

Comparative Punting Kinematics and Pelvic Fin Musculature of Benthic Batoids

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ABSTRACT Although the majority of batoid elasmobranchs, skates and rays, are benthically associated, benthic locomotion has been largely overlooked in this group. Only skates have been previously described to perform a form of benthic locomotion termed “punting.” While keeping the rest of the body motionless, the skate’s pelvic fins are planted into the substrate and then retracted caudally, which thrusts the body forward. In this study, we demonstrate that this form of locomotion is not confined to the skates, but is found across a range of phylogenetically and morphologically diverse batoid species. However, only the clearnose skate, *Raja eglanteria*, and the lesser electric ray, *Narcine brasiliensis*, performed “true punting,” in which only the pelvic fins were engaged. The yellow stingray, *Urobatis jamaicensis*, and the Atlantic stingray, *Dasyatis sabina*, performed “augmented punting,” in which pectoral fin movement was also used to generate thrust. Despite this supplemental use of pectoral fins, the augmented punters failed to exceed the punting capabilities of the true punters. The urobatid and the true punters all punted approximately half their disc length per punt, whereas the dasyatid punted a significantly shorter distance. The skate punted significantly faster than the other species. Examination of the pelvic fin musculature revealed more specialized muscles in the true punters than in the augmented punters. This concordance of musculature with punting ability provides predictive power regarding the punting kinematics of other elasmobranchs based upon gross muscular examinations. In contrast to previous assumptions, our results suggest that benthic locomotion is widespread among batoids. *J. Morphol.* 271:1219–1228, 2010. © 2010 Wiley-Liss, Inc.

KEY WORDS: locomotion; elasmobranch; propterygium; crura

INTRODUCTION

Aquatic vertebrates swim through the water column using a variety of techniques, from turtles flapping their flippers (Zug, 1971) to whales thrusting their tails (Arkowitz and Rommel, 1985). Although most studies have focused on this movement through the water column (Lindsey, 1978; Alexander, 2006), many aquatic vertebrates also use forms of benthic locomotion either as a supplementary or primary mode of transportation. Seals walk on the substrate using their hind flippers (Fish et al., 1988), while their close relatives, the walrus, grip the seafloor with their tusks to thrust themselves forward with a nod of the head (Reidenberg, 2007). Many species of turtle use

both fore and hindlimbs in aquatic walking, which is their primary form of locomotion (Zug, 1971).

We also find several examples of substrate locomotion within fishes. Within the teleosts, batfish (Ogcocephalidae) and searobins (Triglidae) use their pectoral fins, and flying gurnards (Dactylopteridae) use their pelvic fins to walk on the substrate (Helfman et al., 1997; Renous et al., 2000; Ward, 2002). More specialized walking structures have evolved in teleosts that spend some time out of the water, such as the mudskippers (Gobiidae; Moyle and Cech, 1999) and Australian lungfishes (Lepidosirenidae; Pough et al., 2004). Within the elasmobranch fishes, only three families are reported to perform benthic locomotion. The epaulette and bamboo sharks (Hemiscyllidae) and horn sharks (Heterodontidae) use their flexible pectoral and pelvic fins to walk and station-hold on the substrate (Pridmore, 1995; Compagno, 1999; Goto et al., 1999; Wilga and Lauder, 2001). Within the batoids (rays and skates), only members of the family Rajidae, the skates, are reported to use their specialized bilobed pelvic fins, termed crura, to walk (each fin alternately; Lucifora and Vassallo, 2002) and punt (both fins synchronously; Koester and Spirito, 2003) on the substrate. To accomplish these forms of locomotion, the anterior lobe of the fin is protracted cranially, planted into the substrate, and then retracted caudally to thrust the skate forward. The skate then glides and recovers the pelvic fins to prepare for the next cycle. While performing the punt or walk, the rest of the body, including the large pectoral fins, remains motionless (Lucifora and Vassallo, 2002; Koester and Spirito, 2003). This has been observed both in the laboratory and in the wild (Lucifora and Vassallo, 2002; Koester and Spirito, 2003). The only other batoid species thought to perform such

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benthic locomotion is the electric ray, *Typhlonarke*, whose large pelvic fins have been suggested to be modified for walking (Waite, 1909), although no studies have directly tested this.

Although most batoids are benthically associated (McEachran and de Carvalho, 2002), most batoid locomotory studies have largely focused on the role of the pectoral fins for propelling the rays through the water column (Lindsey, 1978; Webb, 1984; Rosenberger and Westneat, 1999; Rosenberger, 2001; Schaefer and Summers, 2005). To address this fundamental shortcoming, we quantified the kinematics of pelvic fin-mediated benthic locomotion and examined the associated pelvic fin musculature in four taxonomically diverse batoid species.

The batoids chosen for this study all feed on similar prey items and are all benthically associated (Compagno, 1999), but they differ in swimming style (Schaefer and Summers, 2005; Fig. 1). The lesser electric ray (*Narcine brasiliensis* Olfers 1831; Narcinidae) is a basal batoid that swims through the water column using axial undulation (Schaefer and Summers, 2005). The clearnose skate (*Raja eglanteria* Bosc 1800; Rajidae) is also basal, but is more derived than the narcinid. It swims through the water column using an intermediate between pectoral fin undulation and oscillation (Schaefer and Summers, 2005). The yellow stingray (*Urolophidae*) is more derived than the skate and swims through the water column using pectoral fin undulation (Schaefer and Summers, 2005). The most derived species in this study, the Atlantic stingray (*Dasyatis sabina* Lesueur 1824; Dasyatidae), performs an intermediate between pectoral fin oscillation and undulation to swim through the water column (Lindsey, 1978).

The species used in this study are phylogenetically and morphologically diverse, and thus will provide us with a greater understanding of the use of punting throughout Batoidea. The goals of this study were i) to determine whether batoids, other than skates, perform pelvic fin locomotion and ii) to determine whether the pelvic fin musculature of batoids correlates to punting performance.

