Norton & Brainerd 1993), the spiny dogfish, *S. acanthias*, uses suction to capture small food items (pieces of shrimp) while a combination of biting and suction is used to capture medium (pieces of herring) and large food items (whole herring) (Wilga 1997). In addition, feeding trials were shorter in duration when capturing small food items compared to large food items. In contrast, RSI values for the leopard shark, *T. semifasciata*, show that relatively greater suction is used to capture medium sized food items than when feeding on small food items. Little modulation in capture kinematics was found in response to elusivity of simulated prey in the leopard shark during suction

feeding, however, the chosen food items may not have been perceived as elusive to the shark (Ferry-Graham 1998b). Food capture kinematics in bonnethead, *S. tiburo*, and juvenile swellsharks, *C. ventriosum*, generally consists of a ram-dominated capture bite that apparently is not modulated by food type or size (Wilga 1997, Wilga & Motta 2000, Ferry-Graham 1997a). Therefore, lemon, blacktip, blacknose, spiny dogfish and leopard sharks appear to be capable of modulating the contribution of suction and ram to capture different sized food items, although not always in accordance with the prey-size hypothesis, while bonnethead and swellsharks do not show modulation.

Kinematic studies using different food types or presentation techniques also provide differing results on the modulatory capabilities of shark feeding behavior. Many sharks have been observed to vary their attack approach in response to the position of the food in the water column (Moss 1972, Tricas & McCosker 1984, Fouts & Nelson 1999, Pretlow-Edmonds 1999). Several different approaches have been observed for the tiger, *G. cuvieri*, lemon, *N. brevirostris*, and dusky, *C. obscurus*, sharks: small food items are picked up from the substrate by impaling them on the lower jaw teeth, small food items in mid-water are taken by simply opening the mouth and swimming at the food, food items at the surface are grasped and bitten as the head and back are quickly elevated, and large mouthfuls are gouged from food items too large to be swallowed whole and are usually accompanied by vigorous shakes of the head and body. White sharks, *C. carcharias*, usually engulf surface bait at normal swimming speeds but may also take the bait in an accelerated rush, while underwater food may be engulfed from an upright posture or after the shark has rolled onto its side. In contrast, the horn shark, *H. francisci*, shows no modulation of suction capture kinematics when presented with food at rest on the substrate, attached to the substrate, or pressed into a feeding tube (Pretlow-Edmonds 1999). However, food capture behavior is altered by the use of additional strikes and vigorous body movements until attached or tube-hidden food is acquired (Strong 1989, Pretlow-Edmonds 1999). Similarly, food capture kinematics of several specialized suction feeding orectolobid and squatid sharks (nurse, *G. cirratum*, spotted wobbegong, *Orectolobus maculatus*, epaulette, *Hemiscyllium ocellatum*, and angel, *Squatina californica*) are also stereotyped and for the nurse shark the kinematics change little despite the presence or absence of food (Wu 1994, Fouts & Nelson 1999, Robinson

1999). Therefore, some sharks show modulation in pre- or post-capture behavior in response to food items rather than in capture mechanism. In addition, morphologically specialized suction and ram feeders appear to have less modulatory ability in the capture mechanism than more generalized feeders that use a combination of these behaviors.

The specific behavior of head and body shaking during feeding varies among shark species (Springer 1961, Moss 1972, Motta et al. 1997, Wilga 1997, Wilga & Motta 1998a). Lemon and bonnethead sharks shake their head rapidly around the pectoral girdle axis. In contrast, tiger, spiny dogfish, and leopard sharks shake the head and entire body back and forth. Still other sharks will roll and spin the body around the prey. This head and body shaking behavior appears to be an efficient means to cut and remove mouth-sized pieces from large prey items.

Differences in the pattern of muscle activity have also been measured during feeding in sharks. Differential activation occurs in the retractor muscles of the palatoquadrate (levator palatoquadrate) and the hyomandibula (levator hyomandibularis) in the spiny dogfish, *S. acanthias*, and the Atlantic guitarfish, *Rhinobatos lentiginosus*, in capture, manipulation, and transport events during feeding (Wilga & Motta 1998a,b). These muscles elevate the upper jaw and hyoid arch respectively retracting the jaws in the recovery phase of capture and transport events. In contrast, these muscles are active during the mouth opening phase in manipulation events. It appears that modulation occurs during manipulatory events when the food is being repositioned within the buccal cavity rather than in the more rapid suction events such as capture and transport. Carcharhinid sharks, such as the lemon shark, *N. brevirostris*, and bonnethead shark, *S. tiburo*, show similar overall motor patterns among the three feeding events (Motta et al. 1997, Wilga 1997, Wilga & Motta 2000). Additional research is needed to determine the extent of this differential muscle activity among feeding behaviors.

