

Evolution and ecology of feeding in elasmobranchs

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Synopsis Paleozoic chondrichthyans had a large gape, numerous spike-like teeth, limited cranial kinesis, and a non-suspensory hyoid, suggesting a feeding mechanism dominated by bite and ram. Modern sharks are characterized by a mobile upper jaw braced by a suspensory hyoid arch that is highly kinetic. In batoids, the upper jaw is dissociated from the cranium permitting extensive protrusion of the jaws. Similar to actinopterygians, the evolution of highly mobile mandibular and hyoid elements has been correlated with extensive radiation of feeding modes in elasmobranchs, particularly that of suction. Modern elasmobranchs possess a remarkable variety of feeding modes for a group containing so few species. Biting, suction or filter-feeding may be used in conjunction with ram to capture prey, with most species able to use a combination of behaviors during a strike. Suction-feeding has repeatedly arisen within all recent major elasmobranch clades and is associated with a suite of morphological and behavioral specializations. Prey capture in a diverse assemblage of purported suction-feeding elasmobranchs is investigated in this study. Drop in water pressure measured in the mouth and at the location of the prey shows that suction inflow drops off rapidly with distance from the predator's mouth. Elasmobranchs specializing in suction-feeding may be limited to bottom associated prey and because of their small gape may have a diet restricted to relatively small prey. Behavior can affect performance and overcome constraints imposed by the fluid medium. Suction performance can be enhanced by proximity to a substrate or by decreasing distance from predator to prey using various morphological and/or behavioral characteristics. Benthic suction-feeders benefit by the increased strike radius due to deflection of water flow when feeding close to a substrate, and perhaps require less accuracy when capturing prey. Suction and ram-suction-feeding elasmobranchs can also use suction inflow to draw prey to them from a short distance, while ram-feeding sharks must accelerate and overtake the prey. The relationship between feeding strategy and ecology may depend in part on ecological, mechanistic or evolutionary specialization. Mechanistic suction-feeding specialist elasmobranchs are primarily benthic, while most epibenthic and pelagic elasmobranchs are generalists and use ram, suction, and biting to catch a diversity of prey in various habitats. Some shark species are considered to be ecological specialists in choosing certain kinds of prey over others. Batoids are evolutionary specialists in having a flattened morphology and most are generalist feeders. Filter-feeding elasmobranchs are ecological, mechanistic, and evolutionary specialists.

Introduction

Arguably, one of the most successful groups of marine vertebrates are chondrichthyan fishes. The evolutionary history of this group spans some 400–450 million years when they diverged from actinopterygians (Long 1995; Nelson 2006). There are two main groups of chondrichthyan fishes: Holocephali (chimeras) and Elasmobranchii (sharks and rays), which are further subdivided into Selachii (sharks) and Batoidea (skates and rays) (Compagno et al. 2005) (Fig. 1). Galean sharks are comprised of horn, carpet, ground, and mackerel sharks, while Squalia include dogfish, angel, saw sharks, and possibly batoids. The goal of this article

is to give a brief review of feeding mechanisms in Chondrichthyes, evaluate prey-capture performance in a diverse assemblage of suction-feeding elasmobranchs, discuss suction-feeding in elasmobranchs and actinopterygians, and relate feeding behavior to ecology. First, the functional morphology of feeding in elasmobranchs and actinopterygians will be reviewed.

Cranial morphology

The elasmobranch cranial skeleton is composed of cartilages forming the upper (palatoquadrate) and lower jaw (Meckel's) suspended from the chondrocranium by the hyomandibulae

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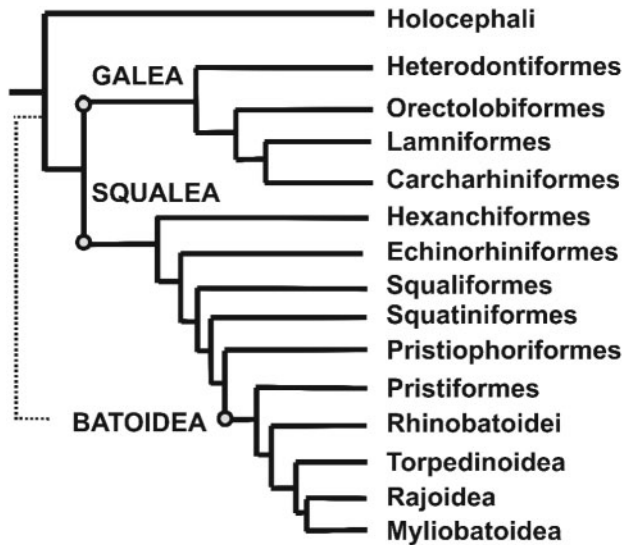


Fig. 1 Cladogram of extant chondrichthyans (after Shirai 1996). The dotted line represents an alternate scenario in which batoids are basal to neoselachians (Douady et al. 2003).

(dorsal element of hyoid arch) posteriorly and by craniopalatine (ethmopalatine) ligaments anteriorly. The hyomandibular cartilages may be oriented more laterally (e.g., squaliforms), more posterolaterally (e.g., carcharhiniforms), or more anterolaterally (e.g., batoids) pivoting on a fossa in the postero-lateral chondrocranial wall. Ligamentously bound to the distal hyomandibulae, the ceratohyals (ventral element of hyoid arch) connect at their distal ends to the unpaired basihyal cartilage. Together with the hypobranchials and basibranchials, the basihyal forms a slightly moveable “tongue” and the floor of the buccal and pharyngeal cavities.

The type of jaw suspension plays an integral role in the feeding mechanism of chondrichthyan fishes. The four taxonomic groups of chondrichthyes have evolved characteristic types of jaw suspension, with *Squalia* evolving two more types (Fig. 2). A hypothetical ancestral autodiastylic condition was proposed for gnathostomes and the common ancestor to the *Holocephali* and *Selachii* because it presented a nonfused autostylic state from which all other types of jaw suspension could be derived (De Beer and Moy-Thomas 1935; Grogan and Lund 2000). The autodiastylic state was predicted in the ancestral form (DeBeer and Moy-Thomas 1935) and was described as the condition in Carboniferous (318 million years old) chondrichthyans (Grogan and Lund 2000). In autodiastyly, the hyoid arch is nonsuspensorial, is similar in morphology to the branchial arches and articulates with the lower jaw. In this state, the upper jaw has ethmoidal and basal articulations with

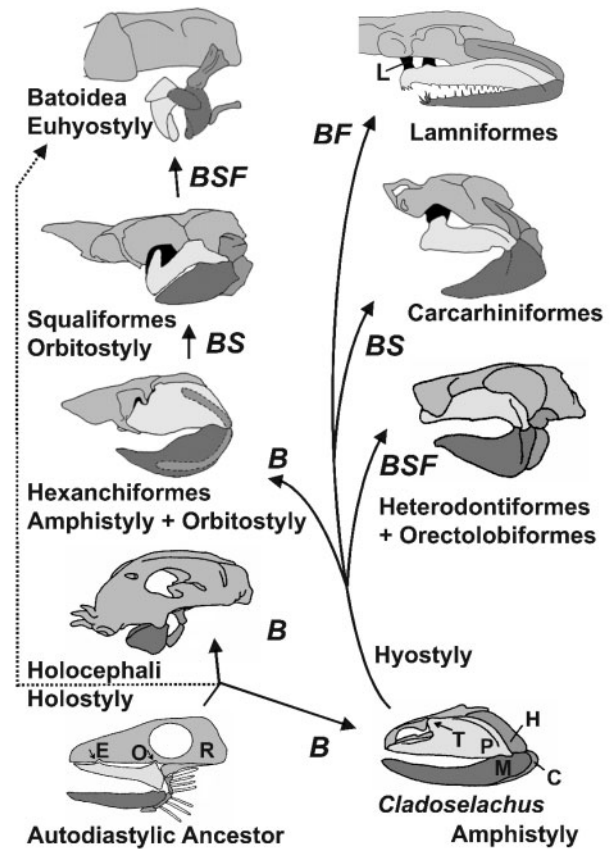


Fig. 2 Morpho-clinal transition predicted for the evolution of jaw suspension and feeding modes in chondrichthyans. Biting appears to be the basal feeding mode. Other feeding modes evolved with hyostyly, orbitostyly and euhystyly. C, ceratohyal; E, ethmoid articulation; H, hyomandibula; L, palatobasal articulation; M, lower jaw; O, orbital articulation; P, palatoquadrate; R, cranium; T, postorbital articulation. *B*, bite; *F*, filter; *S*, suction (Lund and Grogan 1997; Grogan et al. 1999; Grogan and Lund 2000; Wilga 2002, 2005).