MATERIALS AND METHODS

Animal Collection and Husbandry

The four species of benthic batoids that were used for the kinematics study were obtained from several sources. We collected *N. brasiliensis* ($n = 10$) by trawling at Cape Canaveral, FL, and from hand-netting at Long Key, FL. The *U. jamaicensis* specimens ($n = 6$) were collected using hand nets at Long Key, FL. We obtained *D. sabina* specimens ($n = 6$) from seine nets set in Fort Pierce, FL. *Raja eglanteria* specimens ($n = 6$) were obtained from a skate hatchery at Mote Marine Laboratory, Sarasota, FL, and kept in a chilled recirculating system at the Florida Atlantic University Marine Laboratory (Boca Raton, FL). All rays were housed separately in flow-through aquaria at the same facility. They were maintained on a 12L:12D light cycle and were fed daily to satiation on a diet of frozen squid

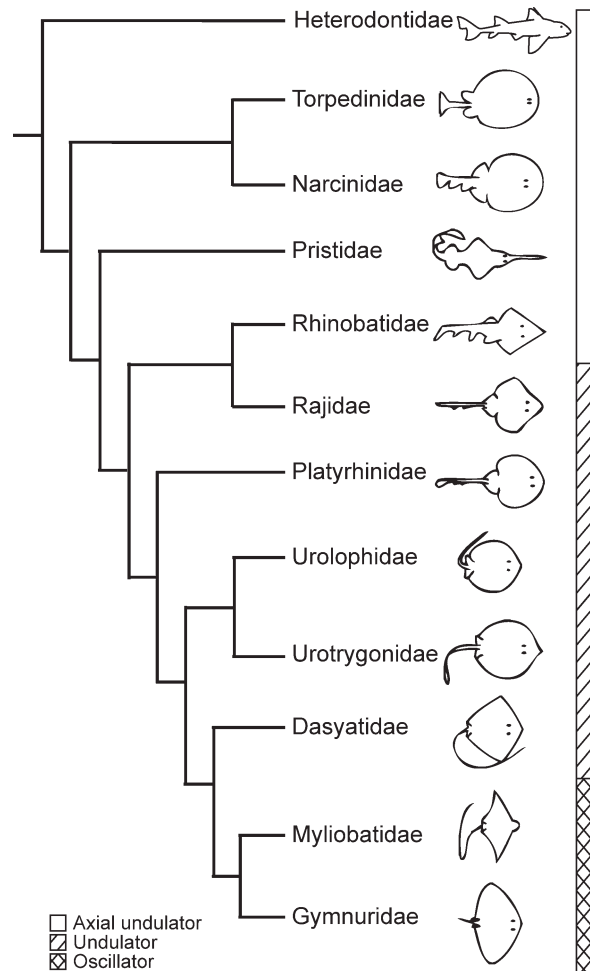


Fig. 1. Cladogram depicting the relationships among batoids and their swimming modes throughout the water column. Axial undulators are the most basal, followed by pectoral fin undulators. The most derived swimming mode is pectoral fin oscillation. A basal shark family, Heterodontidae, is provided as an outgroup. Adapted from Maisey et al. (2004), McEachran and Aschliman (2004), and Schaefer and Summers (2005).

and shrimp. Morphometrics for all animals are provided in Table 1.

Kinematics

To quantify the punting kinematics, the batoids were filmed in a 210-l clear acrylic tank (124.0 cm \times 61.0 cm \times 30.5 cm) with a 5-cm² grid scored onto the base of the tank for scale. A 0.2-mm-thin semirigid plastic netting (1-mm² mesh) was glued at the edges to the bottom of the tank to provide traction while still maintaining a clear ventral view of each animal (after Koester and Spirito, 2003). A video camera was positioned on the floor, 1 m directly beneath the center of the tank, and aimed up, to obtain a ventral view of the tank.

One specimen was introduced to the tank and filmed ventrally at 30 fps (720 \times 480 pixels) for a minimum of 16 punts. A complete punt began when an individual planted the anterior edge of its pelvic fins onto the substrate. The punt was considered complete after the individual swung its pelvic fins forward and repositioned itself for another punting event. Only punts in which both pelvic fins were simultaneously used and in which

TABLE 1. Morphometrics of the four species of batoids used in the kinematics portion of the study

Species	n	Disc width (cm)			Disc length (cm)		
		Max	Min	Mean \pm SD	Max	Min	Mean \pm SD
<i>N. brasiliensis</i>	10	18.3	9.4	14.4 \pm 2.68	17.8	10.5	14.6 \pm 2.30
<i>R. eglanteria</i>	6	27.1	17.1	21.7 \pm 3.92	22.6	13.6	16.9 \pm 3.91
<i>U. jamaicensis</i>	6	13.2	11.5	12.4 \pm 0.53	14.4	13.2	13.9 \pm 0.44
<i>D. sabina</i>	6	32.4	18.9	25.7 \pm 5.22	32.2	17.9	25.3 \pm 5.27

the animal traveled in a straight line, without obstruction by a tank wall, were used in the analysis. Moreover, only punts performed during continuous, steady-state locomotion were used in the analysis. Occasionally, a piece of food was introduced into the tank to stimulate the batoid to locomote. Because the experimental tank lacked filtration or a chiller, the duration of the experiment was limited to 1 h. If the 16 punts were not obtained within that period of time, the animal was returned to its holding tank and the experiment was repeated the following day. The water in the experimental tank was changed after each animal was tested.

From the digital video footage, frames of interest were extracted using Final Cut Pro. We used the software ImageJ (Rasband, 1997) to determine three kinematic variables for individual punts: distance punted, punting speed, and duty factor. Distance and speed were measured in disc lengths (DLs) and DL per second, respectively. The duty factor of a punt was the percentage of the entire punting event in which the anterior edge of the pelvic fin was in contact with the substrate.

