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Scaling of dentition and prey size in the California moray (*Gymnothorax mordax*)

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ABSTRACT

Scaling patterns of tooth morphology can provide insights on prey capture strategy and dietary patterns as species grow through ontogeny. We report the scaling of dentition and diet and how it relates to body size in the California moray, *Gymnothorax mordax*. We sampled lengths, widths, and curvature for teeth lining five distinct regions of the oral jaws across 21 *G. mordax* individuals ranging from 383 to 1110 mm total length. Absolute tooth length in relation to moray size shows positive allometry only for the outer maxillary teeth, while teeth lining the inner maxilla display positive allometry in tooth base width. All other regions exhibit isometric growth in both length and width relative to moray size. Similar to previous descriptions of other moray species, the longest teeth in the oral jaws are the median intermaxillary teeth. This series of three teeth are depressible and rooted in the center of the ethmovomer, the bone that forms the roof of the rostrum. We hypothesize that caudal mobility of the median intermaxillary teeth aids in prey transport by enabling the pharyngeal jaws to remove pierced prey without requiring full abduction of the oral jaws. The predominantly isometric tooth growth in *G. mordax* suggests that the oral teeth grow proportionately as individuals increase in size. Stomach contents from the field suggest that *G. mordax* is highly piscivorous. While a strong positively allometric relationship between vertical gape and head length supports the expectation that moray increase relative prey size over ontogeny, we found no relationship between prey standard length and moray size. This suggests that while larger individuals are capable of consuming larger prey, individual *G. mordax* are opportunistic predators that do not specialize on prey of a specific size over ontogeny.

1. Introduction

Throughout ontogeny, organisms often go through major transformations in morphology (Ponce de León and Zollikofer, 2001; Erickson et al., 2003, 2014; Ward-Campbell and Beamish, 2005) that can have large effects on their biomechanics, behavior, and ecology (Schmidt-Nielsen, 1984; Biewener, 2005). For example, in the common carp, *Cyprinus carpio*, individuals experience a drastic 100-fold change in Reynolds number as they increase in size across ontogeny (Wu, 1977; Fuiman and Batty, 1997). This change in Reynolds numbers affects an individual carp's locomotor behavior, which is associated with a shift from an anguilliform to a carangiform swimming mode. This behavioral shift in swimming results from an increase in overall size which is accompanied by a decrease in muscle shortening velocity thereby affecting the relative force output (Wakeling et al., 1999). As an organism's morphology changes, its growth must also be supported by dietary shifts in prey size which can also lead to the consumption of different prey species (Werner and Gilliam, 1984; Hahn et al., 2000; Erickson et al., 2003). In the American alligator, *Alligator mississippiensis*, individuals go through an impressive 4000-fold increase in body mass, resulting in dietary shifts from insects and small fish to turtles and large mammals (Erickson et al., 2003).

Researchers interested in feeding performance have shown that prey size relative to predator size tends to be the primary limitation during prey intake (Wainwright and Richard, 1995; Hjelm et al., 2003). 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. Developmental changes in jaw and head morphology over ontogeny have been shown to correspond with the ontogenetic shifts in diet observed for some aquatic species (Wainwright and Richard, 1995; Peterson and McIntyre, 1998; Clark and Summers, 2012; Baliga and Mehta, 2014). For example, in the bluegill sunfish,

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Lepomis macrochirus, positive allometric scaling of the jaw-opening in-lever increases feeding efficiency by increasing oral gape and reducing prey handling time (Mittelbach, 1981; Wainwright and Shaw, 1999). Similarly, young banded water snakes, *Nerodia fasciata*, have relatively larger heads than their adult counterparts, which allows them to feed upon comparably 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 (Douglas and Matthews, 1992).

Teeth are informative features often used as a proxy for determining dietary specialization (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). Members of *Roeboides* exhibit teeth along the premaxilla, maxilla, and dentary which migrate to the outside of the mouth as an individual develops and become more rounded in shape. This tooth migration and shape transformation is associated with a transition from a diet of microcrustaceans to an increase in scale consumption, otherwise known as lepidophagy. Therefore, studying intraspecific tooth placement and size over ontogeny can provide insights into changes in resource acquisition and in turn, species interactions.

There has been strong interest in understanding the function and performance of teeth in a variety of fishes (Grubich et al., 2008; Anderson, 2009; Whitenack and Motta, 2010; Galloway et al., 2015). Piscivorous fishes have been shown to be an interesting model for understanding tooth function because it appears that many tooth morphologies have evolved for a piscivorous diet (Helfman et al., 2009). In a recent study using a piscivorous predator, lingcod (*Ophiodon elongatus*), researchers discovered a change in tooth puncture force and draw performance of vomerine and premaxillary teeth over ontogeny. Based on performance testing, it was predicted that juvenile lingcod are expected to use the vomerine teeth for the initial piercing of prey while adults pierce with premaxillary teeth. Adult lingcod are expected to use the vomerine teeth to retain prey while juvenile lingcod are predicted to use the premaxillary teeth (Galloway et al., 2015).

Similar to lingcod, the oral jaws and also the non-jaw cranial bones of moray eels (Muraenidae) are lined with sharp teeth. Upon initial observation, it is apparent that these teeth vary in size and curvature, which presumably has an effect on performance. Therefore, in the current study, we examine tooth scaling patterns and tooth curvature for different regions of the oral jaws and non-jaw cranial bones of the California moray, *Gymnothorax mordax*. In addition to the variation in size, it has been reported that some muraenids exhibit depressible teeth (Smith et al., 2008). However, it is unknown whether depressible teeth are present in the California moray or how consistent this feature is over ontogeny.

Although the California moray is categorized as a piscivore, specific dietary information is lacking (Froese and Pauly, 2015). We propose that examining morphological features that have direct effects on capturing and retaining prey may potentially provide insight into the feeding limitations for this species. Moreover, characterizing dentition over ontogeny can illustrate whether tooth function may change as morays grow as well as indicate ontogenetic shifts in diet or size breadth. The main objectives of the current study are to (1) describe tooth morphometrics within different regions of the oral jaws and non-jaw cranial elements, (2) determine how teeth in these different regions scale in relation to head size, (3) examine the relationship between head size and vertical gape distance for wild-caught morays and (4) determine how these measurements correspond to prey size from stomach contents collected in the field. We predict that tooth morphology and curvature will exhibit allometric changes in relation to head length. We also predict that as *G. mordax* increases in size we will observe a corresponding size increase in prey.