the cranium, which are basal gnathostome characters (Janvier 1996). Subsequently, fusion of the palatoquadrate to the cranium evolved in holocephalans, while elaboration of craniopalatine articulations and modification of the dorsal hyoid element to form a suspensory hyomandibula evolved in sharks (Lund and Grogan 1997; Grogan et al. 1999). Amphistyly is morphologically more derived than holostyly and thus is unlikely to be the preceding morphological condition to holostyly in holocephalans (Lund and Grogan 1997; Grogan et al. 1999; Grogan and Lund 2000). Hexanchiform sharks retained the postorbital articulation while acquiring the orbitostylic articulation, and therefore, possess two jaw suspension types. The orbital articulation became prominent, while the postorbital articulation was lost in orbitostyly and this condition spread

throughout squalan sharks. If batoids are derived squaloids (Carvalho 1996; Shirai 1996), then loss of the orbital articulation and ethmopalatine ligaments creates a modified suspension that is “truly hyostylic” or euhyostylic with the hyomandibula functioning as the sole means of jaw support (Gregory 1904). In addition, the ceratohyal element of the hyoid arch became disconnected from the hyomandibula in euhyostyly. While in galean taxa, loss of the postorbital articulation also occurs in hyostyly (Maisey and Carvalho 1997), while lamniforms gained a single palatobasal ligament connecting the upper jaw to the cranium (Wilga 2005). If batoids are basal neoselachians (Douady et al. 2003), then both the ethmoid and orbital articulations were lost and the ceratohyal became disconnected in batoids but was not retained in sharks.

Cranial mobility

The specific morphology of the craniopalatine articulation is critical in influencing upper jaw kinetics, within, as well as among, different types of jaw suspension. Upper jaw protrusion (Fig. 3 bottom) varies greatly depending on the species, from slight protrusion with bracing by the ethmoid region to extensive protrusion, whereby the upper jaw completely clears the cranium and is attached only by stout craniopalatine ligaments (Fig. 2) (reviewed in Moss 1972; Frazzetta 1994; Frazzetta and Prange 1987; Motta and Wilga 2001; Wilga et al. 2001; Wilga 2002, 2005; Motta 2004). The extent of upper jaw protrusion varies at the level of order or family regardless of type of jaw suspension (Wilga 2002, 2005). For example, lemon sharks, *Negaprion brevirostris*, protrude the upper jaw further than bonnethead sharks do, *Sphyrna tiburo*, even though both are Carcharhiniformes and thus hyostylic (Wilga 2002). Furthermore, spiny dogfish, *Squalus acanthias* (Squalea, orbitostylic) have long ethmopalatine ligaments that allow the upper jaw to protrude just as far as that of Atlantic guitarfishes, *Rhinobatos lentiginosus* (Batoidea, euhyostylic) which lack the ligament. Finally, broadnose sevengill sharks, *Notorynchus cepedianus* (Squalea, amphistylic and orbitostylic) and *S. tiburo* (Galea, hyostylic), have very little upper jaw protrusion. Thus, a long ethmopalatine ligament or complete absence of the ligament allows the upper jaw to protrude further from the cranium (Wilga 2002).

The extent of cranial mobility also appears to be related to loading regimes on the jaw and suspensory cartilages (Huber 2006; Huber et al. 2005, 2006). The ethmoidal articulation remains connected during the full range of motion of the jaws in hyostylic species

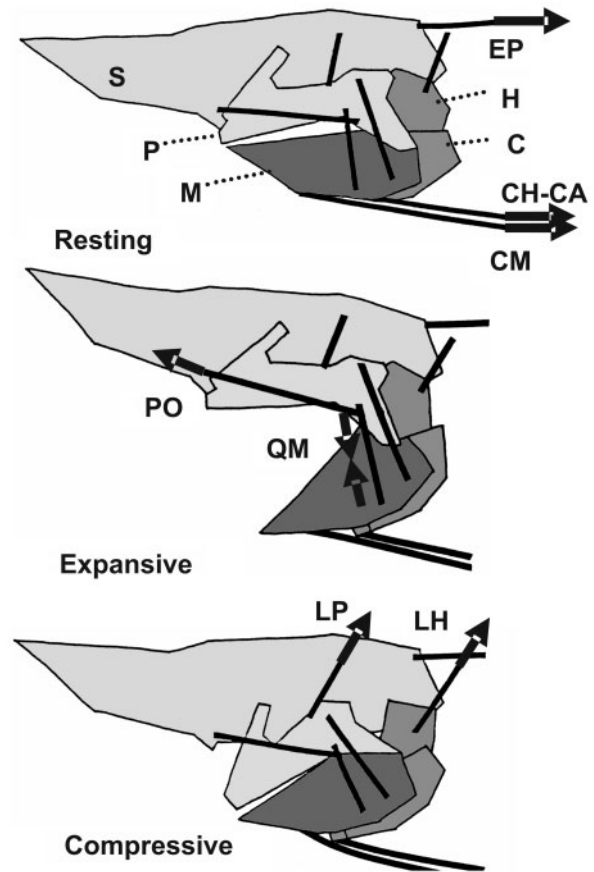


Fig. 3 Generalized feeding mechanism in sharks. Black lines indicate muscles and arrows indicate muscle activity in the associated phases. Skeletal abbreviations as in Fig. 2. CA, coracoarqualis; CH, coracohyoideus; CM, coracomandibularis; EP, epaxialis; LH, levator hyomandibularis; LP, levator palatoquadrate; PO, preorbitalis; QM quadratomandibularis (Wilga and Motta 1998a).

such as bamboo sharks (*Chiloscyllium plagiosum*) and horn sharks (*Heterodontus francisci*) as well as in an amphistylic species, sharpnose sevengill sharks (*Hepranchias perlo*). In these sharks, a static equilibrium analysis indicates that the ethmoid articulation is in compression while the hyomandibulae are in tension. In hyostylic sharks such as carcharhiniforms, the ethmoid articulation disengages, resulting in negligible or no tension on the articulation and considerable compression on the hyomandibulae. Based on current paleontological and evolutionary evidence, the change in loading regime with increased compressive loading on the hyomandibulae may have accompanied the change from amphistylic to hyostylic jaw suspension, resulting in more robust hyomandibulae with trabecular reinforcement and a consequent increased kinesis of the upper jaw (Huber 2006).

