

PECTORAL FIN LOCOMOTION IN BATOID FISHES: UNDULATION VERSUS OSCILLATION

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Summary

This study explores the dichotomy between undulatory (passing multiple waves down the fin or body) and oscillatory (flapping) locomotion by comparing the kinematics of pectoral fin locomotion in eight species of batoids (*Dasyatis americana*, *D. sabina*, *D. say*, *D. violacea*, *Gymnura micrura*, *Raja eglanteria*, *Rhinobatos lentiginosus* and *Rhinoptera bonasus*) that differ in their swimming behavior, phylogenetic position and lifestyle. The goals of this study are to describe and compare the pectoral fin locomotor behavior of the eight batoid species, to clarify how fin movements change with swimming speed for each species and to analyze critically the undulation/oscillation continuum proposed by Breder using batoids as an example. Kinematic data were recorded for each species over a range of swimming velocities (1–3 disc lengths s⁻¹). The eight species in this study vary greatly in their swimming modes. *Rhinobatos lentiginosus* uses a combination of axial-based and pectoral-fin-based undulation to move forward through the water, with primary thrust generated by the tail. The pectoral fins are activated in short undulatory bursts for increasing swimming speed and for maneuvering. *Raja eglanteria* uses a combination of pectoral and pelvic locomotion, although only pectoral locomotion is analyzed here. The other six species use pectoral locomotion exclusively to propel themselves through the water. *Dasyatis sabina* and *D. say* have the most undulatory fins with an average of 1.3 waves

per fin length, whereas *Rhinoptera bonasus* has the most oscillatory fin behavior with 0.4 waves per fin length. The remaining species range between these two extremes in the degree of undulation present on their fins. There is an apparent trade-off between fin-beat frequency and amplitude. *Rhinoptera bonasus* has the lowest frequency and the highest fin amplitude, whereas *Rhinobatos lentiginosus* has the highest frequency and the lowest amplitude among the eight species examined. The kinematic variables that batoids modify to change swimming velocity vary among different species. *Rhinobatos lentiginosus* increases its tail-beat frequency to increase swimming speed. In contrast, the four *Dasyatis* species increase swimming speed by increasing frequency and wavespeed, although *D. americana* also changes wave number. *Raja eglanteria* modifies its swimming velocity by changing wavespeed and wave number. *Rhinoptera bonasus* increases wavespeed, *Gymnura micrura* decreases wave number, and both *Rhinoptera bonasus* and *Gymnura micrura* increase fin-tip velocity to increase swimming velocity. Batoid species fall onto a continuum between undulation and oscillation on the basis of the number of waves present on the fins.

Key words: undulatory locomotion, oscillatory locomotion, pectoral fin locomotion, locomotion, batoid fishes, swimming, kinematics.

Introduction

Batoid fishes (electric rays, sawfishes, guitarfishes, skates and stingrays) are a monophyletic group of over 500 elasmobranch species (Compagno, 1999) nested within sharks (Carvalho, 1996; Shirai, 1996). Batoids are unique among elasmobranch fishes in having dorsoventrally flattened bodies and pectoral fins that are greatly expanded and fused to the head, forming a broad, flat disc. Some members of the group retain a thick, shark-like tail (sawfishes, guitarfishes), whereas others have a greatly reduced tail (skates, stingrays). Despite the commonality of expansion of the fins and flatness of the disc found in batoids, multiple modes of locomotion are found among these species.

Batoids propel themselves through the water primarily either with their body and tail (axial-based locomotion) or with their greatly expanded pectoral fins (pectoral-fin-based locomotion). Axial-based locomotion ('shark-like' swimming) is found in most basal members of the batoid clade including the sawfishes, guitarfishes (Klausewitz, 1965) and electric rays (Roberts, 1969). Some species, such as guitarfishes in the family Rhinobatidae, use a combination of body and fins during locomotion (Klausewitz, 1965). Pectoral-fin-based locomotion has been divided traditionally into two categories: undulation and oscillation. Undulation of the pectoral fins, termed 'rajiform' locomotion (Breder, 1926), is defined by

