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Clinton J. Moran
California State University, Monterey Bay

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CURIOUS FOOD PROCUREMENT IN THE EASTERN NORTH PACIFIC KYPHOSIDAE

A Thesis
Presented to the
Faculty of the
Division of Science and Environmental Policy
California State University Monterey Bay

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Marine Science

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by
Clinton J. Moran
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CALIFORNIA STATE UNIVERSITY MONTEREY BAY

The Undersigned Faculty Committee Approves the

Thesis of Clinton J. Moran:

CURIOUS FOOD PROCUREMENT IN THE EASTERN NORTH PACIFIC KYPHOSIDAE

Gregor M. Cailliet

Gregor Cailliet, Chair
Moss Landing Marine Laboratories

Erika McPhee-Shaw
Moss Landing Marine Laboratories

Lara Ferry
Arizona State University

Marsha Moroh

Marsha Moroh, Dean
College of Science, Media Arts, and Technology

June 20th, 2011

Approval Date

ABSTRACTS

Curious food procurement in the eastern North Pacific Kyphosidae
by
Clinton J. Moran
Masters in Marine Science
California State University Monterey Bay, 2011

Chapter 1:

Prey capture kinematics have been thoroughly described for many suction-feeding fishes. This is not the case for biters and scrapers. *Girella nigricans*, a temperate kyphosid, is known to be an herbivore often scraping or picking microalgae from rocky substrate. The aims of this study were to quantify the kinematics of two feeding behaviors exhibited by *G. nigricans*. A scraping behavior was elicited by allowing *G. nigricans* to scrape from a block of brine shrimp gelatin and a picking behavior was elicited by allowing *G. nigricans* to feed on *Ulva spp.* Measured kinematic variables were cranial elevation, lower jaw rotation, premaxillary protrusion, premaxillary rotation, gape maximum, and intramandibular rotation. Intramandibular rotation was described as any rotation around the articulation between the articular and the dentary. Significant differences in feeding kinematics were seen for every kinematic variable except premaxillary rotation. During feeding events it became apparent that *G. nigricans* does not use, or has lost, the ability to suction feed. When feeding on non-attached diet items they approached their prey with their gape wide open until the prey was in their mouth, likely to reduce the bow wave created in the water. The lack of suction during feeding and the presence of the IMJ has led to the conclusion that *G. nigricans* is a specialized scraper.

Chapter 2:

Herbivory in marine fishes has been studied at the ecological and physiological level but less so at the physical level of algae removal. Previous works conducted on algae scrapers have noted the presence of feeding structure novelties such as the intramandibular joint. The intramandibular joint allows for an increased force produced by the jaw along with an increased residence time of the tooth-bearing surface on the scraped substrates. This study focused on the three species of common eastern North Pacific kyphosids, the scraper; *Girella nigricans*, the grazer; *Hermosilla azurea*, and the picker; *Medialuna californiensis*. Theoretical jaw force production was calculated using the program Mandiblever and comparisons were made among species. *Girella nigricans* had a higher theoretical bite force per unit length than any other species studied. The mechanical advantages for adductor mandibulae two of *H. azurea* and *G. nigricans* were not different from one another but both were higher than *M. californiensis*. This was not the case for adductor mandibulae three as *M. californiensis* was higher than *H. azurea* and *G. nigricans,* which did not differ from each other. The deep jaw structure and the presence of the IMJ in *G. nigricans* set this species apart as a specialized scraper. The separation of each species based on physiological cross-sectional area of the adductor mandibulae two and three and the theoretical force produced during the course of a bite suggests these three species in the family Kyphosidae remove algal dietary items differently.

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Fish Collections were assisted by: Derek, Kevin and Angela Moran, Courtney Anderson, Kyle Dodder, Brandon Theriot, Fernando Gutierrez, Charles Gregory and Josh Guptill. Without their spearfishing expertise the sample size for this study would have never been sufficient. To conclude I would like to thank the Community Hospital of the Monterey Peninsula who provided the digital X-ray images for this project.

CHAPTER 1

KINEMATICS OF HERBIVOROUS FEEDING IN THE EASTERN NORTH PACIFIC KYPHOSID *GIRELLA NIGRICANS*

INTRODUCTION

Suction feeding, the basal mechanism for fish prey capture, is a subject that has now been well–studied from the perspective of how fish capture their food in the aquatic, viscous medium they inhabit (e.g., Alexander 1967, Osse and Muller 1980, Muller et al. 1982, Motta 1984, Lauder 1985, Wainwright and Shaw 1999). This mechanism has afforded fishes tremendous successes with feeding on items both in the water column and on or in biotic and abiotic habitats. Less well understood are the feeding methods associated with biting and scraping, which allow fishes to feed on attached diet items (Alfaro et al. 2001, Konow et al. 2008, Hernandez et al. 2009, Ferry-Graham and Konow 2010). Anatomical changes, such as those that allow for increased contact of the teeth with the substrate, are common, and have been studied in the Cichlidae (Liem 1980, Bouton et al 1998), the Cyprinodontiformes (Hernandez et al. 2009), the Girellidae (Ferry-Graham and Konow 2010), and the Pomacanthidae (Konow and Bellwood 2005).

One anatomical novelty that has evolved independently in many lineages of scraping fishes is the intramandibular joint (IMJ). Typically located between the dentary and articular, the intramandibular joint allows for dorsal bending within the lower jaw that is not seen in most fish species. Fishes that feed on epiphytic diet need to apply the tooth-bearing surface directly to hard surfaces upon which these diet items grow. As the jaw closes, rotation around the intramandibular joint occurs (Gibb et al. 2008). This is thought to increase the maximum gape and allow for a larger tooth-bearing surface to be in contact with the feeding substrate for a longer period of time, in comparison with species without this joint. Other theoretical advantages of the IMJ include a more shallow body angle when feeding on the benthos for increased predator detection and the ability to maintain the ability to suction feed while also being able to scrape (Gibb et al. 2008).

In the eastern North Pacific, specifically off the coast of California, a rich algal food source of green, red and brown algae is available along with various forms of microalgae covering the substrate in the intertidal and subtidal (Barry and Ehret 1993). Of the subtidal fishes there, only two families exploit this eastern North Pacific temperate/subtropic herbivorous food source, the Embiotocidae and the Kyphosidae (Horn 1989, Barry and Ehret 1998). Members of the Embiotocidae are considered to be multivorous, often ingesting algae incidentally while picking invertebrates from the substrate. The Kyphosidae, however, are considered to be primarily herbivorous with multivorous feeding occurring only in the early stages of life (Barry and Ehret 1993, Harris et al. 1984). The subfamily Girellinae is made up of 18 species that span the globe primarily occupying sub-tropical and temperate waters (Yagishita and Nakabo 2003).

The herbivorous *Girella nigricans*, a member of the Girellinae and Kyphosidae, is the focal species for this study. As juveniles and sub-adults, these fish occupy both intertidal and shallow subtidal habitats with a geographic range from central Baja California to Monterey Bay in central California (Eschmeyer et al. 1983). During this life history stage, *G. nigricans* feeds on both plant and animal diet items. As adults these fish are exclusively herbivorous feeding on both micro- and macro-algae (Norris 1963, Barry and Ehret 1993, Behrens and Lafferty 2006). Based on field observations and diet studies, *G. nigricans* have been described as scrapers and biters feeding on the microalgae from the benthos and leafy algae suspended in the water column (Barry and Ehret 1993, Behrens and Lafferty 2006). *Girella nigricans* has an IMJ which allows it to effectively scrape the micro- and small macro-algae from the rocks in the subtidal and up into the intertidal. This is done by a flat tooth-bearing surface being applied to the substrate during feeding facilitated by the IMJ.

The goals of this study were twofold, to describe the: 1) kinematics; and, 2) the morphology of *G. nigricans* during feeding. Specifically, in the laboratory I was interested quantifying differences in feeding kinematics elicited by two very different diet items, brine shrimp gelatin and *Ulva sp.*, which I hypothesized would induce differing degrees of IMJ activation. I then describe the morphology that facilitated the jaw rotation observed in *G. nigricans* and comment on its functional significance.

MATERIALS AND METHODS

Feeding

Ten specimens of *G. nigricans* ranging from 9-14 cm standard length (SL) were collected using rod and reel in Santa Barbara, California. Once captured, the fish were placed in 50-gallon ice chests with a small amount of ice (to slow metabolic rate) for transport to Moss Landing Marine Laboratories (MLML). Once at MLML the fish were held in individual 10-gallon aquaria with flow-through seawater. All fish were taken under the California Department of Fish and Game permit number 9932 and were held and studied under San Jose State University IACUC protocol number 814.

Prior to recorded feeding events, the fish fasted for 48 hours to standardize willingness to feed. Videos were recorded laterally at 250 frames s^{-1} with a Fastec handheld high-speed video camera. Illumination was created by two 650-watt lights. A ruler was placed behind (approximately 5.0 cm) the tanks for scale.

The most consistent way to elicit a scraping behavior was to present the fish with a rectangle of Brine Shrimp gelatin. Brine shrimp was mixed in with K-Knox gelatin before the gelatin hardened. Hardness of the gelatin was controlled by the amount of water that was mixed in with the gelatin. A mixture of 10.0 g of gelatin and 100 ml of boiling water, with 5.0 g of brine shrimp, was prepared and allowed to harden. Optimal hardness was evaluated by the ability of a fish to remove a small amount of gelatin during the scrape without any part of the jaws disappearing from the lateral view of the camera. Rectangles were approximately 43.0 X 28.0 X 1.5 cm and were attached by threading the block to plastic mesh that was clamped to the side of the tank. Three videos were taken from each fish for a total of 30 videos for the gelatin feeding event.

To compare the scraping behavior to a bite and tear method of food procurement, the leafy green alga *Ulva* was chosen. *Ulva* was collected from the Moss Landing jetty and transported back to Moss Landing Marine Laboratories. These algae were stored in flow-through seawater tables until needed for feeding events. In preparation for such feeding events, the *Ulva* was attached to plastic mesh using a needle and thread. The plastic mesh was then clamped to the side of the tank. The algae needed to be attached to ensure the bite took place in the field of view but it was not attached in such a way that would elicit a scraping behavior. The leafy edges of the algae were suspended in the water which would allow for a bite and tear. Three videos were taken of each fish for a total of 30 videos for the *Ulva* feeding event.

Kinematic variables were extracted from the video images using NIH Image J. Measured kinematic variables included: maximum gape; premaxillary protrusion and rotation; cranial elevation; lower jaw depression; and intramandibular rotation (Fig. 1) (Konow and Bellwood 2005). Feeding events were analyzed and averaged to yield an average kinematic profile for both the gelatin and *Ulva* feeding events. Time zero was designated as the frame prior to jaw opening. Variables were measured every four frames which represented 0.016 s between measurements. The end of the feeding event occurred when the jaw had been fully retracted. Angular variables were evaluated by their variation from the resting or closed position. Linear variables were standardized to head length. In keeping with previous studies of fish feeding kinematics, an attempt to quantify the typical motions seen during suction feeding, such as hyoid depression and opercular rotation was made (*sensu* Motta 1984, Ferry-Graham and Lauder 2001).

To test for significant differences between the kinematics elicited by the two food types a Principal Components Analysis (PCA) was used. Kinematic maxima were averaged within an individual for every variable. The outcome was 10 average maxima for each kinematic variable on both diet items. Principal components (PCs) were retained if they accounted for $\geq$ 10% of the total variation. Variables were considered as informative with respect to their PCs if they had a loading score $\geq$ 0.500. When creating the scatter plots, the factor scores were averaged (± S.E.). Comparisons between *Ulva* and gelatin-feeding events and their average factor scores were done using a single Analysis of Variance (ANOVA). Homogeneity of variances were tested with a Levene's test and normality was tested using a Kolmogorov-Smirnov Test.

Anatomy

The morphological portion of this study was conducted on frozen and defrosted specimens. Once defrosted, the fish were manipulated and drawn by hand. A ruler was used to ensure consistent proportionality throughout the figures. Once drawn by hand, the sketches were traced in Adobe Illustrator CS3. I was specifically interested in the mechanisms for jaw opening and jaw closing. Along with normal jaw structure I also looked for novelties that would potentially distinguish scrapers from suction feeders.

RESULTS

Feeding

When *G. nigricans* approached both dietary items, they did so in a similar fashion. The gape was opened to maximum well before contacting the dietary item. While the gape was opened, they closed the distance (~1.0 cm) on the diet item and finished the bite once in contact with it. Prior to contact with the dietary item, the premaxilla and dentary formed a flat tooth-bearing surface. Although approaches initially looked similar, procurement kinematics differed between gelatin- and *Ulva*-feeding events (Fig. 2). On average, cranial elevation maxima were higher when *G. nigricans* fed on *Ulva* (approximately 2°). Maximum cranial elevation was reached around the same time during the course of a feeding event for both diet items (Fig. 2 A.). Larger lower jaw rotation was seen in the gelatin-feeding events (approximately 10°), however, again the maxima were reached at roughly the same time during the bite (Fig. 2 B.). Larger premaxillary rotation was observed when *G. nigricans* fed on the gelatin dietary item when compared to feeding events on *Ulva* (approximately 10°). Average premaxillary rotation reached a peak in *Ulva* feedings prior to the peak seen in gelatin feeding events (Fig. 2 C.). The range of average maximum premaxillary protrusions for both diet items combined was 11.00% - 12.00% (Fig. 2 D.). On average, when *G. nigricans* fed on the gelatin block they utilized a larger gape when compared to feeding on *Ulva* (Fig. 2 E., approximately 0.15 ratio to HL). Flexion around the intramandibular joint only occurred when the fish scraped from the gelatin block with an average of 16° of rotation (Fig. 2 F.).

