# Scaling of Dentition and Prey Size in the California Moray (*Gymnothorax mordax*)

Jacob S. Harrison[a], Ben A. Higgins[a], Rita S. Mehta[a]

[a] Department of Ecology and Evolutionary Biology, Long Marine Laboratory, University of

California Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA

**Introduction:**

Over ontogeny organisms often go through major transformations in their morphology increasing their body length, body mass and cranial dimensions (Erickson et al. 2003, 2014, Ward-Cambell and Beamish 2005, Ponce de León and Zollikofer 2001). These size increases over ontogeny can have large affects on biomechanics, behavior, and ecology (Schmidt-Nielsen 1984, Biewener 2005). For example, the American alligator, *Alligator mississippiensis*, can go through an impressive 4000-fold increase in body mass (Erickson et al. 2003). During this drastic change in body size, they change their diet from insects and small fish to large mammals and aquatic? turtles (Erickson et al. 2003). The Common Carp, *Cyprinus carpio*, experiences a drastic 100-fold change in Reynolds number (Fuiman and Batty 1997, Wu 1977). This change in Reynolds numbers affects locomotion causing the carp to shift from anguilliform to carangiform swimming, which results from an increase in the relative force and power exerted by their muscles (Wakeling et al. 1999).

As organisms age, their growth may be accompanied by dietary shifts in size and species of prey (Werner and Gilliam 1984). However, prey size relative to predator size tends to be the primary limitation during prey intake, rather than prey type (Hjelm et al. 2003, Wainwright and Richard 1995). Studies focused on how different morphological features scale with a metric of body size such as length and mass are potentially useful in providing an understanding of how species interactions change over the course of an animal's life history. Increasing relative head size and gape width may facilitate feeding efficiency and expand the size of potential prey. Changes in jaw and head morphology over ontogeny have been specifically used to provide insights into dietary habits and determine whether individuals undergo ontogenetic shifts in diet (Wainwright & Richard 1995, Peterson & McIntyre 1997, Clark and Summers 2011). In the Bluegill Sunfish (*Leopomis macrochirus*), positive allometric scaling of the jaw-opening in-lever increases feeding efficiency by increasing oral gape and reducing prey handling time (Wainwright and Shaw 1999, Mittelbach 1981). In the banded water snake (*Nerodia fasciata*), younger snakes have relatively larger heads than their adult counterparts, which allows them to feed upon disproportionately

larger prey when they are young (Hampton 2014). These studies show how, morphological changes over ontogeny may be used to understand and even predict changes in resource use over time.

Of the many jaw characteristics, teeth are potentially informative features often used as a proxy for determining dietary specialization in fishes (Evans and Sanson 1998, Massare 2010). Among South American members of the genus *Roeboides*, a gradual change in tooth arrangement has been used to characterize shifts in diet (Hahn et. al 2000). In this genus, teeth along the premaxilla, maxilla and dentary migrate outside of the mouth and change their contour to a mammiform shape. This tooth migration and shape transformation is followed by a transition from a diet of microcrustaceans to an increase in scale consumption, otherwise known as lepidophagy (Hahn et al. 2000). Studying intraspecific tooth placement and size over ontogeny can provide insights into changes in resource acquisition and in turn, species interactions.

In the family muraenidae, the oral jaws contain four tooth bearing bones: the ethmovomer, dentary, right and left maxillae Bohlke et al. 1989). Within these four bones, up to six discrete tooth regions are recognized, though the terminology for these regions have varied for centuries. The anterior portion of the ethmovomer have two regions of teeth: the peripheral intermaxillary teeth, also known as the premaxillary teeth or the ethmoids (Bohlke and Bohlke 2001, McCosker and Randall 2008, Cope 1872), and the median intermaxillary teeth, also known as the medial intermaxillary teeth, "fangs", or "vomerine" teeth (Smith et al. 2008, Bohlke and Bohlke 2001, McCosker and Randall 2008, Bussing 1998, Cope 1872). The posterior shaft of the ethmovomer contains a row of small teeth, previously uncharacterized by Ayres (1859) or Cope (1872), identified as the vomerine region (Bohlke and McCosker 1980, Bohlke and Bohlke 2001, Bussing 1998). Two regions erupt from the maxillae, the outer row of maxillary teeth (Bohlke and Bohlke 2001, McCosker and Randall 2008) and the inner row of maxillary teeth, also known as the medial maxillary teeth (Bohlke and Bohlke 2001, McCosker and Randall 2008, Bohlke and McCosker 1980). Finally, teeth rooted in the dentary are commonly classified as dentary or mandibular teeth (Bohlke and McCosker 1980, Bohlke and Bohlke 2001, McCosker and Randall 2008). Progressing forward we follow Bohlke and Bohlke's 2001 terminology for the 6 different

tooth types: 1) peripheral and 2) median intermaxillary, 3) outer row of maxillary teeth (or outer maxillary teeth), 4) inner row of maxillary teeth (or inner maxillary teeth), 5) vomerine and 6) dentary. The discrete regions are shown in Figure 1. While teeth among theses regions are observably distinct, differences have yet to be quantified.

