

Ecomorphology of the Moray Bite: Relationship between Dietary Extremes and Morphological Diversity*

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ABSTRACT

The pharyngeal jaws of moray eels function exclusively to transport prey from the oral jaws into the esophagus. This functional innovation in the moray pharyngeal jaw system occurred through the loss of some ancestral functions that presumably included prey processing. Therefore, the oral jaws of morays are used to capture and process prey. Dietary accounts suggest that morays can be categorized as either piscivorous or durophagous in feeding habits. These extreme feeding specializations that select for conflicting biomechanical demands on the oral jaws should result in two discrete clusters of cranial form and diet in morphospace. When functional characters underlying the oral jaws were examined for 10 muraenid species, piscivorous and durophagous morays occupied distinct areas of morphospace. Piscivores exhibited longer jaws, narrower heads, and long recurved teeth, while durophagous morays exhibited shorter jaws, greater dentary depths, and short blunt teeth. Durophagous morays process prey in their oral jaws, and their jaw-opening and jaw-closing ratios, along with their enlarged adductors, revealed jaws modified for force transmission. Pharyngeal jaw characters also separated moray species into different areas of morphospace. For example, *Gymnomuraena zebra*, a molluscivore, had more teeth on its pharyngobranchials than all other morays, and these teeth were long and thin compared with those of piscivores. The overall patterns of morphological variation corresponded well with moray dietary breadth. In addition, the range of jaw-opening and jaw-closing ratios revealed that for a clade of obligate carnivores, morays exhibit diverse biting behaviors.

Introduction

Diet has had profound effects on the morphology and behavior of a wide variety of vertebrate taxa (bats: Freeman 1981; Barlow et al. 1997; Dumont 1999; primates: Daegling 1992; Dumont 1995; snakes: Savitsky 1983; Voris and Voris 1983; Coleman et al. 1993; Hosoi et al. 2007; lizards: Dearing 1993; Meyers et al. 2006; fish: Wainwright 1988; Kotrschal 1989; Hugueny and Pouilly 1999; Hulsey and Garcia De Leon 2005). Identifying how dietary habits affect the morphology of the feeding apparatus within a particular clade is an essential step toward understanding the mechanisms contributing to overall patterns of morphological diversity and organismal design. Dietary specialists, often distinguished by their narrow resource use relative to other members within their group, can offer valuable insight into the degree to which complex musculoskeletal systems of the skull can be modified to enhance performance. One might anticipate that successfully capturing or extracting the nutritional benefits from certain prey requires particular anatomical and physiological designs of the feeding apparatus. Understanding the direction of morphological change and the degree of morphological change required to create significant functional shifts in resource use and ecological habit is a central goal of ecomorphology (Bock 1980; Norton and Brainerd 1993; Wainwright 1994).

Teleost fish are one of the most species-rich and morphologically diverse groups of vertebrates (Nelson 2006; Wainwright 2006). Given this diversity, it is not surprising that teleosts have been the subject of many functional morphology and ecological studies related to feeding (Werner 1974; Wainwright 1987, 1988, 1991; Motta 1988; Motta et al. 1995; Wainwright and Richard 1995; Clifton and Motta 1998; Grubich 2003). An important and unifying contribution of many of these studies is the idea that morphology and diet reciprocally illuminate one another once the functionally relevant features of the feeding apparatus are examined.

The majority of bony fish possess a dual-jaw system for feeding. While the oral jaws of fish are primarily used to capture prey, a second set of functioning jaws in the pharynx, the pharyngeal jaws, are used to crush, shred, and prepare prey for digestion (Schaeffer and Rosen 1961). Each musculoskeletal jaw system can contribute independently to functional, morphological, and ecological diversification in teleosts, as exemplified by the partitioning of their functional roles. In addition, the skeletal morphology of the dual-jaw feeding system and associated musculature is strongly correlated with dietary habits (Lauder 1983; Turingan and Wainwright 1993; Wainwright 1996; Ralston and Wainwright 1997; Grubich 2003; Korff and Wainwright 2004).

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In spite of the large number of fish-feeding studies, few studies have examined the morphology of the feeding apparatus in ancient actinopterygian and teleost lineages (Lauder 1979, 1980). Recent studies have shown that some of these earlier lineages exhibit extraordinary diversity in jaw morphology, skull mechanics, and feeding habits (Westneat 2004; Kammerer et al. 2005). Documenting the morphological diversity underlying the feeding apparatus of these lineages is essential to understanding the relationship between morphological diversity and the evolution of trophic diversity in fish-feeding behavior. With this larger goal in mind, this article documents the ecomorphology of moray eels.

Morays (Muraenidae) are a little-studied lineage within a relatively large and early radiation of teleosts, the anguilliforms, otherwise known as the “true eels” (Nelson 2006). Moray eels represent a species-rich group of obligate predatory fish that are found in pantropical waters and are most often found in association with coral reef habitats (Böhlke et al. 1989). Morays are a fascinating group with which to study morphological variation in the feeding apparatus because they are exclusively ram biters and have a reduced capacity to move water through their mouths during prey capture and transport (Mehta and Wainwright 2007a, 2007b). In fact, the oral jaws and the pharyngeal jaws of morays are specialized for biting during both of these distinct phases of feeding (Mehta and Wainwright 2007b), providing an opportunity to examine how dietary habits affect variation in two behaviorally analogous systems. Moreover, literature accounts suggest that morays do not seem to exhibit much variation in dietary habits and are often considered either mostly piscivorous or mostly durophagous (Table 1). However, piscivory and durophagy represent extreme specializations in feeding behavior for many fish groups and often favor conflicting biomechanical demands of the feeding apparatus (Westneat 2003; Wainwright et al. 2004).

Little is known about the morphological variation underlying

the feeding apparatus of morays, let alone how well morphological variation in the oral jaws and pharyngeal jaws reflect moray dietary patterns. One might expect piscivores to exhibit sharp recurved dentition in both the oral and pharyngeal jaws to grip large prey while morays that consume harder prey would exhibit molariform dentition in the oral jaws to process prey while still retaining sharp recurved dentition in their pharyngeal jaws. Both piscivory and durophagy would favor large muscles with which to adduct the oral jaws. Piscivorous morays might also be expected to exhibit larger adductor muscles in the pharyngeal jaws in order to hold and transport large struggling fish prey. This article considers the functional significance of several morphological features of both the oral jaws and pharyngeal jaws to understand how they may shape dietary specialization in morays. Two fundamental questions are as follows: (1) How well are dietary specializations reflected in the morphology of the oral and pharyngeal jaws of morays? (2) Within these dietary specializations, do all morays exhibit similar features?

Material and Methods

Ten muraenid species from six different genera were included in this study: *Echidna catenata*, *Echidna nebulosa*, *Echidna rhodochilus*, *Enchelycore bayeri*, *Gymnomuraena zebra*, *Gymnothorax javanicus*, *Gymnothorax kidako*, *Gymnothorax vicinus*, *Muraena retifera*, and *Rhinomuraena quaesita* (Fig. 1). Species were chosen on the basis of general head shape differences and availability of dietary data. Specimens were obtained from personal collections and the aquarium trade. Dietary habits of morays were surveyed from the literature and used to classify species into discrete dietary groups (Table 1).

A preliminary set of morphological measurements pertaining to the overall size of specimens was first made on a small sample of preserved museum specimens representing all six genera.