Each variable, distance, speed, and duty factor, was square-root-transformed to achieve normality (Kolmogorov-Smirnov test; $P > 0.05$ for all) before statistical analysis. For each variable, a nested ANOVA, using a Satterthwaite approximation for unequal group sizes, was performed to determine differences among species, with Tukey pairwise comparisons to determine significant relationships.

Morphology

For the morphological analysis, we used frozen specimens that were incidental mortalities from other studies.

Surface area. To quantify pelvic fin surface area, the ventral surface of each individual ($n = 6$ per species) was digitally photographed twice. For the first photo, the pelvic fins were positioned on the dorsal surface of the body disc, thereby allowing an unobstructed view of the pectoral fins and disc. In the second photograph, the pelvic fins were positioned naturally ventral to the disc and fully extended. A ruler was included in each frame to calibrate the photos to the nearest millimeter. Surface areas of the pelvic fins (pelvic fins, including area posterior to the puboischiac bar) and of the entire disc (all body area, not including pelvic fins area or tail) were quantified using the program Image J (Rasband, 1997). The ratio of pelvic fin area to entire disc area was calculated and arcsin transformed. We then performed an ANOVA, followed by a Tukey pairwise comparison to determine whether pelvic fin area to entire surface area ratios differed among species.

Musculature. After the pelvic fins were photographed for the surface area analysis, at least three individuals of each species were selected for detailed examination of the pelvic fin musculature. The pelvic fins of each batoid were carefully skinned and dissected to reveal individual muscles. Digital photographs were taken of both the ventral and dorsal surfaces of the pelvic fins throughout the dissection. To ensure that there was no distortion of the muscles during dissection, we obtained MRI scans of two whole pelvic fin samples of *N. brasiliensis* that confirmed muscle positioning in situ. We determined the path of action for each muscle through manual manipulation. The software Adobe Illustrator was used to illustrate the complete pelvic fin musculature and skeletal elements from the dig-

ital photographs. Nomenclature of pelvic fin musculature was based on rajid pelvic fins referred from the study of Lucifora and Vassallo (2002) and epaulette shark pelvic fins referred from the study of Goto et al. (1999). Nomenclature of pelvic girdle skeletal elements was based on myliobatid pelvic girdle descriptions referred from the study of Nishida (1990). At the end of each dissection, all muscles were removed, and the pelvic fin skeletal elements, including the pelvic girdle, were photographed.

RESULTS

Kinematics

All species perform the punting locomotion (Fig. 2); however, the various kinematics, distance, speed, and duty factor, all differ among the species. Moreover, *U. jamaicensis* and *D. sabina* always perform punting with some supplemental pectoral fin movement (Fig. 2). We find significant differences in the punting distances among species (nested ANOVA: $F_{3, 24.74} = 11.51, P < 0.01$). *Narcine brasiliensis* ($\bar{x} = 0.48$ DL \pm 0.266 SE) punts a similar distance as *R. eglanteria* ($\bar{x} = 0.39$ DL \pm 0.215 SE; Tukey post hoc: $P = 0.99$; Fig. 3a), and both species punt significantly longer distances than *D. sabina* ($\bar{x} = 0.32$ DL \pm 0.217 SE; Tukey post hoc: $P < 0.05$ for both). *Urolophus jamaicensis* does not differ from the other three species in punting distance ($\bar{x} = 0.39$ DL \pm 0.047 SE; Tukey post hoc: $P = 0.80$ for *N. brasiliensis*, $P = 0.80$ for *R. eglanteria*, $P = 0.40$ for *D. sabina*).

The four species also punt at different speeds (nested ANOVA: $F_{3, 25.56} = 5.60, P < 0.01$). *Narcine brasiliensis*: $\bar{x} = 0.23$ DL per second \pm 0.012 SE; *U. jamaicensis*: $\bar{x} = 0.20$ DL per second \pm 0.022 SE; and *D. sabina*: $\bar{x} = 0.21$ DL per second \pm 0.020 SE all punt at similar speeds (Tukey post hoc: $P > 0.20$ for all; Fig. 3b), whereas *R. eglanteria* punts significantly faster than the other three species ($\bar{x} = 0.41$ DL per second \pm 0.024 SE; Tukey post hoc: $P < 0.01$ for all).

Lastly, duty factor differs significantly among the species tested (nested ANOVA: $F_{3, 27.69} = 2.37, P < 0.01$). *Raja eglanteria* has a significantly higher duty factor than all three other species ($\bar{x} = 44.2\% \pm 1.72$ SE; Tukey post hoc: $P < 0.01$ for all; Fig. 3c). *Narcine brasiliensis* ($\bar{x} = 37.2\% \pm 2.07$ SE) and *U. jamaicensis* ($\bar{x} = 36.2\% \pm 2.12$ SE) do not differ significantly from each other (Tukey post hoc: $P = 0.98$); however, both have significantly higher duty factors than *D. sabina* ($\bar{x} = 28.9\% \pm 1.35$ SE; Tukey post hoc: $P < 0.01$ for *N. brasiliensis*, and $P < 0.05$ for *U. jamaicensis*).