2. Materials and methods

2.1. Field site and species

66 *G. mordax* were collected using custom-made wire traps 36" × 11" × 9" (Patrick Murphy, Staten Island, NY, USA). We sampled in four sites surrounding Two Harbors, Santa Catalina Island, CA (33°26′45.4″N, 118°29′31.3″W) during the summer months (July–September) of 2012–2015. Traps were baited with thawed northern anchovies, *Engraulis mordax*, and deployed at approximately 1600 hours each night. Captured morays were retrieved the following morning, lightly anesthetized with tricaine methanesulfonate (MS-222) and measured for total length (TL), defined as the distance between the anterior tip of the snout to the posterior tip of the tail. Morays were also measured for head length (HL), defined as the distance between the anterior tip of the snout to the posterior edge of the parabranchial opening, and vertical gape distance (VGD). VGD was measured by manually opening the oral jaws of individual *G. mordax* to their maximum gape with digital calipers (Fig. 1A). 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 overstretched as the jaws were abducted. TL was measured to the nearest 0.1 mm using a retractable tape measure, and HL and VGD measurements were made to the nearest 0.01 mm using a digital caliper. Morays were placed in a 5 gallon bucket for weighing to the nearest 0.01 g with a waterproof digital scale. Each individual was manually palpated for stomach contents and then placed in a 5 gallon bucket of fresh salt water for recovery. Manual palpation is a commonly used non-invasive method for extracting gut contents from snakes (Cruz, 2013; Durso et al., 2013; Rose et al., 2013). Prey items acquired by manual palpation were identified to genera and species whenever possible. Whole prey items were weighed to the nearest 0.01 g and measured for TL 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 their capture sites. Over the course of this study, 21 *G. mordax* spanning an ontogenetic series (TL = 383–1110 mm) were euthanized, formalin-fixed and preserved in 95% ethanol for further morphological analyses. All procedures were approved by the Institute of Animal Care and Use Committee (IACUC) at the University of California, Santa Cruz, USA (#1007). Collection and handling of all specimens was approved by the California Department of Fish and Wildlife (Permit Number: 11366).

2.2. Skull terminology

The original species descriptions of *G. mordax* described the teeth lining the oral jaws, but did not include detailed tooth counts. In the first species description of *G. mordax* (originally named *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 maxilla and two rows within the dentary. McCosker and Rosenblatt (1975) found both *M. mordax* and *M. aquadulcis* to be the same species and subsequently renamed the newly grouped species as *Gymnothorax mordax*.

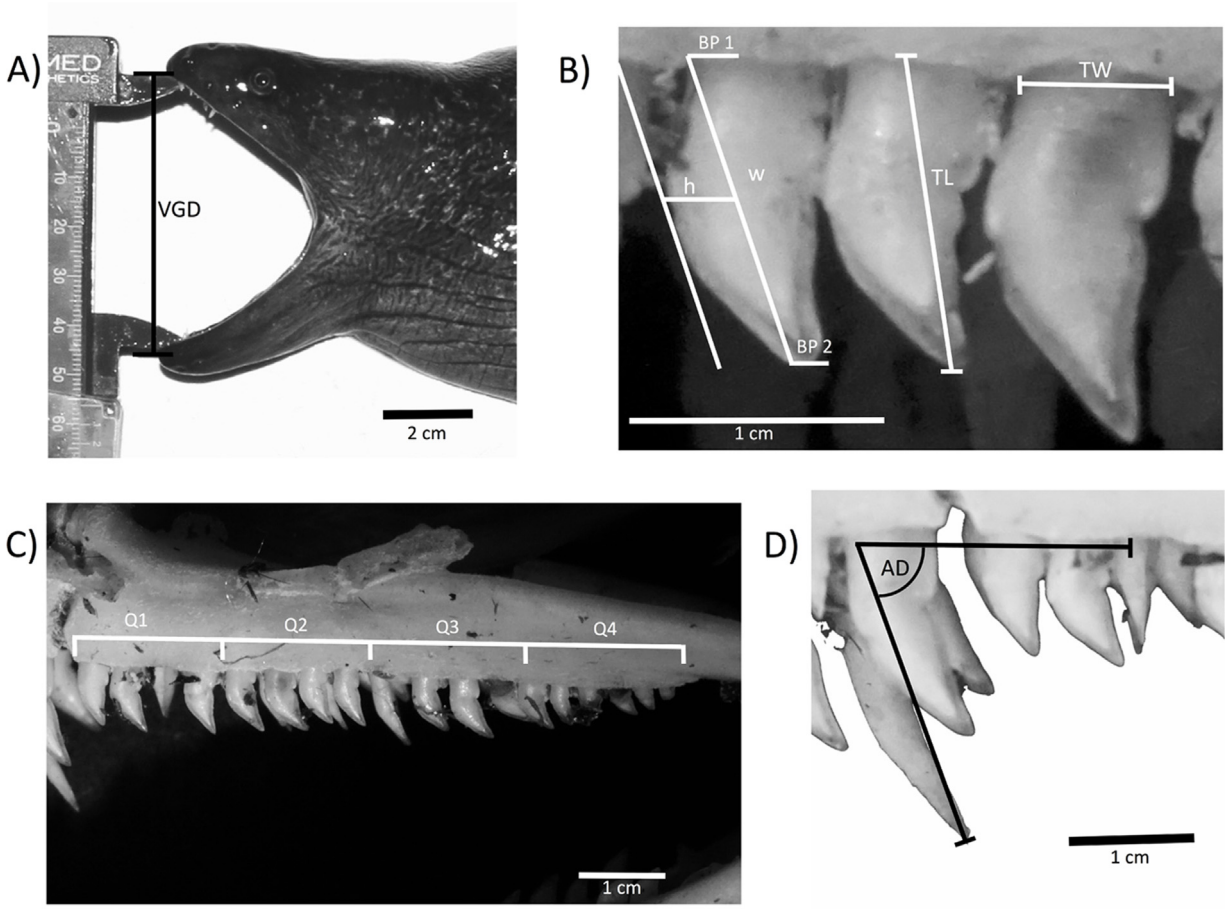

Fig. 1. (A) Photograph illustrating the measurement of vertical gape distance (VGD) in *G. mordax*. (B) Tooth measurements within the oral jaws; BP = bending point, h = arc height, w = arc breadth, TL = tooth length, TW = tooth width. (C) Photograph demonstrating how the maxilla and dentary were split into quarters to determine variation within a tooth region. (D) Photograph illustrating angular deviation (AD) measurement in the median intermaxillary teeth.

In the family Muraenidae, the oral jaws contain four tooth-bearing bones: the ethmovomer, dentary, right, and left maxilla (Böhlke et al., 1989). Within these four bones, up to six discrete tooth regions are recognized, though the terminology for these regions has varied for centuries. The anterior portion of the ethmovomer exhibits two regions of teeth: the peripheral intermaxillary teeth, also known as the premaxillary teeth or the ethmoids (Cope, 1872; Böhlke and Böhlke, 1980; McCosker and Randall, 2008), and the median intermaxillary teeth, also known as the medial intermaxillary teeth, "fangs", or "vomerine" teeth (Cope, 1872; Böhlke and Böhlke, 1980; Bussing, 1998; McCosker and Randall, 2008; Smith et al., 2008). 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 (Böhlke and Böhlke, 1980; Böhlke and McCosker, 2001; Bussing, 1998). Teeth erupt from two regions of the maxillae, the outer row of maxillary teeth (Böhlke and Böhlke, 1980; McCosker and Randall, 2008) and the inner row of maxillary teeth, also known as the medial maxillary teeth (Böhlke and Böhlke, 1980; Böhlke and McCosker, 2001; McCosker and Randall, 2008). Finally, teeth rooted in the dentary are commonly classified as dentary or mandibular teeth (Böhlke and Böhlke, 1980; Böhlke and McCosker, 2001; McCosker and Randall, 2008).