Table 1: Common names, sample sizes, range of standard lengths (SLs), and dietary habits for morays examined

Species	Common Name	<i>n</i>	SL (mm)	Dietary Habits	References
<i>Echidna catenata</i>	Chain moray	4	400–485	Durophagous	Randall 1967, 1968, 1985; Robins and Ray 1986; Böhlke and Chaplin 1993
<i>Echidna nebulosa</i>	Snowflake moray	3	295–308	Durophagous	Randall 1967; Yukihiro et al. 1994
<i>Echidna rhodochilus</i>	White cheek moray	3	235–289	Durophagous	Kottelat et al. 1993
<i>Enchelycore bayeri</i>	Hook jaw moray	3	230–460	Piscivorous	Myers 1991
<i>Gymnomuraena zebra</i>	Zebra moray	3	200–660	Durophagous	Hiatt and Strasburg 1960; Yukihiro et al. 1994; Lieske and Myers 1996
<i>Gymnothorax javanicus</i>	Giant moray	3	260–452	Piscivorous	Hiatt and Strasburg 1960; Yukihiro et al. 1994
<i>Gymnothorax kidako</i>	Kidako moray	3	352–502	Piscivorous	Suyehiro 1942
<i>Gymnothorax vicinus</i>	Purple mouth moray	3	255–357	Piscivorous	Randall 1967; Pattengill et al. 1997; Young and Winn 2003
<i>Muraena retifera</i>	Reticulated moray	4	390–455	Piscivorous	Randall 1985
<i>Rhinomuraena quaesita</i>	Ribbon moray	4	700–723	Piscivorous	Chen et al. 1994

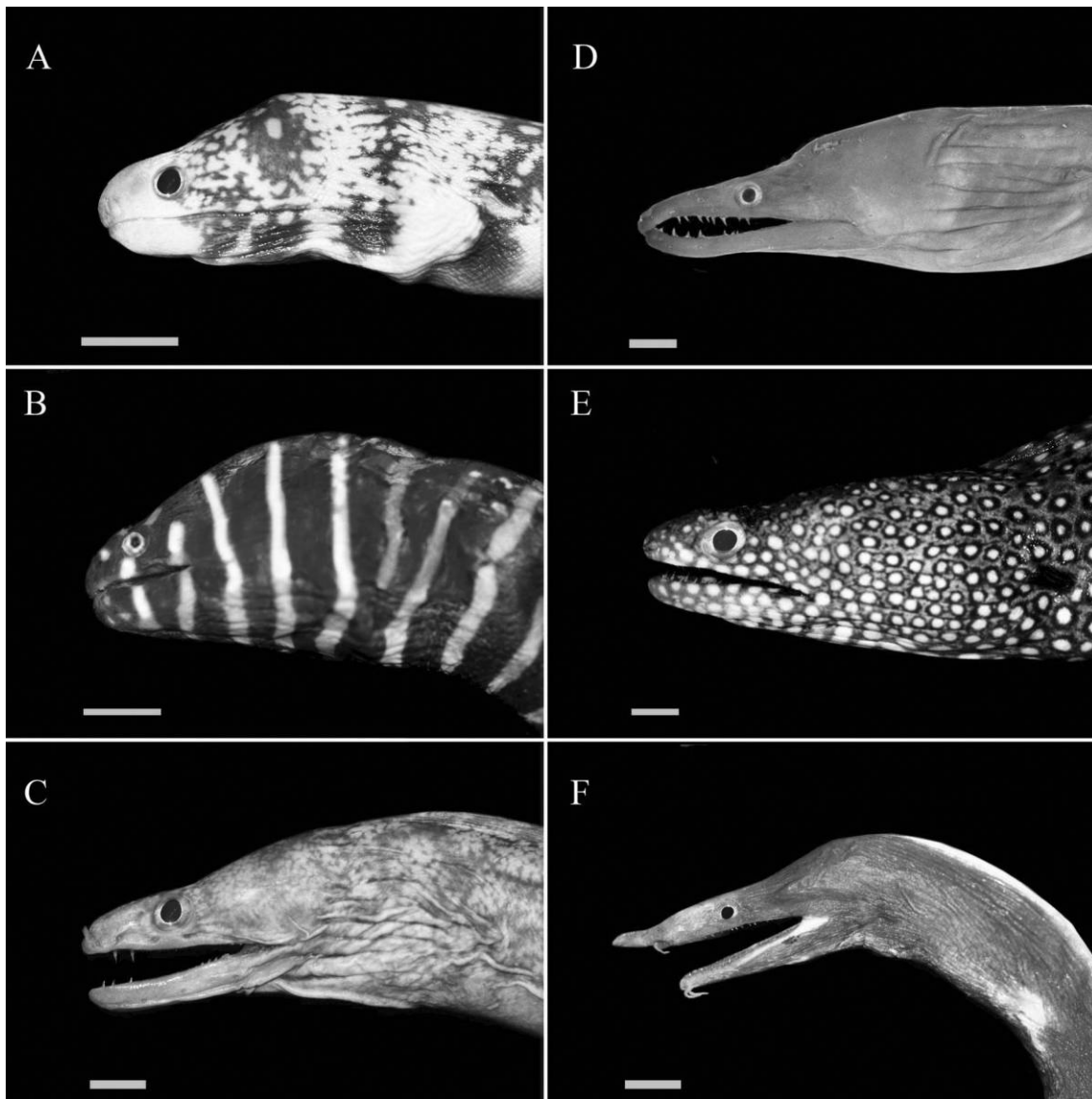


Figure 1. Photographs of freshly killed and preserved specimens depicting general head shape differences for representatives of the six genera of moray eels examined in this study. A, *Echidna nebulosa*. B, *Gymnomuranea zebra*. C, *Gymnothorax kidako*. D, *Enchelycore bayeri*. E, *Muraena retifera*. F, *Rhinomuraena quaesita*. Scale bars = 1 cm.

These measurements were standard length (SL; tip of closed mouth to the beginning of the anal fin rays), head width (HW; width from suspensorium to suspensorium with the mouth closed), head length (HL; distance from the tip of the rostrum to the neurocranium-vertebral joint), and head height (HH; measured from the bottom of the dentary directly below the eye to the top of the head above the eye). A series of least squares regressions were performed on \log_{10} -transformed data to better understand the relationship between head dimensions and overall body size in these extremely elongate fish. Although SL is usually a good indicator of size, the relationship between SL and HL in morays was weak ($r^2 = 0.27$; Fig. 2A). SL was, however, strongly and positively correlated with other head characteristics: HH ($r^2 = 0.72$) and HW ($r^2 = 0.67$; Fig. 2B).

HL was also strongly correlated with HH and HW, but the slopes were negative mainly as a result of the single outlier, *R. quaesita* (Fig. 2C). For a given HL, *R. quaesita* has a very narrow and short neurocranium (Fig. 1F). When *R. quaesita* is removed from the data set, the relationships between HH and HL and HW and HL are positive but weak. I chose to use HL to approximate moray size because the \log_{10} linear relationship between HL and other characteristics corresponded with my own observations of moray head shape. In addition, HL in morays is also more comparable across other fish taxa because few adult fish species grow to approach morays in SL.