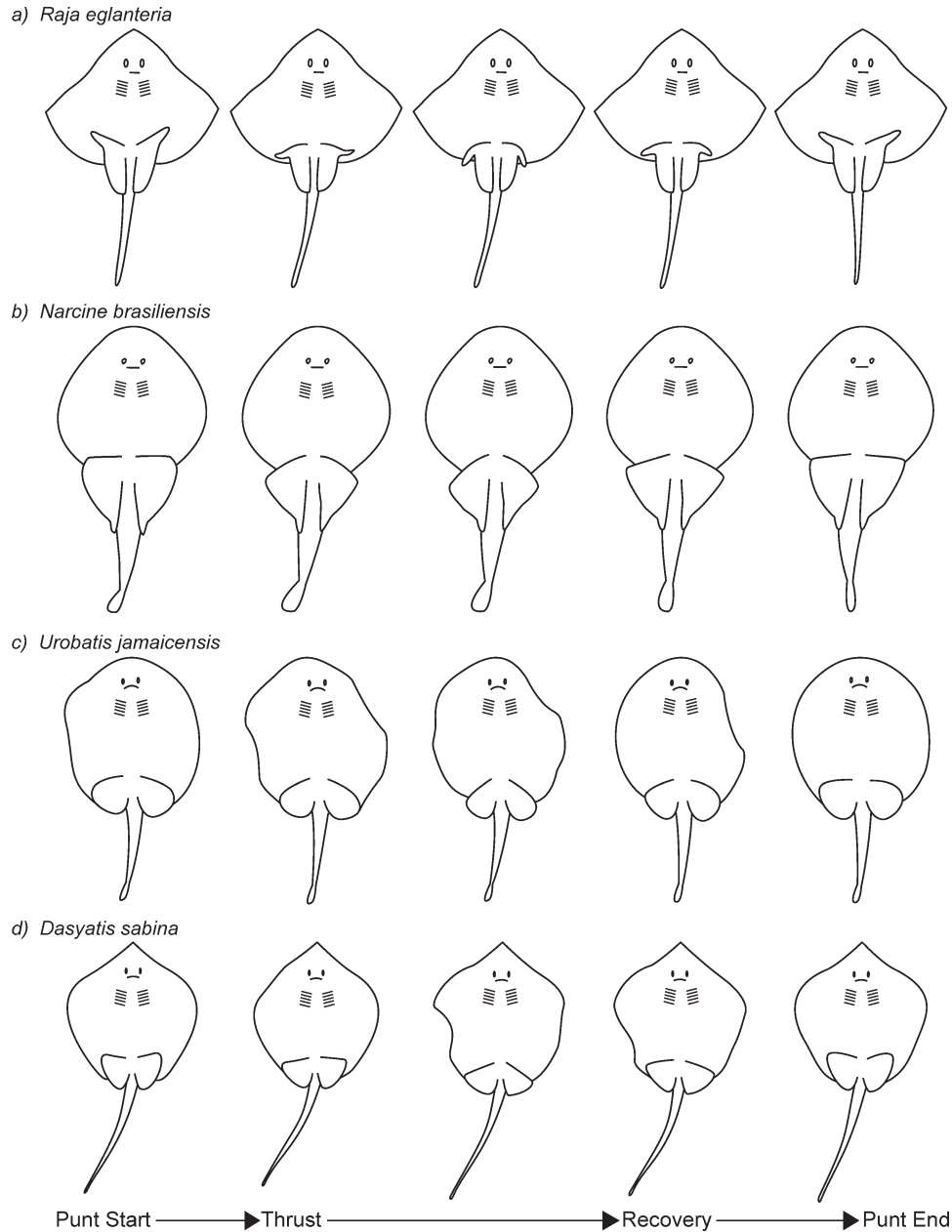


Fig. 2. Ventral view of whole-body kinematics for one punting cycle in the two true punters, (a) *R. eglanteria* and (b) *N. brasiliensis*, and the two augmented punters, (c) *U. jamaicensis* and (d) *D. sabina*. Pelvic fin punting is supplemented with pectoral fin undulation throughout the entire disc in augmented punters. In contrast, the pectoral disc remains rigid throughout the entire cycle for the true punters.

Morphology

In conjunction with differences in punting kinematics, pelvic fin morphology differs among the four species.

Surface area. There are significant differences in pelvic fin surface area (measured as a percent of total disc area) among the four species (ANOVA: $F_{3, 23} = 22.15$, $P < 0.01$). Pelvic fin surface area (Fig. 4) is greatest in *N. brasiliensis* ($\bar{x} = 29.2\% \pm 3.52$ SD; Tukey post hoc: $P < 0.05$). The remaining

three species do not differ significantly from each other in pelvic fin surface area (Tukey post hoc: $P > 0.05$ for all: *R. eglanteria*: $\bar{x} = 15.5\% \pm 0.57$ SD; *U. jamaicensis*: $\bar{x} = 12.2\% \pm 2.63$ SD; *D. sabina*: $\bar{x} = 10.4\% \pm 1.67$ SD).

Musculature. The origin, insertion, and action of the pelvic fin muscles were compared among the species. Musculature on the dorsal surface i) elevates the pelvic fin, ii) elevates the propterygium, or iii) protracts the propterygium. Similarly, mus-

