Biting releases constraints on moray eel feeding kinematics

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Summary

We present an analysis of prey capture functional morphology in eels by comparing two species of moray eels, *Muraena retifera* and *Echidna nebulosa* (Family Muraenidae), to the American eel *Anguilla rostrata* (Family Anguillidae). The skulls of both moray species exhibited extreme reductions of several prominent components of the suction-feeding mechanism, including the hyoid bar, the sternohyoideus muscle and the pectoral girdle. Associated with these anatomical modifications, morays showed no evidence of using suction during prey capture. From 59 video sequences of morays feeding on pieces of cut squid we saw no hyoid depression and no movement of prey toward the mouth aperture during the strike, a widely used indicator of suction-induced water flow. This was in contrast to *A. rostrata*, which exhibited a robust hyoid, sternohyoideus muscle and pectoral girdle, and used suction to draw prey into its mouth. Average prey capture time in morays, about 500 ms, was roughly 10 times longer than in *A. rostrata*, and morays frequently reversed the direction of jaw and head rotation in the midst of the strike. We tested whether the absence of suction feeding reduces temporal constraints on feeding kinematics, permitting greater variance in traits that characterize timing and the extent of motion in the neurocranium, by comparing moray eel species with *A. rostrata*, two Centrarchids and a cichlid. Kinematic variance was roughly 5 times higher in morays than the suction-feeding species. Prey capture by suction demands a rapid, highly coordinated series of cranial movements and the loss of this mechanism appears to have permitted slower, more variable prey capture kinematics in morays. The alternative prey capture strategy in morays, biting, may be tied to their success as predators in the confined spaces of reef crevices where they hunt for cephalopods, crustaceans and fish.

Key words: moray eel, feeding, anatomical reduction, kinematic integration, *Muraena retifera*, *Echidna nebulosa*, *Amphilophus citrinellus*, *Lepomis macrochirus*, *Micropterus salmoides*.

Introduction

Suction feeding is the most commonly used mechanism of prey capture among bony fishes (Ferry-Graham and Lauder, 2001; Lauder, 1985; Liem, 1980; Van Leeuwen, 1984), a fact that has been partly attributed to the demands of feeding in a medium much more viscous and dense than air (Lauder, 1985). However, several fish groups have developed around alternative feeding strategies, including parrotfishes (Scaridae), surgeonfishes (Acanthuridae), gar (Lepisosteidae) and, as we argue in this paper, moray eels (Muraenidae). In each of these groups prey are captured by direct biting, although subsequent transport behaviors may involve hydraulic, suction-based mechanisms (e.g. Lauder, 1983), and comparative research with these groups has provided some insights into how suction feeding shapes and constrains patterns of muscle activity and movement (Alfaro et al., 2001; Lauder, 1980a; Lauder, 1980b; Lauder and Norton, 1980; Porter and Motta, 2004). Because capturing prey by biting and suction rely on different mechanical events (e.g. cranial adduction *vs* abduction, forceful contact of the teeth with the prey *vs* the generation of fluid flow), there may be general differences in the functional patterns that are associated with these behaviors. Biting and suction may be associated with different morphological specializations of the skull that reflect different mechanical demands (De Visser and Barel, 1998; Wainwright and Bellwood, 2002), and this may have implications for kinematics and motor patterns (Alfaro et al., 2001; Rice and Westneat, 2005). In a phylogenetically broad comparative analysis (Alfaro et al., 2001), several features of the muscle activity pattern differed consistently between biting and suction prey capture, including a briefer latency between the activation of expansion and compression phase muscles during suction feeding.

Suction-feeding behavior may also generally be quicker than prey capture by biting. Fishes that rely on high-velocity lunges followed by biting, rather than suction, exhibit longer strike times (Porter and Motta, 2004), and the kinematics of benthic biters appears to typically be slower than suction feeding

(Alfaro et al., 2001; Rice and Westneat, 2005; Konow and Bellwood, 2005).

Successful suction feeding is thought to depend on the ability to generate high water flow velocities, by rapidly expanding the mouth and buccal cavity (Van Leeuwen and Muller, 1984; Wainwright et al., 2001; Van Wassenbergh et al., 2006). A set of inter-related linkage systems (Anker, 1974; Muller, 1989; Westneat, 1994) creates a posterior wave of oral expansion that results in both water and prey being drawn into the buccal cavity. The rate of buccal expansion is directly related to peak fluid speed magnitude (Day et al., 2005), suggesting that the speed of cranial movements of suction feeders during the earliest stages of prey capture can influence their success. Mouth opening speed or peak gape may not affect predatory success in biters as prey capture occurs during jaw adduction after peak gape, rather than during buccal expansion, as in suction feeders. These differences in the timing of coordinated cranial movements during prey capture suggest that the kinematics of successful suction feeding may be constrained, in comparison to biting, such that suction feeders exhibit relatively low variance and tight integration in movement patterns during the period of the strike leading up to prey capture. However, this possibility has not yet been explored in comparative studies of aquatic feeding vertebrates.

Anguilliform eels of the family Muraenidae are a substantial radiation of about 185 species of predatory fishes that mostly live in coral reefs of warm and temperate marine waters (Nelson, 2006; Böhlke et al., 1989). Like all anguilliforms, morays lack pelvic fins, but in addition all muraenids lack a pectoral fin and show a highly reduced pectoral girdle (Böhlke et al., 1989; Fielitz, 2002; Gregory, 1933). In this paper we explore this and other exceptional anatomical features of the moray skull and ask what consequences they have for feeding function. We test for the presence of suction feeding in two moray species by measuring the extent to which prey are transported toward the mouth of striking eels. Skull kinematics and suction ability in the two morays are compared to *Anguilla rostrata*, an anguillid eel that possesses a well-developed pectoral fin and pectoral girdle. We conclude that morays do not use suction during prey capture and we go on to examine the effects that the alternative prey capture strategy, biting, has on moray feeding kinematics. In particular, we test the hypothesis that the absence of suction feeding in morays has reduced constraints on kinematic integration, permitting them to show greater variance in traits that characterize the timing and extent of motion of the skull and jaws. To test the above hypothesis, we compare the feeding kinematics of the two moray eel species to a phylogenetically wide sample of suction feeders, including *Anguilla rostrata*, two centrarchid species well known for being strong suction feeders, and a Central American cichlid.