Feeding mechanism

The musculature that controls the feeding apparatus is highly conserved in chondrichthyans and relatively simple compared to that in actinopterygians, with the exception of the muscles that regulate protrusion of the upper jaw (reviewed in Liem and Summers 1999; Motta and Wilga 2001; Motta 2004). In the expansive phase of the feeding sequence (opening the mouth), the lower jaw is primarily depressed by the coracomandibularis and the hyoid arch by the coracoarcualis and coracohyoideus (Figs. 3 and 4). The mechanism for lower jaw and hyoid depression differs between chondrichthyans and actinopterygians (Wilga et al. 2000). Essentially, elasmobranchs have two independent parallel mechanisms, the lower jaw and the hyoid linkages. In contrast, the two linkages are in-series in actinopterygians; retraction of the hyoid depresses the lower jaw. Depression of the lower jaw in actinopterygians may also be controlled by an opercular linkage not present in elasmobranchs. In both groups, the cranium may be elevated by the epaxialis muscles depending on the relative position of the prey to the predator. The branchial arches play a crucial role in expansion of volume to accept the bolus of water taken in during suction-feeding (Wilga and Sanford, in revision) and are depressed by the coracobranchiales in elasmobranchs. The adductor mandibulae, composed of several preorbitalis and quadratomandibularis divisions, closes the jaws during the compressive phase of feeding. At the same time, the upper jaw is protruded primarily by

the preorbitalis, but also by the adductor mandibulae, when the lower jaw is depressed and fixed, and additionally by the levator palatoquadrati in carcharhinid sharks (Wilga et al. 2001). In orectolobid sharks, however, the upper jaw begins to protrude in the expansive phase. In the recovery phase, the depressed hyomandibulae and jaws are retracted by the levator hyomandibularis and in non-Carcharhinidae by the modified levator palatoquadrati as well. One striking difference in the feeding sequence is that most sharks and guitarfishes protrude the upper jaw during the compressive phase due to mechanical independence of the upper and lower jaws, while actinopterygians protrude in the expansive phase due to a mechanical coupling between the jaws (reviewed in Motta and Wilga 2001; Wilga et al. 2001; Motta 2004). However, similar to actinopterygians, some batoids and orectolobid sharks protrude the jaws during the expansive phase due to a tighter mechanical coupling of the jaws and the loss of craniopalatine articulations (see Batoidea in Fig. 2) (Dean and Motta 2004a, 2004b; Sasko et al. 2006; Duquette and Wilga 2007; Wilga and Sanford, in revision). Protrusion in elasmobranchs has been found to allow faster closure of the jaws and gouging of smaller pieces from prey too large to fit in the mouth (Tricas and McCosker 1984; Frazzetta 1994; Wilga et al. 2001).

Evolution of feeding strategies

Approximately 500 species of sharks occupy a diversity of niches from depths of 3700 m to surface

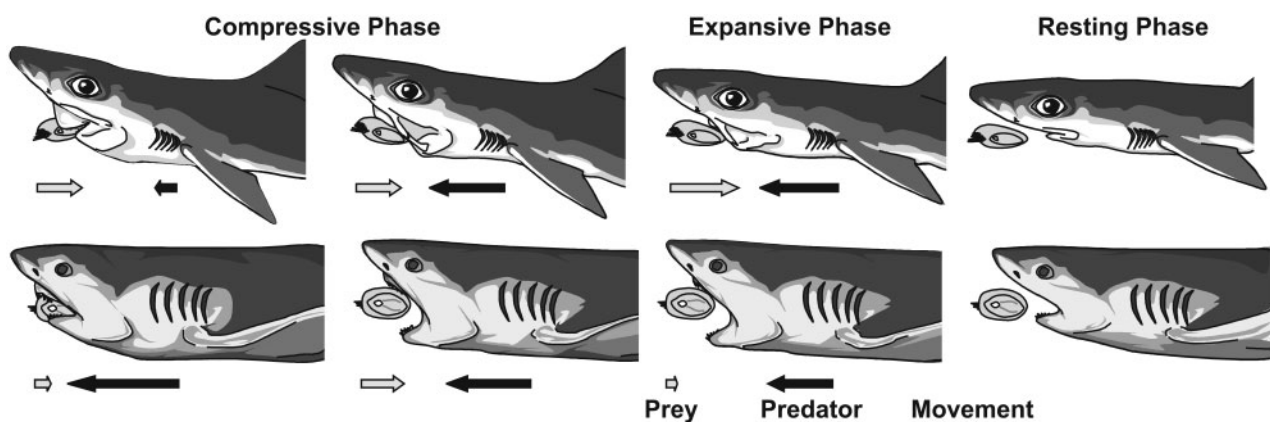


Fig. 4 Feeding sequence in sharks. Suction-bite (above) and bite-feeding (below) exemplified by spiny dogfish, *Squalus acanthias*, and lemon sharks, *Negaprion brevirostris*, respectively. Primarily ram (swimming towards prey) is used to approach prey by *N. brevirostris* while suction is also used to draw the prey to the mouth by *S. acanthias*. Both species use biting to seize the prey. The end of the resting phase just at the start of mouth opening is shown. The mouth is opened to peak gape in the expansive phase. The labial cartilages laterally occlude the gape in the suction-bite feeder. The compressive phase begins when the mouth begins to close and ends at peak protrusion of the upper jaw. Small pieces of food may completely enter the mouth during the expansive phase in suction specialists or the jaw may close on larger pieces as illustrated. (after Wilga and Motta 1998a; Motta et al. 1997). Gray and black arrows indicate relative prey and predator movement respectively from one panel to the next.

tide pools, yet all are carnivorous and stalk, ambush, engulf or chase prey ranging from worms to whales with minimal modification of the feeding apparatus. Central to this evolutionary success is a prey-capture mechanism that has allowed elasmobranchs to radiate into numerous niches encompassing biting, suction-feeding and filter-feeding (Moss 1977; Motta 2004), sometimes in conjunction with ram (movement of the predator towards the prey) (Fig. 4). Captured prey is processed by various mechanisms: blowing and suctioning to reposition the prey; crushing, gouging, and biting that may be coupled with head shaking to reduce the prey. Following numerous early studies on the anatomy of the jaws and head (reviewed by Motta and Wilga 1995, 1999) there has recently been an upsurge in the literature on the kinematics, functional morphology and biomechanics of the feeding mechanism (reviewed in considerable detail by Frazzetta 1994; Liem and Summers 1999; Motta and Wilga 2001; Motta 2004). Capture behavior and cranial morphology superimposed onto an evolutionary history indicates that bite-feeding is the ancestral mode of prey capture for fossil chondrichthyans recovered to date and is retained in most taxa (Fig. 2). There has been a general increase in jaw kinesis as hyostyly and orbitostyly evolved, allowing large gouging bites in Carcharhiniformes and Lamniformes and specialized cutting behaviors in Squaliformes. The ability to suction-feed in addition to bite-feeding has evolved in most groups (Squaliformes, Batoidea, and Carcharhiniformes), while obligate suction-feeding has evolved in Orectolobiformes and Heterodontiformes, and independently in some Batoidea. It is likely that extinct sharks were, and modern chimeras and hexanchiform sharks are capable of generating weak suction by rapidly opening the mouth. This method, however, may not be as effective in these species as biting when capturing prey. Finally, filter-feeding has evolved in at least one species each in Orectolobiformes, Lamniformes, and Batoidea.