In this study we examine tooth scaling patterns for different toothed regions in *Gymnothorax mordax,* the California moray. In the first species description of *G. mordax* (originally name *Muraena mordax*)*,* Ayres,1859, describes the teeth as largest in front, with a row of teeth on the upper and lower jaws, and one or two large teeth on the anterior of the vomer. The same species was described again by Cope (1872) under a different name (*Muraena aquadulcis*) where he reports a single row of teeth along the "ethmoid" (ethmovomer), with two rows along each maxillae and two rows within the dentary. McCosker and Rosenblatt (1975) found both *Muraena mordax* and *Muraena aquadulcis* to be the same species and subsequently renamed the newly grouped species as *Gymnothorax mordax*. *G. mordax* is generally a piscivorous species found in kelp forests and rocky outcroppings from Point Conception in southern California to the southern Baja California in Mexico, attaining lengths up to 1.5 meters (TL) (Froese and Pauly 2015). Our main objectives are to (1) describe teeth within different regions of the oral jaws, (2) determine how teeth in these regions scale in relation to head and body size and (3) examine the relationship between prey size and moray size over ontogeny from data collected in the field.
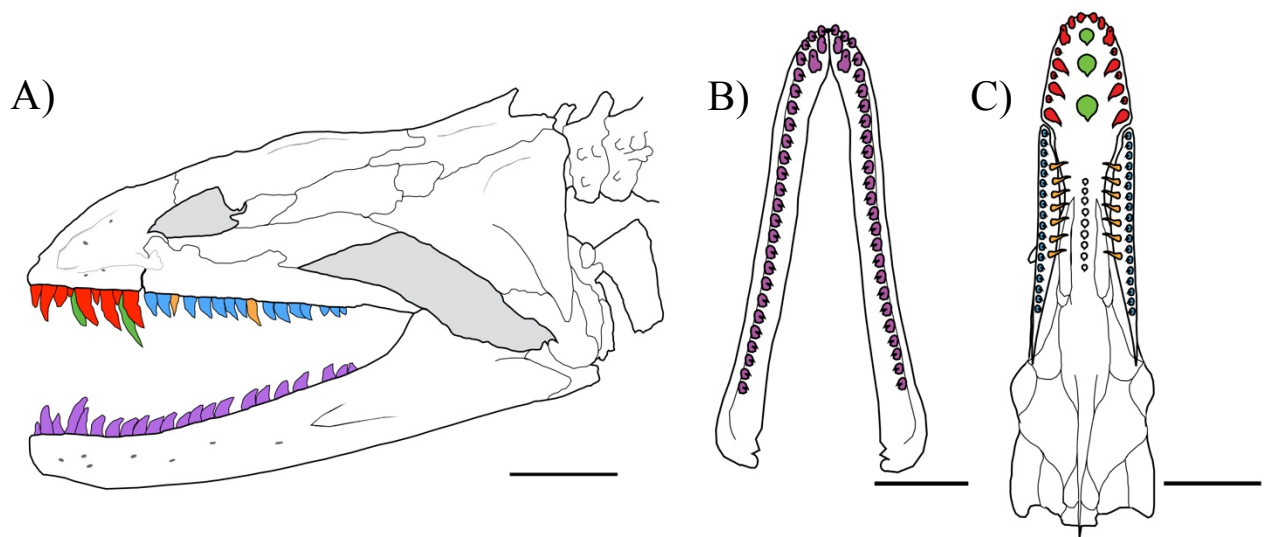


**Figure 1 -** A) Lateral view of the skull of a California moray . Dentition within the oral jaws is shown in B) dorsal view of the lower jaw and C) ventral view of the upper jaw. Different regions of the oral jaws correspond to different colors, Red = peripheral intermaxillary, green = median intermaxillary, purple = dentary, blue = outer maxilla, orange = inner maxilla, white = vomerine. Grayed regions symbolize negative space. All scale bars represent 1 cm.

**Methods:**

*Experimental Site and Species*

G. mordax were collected using custom-made wire traps 36" x 11" x 9" (Patrick Murphy, Staten Island, NY). We sampled in four sites surrounding Two Harbors, Santa Catalina Island, CA (33°26'45.4"N, 118°29'31.3"W) during the late summers (July-September) of 2012-2015. Traps were baited with thawed anchovies, (*Engraulis mordax*) and deployed around 1600 hrs. Upon retrieval the following morning, captured morays were lightly anesthetized with MS-222 and measured for total length (TL), from anterior tip of snout to posterior tip of tail), head length (HL), anterior tip of the snout, to the posterior edge of the pharyngeal opening, and vertical gape distance. Vertical gape distance (VGD) was measured by manually opening the oral jaws of individual *G. mordax* to their maximum gape with the internal-jaws of digital calipers. Oral jaws were not extended past their natural maximum which was controlled by ensuring that the head was completely lateral, and the adductor mandibulae was not over stretched as the jaws were opened. All measurements were made to the nearest 0.01mm using a digital caliper. Total length was measured to the nearest 0.1 mm using a retractable tape measure. Morays were placed in a 5-gal. bucket for weighing to the nearest 0.01 g with a waterproof digital scale. Lastly, each individual was manually palpated for stomach contents and then placed in a 5-gal bucket of fresh salt water for recovery. Manual palpation is a commonly used non-invasive method for extracting gut contents from snakes (Cruz, 2013; Rose et al., 2013; Durso et al., 2013). Prey items acquired by manual palpation were identified to genera. Whole prey items were weighed to the nearest 0.01g and measured for total length to the nearest 0.01 mm. We interpreted that morays had recovered from light anesthesia once individuals were observed freely swimming inside the recovery bucket. Morays were subsequently released near the site of their capture. Over the course of this study, twenty-one *G. mordax* spanning an ontogenetic series (383-1110 TL) were euthanized, formalin fixed and preserved in 95% ethanol for future morphological analyses at the Long Marine Laboratory, University of California Santa Cruz

(UCSC). Collection and handling of all specimens was approved by the California Department of Fish and Wildlife (Permit Number: 11366).

*Tooth Measurements*

Digital photographs of a lateral view of each preserved specimen's head were taken using a Canon EOS Rebel DSLR camera (Canon Aneiva Corporation, San Jose, CA). To understand the relationship between tooth size and moray size, we quantified tooth shape for five of the six toothed regions within the oral jaws: peripheral intermaxillary, median intermaxillary, inner maxilla, outer maxilla and dentary (Fig.1). The vomerine teeth residing on the posterior shaft of the ethmovomer were too obstructed to get accurate photographs, and too small to accurately measure using digital calipers. Therefore, vomerine teeth were not included in this study (Fig. 1). Prior to taking photographs we removed all tissue along the gum line that obstructed the view of the tooth base. We also carefully removed the left maxilla from each individual and photographed both sides (outer and inner) to capture teeth lining the inner and outer maxillary regions.  Only inner maxillary teeth from the left maxilla were measured. Tooth length and width for all teeth in each of the five regions were digitally measured via ImageJ$^©$ (v1.48s) photograph analysis software. Because of the difficulty in acquiring accurate photographs, the median intermaxillary teeth were measured using digital calipers. Tooth length was measured as the distance between the base of the tooth (at center) to the tooth apex. Tooth width was measured as the widest point in the horizontal plane at the base of the tooth. These landmarks for determining tooth length and width are derived from Mehta (2009). Aside from quantifying lengths and widths, we counted the number of teeth in each region. Empty tooth sockets were included in tooth counts because we inferred that at one time, a tooth was present. Broken teeth were included in tooth counts, they were not included in tooth measurements.