We follow Böhlke and McCosker's (2001) terminology for the six different tooth types analyzed in the present study: (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 (Fig. 2). While teeth among these regions are observably distinct, differences have yet to be quantified.

2.3. Tooth measurements

Digital photographs of a lateral view of the *G. mordax* head from each of the 21 preserved specimens were taken using a Canon EOS Rebel t4i DSLR camera (Canon Aneiva Corporation, San Jose, CA, USA). To understand the relationship between tooth size and moray size, we quantified tooth size for individual teeth in five of the six toothed regions within the oral jaws: peripheral intermaxillary, median intermaxillary, inner maxilla, outer maxilla and dentary (Fig. 2). The vomerine teeth residing on the posterior shaft of the ethmovomer were too obstructed to obtain accurate photographs and too short to accurately measure using digital calipers. Therefore, vomerine teeth were not included in the present study. Prior to taking photographs, we removed all tissue along the gum line that obstructed the view of the tooth base. We also removed the left maxilla from each individual and photographed both sides (lingual and labial) to capture teeth lining the inner maxillary region. Only inner maxillary teeth from the left maxilla were measured. Following Mehta (2009), absolute tooth length was measured as the distance between the base of the tooth (at the center) to the tooth apex, and tooth width was measured as the widest distance in the horizontal plane at the base of the tooth (Fig. 1B). Absolute tooth length and width for all teeth in four of the five regions were digitally measured using NIH ImageJ v1.48 (Schneider et al., 2012) photograph analysis software. Because of the difficulty in acquir-

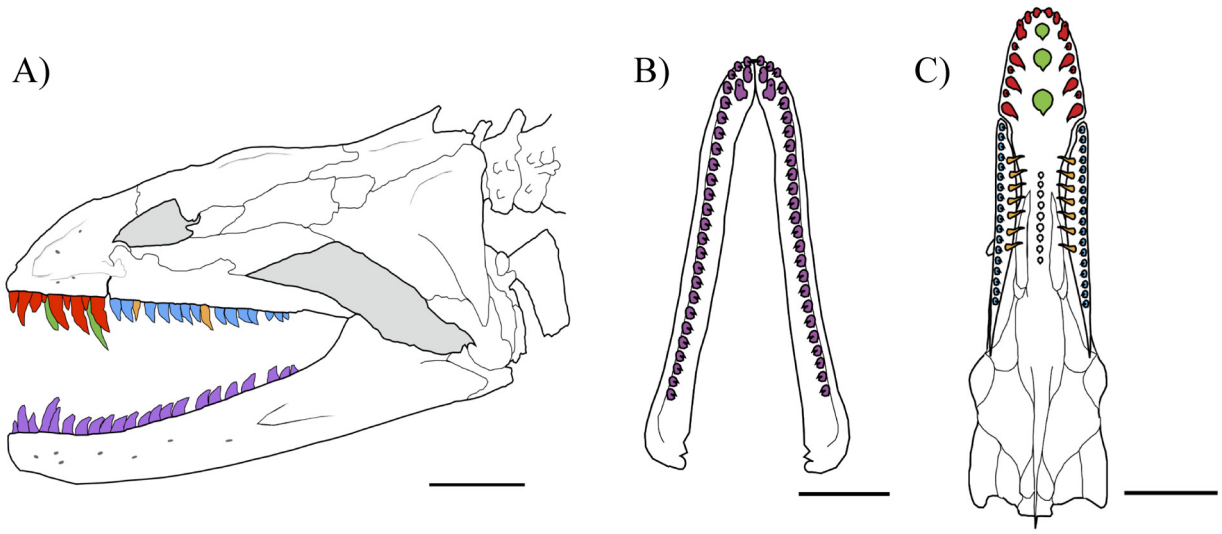

Fig. 2. (A) Lateral view of the skull of *G. mordax*. Dentition within the oral jaws is shown in (B) dorsal view of the lower jaw and (C) ventral view of the neurocranium. Each of the toothed regions is represented by a different color: red = peripheral intermaxillary; green = median intermaxillary; purple = dentary; blue = outer maxilla; orange = inner maxilla; white = vomerine. Grayed regions symbolize negative space. Scale bars = 1 cm.

ing accurate photographs, absolute tooth length for the median intermaxillary teeth was measured using digital calipers.

While we initially set out to compare absolute tooth dimensions across the different regions of the jaws, we observed that not all of the toothed regions were situated on the same plane, which affects how far down into the oral cavity each tooth may protrude. This is especially true for the inner maxillary and median intermaxillary teeth. The inner maxillary teeth, which line the medial side of the maxilla, are rooted more ventrally in the oral jaws than in the outer maxillary, giving the impression that the inner maxillary teeth are only as long as the teeth in the outer maxillary region. The median intermaxillary teeth are located in the center of the ethmovomer; the bases of these teeth are situated higher compared to the teeth in the peripheral intermaxillary region. The peripheral intermaxillary and outer maxillary region both lie on the same plane. We therefore accounted for the inconsistency in tooth plane by standardizing all tooth measurements along a common plane. The teeth along the dentary were not standardized because they all sit along the same plane within the lower jaws. Inner maxillary tooth length was standardized by measuring the difference in height between the base of the central inner maxillary tooth to the base of the outer maxillary teeth below. This distance was then subtracted from the tooth length within the inner maxillary region. Median intermaxillary teeth were standardized by measuring the length of the second median intermaxillary tooth starting from the base of the peripheral intermaxillary teeth. Due to a number of missing median intermaxillary teeth only the second median tooth was measured. All measurements used to standardize regions were completed using NIH ImageJ v1.48 (Schneider et al., 2012).

To determine whether teeth in different regions varied in curvature over ontogeny, we used the formula $(h/w) \times 100$ (Hamrick, 1996; Galloway et al., 2015). This equation provides a dimensionless value of curvature based upon measurements modeled in Fig. 1B. In each region of the oral jaws, up to five anteriormost teeth were measured and included in further statistical analyses. Angular deviation of teeth was acquired in one cleared and stained *G. mordax* individual; multiple observations were taken in the field to corroborate tooth mobility in live specimens. Due to animal preservation, we were unable to measure tooth depressibility over ontogeny. Angular deviation was acquired by measuring the starting angle of each median intermaxillary tooth and then manually depressing the tooth using a dissection probe until the tooth reached the extent of its mobility; an angular measurement is modeled in Fig. 1D. Both tooth angle, before and after manual depression, and linear tooth curvature measurements were acquired using NIH ImageJ v 1.48 (Schneider et al., 2012). Depressibility tests were performed across the ontogenetic series of specimens in order to determine whether mobility was maintained over ontogeny, though tissue preservation made exact measurements imprecise. Tooth counts were made for each oral jaw 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 but were not included in tooth measurements.

