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Scaling of Feeding Performance in Panther Grouper, *Cromileptes altivelis*

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SCALING OF FEEDING PERFORMANCE IN PANTHER GROUPER,
CROMILEPTES ALTIVELIS.

By

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Under the Direction of Dr. Steve Huskey

Submitted to the Honors College of
Western Kentucky University
Spring 2010

CE/T Committee

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ABSTRACT

Fishes demonstrate the greatest change throughout ontogeny in body size of all vertebrates, some becoming twelve times their original length. Panther groupers, *Cromileptes altivelis*, are no exception. This vast size change influences other aspects of their lives including their feeding behavior, the prey they consume, and the capabilities of the mechanisms they use to capture prey. The change in the feeding performance of the panther grouper, *Cromileptes altivelis*, was quantified through buccal pressure recordings and high-speed videography. From this data, we can deduce that the larger juvenile was able to generate greater negative pressure within the mouth. It appears that feeding performance improves as panther groupers increase in body size.

INDEX WORDS: Scaling, Kinematics, Feeding Performance, *Cromileptes altivelis*,
Suction, Pressure

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CHAPTER 1

INTRODUCTION

Scaling

D'Arcy Wentworth Thompson was a leader in mathematical biology, best known for *On Growth and Form* (1917). He showed that in several fish classes, the morphology of related species could be generated by simple geometric transformations. My work focuses on the affine transformation of scaling (Thompson 1984). Scaling is defined as “the structural and functional consequences of a change in size and scale among similarly organized animals” (Biology Reference). Scaling affects all organisms by influencing surface area to volume ratios, metabolic needs, and structural support, among other things. Many features of an organism increase at the same rate, or isometrically. Some demonstrate positive or negative allometry. For example, humans exhibit negative allometry when comparing size and growth rate of our skulls relative to our bodies (Farke 2010). Julian Huxley developed the idea that an organism’s form depends on the differential growth rates of the each part of the body. This idea of the body size dependence of ontogenetic growth was later termed allometric growth, and had the corresponding equation of $Y = Y_0M^b$, where Y is the characteristic you seek such as metabolic rate or life span, Y_0 is a normalization constant, M is body mass and b is the allometric scaling exponent (Huxley 1932). Extensive research on Huxley’s allometry in the 1970’s and 1980’s was compiled into four influential books by: Peters

(1983), McMahon & Bonner (1983), Calder (1984) and Schmidt-Nielsen (1984). These readings reviewed the empirical evidence and found that it overwhelmingly supported quarter-power scaling for BMR and numerous other attributes of organismal form, function, physiology and life history. These scaling affects hold strong influence upon many other capabilities. Locomotion, communication, and feeding are all hindered until our scaling is complete. By studying the scaling affects over the ontogeny of the panther grouper, we will be able to establish how the animal maintains its functional integrity.

According to D'Arcy Thompson:

In an organism, great or small, it is not merely the nature of the *motions* of the living substance which we must interpret in terms of force (according to kinetics), but also the *conformation* of the organism itself, whose permanence or equilibrium is explained by the interaction or balance of forces, as described in statics.

Studies have confirmed that species ability to generate suction pressure varies considerably, with over an order of magnitude range in peak pressure among teleost species (Lauder, '80; Norton and Brainerd, '93; Nemeth, '97; Carroll et al. 2004).

However, less is known about how suction feeding performance scales within species (Richard and Wainwright, '95; Wainwright and Shaw 1999). In essence, we are asking if the fish generate a common suction pressure throughout their lives, or if their capacity to generate suction increases as the fish increases in size. Schmidt and Nielson said that

physical laws must be taken into account because they not only provide opportunity but they also implement constraints (Schmidt-Nielson 1984). For instance, an isometrically growing animal with a fully expanded bucco-pharyngeal cavity exhibits the following relationships: (1) the rate of the bucco-pharyngeal volume change will increase proportionally with the cube of the body length, and (2) the surface area of the mouth, through which the water flows, increases with the square of the body length.

Accordingly, we assume the flow velocity is proportional to the ratio of rate of volume change to the area of the mouth opening (Muller '82 and '84), and then suction flow speed at the mouth would increase linearly with body size. Therefore, large animals would have a substantial advantage over small animals when relating to generating high suction flow speeds. However, the musculoskeletal system and cranial expansions are also subject to scaling effects. Inescapably, large animals will become slower in performing a movement that is similar relative to its body size (Hill '50; Schmidt-Nielson '84). Combined, these opposing effects make it difficult to predict how suction feeding performance will change during ontogeny.