To examine potential morphological patterns associated with diet, a total of 26 morphological measurements were made on the oral jaws and pharyngeal jaws of the 10 species. I examined

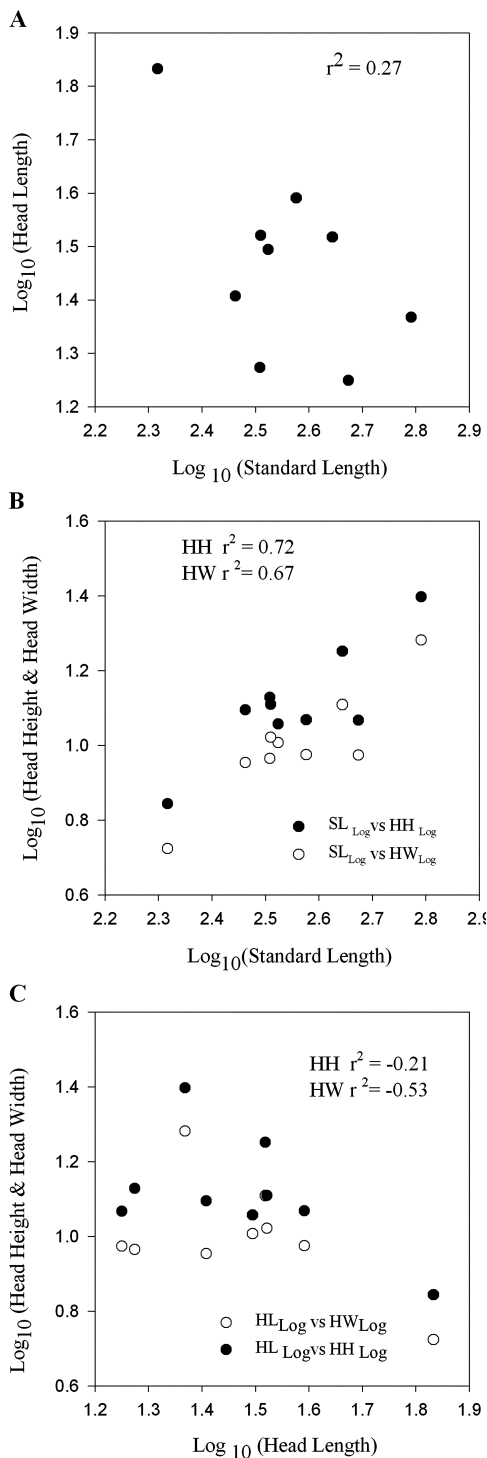


Figure 2. Log₁₀-linear plots of the relationship between (A) log₁₀ (standard length) and log₁₀ (head length), (B) log₁₀ (standard length) and log₁₀ (head height and head width), and (C) log₁₀ (head length) and log₁₀ (head height and head width).

three to four individuals for each species. The moray neurocranium, which is composed of many fused bony elements, is elongate, and the oral jaws are not protrusible (Fig. 3A, 3B). Measurements of the neurocranium and pharyngeal jaws were

made after specimens were cleared and double stained following standard methods (Dingerkus and Uhler 1977; Song and Parenti 1995). This method restored pliability to connective tissue so that the mouths of specimens could be opened to attain realistic measurements of the oral gape. All measurements were taken with an ocular micrometer fitted for a dissecting microscope. The morphological measurements for the oral jaws were HL, HW, rostral length (RL; anteriormost part of the orbit to the tip of the snout), rostral width (RW; width of the rostrum at scarf joint between premaxilla/maxilla), internal vertical gape (VG; distance between the roof of the mouth and the bottom of the lower jaw with the mouth open), internal horizontal gape (HG; distance between the left and right sides of the mouth cavity with the mouth open), total dentary length (TDL; distance from lower jaw symphysis to the posteriormost margin of the dentary), dentigerous dentary length (DDL; length from symphysis to posteriormost tooth on dentary), dentigerous premaxillary length (DPL; length from one scarf joint between maxilla to the other scarf joint), maxilla length (ML; length from scarf joint between premaxilla/maxilla to the tip of the maxilla), dentary depth (DD; length from bottom of dentary to the tip of the coronoid process), and the number of teeth on the maxilla (MT).

The average height and width of the five largest teeth on the upper jaw (UTH, UTW) were also recorded. During different stages of the clearing and staining process, one side of the mandible was removed from specimens (HL > 15 mm) and mounted in putty. A photograph of the medial view of the dentary was taken with a scale bar placed next to the specimen. High resolution digital photographs were taken with a Canon EOS 50-mm lens with a 5-mm extension tube (Fig. 3C). Scanning electron microscopy (SEM) was used for smaller specimens (HL < 15 mm). Jaws from cleared and stained specimens were removed and cleaned of glycerine using soap and water and were dehydrated in 95% ethanol over night. Specimens were then dried, mounted on aluminum stubs, and coated with gold palladium powder. Tooth morphology was examined with SEM (Philips XL30 TMP, FEI) and captured with iTEM software. Images were then imported into Scion Image software, and tooth characters were measured.

The pharyngeal jaws are composed of slender bony elements, and the tooth plates contain recurved teeth, similar to those found in the oral jaws (Fig. 3D). The morphological measures for the pharyngeal jaws were pharyngobranchial length (PBL), pharyngobranchial width (PBW; width just anterior to the attachment site to the epibranchial), epibranchial length (EBL), epibranchial width (EBW; width halfway down epibranchial arm), ceratobranchial length (CBL), ceratobranchial width (CBW; width halfway down ceratobranchial arm), lower tooth plate length (LPL), lower tooth plate width (LPW; width halfway down tooth plate), pharyngobranchial lever arm (PBA; length from point of rotation to the anteriormost end of the pharyngobranchial), number of teeth on upper tooth plate (UT), and number of teeth on lower tooth plate (LT). The average height and width of five teeth on the pharyngobranchial