We observed a gradual decrease in tooth length from anterior to posterior along the dentary and outer maxillary regions. Therefore, the dentary and outer maxilla were divided into four equal quadrants for further analysis; an example of these quadrants is provided in Fig. 1C. Outer maxillary quadrants were determined by first measuring the distance from the anterior scarf joint between the ethmovomer and maxilla to the most posterior tooth of the outer maxilla and then dividing this distance by four. Similarly, quadrants along the dentary were established by measuring the distance between the anteriormost tooth to the posteriormost tooth and dividing this distance by four. Two of the 21 individuals had damaged lower jaws, and we were unable to acquire tooth measurements for the dentary region from these individuals. Because of missing or broken teeth within the median intermaxillary region, we only examined scaling patterns for the second tooth when comparing the different regions of the oral jaws. However, all three median intermaxillary teeth were analyzed to compare tooth sizes within the median intermaxillary region. All teeth in the inner maxillary region from the left maxillae were included in additional statistical analyses. In the peripheral intermaxillary region we observed two distinct alternating size classes of teeth: large and small (Fig. 2). Small teeth were interspersed between larger teeth and were found to be less than half the average length of the larger teeth. Only large peripheral intermaxillary teeth were included in further statistical analysis.

2.4. Statistical analysis

Statistical differences in tooth length and width among the four different quadrants of the dentary and outer-maxillary regions

were determined in each individual 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 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 ($p < 0.05$). Our two observations of feeding behavior in the lab with live octopus prey revealed that morays strike with their anterior teeth. Therefore, we only included the anterior half of the maxilla and the anterior quarter of the dentary in further statistical analysis. No significant differences were found between tooth widths. All data required $\log_{10}$-transformation to pass Levene's test for equal variance. Scaling relationships between tooth length relative to tooth width (including scaling relationships within the median intermaxillary region) and tooth length and width relative to HL were examined using standardized major axis (SMA) regression in the R package SMAtr (Warton et al., 2012; R Core Team, 2014). All regressions were based on a length-to-length relationship; therefore, the predicted isometric slope for all SMA regressions was 1, which assumes geometric similarity and forms our null hypothesis. Scaling relationships that deviate from isometry are allometric (Schmidt-Nielsen, 1984); this includes all relationships whose confidence intervals lie above or below the isometric prediction, resulting in positive and negative allometry, respectively. We interpreted an allometric relationship in tooth length relative to tooth width as a change in tooth aspect ratio, which potentially suggests a change in tooth function across ontogeny. The relationship between tooth curvature and HL was examined using ordinary least squares regressions. The examination of tooth dimensions relative to HL rather than VGD was conducted to detect changes, or the lack thereof, over ontogeny because HL had a much stronger relationship to standard length (SL) compared to VGD (Table 3). In order to account for multiple hypothesis testing we adjusted the p-values for all tooth measurements using methods set by Benjamini and Hochberg (1995) which control for false discovery rates. We also conducted SMA regressions on the 45 individuals captured in the field for diet analyses to examine the relationships between HL and eel TL, VGD and HL, and HL and prey SL. We predicted that the relative increase or decrease of HL and VGD in relation to eel size would directly affect the size of potential prey items.

3. Results

3.1. Distribution of G. mordax dentition

We analyzed 1,364 caniniform teeth across 21 individuals (383–1110 mm TL). Tooth number varied dramatically between each of the five regions. With only three teeth, the median intermaxillary region contained the fewest number of teeth, while the dentary region contained the highest, with up to 24 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, bending caudally into the oral cavity, 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, along with an outer row of 17–18 short, rounded maxillary teeth. The inner maxillary teeth were also found to be mobile in the medial and caudal directions. The left and right dentaries had a single row of 22–24 teeth. The 2–3 anteriormost teeth of the dentary were the largest with smaller teeth interspersed between them. The vomerine region contained 8–9 small teeth organized in a single row. These vomerine teeth were comparable in size to the smaller interspersed anterior teeth of the dentary.

Results of Tukey's HSD revealed that the anterior quarter of the dentary contained significantly longer teeth than the posterior quarter ($p < 0.05$), whereas teeth located on the anterior half of the outer maxilla were significantly longer than those located in the posterior half ($p < 0.05$). Tooth width did not change significantly between the quarters of outer maxillary and dentary region. Average tooth length and width within the five tooth regions of the oral jaws is reported in supplementary Table S1 in the online Appendix.

3.2. Scaling patterns of the G. mordax dentition

Scaling patterns varied between teeth in the five oral jaw regions (Table 1). Absolute tooth length relative to tooth width exhibited isometric growth in four of the five regions. The exception were the teeth in the inner maxillary region, which showed significant negative allometric growth in length relative to width (Fig. 3A). Absolute length for the outer maxillary teeth exhibited positive allometry relative to HL ($p < 0.01$, Table 1). Absolute tooth lengths in the remaining four regions exhibited isometric growth relative to HL (Fig. 3B). Tooth widths for inner maxillary teeth expressed positive allometric growth throughout ontogeny relative to HL ($p < 0.01$, Table 1), whereas tooth width in the remaining four regions showed isometric growth (Fig. 3C). Inner maxillary teeth range from the narrowest (0.34 ± 0.06 mm) in smaller individuals to the widest (1.65 ± 0.48 mm) in larger individuals (Fig. 3C).

After standardizing tooth lengths we found that teeth in the inner maxillary region show strong positive allometry ($p < 0.05$, Table 1) along with the outer maxillary teeth (Fig. 3D). The median intermaxillary teeth, which are the largest teeth in the oral jaws, continue to exhibit isometric growth. Despite the slight differences in scaling patterns between absolute tooth lengths and standardized tooth lengths, the order in which the regions of the upper jaws come in contact with the prey (median intermaxillary, then peripheral intermaxillary, followed by inner and then outer maxillary) is consistent over ontogeny.

The impressive lengths of the median intermaxillary teeth prompted us to further analyze each of these teeth to understand how these teeth scale in relation to one another. However, because of tooth damage, only 10 of our 21 individuals had all three median teeth present; four individuals had only a single median tooth remaining (supplementary Table S1). Using these 10 individuals, we show that median intermaxillary tooth length scales isometrically with tooth width across ontogeny (Fig. 4A and Table 2). Both median intermaxillary tooth length and width also show isometric growth relative to HL (Fig. 4B and Table 2).

There was no relationship between tooth recurvature and SL in the studied morays. This indicates that tooth recurvature in all toothed regions is independent of size. Variation in tooth recurvature ratio presumably reflects wear and tear, which presumably varies between individuals. All teeth lining the periphery of the oral jaws exhibited a larger degree of recurve; these included teeth within the outer maxillary, dentary and peripheral intermaxillary region. The teeth of the inner maxillary and median intermaxillary region showed less recurve and were generally much longer than the teeth in the other regions (Fig. 5).