Materials and methods

We studied the feeding morphology and kinematics of two tropical moray eels, *Muraena retifera* (Goode and Bean) and *Echidna nebulosa* (Ahl). *M. retifera* feeds on fish, cephalopods and shrimp while *E. nebulosa* feeds primarily on crabs and other hard-shelled prey (Randall, 1985; Yukihira et al., 1994). Prey capture morphology and kinematics of the morays were initially compared to those of the anguillid eel *Anguilla rostrata* (Lesueur). *A. rostrata* feeds on a diversity of larval insects as well as gastropods, oligochaetes, amphipods and fish (Page and Burr, 1991). In order to test for the effect of suction feeding on the variability of skull movement during prey capture the two moray eel species were compared to *Anguilla rostrata* and three perciform species: the North American centrarchids, *Lepomis macrochirus* (Rafinesque) and *Micropterus salmoides* (Lacépède), and the Central American cichlid, *Amphilophus citrinellus* (Günther). Both *L. macrochirus* and *M. salmoides* have been the focus of many studies related to suction feeding, and these species are known to differ in their ability to produce suction (Carroll et al., 2004; Higham et al., 2005; Higham et al., 2006a; Higham et al., 2006b; Wainwright and Shaw, 1999). Like the two centrarchids, *Amphilophus citrinellus* is known to use a combination of ram and suction during prey capture (Higham et al., 2006b). We used Centrarchids and Cichlids, percomorph fish that are strong suction feeders and are phylogenetically distant from the anguilliforms, because they provided a robust test of the prediction that there would be differences between biting and suction-feeding taxa in the variability of feeding kinematics.

The *M. retifera* (standard lengths SL = 35.5 and 40.3 cm) were collected in the Florida Keys, *E. nebulosa* (SL = 17.3, 19.5, 28.5 and 35.5 cm) were collected in Hawaii and obtained commercially, *A. rostrata* (SL = 58.2 and 63.6 cm) were collected in Woods Hole, MA, USA, *L. macrochirus* (SL = 15, 15 and 16 cm) and *M. salmoides* (SL = 16.6, 17.3 and 18.4 cm) were collected locally in Yolo County, CA, USA, and the *A. citrinellus* (SL = 8.6, 9.6 and 11.5 cm) were obtained commercially from a pet dealer. At the conclusion of the experiments, all of the specimens were dissected, either while fresh or following formalin fixation, and at least one specimen of each species was cleared and stained for bone and cartilage following a modification of Dingerkus and Uhler (Dingerkus and Uhler, 1977).

Individuals were housed and filmed at 22–27°C in 100 l aquaria at the University of California, Davis using a NAC Memrecam ci digital system (Tokyo, Japan) with illumination from two 600 W flood lights. Video sequences of *A. rostrata*, *L. macrochirus*, *M. salmoides* and *A. citrinellus* were recorded at 500 images s^{-1}, and sequences of the moray eels were recorded at 100 images s^{-1}. Distances in the images were scaled by recording an image of a ruler placed in the field of view. All fish were filmed feeding on pieces of cut squid (*Loligo* sp.).

To quantify feeding kinematics, we analyzed images from the video sequences with the aid of Scion Image software. Due to the diverse cranial morphology of the species in this study, we analyzed only kinematic variables that could be considered homologous across the six taxa. We measured the *x*, *y*

coordinates of six landmarks from the images: (i) the anterior tip of the premaxilla (upper jaw), (ii) quadrate-articular jaw joint, (iii) anterior tip of dentary (lower jaw), (iv) neurocranium-vertebral joint (v) anteriormost margin of the orbit (reference point on the neurocranium), (vi) ventral-most point of the orbit, (vii) ventral-most extension of the floor of the mouth (perpendicular distance between a line at the ventral-most point of the orbit), and (viii) center of mass of the prey. Coordinates of these landmarks were measured at five points in time: (i) onset of the strike characterized by the onset of fast lower jaw rotation, (ii) time of peak jaw abduction, (iii) time of peak cranial elevation, time of peak gape, (iv) peak hyoid displacement, and (v) time of prey capture, defined as the frame in which the prey completely entered the predator's mouth or, in eels, the frame in which the upper and lower jaws made contact with the prey.

As an indication of the use of suction in prey capture we measured 'suction distance', the distance the prey moved toward the plane of the open mouth during the strike. Suction distance has been used extensively as a functional measure of the contribution of suction-induced flow to the movement of prey into the oral cavity (Norton and Brainerd, 1993; Svanbäck et al., 2002; Wainwright et al., 2001). While the absence of suction distance does not necessarily imply the inability to generate suction pressures inside the buccal cavity, greater suction distances do imply stronger suction pressures for an individual fish (Van Wassenbergh et al., 2006; Wainwright et al., 2001). Thus, from each prey capture sequence, we determined the rotational excursions of the lower jaw and the neurocranium, peak hyoid depression and gape distance, and the time from the onset of jaw depression to peak jaw rotation, peak cranial rotation, peak hyoid depression and prey capture. In addition, we counted the number of times the direction of head and jaw excursion was temporarily reversed in the time between the onset of jaw depression and the time of peak jaw and head rotation, respectively. We analyzed only those sequences in which a lateral view of the fish could clearly be seen in the image and the head of the fish was oriented approximately perpendicular to the camera. A total of 169 prey capture sequences were analyzed in this study, with sample sizes ranging between 9–10 for each individual.