We observed a gradual decline (from anterior to posterior) in tooth length along the dentary and outer maxillary regions. Therefore, the dentary and outer maxilla were divided into four equal quadrants for further analysis. Maxillary quadrants were determined by measuring the distance from the anterior scarf joint between the ethmovomer and maxilla, to the most posterior tooth of the outer maxilla and

dividing by four. Quadrants along the dentary were established by measuring the distance between the most anterior tooth, to the most posterior tooth and dividing this distance by four. Two of the twenty-one individuals were found with damaged lower jaws, therefore we were unable to acquire tooth measurements for the dentary region from these individuals. Due to missing or broken teeth within the median intermaxillary teeth, we only examined scaling patterns for the secondary tooth. However, all three median intermaxillary teeth were analyzed to compare sizes within the region. All teeth in the inner maxillary region were included in additional statistical analyses. In the peripheral intermaxillary region we observed two distinct alternating size classes of teeth: large and small (see Fig. 1). Small teeth are interspersed between the larger teeth, and were found to be less than half the length of the average of the larger teeth. Only large peripheral intermaxillary teeth were included in further statistical analysis.

Table 1 - Scaling relationships of tooth length and width in the five oral jaw regions of *G. mordax.* Bolded rows show significance. For scaling patterns, IS = Isometry, PA = Positive Allometry, NA = Negative Allometry.

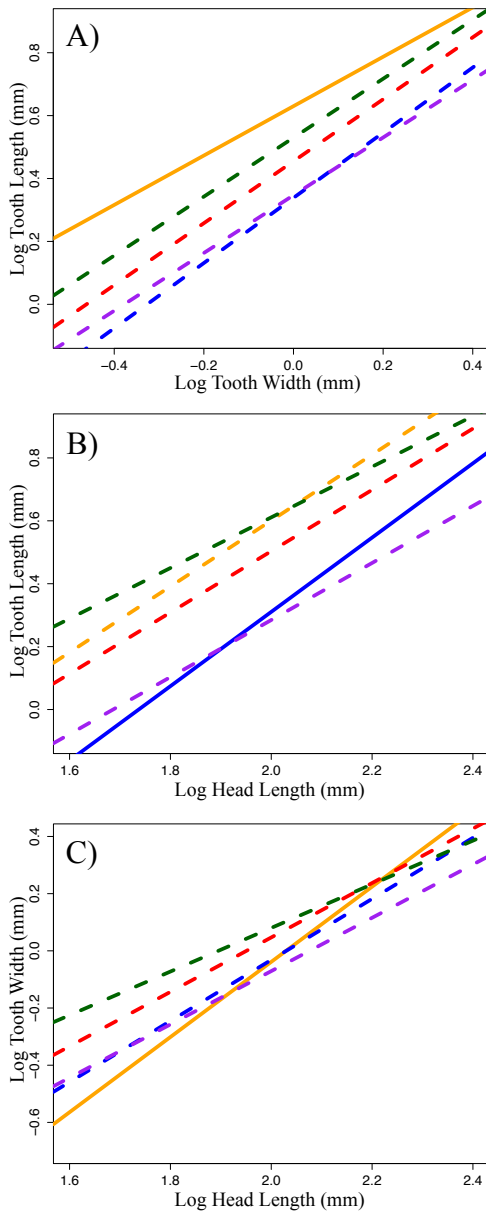| | Scaling Relationships | | | | |
|---|---|---|---|---|---|
| | Slope (95% CI) | $R^2$ | *P* | Isometric Prediction | Scaling Pattern |
| **A) *Tooth Length against Tooth Width*** | | | | | |
| Outer Maxilla | 1.08 (0.95-1.23) | 0.92 | 0.25 | 1 | IS |
| Inner Maxilla | **0.80 (0.73-0.88)** | **0.96** | **0.0001** | **1** | **NA** |
| Dentary | 0.97 (0.82-1.14) | 0.90 | 0.69 | 1 | IS |
| Peripheral Intermaxillary | 1.04 (0.89-1.22) | 0.89 | 0.59 | 1 | IS |
| Medial Intermaxillary | 1.13 (0.86-1.49) | 0.68 | 0.35 | 1 | IS |
| **B) *Tooth Length against Head Length*** | | | | | |
| Outer Maxilla | **1.21 (1.09-1.34)** | **0.95** | **0.001** | **1** | **PA** |
| Inner Maxilla | 1.11 (0.95-1.3) | 0.89 | 0.18 | 1 | IS |
| Dentary | 0.95 (0.81-1.12) | 0.90 | 0.57 | 1 | IS |
| Peripheral Intermaxillary | 1.09 (0.88-1.34) | 0.80 | 0.42 | 1 | IS |
| Medial Intermaxillary | 0.97 (0.74-1.27) | 0.69 | 0.81 | 1 | IS |
| **C) *Tooth Width against Head Length*** | | | | | |
| Outer Maxilla | 1.12 (0.97-1.3) | 0.90 | 0.12 | 1 | IS |
| Inner Maxilla | **1.39 (1.19-1.61)** | **0.90** | **0.0002** | **1** | **PA** |
| Dentary | 0.99 (0.84-1.17) | 0.89 | 0.87 | 1 | IS |
| Peripheral Intermaxillary | 1.04 (0.86-1.27) | 0.83 | 0.66 | 1 | IS |
| Medial Intermaxillary | 0.85 (0.67-1.06) | 0.80 | 0.15 | 1 | IS |

**Figure 2 -** The variation in tooth dimensions across the skull and the scaling patterns of teeth within these regions. Scaling relationship **A)** of tooth length against tooth width. Scaling relationships **B)** of tooth length against head length and of **C)** tooth width against head length. Allometric growth as determined by standardized major axis regression is represented as solid lines, isometric growth is represented as dashed lines. Negative allometric growth was found in the inner maxillary region in part A. Positive allometry was only in tooth width in the inner maxillary region regressed against HL and tooth length in the outer maxillary region regressed against HL. Color of regression lines correspond to different regions highlighted in figure 1, scaling relationships are represented in Table 2. N = 21.