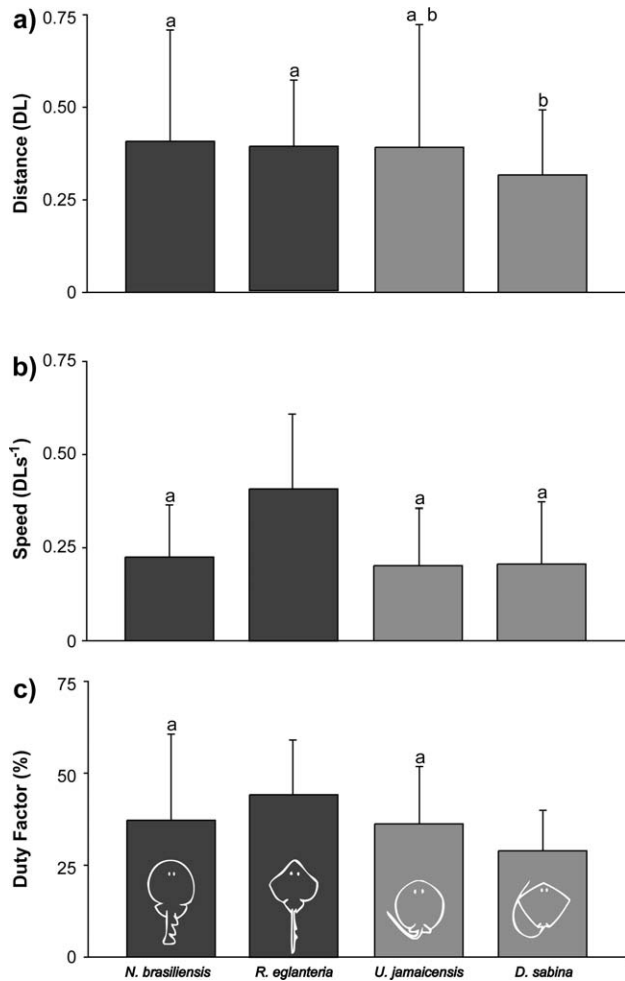


Fig. 3. Punting kinematics variables for four species of benthic batoids (mean + SD). Dark gray bars indicate true punters, which use only their pelvic fins during each cycle; light gray bars indicate augmented punters, which use supplemental pectoral fin movement during each punt. Species that are not statistically different from each other share a common letter. (a) The batoids are all quite consistent with the distance punted during each cycle; however, *D. sabina* punts a significantly shorter distance than *R. eglanteria* and *N. brasiliensis*. (b) The skate, *R. eglanteria* is significantly faster than all other batoids when punting. (c) *R. eglanteria* spends a significantly longer amount of time per cycle in the thrust phase, as indicated by a significantly greater duty factor than the other three batoids, whereas *D. sabina* has a significantly lower duty factor than the other species.

culature on the ventral surface of the pelvic fin is found to i) depress the pelvic fin or ii) depress the propterygium. Retractors of the propterygium are found on both the dorsal and ventral surfaces. The skate species in this study, *R. eglanteria*, possesses the characteristic bilobed pelvic fin, with an anterior leg-like lobe and posterior fin-like lobe, and does not show major differences in musculature from the *Psammobatis* spp. described by Lucifora and Vassallo (2002). However, in *R. eglanteria*, the propterygium retractors and protractors are pres-

ent on both the ventral and dorsal surfaces of the fins, as opposed to earlier reports of their location exclusively on the ventral and dorsal surfaces, respectively (Lucifora and Vassallo, 2002).

N. brasiliensis, although lacking the divided lobes of the pelvic fins, is similar to the skate species in that it also possesses a functional joint and robust skeletal element at the distal end of the propterygium. Therefore, like *R. eglanteria* (Fig. 5a), *N. brasiliensis* also possesses a distal and a proximal propterygium depressor on the ventral surface of the pelvic fins (Fig. 5b and Table 2). However, in contrast to *R. eglanteria*, the propterygium protractor originates from the linea alba and puboischiac bar. Also, *N. brasiliensis*' dorsal musculature (Fig. 5a and Table 3) differs from *R. eglanteria* with the distal and proximal propterygium levators originating from the anterior region of the lateral pelvic processes of the pelvic girdle. The propterygium retractor of *N. brasiliensis* originates from the iliac process of the puboischiac bar.

U. jamaicensis and *D. sabina* share similar musculature (Fig. 5c,d, respectively; Tables 2 and 3). Because they both lack the segmented propterygia, they possess only one muscle to depress the entire propterygium, which originates from the iliac process of the puboischiac bar and inserts along the entire ventral length of the propterygium. The propterygium retractor for both of these species originates from the medial region of the puboischiac bar. Also, the propterygium protractor differs from the true punters in which it originates directly from the puboischiac bar. Musculature on the dorsal surface also differs because of the lack of segmented propterygia (Fig. 5c,d and Table 3). The general propterygia levator originates from the puboischiac bar and inserts along the dorsal length of the propterygium.

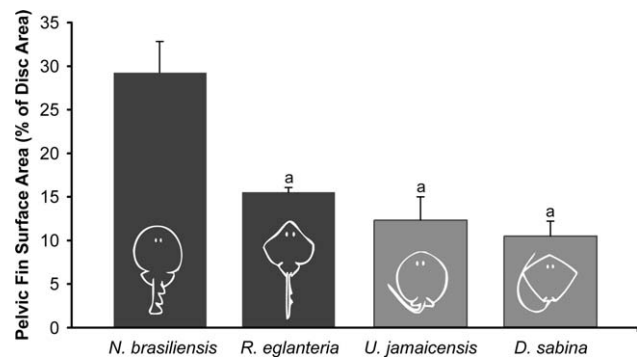


Fig. 4. Pelvic fin surface area (mean + SD) of four benthic batoids ($n = 6$, each spp.), expressed as percent of total disc area. Species that are not statistically different from each other share a common letter. The lesser electric ray, *N. brasiliensis*, has significantly larger pelvic fin surface area than the other three batoids. True punters are in dark gray bars; augmented punters are in light gray bars.