We used a nested analysis of variance (ANOVA), with individuals nested within species to compare the average value for each kinematic variable between moray eels and *A. rostrata*. Kinematic data were $\log_{10}$ transformed before analyses to help normalize variances. We used a sequential Bonferroni correction to adjust the probability values for the use of multiple statistical tests. Prior to running the nested ANOVAs, data were inspected for normality and Levene's tests were performed to assess equality of variances. Although ANOVA is generally robust to some departures from the assumption of equal variances, we also performed Kruskal–Wallis non-parametric comparisons on average kinematic variables.

To identify independent axes of kinematic variation between moray eels and *A. rostrata*, we conducted a principal component analysis (PCA) on the correlation matrix of a reduced set of variables from the entire data set. In this analysis we included jaw rotation, head rotation, the number of reversals of jaw rotation and head rotation, time to peak jaw rotation, time to peak head rotation, time to peak gape, and time to prey capture. Predator size has been shown to have strong effects on feeding kinematics and is therefore a potentially confounding factor. For suction-feeding fish, scaling effects are most acute for duration variables such as time to peak gape and peak hyoid displacement (Richard and Wainwright, 1995; Van Wassenbergh et al., 2005). We tested for body size effects in the data set by regressing principal component scores against the logarithm of fish body mass (M_b).

In order to test for differences among all six species in the variability of prey capture kinematics, we ran a nested ANOVA on kinematic variance calculated for each individual fish. Kinematic variance was calculated for each fish by summing the variances for scores on each of the first four principal component axes (these PCs had eigenvalues greater than 1.0) of a PCA that was conducted on the kinematic data set for all six species. A nested ANOVA was then run on kinematic variance with species nested within group, where the two groups were moray eels (non-suction feeders) and the suction feeders. A significant test of the group effect in this ANOVA would indicate that the variance of prey capture kinematics differs between the morays and the four suction-feeding teleosts. We used SYSTAT version 9 (SPSS Inc., Chicago, IL, USA) for all statistical analyses.

Results

The cranial anatomy of moray eels shows a number of modifications relative to the generalized teleost condition that appear to be strongly related to prey capture behavior. In both moray species, the premaxillae are fused to the ethmoid and vomer and are immobile (Fig. 1A,C). The maxillae attach to the neurocranium just posterior to the premaxillae with a joint that permits some ventral rotation of the distal part of this bone. The premaxillae, maxillae and vomer bear large recurved teeth that are arranged in many rows in *M. retifera* and a combination of smaller conical teeth arranged in either a single or many rows in *E. nebulosa*. The parasphenoid is elongate and forms the floor of the orbit. The suspensorium in both morays is reduced anteriorly and is dominated by a large hyomandibula that can flex laterally at its joint with the neurocranium. The opercular series is reduced but present. The opercles are small and rounded. Muraenidae is the only anguilliform family in which all members lack pectoral fins (Fielitz, 2002; Nelson, 2006). In accordance with Fielitz (Fielitz, 2002), we found the pectoral girdle to be greatly reduced with only one pectoral bony element present in both *E. nebulosa* and *M. retifera*. Ventral elements of the hyoid arch and the three gill-bearing branchial arches are greatly reduced in size. The hyoid is long, thin (0.11–0.4 mm in their thickest dimension in our specimens), and flexible (Fig. 1B,D). The sternohyoideus, which attaches anteriorly to the hyoid arch, is represented by