Scaling of feeding kinematics

Ontogenetic changes in diet (Wetherbee et al.², Simpfendorfer 1992, Lowe et al. 1996) feeding behavior (McCosker 1985), suction forces (Tanaka 1973), and feeding mechanisms (Beebe 1941, Raschi et al. 1982, Tricas & McCosker 1984, Ellis & Shackley 1995) have been found in some shark species. However,

the effect of scale on the feeding mechanics of sharks has only recently been addressed. The magnitude of head and jaw kinematics during feeding of hatchling and one-year-old swellsharks, *C. ventriosum*, doubled with a doubling of shark length (Ferry-Graham 1998a). Subsequent scaling analysis found that growth in the swellshark scaled isometrically. However, hatchling food captures were predominately ram while one-year-old captures were predominately suction. Hatchlings were more active during capture and may be overtaking the food before it can be drawn into the mouth by suction inflow. Alternatively, hatchling sharks may be too small to use suction effectively, suggesting that there may be an absolute size at which a particular food capture behavior may be effective (Ferry-Graham 1998a). In addition to this assessment of predator-size scaling with prey size, data on prey-size scaling with predator size will provide information on modulatory abilities of sharks.

In a broad ontogenetic study of the feeding mechanics (12 individuals ranging from 33 cm to 254 cm total length), it was found that the feeding apparatus and kinematics of the nurse shark, *G. cirratum*, also scaled isometrically (Robinson 1999). However, the duration of the feeding events had a tendency to increase with negative allometry, i.e., larger sharks tended to take longer to perform the same kinematic feeding sequence than smaller nurse sharks. Physiological constraint on muscular contraction dynamics was suggested as the underlying factor causing the increase in the timing variables (Robinson 1999), supporting a model proposed by Wainwright & Richards (1995) for teleost fishes. Similar results were found in the bonnethead shark, *S. tiburo*, where peak kinematic events were attained later in larger sharks than smaller sharks (Wilga 1997, Wilga & Motta 2000). The ecological implications of scaling of prey capture kinematics, if any, are not clear.

Mechanics and function of jaw protrusion

Protrusion of the upper jaw away from the cranium during the jaw closing phase is an integral part of feeding behavior in most sharks and likely serves numerous functions. Protrusion may shift the entire jaw apparatus away from the cranium and expose the teeth to allow more efficient bites and manipulation of prey (Frazzetta 1994). Protrusible jaws might provide the shark with a versatile yet hydrodynamic subterminal mouth (Tricas & McCosker 1984). Protrusion of the

upper jaw is also believed to facilitate the cutting action of the teeth and allow deep gouging bites to be made into oversized prey (Moss 1977, Tricas & McCosker 1984). Upper jaw protrusion may enable the shark to grasp items from the substrate with more precision (Moss 1972). The teeth may be reoriented during protrusion of the upper jaw for increased grasping ability (Frazzetta & Prange 1987). In addition, nearly simultaneous protrusion of the upper jaw while the lower jaw is elevating may also provide the shark with a better grasp of struggling or elusive prey (Frazzetta & Prange 1987). However, few of these ideas have been experimentally tested.

There are quantitative data to suggest that one function of upper jaw protrusion in some sharks may be to assist in jaw closure as Frazzetta & Prange (1987) hypothesize. In the spiny dogfish *S. acanthias*, the lemon shark *N. brevirostris* and the Atlantic guitarfish *R. lentiginosus* protrusion of the upper jaw significantly decreases the jaw closing distance necessary for the lower jaw to travel before meeting the upper jaw by 27–64% (Motta et al. 1997, Wilga & Motta 1998a,b). However, in sevengill *N. cepedianus* (16%) bonnethead *S. tiburo* (14%) and swell *C. ventriosum* sharks upper jaw protrusion is slight and does not contribute significantly to decreasing this distance (Ferry-Graham 1997a, Wilga 1997, Wilga & Motta 2000). Note that protrusion of the upper jaw occurs independently of cranial depression (Motta et al. 1997, Ferry-Graham 1998b, Wilga & Motta 1998a,b).