Background

Commonly known as the panther grouper, *Cromileptes altivelis*, are found in the Indo-Pacific region. This species is very popular for aquariums due to their hardy disposition and long lives, being able to grow up to 70 cm (Heemstra and Randall 1993). In the wild, panther groupers are one of many types of fish that dwell in and around reefs, lagoons, and tide pools ranging from 2-40 meters in depth (Lieske and Myers

1994). Panther grouper capture their prey out of the many crevices in the reef and typically consume small, reef-dwelling fishes and crustaceans (Myers 1999). To accomplish this task they have a narrow morphology and a pointed skull that allows them to generate enough suction to draw their prey out of the nooks in the reef.

The flexibility, precision and distinct movements of the pectoral fins allows the panther grouper to discretely turn back to the reef and sneak into perfect alignment to suction feed on their prey. The spotted coloration and body shape of the panther grouper allows them to easily conceal themselves against the changing patterns of the reef. The reef serves as a source of shelter and food for the panther grouper. Its solitary lifestyle reveals a territorial predator that can strike from his home with great precision (ARKive, 2010). Despite these strengths, the panther grouper is currently listed as vulnerable on the IUCN Red List of Threatened Species (Sadovy et al. 2008). This is mainly justified by high rates of harvesting, driven by panther grouper's high value in the fish markets, and expansive habitat degradation, most notably in Southeast Asia.

My goals were to quantify the maximum suction ability and feeding kinematics in panther groupers of different lengths to see if scaling affects their feeding performance. My null hypothesis was that there would be no difference in the feeding performance of panther groupers of different sizes. While my alternative hypothesis is that feeding performance is dependent on the size of the panther grouper.

MATERIALS AND METHODS

Experimental Set Up

Two juvenile panther groupers were studied in the WKU Functional Morphology Laboratory. Each juvenile was housed in a 175 liter tank at a room temperature of 20 degrees Celsius where the water was regularly changed and maintained. On both tanks, 1 cm squares were taped to the back of the tank to provide a scale for analyzing the video footage. For the larger juvenile there was also a piece of mirror placed in the bottom of the tank at a 45 degree angle to allow for simultaneous recordings of lateral and ventral views.

Before we actually recorded any data, we first had to insert a plastic cannula into each juvenile. This allowed a consistent access point to the buccal cavity for the pressure transducer during recorded feedings. After a few days of initial adjustment to our laboratory tanks we gave each juvenile anesthetic and implanted the plastic cannula through the buccal cavity. Specifically, it was placed just anterior to the orbit through the dorsal surface of the buccal cavity, just lateral to the parasphenoid and posterior to the vomer. A catheter-tipped pressure transducer was threaded into the cannula and held in place with a silicon sleeve, pushed over to expose the end of the cannula; thus allowing the measurement surface of the pressure transducer to be held in position on the inside of the roof of the buccal cavity (Wainwright et al. 2006).

After surgery, the grouper were allowed to recuperate in their tanks. Next, we refrained from feeding the fish for a few days until they seemed willing to feed. This was

usually evident when we would enter the room, and they would follow us, coming to the top of the tank awaiting a meal. We began to train them to capture small, peeled shrimp surrounded by the two high powered Lowell Pro lights, each providing 250 watts of light to illuminate the tank. Following this acclimation, we collected data through feedings on live common goldfish in the larger juvenile and small ghost shrimp for the smaller juvenile. Prey was scaled relative to overall body length of each predator, hence the application of two different prey-types. This also keeps the smaller fish from having to compensate in terms we are not measuring in order to capture the same prey. We waited one week between data collected feedings to make sure the fish would attack aggressively, just like in a natural environment.

To capture the kinematics, we used a Redlake MotionPro high-speed digital video camera, shooting 500 frames per second, with 1280 x 1024 resolution, 250 watt lamps, and analyzed data through MiDAS software program. The pressures were recorded digitally also at 5,000Hz using an analog-to-digital conversion system. Nineteen video sequences were recorded for the first juvenile, while we collected seventeen for the second, smaller juvenile. We collected 28 pressure data entries for the first juvenile and 21 for the second juvenile, all within 12 months.

Analysis

For the videos we measured maximum gape, time to maximum gape, maximum hyoid depression, time to maximum hyoid depression, maximum cranial elevation, time to maximum cranial elevation, prey velocity before and after suction, and total gape

cycle time (Richard and Wainwright 1993). Centimeters were used to measure all of the distances, seconds were used for the timing, and kPa was used to measure the pressure generated. To begin the kinematic measurements we defined time zero as the moment right before the jaw opens for the feeding cycle (Figure 1). Next, we measured the maximum gape as the time at which the fish's jaws expanded furthest (Figure 2). Maximum hyoid depression was the frame at which the greatest depression of the hyoid arch was reached (Figure 3). The time to maximum cranial elevation was found as the frame in which the cranium was at its greatest height relative to the body (Figure 4). The total gape cycle was found by starting at time zero and stopping time at the moment when the fish closed its jaws together immediately after feeding. Also we measured the velocity of the prey before suction and during suction. We did this by using the formula of velocity equals distance divided by time. We measured the distance that the prey traveled over a set of frames before the feeding began, and again during frames at which it was being sucked into the buccal cavity. The grid in the background, a centimeter scale, was used as a reference for the MiDAS program to properly calculate the distances.

