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Mechanics of suction generation during feeding in Little skates

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Abstract

Feeding mechanisms of aquatic vertebrates has been extensively studied in the past, while that of elasmobranchs remains limited. Skates and rays are believed to have evolved from a shark ancestor, thus they represent the most derived group. All skates are dorsoventrally compressed, have a unique jaw suspension type and head skeleton and live in benthic environments. It is unknown whether these derived features of skates have altered the ancestral shark feeding mechanism. Comparing feeding mechanisms in skates and sharks may shed light on morphological transformations that have arisen after the evolutionary split of these two groups.

In this study prey capture and manipulation behaviors are compared and contrasted with the white-spotted bamboo shark. Jaw kinematics and buccal pressure during feeding events are investigated using sonomicrometry simultaneously with pressure transducers. Little skates capture prey primarily using biting but sometimes utilize weak suction as well. Pressure in the buccal cavity during prey capture varies around ambient ranging from slightly positive to slightly negative. In contrast bamboo sharks always use strong suction to capture prey with greater subambient buccal pressures. However, both species extensively process prey using strong suction alternately with compression. Such cycles can last several seconds, eventually ending in transport of the prey item. Greater subambient pressure develops in the buccal cavity during manipulation, indicating that skates are capable of generating stronger suction than that used to capture prey. Gape area during capture events is greater than during manipulation. Hyoid area attains similar magnitudes in both capture and manipulation events. Time of mean onset and peak gape and hyoid expansion occurs prior to peak buccal pressure in captures and manipulations. Although both occupy benthic regions of the ocean, prey capture in the two species appears to be quite different while manipulations are similar. Morphological differences in the jaw and hyoid apparatus of sharks and skates may be partly responsible for the functional differences in the generation of suction.

Introduction

While studies on sharks are slowly increasing, relatively little is known about the mechanics of prey capture of skates and rays (Motta and Wilga, 2001; Motta, 2004). Skates and rays are believed to have evolved from a shark ancestor (Shirai 1996; McEachran et al. 1996; but see Douady et al. 2003), thus they represent the most derived group of elasmobranchs (sharks and rays). All skates are dorsoventrally compressed, have a unique jaw suspension type and head skeleton and live in benthic environments

(Compagno, 1977; Motta, 2004; Wilga, 2002). While some sharks are benthic, very few are dorsoventrally compressed (Compagno, 1984). It is unknown whether these derived features of skates have altered the ancestral shark feeding mechanism. Comparing the feeding mechanisms of skates and sharks may shed light on anatomical and functional transformations that have arisen after the evolutionary split of these two groups.

In general, we investigate the mechanics of suction generation during feeding in Little skates, *Leucoraja erinacea*. We also compare prey capture and manipulation behaviors in *L. erinacea* to that of a benthic feeding shark, white-spotted bamboo sharks, *Chiloscyllium plagiosum* (Wilga and Sanford, In review). More specifically, we ask several questions that test previous hypotheses. 1) Does the progression of maximum pressure in little skates parallel the anterior to posterior progression of kinematic movement observed in sharks, bony fishes and salamanders? 2) Is the temporal and spatial relationship between movement of the oropharyngeal cavities and the resulting pressure generated in little skates similar to that of sharks and bony fishes? 3) Does the time of peak velocity of buccal expansion coincide with the time of maximum pressure in the oral cavity as has been found in sharks and bony fishes? This study will increase our understanding of the relationship between morphology and feeding behavior in elasmobranchs, as well as in bony fishes. This study will also provide a better understanding of the impact of *L. erinacea* on the ecosystem of Narragansett Bay.