Principal component one (PC1) accounted for 34.5% of the variation in my data set. PC1 had significant component loadings for lower jaw rotation (0.789) and gape distance (0.816). Principal component two (PC2) accounted for 28.4 % of the variation in my data set. PC2 had significant loadings of cranial elevation (0.809) and premaxillary protrusion (0.598). Principal component three (PC3) accounted for 13.04% of the variation in my data set. PC3 included premaxillary rotation (-0.840) alone. Based on the results of the ANOVA conducted using the factor scores as variables, gelatin- and *Ulva*-feeding events differed significantly for PC1 ($p< 0.05$, $F=7.629$) and PC2 ($p<0.005$, $F=11.209$) but not for PC3 ($p>0.5$, $F=0.345$) (Fig. 3 and 4).

Qualitatively, *G. nigricans* displayed ram-feeding behavior on both diet items, producing little to no observable suction during feeding events. Small amounts of suction were detectable in some (but not all) *Ulva*-feeding events, but only at the moment that the leafy portions of *Ulva* were crossing the plane of the open mouth. There were no obvious regions of cranial expansion in *G. nigricans* during prey capture.

Anatomy

In all of the videos it was apparent that *G. nigricans* was using a ram feeding method of feeding and that jaw opening and closing was qualitatively different than that seen in suction feeders. During jaw opening, prior to making contact with the diet item, a large amount of premaxillary rotation but almost no premaxillary protrusion was seen. This rotation was facilitated by potentially unique soft tissue in conjunction with the typical bony elements.

In *G. nigricans,* the medial base of the maxilla connects with the articular in a manner similar to a ball and socket joint. When the lower jaw rotates ventrally the articular rotates in the anterior direction forcing the maxilla toward the anterior of the fish (Fig. 5). Along with the resting position of the maxilla, there is connective tissue that connects the medial face of the base of the maxilla to the lateral face of the articular (Fig. 5 A., B., C.). The material properties of this tissue are unclear, but rotation in the maxilla is facilitated by this piece of tissue. Because the tissue between the maxilla and premaxilla is relatively stiff, movement seen in the maxilla translates to movement in the premaxilla. I also observed a tissue that assists in the last approximately 25% of premaxillary rotation during jaw opening (Fig 5 C.). Once the mouth is open to about 75% of maximum gape, the dentary and articular rotate further while tightening a connective tissue that connects the dentary to the base of the premaxilla. As the dentary rotates, this tissue tightens and pulls the base of the premaxilla forward creating a flat tooth-bearing surface on the diet item. During closing, this flat surface is maintained through rotation of the dentary around the IMJ (Fig 6).

Based on the results seen in Fig. 2 F. and this dissection I concluded that the IMJ is a passive joint. There appeared to be no musculature associated with rotation of the dentary around the articular. The video suggests that no intramandibular rotation occurred during *Ulva* feeding events. Intramandibular rotation only occurred when a force was applied to the tip of the dentary.

DISCUSSION

During scraping events, *G. nigricans* displayed a feeding behavior similar to that seen in a typical ram feeder. While utilizing maximum gape in most strikes on the gelatin, *G. nigricans* attacked the gelatin with all kinematic variables at their maxima. IMJ activity was seen during the scrape as the fish drew its mouth closed (Fig 2 F.). Rotation around the IMJ allowed for a larger tooth-bearing surface on the diet item for a longer period of time when compared to scrapers without the joint. Based on Fig. 2 D, very minimal amounts of premaxillary protrusion occurred throughout most of the bites. For a scraper, this is very important. If the jaws were to protrude, the force that *G. nigricans* could apply to the substrate would be less than if there was no protrusion. By having very little distance between the premaxilla and the body, the fish can provide force to the scrape with the body rather than just the jaws. Instead of the force of the bite now being completely controlled by the jaws there is a significant contribution provided by lateral movement of the caudal fin.

Based on the current study and video from Ferry-Graham and Konow (2010), it was clear that *G. nigricans* has lost the ability to produce suction during feeding events. Ferry-Graham and Konow (2010) offered their fish brine shrimp suspended in the water column and they produced very little suction. This result was similar to that seen in this study with *Ulva*-feeding events. Suction only occurred once the diet item was approximately half way into the mouth. It is possible that this suction could simply be a product of the fish opening its mouth in water. Their feeding style on suspended algal and animal dietary items is similar to that seen in aquatic snakes (Drummond 1983, Alfaro 2002). Aquatic snakes that cannot create suction during feeding, attack their prey with their gape held open to prevent a bow wave. *Girella nigricans* approached the suspended dietary item in a similar manner eliminating the effects of a bow wave on prey capture. Further evidence for the lack of suction during feeding events is the absence of any recognizable pattern of cranial elevation, premaxillary protrusion, hyoid depression, or opercular rotation. All of these factors contribute to producing suction in the buccal cavity but are either absent or unrecognizable in *G. nigricans*. Based on these results, it is apparent that *G. nigricans* is specialized for scraping and has potentially lost the ability to generate the amount of suction necessary to feed on elusive mid-water prey.

A number of morphological features of *G.* nigricans indicated that it has shifted towards an obligate reliance on scraping as a mechanism of food procurement. The most pronounced morphological modification is the deep jaws (taller than they are longer), which facilitate large amounts of jaw rotation. The amount of premaxillary rotation is also critical in a scraping bite, as it allows for a flat tooth-bearing surface that can be placed on the substrate. With the lower jaw apparatus, rotation of the IMJ during closure effectively matched rotation of the premaxilla (Fig.2). This coupled rotation around the IMJ and rotation in the premaxilla further created a flat tooth-bearing surface which is critical for fishes that scrape (Gibb et al. 2008). The functional importance of a flat tooth-bearing surface was lost when feeding on *Ulva,* yet *G. nigricans* produced a similar flat bite surface. This suggests that the modifications to the anatomy of *G. nigricans* have led to trade-offs in terms of suction feeding and scraping as the method of food procurement. Such trade-offs are not apparent for all scrapers and biters. Tropical wrasses and temperate greenlings, for example, have been shown to bite at attached prey while increasing suction production (Nemeth 1997, Ferry-Graham et al. 2002). Yet, in *G. nigricans*, the changes described here allow them to take advantage of an abundant food source that is virtually untapped in the eastern North Pacific.

CONCLUSION

The truly herbivorous kyphosid, *Girella nigricans*, utilizes a slightly different bite depending on the diet item that they are feeding upon. Based on the kinematics of the feeding events, *G. nigricans* used a different bite when feeding on a diet item that must be scraped versus a diet item that was suspended in the water column. Even when a diet item was suspended in the water column, *G. nigricans* did not appear to use any type of suction. This is surprising as suction is the basal method of fish feeding. By investigating the morphology of jaw opening and closing, it was confirmed that this species is highly adapted for scraping, with pronounced premaxillary rotation in addition to rotation around the IMJ. During jaw closure, rotation around the IMJ allows for a flat tooth bearing surface until the gape has been fully closed. Functionally, this allows more algae per bite than if the joint was not present in this species.

LITERATURE CITED

Alexander, R.McN. 1967. The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. J. Zool. 151, 43–64.

Alfaro., M. E. 2002. Forward attack modes of aquatic feeding garter snakes. Functional Ecology, 16: 204–215.

Alfaro, M.E., Janovetz, J., Westneat, M.W. 2001. Motor control across trophic strategies: Muscle activity of biting and suction feeding fishes. Am. Zool. 41: 1266–1279.

Barry, J.P., Ehret, M. J. 1993. Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California. Environ. Biol. of Fish. 37: 75-95.

Behrens, M.D., Lafferty, K.D. 2007. Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. Can. J. Fish. Aquat. Sci., 64: 868-873.

Bouton, N, Van Os N, Witte, F. 1998. Feeding performance of Lake Victoria rock cichlids: Testing predictions from morphology. J. Fish. Biol. 53: 118-127.

Drummond, H. 1983. Aquatic Foraging in Garter Snakes: A Comparison of Specialists and Generalists. Behavior. 86: 1-30.

Eschmeyer, W.N., Herald, E.S., Hammann, H. 1983. A field guide to pacific coast fishes of North America. Houghton Mifflin Company, Boston. pp. 221.

Ferry-Graham, L.A., Konow, N. 2010. The intramandibular joint in Girella: A mechanism for increased force production. J Morph 271: 271-279.

Ferry-Graham, L.A., Lauder, G.V. 2001. Aquatic prey capture in ray-finned fishes: A century of progress and new directions. J. Morph. 248: 99-119.

Ferry-Graham, L.A., Wainwright, P.C., Westneat, M.W., Bellwood, D.R. Mechanisms of benthic prey capture in wrasses (Labridae). Mar. Biol. 141: 819-830.

Gibb, A. Ferry-Graham, L.A., Hernandez L.P., Romansco R., Blanton, J. 2008. Functional significance of intramandibular bending in poeciliid fishes. Environ. Biol. Fish. 83: 507-519.

Harris, L.G., Ebeling, A.W., Laur, D.R., Rowley, R. J. 1984. Community Recovery after Storm Damage: A Case of Facilitation in Primary Succession. Science 224: 1336-1338.

Hernandez, L.P., A.C. Gibb, and L.A. Ferry-Graham. 2009. Trophic apparatus in cyprinodontiform fishes: functional specializations for picking and scraping behaviors. J. Morph. 270: 645-661.

Horn, M.H. 1989. Biology of marine herbivorous fishes. Oceanog. Mar. Biol. Ann. Rev. 27: 167-272.

Kanda, M., Yamaoka, K. 1995. Tooth and gut morphology in relation to feeding in three girellid species (Perciformes, Girellidae) from Southern Japan. Neth. J. Zool. 45: 495- 512.

Konow, N., Bellwood, D.R. 2005. Prey-capture in Pomacanthus semicirculatus (Teleostei, Pomacanthidae): functional implications of intramandibular joints in marine angelfishes. J. Exp. Biol. 208: 1421-1433.

Konow, N., Bellwood, D.R., Wainwright, P.C., Kerr, A.M. 2008. Evolution of novel jaw joints promote trophic diversity in coral reef fishes.

Lauder, G.V. 1985. Aquatic feeding in lower vertebrates. In Functional Vertebrate Morphology (ed. M. Hildebrand, D. Bramble, K. Liem and D. Wake), pp. 210-229. Cambridge, Mass.:Harvard University Press.

Liem, K.F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. Am. Zool. 20: 295–314.

Motta, P.J. 1984. Mechanics and function of jaw protrusion in teleost fishes: a review. Copeia 1984: 1-18.

Muller, M. Osse, J.W.M., Verhagen, J.H.G. 1982. A quantitative hydrodynamical model of suction feeding in fish. J. Theor. Biol. 95: 49-79.

Nemeth, D.H. 1997. Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, Hexagrammos decagrammus. J. Exp. Biol. 200: 2155-2164.

Norris, K.S. 1963. The Functions of Temperature in the Ecology of the Percoid Fish Girella nigricans (Ayres). Ecol. Mono. 33: 23-62

Osse, J.W.M. and Muller, M. 1980. Functional anatomy of the head of the perch (Perca fluviatilis L.); an electromyographic study. Neth. J. Zool. 19: 289-392.

Wainwright, P.C. and Shaw S.S. 1999. Morphological basis of kinematic diversity in feeding sunfishes. J. Exp. Biol. 202: 3101-3110.

Yagishita, N. and Nakabo, T. 2003. Evolutionary trend in feeding habits of Girella (Perciformes: Girellidae). Ichthyol. Res. 50: 358-366.