Suction-feeding in actinopterygian fishes

Suction-feeding is the most prevalent form of prey capture in actinopterygians (Liem 1980a, 1980b; Lauder 1985). Pelagic, epibenthic, and benthic actinopterygians commonly use suction to capture suspended, attached and elusive prey (Liem 1980a; Norton 1995; Ferry-Graham and Lauder 2001). Suction-feeding is characterized by a rapid expansive phase, lasting 50–100 ms, followed by a compressive phase when the mouth closes (Ferry-Graham et al. 2003; Westneat 2006). Sometimes the expansive phase is preceded by a preparatory phase, where

the mouth cavity volume slightly decreases maximizing volume change during the expansive phase. Head motions during the expansive phase include neurocranial elevation, opercular rotation and abduction, abduction of the suspensorium, hyoid depression, depression of the lower jaw, and protrusion of the upper jaw. The gape is occluded laterally by the premaxilla, maxilla, and soft tissue in suction-feeders, such that a tubular opening is formed (Lauder 1979). Suction-feeding is enhanced by fishes with a small gape and large mouth opening muscles as in bluegill sunfish, *Lepomis macrochirus*, but large mouthed fishes with large mouth closing muscles like largemouth bass, *Micropterus salmoides*, or tarpon, *Megalops atlanticus*, combine suction with ram. A trade-off exists between gape size for high-velocity, low-volume suction versus low-velocity, high-volume suction, respectively (Liem 1980a; Lauder 1985; Grubich 2001; Carroll et al. 2004; Higham et al. 2005, 2006a, 2006b; Westneat 2006). Small-mouthed predators with larger epaxial cross-sectional areas are able to generate higher forces and thus rapid fluid speeds and greater pressure during suction. In contrast, large mouthed predators with linkage systems that favor large movements ingest a larger volume of water, but also use ram to compensate for the lower velocity of fluid flow.

Numerous studies have tested theoretical models of suction-feeding in actinopterygian fishes (Muller et al. 1982; Van Leeuwen and Muller 1983, 1984; Muller and Osse 1984). These findings have revealed that water pressure decreases rapidly as the mouth opens, resulting in large drops of 10–30 kPa (Alexander 1969, 1970; Lauder 1980, 1983; Liem 1980b; Van Leeuwen and Muller 1983; Muller and Osse 1984; Nemeth 1997a; Sanford and Wainwright 2002; Higham et al. 2005, 2006a; Westneat 2006). The greatest subambient pressure and thus fluid speed at the mouth occurs early in the strike cycle, when the rate of buccal expansion and hyoid depression is the greatest just prior to peak gape (Van Wassenbergh et al. 2005, 2006). Water is drawn into the mouth from a spherical shaped region around the mouth of a suction-feeding fish in the water column (Ferry-Graham et al. 2003; Higham et al. 2005). Since the velocity of water flow drops off exponentially with distance, suction is only effective within approximately one mouth width distance in front of the mouth. Additional velocity due to ram at the same time as suction results in a more elongate but more narrow volume of water taken in at higher fluid speeds than by suction alone (Higham et al. 2005). This allows the predator to close more quickly on the prey, while still using suction, facilitating the

capture of more elusive prey (for example, Wainwright et al. 2001; Svanback et al. 2002; Ferry-Graham et al. 2003; Carroll et al. 2004; Day et al. 2005; Higham et al. 2006a, 2006b, 2007). At least for one species of actinopterygian fish, common snook *Centropomus undecimalis*, suction pressure does not scale with total length (Wainwright et al. 2006). The volume of water ingested, however, increases with size. In catfish, *Clarias gariepinus*, the absolute distance from which prey can be sucked into the mouth increases with size of predator due to more sustained suction flow (Van Wassenbergh et al. 2006). These findings support the notion that larger fish generate a higher volume of flow, presumably making them more effective at capturing larger prey and from greater distances (Wainwright et al. 2006).

The mechanism for suction-feeding in elasmobranchs and actinopterygians differs due to fundamental differences in the cranial skeleton that controls the feeding apparatus (Wilga and Sanford, in revision). A recent study found that *C. plagiosum* is able to generate large suction pressures, while paradoxically compressing the hyoid cavity laterally (Wilga and Sanford, in revision). Differences in the architecture of jaw suspension means that in elasmobranchs, only ventral depression of the hyoid takes place during suction feeding in *C. plagiosum*, while in actinopterygians the hyoid cavity expands both laterally and ventrally. This paradoxical mechanism of expansion in elasmobranchs leads to a delay in the generation of peak suction pressure in *C. plagiosum* compared to actinopterygians and represents a significant divergence in the suction-feeding mechanism of elasmobranch and actinopterygian fishes (Wilga and Sanford, in revision).

Materials and methods

Animals

Spiny dogfish, *Squalus acanthias*, and little skates, *Leucoraja erinacea*, were obtained by otter trawl from Narragansett Bay. Dogfish and skates were housed separately in 38,611 and 4826 liter (16°C) circular tanks, respectively, and maintained on a diet of squid (*Loligo*, sp.) and fish (*Menidia menidia*, *Clupea harengus*). Three dogfish and three skates with mean total lengths of 78 cm (77, 77, 86) and 46 cm (45, 46, 48), respectively, were studied. Food was withheld from individuals for four days prior to the experiment. Each individual fish was acclimated to the experimental tank prior to each experiment. Bamboo shark, *Chiloscyllium plagiosum* data is from Sanford and Wilga (in review) and Wilga and Sanford (in revision). These animals had a mean

total length of 73 cm (69, 71, 74, 76 cm) and were fed squid *Loligo* sp. pieces. Nurse sharks, *Ginglymostoma cirratum*, with a mean total length of 89 cm (82, 83, 103) were fed with pieces of Atlantic herring (data from Motta et al., manuscript in preparation).

Pressure with simultaneous video

Each fish was initially anesthetized for surgery with a 0.1 g l⁻¹ solution of tricaine methanesulfonate (MS-222), diluted to 0.05 g l⁻¹ during implantation of the pressure transducer. Width of the mouth and total length of the body were measured. Two Millar SPR-799 microcatheter side-tipped pressure transducers were used, one transducer was surgically placed in the buccal cavity of the fish and the second transducer was positioned at the site of the prey. For the buccal cavity, the pressure transducer was threaded through a plastic cannula, inserted through one of the fifth gill slits, and then sutured to the midline of the roof of the mouth just behind the jaws. The transducer was also fixed to the skin above the pectoral fin by suture. The second transducer was taped to a two-pronged stick with the food placed on one prong and the transducer on the other with the sensor facing upwards. A similar arrangement was used for *Chiloscyllium plagiosum* (Wilga and Sanford, in revision), while for *Ginglymostoma cirratum* (Motta et al., manuscript in preparation) the transducer was fixed inside a PVC pipe with the food placed behind the transducer from which the shark sucked the prey out. The signals from the pressure probes were amplified (Millar PCU-2000) and then connected to a data-acquisition unit (National Instruments or Sonometrics Corp.). Video recordings were recorded in ventral view using a Photron Fastcam 1280 PCI model or a Redlake PCI 500 Motionscope high-speed camera at 250 field s⁻¹. Video and pressure data were recorded simultaneously and synchronized either by the National Instruments data-acquisition unit or by a custom-made (by Mike Boller) microcontroller wave-form generator that provided coded output to the video image and data-acquisition unit, simultaneously. After the 10 min surgery to implant the transducer, the fish was allowed to recover in the experimental tank until normal swimming behavior commenced, usually 1 h. Experiments began by feeding the fish with squid cut into pieces 1 mw by ½ mw.

Recordings of pressure in the buccal cavity and at the location of the prey relative to ambient were analyzed using Photron Motion Tools (Photron USA V. 1.2) or SonoVIEW (Sonometrics V. 3.3.4). The variables were: magnitude of ambient pressure,

time of onset, time of peak, and magnitude of peak subambient pressure. Video recordings were digitized using Didge (Alistair Callum) for the following kinematic variables: time of onset of lower jaw depression, time of peak lower jaw depression; position of the left corner and right corner of the mouth, and the position of the transducer sensor at the time of peak depression of the lower jaw. The distance of the transducer to the center of the mouth was calculated as the distance from the sensor to a point at the center of the mouth calculated at the midpoint between the left and right corners of the mouth. Time variables were standardized using peak buccal pressure as “time zero”. Scaled peak subambient pressure (divided by mw) in the buccal cavity was calculated for *Chiloscyllium plagiosum* and *Ginglymostoma cirratum*. These two species of suction-feeders are closely related and are morphologically similar, but differ in mw and body size.