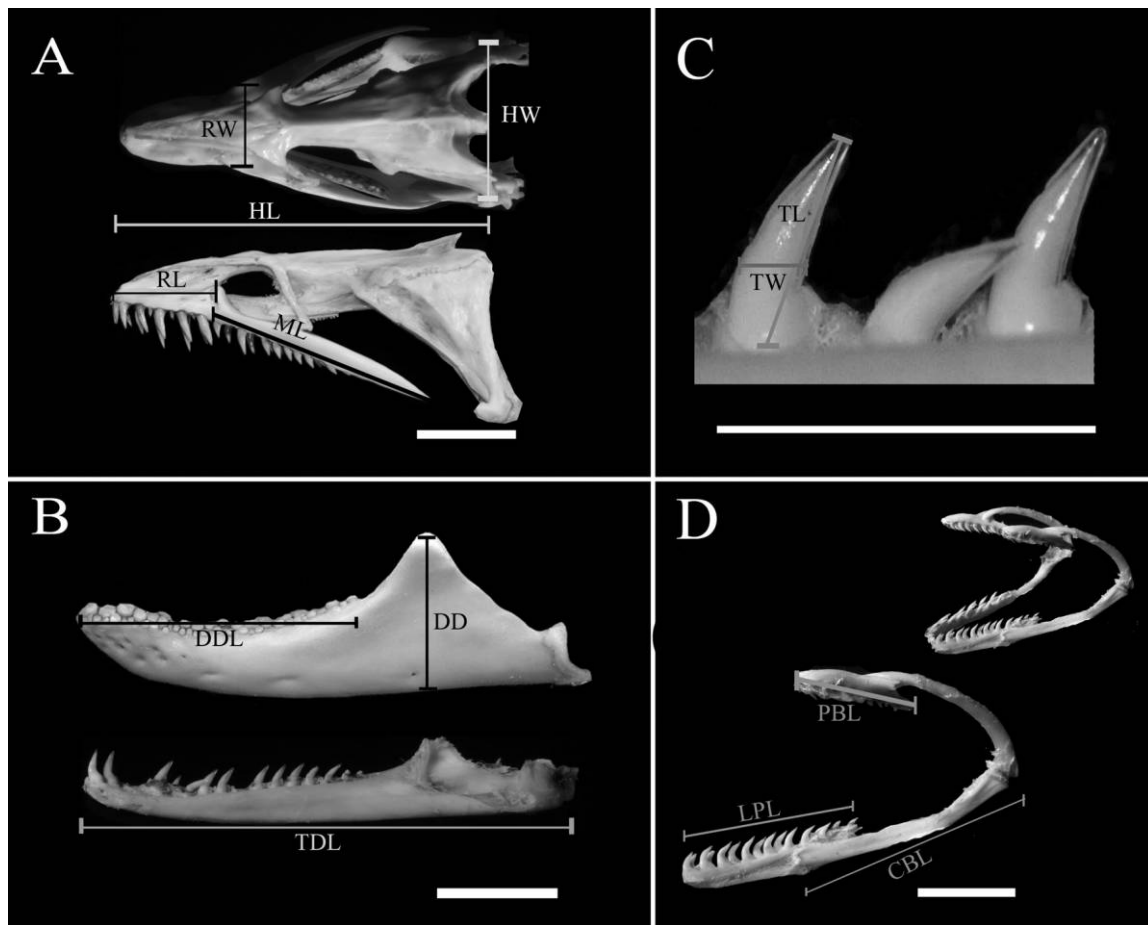


Figure 3. Photographs of different components of the moray feeding apparatus examined in this study. A, Dorsal (*top*) and lateral (*bottom*) views of the neurocranium of *Gymnothorax javanicus* depicting some of the morphological variables measured: rostral width (RW), head width (HW), head length (HL), rostral length (RL), and maxillary length (ML). B, Lateral view of the dentary of *Gymnomuraena zebra* (*top*) and medial view of the dentary of *Muraena retifera* (*bottom*) depicting the following three morphological variables measured: dentigerous dentary length (DDL), dentary depth (DD), and total dentary length (TDL). C, Medial view of three caniniform and slightly recurved teeth on the lower tooth plate of the pharyngeal jaw depicting how tooth length (TL) and tooth width (TW) were measured. D, Oblique view of the pharyngeal jaw apparatus (*upper right*) and lateral view of the left side of the pharyngeal jaw of *G. javanicus* depicting three of the 13 morphological variables measured: pharyngobranchial length (PBL), ceratobranchial length (CBL), and lower tooth plate length (LPL). Scale bars = 1 cm.

(PJTL, PJTW) were also recorded for each specimen using digital photograph techniques and SEM.

The adductor mandibulae is a large muscle complex that acts to adduct the oral jaws and is therefore the muscle that powers biting (Alfaro et al. 2001; Westneat 2003). Previous studies have shown that species with greater adductor mandibulae masses, all other features remaining the same, exhibit greater force-generating capacity (Wainwright 1988; Grubich 2003). Unlike the majority of fish, morays only have the A2 division of the adductor mandibulae. In muraenids, the adductor mandibulae (AM2) is the largest superficial muscle of the neurocranium. The left and right sides of the adductor are connected at the dorsal midline of the skull. In morays, the A2 originates from the hyomandibular, symplectic, and skull. The superficial muscle fibers insert on the coronoid process of the dentary and the posterior margin of the angular. The inner fibers insert into the Meckelian fossa and consolidate as a tendon extending throughout the Meckelian fossa (Wu and Shen 2004).

With the exception of the greatly hypertrophied obliquus dorsalis and the fifth adductor (AD5), the pharyngeal muscles of morays are extremely long. The fifth adductor functions to adduct the pharyngeal jaws during initial prey contact and also to maintain a grip on prey while transporting prey from the oral jaws into the oesophagus. The fifth adductor originates on the dorsal epibranchial and inserts onto the lateral side of the ceratobranchial (Mehta and Wainwright 2007b). In a separate analysis with a more limited number of specimens, I carefully removed and weighed the right AM2 of the oral jaws and the AD5 of the pharyngeal jaws for 10 moray species to determine whether dietary specialization is correlated with the mass of these muscles.

To characterize the mechanical diversity in the feeding apparatus, the mechanical advantage (MA) of jaw opening and jaw closing were measured for the oral jaws (Westneat 2003, 2004). The inlever for jaw opening was calculated as the distance from the jaw joint to the attachment midpoint of the

Table 2: Loadings of the 13 oral jaw variables on the first two principal components (PC1, PC2)

Variables	PC1 (42%)	PC2 (18.3%)
Head width	-.60	.37
Rostral length	.73	.14
Rostral width	-.69	.25
Vertical gape	.81	-.13
Horizontal gape	.63	.21
Total dentary length	.72	-.34
Dentigerous dentary length	.66	-.14
Premaxillary length	.16	-.55
Maxillary length	.83	.30
No. teeth on maxilla	.67	.24
Dentary depth	-.85	.04
Tooth length	.48	.82
Tooth width	-.10	.92

interopercular mandibular ligament on the posteriormost portion of the dentary. The inlever for jaw closing was the attachment midpoint of the adductor mandibulae muscle on the coronoid process of the dentary to the center of the quadrate-articular joint. To obtain the moment arm for both jaw opening and jaw closing, I measured the distance from the jaw joint to the tip of the anteriormost tooth on the dentary. The MA of jaw opening was calculated as the ratio of jaw-opening inlever to outlever, and the MA of jaw closing was the ratio of the jaw-closing inlever to outlever. Although it has been shown that calculating simple lever models overestimates force and underestimates velocity transmission for most fish (Westneat 2003), simple mechanical advantages are calculated here in order to make broad phylogenetic comparisons across actinopterygian groups for which jaw-opening and jaw-closing MAs have already been examined using this simple lever method.

Statistical Analyses

Two principal components analyses (PCAs) were conducted on 13 oral jaw characters and 13 pharyngeal jaw characters. All data were \log_{10} transformed with the exception of the MT and the number of teeth on the upper and lower pharyngeal tooth plates, which were square root transformed (Sokal and Rohlf 1995). Each morphological variable, with the exception of meristic characters (tooth counts), was regressed with HL, and the resulting residuals were used in all analyses. Because the data set was a combination of linear and meristic variables, the correlation matrix was used to extract principal components. In this data set, the purpose of PCA was to reduce the fairly large set of morphological variables for the oral and pharyngeal jaws to a smaller data set while maintaining the variance. In order to do this, I used the "eigenvalue greater than 1" rule (Conway and Huffcutt 2003), which, in these analyses, was the same as retaining the number of factors that accounted for the highest proportion of variance. To determine whether morphological variance differed between durophagous and piscivorous

morays, the variance of scores on each principal components axis was calculated for each species within each diet grouping, and the cumulative variance for all the axes was summed for each morphological data set. A nested ANOVA with individuals nested within species was conducted on the total morphological data set to determine whether the average value for each morphological variable was significantly different