Another function of protruding the upper jaw may be to disable prey. Capture of large prey often elicits vigorous lateral head shaking in the tiger *G. cuvieri*, white *C. carcharias*, blacknose *C. acronotus*, blacktip *C. limbatus*, lemon *N. brevirostris*, bonnethead *S. tiburo*, spiny dogfish *S. acanthias*, leopard *T. semifasciata* sharks as well as other sharks (Springer 1961, Moss 1972, Frazzetta & Prange 1987, Frazzetta 1994, Motta et al. 1997, Wilga 1997, Wilga & Motta 1998a, Wilga & Motta 2000). This head shaking behavior is thought to be used for cutting or gouging smaller pieces from large prey. Cutting is facilitated by protrusion of the upper jaw into the prey (Springer 1961, Hobson 1963, Gilbert¹, Moss 1972, 1977, Tricas & McCosker 1984, Frazzetta & Prange 1987, Frazzetta 1988, 1994, Powlik 1995). Vigorous lateral head shaking with the prey grasped between the lower jaw and the protruded upper jaw results in the prey being cut in two pieces in the spiny dogfish, *S. acanthias*, and the lemon shark, *N. brevirostris* (see pp. 142–145) (Motta et al. 1997,

Wilga & Motta 1998a). Rapid upper jaw protrusion in the horn shark, *H. francisci*, may be used like a striking chisel to remove attached prey, such as sea urchins, from the substrate (Pretlow-Edmonds 1999). Furthermore, the white shark, *C. carcharias*, may prolong head elevation when feeding on whales in order to deliver multiple bites by repeated protrusion and retraction of the upper jaw until a consumable chunk is removed (Pratt et al. 1982).

Several mechanisms of jaw protrusion have been described from observational and manipulative studies of feeding in sharks (Luther 1909, Haller 1926, Zlabek 1931, Alexander 1967, Moss 1972, Nobiling 1977, Tricas & McCosker 1984, Frazzetta & Prange 1987, Frazzetta 1994, Shirai & Okamura 1992, Wu 1994). Some of these hypotheses have been supported by a few functional studies that have correlated head and jaw movements during feeding with simultaneous muscle activity. The feeding mechanism of the spiny dogfish, *S. acanthias*, may serve as a general mechanism for squaliform sharks (Wilga & Motta 1998a). The preorbitalis muscle [homologous to the ventral preorbitalis in carcharhiniform sharks (Moss 1972, Compagno 1988)] produces an anteriorly directed force near the posterior region of the jaw (Figure 13). This forces the orbital process of the upper jaw to slide ventrally along the orbital wall and ethmopalatine groove to protrude the upper jaw. As the upper jaw is protruding, the orbital process slides ventrally within the sleeve-like ethmopalatine ligament until the ligament becomes taut at which time upper jaw protrusion is complete. As the upper jaw protrudes, the entire jaw moves anteroventrally while the hyomandibula passively follows. The distal end of the hyomandibula is pulled ventrally and only slightly anteriorly. Since the action of an adductor muscle is to bring two elements closer together, contraction of the quadratomandibularis not only elevates the lower jaw, but may also pull the upper jaw away from the cranium toward the lower jaw. In this way, the quadratomandibularis may assist the preorbitalis in protruding the upper jaw, which can be protruded a considerable distance.

The mechanism of upper jaw protrusion in carcharhiniform sharks differs slightly from that in squaliform sharks. The carcharhiniform mechanism has been proposed in several studies (Luther 1909, Moss 1972, Frazzetta & Prange 1987, Frazzetta 1994) and has largely been supported in functional studies of feeding in the lemon shark, *N. brevirostris*, and the bonnethead shark, *S. tiburo* (Motta et al. 1997, Wilga 1997,