The ram–suction index (RSI) is commonly used to assess the relative contribution of ram due to movements of the predator and prey versus suction due to the prey’s movement (Norton and Brainerd 1993). RSI values were calculated for each feeding event as well as from the literature (see Results section): $RSI = (D_{\text{predator}} - D_{\text{prey}}) / (D_{\text{predator}} + D_{\text{prey}})$, where D is the distance moved by the predator or prey during the strike.

Results

The four elasmobranchs used in this study are suction ventilators, thus the precise onset of lower jaw depression was difficult to assess during feeding. Therefore, the onset of lower jaw depression was calculated as the time that the gape reaches 10% of its peak, usually corresponding to the fast-opening phase of the expansive phase (Sanford and Wainwright 2002; Wilga and Sanford, in revision). Little skates, *Leucoraja erinacea*, routinely capture prey using a combination of biting and suction. Depression of the lower jaw occurs very early at a mean of -74 ± 30 ms, with the onset of subambient buccal pressure following shortly thereafter at -53 ± 27 ms (Fig. 5). As *L. erinacea* grasped the prey with the jaws, relatively weak subambient pressure was recorded in the buccal cavity (mean -1.4 ± 0.94 kPa, up to -3.7 kPa). Mean duration of lower jaw depression is 66 ± 28 ms with peak lower jaw depression occurring at -8 ± 38 ms. There is no relationship between external pressure at the prey (kPa) and distance ($\text{cm } mw^{-1}$) ($r^2 = 0.01$, $P = 0.60$). Mean RSI is -0.14 with a range of -0.61 to 0.52 .

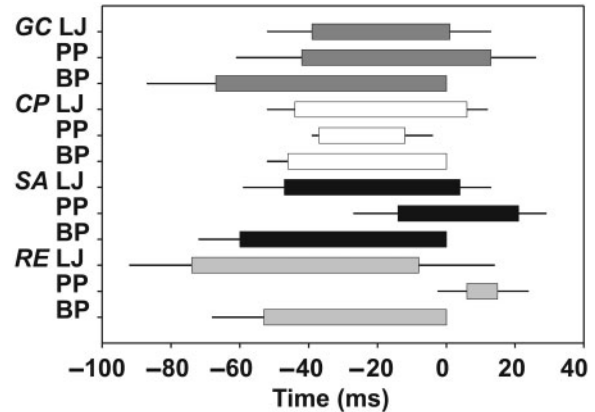


Fig. 5 Bar plot of mean pressure and kinematic variables in four elasmobranchs. CP, *C. plagiosum* white bars; GC, *G. cirratum* dark gray bars; RE, *L. erinacea* light gray bars; SA, *S. acanthias* black bars. The left side of the bar represents mean onset of activity and the right side of the bar represents mean peak activity. The lines indicated one standard error of onset and peak activity at the left and right sides of the bar, respectively. BP, buccal pressure (peak is time 0); LJ, lower jaw depression (the time that 10% of peak gape has been reached); PP, pressure at the prey.

Spiny dogfish, *Squalus acanthias*, also routinely capture prey using a combination of suction and bite mechanisms. Although, *S. acanthias* uses weak to moderate suction to bring the prey closer to the mouth while swimming, the jaws typically close on the prey. Lower jaw depression occurs at a mean of -47 ± 21 ms with the onset of subambient buccal pressure occurring at -60 ± 21 ms (Fig. 5). Relatively, weak subambient pressure was recorded in the buccal cavity (mean -2.08 ± 1.14 kPa, up to -4.46 kPa). Mean duration of lower jaw depression is 56 ± 25 ms with peak depression of the lower jaw occurring at 4 ± 15 ms. There is no relationship between external pressure at the prey (kPa) and relative probe distance ($\text{cm } mw^{-1}$) ($r^2 = 0.13$, $P = 0.96$). Mean RSI is 0.237 with a range of -0.32 to 0.74 .

Whitespotted bamboo sharks, *Chiloscyllium plagiosum*, always captured prey using suction and had the shortest capture duration. Depression of the lower jaw occurs early at a mean of -44 ± 16 ms with the onset of subambient buccal pressure occurring almost simultaneously at -46 ± 11 ms. Relatively, strong subambient pressure was recorded in the buccal cavity (mean -20.60 ± 11.95 kPa, up to -45.46 kPa). Scaled peak subambient pressure (divided by mw) in the buccal cavity is -8.94 ± 5.06 kPa mw^{-1} (up to -18.94). Mean duration of lower jaw depression is 37 ± 11 ms with peak lower jaw depression occurring at 6 ± 12 ms. The best fit relationship between external pressure

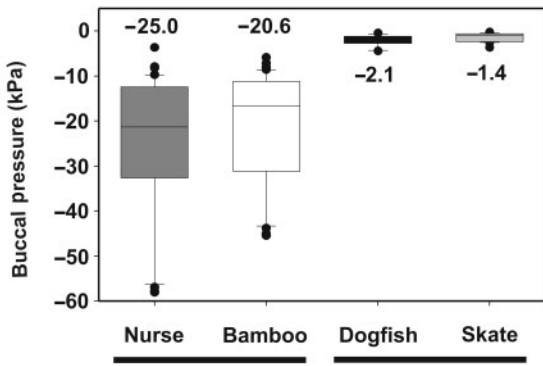


Fig. 6 Whisker plot of buccal pressure in four elasmobranchs. Numbers indicate mean pressure. Bars that do not overlap indicate significant differences among species ($P < 0.001$). Nurse sharks and bamboo sharks generate similar buccal pressures that are greater than those of dogfish and skates, which also generate similar buccal pressures ($P < 0.001$). When scaled to size of the mouth opening, *C. plagiosum* (because of its smaller mouth) generates greater buccal pressure than does *G. cirratum*.

at the prey (kPa) and relative probe distance (cm mw^{-1}) is a third-order polynomial regression ($r^2 = 0.244$, $P = 0.002$, $y = -11.217 + (25.602 \times x) - (20.125 \times x^2) + (5.251 \times x^3)$). Mean RSI is -0.53 with a range of -0.93 to -0.05 .

Nurse sharks, *Ginglymostoma cirratum*, also always captured prey using suction. Lower jaw depression occurs early at a mean of -39 ± 23 ms with the onset of subambient buccal pressure occurring at -67 ± 35 ms. Relatively strong subambient pressure was recorded in the buccal cavity (mean -25 ± 16 kPa, up to -68 kPa). Scaled peak subambient pressure (divided by mw) in the buccal cavity is -4 ± 3 kPa mw^{-1} (up to -11). Mean duration of lower jaw depression is 40 ± 26 ms with peak lower jaw depression occurring at 1 ± 20 ms. Distance of the external pressure probe in front of the shark was not recorded for this species. Mean RSI is -0.42 with a range of -0.24 to -0.55 (Robinson and Motta 2002).

One-way analysis of variance (ANOVA) tests reveal several differences in the time and magnitude of responses among the elasmobranch species (Fig. 5). Depression of the lower jaw begins earlier in *L. erinacea* than in *S. acanthias*, *C. plagiossum* and *G. cirratum* ($P < 0.001$). The duration of lower-jaw depression is shorter in *C. plagiosum* and *G. cirratum* than in *L. erinacea* than *S. acanthias* ($P = 0.001$). Peak lower jaw depression occurs earlier in *L. erinacea* compared to the others ($P = 0.005$). Peak subambient pressure in the buccal cavity is greater in *C. plagiosum* and *G. cirratum* than in *L. erinacea* and *S. acanthias* ($P < 0.001$), with *C. plagiosum* greater than *G. cirratum* when scaled to mw ($P < 0.001$) (Fig. 6).