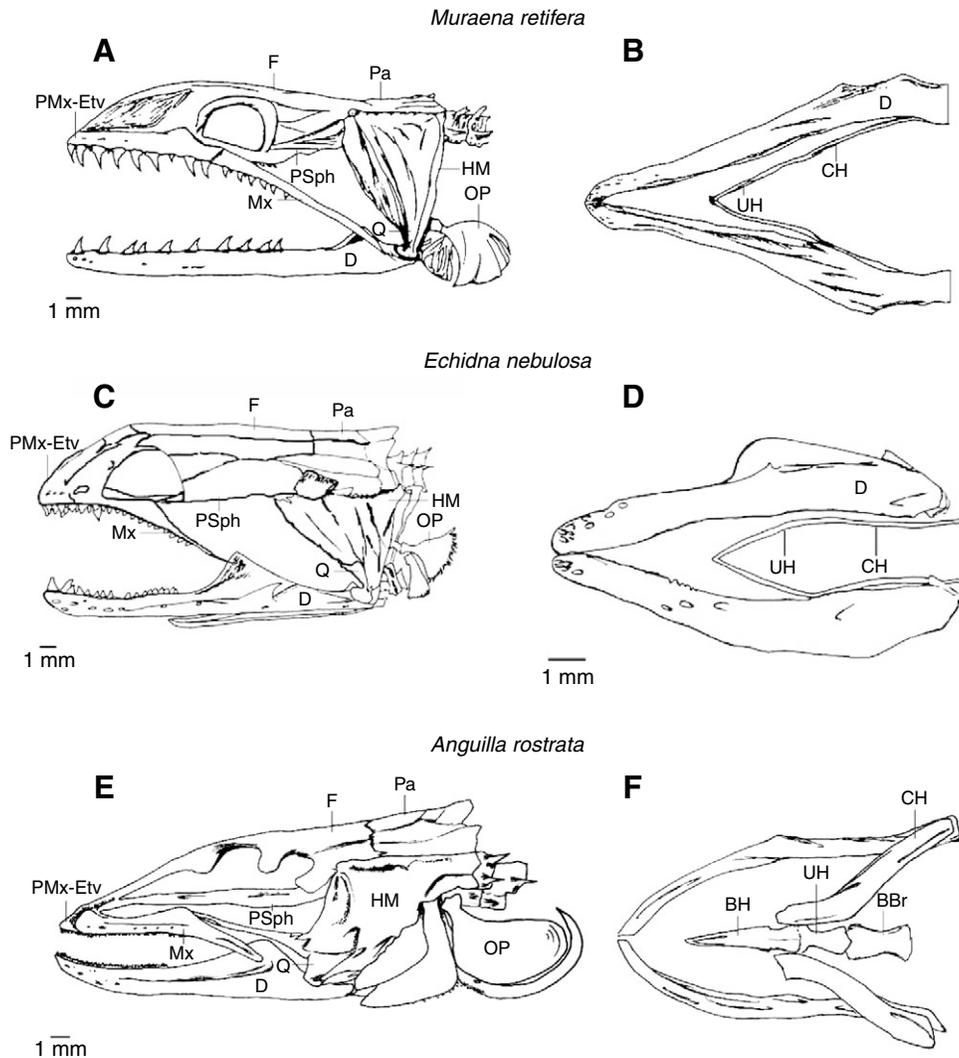**Muraena retifera**

Echidna nebulosa

Fig. 1. Lateral and ventral illustrations of the skull for *Muraena retifera* (A,B), *Echidna nebulosa* (C,D) and *Anguilla rostrata* (E,F). Note the well-developed hyoid bar in *Anguilla*, as compared to the thin hyoid in *Muraena* and *Echidna*. Abbreviations of skeletal elements follow Gregory (Gregory, 1933). Lateral view (A,C,E): D, dentary; F, frontal; HM, hyomandibular; Mx, maxilla; OP, opercle; Par, parietal; PMx-Etv, premaxillo-ethmovomerine complex; PSph, parasphenoid; Q, quadrate. Ventral view (B,D,F): BBr, basibranchial; BH, basihyal; CH, ceratohyal; D, dentary; U, urohyal.

Anguilla rostrata

ventrolateral extensions of the hypaxial musculature. The sternohyoideus muscle is small compared to other teleosts and the fibers appear continuous with the hypaxialis.

In *Anguilla rostrata*, the premaxillae of the upper jaw is fused with the ethmovomer complex and is immobile (Fig. 1E). The maxillae attach to the neurocranium just posterior to the premaxillae *via* the premaxillae-ethmovomer complex and is slightly mobile. The premaxillae, maxillae and mandible bear very small sharp teeth arranged in many rows. There is also a narrow patch of very small sharp densely packed teeth on the vomer. The suspensorium is narrow. The pterygoid is well-developed and the hyomandibula and quadrate are directed anteriorly so the lower jaw is more compact. The opercular series is well developed and the opercles are large and crescent-shaped. The hyoid complex is long and robust. The basihyal is elongate while the urohyal and ceratohyals are thick (Fig. 1F). A well-developed sternohyoideus muscle originates on a robust pectoral girdle and attaches anteriorly to the hyoid arch.

All eels initiated the strike with lower jaw depression, accompanied by cranial elevation. Neither of the two moray species exhibited any hyoid depression during the strike and

prey did not enter the oral jaws until some time after peak gape (Figs 2, 3 and 4). The kinematics of prey capture for *A. rostrata* followed a familiar pattern of events, which included hyoid depression (Figs 2 and 3). In fact, *A. rostrata* synchronized lower jaw depression and cranial elevation with depression of the hyoid, which reached maximum a few milliseconds after peak jaw rotation, a pattern observed in suction-feeding perciforms (Table 1; Fig. 3). As with other suction feeders, prey entered the oral cavity of *A. rostrata* near the time of peak gape.

Although the order of kinematic events was similar in morays and the anguillid eel, all average magnitudes and timing events for kinematic variables were significantly different between morays and *A. rostrata* (Table 1). Jaw rotation in morays was nearly three times that of *A. rostrata*, which exhibited very small angular excursions of the lower jaw. Head rotation was also four times greater in morays compared to *A. rostrata*, which exhibited modest head excursions ranging from 1.19–6.34°. Over all, morays exhibited significantly slower skull movements during prey capture compared to *A. rostrata* (Figs 2, 3 and 4).
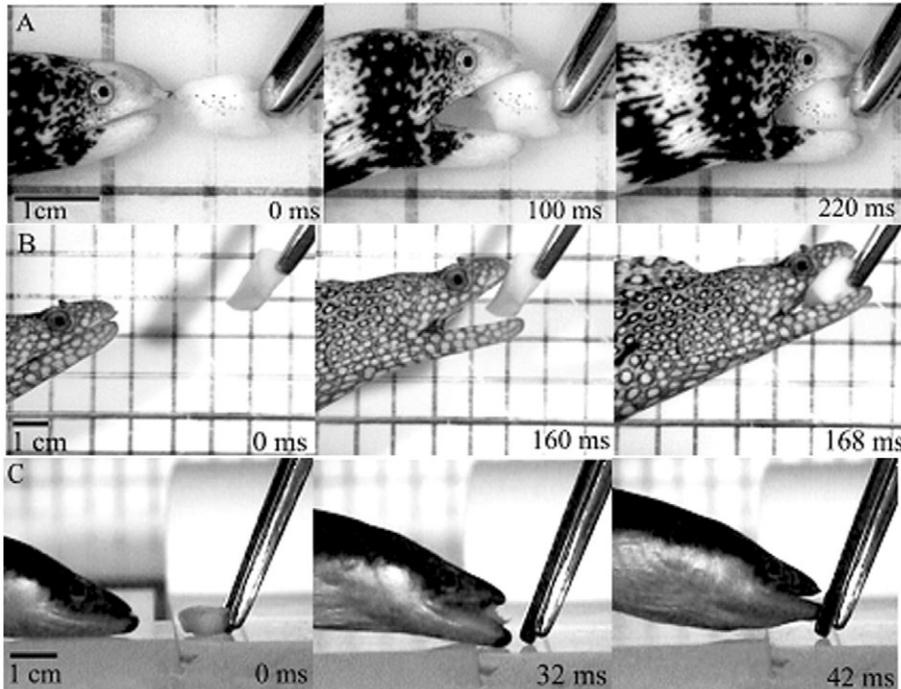
Fig. 2. Kinematic examples of a prey capture event for (A) *Echidna nebulosa*, (B) *Muraena retifera* and (C) *Anguilla rostrata*. Note the differences in time to peak gape (center panels) and prey capture time (right panels) between the three eel species. Also note the lack of hyoid depression in the two morays.