All of this data was recorded into Microsoft Excel spreadsheets. From the 36 total video data points over the 12 month period we established two sets of data, one from the first, larger juvenile at 24.62 cm and one from the second, smaller juvenile which is half of the length of the first at 11.13 cm. Additionally two more sets of data were collected from the 49 total pressure entries.

Figure 1. Juvenile 2 at time zero. Beginning of Feeding Cycle.

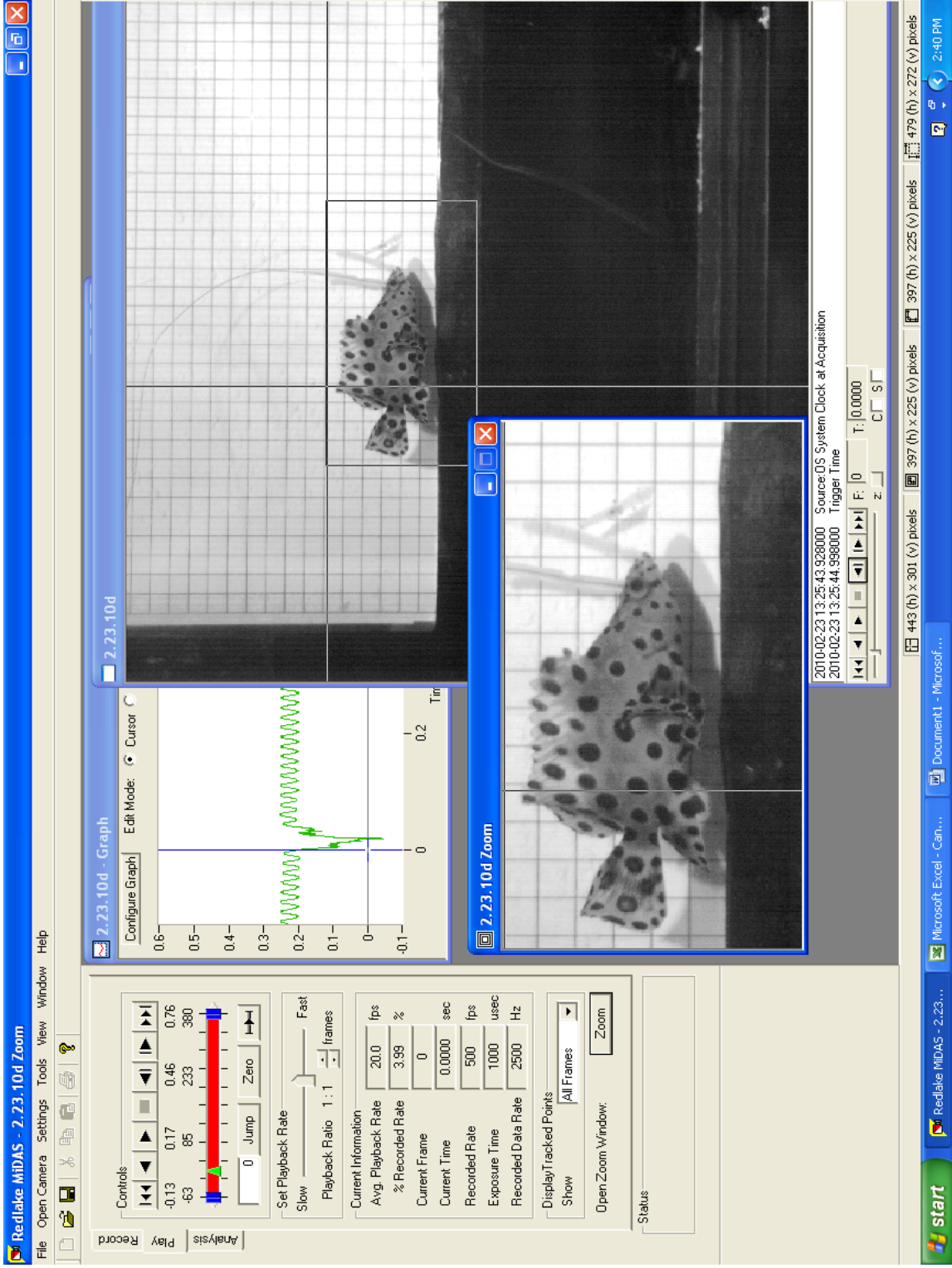


Figure 2. Maximum Gape at time 0.014 seconds.