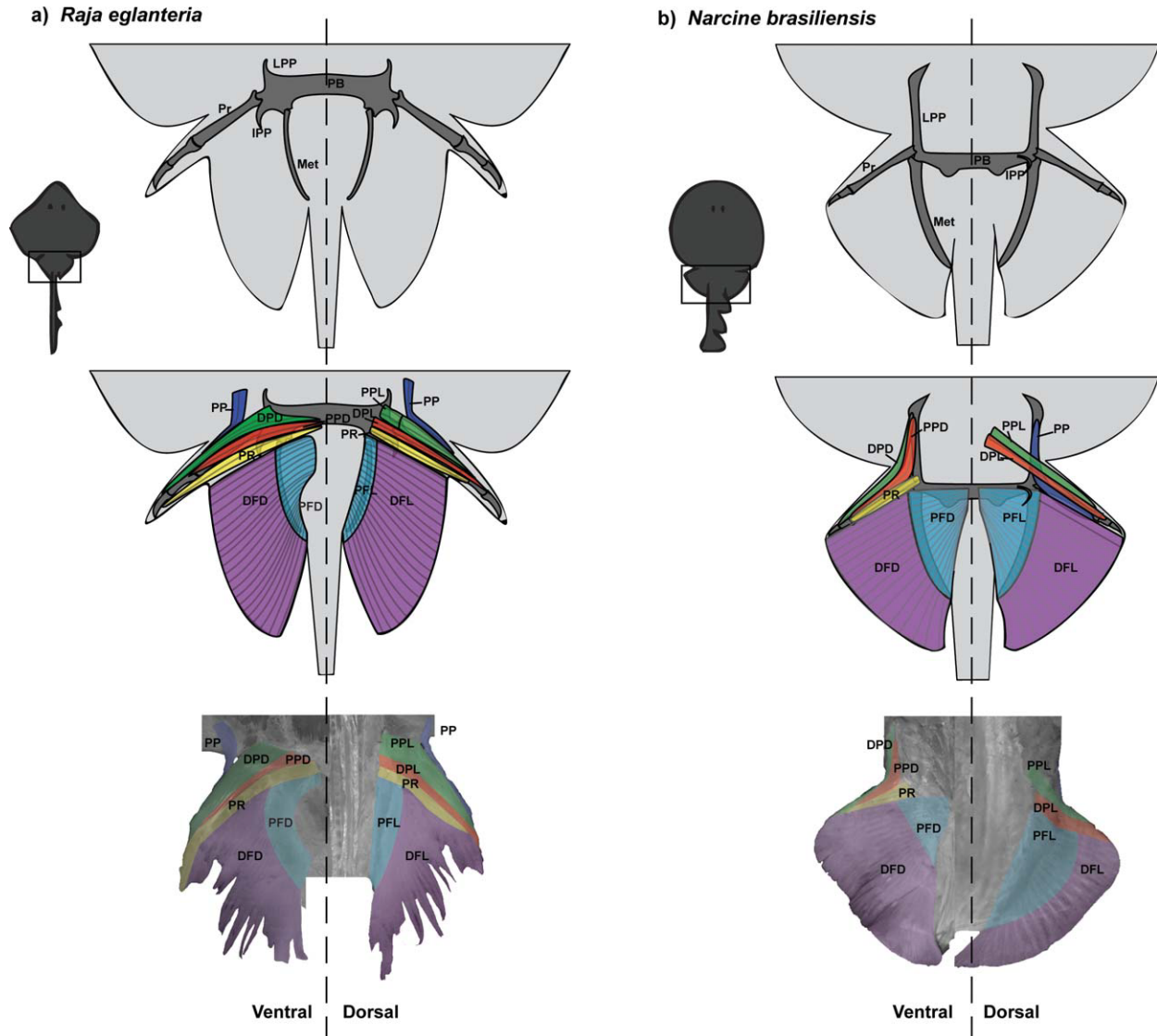


Fig. 5. Schematic representation and photographs of pelvic fin skeletal elements and musculature of four benthic batoids: true punters (dark gray inset): (a) *R. eglanteria* and (b) *N. brasiliensis*; and augmented punters (light gray inset): (c) *U. jamaicensis* and (d) *D. sabina*. In each species' pair of illustrations, the ventral surface is shown on the left and the dorsal surface is shown on the right. Pelvic girdle and associated skeletal elements are shown on the top half of each species' pair of illustrations: puboischiac bar (PB), iliac pelvic process (IPL), lateral pelvic process (LPP), metapterygium (Met), propterygium (Pr). Pelvic musculature is shown in the bottom half of each species' pair of illustrations: ventral muscles: proximal fin depressor (PDF, turquoise), distal fin depressor (DFP, purple), distal propterygium depressor (DPD, green), proximal propterygium depressor (PPD, red), and general propterygium depressor (GPD, green); dorsal muscles: proximal fin levator (PFL, turquoise), distal fin levator (DFL, purple), proximal propterygium levator (PPL, green), distal propterygium levator (DPL, red), and general propterygium levator (GPL, green). The propterygium retractors (PR, yellow) and protractors (PP, blue) were found on both dorsal and ventral sides (PP is occluded from view in the dorsal photograph of *N. brasiliensis*). Only the true punters possess specializations in propterygium depressors and levators, whereas the augmented punters possess only a generalized muscle for each of these actions.

Dissection of these four species revealed that *N. brasiliensis* and *R. eglanteria* both have apparently more specialized musculature supporting their pelvic fin skeletal elements which allow for movement of the jointed propterygia. In contrast, the musculature of the augmented punters is relatively smaller and more generalized, especially in the muscles responsible for the retraction and protraction of the anterior edge of the pelvic fins.

DISCUSSION

Punting and walking in batoids were thought to be a specialized form of locomotion performed only by skates (Rajidae) because of their specialized musculature and skeletal elements (Holst and Bone, 1993). Previous claims that other batoids would not share this locomotory mode (Holst and Bone, 1993) were based on life histories of the