Morays interrupted the expansion phase of the strike with temporary reversals of both jaw and head rotation that occurred at any point between the onset of jaw depression and the moment of prey capture. In some trials both the lower jaw and neurocranium reversed directions (e.g. Fig. 4) whereas in other trials, only one morphological unit (jaw or neurocranium) would reverse direction. Head reversals were slightly more frequent than jaw reversals. The number of reversals was not correlated with strike initiation distance (r^2=0.01). Reversals of jaw or head rotation were never seen in *A. rostrata* and have yet to be documented in any suction-feeding species.

Anguilla rostrata used considerable suction during prey capture, as indicated by suction distances between 10–13 mm in front of the mouth aperture (Table 1). These suction distances corresponded to a range of 44–71% of peak gape distance. In contrast, there was no evidence of prey moving toward the mouth of either moray species in any of the video sequences, indicating no use of suction to transport prey during capture.

The first principal component revealed complete separation in kinematic space between the morays and *A. rostrata*, with morays having higher scores on this axis (Fig. 5). All of the angular excursions and timing variables loaded heavily and positively on PC1 (68%) while the kinematic reversals loaded strongly on PC2 (Table 2). PC1 reflected the longer times in the moray feeding sequences, which were more spread out, reflecting greater variability. The second axis of variation, PC2 (17%), loaded heavily on the number of angular reversals, which also varied between moray feeding sequences. There was no relationship between body mass on either of the PC axes: PC1 (r^2<0.02, $F_{1,8}$=0.21, P=0.76) or PC2 (r^2<0.010, $F_{1,8}$=0.32, P=0.69). Thus, these principle components identified size-independent patterns of variation among the three anguilliform taxa.

Time to prey capture in *A. rostrata*, the two centrarchids and the cichlid ranged from 16–70 ms from the onset of jaw depression, while the two moray species ranged from 189–1186 ms. A regression analysis indicated that there was no relationship between body mass and average prey capture time for all fish (r^2=0.02, $F_{1,15}$=0.35, P=0.56). A nested ANOVA comparing averages of the kinematic variables in morays to the four suction-feeding species indicated significant differences in all kinematic variables, with the exception of cranial elevation (Table 1). However, cranial elevation showed significant differences in variance across the two groups in the Levene's test. Kuskal–Wallis non-parametric tests showed differences in all six kinematic variables between morays and the other four species (all P<0.001).

A nested ANOVA with individual nested within group (morays *vs* suction feeders), indicated that the variance in feeding kinematics differed in the two groups ($F_{1,3}$=60.11, P<0.005). Summed variance on the first four principal components was about 5 times higher for the morays, averaging 4.42 per species as compared to 0.837 for the suction feeders (Table 1).

Discussion

The moray eels examined in this study exhibited striking reductions in a suite of morphological characters that are usually associated with the ability to suction feed, including a highly reduced hyoid bar, pectoral girdle and sternohyoideus muscle. *E. nebulosa* and *M. retifera* exhibited only a single bony element representing a vestigial remnant of the pectoral

Table 1. *Kinematic variables from prey capture in six teleost species*

Variables examined	Echidna nebulosa	Muraena retifera	Anguilla rostrata	Micropterus salmoides	Lepomis macrochirus	Amphilophus citrinellus	F-ratio[1] Morays vs Anguilla	Morays vs other species
Jaw rotation (deg.)	23.52±1.89	21.5193±1.74	8.18±0.67	40.1±0.99	39.85±1.03	37.29±1.29	0.886*	0.167
Cranial elevation (deg.)	13.68±1.07	12.26±1.58	3.58±0.4	9.49±0.89	2.67±0.19	8±0.668	0.936*	3.46
Hyoid displacement (cm)	0	0	0.41±0.02	1.25±0.23	0.71±0.27	0.37±0.37	NA	NA
Peak jaw excursion time (ms)	407.56±20.89	345.05±45.44	32±2.14	38.06±1.22	46.76±1.76	51.06±1.77	6.57**	120.132**
Peak head excursion time (ms)	417.72±20.82	355.7±46.08	43.7±2.37	44.7±1.44	28.33±2.31	36.8±2.92	5.71**	186.94**
Gape distance (dm)	0.920±0.04	1.07±0.08	0.88±0.36	2.63±0.04	1.68±0.03	1.36±0.04	NA	NA
Peak gape time (ms)	413.72±20.94	347.05±37.14	36.35±2.34	38.2±1.23	45.56±1.82	30.5±2.43	6.19**	156.55**
Jaw reversals	0.67±0.13	1.1±0.21	0	0	0	0	NA	NA
Head reversals	1±0.14	1.05±0.20	0	0	0	0	NA	NA
Capture time (ms)	512±32.13	476.55±57.42	42.3±2.88	38.2±1.23	46.06±1.76	29.6±2.49	5.93**	189.16**
Suction distance (cm)	0	0	1.13±0.11	1.51±0.08	1.11±0.052	0.58±0.033	NA	NA
Summed kinematic variance[2]	3.75	5.09	1.16	0.67	0.54	0.98	NA	60.11*
N	39	20	20	30	30	30		

Values are means ± s.e.m. NA, not applicable.

[1]Represents Bonferroni corrected level of significance at *P=0.05, **P=0.001.

[2]Summed kinematic variance is based on summed PC scores for individual fish.

girdle. The extensive reduction in these ventral structures of the skull result in loss of the ability to ventrally expand the buccal cavity forcefully, the primary mechanism of buccal expansion in most suction-feeding teleosts (Lauder, 1980a; Lauder, 1985; De Visser and Barel, 1998; Sanford and Wainwright, 2002). The apparent reduction in suction-feeding ability was supported by the analyses of prey capture kinematics that revealed no hyoid depression and no movement of prey toward the eel's mouth in the 59 moray feeding sequences collected in this study (Table 1). *E. nebulosa* and *M. retifera* did not use suction-induced water flow to help close the distance between them and their prey, but rather, apprehended their prey by direct biting.