Materials and Methods

Four Little skates, *Leucoraja erinacea*, were obtained from Narragansett Bay, RI. Skates were trained to feed from tongs in the experimental tank. Food was withheld from each skate for 2-3 days prior to the experiment. Each skate was anesthetized in a 0.05 g l-1 tricaine methansulfonate (MS-222) initially, then diluted to a 0.025 g l-1 dose for surgery. Seven 2 mm sonometric crystals and one pressure transducer were implanted in the oropharyngeal cavity of the skate and secured by sutures. Implantation of the 7 crystals was as follows: 1- anterior cranium, 2- upper jaw, 3- lower jaw, 4- posterior cranium, 5 and 6 – left and right hyomandibular-ceratohyal joints, 7- basihyal, transducer - anterior cranium (Fig. 2). Crystals and transducer were threaded through the 4th and 5th gill slits. The skate was allowed to recover and then fed 1-2 cm cut pieces of squid, *Loligo*, sp., or fish Atlantic silversides, *Menidia menidia,* to satiation. Pressure and kinematic data was recorded simultaneously using a sixteen channel sonomicrometer (Sonometrics Corp.). Four capture and four manipulation events for each of three individuals was analyzed using SonoVIEW (Sonometrics Corp.) and exported to Excel where the values for duration of gape and pressure, peak onset of gape and pressure, hyoid area were calculated. Plots were constructed using SigmaPlot (Jandel Corp.). Means and One-way ANOVA statistical tests were run using SigmaStat.

Fig 1. 140 cm Millar microtip pressure transducer.

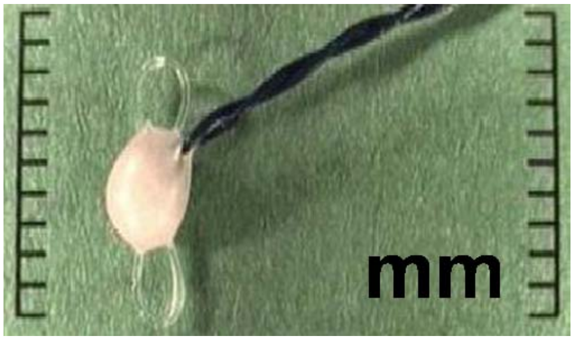


Fig 2. 2 mm sonometric crystal with suture loops.

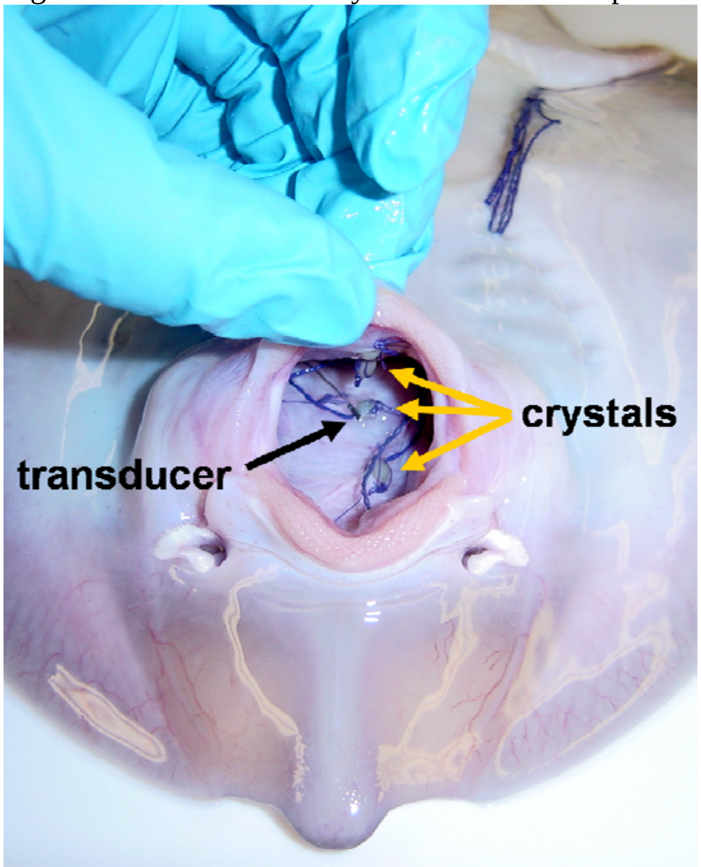


Fig 3. Crystals and transducer in mouth of skate.