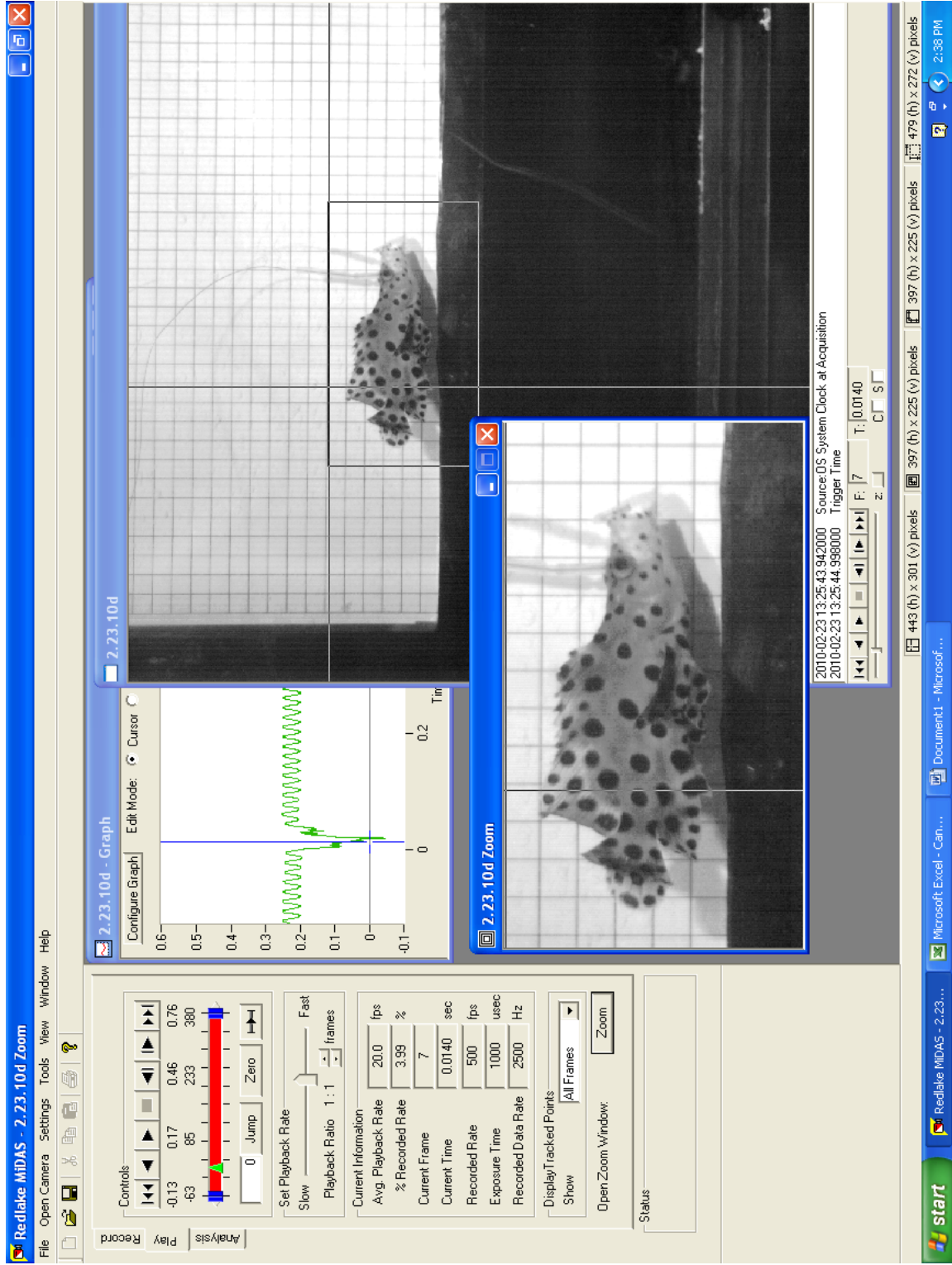


Figure 3. Maximum Hyoid Depression at time .018