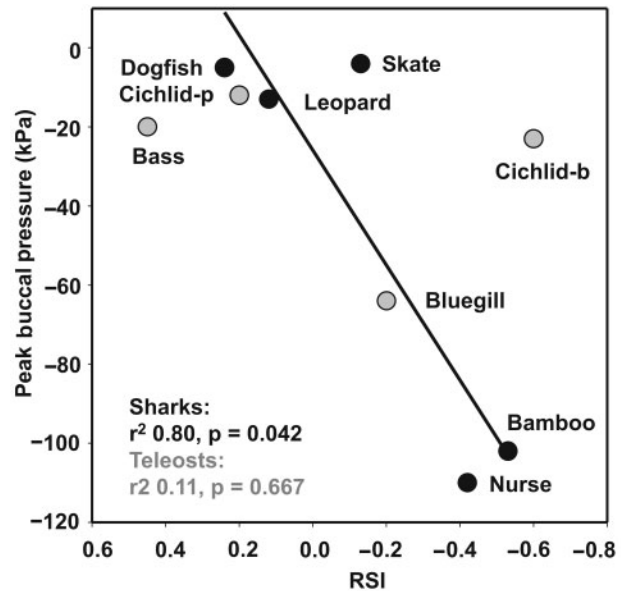


Fig. 7 Plot of ram-suction index (RSI) versus peak buccal pressure in fishes. Black circles indicate elasmobranchs and gray circles represent teleost fishes. Bamboo, *Chiloscyllium plagiosum*; Bass, largemouth *Micropterus salmoides*; Bluegill *Lepomis macrochirus*; Cichlid -b, banded *Heros severus*; Cichlid-p, peacock cichlid *Aulonocara hansbaenschii*; Dogfish, *Squalus acanthias*; Leopard, *Triakis semifasciata*; Nurse, *Ginglymostoma cirratum*; Skate, *Leucoraja erinacea* (Lauder 1980; Ferry-Graham 1998; Norton and Brainerd 1993; Sanford and Wainwright 2002; Robinson and Motta 2002; Svanback et al. 2002; Dean and Motta 2004; Carroll and Wainwright 2006; Higham et al. 2006; Wainwright et al. 2006; Wilga and Sanford, In revision; Lowry et al., manuscript in preparation; Motta et al., manuscript in preparation).

Ram-suction index values are inversely related to peak buccal pressure for elasmobranchs ($r^2 = 0.80$, $P = 0.042$) but not for teleosts ($r^2 = 0.11$, $P = 0.667$) as indicated by values from the present study and from the literature (Fig. 7) (Lauder 1980; Ferry-Graham 1998; Norton and Brainerd 1993; Sanford and Wainwright 2002; Robinson and Motta 2002; Svanback et al. 2002; Dean and Motta 2004b; Carroll and Wainwright 2006; Higham et al. 2006b; Wainwright et al. 2006; Wilga and Sanford, in revision; Lowry et al., manuscript in preparation; Motta et al., manuscript in preparation).

A third-order relationship between external pressure at the prey and the relative distance of the probe from the mouth was found in *C. plagiosum* ($r^2 = 0.244$, $P = 0.002$) (Fig. 8). In contrast, no relationship exists between external pressure and distance in *S. acanthias* ($r^2 = 0.130$, $P = 0.96$) and *L. erinacea* ($r^2 = 0.01$, $P = 0.60$) (Fig. 8).

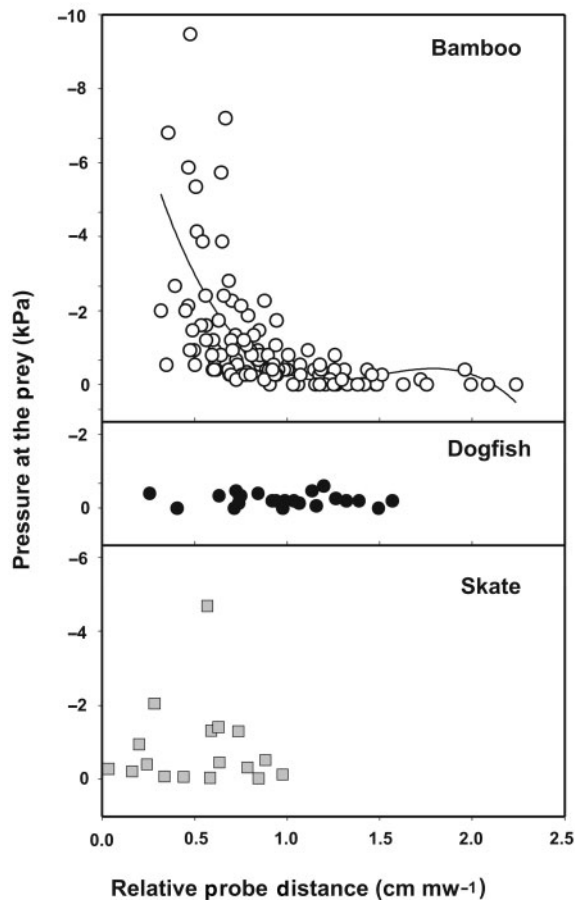


Fig. 8 Plots of pressure at the prey versus distance for three elasmobranchs. A third-order relationship exists for *Chiloscyllium plagiosum* (Bamboo), while no relationship exists for *S. acanthias* (Dogfish) and *L. erinacea* (Skate).

Discussion

Prey capture performance

Suction capture performance varied widely among four diverse supposed suction-feeding elasmobranchs. *C. plagiosum* and *G. cirratum* (Orectolobiformes), always used strong suction (mean -21 and -25 kPa, respectively) to capture the prey, as has been found in previous studies on orectolobiform species (Motta et al. 2002; Robinson and Motta 2002; Nauwelaerts et al. 2007). In contrast, primarily ram, i.e., swimming towards the prey as the mouth opens, coupled with weak to moderate suction (mean -2.1 kPa) and biting was used by adult *Squalus acanthias* here (Squaliformes), in contrast to a previous study in which the prey frequently was observed to be drawn rapidly into the mouth of juvenile *S. acanthias* (Wilga and Motta 1998a). Either an ontogenetic change in feeding mechanism occurs in *S. acanthias* or the prey was not offered in such a way as to elicit a similar

behavior. Interestingly, *L. erinacea* (Rajoidea) captured the prey by rapidly grasping it between the jaws and elevating the head, i.e., biting combined with weak suction (mean -1.5 kPa). Stronger suction was used to transport the prey (mean -5.9 kPa) as was found previously (Duquette and Wilga 2007). The basal batoid, *Rhinobatos lentiginosus* (Rhinobatoidei), uses suction combined with ram to capture prey with similar RSI values (mean -0.11), while an intermediate species, lesser electric rays *Narcine basiliensis* (Torpedinoidea) always uses strong suction to capture prey (mean -22 kPa) (Wilga and Motta, 1998b; Dean and Motta, 2004b). These batoids probe the substrate for infauna and thus there appears to be a species-specific preference in the use of suction and biting to extract prey from the substrate.

The obligate suction-feeders can be distinguished from those species in the present study that use a combination of biting and suction in feeding (Fig. 5). Subambient pressure generated in the buccal cavity depends on rapid opening of the mouth and expansion of the buccal cavity to draw water rapidly into the mouth. Accordingly, jaw kinematics and pressure patterns for the obligate suction-feeders *C. plagiosum* and *G. cirratum* are similar in having a shorter duration of mouth opening and an earlier generation of subambient pressure that rapidly drags the prey into the mouth. In contrast, *S. acanthias* and *L. erinacea* open their mouths earlier and hold them open for a longer duration as is typical of bite-feeders with relatively weaker suction pressure generated later in the feeding event than the obligate suction-feeders. These bite-suction-feeders use ram to move towards the prey and seize the prey with the jaws. The drop in buccal pressure well before lower jaw depression in *G. cirratum* and *L. erinacea* may be explained by several factors. The onset of lower jaw depression used (the time at which 10% of peak gape was attained) artificially delays the time of onset. Alternately, ram or other movements by the predator (Van Leeuwen and Muller 1983) or early expansion of more posterior regions could affect suction pressure.