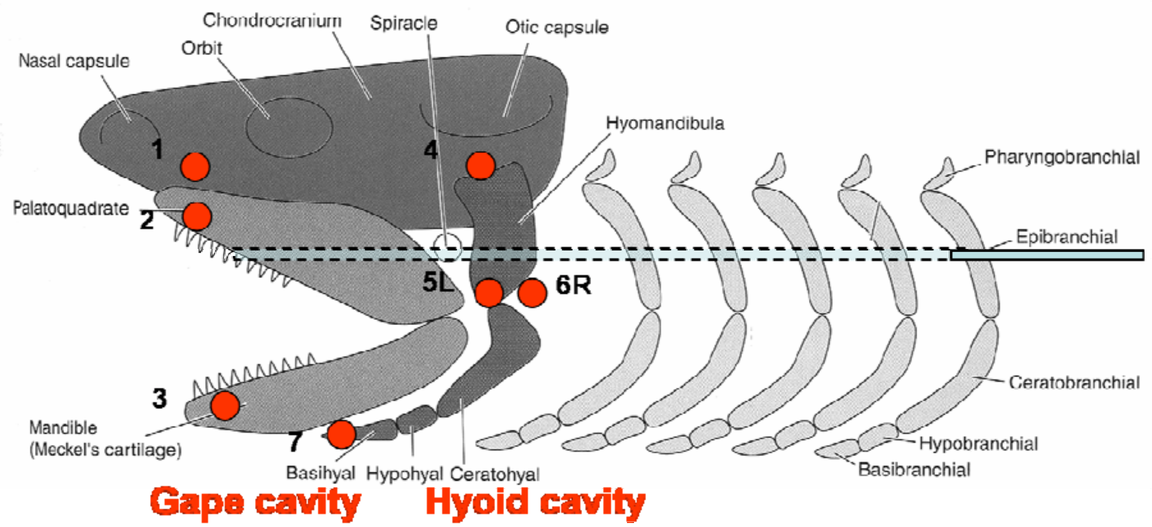


Fig 4. Sonometric crystal placement (fig. after Liem et al. 2001)

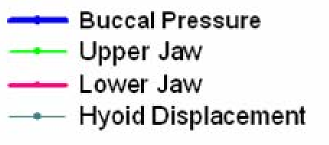
Results

Little skates, *Leucoraja erinacea*, use a combination of bite and ram mechanisms to seize fish and squid pieces rather than relying on suction. Pressure in the buccal cavity during prey capture has a wide range of positive and negative peaks (-0.93 to 1.2 kPa) with a mean of -0.14 kPa. During prey capture, the mouth undergoes a long phase of slow opening followed by a shorter phase of fast opening. Mean fast opening phase corresponds with the mean onset of buccal pressure (paired t-test, p=0.696). Upper jaw protrusion begins simultaneously with lower jaw depression. Extensive upper jaw protrusion and lower jaw depression contribute to the large gape area (178 mm2). Although, the mean slow mouth opening phase begins just prior to mean expansion of the hyoid cavity, the difference is not significant (paired t-test, p=0.280). Mean area of the hyoid arch is 40% larger than that of the gape.

In contrast, primarily suction is used to manipulate prey after capture. Pressure in the buccal cavity during manipulation events has a larger range of only negative peaks (-1.47 to -8.8 kPa) with a mean of -6 kPa. The gape cycle is short, due to the prey already being grasped between the jaws after capture. The onset of slow mouth opening and buccal pressure occur together (paired t-test p=0.307). Little upper jaw protrusion and lower jaw depression result in a relatively small gape area (106 mm2) of short duration. The time of fast mouth opening and the onset of hyoid expansion occur together (p = 0.411). Mean area at the hyoid arch is 58% larger than that of the gape.

Bite/ram prey capture events (mean 392 ms) are longer than that of suction manipulation events (280 ms) (ANOVA, p=0.033) (Fig. 10). The duration of hyoid and gape expansion to peak are significantly different in capture and manipulation events (p=0.0005, and p=0.0007 respectively). The rate of change for hyoid area expansion is much faster in manipulation events (9.37 mm2 ms-1) than in capture events (3.93 mm2 ms-1) (p=0.0071). The magnitude of peak buccal pressure is greater in manipulation events compared to capture events ($p<0.0001$). The range of buccal pressure is narrow with positive and negative values in captures, while manipulations have a much broader range of only negative pressures.

Capture **Manipulation**



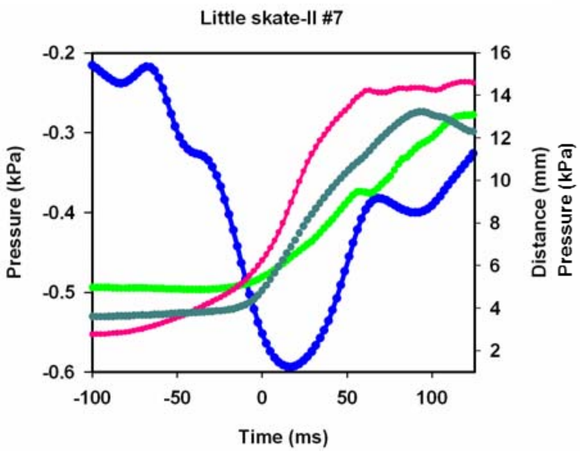


Fig 5. Representative plot of kinematic data from prey capture event.