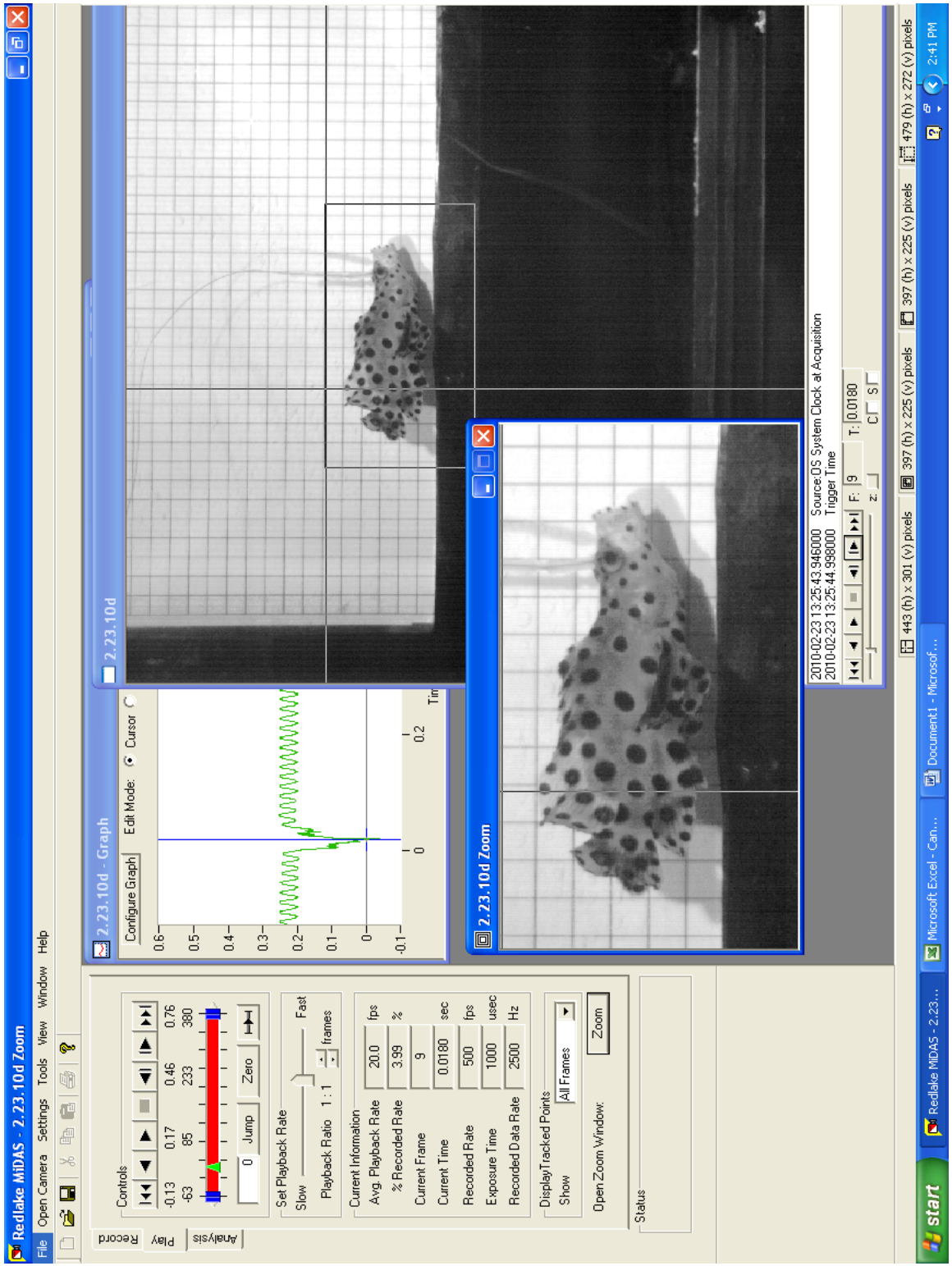
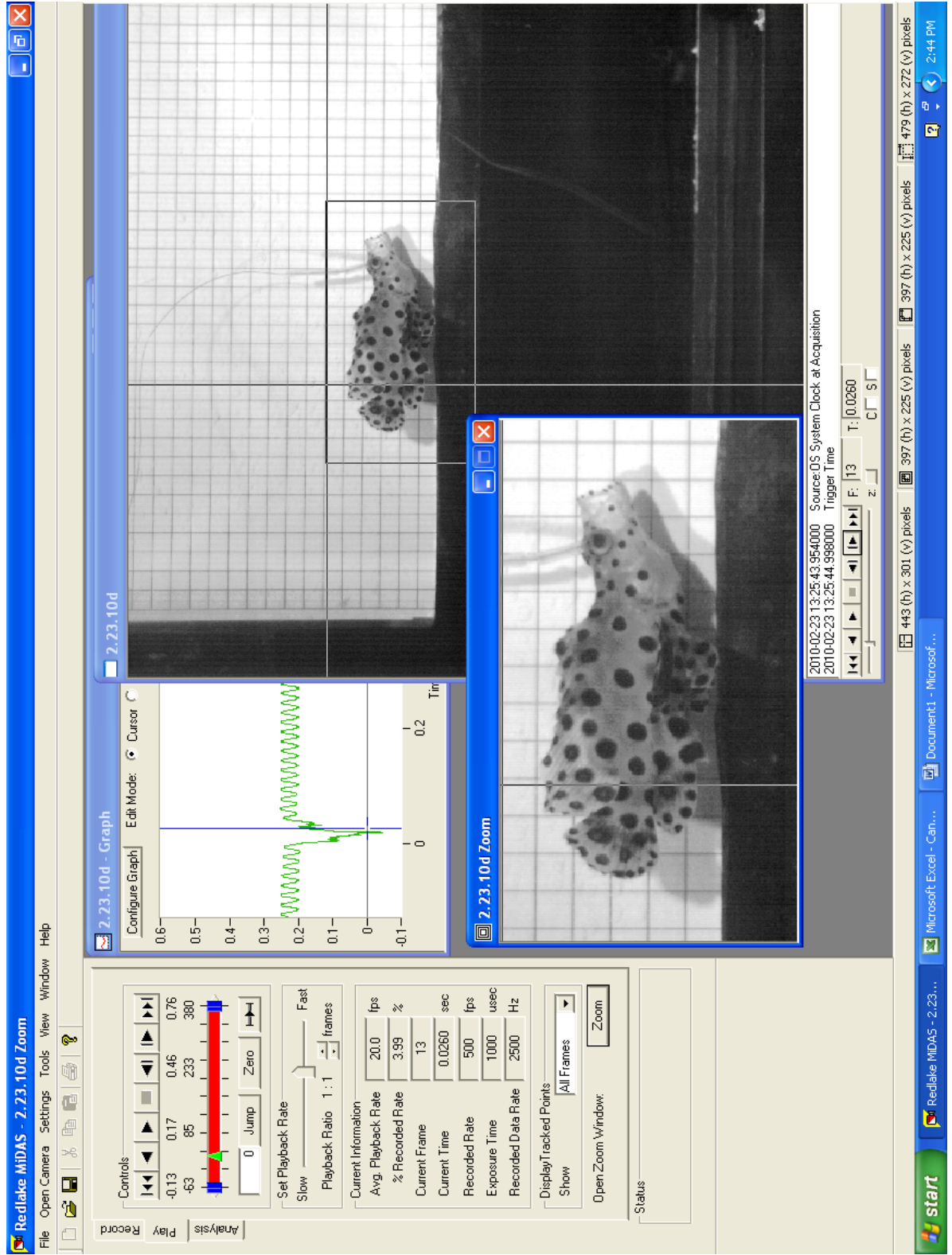