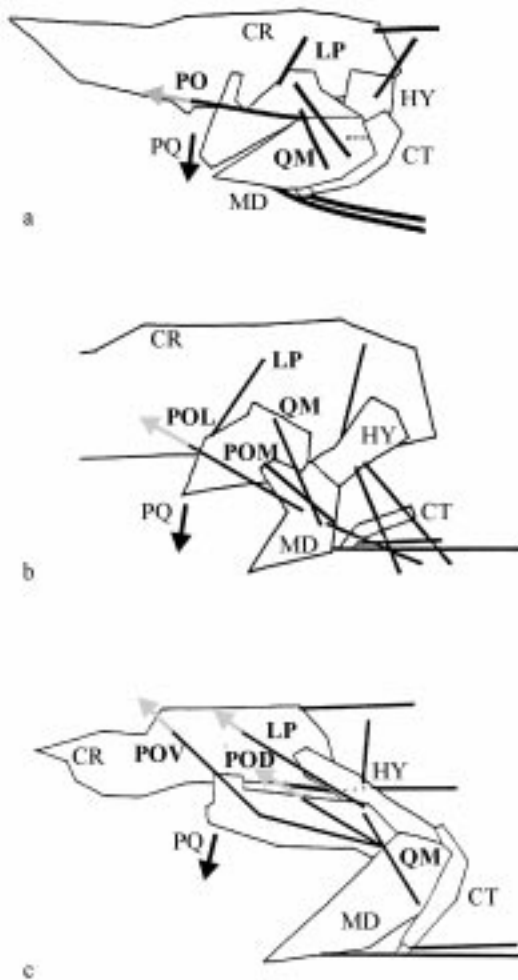


Figure 13. Mechanisms of upper jaw protrusion in elasmobranchs: a – spiny dogfish, *Squalus acanthias*. The PO muscle pulls the upper jaw anteriorly, forcing the orbital process of the upper jaw to slide ventrally along the orbital wall to protrude the upper jaw. As the upper jaw protrudes, the entire jaw moves anteroventrally while the distal hyomandibula is pulled passively ventrally and slightly anteriorly. b – Atlantic guitarfish, *Rhinobatos lentiginosus*. The POL muscle pulls the upper jaw anteriorly while the POM pulls the upper jaw ventrally. As the upper jaw protrudes, the entire jaw moves ventrally while the distal hyomandibula is pulled passively ventrally and slightly posteriorly. c – bonnethead shark, *Sphyrna tiburo*. The POD pulls the upper jaw ventrally while the POV and LP muscles pull it anterodorsally, forcing the orbital process of the palatoquadrate to glide on the ethmopalatine groove driving the upper jaw anteriorly and ventrally. During upper jaw protrusion, the jaws and the distal hyomandibula also swing anteroventrally to a greater extent than the spiny dogfish. Note that the QM can assist in protruding the upper jaw in all three species by pulling the upper jaw towards the lower jaw. Solid black lines indicate muscles with gray arrows

Wilga & Motta 2000). Carcharhiniform sharks have a derived condition in which the levator palatoquadrate muscle is oriented more anteroposteriorly instead of dorsoventrally as in dogfish (Nakaya 1975, Moss 1972, Compagno 1988). In this orientation, the levator palatoquadrate muscle can assist the dorsal and ventral preorbitalis muscle (carcharhiniform sharks have two divisions of the preorbitalis muscle) in protruding the upper jaw (Figures 5, 8, 13). The dorsal division of the preorbitalis pulls the palatoquadrate ventrally as the ventral division of the preorbitalis and the levator palatoquadrate muscles pull it anterodorsally. Similar to the dogfish, the orbital process of the palatoquadrate is forced to glide on the ethmopalatine groove, and the resultant reaction force drives the upper jaw anteriorly and ventrally to protrude it. As the upper jaw is protruded, the rope-like ethmopalatine ligament unfolds (folded in the resting position) until it becomes taught, halting upper jaw protrusion. As the upper jaw protrudes, the jaws and the distal end of the hyomandibula also swing anteroventrally but to a greater extent than the spiny dogfish. Contraction of the quadratomandibularis muscle might also assist upper jaw protrusion as described above (Moss 1965).

Still another mechanism for protruding the jaws was proposed for orectolobiform sharks using cineradiography to visualize cartilage movements of the head and jaws in the spotted wobbegong, *O. maculatus* (Wu 1994). Compression of the two sides of the hyomandibula and lower jaw by the interhyoideus and intermandibularis muscles, respectively, is thought to protrude the jaws anteriorly, resulting in a more acute symphyseal angle. Concomitant with hyomandibular compression is rotation of the ceratohyal around a posterior process on the lower jaw that may push the hyomandibulae and jaws anteroventrally to protrude the jaws. However, the orectolobiform mechanism, as well as heterodontiform and lamniform mechanisms, await confirmation by detailed functional studies. The mechanics of upper jaw protrusion differ among taxa,

indicating direction of action. Back arrows indicate direction of cartilage movement. Muscle names are in bold font, skeletal elements are in normal font. CR = cranium, CT = ceratohyal, HY = hyomandibula, LP = levator palatoquadrate, MD = mandible, PO = preorbitalis, POD = preorbitalis dorsal division, POL = preorbitalis lateral division, POM = preorbitalis medial division, POV = preorbitalis ventral division, PQ = palatoquadrate, QM = quadratomandibularis (reproduced with permission from Wilga 1997).

presumably due to the evolutionary differences in the suspensory apparatus and myology.