FIGURES:

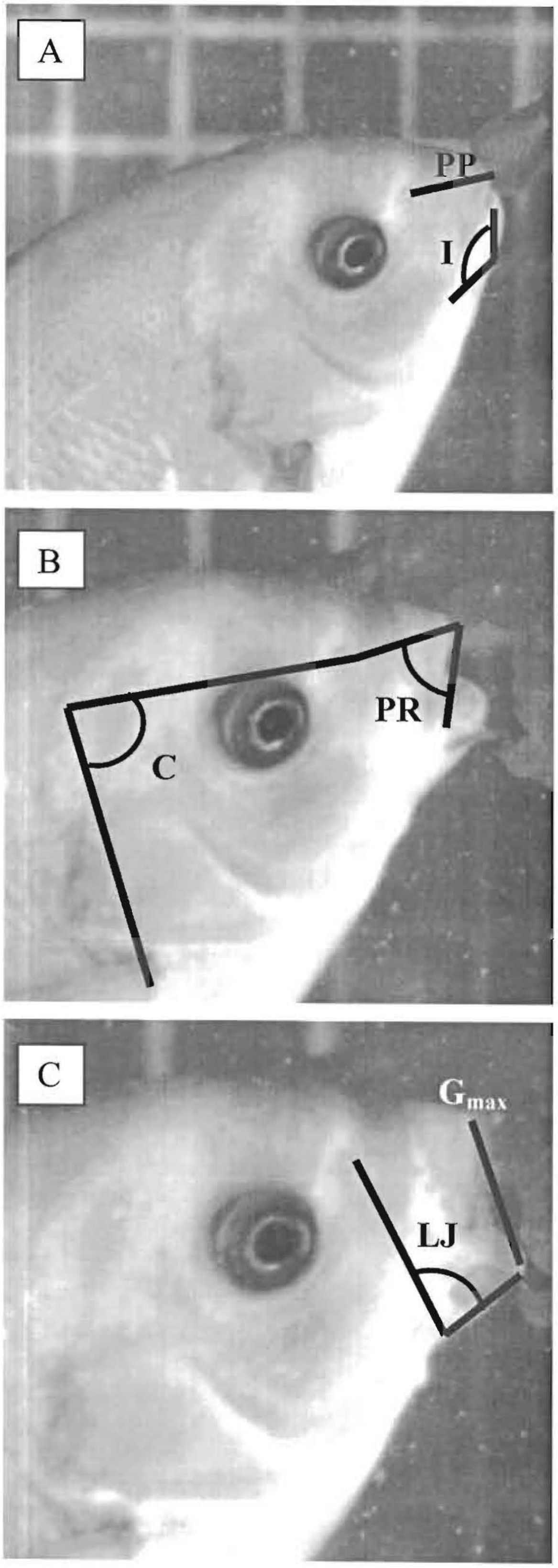
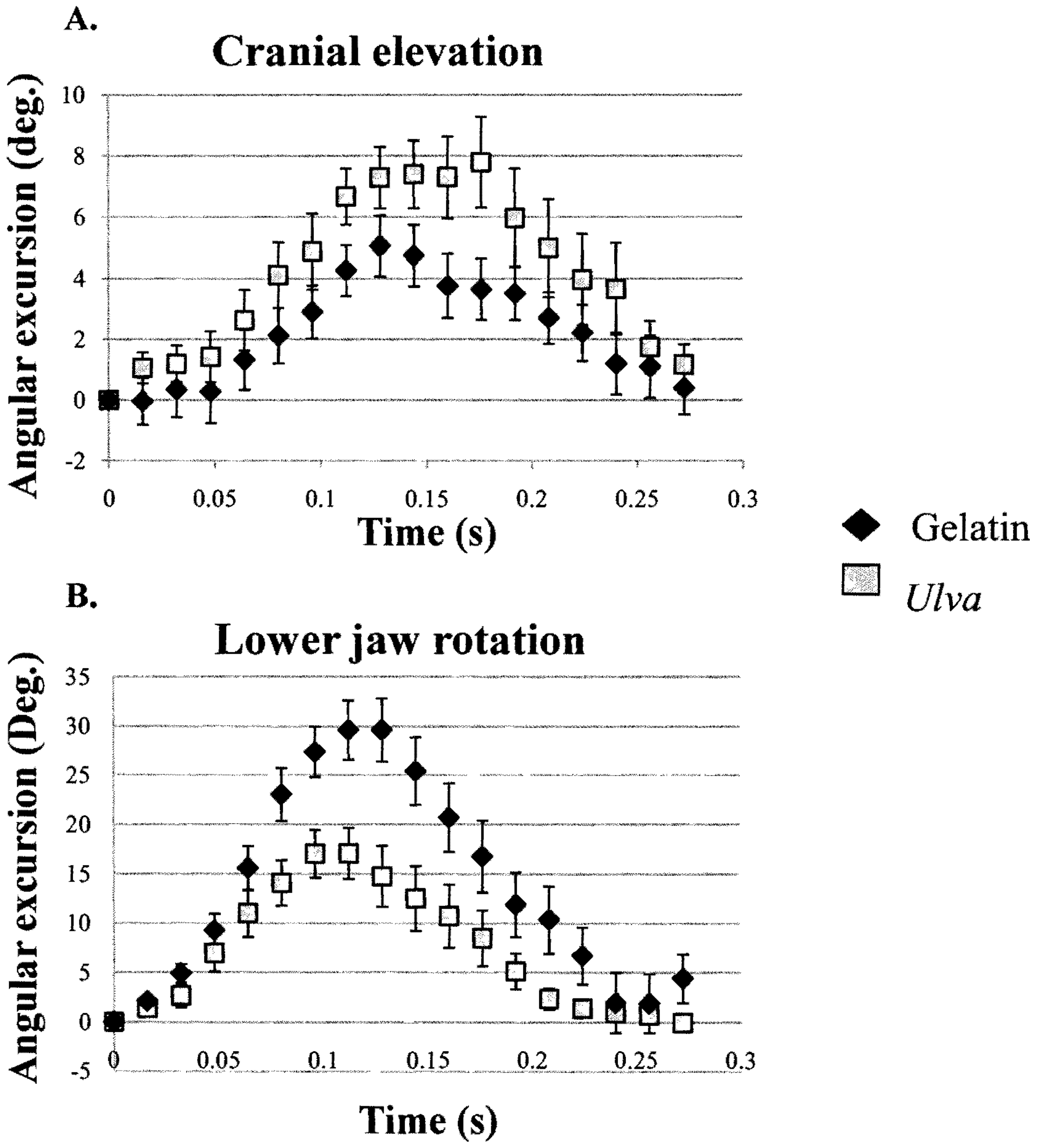
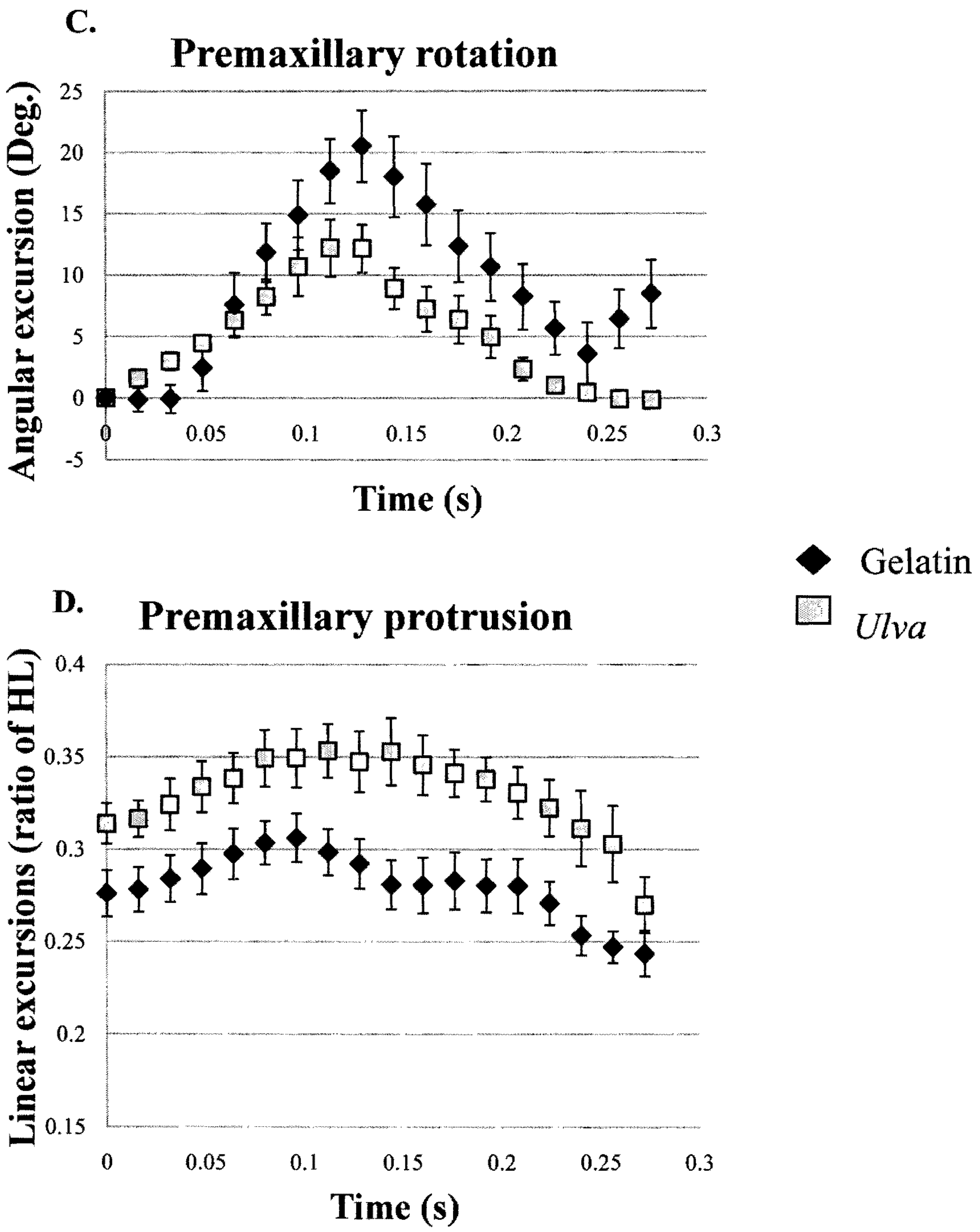


Figure 1: Images taken from a feeding event on *Ulva* by *Girella nigricans*. Represented are the measurements that were taken during all feeding events. (A) PP= premaxilla protrusion which was measured from the nasal to the tip of the premaxilla and I= intramandibular rotation which was measured from the lower jaw articulation to the intramandibular joint to the tip of the dentary. (B) PR= premaxilla rotation which was measured from the nasal to the tip of the premaxilla to the base of the premaxilla and C= cranial elevation which was measured from the pectoral fin to the origin of the opercula to the nasal. (C) LJ= Lower jaw depression which was measured from the nasal to the lower jaw articulation to the tip of the dentary and G_{max}= Gape maximum which was measured from the tip of the premaxilla to the tip of the dentary.


A.
Cranial elevation
Angular excursion (deg.)
10
8
6
4
2
0
-2
0
0.05
0.1
0.15
0.2
0.25
0.3
Time (s)
B.
Lower jaw rotation
Angular excursion (Deg.)
35
30
25
20
15
10
5
0
-5
0
0.05
0.1
0.15
0.2
0.25
0.3
Time (s)
◆ Gelatin
▨ *Ulva*



Premaxillary rotation

Premaxillary protrusion

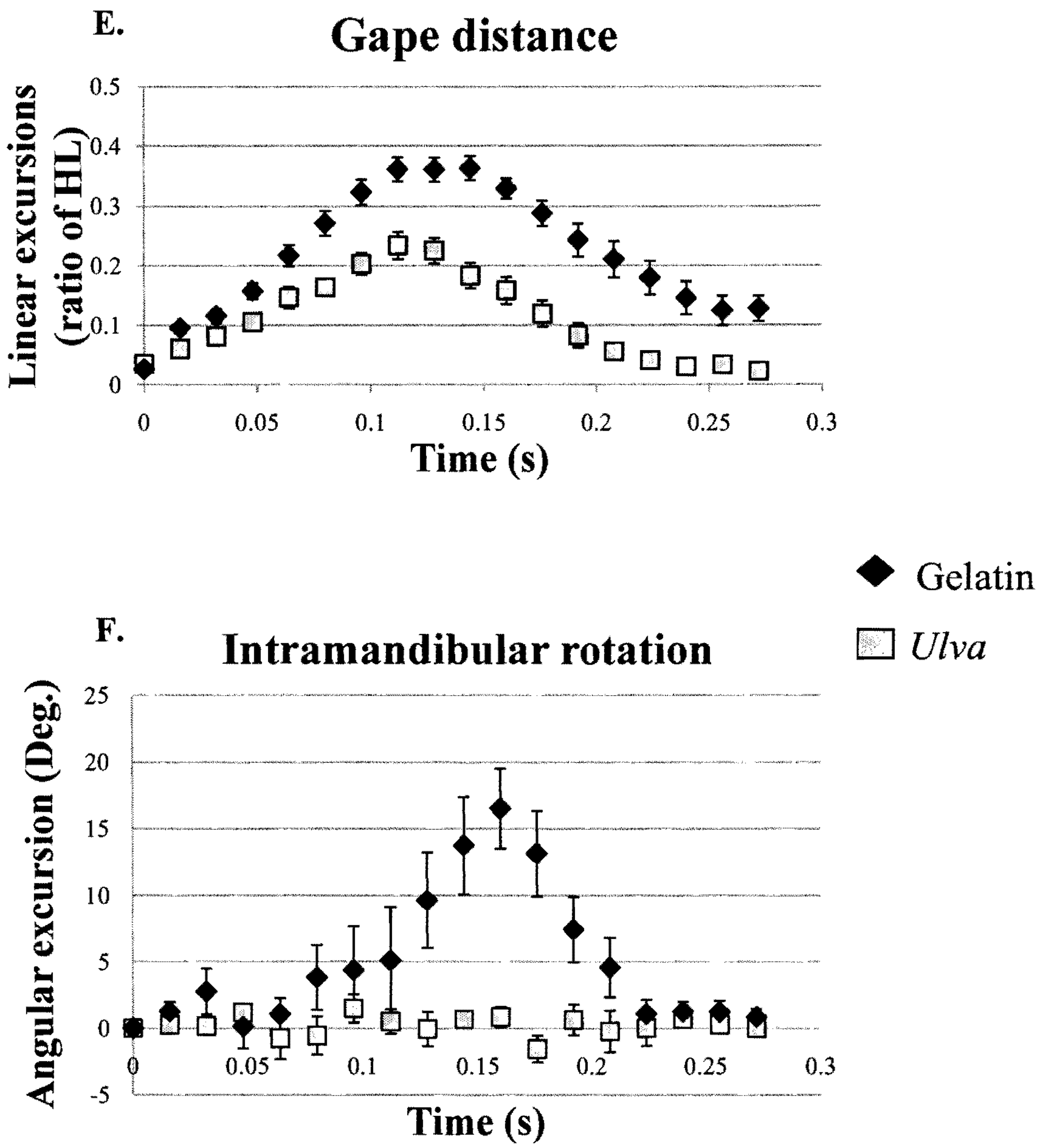


Figure 2: Average kinematic profiles for gelatin and *Ulva* feeding events (n=30 for each). Black diamonds are gelatin-feeding events and grey squares are *Ulva*-feeding events. A. Cranial elevation, B. Lower jaw rotation, C. Premaxillary rotation, D. Premaxillary protrusion. E. Height of gape during a feeding event, F. Intramandibular rotation.