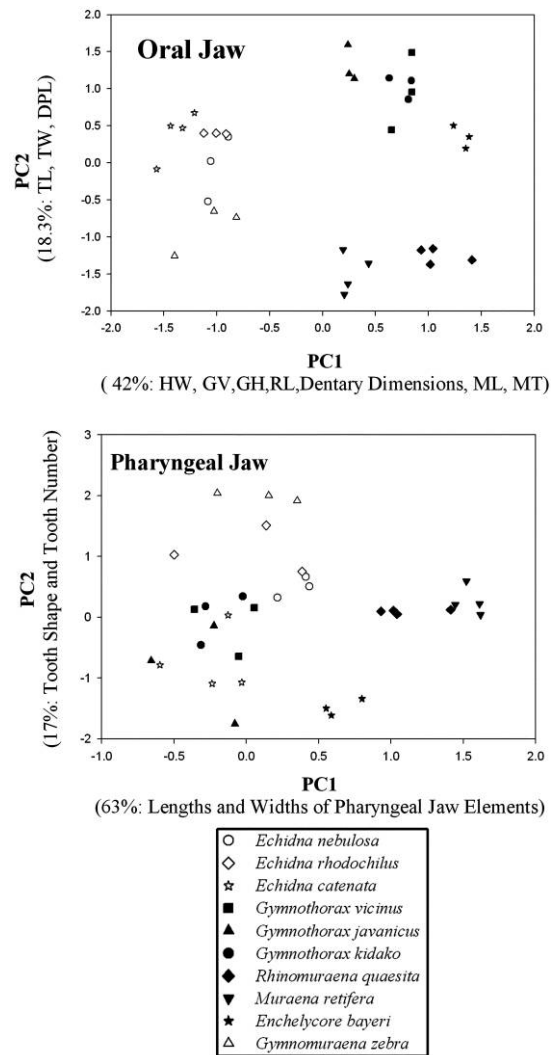


Figure 4. A, Plot of principal components 1 (PC1) versus 2 (PC2) for 13 morphological variables associated with oral jaw characters used during feeding. Species separate on PC1 primarily by vertical and horizontal gape distance, rostral length, dentary dimensions (dentary length, dentigerous dentary length, dentary depth), maxillary length, and number of maxillary teeth. Oral jaw characteristics such as tooth length and tooth width loaded highly and positively on PC2, while total dentary length and premaxillary length loaded negatively. Open symbols represent moray species that exhibit diets composed mostly of crustaceans and hard-shelled prey. Filled symbols represent mostly piscivorous morays. B, Plot of PC1 versus PC2 for 13 morphological variables associated with pharyngeal jaw characters. Moray species separated along PC1 by lengths and widths of the pharyngeal jaw elements; pharyngeal jaw tooth length, tooth width, and number of teeth on both the upper and lower jaw separated moray species along PC2.

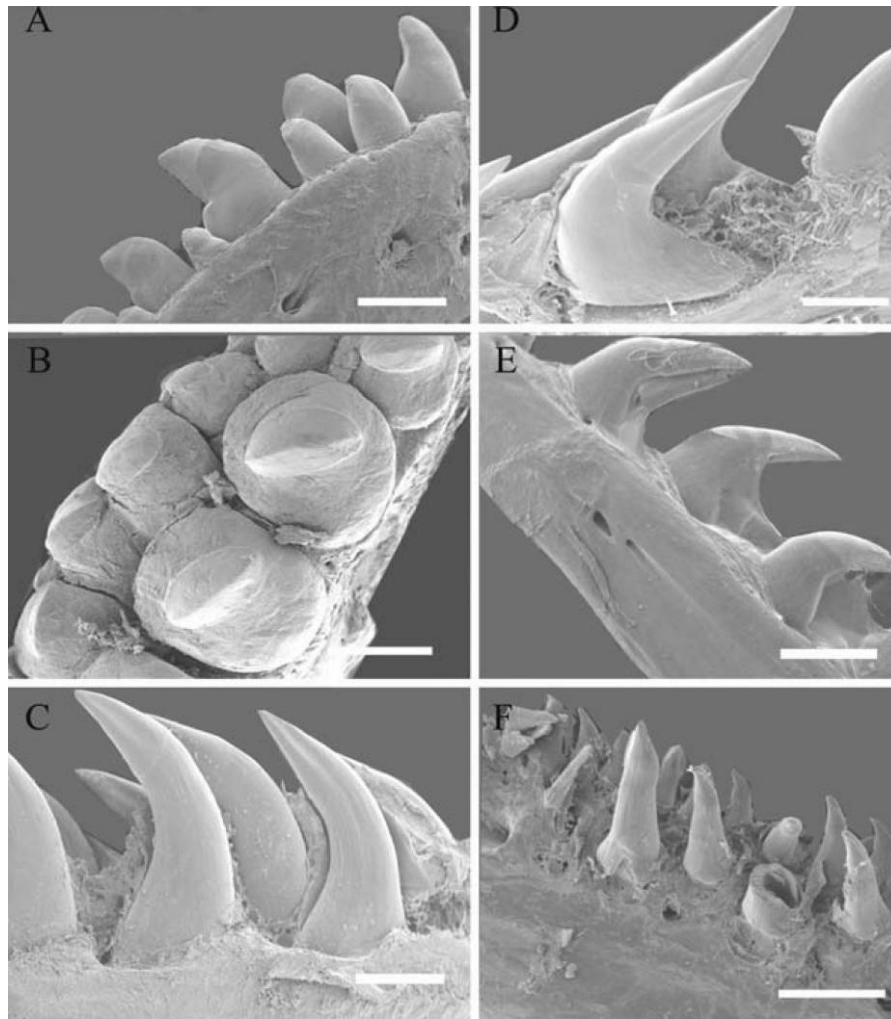


Figure 5. Scanning electron micrographs of the upper oral jaw teeth of six representative moray genera. A, *Echidna*. B, *Gymnomuraena*. C, *Gymnothorax*. D, *Enchelycore*. E, *Muraena*. F, *Rhinomuraena*. Scale bars = 1 mm.

across species and across dietary groups. A sequential Bonferroni correction was used to adjust for multiple statistical tests. An ANOVA was also used to test for differences in mechanical advantage for both jaw opening and jaw closing between dietary groups. SPSS (ver. 13.0; SPSS, Chicago) was used for all statistical analyses.

Results

Dietary Survey

On the basis of results of a literature survey, morays were separated into two distinct dietary specializations: piscivory and durophagy (Table 1). Piscivorous morays were those that fed mostly, rather than exclusively, on fish. Many of the piscivorous morays examined in this study are also known to consume cephalopods (*Gymnothorax javanicus*, *Gymnothorax kidako*, *Gymnothorax vicinus*, *Muraena retifera*). At least one of the piscivorous morays has been found to consume crabs in certain geographic locations for which their dietary habits have been

examined (*G. javanicus*; Table 1). Durophagous morays were those that mostly fed on crustaceans and other hard-shelled invertebrate prey. Some of the morays that were grouped as durophagous were also known to consume small fish (*Echidna catenata*, *Echidna nebulosa*). Although these dietary habits, piscivory and durophagy, are by no means discrete in natural populations, these dietary groupings provide insight into the relative functional demands placed on the feeding apparatus for each species.

Morphological Analyses

A PCA resulted in four axes explaining 87% of the morphological variation in the oral jaws, with PC1 and PC2 explaining 60.3% of the variation among the 13 morphological variables (Table 2). A plot of the scores on the first two PCs revealed complete separation of durophagous and piscivorous species in morphospace (Fig. 4A). PC1 accounted for 42% of the variation in the oral jaws. Moray species separated along PC1 by

Table 3: Loadings of the 13 pharyngeal jaw variables on the first two principal components (PC1, PC2)

Variables	PC1 (63%)	PC2 (17%)
Pharyngobranchial length	.95	-.03
Pharyngobranchial width	.31	.48
Epibranchial length	.99	.04
Epibranchial width	.67	.13
Ceratobranchial length	.87	.21
Ceratobranchial width	.70	.34
Lower tooth plate length	.89	-.14
Lower tooth plate width	.72	-.05
Pharyngobranchial lever arm	.91	-.10
No. teeth on upper tooth plate	-.05	.79
No. teeth on lower tooth plate	-.15	.59
Tooth length	.21	-.82
Tooth width	-.10	-.82

HW, gape dimensions, rostral dimensions, dentary characters, maxillary length, and MT. PC1 was most highly and positively correlated with TDL, DDL, RL, maxillary length, MT, and gape dimensions and was most negatively correlated with DD, RW, and HW (Fig. 4A). PC2 accounted for 18.3% of the variation among morphological variables. Oral jaw characteristics, such as tooth length and tooth width, loaded highly and positively on PC2, while TDL and premaxillary length loaded negatively. Piscivores exhibited longer and sharper cranial features in comparison with morays that consume mostly crustaceans and other hard-shelled prey. The oral jaw dentition of *Gymnomuraena zebra*, a moray that specializes on hard-prey types, and *Rhinomuraena quaesita*, a piscivore that specializes on smaller fish, were markedly different from all other moray species. SEM of the teeth of a small *G. zebra* specimen revealed pebblelike dentition that was extremely worn on the dorsal surface, while the teeth of *R. quaesita* were short, relatively straight, and thin (Fig. 5B, 5F). The total variance calculated from PC scores was twice as great for piscivores (0.043) compared with durophagous eels (0.024), revealing that the oral jaws of piscivores exhibit greater diversity.