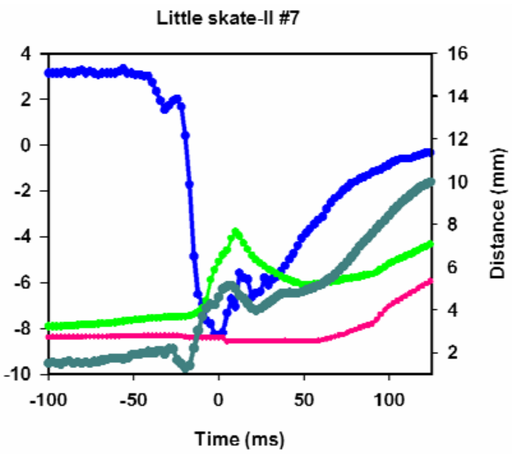
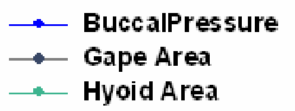


Fig 6. Representative plot of kinematic data from a prey manipulation event.

Capture **Manipulation**



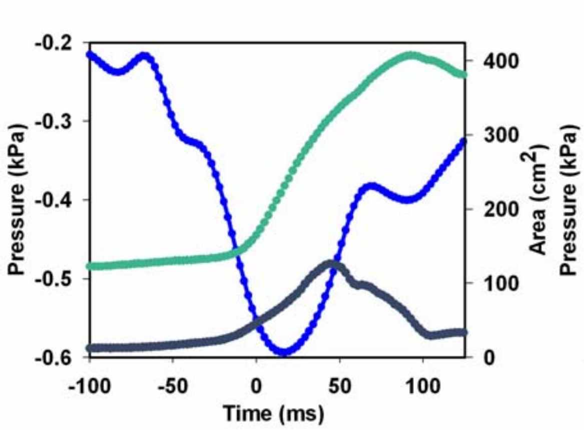


Fig 7. Plot of hyoid, gape area and buccal pressure vs. time during a capture event.

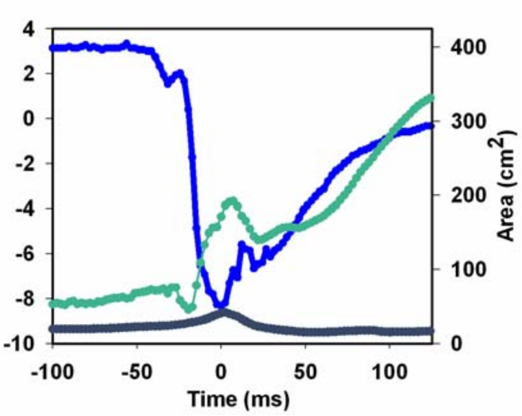


Fig 8. Plot of hyoid, gape area and pressure vs. time during a manipulation event.

Discussion

In Little skates, *Leucoraja erinacea*, prey captures are bite dominated with little or no suction pressure generated. In contrast, other batoids have been found to use primarily suction to capture prey. Atlantic guitarfishes, *Rhinobatos lentiginosus*, use suction to capture prey (Wilga and Motta, 1998). Another benthic batoid, lesser electric ray, *Narcine brasiliensis*, captures prey using relatively stronger suction (mean -22 ± 2.7 kPa) (Dean and Motta, 2004). A pelagic stingray, cownose *Rhinoptera bonasus*, also uses suction to capture prey (Sasko et al, 2006). Compared to spiny dogfish sharks (closest shark relative) and teleosts (Table 1), *L. erinacea* has relatively weak suction pressure during capture, but generates similar suction pressure during manipulation events. Strong suction feeding sharks have comparable buccal pressures to that of *N. brasiliensis*, a specialized suction feeding batoid.