Biting is associated with several novel features in the prey capture kinematics of morays. Although the basic kinematic sequence of jaw depression and cranial elevation did not differ from that seen in a representative suction-feeding eel, *Anguilla rostrata*, and was similar to both centrachids and *A. citrinellus*, cranial movements were distinguished by being significantly slower and more variable. Relatively slow movements have been found in other teleost taxa that apprehend their prey by biting. For example, time to maximum gape or peak lower jaw depression takes over 200 ms in the wimple piranha (Janovetz, 2005), about 150 ms in the redfin needlefish (Porter and Motta, 2004), over 300 ms in the koran angelfish (Konow and Bellwood, 2005), and about 80 ms in the bucktooth parrotfish (Rice and Westneat, 2005).

Effective suction feeding involves a rapid and coordinated anterior-to-posterior expansion of the mouth, buccal and opercular cavities (Lauder, 1980a; Lauder, 1985; Svanbäck et al., 2002). The velocity of water flow that is generated, and hence the speed with which a prey item is transported to the mouth, is directly dependent on the rate of expansion of the buccal cavity (Muller et al., 1982; Van Wassenbergh et al., 2006). Prey capture and time to peak gape expansion in suction-feeding teleosts typically occur in less than 60 ms from the onset of mouth opening (Gibb and Ferry-Graham, 2005; Lauder, 1985; Wainwright et al., 2001) and occurred in less than 50 ms in the species studied here. In contrast, morays captured prey in about 500 ms, approximately an order of magnitude longer in time than seen in *A. rostrata*, the two centrachids and the cichlid. We have been unable to find any examples of similar sized suction-feeding teleosts in the literature with strike times as long as 500 ms.

The suction feeders examined in this study captured their prey by depressing the hyoid apparatus and expanding the oral cavity, thus manipulating the water around the prey, whereas moray eels captured prey by biting them. While a suction feeder can begin physically influencing the prey with the onset of water flow that begins with the onset of buccal expansion, moray eels do not appear to physically interact with the prey until their upper and lower jaws come in contact with the prey during the bite. This difference in prey capture mechanism, biting *versus* producing suction, appears to be associated with a relaxation in temporal constraints on eel feeding kinematics that are usually present in the kinematics of suction feeders.
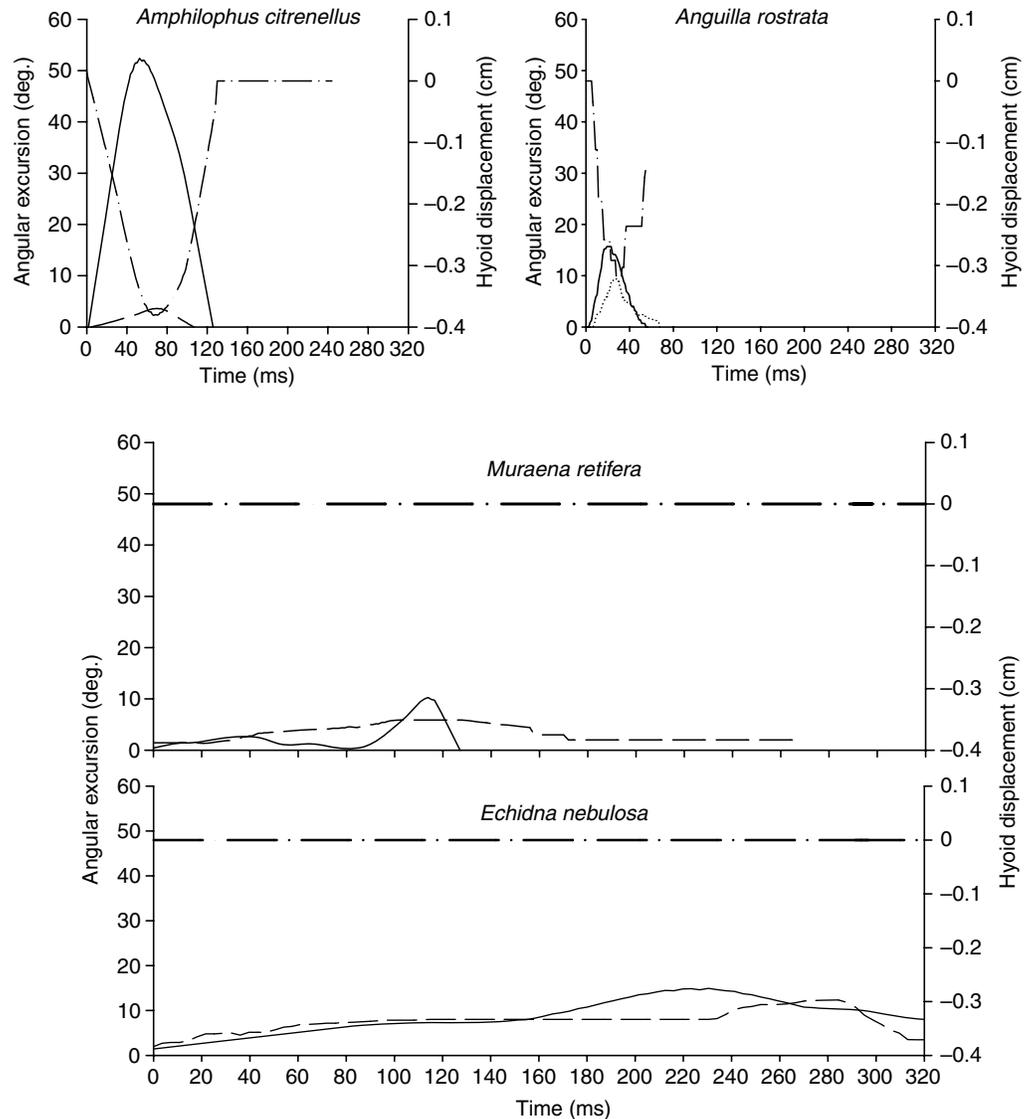
Fig. 3. Kinematic profiles representative of the cichlid *Amphilophus citrinellus*, the anguillid *Anguilla rostrata* and the two moray eels, *Muraena retifera* and *Echidna nebulosa*. Dash-dot lines represent hyoid movement. Bold-face dash-dot lines indicate the lack of hyoid movement during prey capture for morays. Solid black lines represent lower jaw depression. Broken lines and dotted lines represent cranial elevation. Data are smoothed using the running average.