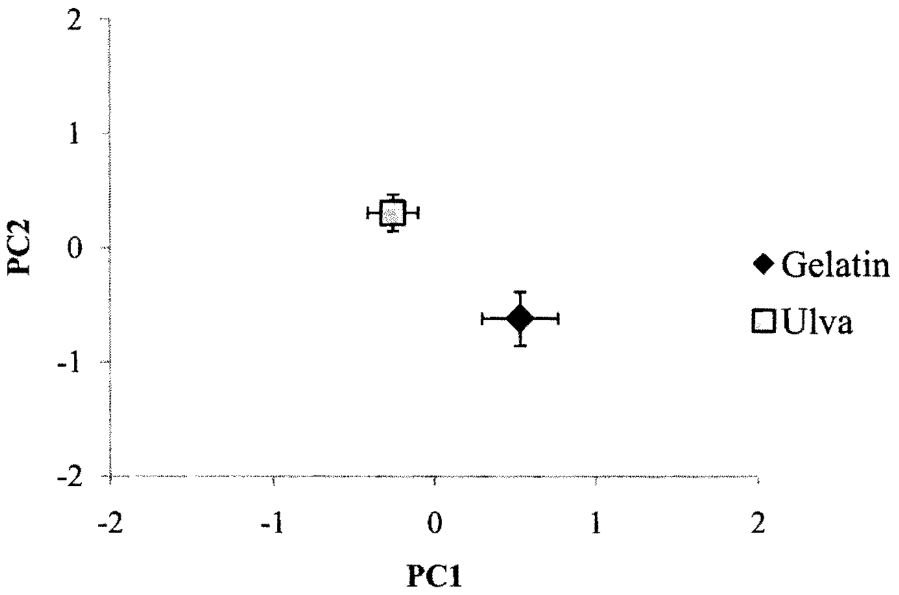


Figure 3: A graphical representation of PC1 and PC2. PC1 is represented by lower jaw rotation and gape distance both of which increase in the positive x direction. PC2 is represented by cranial elevation and premaxillary protrusion both of which increase in the positive y direction. Significant differences were seen for both PC1 and PC2 between feeding events.

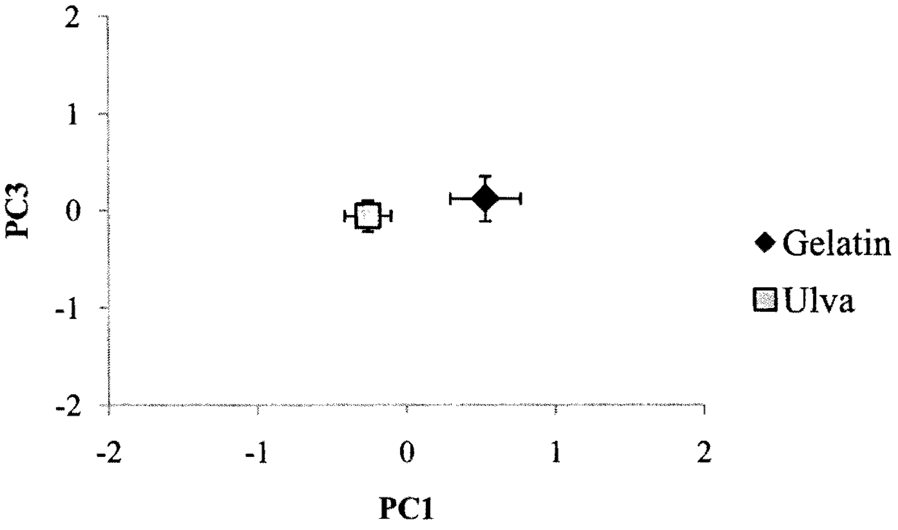
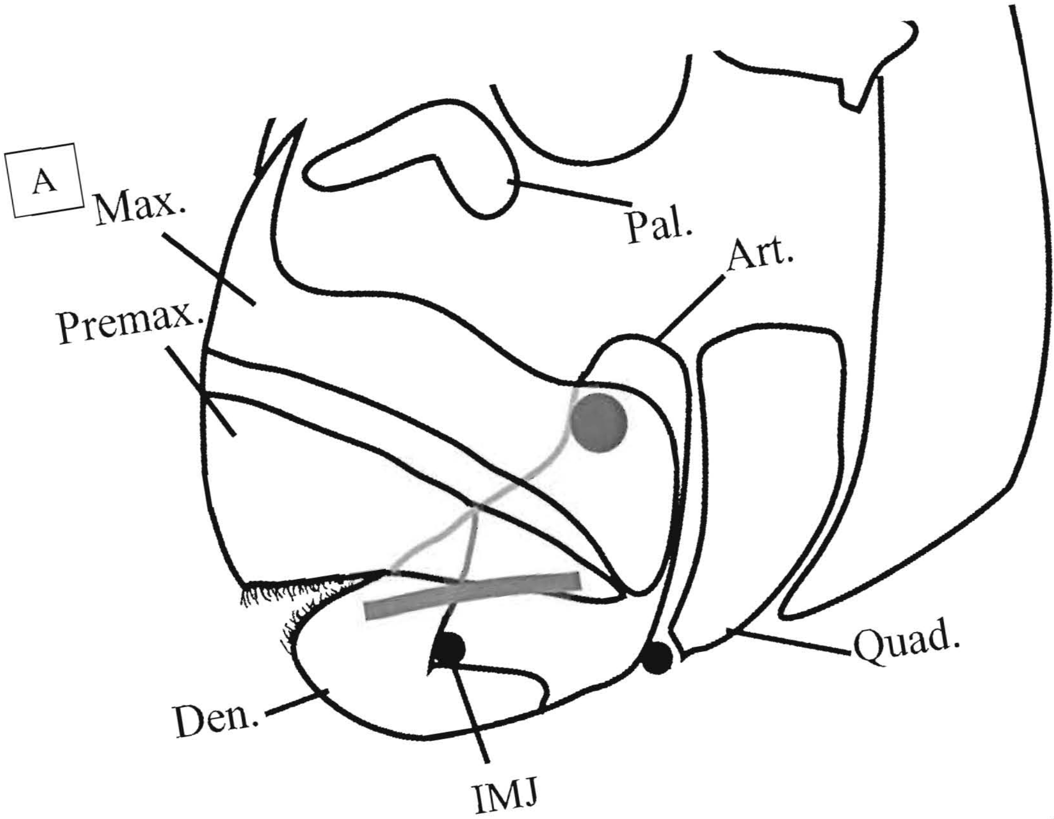


Figure 4: A graphical representation of PC1 and PC3. PC1 is represented by lower jaw rotation and gape distance both of which increase in the positive x direction. PC3 is represented by premaxillary rotation which increases in the negative y direction. A significant difference was seen in PC1 but not PC3.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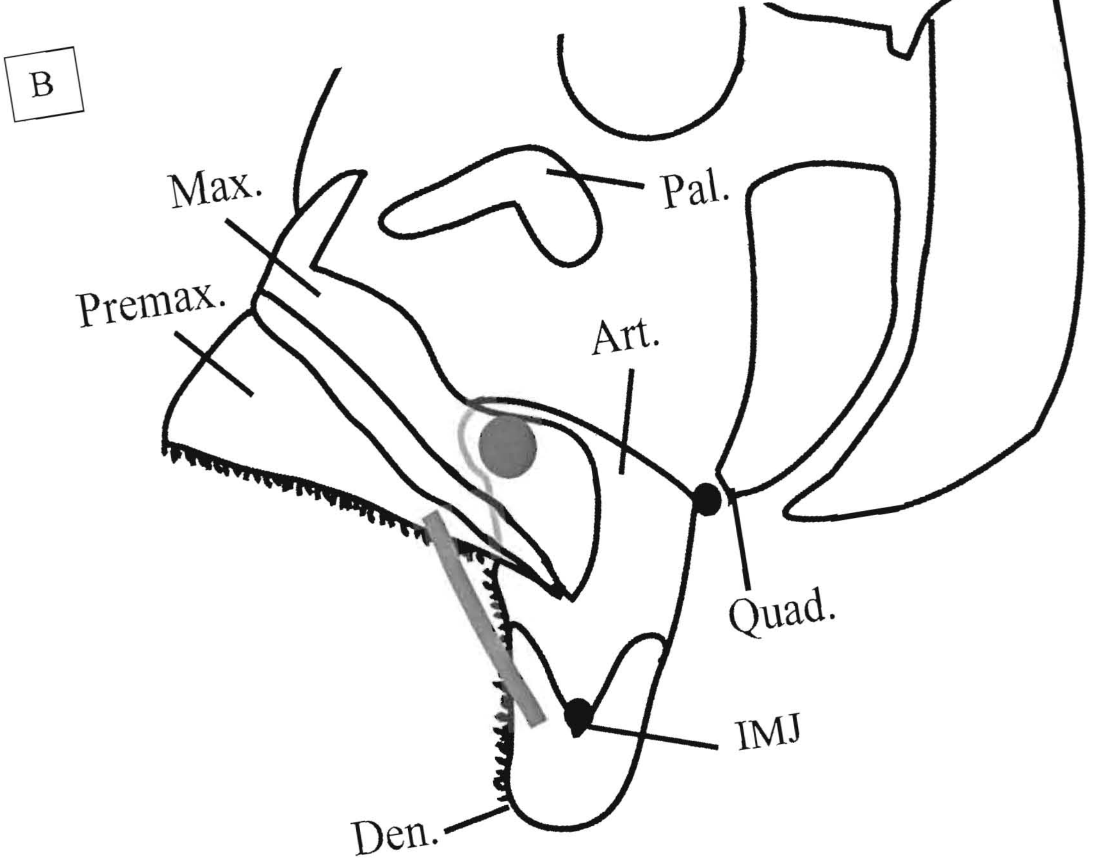
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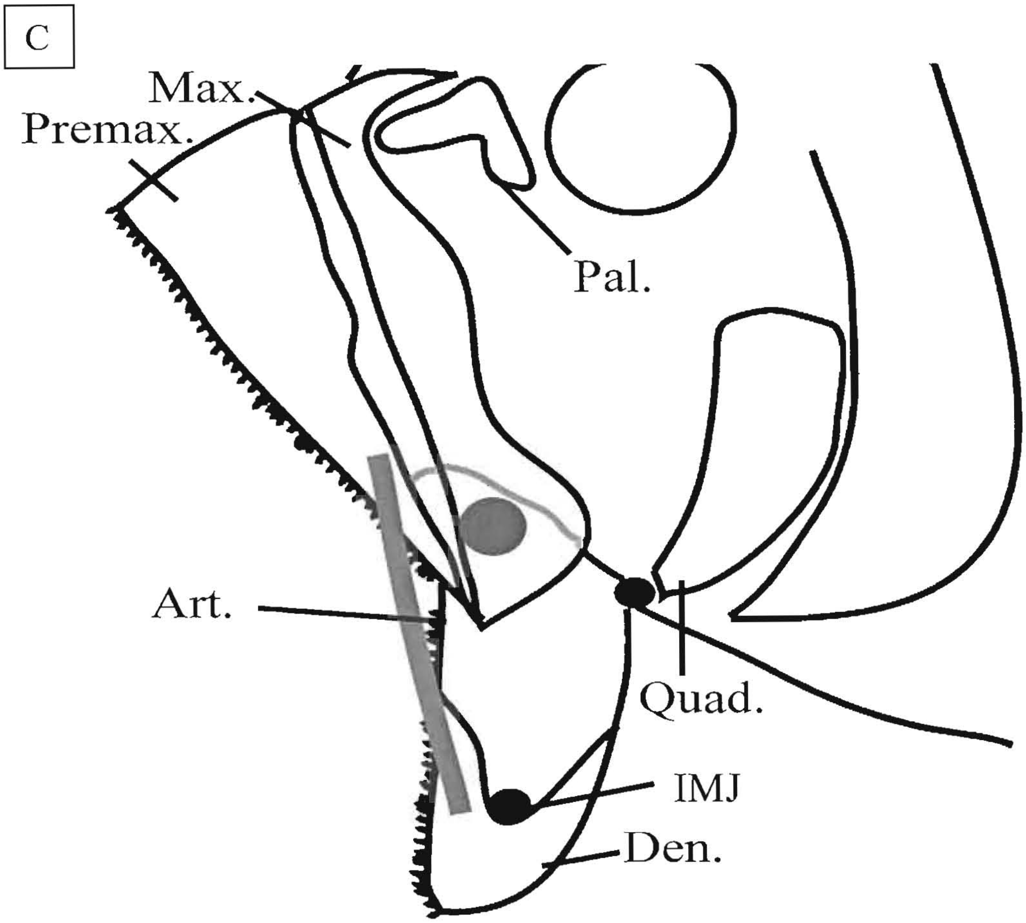

Figure 5: Line drawings from defrosted *G. nigricans*. Drawings were done from the closed position (A.) from the halfway open position (B.) and the fully open position with the last 25% of jaw opening assisted by the rectangle (C.). The Circle between the articular and maxilla represents the piece of tissue that allows for rotation between those two jaw elements. The rectangular line connecting the dentary to the premaxilla represents a piece of connective tissue that when pulled tight by ventral rotation of the lower jaw creates anterior rotation in the maxilla and premaxilla unit.