As expected, peak subambient buccal pressure is far greater in the obligate suction-feeders than the suction-bite feeders. Subambient suction pressure as low as -109 and -102 kPa have been recorded for *G. cirratum* and *C. plagiosum* respectively (Tanaka 1973; Lowry and Motta, manuscript in preparation; Motta et al., manuscript in preparation; Wilga and Sanford, in revision). The two closely related orectolobid species, *C. plagiosum* and *G. cirratum*,

have similar enlarged muscles that expand the buccal cavity (Motta and Wilga 1999; Sanford and Wilga in review), but *C. plagiosum* has a relatively smaller mouth. When scaled to size of the mouth opening, *C. plagiosum* generates greater buccal pressure than does *G. cirratum*, suggesting that in morphologically similar species, smaller mouthed predators can generate higher suction pressures (Higham et al. 2006b).

In leopard sharks, *Triakis semifasciata*, and *C. plagiosum*, maximum suction pressure increases with body size, to a greater extent in the latter which is an obligate suction-feeder (Lowry 2005; Ramsay and Wilga 2006; Motta et al., manuscript in preparation; Sanford and Wilga, in review). Faster expansion of the mouth and hyoid depression results in stronger suction pressure in these species. The shape of the parcel of water drawn into the mouth did not change with growth regardless of size in *T. semifasciata* or *C. plagiosum*, with the former being more elliptical and the latter more rounded (Lowry 2005). The forward ram component of the strike in *T. semifasciata* focuses the parcel of water moved into the mouth into a more elliptical shape, similar to that in bony fishes (Higham et al. 2005; Lowry 2005).

RSI correlates to peak buccal pressure

Ram-suction index values are a good predictor of maximum buccal pressure for elasmobranchs although not for teleosts (Fig. 7). RSI is inversely related to maximum buccal pressure for elasmobranchs with no clear relationship for teleosts as shown by the present study and data from others (see Fig. 7 caption). The further the prey is drawn towards the predator and the less predator movement, the smaller the RSI value, regardless of the magnitude of subambient suction generated. The obligate suction-feeding elasmobranchs, *C. plagiosum* and *G. cirratum*, group together in the part of the graph denoting high suction pressure and low RSI in the RSI-pressure plot. These two species sit relatively still on the bottom when feeding and hence have a smaller ram component. *Leucoraja erinacea* is also benthic, but protrudes the jaws to catch prey rather than using suction; it appears in the part of the plot denoting low suction pressure and intermediate RSI. While *S. acanthias* will take prey from all water levels, *T. semifasciata* is epibenthic and thus swimming towards the prey is an essential part of capture of prey as reflected by their values grouping in the part of the graph denoting low suction pressure and high RSI. Similarly, some suction-feeding teleosts use

ram to approach the prey thus their values are widely scattered on the pressure-RSI plot.

Suction-feeding in elasmobranch and actinopterygian fishes

Suction-feeding in elasmobranchs apparently differs from actinopterygians in that specialization for capture by suction only is primarily confined to benthic species, with the exception of whale sharks *R. typus*. Epibenthic species may employ suction in conjunction with biting, while using ram and apparently are not as specialized for suction as are benthic species (Motta 2004). Suction specialists have terminal or subterminal mouths that are laterally occluded by large labial cartilages to form a rounded gape ringed by relatively small teeth and hypertrophied abductor muscles that generate great expansive forces (Fig. 9) (reviewed in Motta and Wilga 2001; Motta 2004). It is interesting to note, however, that benthic elasmobranchs such as chain catsharks, *S. retifer*, which have a morphology typically associated with bite-feeding are strong suction-feeders (Ajemain and Sanford, 2007). The duration of mouth opening in suction-feeding specialist sharks is shorter than that in bite-feeding sharks, regardless of size, and ranges from 30–100 ms. Elevation of the cranium and protrusion of the upper jaw generally do not contribute to buccal expansion in sharks that are suction specialists as cranial elevation and upper jaw

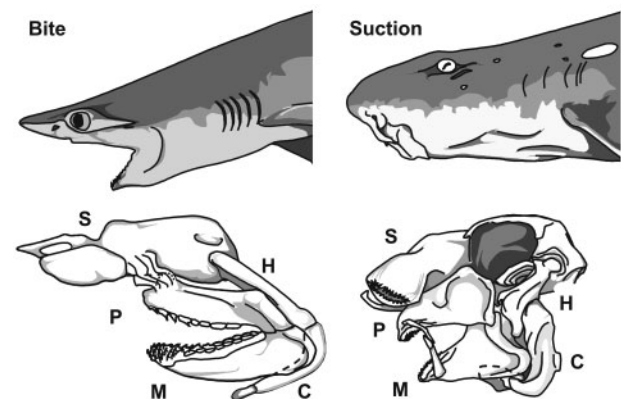


Fig. 9 Cranium and feeding apparatus of bite-feeding and suction-feeding specialists. Top, head of the bite-feeding bonnethead shark *Sphyrna tiburo* (left) and a suction-feeding whitespotted bamboo, *C. plagiosum* (right) at peak gape. In *C. plagiosum*, the large labial cartilages laterally occlude the gape in and there is little or no cranial elevation. Bottom, cranial morphology of the same species shown above. Note the protrusible upper jaw of *S. tiburo* that loses its firm connection to the cranium, whereas the upper jaw of *C. plagiosum* slides forward at its ethmoidal articulation but does not dissociate from the cranium. Skeletal abbreviations as in Fig. 2.

protrusion are often absent or slight (Wu 1994; Motta et al. 2002; Motta 2004; Lowry 2005; Wilga and Sanford, in revision). However, simultaneous protrusion of the upper and lower jaws may occur during the expansive phase in some batoids, thereby augmenting volume and also increasing ram in specialized suction-feeders (Dean and Motta 2004b) as well as expanding the gape in bite-feeders (Duquette and Wilga 2007). Bite-feeding specialists have larger mouths that open laterally to allow a larger bite (Fig. 9) and typically elevate the cranium to increase the gape. Adductive bite force is not simply related to prey capture method, prey processing methods must also be considered. A species that suction captures and crushes hard prey, *Heterodontus francisci*, and a bite-feeding species, sharpnose sevengill sharks *Heptranchias perlo*, generate greater adductive bite force than another bite-feeding, *Negaprion brevirostris*, and suction-feeding species, *C. plagiosum* (Huber 2006).

For suction-feeding to be effective, a parcel of water must be moved rapidly enough into the mouth of the predator to minimize the chance of the prey escaping (Muller et al. 1982; Van Leeuwen and Muller 1984). In *C. plagiosum*, suction pressure drops exponentially with distance from the mouth, with weak suction pressure similar to the buccal pressures generated by *S. acanthias* and *L. erinacea* measured up to 2.0 mw distant (Fig. 8). However, the distance of the flow field generated by *C. plagiosum* during suction-feeding on the substrate is increased up to 2.5 mw, when truncated by a substrate compared to that in the water column (Fig. 10) (Nauwelaerts et al. 2007). Feeding near a substrate extends the distance over which suction is effective, particularly when combined with a long pre-oral snout (Nauwelaerts et al. 2007). This feeding strategy can benefit benthic predators by increasing the radius of the strike and reducing the accuracy necessary for capturing prey successfully (Nauwelaerts et al. 2007). The benthic suction specialist, *G. cirratum*, captures pieces of food up to 3.0 cm away or 1.4 mw, regardless of shark size (Motta et al., manuscript in preparation). Similarly, an epibenthic shark, *T. semifasciata*, also successfully captures prey by suction from the substrate up to 4.5 cm away or 1.7 mw (Lowry 2005). In contrast, there is no relationship between suction pressure and distance for *S. acanthias* and *L. erinacea*, which in this study used little suction but greater bite and ram.