Figure 4. Maximum Cranial Elevation at time 0.026



RESULTS

The time at which each noted measurement was met usually took longer for the smaller juvenile, most likely due to his smaller muscles used to quickly expand the buccal cavity. However, the total cycle time took longer for the first, larger juvenile. The increments measured leading up to the capture of the prey, time to cranial elevation and time to hyoid depression, do not seem to equate to fish 1's extended total gape cycle time, thus we can infer the slowness of the feeding action occurs in the closing of the jaws and not in the rapid expansion which causes the negative pressure in the buccal cavity. The first juvenile was measured at 24.62 cm while the second juvenile had a total length of 11.13 cm. Noting this considerable difference in length, the kinematic measurements do not seem to be as differentiated as one might expect (Table 1).

Table 1: Summary of Juvenile Kinematic Averages

Sequence	Predator Characteristics		Mean Skull Kinematics								
			No.	TL (cm)	HL (cm)	Max gape (cm)	Max gape timing	Prey mean velocity, prior to attack (cm/s)	Prey mean velocity during attack (cm/s)	Hyoid depression distance	Hyoid depression timing
Fish 1 Mean	24.62	8.28	2.613	.0115	10.289	355.23	.480	.0151	19.20	.0188	.043
Fish 2 Mean	11.13	2.61	1.039	.0111	3.039	102.25	.351	.016	26.67	.0256	.037

The mean suction pressure generated by the larger specimen was 18.26 kPa, and only 14.02 kPa for the second, smaller specimen. It seems there is a notable difference in the capabilities of the fish as they grow (Table 2). This may also be backed by the mean velocity of the prey. Juvenile one generated an impressive mean movement of prey during feeding of 355.3 cm/s, while the second juvenile only generated 102.25 cm/s (Table 1). This differentiates from the Snook who maintained a relatively constant suction capacity throughout their growth.