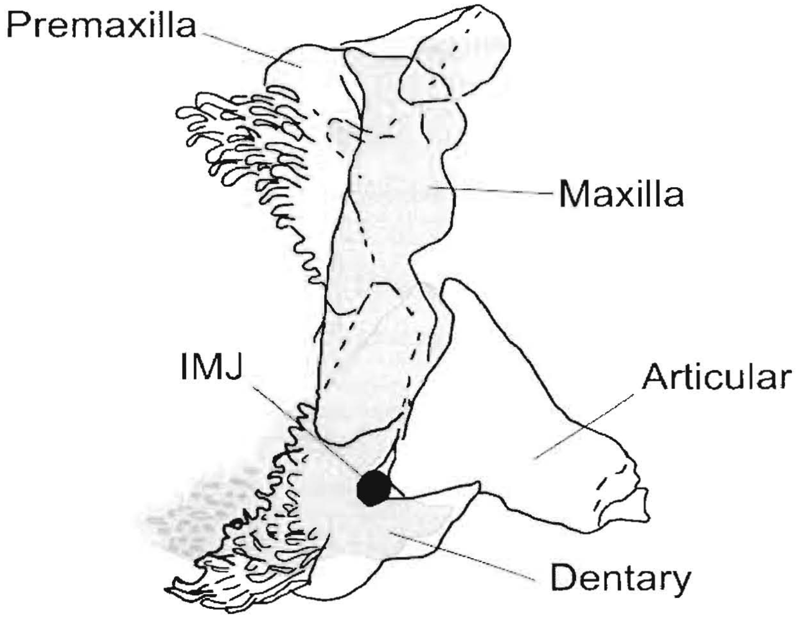

Figure 6: Modified after Ferry-Graham and Konow 2010. A drawing of *G. nigricans* jaws with intramandibular rotation occurring around the IMJ. The grey section of the drawing represents where the jaw naturally opens to and the white portion represents where the jaw extends to during rotation. For this species rotation only occurred when a force was applied to the dentary.

CHAPTER 2

THEORETICAL BITE FORCE PRODUCTION IN THE COMMON EASTERN NORTH PACIFIC KYPHOSIDAE

INTRODUCTION

Marine herbivorous fishes seem to play a considerable role in the biological formation and structure of shallow water reef habitats (Gaines and Lubchenco 1982, Horn 1989, Vial and Ojeda 1990, Clements and Choat 1997). We know a great deal about the mechanics of herbivory (sensu Wainwright (Lewis and Wainwright 1985, Wainwright 1988, Price et al. 2010), Westneat (Westneat 1990, Alfaro et al 2001, Westneat 2003), and Bellwood (Purcell and Bellwood 1993, Mantyka and Bellwood 2007, Konow et al. 2008, Hoey and Bellwood 2010)). Also, the physiology of herbivory (Gaines and Lubchenco 1982, Horn 1989, Vial and Ojeda 1990, Harmelin-Vivien 2002, Moran and Clements 2002, Behrens and Lafferty 2007, Clements et al. 2009) and the ecological niche formed by herbivorous fish species in both the tropical and temperate realms (Barry and Ehret 1993, Harris et al. 2002, Pèrez-Matus et al. 2007) have been well described.

However, at temperate latitudes, herbivorous fishes do not play as big of a role in the biological formation of reef structure, and many herbivorous niches appear to exist and are virtually untapped (Barry and Ehret 1993, Harmelin-Vivien 2002, Floeter et al. 2004, Pèrez-Matus et al. 2007, Mora 2008, Clements et al. 2009, Tolentino-Pablico et al. 2008). Multiple theories exist on the causes of this difference between the temperate and tropical regimes. The predominant idea is that algal material cannot be digested in cold temperatures due to the high amounts of energy it takes to break down a low quality diet item (Clements et al. 2009). Low temperatures cause slow enzyme function, which slows digestion. As a result, low quality dietary items such as algal material are generally not consumed at high latitudes (Clements et al. 2009). Another prominent theory is that algal material is of a different composition at higher latitudes, and therefore may be tougher to remove from the substrate (Clements et al. 2009). Because of this theory, many (Liem 1978, Purcell and Bellwood 1993, Ferry-Graham and Konow 2002, Konow et al. 2008, Ferry-Graham and Konow 2010) have investigated the mechanics of removing tough algal material.

The mechanics of algal removal by fishes is ultimately limited to the simple problem of fish muscles exerting forces on fish bones (i.e., the lower jaw), and ultimately causing rotation around a joint (i.e., the jaw articulation; Westneat 2003). Thus, a lever approach can be used to model force production and the subsequent ability to remove such food items. In the feeding apparati of fishes, the variation between and within a species has made modeling of lever systems a dynamic area of research (Delsman 1925, Alexander 1967, Liem 1978, 1980; Lauder 1980, Wainwright and Lauder 1986, Westneat 1990, 1991). Modeling is invaluable as it provides testable hypotheses of the connection between morphology and ecology, while expanding exploration of structural and physiological variation (Westneat 1995). Biting as a mode of prey capture is less common than other modes such as ram or suction feeding, and is often associated with an additional increase in muscular and skeletal complexity when compared to phylogenetic relatives that use ram or suction feeding (Alfaro et al. 2001, Wainwright and Bellwood 2002, Ferry-Graham and Konow 2010).

Feeding structure complexity can be seen in both the musculature and bone structure of herbivorous fishes. Characteristics such as well developed adductor mandibulae muscles accompanied by robust jaw bones in benthic feeding wrasses, (Westneat 1994, Wainwright and Richard 1995, Ferry-Graham 2002) and the intramandibular joint (IMJ) in the girellids (Vial and Ojeda 1990), pomacanthids (Konow and Bellwood 2005), and acanthurids (Purcell & Bellwood 1993) are examples of how biters and scrapers use their herbivorous benthic prey array. The IMJ is a novelty joint that allows for rotation between the articular and dentary. Flexion about this joint allows for increased performance of the feeding apparatus both in the form of force production and increased time of the tooth bearing surface contacting the diet item (Ferry-Graham and Konow 2010).

In the temperate eastern North Pacific, a few intertidal and subtidal fish families such as the Kyphosidae, Pholidae, and Stichaeidae, have been able to exploit the huge and underused herbivorous trophic resource (Barry and Ehret 1993). A sub-family of the Kyphosidae that has occupied sub-tropical and temperate waters while maintaining herbivory and the IMJ is the Girellinae, specifically *G. nigricans*. Two other members of the Kyphosidae that exhibit herbivory but do not have the intramandibular joint are *Hermosilla azurea* (zebraperch) and *Medialuna californiensis* (halfmoon). All three species occupy the shallow rocky reef and kelp bed habitats and are considered to be multivorous; the levels of herbivory begin to vary as these fishes become juveniles and on into adulthood. *Girella nigricans* is considered to be a benthic grazer that scrapes the highly nutritious microalgae off of rocky substrates (Clements et al. 2009). *Hermosilla azurea* is considered to be a benthic browser constantly moving and feeding on small macroalgae (Barry and Ehret 1993, Clements et al. 2009, Horn 1989). *Medialuna californiensis* has a markedly different feeding behavior, picking out invertebrates from kelp stalks and feeding on newly settled macroalgae (Harris et al. 1984).

The aims for this study were to quantify and compare the theoretical forces created by *G. nigricans, H. azurea* and *M. californiensis.* I compared mechanical advantages and physiological cross sectional areas of adductor mandibulae numbers two and three, testing the hypothesis that there is a quantifiable difference between the three species. I then compared, among species, the total theoretical force produced at the tip of the dentary to investigate the different potential output forces. I concluded this study with a comparison of force production during the course of the bite. To supplement the force data, I provided morphological descriptions to better understand the mechanisms of force production in each species.

MATERIALS AND METHODS

Animal Collection and Imaging

All fishes were collected using a spear gun in Laguna Beach, California under the California Department of Fish and Game scientific collecting permit number 9932 and held under San Jose State University IACUC protocol number 814. Twenty six *Girella nigricans* (26.0-63.00 mm, head length (HL)), 10 *Hermosilla azurea* (54.00-69.00 mm HL), and 10 *Medialuna californiensis* (42.00-70.00 mm HL), were speared, then frozen, and transported to Moss Landing Marine Laboratories. The fishes were then defrosted and dissected. One side of each fish was dissected at a time. All dissections began by removing and weighing adductor mandibulae two (AM2) and three (AM3) to the nearest 0.001 g. Each muscle was patted dry before weighing. AM2 and AM3 from the right and left sides were averaged to yield a single weight value for each muscle from each fish. After the musculature had been removed, photos were taken using a Cannon digital SLR placed laterally over the fish's head with a ruler in view for scale. Digital X-ray was used on one specimen of each species to further assist in visualization of the lower jaw apparatus and associated anatomy. Digital X-radiography was provided by the Community Hospital of the Monterey Peninsula.

Physiological cross-sectional Area

Muscle physiological cross-sectional area (PCSA) can be used as a metric for comparison of the applied muscle mass (Powell et al. 1984). To calculate physiological cross-sectional area for all fishes, the following equation was used:

$$\text{PCSA} = (\text{muscle mass}/\text{muscle density}) \times (\cos \Theta) \times (1/\text{fiber length})$$

where Θ is equal to the average pennation angle from the central tendon. As described in Westneat (2003), pennation angle is the angle or orientation of the muscle fibers. The best estimation of fish muscle density is 1.05 g cm^{-3} (Powell et al. 1984 and Wainwright 1988). Fiber length was observed by patting the muscle dry and measuring 10 muscle fibers and then averaging them to yield one fiber length per muscle. The average pennation angle for all individuals was zero. PCSA calculations were averaged for each side of the head to yield one value for AM2 and one value for AM3 for each fish. An analysis of covariance (ANCOVA) was used to test the hypothesis that there was no species effect on the PCSA for each muscle. Head length was used as the fixed factor with muscle PCSA as the dependent variable.

Modeling Lower Jaw Force Production

Once photos were taken for all fishes, they were digitized using Image J (NIH). The lower jaw was modeled as a third order lever system and the biomechanics of the jaw were modeled in the program Mandiblever 3.3 (Westneat 2003; Fig. 1). The following measurements were taken to the nearest 0.001 cm while the jaw was closed: (1) in-lever A2, from quadrate-articular joint to A2 insertion on the articular; (2) in-lever A3, from quadrate-articular join to A3 insertion on the medial face of the articular; (3) in-lever open, from quadrate-articular joint to the posteroventral margin of the articular; (4) out-lever, from quadrate articular joint to dentary tip; (5) A3 length, from origin on preopercle to insertion on the ascending process of the articular; (6) A3 total length, From origin on preopercle and hyomandibular to insertion on the medial face of the articular; (7) A3 tendon, from tendon insertion on medial face of articular to tapering end into A3 fibers; (8) A2-joint distance, from A2 origin at preopercle to quadrate-articular joint; (9) A3 joint distance, from origin of A3 to quadrate-articular joint; (10) A2-A3 ins, from A2 to A3 insertion; (11) LJtop length, from the tip of the articular to the most distal part of the dentary; and (12) LjBot length from postventral margin of the articular to the tip of the dentary. These variables were used by Mandiblever to estimate the force produced in the closed position, open 10°, 20°, and 30° for each fish. Mandiblever calculated force using the equation:

$$F_{\text{output}} = F_{\text{acting musle}} \times \sin(a) \times MA$$

Where (a) is the action angle of the muscle and MA is the mechanical advantage of that muscle. A force calculation was made for each muscle and then added to yield a unilateral force produced at the tip of the dentary. This value was then added to the opposite side of the head to yield a bilateral force produced at the tip of the dentary. Mandiblever was also used to provide the mechanical advantage for AM2 and AM3 for each fish. One rosy rockfish (*Sebastes rosaceus*), a generalized, non-modified species, was included as a baseline for my comparisons.

To test the hypothesis that there were no significant differences in bite force production among species, an analysis of covariance (ANCOVA) was run in which HL was a fixed factor and force produced in the closed position was the dependent variable. To test the hypothesis that a species effect persisted in the mechanical advantages, the mechanical advantages for AM2 and AM3 were averaged for each species. An analysis of variance (ANOVA) was used to compare average mechanical advantage among the three species. In the case in which significant differences were detected, LSD post-hoc tests were used to further examine trends. To compare among species at each point in the bite, I averaged the force values for each individual in their respective bite phase. This yielded a single value for each species at open 30°, 20°, 10°, and closed. To control for the confounding variable of size, only individuals that were within the range of 42.0-70.0 mm HL were included. This yielded a new sample size of 10 for each species. By doing this the smallest *Girella nigricans* were included. To test for significant differences between species during the bite, a one-way ANOVA was used for every measured point during the bite, followed by LSD post-hoc tests.