*Statistical Analysis*

Statistical differences in tooth length and width among the four different quadrants of the dentary and outer-maxillary regions were determined using one-way Analysis of Variance (ANOVA), followed by a Tukey's honest significant difference (HSD) post-hoc test. Tooth length in the anterior half of the maxilla was found to be significantly longer when compared to tooth length in the posterior half ($P < 0.05$), and tooth length in the anterior quarter of the dentary was shown to be significantly longer than tooth length in the posterior quarter ($P<0.05$). Therefore, we only included the anterior half of the maxilla and the anterior quarter of the dentary in further statistical analysis. All data required $\log_{10}$-transformation to pass Levene's test for equal variance. Allometric scaling relationships between tooth length relative to tooth width (including scaling relationships within the median intermaxillary region) were tested using standardized major axis (SMA) regression in the R package SMAtr (R Core Team, 2014). The predicted isometric slopes for all SMA regressions was 1 which assumes geometric similarity and forms our null hypothesis. Scaling relationships that deviated from isometry are allometric (Schmidt-Nielson 1984). An allometric relationship in tooth length relative to tooth width would signify a change in tooth aspect ratio, which potentially suggests a change in tooth function across ontogeny. We also conducted SMA regressions to examine the relationship between head length

and eel total length and vertical gape distance and head length. We predicted that the relative increase or decrease of head length and vertical gape distance in relation to eel size would directly affect the size of potential prey items.

**Results**:

*Distribution of Dentition for G. mordax*

We analyzed 1,364 teeth across 21 individuals (size range 383 mm – 1110 mm TL). Tooth number varied dramatically between each of the five regions; median intermaxillary contained the least number of teeth with only three, while the dentary contained the highest with up to 23 teeth per side. Peripheral intermaxillary teeth, of which there were 5-6 per side, increased in size from anterior to posterior, with smaller teeth interspersed between them. The three median intermaxillary teeth were long and thin and increased in size anterior to posterior; these teeth were also somewhat depressible with the third tooth having the greatest mobility. On the maxilla, we observed a row of 6-7 tall, slender and well-spaced inner maxillary teeth, and an outer row 17-18 short, rounded maxillary teeth. The dentary on each side had one row of 20-22 teeth with the 2-3 anterior teeth being the largest. Vomerine teeth, of which there were 8-9 were small, comparable in size to the anterior teeth of the dentary, and organized in a single row. All teeth lining the periphery of the oral jaws exhibited a large degree of recurve towards the
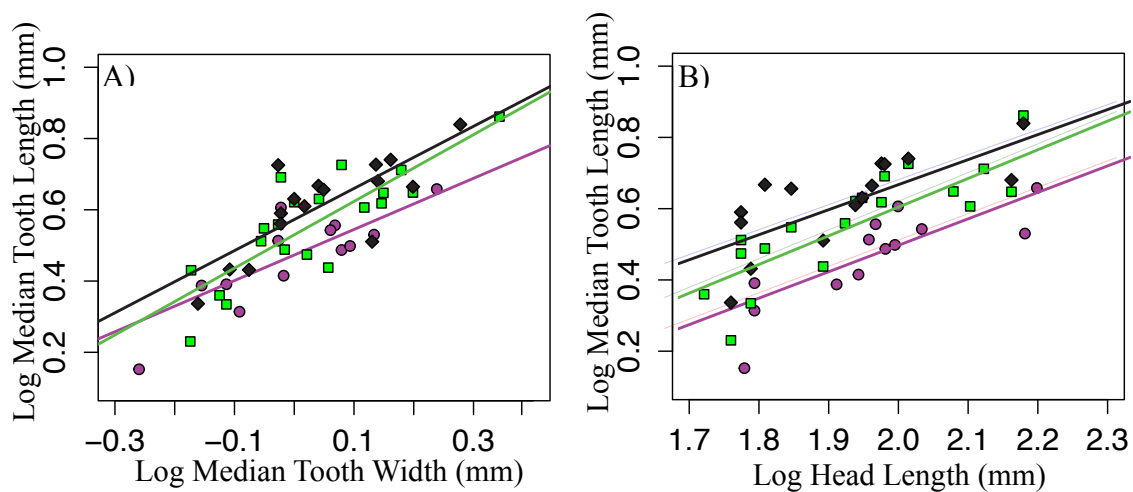


**Figure 3 -** The variation in tooth dimensions and scaling relationships of the three median intermaxillary teeth within the vomerine region. Scaling relationship **A)** of tooth length against tooth width and scaling relationships **B)** of tooth length against head length. Colors represent the three different teeth within the median intermaxillary region, the primary, secondary and tertiary teeth are shown by purple, green, and black respectively. Scaling relationships are represented in Table 2, all regressions were found to be isometric. N= 20.