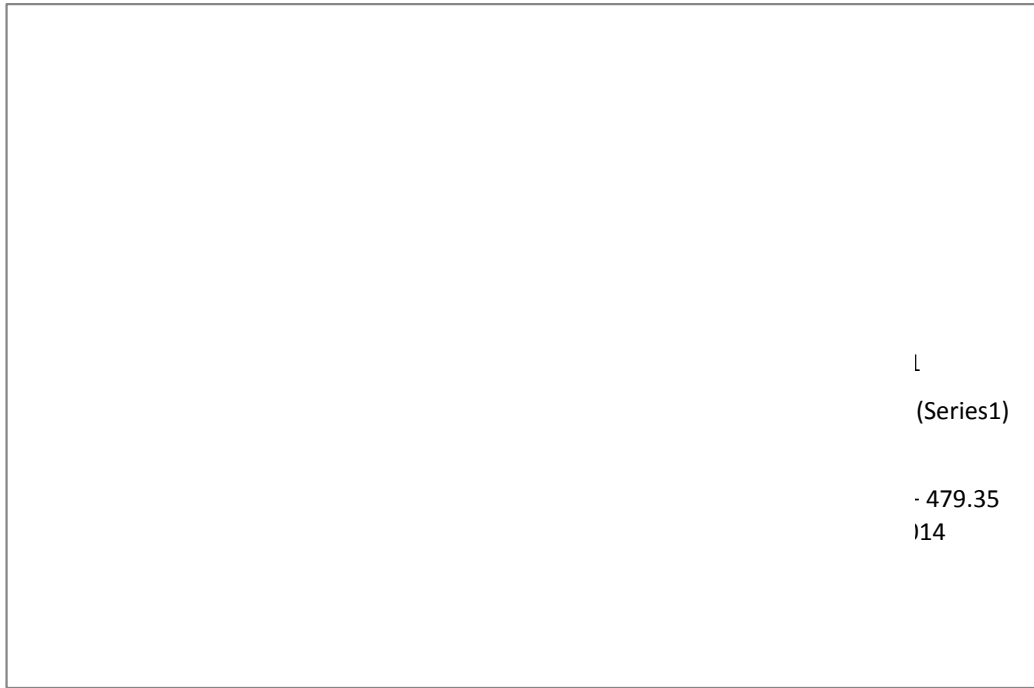
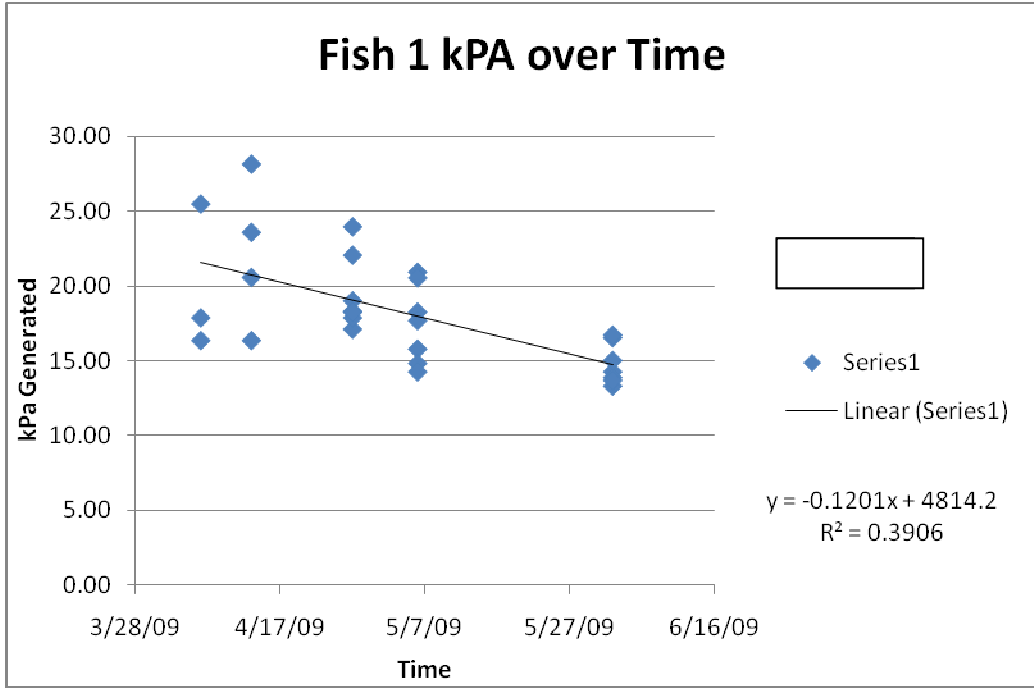
Due to the buccal cavity's size and shape change during the course of an attack (Sanford and Wainwright, 2002) and the flow changes in velocity (Day et al., 2005) we cannot use the apply the Bernoulli principle, and hence the need for direct measurements of pressure speed.