Relationship of jaw suspension to feeding

As noted above, upper jaw protrusion is a key feature of feeding behavior in most sharks. In turn, jaw suspension has been presumed to be a major factor in determining the extent of upper jaw protrusion, as well as the magnitude of the gape (Schaeffer 1967, Moss 1972, Maisey 1980). The types of jaw suspension present in sharks are defined primarily by the amount of support that the hyomandibular element of the hyoid arch gives to the mandibular arch and secondarily by the number of connections and ligaments between the palatoquadrate and the cranium (Figure 14) (Huxley 1876, Gregory 1904, Maisey 1980, Lund & Grogan 1997, Grogan et al. 1999). In amphistylic jaw suspension (i.e., *Paleospinax*), the palatoquadrate or upper jaw is suspended from the cranium by an ethmoid articulation with the ethmoid region of the cranium anteriorly, by a relatively small hyomandibula that is presumed to

contribute little to jaw support posteriorly, and by a postorbital articulation between the cranium and palatoquadrate (Figure 14a). Some researchers propose that the tight postorbital articulation severely limits or prevents protrusion of the upper jaw in amphistylic sharks (Compagno 1977) while others suggest that limited upper jaw protrusion is present (Moss 1972, 1977, Zangerl & Williams 1975). In contrast, the relatively large hyomandibula is thought to contribute more to supporting the jaws than the anterior ethmoid articulation in hyostylic jaw suspension (i.e., carcharhiniform, lamniform, orectolobiform, and heterodontiform sharks) (Figure 14b). In hyostyly, the ethmoid articulation is relatively loose and all researchers agree that these sharks have freely protractile jaws (Huxley 1876, Maisey 1980, Compagno 1988). Orbitostylic jaw suspension is similar to hyostyly except instead of an ethmoid articulation, there is an orbital articulation between the palatoquadrate and orbital region of the cranium (i.e., squaliform sharks) (Figure 14c) (Maisey 1980). Some presume that the orbital articulation is so tight as to limit protrusion of the upper

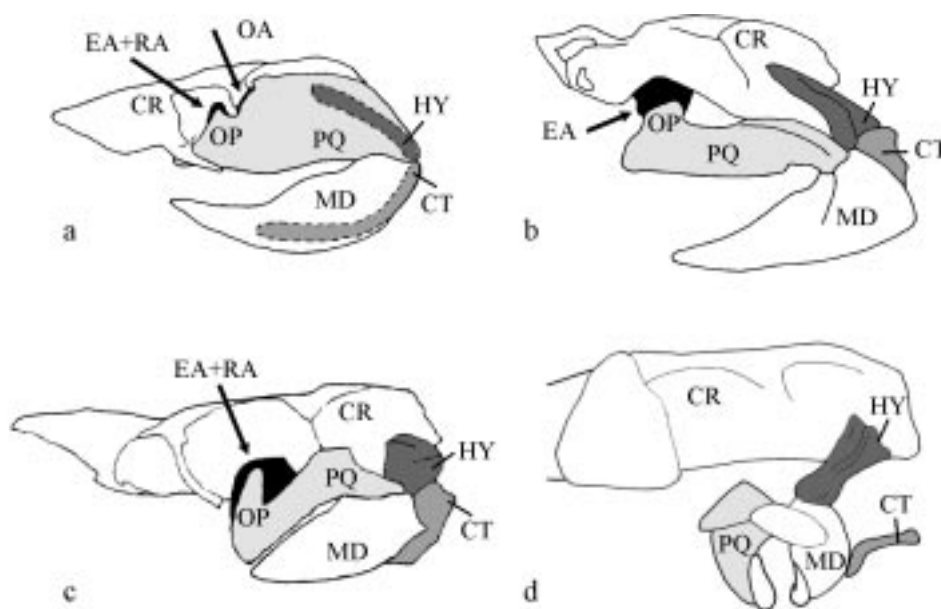


Figure 14. Jaw suspension type in: a – Hexanchiformes (amphistylic), b – Carcharhiniformes (hyostylic), c – Squaliformes (orbitostylic), d – Batoidea (euhyostylic). Black = ethmopalatine ligament, light gray = palatoquadrate or upper jaw, medium gray = ceratohyal, dark gray = hyomandibula, white = cranium and mandible. CR = cranium, CT = ceratohyal, EA = ethmopalatine articulation, HY = hyomandibula, MD = mandible or lower jaw, OA = otic articulation, OB = orbital process, PQ = palatoquadrate or upper jaw, RA = orbital articulation (reproduced with permission from Wilga 1997).