**Table 2** - Scaling relationships of tooth length and width within the median intermaxillary region in *G. mordax*. For scaling patterns, IS = Isometry.

| | | Scaling Relationships | | | |
|---|---|---|---|---|---|
| | Slope (95% CI) | $R^2$ | *P* | Isometric Prediction | Scaling Pattern |
| **A)** *Tooth Length against Tooth Width* | | | | | |
| Primary Tooth | 0.86 (0.61-1.2) | 0.70 | 0.34 | 1 | IS |
| Secondary Tooth | 1.13 (0.86-1.49) | 0.68 | 0.35 | 1 | IS |
| Tertiary Tooth | 1.11 (0.78-1.56) | 0.62 | 0.55 | 1 | IS |
| **B)** *Tooth Length against Head Length* | | | | | |
| Primary Tooth | 0.90 (0.64-1.28) | 0.68 | 0.54 | 1 | IS |
| Secondary Tooth | 0.97 (0.74-1.27) | 0.69 | 0.81 | 1 | IS |
| Tertiary Tooth | 0.90 (0.64-1.28) | 0.61 | 0.55 | 1 | IS |
| **C)** *Tooth Width against Head Length* | | | | | |
| Primary Tooth | 1.05 (0.83-1.34) | 0.85 | 0.66 | 1 | IS |
| Secondary Tooth | 0.85 (0.69-1.06) | 0.80 | 0.15 | 1 | IS |
| Tertiary Tooth | 0.82 (0.58-1.15) | 0.64 | 0.22 | 1 | IS |

interior of the mouth; these include teeth within the outer maxillary, dentary and peripheral intermaxillary region. The inner maxillary and median intermaxillary region showed less recurve and were generally much longer and straighter than teeth in the other regions. Which teeth were the straightest? Was there a specific region where missing teeth were common?

Results of the Tukey's HSD showed that the anterior quarter of the dentary contained significantly longer teeth than in the posterior quarter ($P < 0.05$), whereas teeth located on the anterior half of the outer maxilla had significantly longer teeth than in the posterior half ($P < 0.05$). Tooth width did not change significantly throughout the oral jaw. Average tooth length and width within the five regions is reported in supplementary table 1.

Scaling patterns varied between teeth in the five oral jaw regions (Table 1). Tooth length relative to tooth width exhibited isometric growth in four of the five regions. The exception was teeth in the inner maxillary region, which showed significant negative allometric growth in length relative to width (Fig. 2A). Length for the outer maxillary teeth exhibited positive allometry relative to head length. ($P \leq 0.001$, Table 1); tooth lengths in the remaining four regions exhibited isometric growth relative to HL (Fig. 2B). Widths for inner maxillary teeth expressed allometric growth throughout ontogeny relative to head length ($P < 0.001$, Table 1), whereas tooth width in the remaining four regions showed isometric growth (Fig. 2C). Inner maxillary teeth range from the narrowest (0.34± 0.06 mm) in smaller individuals, yet grow to be the widest (1.65± .48 mm) in larger individuals (Fig. 2C).

The medianintermaxillary teeth were the largest teeth in the oral jaws and they were further analyzed to understand scaling patterns within the median intermaxillary region. However, due to tooth damage, only ten of our twenty-one individuals had all three median teeth present; four individuals had a only a single median tooth remaining (Supplementary Table 1). Median intermaxillary tooth length showed isometric growth relative to tooth width across ontogeny (Fig. 3A, Table 2). Both tooth dimensions showed isometric growth relative to head length in the median intermaxillary region across ontogeny (Fig 3A and 3B, Table 2).

*Prey size in relation to moray size*

We collected dietary data for 45 individuals that varied in TL (480-1114 mm). This size range was similar to the ontogenetic series for which we quantified tooth dimensions. As predicted, we found a strong positive allometric relationship between *G. mordax* HL and TL (Table 3, Fig. 4A). We also found

**Table 3** - Scaling relationships of head length and vertical gape distance in *G. mordax.* For scaling patterns, PA = Positive Allometry

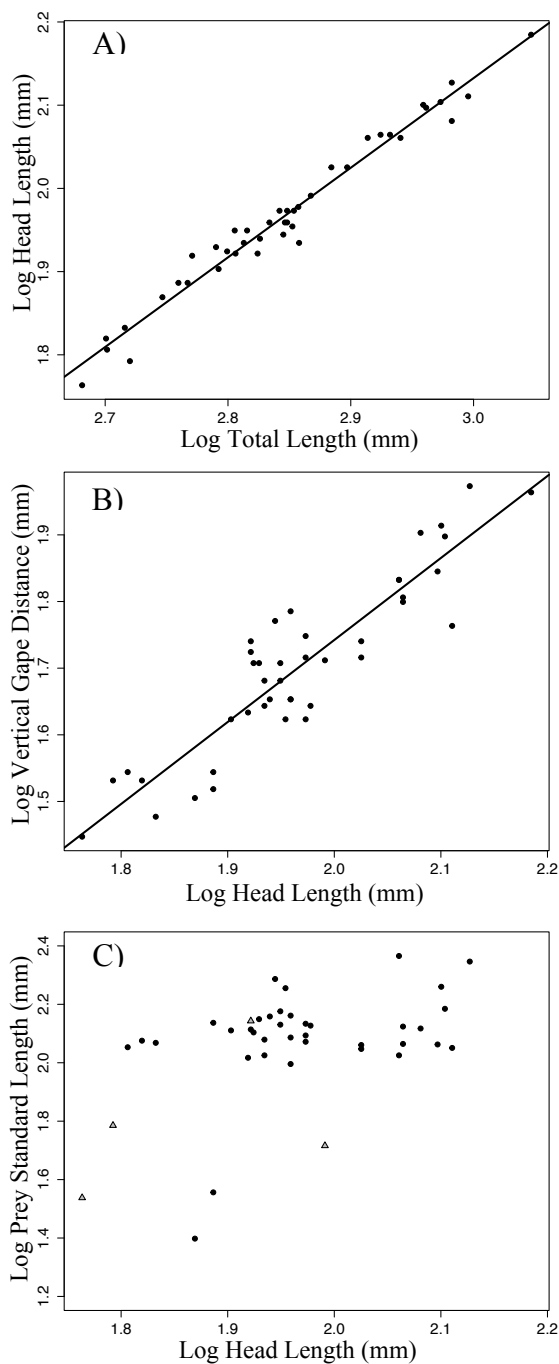| | Scaling Relationships | | | | |
|---|---|---|---|---|---|
| | Slope (95% CI) | $R^2$ | *P* | Isometric Prediction | Scaling Pattern |
| *Head Length against Total Length* | 1.09 (1.03-1.16) | 0.97 | 0.002 | 1 | PA |
| *Vertical Gape Distance against Head Length* | 1.35 (1.18-1.49) | 0.83 | >0.001 | 1 | PA |