IMJ and Force Production

In this study, *Girella nigricans* was the only species that possessed the intramandibular joint. As rotation occured around the IMJ, the out-lever length shortened (Fig. 2). If the same force of the muscle was applied to a shortened out-lever, the result was an increased force production at the tip of the dentary (Ferry-Graham and Konow 2010). To determine the ramifications of this biomechanical property, the articular was held still with forceps while applying a force to the tip of the dentary. Rotation around the IMJ continued until the ventral section of the dentary made contact with the articular, which is where the rotation was stopped. Photos were taken at the point of maximum rotation and analyzed using Image J. The measurements that changed were: (4) out-lever, from quadrate articular joint to dentary tip; (11) LJtop length, from the tip of the articular to the most distal part of the dentary; and (12) LjBot length from postventral margin of the articular to the tip of the dentary, with all other variables staying the same (Fig. 1). This new information was added to the previous information in Mandiblever 3.3. The new output force, as predicted by Mandiblever, was recorded for the jaw in the 30° open position.

Force was estimated for the fully open jaw position (the maximum angle of rotation around the IMJ) because this moment is when intramandibular bending is of most ecological and biomechanical significance. At maximum gape, the output force created by the lower jaw is necessarily the weakest, due simply to the mechanical advantage of the jaw in that orientation. Conversely, the shortened jaw lever arm created by intramandibular rotation may increase the force that can be applied to the substrate. Additionally, there are changes in the lateral forces during the bite. When the dentary first makes contact with the substrate the highest amount of lateral force will be applied to the substrate. This will necessarily occur at the onset of a scraping event, when the gape is likely maximally opened. As the scrape continues, the force of the jaw acts, in some part, lateral to the body, thereby forcing the fish away from the substrate. As this occurs intramandibular bending is reduced (pers. obs.).

To test the hypothesis that intramandibular bending increases force production at the tip of the dentary, a Student's t-test was used. The average force produced in the open position (30°) with no intramandibular bending was compared to the average force at the output in the same position with flexion around the joint. All individuals of *Girella* were used for this part of the study (n = 26).

RESULTS

Physiological Cross-Sectional Area

For all the sampled species and all individuals, AM2 had a larger PCSA than AM3. Physiological cross-sectional area showed a linear relationship when plotted against head length. Of the three species tested, *Girella nigricans* had the largest PCSA for both AM2 and AM3 for a given unit of head length (Fig. 3). *Medialuna californiensis* and *Hermosilla azurea* had similar PCSAs for both AM2 and AM3. Based on the results of the ANCOVA, the slopes for AM2 and AM3 were not significantly different among species and among one another

(Muscle effect for AM2: $F = 2.410$, $p > 0.05$; Muscle effect for AM3: $F = 2.272$, $p > 0.05$; Species effect for AM2: $F = 0.75$, $p > 0.05$; Species effect for AM3: $F = .744$, $p > 0.05$). There were no species effects on adductor PCSA based upon the individuals sampled.

Lower Jaw Force Production

The differences seen in mechanical advantages of both AM2 and AM3 differed among species. With respect to AM2, *G. nigricans* and *H. azurea* were not significantly different from one another, but both were significantly larger than *M. californiensis* (ANOVA: $F = 6.06$, $p < 0.05$; Fig. 4). Conversely, for AM3, *G. nigricans* and *H. azurea*, again, did not differ from each other but had a lower mechanical advantage than *M. californiensis* (ANOVA: $F = 37.96$ $p < 0.005$; Fig. 4).

The interpretation of species-effects in this model is difficult because when lower jaw maximum force production was plotted against head length (Fig. 5), the interaction term in the ANCOVA yielded a significant result ($F = 9.114$, $p < 0.05$). However, it was apparent that *G. nigricans* had higher forces per unit head length than the other species and *Medialuna californiensis* and *Hermosilla azurea* had similar force out-puts per unit head length with no recognizable trend between them. Based on the significant interaction term, the rate of change through ontogeny is different in the three species tested. Thus, they were not compared further statistically.

In the bite sequence data, *G. nigricans* plotted significantly higher than both species tested. Differences occurred at all points during the bite (30°: $F = 10.996$, $p < 0.005$; 20°: $F = 17.161$, $p < 0.005$; 10°: $F = 21.530$, $p < 0.005$; Closed: $F = 22.343$, $p < 0.005$; Fig. 6). The ANOVAs also revealed that *H. azurea* and *M. californiensis* were not significantly different from one another at any point during the bite (Fig. 6, $p > .05$). Note that *S. rosaceus* was not included in the statistical analysis because I only had one individual. However, this species clearly falls between *M. californiensis* and *H. azurea*.

IMJ and Force Production

In *Girella nigricans*, on average, approximately 5 degrees of rotation around the IMJ occurred. This rotation resulted in a 20 to 25 percent decrease in the out-lever length, in keeping with the estimates of Ferry-Graham and Konow (2010). This consistently led to an increase in force produced at the tip of the dentary (Fig. 7), though not statistically significant.

DISCUSSION

The collective findings documented here further support the theory that *G. nigricans* is a scraping specialist. Mandiblever revealed significantly higher forces generated by the lower jaw for this species. Examination of the dentition work (Norris and Prescott 1959) and jaw structure (Ferry-Graham and Konow 2010) had previously suggested this hypothesis. The Mandiblever findings detailed here add biomechanical credence to this notion. As seen in Fig. 4 the PCSA, for AM2 and AM3, per unit head length was larger in *G. nigricans* than any other species tested. This further suggested that *G. nigricans* can produce high forces that may assist in scraping. Based on the high (> 0.6) mechanical advantage of AM2 in *G. nigricans* and its large PCSA one might expect this to be the primary jaw closing muscle. *Girella nigricans* has a deep jaw that possibly assists in rotation rather than protrusion. As a result, the mechanical advantage of AM3 was small for a biter (~ 0.4) which may suggest AM3 is a supplemental closing muscle rather than contributing significantly to jaw closure. Although the force produced by *G. nigricans* was not significantly larger than the other species tested here, the force calculations produced a higher force in *G. nigricans* than any other species per unit head length. This further suggests that these fish are algae removing specialists as the force required to remove these diet items are high.

Medialuna californiensis, by contrast, is a picker. This species is often found in the middle of the water column feeding on the invertebrates in the kelp (Harris et al. 1984). As potentially expected, *M. californiensis* data tended to resemble those from the generalized *S. rosaceus* (Fig. 6). *Sebastes rosaceus* is known to pick invertebrates from the benthos, which might lead to further similarity among the species. The low (~ 0.5) mechanical advantage for AM2 and AM3 suggested that the *M. californiensis* jaw is built more for speed than power. Ecologically, this is critical as a speedy suction feeding event is necessary to pick invertebrates from the kelp (Harris et al. 1984). Although the mechanical advantages were low in *M. californiensis*, they still possess what one would expect to be large enough adductor muscles to supplement their diets with algal material. Both the PCSA of AM2 and AM3 (Fig. 3) and the total forces produced (Fig. 5) plot *H. azurea* and *M. californiensis* close to each other, but ecologically they are very different.

Hermosilla azurea is an inshore species, often seen feeding on the benthos. Therefore, one might expect them to be able to produce forces more similar to *Girella nigricans,* both in terms of total bite force and forces produced during the course of a bite. Based on the analysis of the diet of *G. nigricans* and *H. azurea* in Barry and Ehret (1993), they eat similar algal dietary items, but with *H. azurea* feeding more on the 'leafy' green algae. These softer green algae are likely more easily removed than the diet items that must be scraped by *G. nigricans*, and thusly weaker bite forces might result. It is also noteworthy that the dentition of *H. azurea* is located more posteriorly within the oral cavity when compared to *G. nigricans* (Fig. 8). This suggests that *H. azurea* is not as well equipped for scraping as *G. nigricans*. In *H. azurea* the mechanical advantages for AM2 and AM3 were not statistically different from *G. nigricans*, which might suggest that they can produce similar forces. The results from Fig. 5 suggest that, per unit head length, *H. azurea* cannot match *G. nigricans* in force production and thus is not as well equipped muscularly for scraping as *G. nigricans*. Ecologically, the results suggest that these fish are likely not scraping but picking or biting algae from the benthos.

Morphological novelties such as the IMJ have been a growing topic in the field of functional morphology. This study adds to that knowledge base as it connects evolutionary developments to their functional implications. In the case of the IMJ in *G. nigricans,* flexion of the IMJ shortened the out-lever which increased the force at the tip of the output. Surprisingly, no significant difference was found in the force produced as a result of flexion around the IMJ. It is noteworthy that there appeared to be no musculature associated with the generation of rotational movement about the IMJ. Many researchers (Vial and Ojeda 1990,Yagishita and Nakabo 2003, Ferry-Graham and Konow 2010) have suggested the possibility that flexion of the dentary around the IMJ could be facilitated by an intramandibular adductor in the genus *Girella*. This does not seem to be the case with *G. nigricans* as no such muscle inserts onto the dentary. Observations made on the insertion of AM3 indicated that the insertion occurs on the most anterior surface of the articular. This, along with high-speed video events of the scraping behavior, suggests that intramandibular bending in *G. nigricans* is passive and only occurs once the lower jaw is pressed against the surface. Although I saw no significant increase in force produced as a result of intramandibular rotation, the functional significance of the IMJ remains imperative. As the fish scrapes the surface of a rock, rotation of the dentary around the IMJ allows for a larger tooth-bearing surface to remain on the substrate for a longer period of time compared to a situation where no bending occurred. The longer residence time of the dentition on the substrate means the individual may consume more food per bite than if rotation does not occur. Feeding efficiency can be functionally significant to a species as it allows for less time feeding which is a time of low predator detection. Based on Fig. 6, *G. nigricans* had high force production when compared to different species in the same size range. One can imagine how different *Girella nigricans* theoretical force production becomes when intramandibular rotation is factored in. The out-put force production created by *G. nigricans* would make the gap between itself and all other species tested even larger.

Based on mitochondrial DNA phylogenetics in Yagishita and Nakabo 2003, *G. nigricans* is most closely related to *G. elevata* and *G. tricuspidata* which are both native to the south eastern coast of Australia. In the previously mentioned paper the authors made dentition morphological comparisons and found that the tricuspid shaped teeth exist in the three species. It is unclear as to how *G. nigricans* is related to *H. azurea* and *M. californiensis* as no phylogenies exist. Based on the arguments made in Yagishita and Nakabo 2003, I believe that *G. nigricans* is more closely related to their southern ocean relatives than to *H. azurea* or *M. californiensis.* Because *M. californiensis* and *H. azurea* belong to different families, I believe their evolutionary story is similar to *G. nigricans.* Phylogenies do not exist for either species but I believe they have a closely related relative in the southern Pacific. Over evolutionary time they found suitable habitat along the eastern North Pacific which is where they live today.

CONCLUSION

Girella nigricans is specialized for scraping and can produce more jaw closing force than any other eastern North Pacific kyphosid. Based on the location of the dentition and the high force production during the bite, *G. nigricans* is well equipped to scrape algal dietary from the benthos. The results of this study suggest that the comparative kyphosid species, *Medialuna californiensis* and *Hermosilla azurea*, feed in different manners from each other and from *G. nigricans*. The jaw of *M. californiensis* is built for speed rather than power normally exhibited by an herbivore. This result is supported ecologically as they pick invertebrates from the kelp stalks as adults while supplementing their diet with algal material. *Hermosilla azurea* is a benthic grazer and appears to fit in between the two previously mentioned species. These fish are commonly seen feeding on leafy algae growing on the benthos. This intermediate species has a deep jaw that appears to be well equipped for a bite and tear method of food procurement. Intramandibular bending occurred only in *G. nigricans*. Based on the amount of flexion allowed around the joint there was not a significant force increase during the bite. This, however, does not deter from the functional significance of the joint as it allows for a longer residence time of the tooth bearing surface on the scraped surface.

LITERATURE CITED

Alexander, R.McN. 1967. The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. J Zool 151, 43–64.

Alfaro, M.E., Janovetz, J., Westneat, M.W. 2001. Motor control across trophic strategies: Muscle activity of biting and suction feeding fishes. Am Zool 41: 1266–1279.

Barry, J.P., Ehret, M. J. 1993. Diet, food preference, and algal availability for fishes and crabs on intertidal reef communities in southern California. Environ Biol of Fish 37: 75-95.

Behrens, M.D., Lafferty, K.D. 2007. Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. Can J Fish Aquat Sci, 64: 868-873.

Clements, K.D., Choat, J.H. 1997. Comparison of herbivory in the closely-related marine fish genera *Girella* and *Kyphosus*. Mar Biol vol. 127; 4: 579-586.

Clements, K.D., Raubenheimer, D., Choat, J.H. 2009. Nutritional ecology of marine herbivorous fishes: ten years on. Funct ecol 23: 79-92.

Delsman, H.C. 1925. Fishes with protrusile mouths. Treubia 98–106.

Ferry-Graham, L.A., Konow, N. 2010. The intramandibular joint in Girella: A mechanism for increased force production. J Morph 271: 271-279.

Ferry-Graham, L.A., Wainwright, P.C, Westneat, M.W., Bellwood, D.R. 2002. Mechanisms of benthic prey capture in wrasses (Labridae). Mar Biol 141: 819-830.

Floeter, S.R., Ferreira, C.E.L., Dominici-Arosemena, A., Zalmon, I.R. 2004. Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. J Fish Biol 64: 1680-1699.