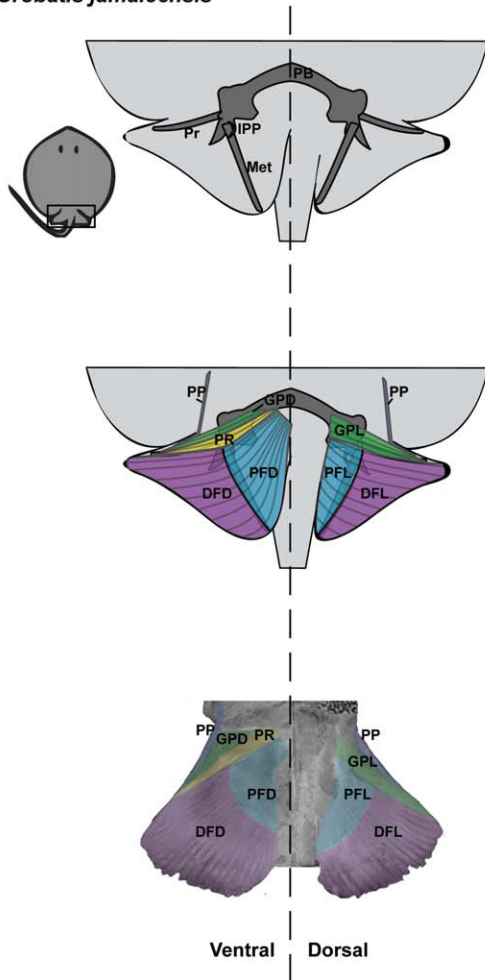
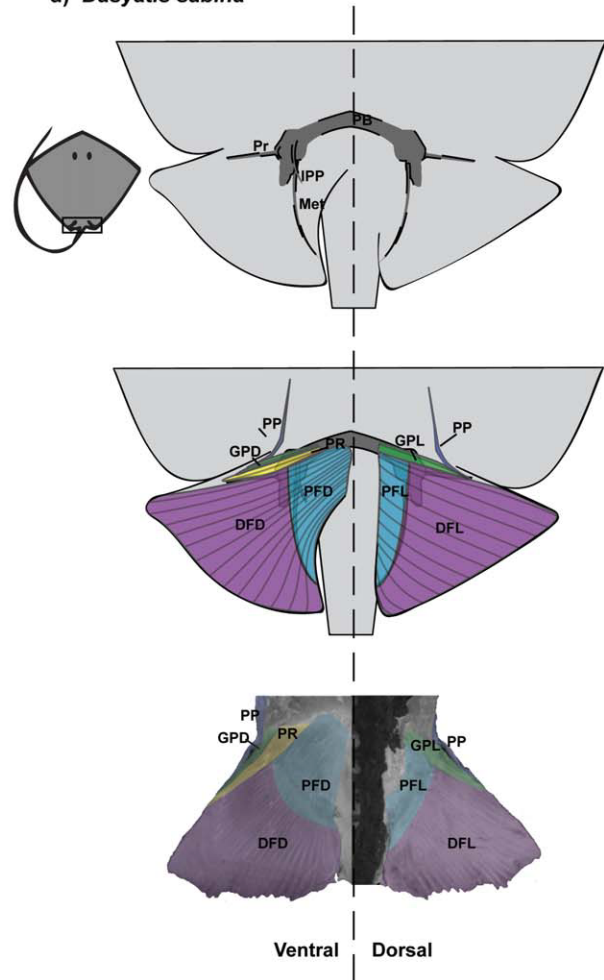
c) *Urobatis jamaicensis*d) *Dasyatis sabina*

Fig. 5. (Continued.)

largely pelagic myliobatids (Bigelow and Schroeder, 1953). However, our study involved batoids that shared similar habitat and prey items with the skates and found that, indeed, other batoids do perform pelvic fin locomotion on the substrate. This behavior is likely representative of the Batoidea, as the majority of batoids are benthically associated and feed on small benthic fishes, crustaceans, and other invertebrates (McEachran and de Carvalho, 2002).

Punting locomotion confers numerous advantages to benthic batoids when compared with pectoral fin or axial body locomotion. Punting provides fine-scale maneuverability when locomoting on the substrate, which facilitates prey detection and localization. Moreover, because punting requires little to no movement of the large pectoral fins, a punting batoid creates a minimal mechanical disturbance in the water. It is thus a more stealthy form of locomotion that could reduce detection by both predators and prey. Punting may also provide an advantage in the electrosensory

detection of prey. All elasmobranchs are able to detect the weak bioelectric fields of their prey (Bullock, 1973) via their electrosensory system located on their pectoral disc and cranial region (Kalmijn, 1966). By reducing movement of the pectoral disc, they minimize self-generated electric noise and may therefore be able to more easily detect their prey (New and Bodznick, 1990). The same principle applies to the lateral line system, which is also distributed over the pectoral disc (Jordan et al., 2009). Maintaining an electrically quiet environment may be especially important for the two true punters examined in this study, as both are thought to use their small electrogenic organs in intraspecific communication (Bratton and Ayers, 1987; Macesic and Kajiura, 2009). Lastly, because only relatively small muscles are used during punting and because this is an intermittent form of locomotion, punting may reduce swimming energetics (Videler and Weihs, 1982). These potential advantages of punting suggest that this form of

TABLE 2. Ventral pelvic fin musculature in four species of benthic batoids

Ventral muscle	Found in	Origin	Insertion	Action
Proximal fin depressor	<i>Re, Nb, Uj, and Ds</i>	Linea alba and puboischiac bar	Metapterygium	Depresses pelvic fin (proximal region)
Distal fin depressor	<i>Re, Nb, Uj, and Ds</i>	Metapterygium	Radials and ceratotrichia	Depresses pelvic fin (distal region)
Distal propterygium depressor	<i>Re and Nb</i>	<i>Re</i> : iliac process of puboischiac bar <i>Nb</i> : lateral pelvic process	Propterygium (distal tip)	Depresses propterygium (distal tip)
Proximal propterygium depressor	<i>Re and Nb</i>	<i>Re</i> : iliac process of puboischiac bar <i>Nb</i> : lateral pelvic process	Propterygium (proximal region)	Depresses propterygium (greater proximal region)
General propterygium depressor	<i>Uj and Ds</i>	Iliac process of puboischiac bar	Along length of propterygium	Depresses propterygium (entire element)
Propterygium retractor (also on dorsal surface)	<i>Re, Nb, Uj, and Ds</i>	<i>Re</i> : axial musculature (ventral longitudinal bundle) <i>Nb</i> : iliac process of puboischiac bar <i>Uj and Ds</i> : puboischiac bar	Propterygium	Adducts propterygium from anteriorly extended position

Abbreviations: *Re, Raja eglanteria*; *Nb, Narcine brasiliensis*; *Uj, Urobatis jamaicensis*; *Ds, Dasyatis sabina*.

locomotion is, as we found, actually widespread but previously overlooked among benthic batoids.