**Figure 4 -** Scaling relationships **A)** of moray head length against total length and **B)** of vertical gape distance against head length. Both lines represent positive allometric growth as determined by standardized major axis regression. **C)** The relationship between standard lengths of prey item and CA moray. Circles represent various fish species and triangles represent six invertebrates (5 red rock shrimp, 31 - 61mm and the California spiny lobster, 139 mm). N = 45.

a strong positive allometric relationship between VGD and HL (Table 3, Fig. 4B). Thus, as *G. mordax* grows in size, both HL and VGD increase their relative size across ontogeny. The relative increase in head length and VGD suggests the potential to increase relative maximum prey size in larger individuals. The dietary items found in the stomachs of *G. mordax* consisted mainly of fishes (83 % of which was Calico bass) and few invertebrates (5 Red Rock Shrimp, 12-61 mm, and 1 California Spiny Lobster 139 mm) ranging from 12-232 mm standard length. Each prey item was collected from a single *G. mordax* individual; there were not multiple prey items removed from the stomach of a single eel. There was no relationship between prey standard length and *G. mordax* HL (Fig. 4C). As we anticipated, as *G. mordax* grow larger, larger prey items are consumed. However, smaller dietary items are retained in the diet showing that individuals of *G. mordax* do not specialize on a particular size of prey as they increase in size.

**Discussion:**

We discovered that while teeth in the different regions of the oral jaws of *G. mordax* exhibit great variation in number, shape, and size, these regions do not vary much over ontogeny. Within the different regions of the oral jaws the teeth may specialize in different functional roles. Teeth along the outer edges of the jaws display a large amount of tooth recurvature directed towards the interior of the oral

cavity; this includes teeth lining the outer maxillae peripheral intermaxillary and dentary. Tooth recurvature is prevalent in piscivorous fish species (Blaber et el. 1994, Galloway 2015, Ramsay and Wilga 2007), and functions to maintain a prey item within the jaws (Ramsay and Wilga 2007). This suggests the recurved peripheral teeth of *G. mordax* may function to retain prey. Teeth in the inner maxillary and median intermaxillary regions, however, show little tooth recurvature. Less recurvature may make these teeth more effective in piercing prey items, allowing the teeth to embed themselves deeply into the prey. The three teeth in the median intermaxillary region were among the longest teeth in the oral jaws (Supplementary Table 1). Their position in the jaws, just posterior to the peripheral intermaxillary? and their length may be the first to puncture a prey item. Teeth in the median intermaxillary and inner maxillary regions are also relatively more spaced out than teeth in the other oral jaw regions. Teeth that are spaced out are able to puncture much more readily than teeth that are closely compacted together (Anderson 2009).

   If different teeth are responsible for varying functional roles within the oral jaws, it is important for morays to maintain their teeth in order to maintain functionality. To preserve functionality of the oral jaws, species must either reduce the risk of tooth fracture or have the ability to replace their teeth over time. In species of the clade muraenidae, replacement teeth have been found to develop beneath and lingual to functional teeth (Trapani 2001). However, tooth replacement has not been documented in all species of muraenidae. Upon inspection of several *G. mordax* individuals, including both osteological and cleared and stained specimens, we found no evidence of tooth replacement. No tooth budding was present in any of the specimens analyzed, and in the cleared and stained *G. mordax* specimens no teeth were seen developing beneath existing teeth. Without tooth replacement, *G. mordax* must either fortify their teeth, or change the functional roles of the teeth in order to maintain feeding efficiency. The scaling patterns for teeth may potentially provide insight into whether tooth fortification was occuring over ontogeny. If this was the case, we would expect to observe positive allometric patterns between tooth length and width.

The majority of scaling relationships within the oral jaws of *G. mordax* showed isometry. Teeth along the dentary, peripheral intermaxillary, and median intermaxillary region all maintain the same shape over ontogeny (Table 2), which implies no functional change as *G. mordax* individuals grow. The only regions to show allometric relationships with HL were teeth lining the maxilla (Table 2). Along the outer maxillary region, teeth are getting longer relative to head length as morays grow. Over ontogeny these teeth are increasing in length slightly, but not increasing their relative width. In the outer maxillary region, teeth exhibit a large amount of recurvature; lengthening of the outer maxillary teeth may assist in prey retention by making these teeth more effective within the oral jaws. This is especially important as individuals age, as any tooth damage could pose challenges for prey retention. Longer more prominent outer maxillary teeth could be a way to enhance prey retention ability, and limit the affect that broken or missing teeth have on feeding.

We also see allometric growth in the inner maxillary region, where tooth width is increasing relative to both tooth length and head length across ontogeny. The median inner maxillary teeth are some of the longest teeth in the oral jaw region (Fig. 2A, B); however, they develop from the thinnest teeth within the oral jaws into the widest (Fig. 2 C). Widening the base of a tooth relative to its length is one way to reduce the risk of fracture, which is especially important in species where there is no tooth replacement. This drastic change in tooth aspect ratio could be a way to increase tooth stability and lessen the risk of tooth damage in this region. Another possible reason for the relative increase in width could be a lack of tooth crowding. In the dentary and outer maxillary regions teeth form a compact line. Each tooth is in close succession with those on either side, often coming into contact with its neighboring teeth. However, teeth in the median and inner maxillary region are not crowded. Because these teeth are spaced out, the extra room could facilitate uninhibited growth in tooth width. This spacing between teeth also makes them more efficient in puncturing materials (Anderson 2009). If the functional role of the inner maxillary teeth is to puncture, it would validate the reason for the relatively large spacing between teeth which provides an alternative theory on why these teeth are placed so sparsely.