Gaines, S.D., Lubchenco, J. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. Ann Rev Ecol System 13: 111-138.

Harmelin-Vivien, M.L. 2002. Energetics and fish diversity on coral reefs. In coral reef fishes: dynamics and diversity in a complex ecosystem. Academic press, New York. pp. 265-274.

Harris, L.G., Ebeling, A.W., Laur, D.R., Rowley, R. J. 1984. Community Recovery after Storm Damage: A Case of Facilitation in Primary Succession. Science 224: 1336-1338.

Hoey, A.S., Bellwood, D.R. 2010. Among-habitat variation in grazing intensity on Sargassum spp. on a mid-shelf reef in the northern Great Barrier Reef. Mar Biol 157: 189-200.

Horn, M.H. 1989. Biology of marine herbivorous fishes. Oceanog Mar Biol Ann Rev 27: 167-272.

Horn, M.H., Ojeda, F.P. 1999. Herbivory. *In* intertidal fishes: Life in two worlds. *Edited by* M.H. Horn, K.L.M. Martin, and M.A. Chotkowski. Academic Press, New York, pp. 197-222.

Konow, N., Bellwood, D.R., Wainwright, P.C., Kerr, A. 2008. Evolution of novel jaw joints promote trophic diversity in coral reef fishes. Biol J Linnean Soc 93: 545–555.

Lauder, G.V. 1980. Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of polypterus, lepisosteus, and amia. J Morph 163: 283–317.

Lewis, S.M. and P.C. Wainwright. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. J Exp Mar Biol Ecol. 87: 215-228.

Liem, K.F. 1978. Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlids. I. Piscivores. J Morph 158: 323–360.

Mantyka, C.S., Bellwood, D.R. 2007 Direct evaluation of macroalgal removal by herbivorous coral reef fishes. Coral Reefs (published online).

Mora, C. 2008. A clear human footprint in the coral reefs of the Caribbean. Proc Royal Soc B 275: 767-773.

Moran, D., Clements, K.D. 2002. Diet and endogenous carbohydrases in the temperate marine herbivorous fish *Kyphosus sydneyanus*. J Fish Biol 60: 1190-1203.

Norris, K.S., Prescott, J.H. 1959. Jaw structure and tooth replacement in the opaleye, *Girella nigricans*, (Ayrea) with notes on other species. Copeia 4: 275-283.

Pèrez-Matus, A., Ferry-Graham, L.A., Cea, A., Vasquez, J.A. 2007. Community structure of temperate reef fishes in kelp-dominated subtidal habitats of northern Chile. Mar Fresh Res 58: 1069-1085.

Powell, P.L., Roy, R.R., Kanim, P., Bello, M.A., Edgerton, V.R., 1984. Predictability of skeletal muscle tension from architectural determinations in guinea pigs. J Appl Physiol 57: 1715–1721.

Price, S. A. , P. C. Wainwright, D. R. Bellwood, E. Kazancioglu, D. C. Collar, T. J. Near. 2010. Functional innovations and morphological diversification in parrotfishes. Evolution. 64-10: 3057-3068.

Purcell, S.W., Bellwood, D.R. 1993. A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). Envir Biol Fish 37: 139–159.

Tolentino-Pablico, G., Bailey, N., Froese, R., Elloran, C. 2008. Seaweeds preferred by herbivorous fishes. J App Phycol DOI 10.1007/s10811-007-9290-4.

Vial C.I., Ojeda F.P. 1990. Cephalic anatomy of the herbivorous fish *Girella laevifrons* (onteichthyes: Kyphosidae): mechanical considerations of its trophic function. Revista Chilena de Historia Natural 63: 247-260.

Wainwright, P. C. 1988. Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. Ecol 69: 635–645.

Wainwright, P.C., Lauder, G.V. 1986. Feeding biology of sunfishes: patternsof variation in the feeding mechanism. Zool J Linn Soc 88: 217–228.

Wainwright, P.C., Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. *Envir.* Biol Fish 44: 97-113.

Westneat, M.W. 1990. Feeding mechanics of teleost fishes (Labridae): a test of four-bar linkage models. J Morphol 205: 269–295.

Westneat, M.W. 1991. Linkage mechanics and evolution of the unique feeding mechanism of Epibulus insidiator (Labridae: Teleostei). J Exp Biol 159: 165–184.

Westneat, M. W. 1994. Transmission of force and velocity in the feeding mechanisms of labrid fishes. Zoomorph 114: 103-118.

Westneat, M.W. 1995. Feeding, function, and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. Syst Biol 44: 361–383.

Westneat, M.W. 2003. A biomechanical model for analysis of muscle force, power output and lower jaw motion in fishes. J Theor Biol 223: 269-281.

Yagishita, N. and Nakabo, N. 2003. Evolutionary trend in feeding habits of *Girella* (Perciformes: Girellidae). Ichthyol Res 50: 358-36

FIGURES

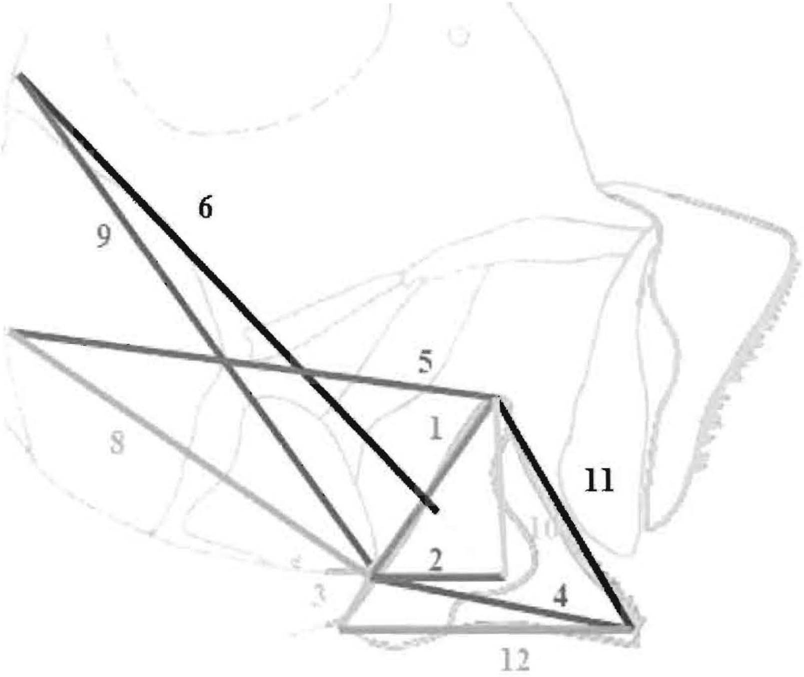

Figure 1: A visual representation of the morphometrics used in the program Mandiblever 3.3. Measurements are described on page 6.

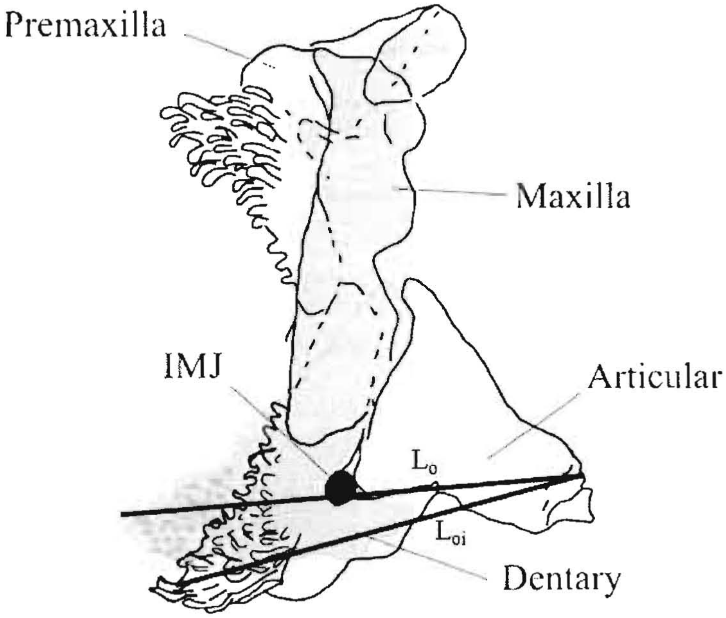

Figure 2: A visual representation of intramandicular bending modified after Ferry-Graham and Konow 2010. The gray illustration of the dentary is the lower jaw of *G. nigricans* without bending and the white illustration of the dentary represents bending around the IMJ. L_o: Original outlever, L_{oi}: The shortened out-lever after the dentary rotates around the intramandibular joint.

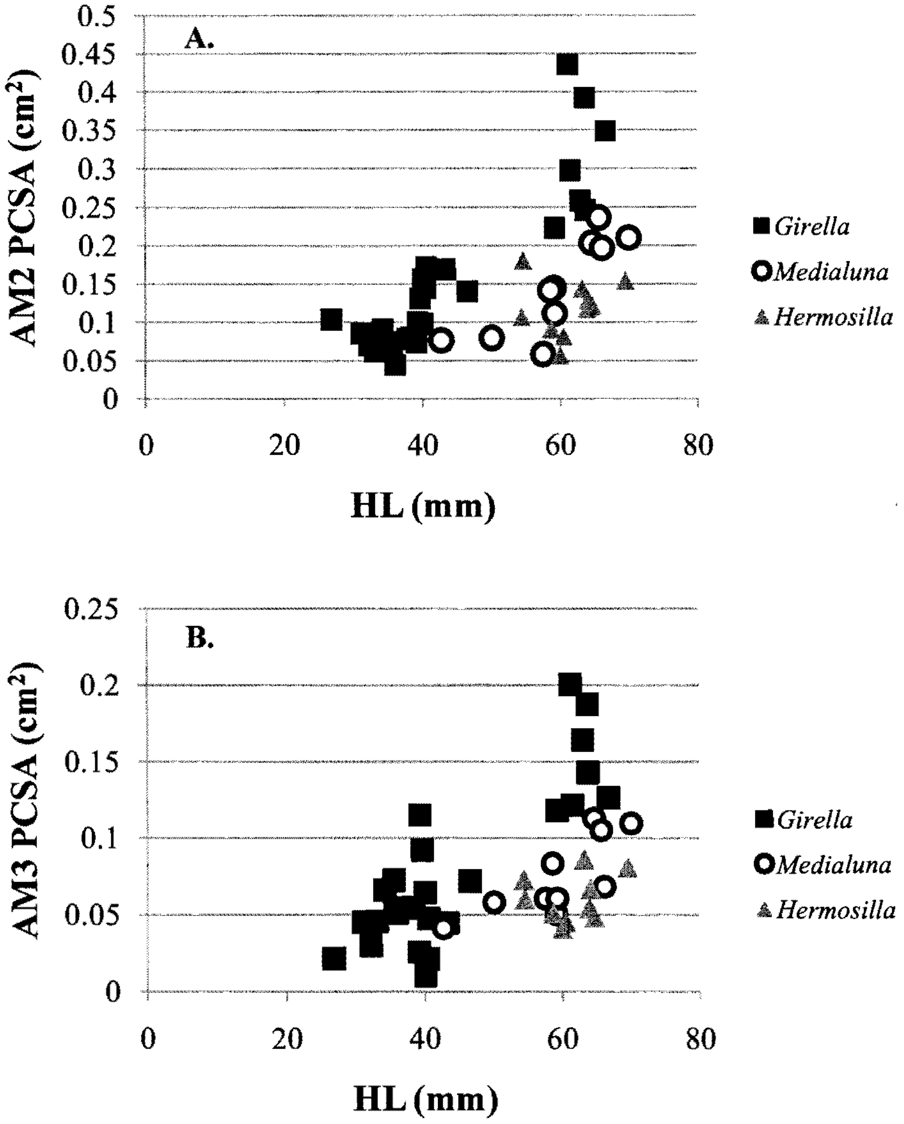

Figure 3: Physiological cross-sectional areas for AM2 (A) and AM3 (B) relative to head length (HL). Each point represents the average for both sides of the head for one individual. Error bars were left off for clarity. Black squares represent *G. nigricans*, circles represent *M. californiensis*, and grey triangles represent *H. azurea*.