Testing tooth depressibility in the median intermaxillary region of a cleared and stained *G. mordax* individual revealed that the primary tooth had an angular deviation of 15°. The secondary tooth showed an angular deviation of 63°, and the tertiary tooth had an angular deviation of 83°. The tertiary tooth was able to depress fully against the roof of the oral jaws. Our observations of tooth depressibility on a wide size range of anesthetized individuals from the

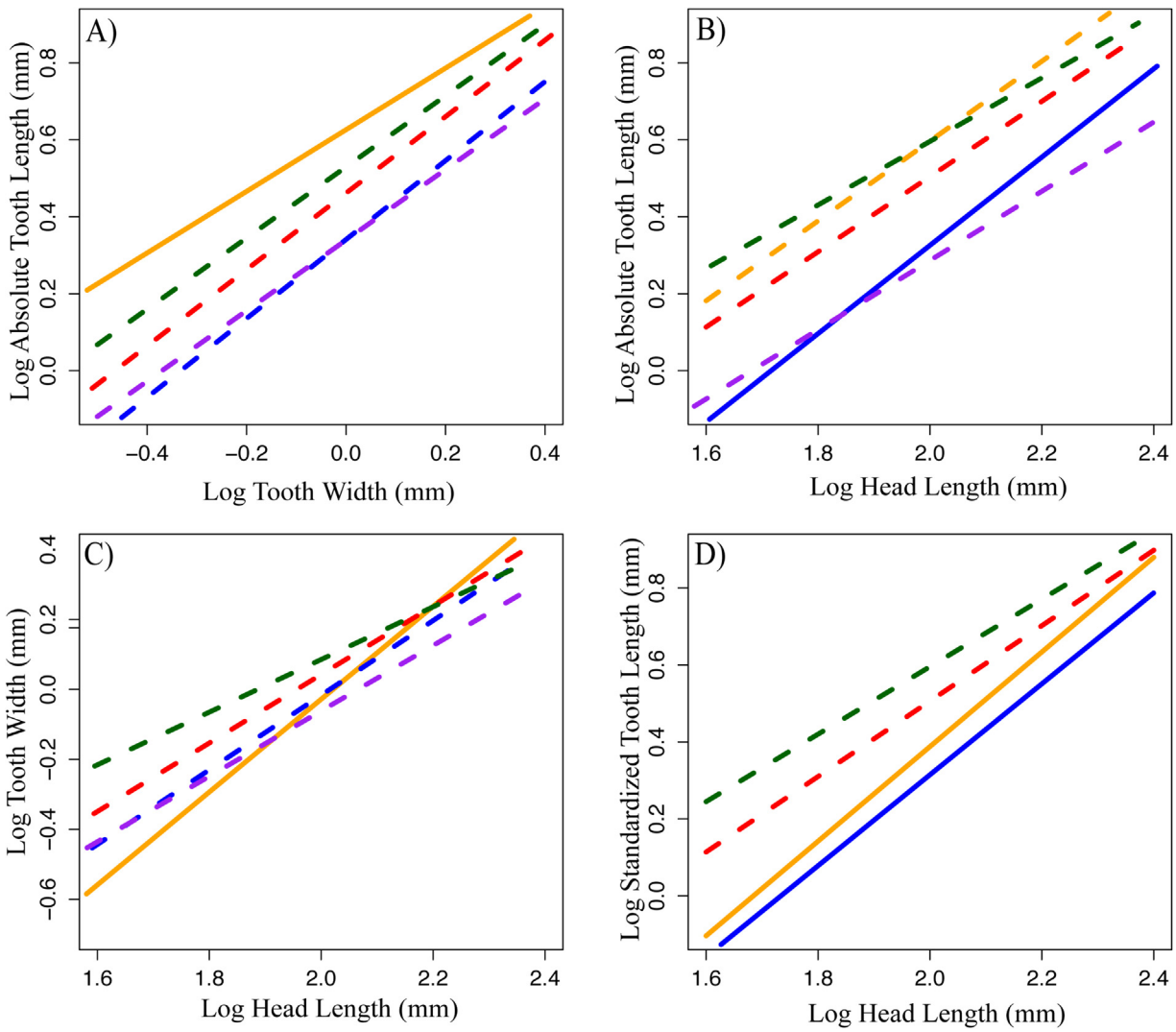

Fig. 3. Variation in tooth dimensions across the skull and scaling patterns of teeth within the regions depicted in Fig. 2. Scaling relationship of (A) tooth length vs. tooth width; inner maxillary teeth exhibit negative allometry, (B) tooth length vs. head length; outer maxilla exhibits positive allometry, (C) tooth width vs. head length; inner maxillary teeth exhibit positive allometry, and (D) standardized tooth length vs. head length; inner maxillary teeth exhibit positive allometry. Allometric growth determined by standardized major axis regression is represented by solid lines, and isometric growth is represented by dashed lines. Colors of regression lines correspond to the different regions highlighted in Fig. 2; scaling relationships are represented in Table 1. The dentary was not standardized and was therefore not included in (D). $N = 21$.

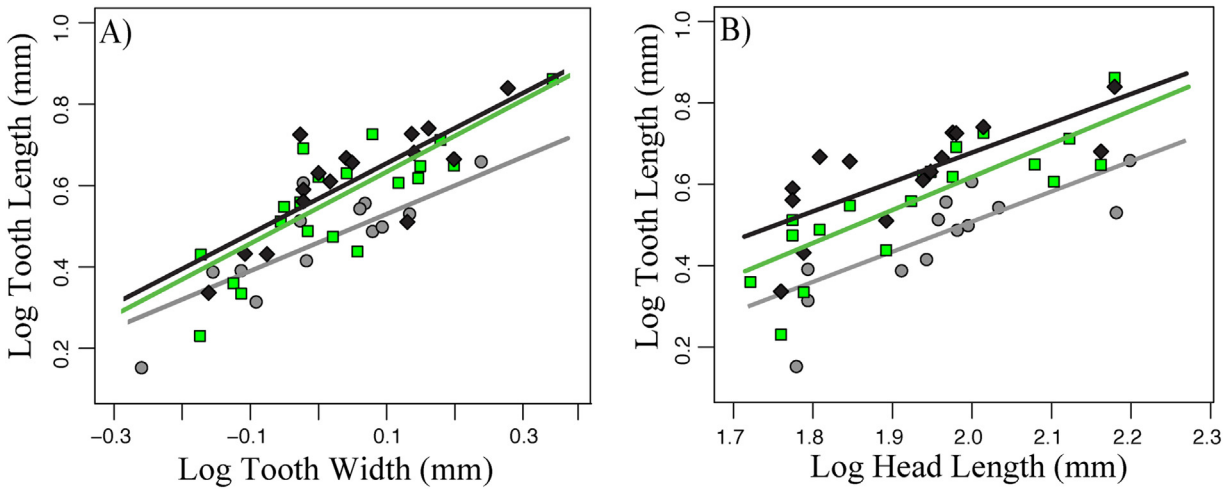

Fig. 4. Variation in tooth dimensions and scaling relationships of median intermaxillary teeth in *G. mordax*. Scaling relationship of (A) tooth length vs. tooth width and (B) tooth length vs. head length. Colors represent the three different teeth within the median intermaxillary region: the primary, secondary and tertiary teeth are shown by gray, green, and black colors, respectively. Scaling relationships are represented in Table 2; all regressions were found to be isometric. $N = 20$.