As stated earlier, though few in number, the median intermaxillary teeth are some of the largest teeth within the oral jaws of *G. mordax*. Their scaling relationships show that they exhibit isometric growth in both length and width relative to head length across ontogeny (Table 3). However, there was a large amount of variance in the lengths and widths of the median intermaxillary teeth (Fig 3, Table 3), some of which may be attributed to the challenges of taking measurements of teeth still attached to the jaws. The median intermaxillary teeth sit in the center of the ethmovomer jutting down like daggers from the roof of the mouth. We hypothesize these teeth are specialized in puncturing; the overall "fang-like" morphology and the relatively high tooth spacing allows them to puncture easily (Anderson 2009). It is intriguing that the median intermaxillary teeth sit directly in the path of a potential prey item, making them a potential hindrance for feeding unless the oral jaws are fully abducted and the gape is large just before the time of prey capture. However, the median teeth also show a large amount of flexibility, they are able to bend caudally and depress towards the roof of the oral jaws. The degree of this movement increases in each tooth as you move caudally, with the third median intermaxillary tooth being the most mobile. Depressible teeth may allow for large prey items to easily pass the oral jaws into the esophagus without the median intermaxillary teeth obstructing the passage, ultimately allowing *G. mordax* to feed on potentially larger prey items. This was found in all specimens in the present study and depressible teeth are found in other species of muraenidae (Smith 2008). The trait is also present in the White-Spotted Bamboo Shark, *Chyloscyllium* plagiosum, where teeth depress against the roof of the mouth when coming into contact with a hard prey item (Ramsay and Wilga 2007). When the teeth depress in *C. plagiosum* it reduces the forces placed on the tooth tip, the flat side of the tooth comes into contact with the prey item and can be used to crush hard prey. The depressible teeth in *G. mordax* would be advantageous by reducing the forces put on the tooth tip. This may be especially beneficial if a prey item is too hard for the tooth to penetrate, the tooth can respond by folding back. This would reduce the rate of fractures in teeth within this region, which is important for species that lack tooth replacement which still remains to be determine in this species.

The predominantly isometric patterns of tooth growth in the oral jaws suggest no ontogenetic change in feeding behavior. However, we see that over time there is positively allometric scaling of head length and vertical gape distance relative to TL over ontogeny. Head length relative to TL shows very slight positive allometric scaling, with a scaling coefficient of only 1.09 (isometric scaling = 1), yet is still significant ($P < 0.01$). We see a much more drastic positively allometric relationship when looking at vertical gape distance (VGD), which shows a scaling coefficient of 1.35 (isometric scaling = 1). The correlation is strong ($R^2 = 0.83$) and shows significant deviation from isometric predictions ($P < 0.001$).

Thus *G. mordax* individuals can potentially consume larger prey as they grow. Typically, in snakes' the younger individuals have larger heads relative to their body size than older individuals; this allows them consume relatively larger prey when they are small (King et al. 1999; Hampton 2014?). Increased head size across ontogeny will not only assist in potentially larger relative prey size, but assist in consuming smaller prey items at a faster rate (Pough and Grooves 1983, Forsman and Lindell 1993). Our diet data show that morays predate upon larger prey as they grow; however, smaller prey are retained in the diet. This suggests that as morays increase in size they are expanding the size range of prey that they will feed upon, also known as ontogenetic 'telescoping' (King 2002). This is often seen in predatory fish, where as the predator grows they will increase the maximum size of their prey but continue to feed on a very wide range of prey sizes (Sharf et al. 2000). The inclusion of small-bodied prey items in the larger *G. mordax* probably shows a generalist foraging behavior.

In studies focused on diet over ontogeny it is important to capture the diet within the different life stages of a species. Unfortunately, little is known about the life history of *G. mordax*. However, we may be able to draw some insight from studies of , *Muraena helena,* another temperate moray species with a well documented life history. The maximum length of *M. helena* is 1.5 meters, though the minimum size when the species transitions to the elver stage (juvenile eels) is unknown. Matic-Skoko et al. (2011) found that *M. helena* sexually matures around 78 cm. The maximum recorded size of a *G. mordax* individual is also 1.5 meters in length

(Eschmeyer et al 1983), though there is no recorded minimum size. Because of the size

similarities between the two species, we are confident that our sampling covered the transition

from the juvenile to the adult stage. Though without knowing the size at which *G. mordax*

transitions from leptocephali (larval stage) to elver stage we cannot be confident that we have

fully captured the juvenile state. However, we can say with confidence that during the transition

between the juvenile to adult stage of *G. mordax*, most teeth maintain their aspect ratios and

scale isometrically with body size corroborating the lack of an ontogenetic shift in diet.

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Supplementary Table 1 - Average tooth length and width across five regions of the oral jaws in *G. mordax* ± standard error