A PCA resulted in two axes explaining 80% of variation among the 13 morphological variables used to characterize the pharyngeal jaws (Table 3). PC1 accounted for 63% of the variation in the pharyngeal jaws, and the majority of the variables loaded positively along PC1. Moray species separated along PC1 by lengths and widths of the pharyngeal jaw elements. PC2 accounted for 17% of the variation among morphological variables. Pharyngeal jaw tooth length, tooth width, and number of teeth on both the upper and lower jaw separated moray species along PC2 (Fig. 4B). The number of teeth on both the upper and lower jaws loaded highly and positively on PC2, while tooth width and tooth length loaded strongly but negatively. Hard prey specialists had more teeth on the pharyngobranchials, and these teeth were longer and wider compared with those of piscivores (Fig. 6). The variance in PC scores for

the pharyngeal jaws was similar in piscivores (0.0032) and durophagous morays (0.0028).

An ANOVA revealed significant differences in mean oral jaw and pharyngeal jaw characters across moray species (oral jaw: $F_{9,20} = 6.13$, $P < 0.001$; pharyngeal jaw apparatus: $F_{9,20} = 5.62$, $P < 0.001$) and between dietary specializations (oral jaw: $F_{1,25} = 4.23$, $P < 0.001$; pharyngeal jaw apparatus: $F_{1,25} = 5.14$, $P < 0.001$). Post hoc tests revealed that *Enchelycore bayeri* and *R. quaesita* exhibited the greatest differences in oral jaw characteristics when compared with other piscivorous morays. These two species were distinctly different from all other piscivores in that they exhibited the longest jaws and maxilla, extremely narrow heads, and very narrow teeth.

When species were grouped by diet, there were significant differences between all morphological elements of the oral jaws between piscivores and durophagous morays, while only three morphological characters of the pharyngeal jaws differed across the dietary groups. These characters were number of teeth on the upper pharyngeal tooth plate, tooth length, and tooth width. Crustacean specialists exhibited short maxillae, a tall dentary, and short teeth for processing prey in the oral jaws.

Adductor Muscles

As noted earlier, the left and right sides of the adductor are connected at the dorsal midline of the skull in muraenids. This connection increases AM2 attachment area, enabling hypertrophy of the AM2, which presumably results in increased stability of the neurocranium during biting (Fig. 7A). In the durophagous moray *G. zebra*, the supraoccipital extends several millimeters past the neurocranium and allows for an even larger attachment surface for the AM2 (Fig. 7B). Morays exhibited a strong positive relationship between HL and AM2 mass ($r^2 = 0.62$). An ANOVA revealed significant differences in AM2 mass between the two dietary groups ($P < 0.01$), with piscivores exhibiting smaller AM2 muscles compared with durophagous morays. Interspecific differences in AD5 mass of the pharyngeal jaws were not detected ($P = 0.14$). There appeared to be a slight trend favoring larger AD5 masses in piscivores, although an ANOVA did not detect any significant differences ($P = 0.063$).

Jaw Mechanics

The 10 moray species examined in this study exhibited a wide range of jaw mechanics. Mechanical advantage of jaw opening ranged from 0.04 to 0.21, while jaw-closing ratios ranged from 0.12 to 0.38. Jaw-closing transmission properties indicate that at least 12% of adductor muscle force is transmitted to the anterior tip of the dentary in *E. bayeri*, whereas 38% of the adductor force is transmitted to the dentary tip in *G. zebra*. When morays were grouped by dietary specialization, there was a highly significant difference between jaw-opening ($F_{1,9} = 9.39$, $P = 0.013$) and jaw-closing ($F_{1,9} = 26.8$, $P = 0.001$) ratios for the two groups. Morays that consumed mostly hard-shelled prey exhibited slower jaw-opening mechanics and a force-modified, jaw-closing lever system that translated into high

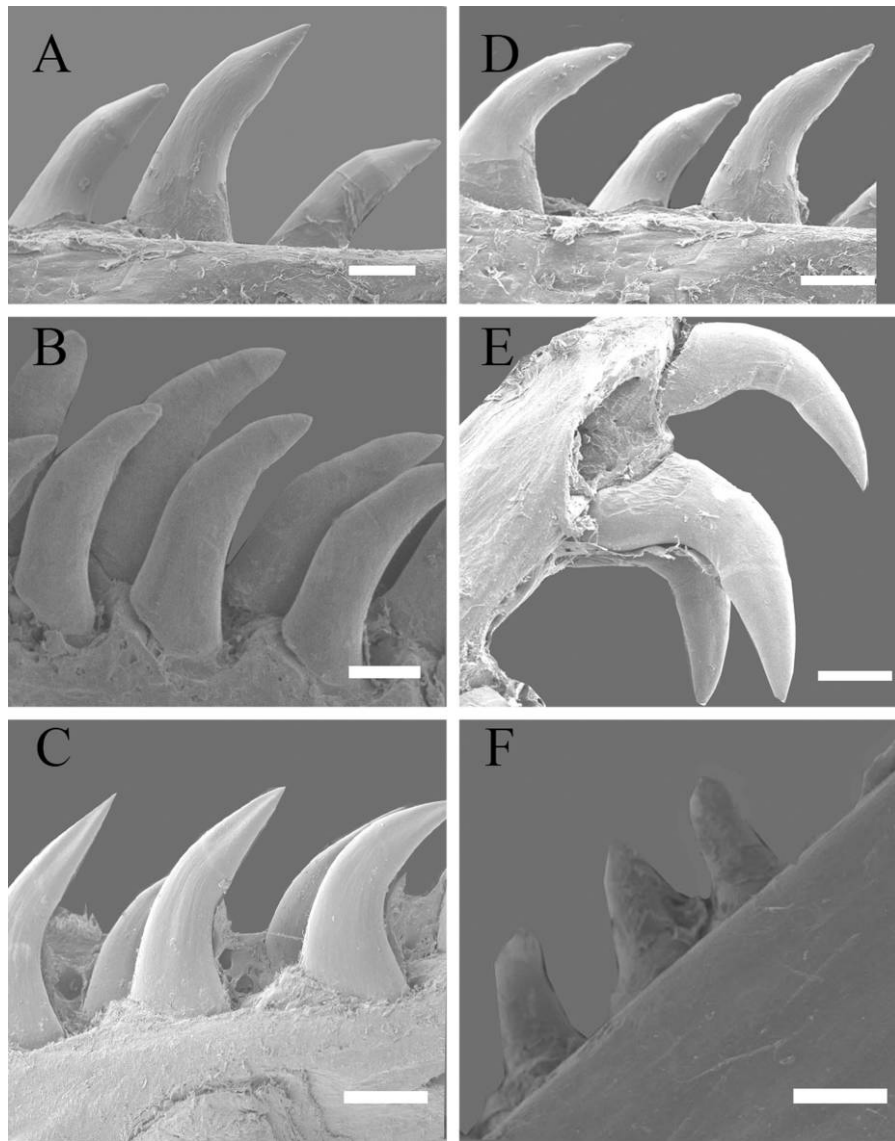


Figure 6. Scanning electron micrographs of the pharyngeal teeth of six representative moray genera. A, *Echidna*. B, *Gymnomuraena*. C, *Gymnothorax*. D, *Enchelycore*. E, *Muraena*. F, *Rhinomuraena*. Scale bars = 1 mm.