Table 1
Scaling relationships of tooth length and width in the five oral jaw regions of *G. mordax*.

	Slope (95% CI)	Scaling relationships			Scaling pattern
		R^2	P	Isometric prediction	
A) *Tooth length against tooth width*					
Outer maxilla	1.08 (0.95–1.23)	0.92	0.64	1	IS
Inner maxilla	**0.80 (0.73–0.88)**	**0.96**	**0.002**	**1**	**NA**
Dentary	0.97 (0.82–1.14)	0.90	0.79	1	IS
Peripheral intermaxillary	1.04 (0.89–1.22)	0.89	0.79	1	IS
Medial intermaxillary	1.13 (0.86–1.49)	0.68	0.73	1	IS
B) *Tooth length against head length*					
Outer maxilla	**1.21 (1.09–1.34)**	**0.95**	**0.008**	**1**	**PA**
Inner maxilla	1.11 (0.95–1.3)	0.89	0.59	1	IS
Dentary	0.95 (0.81–1.12)	0.90	0.79	1	IS
Peripheral intermaxillary	1.09 (0.88–1.34)	0.80	0.79	1	IS
Medial intermaxillary	0.97 (0.74–1.27)	0.69	0.89	1	IS
C) *Tooth width against head length*					
Outer maxilla	1.12 (0.97–1.3)	0.90	0.55	1	IS
Inner maxilla	**1.39 (1.19–1.61)**	**0.90**	**0.002**	**1**	**PA**
Dentary	0.99 (0.84–1.17)	0.89	0.91	1	IS
Peripheral intermaxillary	1.04 (0.86–1.27)	0.83	0.79	1	IS
Medial intermaxillary	0.85 (0.67–1.06)	0.80	0.58	1	IS
D) *Standardized tooth lengths against head length*					
Inner maxilla	**1.35 (1.11–1.62)**	**0.84**	**0.02**	**1**	**PA**
Peripheral intermaxillary	1.01 (0.78–1.3)	0.74	0.93	1	IS

Bolded rows show significance. For scaling patterns, IS = isometry, PA = positive allometry, NA = negative allometry. *P*-values have been adjusted for multiple hypothesis testing following Benjamini and Hochberg (1995).

Table 2
Scaling relationships of tooth length and width within the median intermaxillary region of *G. mordax*.

	Slope (95% CI)	Scaling relationships			Scaling pattern
		R^2	P	Isometric prediction	
A) *Tooth length against tooth width*					
Primary tooth	0.86 (0.61–1.2)	0.70	0.73	1	IS
Secondary tooth	1.13 (0.86–1.49)	0.68	0.73	1	IS
Tertiary tooth	1.11 (0.78–1.56)	0.62	0.79	1	IS
B) *Tooth length against head length*					
Primary tooth	0.90 (0.64–1.28)	0.68	0.79	1	IS
Secondary tooth	0.97 (0.74–1.27)	0.69	0.89	1	IS
Tertiary tooth	0.90 (0.64–1.28)	0.61	0.79	1	IS
C) *Tooth width against head length*					
Primary tooth	1.05 (0.83–1.34)	0.85	0.79	1	IS
Secondary tooth	0.85 (0.69–1.06)	0.80	0.58	1	IS
Tertiary tooth	0.82 (0.58–1.15)	0.64	0.63	1	IS

For scaling patterns, IS = isometry. *P*-values have been adjusted for multiple hypothesis testing following Benjamini and Hochberg (1995).

Table 3
Scaling relationships of head length and vertical gape distance in *G. mordax*.

	Slope (95% CI)	Scaling relationships			Scaling pattern
		R^2	P	Isometric prediction	
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**

For scaling patterns, PA = positive allometry. Bolded rows indicate significant allometry.

field helped us verify that the ability of the tertiary tooth to flatten against the roof of the oral jaws was consistent across ontogeny.

3.3. Prey size in relation to moray size

We collected dietary data for 45 *G. mordax* individuals that varied in TL (range: 480–1114 mm). The size range of specimens used for diet samples was similar to the ontogenetic series for which we quantified tooth dimensions. We found a strong positive allometric relationship between *G. mordax* HL and TL ($p < 0.01$, $R^2 = 0.97$, Fig. 6A). We also found a strong positive allometric relationship between VGD and HL ($p < 0.001$, $R^2 = 0.83$, Fig. 6B). Thus, as *G. mordax* grows in body size, both HL and VGD disproportionately increase over ontogeny. The dietary items found in the stomachs of *G. mordax* consisted mainly of fishes (83% of which was Calico bass, *Paralabrax clathratus*) and a few invertebrates (5 red rock shrimp, *Lysmata californica,* 12–61 mm, and 1 California spiny lobster, *Panulirus interruptus*, 139 mm). Size of prey from stomach contents ranged from 12 to 232 mm in standard length. Each prey item was collected from a single *G. mordax* individual. No single eel had multiple prey items in their stomach. We found no relationship between prey standard length and *G. mordax* HL (Fig. 6C).

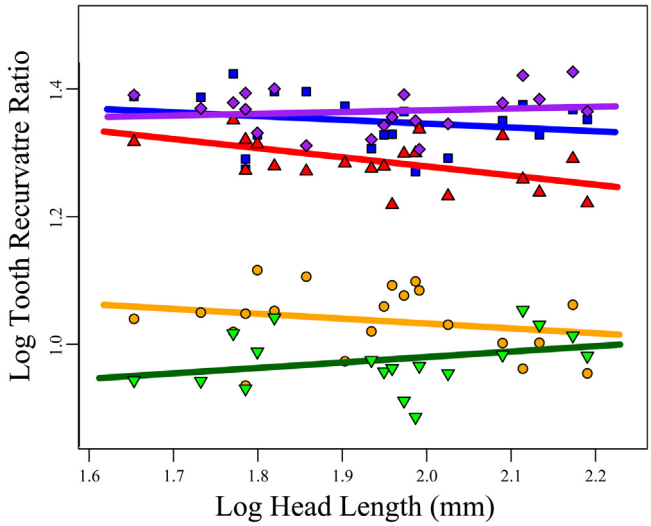

Fig. 5. Variation and scaling relationships of tooth recurvature vs. head length in *G. mordax*. Tooth recurvature is a unitless metric because it is a ratio. Colors correspond to the regions in Fig. 2. Solid lines represent ordinary least-square regressions. No regressions were found to be significant. $N = 21$.