The loss of suction in morays is associated with greater variation in kinematic movement patterns, which may contribute to the ability of these elongate predatory fish to capture prey exceeding the size of a suction feeder's flow field.

Our prediction that the pattern of moray eel feeding kinematics is less constrained than that of suction feeders was supported by the finding that kinematic variance in the morays was significantly higher than *Anguilla*, centrarchids and cichlid (Table 1). In addition to this difference in overall kinematic variation, morays frequently showed reversals of head and jaw rotation during the expansive phase of the strike, something that to our knowledge has never been reported in a suction-feeding fish. The relative timing and continuous movement of head and jaw excursion creates unidirectional water flow into the buccal cavity of suction feeders (Lauder, 1980a; Lauder and Clark, 1984; Ferry-Graham and Lauder, 2001; Ferry-Graham et al., 2003). Temporary reversals in head and jaw rotation would substantially disrupt the development of suction-feeding flow patterns because the water flow is so intimately tied to buccal expansion.

The reduction of the hyoid bar, sternohyoideus muscle and pectoral girdle, together with the absence of hyoid depression and the absence of suction as a prey capture strategy, represent a radical departure from the nearly ubiquitous reliance on hyobranchial depression and suction feeding among teleost fishes. We speculate that the anatomical modifications seen in the morays have greatly reduced their suction-feeding ability. In suction-feeding fish, the cross-sectional area of the hyoid bar must be relatively thick in order to withstand the forces exerted by a well-developed sternohyoideus muscle, which delivers an expansive force to the buccal cavity during suction production (Wainwright et al., 2006). In morays, it is unlikely that the sternohyoideus muscle delivers any major expansive forces to the buccal cavity because the muscle is not only reduced, but the slender hyoid bar does not seem able to withstand the forces necessary to depress the ventral region of the buccal cavity or counteract the forces exerted by the epaxialis during dorsal rotation of the neurocranium (Carroll et al., 2004). This is further supported by the fact the *A. rostrata*, which is more
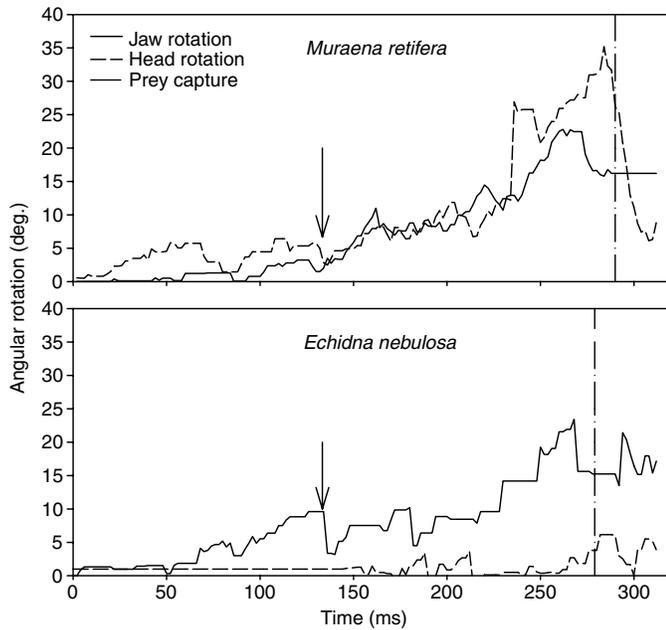
Fig. 4. Kinematic events during prey capture for *Muraena retifera* and *Echidna nebulosa*. Note the high frequencies of reversals in rotation of the jaw and head rotation in the time between onset of the strike and peak mouth opening. In the *M. retifera* plot, the arrow indicates a cranial reversal event and in the *E. nebulosa* plot, the arrow indicates a jaw reversal event.
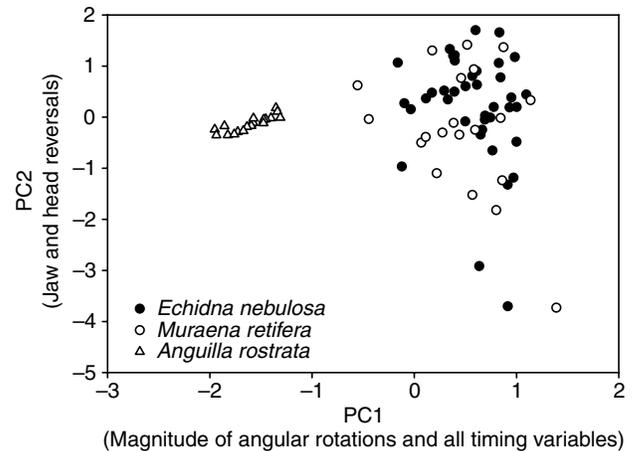

Fig. 5. Axes of kinematic variation in prey capture as revealed by PCA. Each point represents a feeding sequence on the respective axes for the species examined. Note the separation of morays from *A. rostrata* on PC1. Magnitude of angular excursions and all timing variables load positively on PC1 for morays and negatively for *Anguilla rostrata*. Head loaded strongly and negatively on PC2. Moray eels, *Muraena retifera* and *Echidna nebulosa*, exhibited more variable kinematics than the suction-feeding *Anguilla rostrata*.

closely related to morays than to the other three perciform fish used in this study, shares some skull modifications with morays but has a robust hyoid system and used suction to capture prey. Also, the tarpon, *Megalops atlanticus*, an elopomorph member of the sistergroup to anguilliforms, uses suction to capture prey, has a large hyoid bar, and reaches peak gape in about 40 ms (Grubich, 2001).