mechanical advantage for both behaviors. On the other hand, piscivorous morays exhibited jaws modified for velocity transmission as observed by the low mechanical advantage calculated for jaw opening and jaw closing. The variance in jaw-closing mechanics was greater in piscivorous species compared with crustacean eaters (0.0027 vs. 0.0012). When the residuals for HL and AM2 were regressed against jaw-opening and jaw-closing ratios, morays with higher mechanical advantage for both behaviors (durophagous morays) had larger adductors (Fig. 8). *Rhinomuraena quaesita* exhibited the smallest adductor muscles for a given HL, while the mechanical advantage of jaw opening and jaw closing for this species grouped together well with other piscivores.

Discussion

The goal of this study was to investigate the relationship between dietary breadth and morphological variation between the oral and pharyngeal jaws of moray eels, a highly specialized group of biters. To accomplish this, I used an established set of characteristics for the oral jaws and pharyngeal jaws from previous ecomorphology and functional morphology studies (Motta et al. 1995; Wainwright and Richard 1995; Clifton and Motta 1998; Grubich 2003; Grubich and Westneat 2006). In addition to these characters, I used characters such as RW, RL, and tooth characteristics that were potentially informative for understanding interspecific differences in the feeding habits of

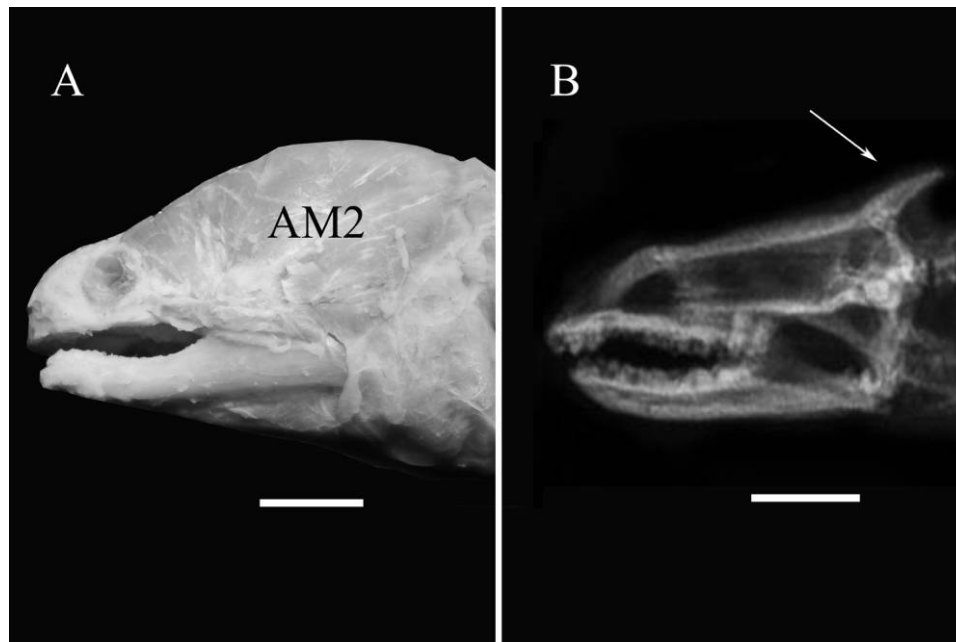


Figure 7. A, Photograph of a skinned *Gymnomuraena zebra*, a durophagous moray, in lateral view, showing an enlarged adductor mandibulae (AM2). B, Radiograph of *G. zebra* revealing an extended supraoccipital, which provides a greater surface area for attachment of the AM2. Scale bars = 1 cm.

morays. The 26 morphological characters measured in the oral and pharyngeal jaws were very good predictors of dietary specialization for the morays examined in this study. This study shows that although dietary specialization may not be a clear dichotomy in nature, the functional demands of piscivory and durophagy strongly shape the feeding apparatus of morays, resulting in two discrete clusters of cranial form and diet in morphospace.

The first PC analysis using morphological characters of the oral jaws clearly separated individuals into distinct species clusters. In addition to species separation, the durophagous and piscivorous morays examined in this data set occupied different areas of morphospace. The lack of overlap in morphospace revealed that the morphological properties of the moray oral jaws reflect different functional demands associated with diet (Fig. 4A). Piscivorous morays exhibited greater variance in oral jaw PC scores than durophagous morays. In this data set, the overall variance for piscivores was twice as great as the variance for those that consumed crustaceans and other hard-shelled prey, suggesting that the functional demands of durophagy may limit morphological variation of the oral jaws relative to piscivory, although a larger data set is necessary to test this hypothesis.

Despite extreme functional specialization of the moray pharyngeal jaw system, characteristics such as tooth length and tooth width revealed axes of divergence across morays. Durophagous morays had more teeth on their pharyngobranchials, and these teeth were longer, less recurved, and wider compared with piscivores (Fig. 6). This difference in pharyngeal jaw tooth morphology between durophagous and piscivorous morays

may be associated with the prey processing that takes place in the oral jaws of durophagous morays. Because durophagous morays must crack the shells of their prey before consuming them, prey are in smaller fragments in the oral jaws before intraoral transport. Therefore, more teeth that are less recurved on the pharyngobranchials may aid in effectively grabbing prey fragments. On the other hand, piscivores mainly consume their prey whole, and sharp recurved teeth in the oral jaws and on

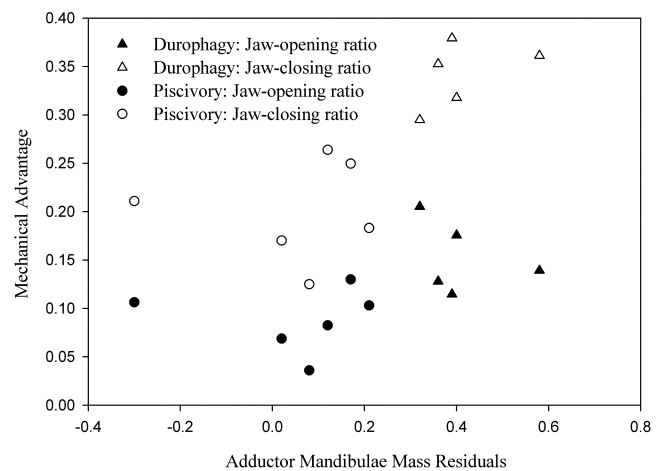


Figure 8. Scatterplot of the relationship between the residuals of adductor mandibulae mass and jaw mechanics for 10 moray species. Triangles represent durophagous morays, and circles represent piscivorous morays. Note that the durophagous morays have high jaw-closing ratios and occupy a different area of the scatterplot.

the pharyngeal tooth plates enable piscivores to maintain a grip on struggling prey at all times (Mehta and Wainwright 2007b). In both morphological data sets, *Enchelycore bayeri*, *Muraena retifera*, and *Rhinomuraena quaesita* were distinctly different from all other piscivorous morays in morphospace (Fig. 4A, 4B). *Enchelycore* and *Rhinomuraena* exhibited extremely long oral jaws, while *Muraena* and *Rhinomuraena* exhibited relatively short teeth. *Enchelycore bayeri*, *M. retifera*, and *R. quaesita* also exhibited rather long pharyngeal elements relative to all other morays. These differences reveal that morays can vary greatly in morphology even within dietary specializations.