jaw (Schaeffer 1967, Compagno 1977) while others report that the jaws are freely protractile (Haller 1926, Moss 1977). Note that there is an ethmopalatine ligament interconnecting the cranium and the palatoquadrate in ethmoid and orbital articulations. Batoids (skates, rays and guitarfishes) have an euhyostylic type of jaw suspension in which the jaws are suspended solely by the hyomandibulae and lack any ligamentous connections or articulations between the palatoquadrate and the cranium (Figure 14d) (Gregory 1904, Luther 1909, Schaeffer 1967). Accordingly, most agree that euhyostylic batoids are capable of extreme jaw protrusion.

Contrary to popular belief, jaw suspension type is not a good predictor of mobility of the jaws (as measured by upper jaw protrusion distance during feeding in sharks) as concluded by a quantitative study of kinematic and morphological variables of five elasmobranchs (Wilga unpublished). The bonnethead *S. tiburo* is a hyostylic shark and has nearly the same weak jaw protrusion (10% head length, HL) as the sevengill *N. cepedianus* (9% HL), which is an orbitostylic shark (some categorize it as amphistylic). In addition, the spiny dogfish *S. acanthias* (29% HL), which is an orbitostylic shark (some categorize it as hyostylic) and the Atlantic guitarfish *R. lentiginosus* (26% HL), which is euhyostylic, both have extensive upper jaw protrusion. Furthermore, the lemon shark *N. brevirostris*, another hyostylic shark, has only intermediate protrusion (18% HL). Anatomical dissection reveals that the spiny dogfish has a relatively longer ethmopalatine ligament than the lemon shark, which has a longer ligament than the bonnethead and sevengill, with the ligament being absent in the guitarfish. Thus, in this study, the best predictor of jaw mobility appears to be either the presence of a long ethmopalatine ligament or its complete absence, both of which permits the upper jaw to move further from the cranium.

Studies based on anatomy of heterodontiform and orectolobiform sharks, both of which are classified as hyostylic, suggest that their extensive ethmoid articulation greatly restricts upper jaw protrusion and makes the jaw suspension functionally amphistylic (Holmgren 1940, 1942, Smith 1942, Schaeffer 1967, Maisey 1980). As predicted, several of these sharks, horn *H. francisci* (Heterodontiformes, 7% HL), nurse *G. cirratum* (Orectolobiformes, 12% HL) and the epaulette *H. ocellatum* (Orectolobiformes, 9% HL) have relatively little upper jaw protrusion (Wu 1994, Pretlow-Edmonds 1999). However, the spotted

wobbegong *O. maculatus* (Orectolobiformes) can protrude its upper jaw up to 33% of its head length (Wu 1994). It appears that there is a wide range of variation in the extent of upper jaw protrusion within any particular jaw suspension type and generalizations regarding jaw suspension and upper jaw protrusion ability are not supported.

Long posteriorly directed hyomandibulae has been presumed to allow the jaws to swing forward and protrude the upper jaw a greater distance compared to species with shorter more laterally directed hyomandibulae, and secondly to swing laterally when the mouth opens increasing the lateral and vertical gape distance (Moss 1972, 1977). A recent study on the morphology of the jaw suspension shows that long posteriorly directed hyomandibulae do not promote greater jaw protrusion during feeding in the five species examined (Wilga unpublished), but they do correlate directly with a larger vertical gape. This is because having a longer hyomandibula is simply a function of having a longer jaw. The hyomandibula connects the jaws to the cranium and therefore a longer jaw at the same angle of mouth opening will have a larger vertical gape. The sevengill, bonnethead, and lemon sharks all have long posteriorly directed hyomandibulae, long jaws and larger vertical gapes. In contrast the spiny dogfish has short laterally directed hyomandibulae and a smaller vertical gape, while the guitarfish has anteriorly directed intermediate length hyomandibulae but also has a small vertical gape (Wilga 1997). According to this study, longer hyomandibulae do appear to confer a larger vertical gape but have no effect on jaw protrusion.