4. Discussion

4.1. Tooth size and scaling relationships

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 maintained the same shape over ontogeny (Table 1), which implies no functional change as *G. mordax* individuals grow. The only teeth to show allometric relationships with HL were teeth lining the maxillae (Table 1). Over ontogeny, teeth along the outer maxillary region are getting longer relative to HL, but do not increase their relative width; lengthening of the outer maxillary teeth may assist in prey retention by making these teeth more prominent within the oral jaws. In the outer maxillary region, teeth also exhibit some of the greatest recurvature, which may further aid in prey retention (Fig. 5).

We found that the inner maxillary teeth are some of the longest in the oral jaws (Fig. 3A and B). Inner maxillary tooth widths increase relative to both tooth length and HL across ontogeny. The inner maxillary teeth begin as some of the thinnest teeth and grow to be the widest (Fig. 3C). Widening the tooth base over ontogeny may be a way to fortify teeth and reduce tooth loss in the inner maxillary region. While we found that the absolute length of the inner maxillary teeth exhibits isometric growth, indicating that tooth length is proportional to HL over ontogeny, standardization of the inner maxillary teeth revealed positive allometric growth. This disproportional increase in tooth length may enable the inner maxillary teeth to contact the prey item in synchrony with the outer maxillary teeth.

Unlike teeth in the other regions, teeth in the inner maxillary and median intermaxillary regions are long and straight and show the least amount of tooth recurvature of any region. Higher-aspect ratio teeth in elasmobranchs have been shown to be more effective in piercing materials (Whitenack and Motta, 2010). Presumably, the high-aspect ratio teeth that line the inner maxillary and median intermaxillary regions are more effective at puncturing, and can embed deeply into a prey item. Though few in number, the median intermaxillary teeth are the longest teeth within the oral jaws of *G. mordax* (supplementary Table S1). The position of the three median intermaxillary teeth, just posterior to the peripheral intermaxillary,

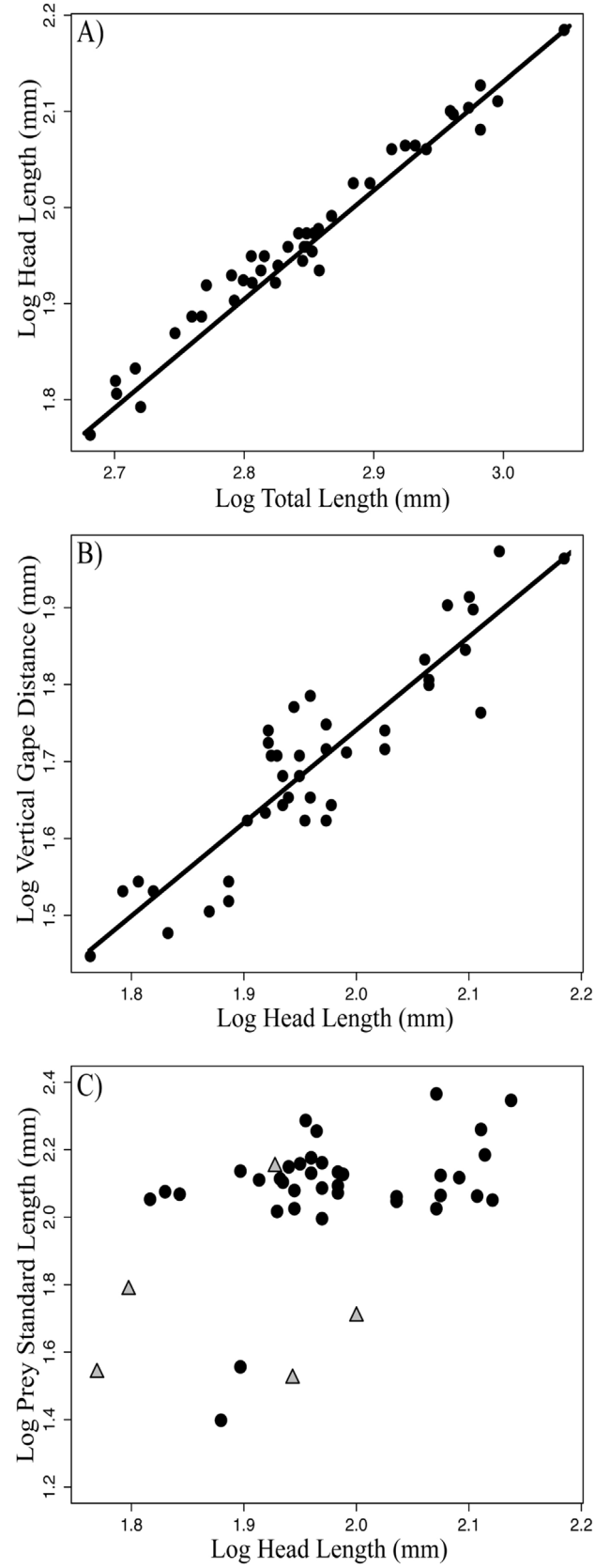

Fig. 6. Scaling relationships of (A) moray head length vs. total length, (B) vertical gape distance vs. head length, and (C) standard lengths of prey items and California morays. Circles represent various fish species and triangles represent six invertebrates (5 red rock shrimp, 31–61 mm; and the California spiny lobster, 139 mm). $N = 45$.

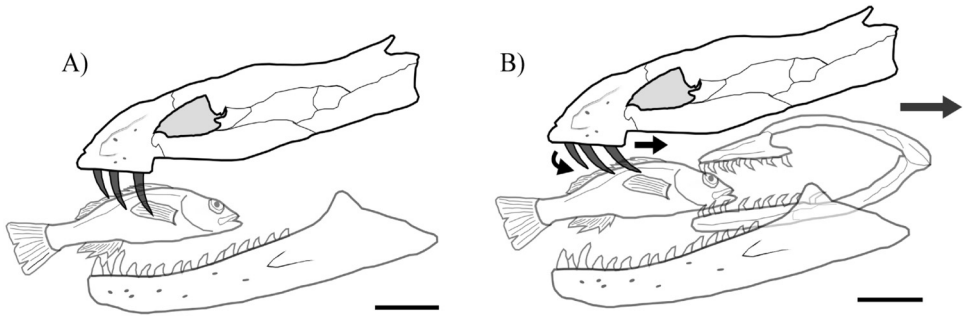

Fig. 7. (A) Lateral view of a *G. mordax* skull. The maxillae and hyomandibular have been removed along with the peripheral intermaxillary teeth in order to highlight the median intermaxillary teeth. Fish represents a potential prey item caught within the oral jaws. (B) Arrows represent the movement of the prey item and the direction of movement of the median intermaxillary teeth. Scale bars = 1 cm.

suggests that they may be the first to come into contact with a prey item. We found a large amount of variance in the lengths and widths of the three median intermaxillary teeth (Fig. 4 and Table 3). These teeth were often observed to be chipped or broken off at the tooth base in our specimens; only 10 individuals had all three median intermaxillary teeth present.