Durophagy has strong effects on the musculoskeletal system in fish, and these effects can be observed in either the oral jaws (Turingan 1994; Hernandez and Motta 1997; Cutwa and Turingan 2000) or the pharyngeal jaws (Liem and Kaufman 1984; Liem and Sanderson 1986; Wainwright 1987, 1988; Grubich 2003). In morays, the oral jaws were strongly reflective of durophagous habits. Although morays in general seem to have very well-developed adductor mandibulae muscles, AM2 muscle masses were larger in durophagous morays than in piscivorous species. Durophagous morays exhibited additional features of the neurocranium, such as an extended supraoccipital process on the skull and a high coronoid process on the dentary, that increased AM2 attachment area, thereby enabling additional hypertrophy of the adductors.

I hypothesized that piscivorous morays might exhibit greater adductor masses in their pharyngeal jaws to transport large fish prey. An ANOVA did not detect any differences in AD5 mass between piscivorous and durophagous morays. The reason for this lack of difference in pharyngeal adductor mass between piscivorous and durophagous morays may have been due to the small specimens examined in this study (200–723 mm). Smaller morays are presumably consuming smaller prey. Differences in AD5 mass may be more obvious in larger specimens, which can presumably consume larger prey. Future studies aimed at determining whether muscular components of the pharyngeal jaws reflect functional differences between species will provide useful insight into the relationship between dietary specialization and morphological diversity in the pharyngeal jaw apparatus of morays.

Morphological Diversity Underlying Biting Behavior

The morphological variation underlying the mechanical advantage of jaw opening and closing was also reflective of dietary specialization. Despite the fact that some piscivorous morays consume crabs and some durophagous morays may consume small fish, there is absolutely no overlap in MA for jaw closing and very little overlap in MA for jaw opening (Fig. 8). Piscivore jaw mechanics revealed relatively fast mouth opening and faster mouth closing systems, while durophagous morays exhibited slower jaws with increased force-transmitting capacities. The greater mechanical variation found in the piscivore jaw system implies that ram biting does not constrain biomechanical variation in the jaws of morays.

A recent comparative study of the evolution of biomechan-

ical feeding systems in actinopterygian fish revealed that there is a large degree of mechanical diversity and convergence across disparate fish groups (Westneat 2004), and this mechanical variation mirrors the biomechanical diversity of the jaws for the select fish groups that have been examined (Wainwright and Richard 1995; Westneat 1995; Wainwright et al. 2004). In terms of biomechanical diversity, this study reveals that a skull modified for biting and with little kinesis can still be functionally diverse. The MA of jaw opening ranged from 0.036 to 0.21, while the MA of jaw closing ranged from 0.12 to 0.37. The MAs for both jaw opening and closing exhibit range values that span the actinopterygian tree and are shared with taxa with cranial morphologies as diverse as gar (Lepisosteidae) and large percomorph fish such as barracuda (Sphyraenidae) and groupers (Serranidae). Other monophyletic clades of biters, such as scarid wrasses, reveal greater mechanical diversity in jaw-closing ratios when compared with their suction-feeding relatives (Wainwright et al. 2004). These examples suggest that biting need not constrain the morphological and mechanical variation underlying the feeding apparatus of fish.

Body Size Considerations and Prey Size

Body size has been shown to play a large role in determining diet in fish (Wainwright and Richard 1995). HL was used as a measure for body size in this study. Each morphological variable was regressed with HL, and the resulting residuals were used in all analyses. Rather than SL, HL was used to remove some aspects of size effects because there was a very weak correlation between SL and HL for morays (Fig. 2A). For example, some moray species, such as the ribbon eel *R. quaesita*, were extremely long for a given HL. Although SL may not reliably predict all cranial features in morays, SL must play an important role in moray feeding habits because the longer the moray, the greater the energetic requirements.

Two major points that were not addressed in this study are changes in body size, including ontogenetic shifts in diet, and the effects phylogeny may have on the relationship between diet and morphology in morays. Ontogenetic shifts in diet are prevalent in many fish groups, and these shifts are ecologically important for many reasons, not least of all because they affect the changing relationship between predators and their prey (Werner 1974, 1977; Grossman 1986; Wainwright 1991). How ontogenetic changes in the diet of morays reveal shifts in prey type or prey size within a particular prey category is unknown. We also know very little about how morphological features of the feeding apparatus scale throughout ontogeny in morays. The allometry of oral and pharyngeal features will presumably have an effect on moray diet, particularly throughout the elver stage.

What determines prey size in morays? As in most fish, prey size can be predicted by mouth gape. In the size-corrected PC analysis, piscivorous morays exhibited a larger oral gape than durophagous morays. Thus, on the basis of morphological features alone, this data set suggests that piscivorous morays can consume much larger prey than durophagous morays.

Novel behavior patterns are often associated with dietary specialization in many vertebrate groups (Liem 1973; Greene and Burghardt 1978; Hoso et al. 2007). At least four genera of moray eels (*Echidna*, *Enchelycore*, *Gymnothorax*, and *Muraena*) have been shown to use novel behavior patterns, such as rotational feeding and knotting, to immobilize and remove smaller pieces from large prey (Miller 1987, 1989). This suggests that although gape size may be a predictor of prey size for many moray species, the size of prey a moray can consume may not ultimately be limited by gape. Future behavioral studies in addition to studies on the predator-prey relationships of morays will be useful for understanding the relationship between gape limitation and trophic ecology in elongate predators.

This study used morphological features to identify the primary axis of variation for a small sample of moray species. However, the phylogenetic relationships of species in this ecomorphological study are not well known, and the congruence between diet and morphology may be confounded by phylogeny. This is especially problematic for durophagous morays because only four species representing two genera were examined.

Although this study revealed that *Gymnomuraena zebra* shares many morphological characteristics with species of *Echidna*, this similarity may be due to shared ancestry in addition to convergence in feeding habits. Previous studies have noted morphological and behavioral differences in *G. zebra* compared with species of *Echidna* (Böhlke et al. 1989; Miller 1989). Whether durophagy evolved in muraenids once or multiple times is currently unknown. Despite these phylogenetic questions, these data reveal that morays exhibit species-specific characteristics of the feeding apparatus and that the dual-jaw feeding apparatus is shaped by dietary specialization. Furthermore, although dietary demands may strongly shape the morphology of the moray eel feeding apparatus, variation within dietary breadth is present. Future phylogenetic studies of morays will greatly contribute to understanding the ecomorphology and morphological diversity underlying this diverse and functionally specialized group of biters.

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Appendix

Museum Accession Numbers

CAS: California Academy of Sciences, San Francisco.

CAS-SU: Stanford University, housed at the CAS.

Echidna leucotaenia. CAS 90431, CAS 99269.

Gymnomuraena zebra. CAS 37273, CAS 37275, CAS-SU 8954.

Enchelycore bayeri. CAS 37237, CAS 37236.

Echidna catenata. CAS 201793, CAS 59206.

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