While the manipulation events that were analyzed here are suction dominated, little skates use a variety of other mechanisms to process prey, such as bite, blow, compression and ram. These appear to be commonly used behaviors by skates and rays to process prey (Wilga and Motta, 1998; Dean and Motta, 2004; Sasko et al, 2006). While individual manipulation events are shorter in duration than captures, the entire duration of processing the prey for swallowing is much longer. The mouth only needs to open just enough to release the prey so that it can be moved further into the mouth, which is why the gape cycle in manipulation events is shorter than captures.

There appears to be a dichotomy in the timing of upper jaw protrusion in elasmobranchs. Like *N. brasiliensis and R. bonasus* (Dean and Motta, 2004; Sasko, Dean, Motta and Hueter, 2006), upper jaw protrusion and lower jaw depression occur simultaneously in *L. erinacea*. In contrast, the upper jaw does not begin to protrude until peak lower jaw depression is reached in *R. lentiginosus* and most sharks (Wilga and Motta, 1998; Motta and Wilga, 2001; Motta, 2004). This dichotomy in the time of upper jaw protrusion is not associated with feeding mechanism (ram, bite, suction) or behavior (capture, manipulation, transports); more investigation is needed to understand this phenomenon.

Future research will involve analyzing other types of manipulation events, such as bite, compression and suction transports as well as measuring pressure in the pharyngeal cavity during feeding in *L. erinacea*.

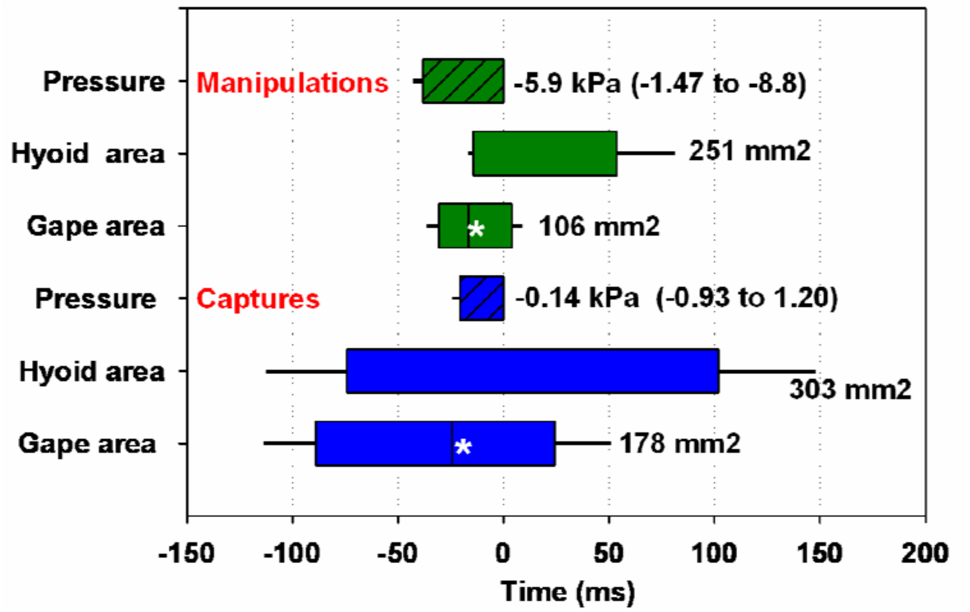


Fig 9. Mean bar plot of area and pressure during capture and manipulation in skates.
*Indicates fast opening phase of gape.

Table 1. Capture Pressure in Fishes	Buccal Pressure (kPa) mean	range
Little Skates cap.	-0.14	-0.93 to 1.20
Little Skates man.	-5.9	-1.47 to -8.8
Lesser electric ray (Dean and Motta, 2004)	-22	to -31
Lesser electric ray (Dean and Motta, 2004)	-21	to -34
Spiny Dogfish (Wilga, Motta and Sanford in prep)	-2.1	-0.5 to -4.5
Bamboo sharks (Wilga and Sanford, in review)	-31	-11 to -102
Nurse sharks (Mattot et al. 2005)	-110	
Largemouth bass (Sanford and Wainwright, 2002)	-5	-2 to -15
Largemouth bass (Svanback et al. 2002)	-5	-1 to -6
Peacock cichlid **Banded cichlid** (Norton and Brainerd, 1993)	-5 -10	
Bluegill sunfish (Lauder, 1980)		(3 – 17)

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