4.2. Tooth functional roles

Variation in length in caniniform teeth across different regions of the oral jaws in *G. mordax* suggests teeth in these regions exhibit different functional roles for prey capture and prey retention. Research focused on another marine piscivore, the great barracuda (*Sphyraena barracuda*), showed that caniniform teeth in the oral jaws were more triangular along the dentary and palatine. These triangular teeth formed a set of shears, which function to slice through their prey when the jaws adduct (Grubich et al., 2008). However, caniniform teeth in the oral jaws of the moray appear better designed for gripping. Teeth along the periphery of the jaws (outer maxillae, peripheral intermaxillary, and dentary) display tooth recurvature directed towards the interior of the oral cavity. Tooth recurvature is prevalent in piscivorous fishes (Blaber et al., 1994; Ramsay and Wilga, 2007; Galloway et al., 2015), where recurved teeth function to maintain prey within the jaws (Ramsay and Wilga, 2007).

The median intermaxillary teeth are rooted in the center of the ethmovomer, emerging from the roof of the mouth. We hypothesize that these teeth are specialized for puncturing prey items. Narrow high-aspect ratio teeth have been shown to require less force to puncture materials in both elasmobranchs and mammals (Freeman and Leeman, 2007; Whitenack and Motta, 2010). By having fewer high-aspect ratio teeth and increasing the spacing between them, the relative stress applied at each tooth focal point can be increased. This allows each tooth to puncture more effectively, rather than if the teeth were densely packed together (Anderson, 2009; Galloway et al., 2015). The overall "fang-like" morphology and the relatively wide spacing of teeth in the median intermaxillary region strongly suggest that the median intermaxillary teeth are used to puncture prey.

A trade-off of the median intermaxillary teeth puncturing deep into a prey item is that it will make it more challenging for the moray to remove the prey from the teeth to transport the food to the back of the throat. However, the median teeth show a large amount of mobility, as they are able to depress towards the roof of the skull. The degree of this movement increases caudally, with the third median intermaxillary tooth being able to completely depress against the roof of the skull. Inner maxillary teeth are also highly mobile in the caudal and medial directions. Depressible teeth may allow for large prey items to be easily transported from the oral cavity into the esophagus without obstructing transport. Depressible teeth were found in all specimens in the present study and are also found in other muraenids (Smith et al., 2008). This depressibility may be enabled by the ring of predentine and collagen found between the tooth base and the bone, which is a character shared by the Elopomorpha (Fink, 1981).

In Muraenidae, a set of pharyngeal jaws are used to transport prey items from the oral jaws into the esophagus (Mehta and Wainwright, 2007; Mehta, 2009). We presume that depressible teeth in the median intermaxillary region facilitate prey transport by the pharyngeal jaws so that prey captured and punctured in the oral jaws can be transported and retracted into the esophagus (Fig. 7). Possessing depressible teeth prevents the moray from having to fully abduct the upper and lower jaws to release the pierced prey in order for the pharyngeal jaws to transport it.

A possible alternative benefit conveyed by depressible teeth is protection from tooth damage when consuming tougher prey. For example, in the white-spotted bamboo shark (*Chyloscyllium plagiosum*), teeth depress against the roof of the mouth when coming into contact with a hard prey item (Ramsay and Wilga, 2007). In *C. plagiosum*, teeth depress to reduce the forces placed on the tooth tip; when the tooth is depressed, the broad side of the tooth comes into contact with the prey item and is then used to crush hard prey. Due to the shape of these teeth in morays, it is highly unlikely that the purpose of median intermaxillary tooth depression is to reduce the forces put on the tooth tip. If a prey item is too hard for the tooth to penetrate, a median intermaxillary tooth can presumably still break, even though the tooth can respond by simply folding back against the roof of the skull. In fact, we commonly observed tooth fracturing within the median intermaxillary region as most *G. mordax* specimens used in the present study were found to be missing one or more median intermaxillary teeth. In durophagous organisms, a high narrow cusp on a tooth reduces the force required to crush a prey item, though ultimately increasing the likelihood of tooth fracture (Crofts and Summers, 2014). High-aspect ratio teeth like those found in the median intermaxillary region in the California moray are under greater risk of fracture, suggesting a trade-off between tooth failure and maintaining low puncture forces. The scaling patterns for tooth aspect ratio in the oral jaws and non-jaw cranial elements we quantified do not suggest that tooth fortification occurs over ontogeny, with the exception of the inner maxillary teeth, which show an increase in relative tooth width as morays increase in size.

4.3. Moray diet

The predominantly isometric patterns of tooth growth in the oral jaws suggest that feeding behavior remains relatively constant over ontogeny. This tooth scaling pattern in conjunction with the

disproportionate increase in HL and VGD relative to eel TL suggests the potential to increase relative maximum prey size over ontogeny (supplementary Table S2). This pattern is opposite to that of some species of snakes for which ontogenetic trajectories have been examined. E.g., in species of natricine water snakes, younger individuals tend to have larger heads relative to their body size compared to older individuals, allowing them to consume relatively larger prey when they are small (King et al., 1999; Hampton, 2014). Increased head size in snakes not only facilitates the consumption of relatively larger prey sizes, but also assists in consuming smaller prey items at a faster rate (Pough and Groves, 1983; Forsman and Lindell, 1993).

We demonstrate that smaller prey are retained in the diet of *G. mordax*, suggesting that this species does not specialize on a particular size of prey at any point over ontogeny. Rather, as morays increase in size they are expanding the size range of prey consumed, also known as ontogenetic 'telescoping' (King, 2002). This pattern of feeding on a wide range of prey sizes is thought to be typical of predatory fish (Scharf et al., 2000). The inclusion of small-bodied prey items in larger *G. mordax* suggests an opportunistic foraging behavior. An observation that supports the idea that California morays may be opportunistic foragers is the sighting of individuals hunting smaller pelagic crabs (*Pleurincodes planipes*), roughly 5–7 cm in carapace length, within the shallow rocky intertidal during daylight hours (R.S.M and J.S.H., personal observation). These pelagic crabs, otherwise known as tuna crabs, are soft-shelled and their appearance coincided with an El Niño event.

5. Conclusion

The California moray exhibits caniniform teeth that vary in size in the oral jaws, with the inner maxillary and median intermaxillary teeth being the longest. The scaling patterns of teeth across five distinct regions of the oral jaws exhibit mostly isometry, except for the maxillary region. The teeth also do not vary in their aspect ratio over ontogeny. The median intermaxillary teeth, of which there are only three, appear to be used for puncturing prey. Interestingly, these teeth are highly depressible. Teeth along the periphery of the oral jaws, peripheral intermaxillary, outer maxillary, and dentary are more curved and appear to be effective in prey retention. Gut contents from California morays in the field revealed that kelp bass were the dominant prey. The relationship between vertical gape distance, head length and eel total length exhibits strong positive allometry, suggesting that larger morays consume larger prey. However, we find no relationship between prey size and moray size. Thus, the predominantly isometric tooth growth in the oral jaws of the California moray supports a wide size range of prey. Here, we provide another example of how scaling patterns of dentition can support tooth function and lend insight into whether predators undergo ontogenetic shifts in diet.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.zool.2017.02.002.

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