Table 2: Summary of Juvenile Pressure Averages

	Baseline	Max Negative	Absolute Change	20mm Hg scale	kPa generated
Fish 1 Mean	.1283	-0.1059	-0.2342	.0342	18.257
Fish 2 Mean	.2365	.0567	-.1716	.0342	14.0176

To our knowledge thus far we can infer that despite the larger juveniles greater gape distance, larger and heavier bone structure, and greater amount of water to displace, the species must develop relative cranial and jaw musculature to sustain a speed and force necessary for effective suction feeding speed and pressure that we measured (Figures 1 and 2). From our data, you can also note that as the fish grew, and

as they adapted to the noncompetitive tank environment, their maximum negative suction pressure generated decreased (Graph 1 and 2). The difference is more notable for fish one, who not only grew more, but also had longer to adapt to the tank.



DISCUSSION

Hyoid depression measurements must be studied in this experiment to understand the implications of the buccal expansion used during feeding. Cranial elevation increase contributes to an increased mouth gape during suction (Richard and Wainwright, 1994). Gape distance is also measured because it can help indicate the maximum size of the prey able to be captured. Analyzing these factors together is necessary to determine the kinematics of feeding performance in fishes. Using these measurements in combination with the timing of each we can find the extent of scaling, within the juvenile size range.

Parallel to a few other specialized species, the panther groupers seem to be an exception to the common fish, who changes feeding styles as fish grow (Wainwright et al. 2006). Despite the extended time needed to open and close their mouths during feeding, they continue to use the same method, suction feeding. Unlike other grouper such as the goliath grouper, that may change to become ram feeders, using explosive speed to ambush and capture prey (Bullock and Smith, 1991), the panther grouper is able to maintain a suction feeding lifestyle throughout its ontogeny (Huskey and Turingan, 2001). It has been suggested by Wainwright and Richard (1994) that one can expect a larger fish to have slower movements based only on its larger body size where larger, heavier body elements must impart greater volumes of water. Our data, as previously noted in table one, total gape cycle, concurs with Wainwright and Richard's conclusion.

You can note in Figures 5 and 6 the bone structure of Fish 1, which exemplifies the anterior cranial surface for maximum amount of muscle attachment, thus great muscle capabilities to quickly expand the buccal cavity thereby creating an intense negative suction pressure to capture their prey. Although the time to max gape increases with maximum gape distance, these are seemingly proportional, and directly related to the size of the fish. This altogether unique design is the basis for allowing the panther grouper to sustain a suction feeding predation style throughout its life. As the panther grouper grows and the maximum gape distance increases, larger prey can be consumed. Panthers are obviously able to capture larger prey as they increase in body size.

Lateral and rostral views of the skeleton of the larger juvenile, Fish 1, used in this experiment.

Figure 5



Figure 6



Due to the negative allometry demonstrated by their suction capacity, it appears that the tank environment had a much greater impact on the pressure measured than we had originally estimated. The larger juvenile demonstrated a less aggressive attack as he acclimated to his noncompetitive environment, yet continued to maintain at least an average 15 kPa of suction, which is similar to how the smaller juvenile was performing. Inferring from this data we can say that the capabilities of the fish's performance increase with size, despite the fact that one might not always exhibit that capacity if it is not required.

Thus far in this investigation it seems as though the null hypothesis is false. For a direct defense we can note the times the larger fish was faster, the mean prey velocity

during attack, and the suction pressure exhibited. These quantities all agree that scaling does have an impact on the panther grouper's performance, yet as previewed in the introduction there are many physical laws in place that we have yet to test to verify our results thus far.

The studies discussed in this work, and soon this work also, allow for a firm knowledge that one cannot assume a species will have a specific capacity for generate suction pressure; some will change and others will stay stagnant. Although this creates challenges for attempts to generate comparative data, it entails the need for suction pressure capacity to be expressed in relation to a particular body size of that species.

This project must expand to include more fish and especially those of many sizes ranging from 10 cm to up to 50 cm. In this project we were able to place a cannula in the cranium of one of the smallest fishes ever studied, so the species is obviously very accommodating. From here we must increase the number of replications within our experiment, as well as expand our experimental set-up to include more calculations to help us decrease the variables and increase our specificity to the cause and relationships in order to verify the panther grouper's feeding ontogeny strategies and capacities.

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