In *A. rostrata*, the two centrarchids and cichlid included in this study, and in other suction-feeding teleosts that have been described, the pectoral girdle forms a robust skeletal foundation for the actions of the sternohyoideus muscle that originates on the anterior face of the cleithrum and inserts on the medial region of the hyoid. The sternohyoideus can depress the hyoid by its contractions, or act as an antagonist to cranial elevation, also resulting in hyoid depression (Carroll and Wainwright, 2006). *Echidna nebulosa* and *M. retifera* possess a highly reduced pectoral girdle and while the sternohyoideus muscle is present, it is small with its primary origin in the anterior hypaxial muscles. Manual, posteriorly and ventrally directed tension on the sternohyoideus of fresh specimens of the two moray species revealed that this action cannot depress the floor of the buccal cavity, as it does in *A. rostrata,* centrarchids and cichlids, because the hyoid is held within the tissues forming the floor of the buccal cavity and is too flexible to transmit this motion. The rami of the hyoid bar are thin and bent readily when the floor of the buccal cavity was manually depressed.

Although it was not measured in our lateral-view videos, we did observe lateral rotation of the suspensoria during moray eel

feeding. Suspensorial abduction is a key component of buccal expansion in most teleosts (Lauder, 1985) that is retained in moray eels, along with a well developed levator arcus palantini muscle that is positioned to abduct the suspensorium. Lateral motion of the suspensorium was observed in morays during respiration, but in spite of this ability to expand the buccal cavity somewhat by suspensorium abduction, these movements appeared to be too slow to result in sufficient suction flow velocities to move prey items.

Some authors have suggested that the absence of measurable suction distance may underestimate the role of suction in prey capture, if the predator is using suction to compensate for forward movement of the body during the strike (Aerts et al., 2001; Summers et al., 1998). However, compensatory suction is unlikely to be a major component of feeding in morays because of the unusual shape of the moray mouth. Suction-feeding teleosts are often observed to have a planar, almost circular mouth aperture (Higham et al., 2006a; Van Wassenbergh et al., 2006). The mouth opening of moray eels always reveals a distinctive, deep lateral notch that exposes most of the mandibular tooth row when seen in lateral view (Figs 1 and 2). The left and right mandibles form an anterior apex such that the majority of the mouth aperture is oriented laterally. We suspect that anterior motion of the moray head with the jaws abducted results in water spilling out the posterior-lateral part of the mouth opening. This unusual jaw morphology and mouth shape may result in a greatly reduced bow wave, possibly eliminating the need for compensatory suction, and allowing morays to move their jaws into a biting position without pushing potential prey away from the opened mouth.

Table 2. *Loadings of the kinematic variables on the first two Principal Components*

Variables	PC1 (68%)	PC2 (17%)
Jaw rotation	0.745	0.313
Head rotation	0.727	0.270
Time to peak jaw rotation	0.979	0.313
Time to peak head rotation	0.978	0.093
Time to peak gape	0.978	0.093
Jaw reversal	0.544	–0.754
Head reversal	0.563	–0.754
Capture time	0.945	0.128

Implications for alternative feeding strategies

Moray eels are dominant predators in many coral reef communities (Carr and Hixon, 1995; Parrish et al., 1986). The alternative prey acquisition behavior, biting, has a number of implications for prey capture kinematics and for feeding biology in this highly successful lineage. Whether fishes rely on suction or use a ram–suction strategy, the sequence of cranial events is conserved and the relative timing of kinematic events appears to be highly constrained to a period of less then 100 ms. In this study, all timing variables and jaw rotation variables loaded together on the first principal component, clearly separating morays from *A. rostrata*. *A. rostrata* clustered tightly together on both PC1 (magnitude of angular rotation and timing) and PC2 (jaw and head reversals), indicating that suction production relies on a more restricted range of head movements (Fig. 5). Studies of prey capture kinematics in other suction-feeding teleosts have revealed similar patterns, also suggesting that tight integration of head movements is a general feature of suction-feeding kinematics (reviewed in Gibb and Ferry-Graham, 2005). The present study suggests that biting results in less integrated, and more temporally variable feeding patterns. Moray eels exhibited longer prey capture cycles and reversals of jaw and head movements during feeding events. The frequency of jaw and head reversals during moray feeding sequences was not correlated with capture times and may be involved in attempts by morays to track their prey while they position posterior regions of their body for the strike. Whether jaw and head reversals are associated with prey detection and tracking necessitates further investigation.

What selection pressures may have shaped the extensive use of biting rather than suction during prey acquisition in moray eels? In order for suction feeding to be effective, the predator must place itself directly in front of the prey item so that the prey is contained within the volume of water that is captured during the suction-feeding strike (Higham et al., 2006a). Body elongation coupled with the active hunting strategies of morays may have played some role in the loss of suction feeding. Moray eels live within the deep recesses of rocky and coral reefs where they hunt in confined spaces. Biting has been suggested as a strategy for overcoming restrictions that maximum gape size places on diet (Alfaro et al., 2001). Studies of moray stomach contents indicate that they prey upon cephalopods, crabs, shrimp and fishes, often consuming relatively large prey items (Randall, 1967; Randall, 1985; Young and Winn, 2003). Suction feeding may be of limited effectiveness for capturing particularly large prey that can easily escape the flow field in front of a moray's mouth. Suction feeding presumably works best when the prey is small enough to fit within the volume of water contained within one mouth diameter away from the predator's mouth (Day et al., 2005; Higham et al., 2006a; Van Leeuwen, 1984). Reliance on directly biting prey rather than capturing prey with suction may represent an important behavioral adaptation enabling morays to subdue relatively large prey in confined spaces.

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