Behavior may affect performance and overcome the constraints imposed by the fluid medium. Suction performance may be enhanced by proximity

to a substrate or by decreasing distance between predator and prey using morphological and/or behavioral characteristics. Bottom-feeding nurse sharks, *G. cirratum*, push their heads into reef crevices to suck out prey (Cathy Church, personal communication), a behavior that may effectively extend the suction distance by truncating flow, as demonstrated for *C. plagiosum* (Nauwelaerts et al. 2007). Many skates and rays use suction and blowing to fluidize the sediment and extract prey concealed therein (Sasko et al. 2006). Cownose rays use the cephalic lobes to form a chamber around the mouth and use suction to capture prey (Motta 2004; Sasko et al. 2006). Extension of the lobes may act to increase the effective suction distance by deflecting the flow between the lobes, thus acting as substrates. Specialized suction-feeding elasmobranchs may be restricted in dietary choice to smaller prey due to the relatively small gape (Dean and Motta 2004b; Motta et al., manuscript in preparation). However, suction, suction-ram, and suction-bite-feeding elasmobranchs can use suction inflow to draw prey to them a short distance, and therefore, do not have to get as close to the prey as bite-feeding sharks which must use ram in the form of ambushing or chasing prey close enough to grab them in the jaws.

Several factors related to fundamental morphological differences appear to distinguish suction-feeding behavior in chondrichthyans and actinopterygians. A relationship between RSI and peak buccal pressure

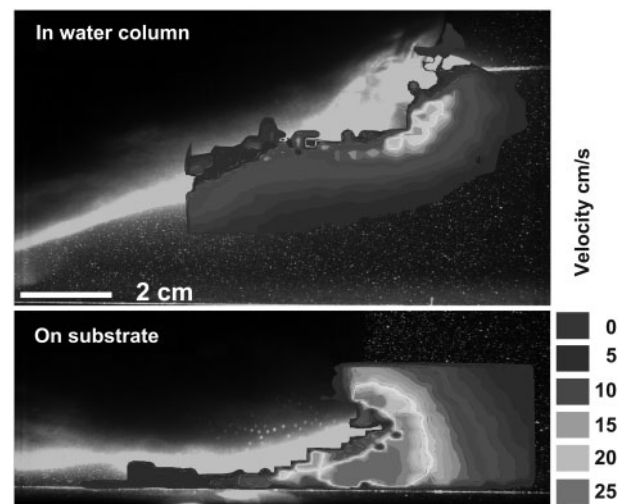


Fig. 10 Fluid dynamics of suction-feeding. Feeding near a substrate extends the distance over which suction is effective by up to 2.5 times compared to that in (anterior is to the right) of the head of *C. plagiosum* feeding in the water column and on the substrate. Intensity of shading represents water velocity into the mouth. Bar = 2 cm (Nauwelaerts et al. 2007).

may not hold for teleosts because suction-feeding may be accompanied by ram in these neutrally buoyant fishes, however buoyancy can fluctuate depending on use of the swim bladder. However, comparable studies on suction-feeding teleosts near a substrate would likely improve the relationship between RSI and peak buccal pressure. In contrast, the negative buoyancy of most elasmobranchs has primarily limited obligate suction-feeding behavior to benthic species that are more stationary. Epibenthic and pelagic elasmobranchs generally remain in motion in the water column due to their negative buoyancy and consequently employ some ram during prey capture.

Relationship of feeding behavior and ecology

The relationship between feeding strategy and ecology may depend in part on the degree and type of specialization. *C. plagiosum* and *G. cirratum*, and presumably all orectolobiform and heterodontiform species, use suction to capture small benthic prey because they are mechanistic and evolutionary specialists (Ferry-Graham et al. 2002). *Chiloscyllium plagiosum* and *G. cirratum* are specialized suction-feeders and occupy benthic habitats due to the orectolobiform and heterodontiform familial lineage including a cranial anatomy comprised of small mouths and teeth, little upper jaw protrusion, large labial cartilages, low aspect tail, large blunt head, long body, and flexible fins more suited for resting on the substrate and making short swimming forays (Moss 1977; Thomson and Simanek 1977). A mechanistic specialist is excluded from a set of resources when it is not capable of utilizing the resource due to anatomical or behavioral constraints (Ferry-Graham et al. 2002). *Chiloscyllium plagiosum* and *G. cirratum* have agile locomotor morphology which is better suited for maneuvering on the substrate. An evolutionary specialist is excluded from a set of resources by heritable constraints acting on the organism (Ferry-Graham et al. 2002).

Most shark species, such as *S. acanthias*, exhibit intermediate aspects of feeding behavior, locomotor morphology and ecology typical of generalists which are characterized by their versatility (Nemeth 1997b). *Squalus acanthias* is a trophic generalist that takes a wide range of prey including fishes, crustaceans and mollusks as it forages in benthic and pelagic environments (Link et al. 2002) with a locomotor morphology including an intermediate aspect tail and a wide range of cruising speeds (Thomson and Simanek 1977). A diversity of prey capture behaviors from suction to biting coupled with ram that may include head shaking are used by *S. acanthias* in

accordance with its cranial morphology that has suction (moderate labial cartilages and mouth cavity) and bite characteristics (large mouth and upper jaw protrusion, large cutting teeth) (Wilga and Motta 1998a).

Most batoids (Pristiformes to Rajoidea) are evolutionary specialists (Ferry-Graham et al. 2002) that evolved a flattened morphology that allows them to cover and conceal themselves in soft bottom environments. *Leucoraja erinacea* and *R. lentiginosus*, and presumably all rhinobatoids and rajoids, appear to be generalist feeders that use bite and suction, hence the relatively large mouth open laterally, extensive upper jaw protrusion and small teeth, which facilitate extracting prey from sandy substrates (Wilga and Motta 1998b). However, lesser electric rays *Narcine basiliensis*, and maybe all Torpedinoidea, are mechanistic specialists for suction-feeding (Dean and Motta 2004a, 2004b).

Some shark species are considered to be ecological and mechanistic specialists by their behavior in choosing certain kinds of prey and by their specialized biting or crushing behavior. White sharks *Carcharodon carcharias*, use extensive upper jaw protrusion to cut or gouge mouth size pieces from prey that are too large to fit into the mouth like seals or whales (Tricas and McCosker 1984). Similarly bonnethead sharks, *Sphyrna tiburo*, have crushing teeth and feed nearly exclusively on crabs (Cortes et al. 1996). Bite specialists have large mouths that are open laterally, large blade-like teeth, and high-velocity locomotor morphology (high aspect tail, conical head, torpedo shaped body, stiff fins) necessary to catch fast pelagic prey like seals (Moss 1977; Thomson and Simanek, 1977). Likewise, bonnethead sharks have large mouths that are open laterally and molariform teeth coupled with a high aspect tail and stiff fins suitable for catching and feeding on swimming crabs Wilga and Motta 2000. Filter-feeding elasmobranchs are ecological specialists because their zooplankton prey is suspended in the water column, mechanistic specialists because they only choose zooplankton prey that is strained through a filtering apparatus and evolutionary specialists because they have evolved the morphology for filter-feeding.

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