All species in this study performed the same broad pelvic fin kinematics, wherein the anterior edge of the fins is protracted, planted into the substrate, and then retracted to generate thrust, which propels the animal forward. This is the same pattern that has been described for several skate species (Holst and Bone, 1993; Lucifora and Vassallo, 2002; Koester and Spirito, 2003). Moreover, this is the same pattern described for walking and crawling benthic sharks (Pridmore, 1995; Goto et al., 1999; Wilga and Lauder, 2001). These sharks have relatively flexible pectoral and pelvic fins when compared with other pelagic sharks; however, they do not possess any specialization such as the crura seen in skates.

Published values for the rajid punting speed range from 0.30 to 0.40 DL per second (Holst and Bone, 1993; Koester and Spirito, 2003). In the species that we examined, *R. eglanteria* punted at the faster end of this range (0.41 DL per second), whereas the three others were significantly slower (0.20–0.23 DL per second). These values are all substantially lower than values reported for the epaulette shark, which can crawl at a speed of approximately 0.64 body lengths (BL) per second (Pridmore, 1995). The two slowest species in this study, *U. jamaicensis* and *D. sabina*, performed augmented punting, in which pectoral fin undulations were used at the same time as the pelvic fin punts, likely increasing forward thrust. This may be necessary for effective benthic locomotion in these species, when considering their relatively di-

TABLE 3. Dorsal pelvic fin musculature in four species of benthic batoids

Dorsal muscle	Found in	Origin	Insertion	Action
Proximal fin levator	<i>Re, Nb, Uj, and Ds</i>	Metapterygium	Radials and ceratotrichia	Elevates pelvic fin (deep region)
Distal fin levator	<i>Re, Nb, Uj, and Ds</i>	Axial musculature	Radials and ceratotrichia	Elevates pelvic fin (superficial region)
Proximal propterygium levator	<i>Re and Nb</i>	<i>Re</i> : iliac process of puboischiac bar <i>Nb</i> : lateral pelvic process	Propterygium (proximal region)	Elevates propterygium (greater proximal region)
Distal propterygium levator	<i>Re and Nb</i>	<i>Re</i> : iliac process of puboischiac bar <i>Nb</i> : lateral pelvic process	Propterygium (distal tip)	Elevates propterygium (distal tip)
General propterygium levator	<i>Uj and Ds</i>	Puboischiac bar	Along length of propterygium	Depresses propterygium (entire element)
Propterygium protractor (also on ventral surface)	<i>Re, Nb, Uj, and Ds</i>	<i>Re</i> : axial musculature (ventral longitudinal bundle) <i>Nb</i> : linea alba and puboischiac bar <i>Uj and Ds</i> : puboischiac bar	Propterygium	Protracts propterygium anteriorly

Abbreviations: *Re, Raja eglanteria*; *Nb, Narcine brasiliensis*; *Uj, Urobatis jamaicensis*; *Ds, Dasyatis sabina*.

minutive pelvic fin musculature. Our results demonstrate that despite the addition of pectoral fin undulation, augmented punters performed worse than the true punters.

The specialized musculature seen in *R. eglanteria* is similar to that previously described in other skate species (Lucifora and Vassallo, 2002); however, it appears that *N. brasiliensis* also possesses anatomical specializations for punting. In particular, the propterygium, like the crus of the skate, possesses a small, but robust, distal skeletal element, attached by a condyloid joint. Specialized musculature, likely controlling the proximal, mid, and distal regions of the propterygium, is also similar to that of *R. eglanteria*. These specialized propterygium levators and depressors, along with the propterygium protractor, all originate from the anterior portion of the lateral processes of the pelvic girdle. These processes are approximately three times longer than those found in *R. eglanteria*, although other skate species also possess similarly long processes (Hulley, 1972; McEachran and Miyake, 1990; Nishida, 1990). This may enable these batoids to protract their pelvic fins with a minimum amount of force exerted in the lateral plane and more force directed anteriorly. Even though we do not see distinct skate-like lobes, narcinid rays do possess distinct specializations for punting, as Waite (1909) had suspected.

The augmented punters, *U. jamaicensis* and *D. sabina*, possess very similar musculature to each other, although they differ from the true punters. In contrast to the specialized true punters, only a single general muscle is responsible for movement of the entire propterygium in these batoids. The propterygium is composed of a single skeletal element and is not segmented into any other functional smaller elements. This reduces the amount of fine motor movements possible in these augmented punters. Moreover, the lateral pelvic processes of the pelvic girdles are greatly reduced or absent, and therefore, the propterygium depressors, levators, and protractors originate from the puboischiac bar. When the fins are in a resting position, this site of origin is only slightly more anterior than the insertion point on the propterygium itself, indicating that there may be a substantial amount of wasted lateral force produced when protracting the pelvic fin to initiate a punt cycle. Additionally, the augmented punters' protractors and retractors are much smaller than those in true punters, thus generating less force. Again, this illustrates the need for the supplemental pectoral fin movements to approach the performance of the true punters.

The species chosen for this study span a variety of swimming styles from axial undulation in *N. brasiliensis* to pectoral fin undulation in *U. jamaicensis* and approaching pectoral fin oscillation in *D. sabina*. These swimming styles have evolved in this

pattern, with axial undulation being the most basal and full pectoral fin oscillation being the most derived (Rosenberger, 2001; Schaefer and Summers, 2005). From this study, we find a similar locomotory trend, in which the most basal batoids, the narcinids and rajids (McEachran and Aschliman, 2004), both perform true punting. Augmented punting is found only in the more derived batoids, the urobatids and dasyatids. The most derived batoids, the myliobatids, are almost exclusively pelagic and have likely lost the capacity for benthic locomotion altogether. Therefore, barring other selective pressures, we predict that the myliobatids likely possess generalized and reduced pelvic fin musculature. We therefore propose that punting is a basal form of locomotion within Batoidea. Moreover, examples of punting or walking in multiple shark families indicate that this behavior confers considerable advantages for benthic species and has convergently evolved multiple times within Elasmobranchii.

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