| | | Length | | | | | | Width | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total Length | Head Length | Peripheral Intermaxillary | Medial Intermaxillary | | | Outer Maxilla | Inner Maxilla | Dentary | Peripheral Intermaxillary | Medial Intermaxillary | | | Outer Maxilla | Inner Maxilla | Dentary |
| | | | 1 | 2 | 3 | | | | | 1 | 2 | 3 | | | |
| 383 | 45 | 1.28± 0.14 | 2.06 | 2.69 | 2.71 | 0.68±0.04 | 1.66±0.31 | 0.95±0.09 | 0.57±0.08 | 0.45 | 0.67 | 0.78 | 0.40±0.02 | 0.34±0.06 | 0.45±0.04 |
| 470 | 54 | 1.67±0.18 | | 2.29 | | 0.93±0.08 | 2.11±0.48 | 1.06±0.17 | 0.59±0.07 | | 0.75 | | 0.45±0.03 | 0.41±0.09 | 0.51±0.07 |
| 455 | 59 | 1.32±0.12 | 1.42 | 1.70 | 2.17 | 1.05±0.11 | 1.86±0.30 | 1.18±0.21 | 0.50±0.05 | 0.55 | 0.67 | 0.69 | 0.42±0.04 | 0.37±0.06 | 0.49±0.08 |
| 533 | 61 | 2.13±0.21 | 2.46 | 3.25 | 3.89 | 1.38±0.11 | 2.85±0.83 | 1.27±0.18 | 0.64±0.06 | 0.77 | 0.88 | 0.95 | 0.60±0.05 | 0.53±0.15 | 0.58±0.09 |
| 480* | 61 | 2.35±0.31 | 2.06 | 2.98 | 3.64 | 1.23±0.11 | 2.96±0.86 | | 0.80±0.11 | 0.81 | 1.05 | 0.95 | 0.72±0.10 | 0.56±0.16 | |
| 510 | 63 | 2.05±0.37 | | 2.16 | 2.7 | 1.15±0.13 | 2.33±0.37 | 1.17±0.21 | 0.69±0.12 | | 0.77 | 0.84 | 0.53±0.04 | 0.45±0.07 | 0.53±0.07 |
| 533* | 66 | 2.03±0.28 | | 3.08 | 4.65 | 1.28±0.12 | 2.45±0.45 | 1.39±0.13 | 0.91±0.12 | | 0.96 | 1.10 | 0.75±0.07 | 0.56±0.10 | 0.68±0.06 |
| 680 | 72 | 2.93±0.44 | | 3.53 | 4.5 | 1.50±0.11 | 3.03±0.41 | 1.24±0.20 | 0.94±0.15 | | 0.89 | 1.12 | 0.61±0.04 | 0.69±0.09 | 0.55±0.08 |
| 612* | 80 | 2.95±0.56 | 2.44 | 2.74 | 3.24 | 1.70±0.13 | 2.80±0.46 | | 0.94±0.18 | 0.7 | 1.14 | 1.35 | 0.75±0.06 | 0.71±0.11 | |
| 680 | 86 | 2.59±0.28 | 2.6 | 3.62 | | 1.46±0.08 | 2.96±0.55 | 1.50±0.21 | 0.90±0.10 | 0.96 | 0.94 | | 0.66±0.04 | 0.60±0.11 | 0.59±0.08 |
| 687 | 89 | 2.76±0.37 | 3.26 | 4.18 | 4.10 | 1.80±0.15 | 3.34±0.75 | 2.13±0.28 | 0.86±0.12 | 0.94 | 1.00 | 1.04 | 0.77±0.07 | 0.67±0.15 | 0.74±0.08 |
| 780 | 91 | 3.97±0.63 | 3.6 | 4.27 | 4.27 | 1.78±0.15 | 4.50±1.02 | 2.03±0.26 | 1.30±0.21 | 1.17 | 1.10 | 1.0 | 0.84±0.07 | 0.97±0.22 | 0.78±0.09 |
| 695* | 94 | 3.15±0.48 | 3.07 | | 4.62 | 2.00±0.17 | 3.79±0.70 | 1.67±0.21 | 0.96±0.15 | 1.2 | | 1.58 | 0.90±0.07 | 0.85±0.16 | 0.67±0.07 |
| 757 | 97 | 3.36±0.68 | 3.15 | 4.15 | 5.33 | 2.09±0.20 | 3.49±0.79 | 2.04±0.29 | 1.24±0.23 | 1.24 | 1.40 | 1.37 | 0.91±0.09 | 0.84±0.20 | 0.86±0.11 |
| 770 | 98 | 2.67±0.23 | 4.04 | 4.91 | 5.31 | 1.82±0.11 | 4.02±0.74 | 1.93±0.29 | 0.90±0.10 | 0.95 | 0.95 | 0.94 | 0.77±0.05 | 0.75±0.14 | 0.72±0.10 |
| 850 | 106 | 3.51±0.56 | 3.49 | 5.32 | 5.5 | 2.45±0.17 | 3.63±0.68 | 2.08±0.26 | 1.04±0.17 | 1.15 | 1.20 | 1.45 | 1.00±0.07 | 0.75±0.14 | 0.85±0.10 |
| 964 | 123 | 4.10±0.88 | | 4.45 | | 2.65±0.16 | 6.04±1.37 | 2.23±0.21 | 1.68±0.37 | | 1.58 | | 1.34±0.08 | 1.61±0.36 | 1.14±0.09 |
| 985 | 130 | 2.97±0.38 | | 4.04 | | 2.66±0.25 | 5.75±1.66 | 2.23±0.23 | 1.18±0.13 | | 1.31 | | 1.31±0.09 | 1.44±0.43 | 1.15±0.10 |
| 1105 | 136 | 5.22±0.68 | | 5.15 | | 3.15±0.20 | 6.02±1.38 | 3.15±0.30 | 1.65±0.23 | | 1.51 | | 1.33±0.07 | 1.59±0.40 | 1.42±0.11 |
| 1100 | 149 | 4.49±0.55 | 3.39 | 4.44 | 4.79 | 3.33±0.19 | 5.41±1.27 | 2.81±0.30 | 1.58±0.22 | 1.36 | 1.41 | 1.38 | 1.39±0.08 | 1.34±0.34 | 1.27±0.14 |
| 1110 | 155 | 4.24±0.58 | 4.551 | 7.27 | 6.91 | 2.93±0.16 | 5.83±1.70 | 2.36±0.20 | 1.73±0.22 | 1.73 | 2.21 | 1.90 | 1.42±0.08 | 1.65±0.48 | 1.23±0.10 |

*Median intermaxillary region is represented by the three teeth present in that region, 1st being the primary and the 3rd being the tertiary tooth. Because these teeth were not averaged they do not have standard error. Any missing data was due to either broken or missing teeth and/or bones. The asterisk (*) denotes those individuals who were missing the caudal region of the body and so their total length was supplied by comparing their head length to regression line from a larger data set consisting of 885 individuals