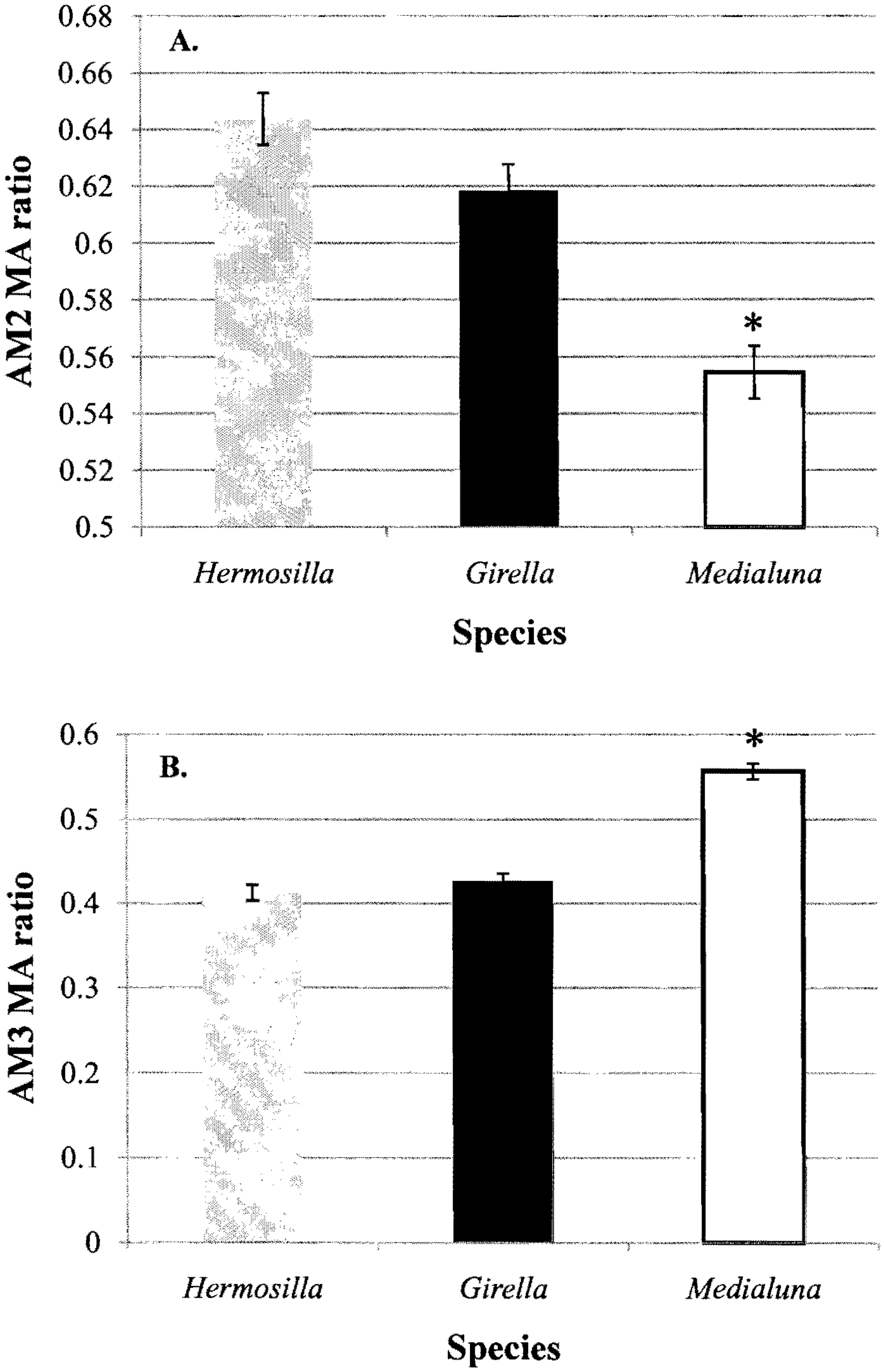

Figure 4: Mechanical advantages for AM2 (A) and AM3 (B) for each species tested. Data are represented by the average for all individuals tested (± S.E.). The asterisk denotes a significant difference ($\alpha = 0.05$).

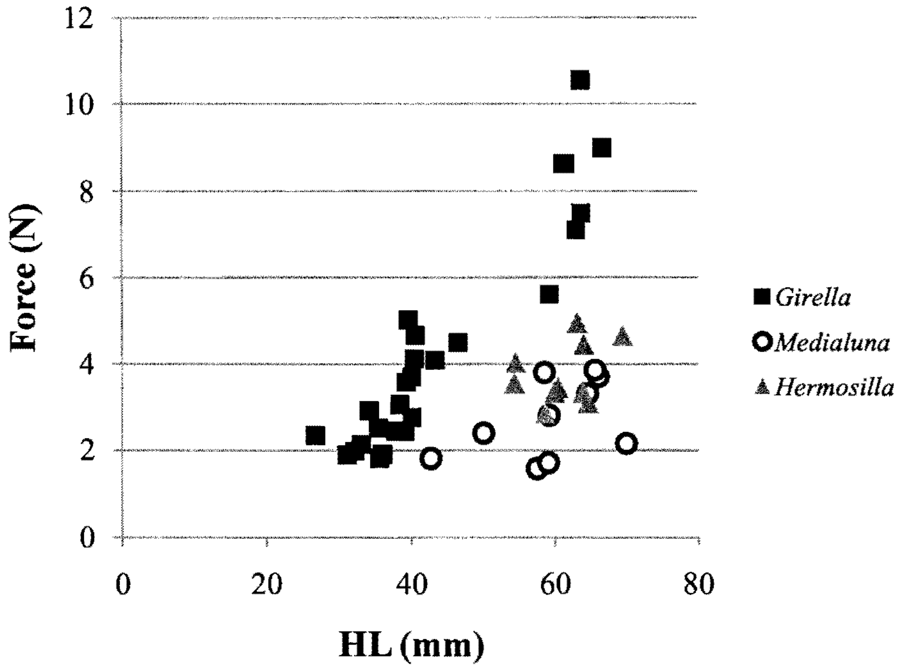

Figure 5: Maximum force at the out-put for each individual sampled relative to head length (HL). Each point represents the average for both sides of the head for one individual. Error bars were left off for clarity. Black squares represent *G. nigricans*, circles represent *M. californiensis*, and grey triangles represent *H. azurea.*

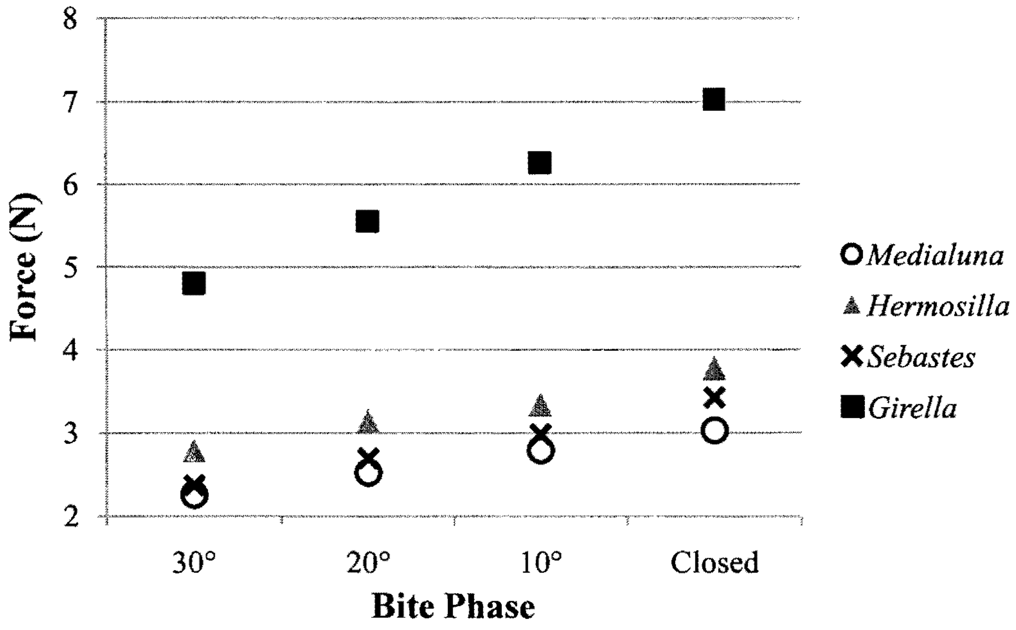

Figure 6: Bite sequence data for all species tested including *S. rosaceus* (X marks). Each data point represents an average from individuals in the size range of 42.00-70.00 mm head length within each species. Error bars were left off for clarity of the figure. Black squares represent *G. nigricans*, circles represent *M. californiensis*, and grey triangles represent *H. azurea.* At every point during the bite *G. nigricans* had significantly higher force values than any species tested. There were no significant differences between the other three species.

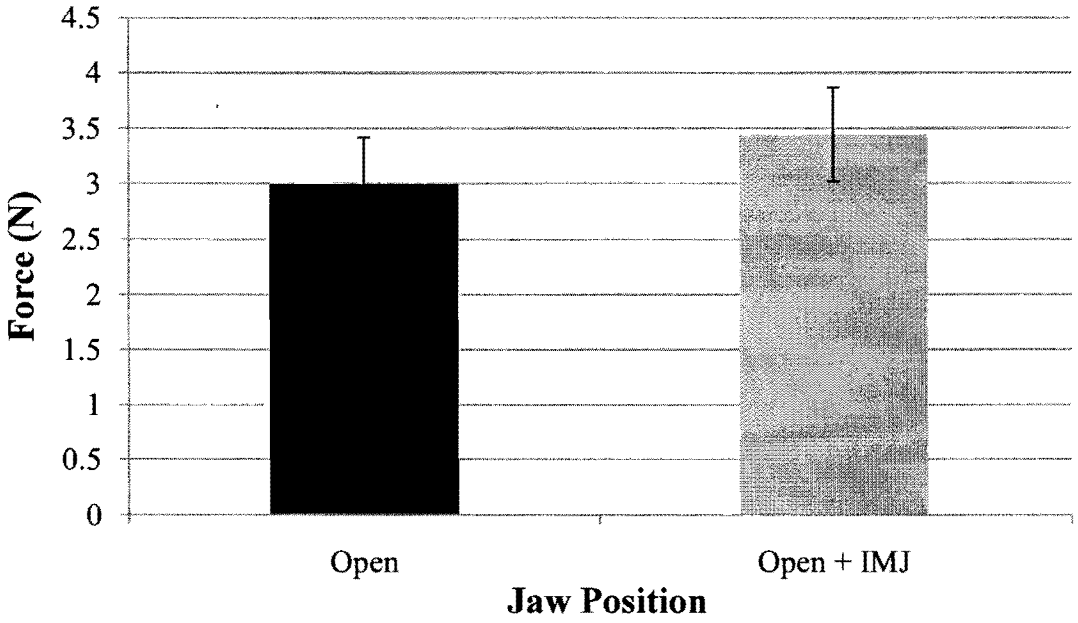

Figure 7: Increased force production as a result of intramandibular bending. Data were gathered from individuals in the species *G. nigricans*. Size range of the sample size was 32.00-69.00 mm head length. Measurements were taken in the open position (30°). No significant difference was found.

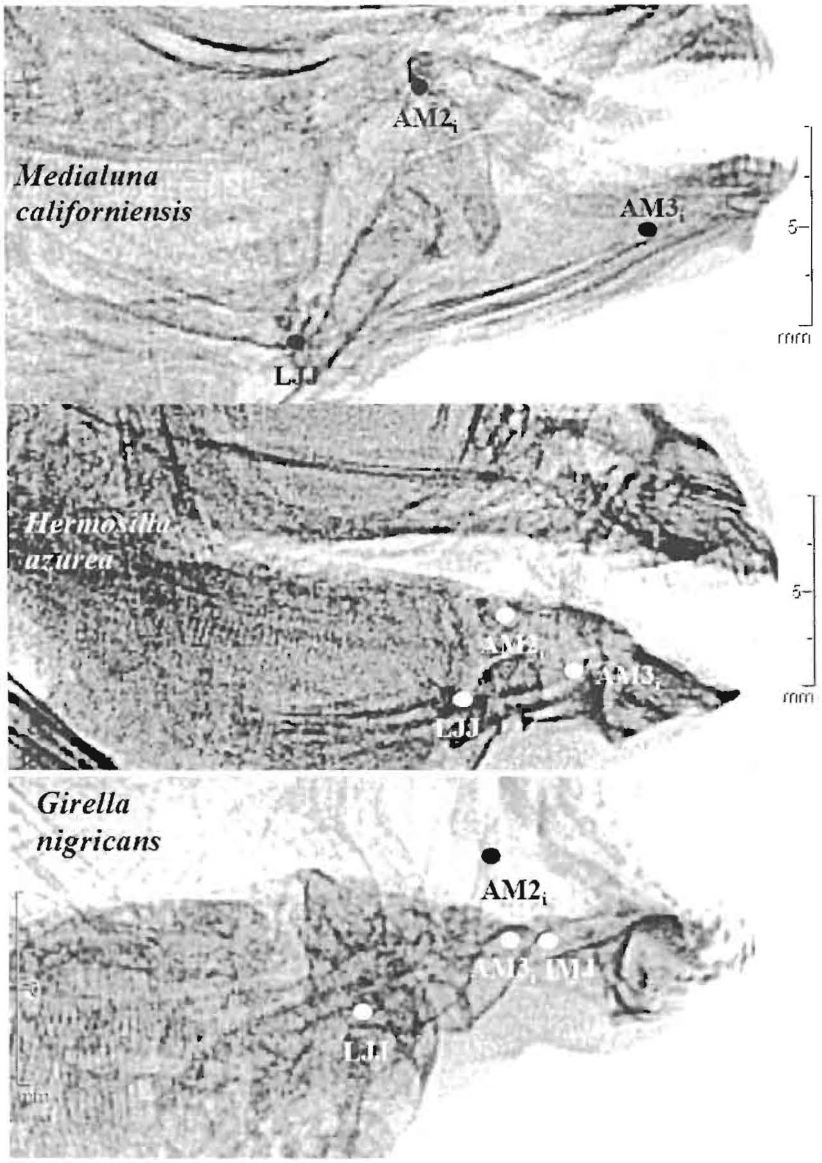

Figure 8: Digital X-rays taken for each species tested in the study. LJJ: lower joint; AM2$_i$: the insertion site for Adductor Mandibulae II; AM3$_i$: insertion site for Adductor Mandibulae III; IMJ: intramandibular joint. Notice the differences in insertion sites of *H. azurea* and *G. nigricans* to that of *M. californiensis.* Insertion sites drive the differences seen in mechanical advantage ratios.