Interestingly, those sharks studied with relatively longer jaws also capture prey using bite or ram feeding, while those sharks with shorter jaws use inertial suction to capture food. In bony fishes, characteristics such as relatively long jaws with restricted jaw mobility have been predicted to be specializations for ram feeding, while fishes with small gapes and kinetic jaws are proposed to be specialized for suction feeding (Norton 1995). Larger gapes are proposed to improve the capture success of ram or biting predators by increasing the volume of the capture apparatus (Norton 1991, 1995). In contrast, smaller gapes improve the capture success of suction feeding predators by increasing the velocity of water flow into the mouth (see pp. 134–137). More research is needed on the morphology of the feeding apparatus and feeding mechanics before such generalizations can be accepted.

Thus, upper jaw mobility varies widely by jaw suspension type and predictions of jaw mobility based on jaw suspension type are usually not supported. More detailed morphological and functional analyses are needed to further investigate the relationship of the jaw suspension to the feeding mechanism, in particular, studies are lacking on lamniform sharks.

Future directions

Our knowledge of the feeding behaviors, mechanisms, and mechanics of sharks has increased immensely since the early 1900s. There now exists a relatively good understanding of the diet of a subset of species, we have begun to model the mechanics of the feeding apparatus of a handful of species, and understand dental structure, tooth replacement and growth. An understanding of feeding behavior still lags behind many other aspects of their feeding biology, primarily because of the difficulty of recording natural feeding behavior of these predators. Consequently, a great deal of the data collected on their feeding behavior and kinematics is gleaned from their diets, fortuitous observations, and a handful of controlled feeding experiments either in the laboratory or field. As much as we have advanced in our understanding of these predators we have just begun in other areas of research. For example, we have little understanding of the evolution of feeding behaviors such as suction, ram, and biting in elasmobranchs. We therefore pose a variety of hypotheses and questions that remain to be addressed.

The functional specialization for suction-feeding hypothesis

Paleontological evidence and preliminary data on prey capture by more basal sharks including sixgill and sevengill sharks indicates that early sharks primarily grasped their prey with negligible suction. We hypothesize that from an early shark ancestor that was morphologically suited for biting and tearing its prey yet could undoubtedly employ some suction, morphological and functional specialization for suction feeding has arisen repeatedly in numerous elasmobranch clades.

The aquatic suction-feeding functional convergence hypothesis

Sharks have a relatively simple feeding apparatus composed of fewer anatomical elements compared to that of teleost fishes. Despite this, we hypothesize that due to

hydrodynamic constraints placed upon aquatic feeding vertebrates, many of the morphological and functional specializations for suction feeding that have arisen in sharks are convergent with those of inertial suction feeding bony fishes.

The feeding modulation hypothesis

Ram and biting carcharhinid and lamnid sharks appear to have a versatile and modulated prey capture kinematic sequence that varies with prey or food type, size and location. Conversely, suction feeding sharks appear to have capture events of shorter duration that are more stereotyped. We hypothesize that sharks which are morphologically specialized for inertial suction will have capture events that are more stereotyped with less modulatory ability than capture events from sharks that ram or bite. Furthermore, rapid suction captures will be pre-programmed stereotyped bites that go to completion once initiated, regardless of sensory input.

The independence of jaw suspension and feeding behavior hypothesis

Traditional studies have categorized different shark taxa based upon the anatomical arrangement of the jaws and cranium, and the suspension of the jaws. Preliminary work indicates that the extent of jaw protrusion, which has been proposed to be related to different prey capture behaviors, is not simply related to traditional jaw suspension types. We hypothesize that the overly simplistic categorization of traditional jaw suspension types (amphistylic, hyostylic) is not a good predictor of jaw mobility, and has a complex relationship with prey capture behavior (suction, ram biting, biting and gouging, filter feeding) and feeding performance.

In addition to these hypotheses we also pose questions that remain to be addressed: (1) How does prey capture differ among sharks, and are there still unexplored methods of prey capture yet to be revealed? (2) How do teeth function during prey capture and manipulation in the different feeding types? (3) Do most sharks have modulatory abilities similar to bony fishes? and (4) What are the functions of upper jaw protrusion in sharks? These hypotheses, questions, and their answers will help to guide research on the feeding biology of sharks into the next millennium.

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