having more than one wave present on the fins at a time (Webb, 1994). Skates (Daniel, 1988) and most stingrays (Marey, 1893; Magnan, 1930; Campbell, 1951; Rosenberger and Westneat, 1999) are thought to use this mode of locomotion. Oscillation of the pectoral fins, termed 'mobuliform' locomotion (Webb, 1994) is more similar to flapping in birds; the fins move up and down with less than half a wave on the fins. Pelagic stingrays, such as manta (Klausewitz, 1964), cownose (Heine, 1992), eagle and bat rays, use the oscillatory mode. Many fishes, including some batoids, use modes of locomotion that do not fit into the categories of 'undulatory' and 'oscillatory' in that there is between half a wave and one wave present on the fins or body; however, no name has been given to this broad category, so I will refer to this middle mode as 'intermediate'.

Breder (1926) was the first to categorize the different locomotor modes of fishes on the basis of the parts of the body (paired and median fins or body/caudal) used for propulsion (Breder, 1926). These locomotor categories (Breder, 1926) have since modified on the basis of more recent studies in fish locomotion (Lindsey, 1978; Webb, 1994; Webb, 1998). The recognition of discrete categories of pectoral fin locomotion suggests a continuum between undulation and oscillation for fishes in general. Although two extremes of locomotion between undulation and oscillation have been recognized, all fishes are true undulators in that waves are passed down the body or fins. The difference lies in the number of waves present. When the number of waves is small (less than half a wave), the motion appears to look like an oscillating plate, and this mode has been called 'oscillatory'. Alternatively, when the wave number is larger, the fin looks more undulatory. Most taxonomic groups of fishes are assigned to one category or the other and lack representatives along the continuum. Batoids are one of the few groups of fishes with representatives at each extreme of the continuum, making them ideal for comparing undulatory and oscillatory kinematics within a group of closely related fishes. Although the categories of undulation and oscillation accurately describe the fin kinematics of some species of batoids, other species appear to be intermediate between the two extremes.

Previous studies on locomotion in batoid fishes have focused on one or two species (Marey, 1893; Magnan, 1930; Campbell, 1951; Klausewitz, 1964; Klausewitz, 1965; Roberts, 1969; Daniel, 1988; Heine, 1992; Rosenberger and Westneat, 1999). Rosenberger and Westneat (1999) examined pectoral fin undulation in the blue-spot stingray *Taeniura lymma* to quantify its kinematic behavior and to document the muscle activation patterns associated with undulatory locomotion. Their study found that, as swimming velocity increased, fin-beat frequency, wavespeed and stride length increased, the number of waves decreased and amplitude remained constant. They also discovered a trade-off between frequency and amplitude among *T. lymma* individuals (Rosenberger and Westneat, 1999). The detailed kinematic data for *T. lymma* provide a foundation for quantitative comparative studies of locomotion in batoids that exhibit different locomotor modes. The present study examines the kinematics of pectoral fin

locomotion in eight species of batoids that differ in swimming behavior and lifestyle. The specific goals of this study were (i) to describe the general swimming behavior and test for differences in pectoral fin locomotion for the eight species, (ii) to determine how the different species change their swimming behavior to increase swimming velocity, and (iii) to analyze the continuum between undulation and oscillation in diverse batoid fishes.

Materials and methods

Kinematics

Pectoral locomotion was examined in eight batoid species (Fig. 1): *Dasyatis americana* (southern stingray), *D. sabina* (Atlantic stingray), *D. say* (bluntnose stingray), *D. violacea* (pelagic stingray), *Rhinobatos lentiginosus* (guitarfish), *Raja eglanteria* (clearnose skate), *Gymnura micrura* (smooth butterfly ray) and *Rhinoptera bonasus* (cownose ray). Sample size, disc measurements and capture locality and methods for the eight batoid species are presented in Table 1. Batoids were purchased from a Chicago fish wholesaler, donated by or studied at aquariums, or captured by way of hook and line, beach seining or otter trawling. Batoids caught by hook and line were allowed to recover for a minimum of 5 days before experiments were performed. *Rhinobatos lentiginosus* and the five *D. americana* individuals donated by the National Aquarium in Baltimore were studied in a flow tank (working area of 30 cm×30 cm×120 cm; 360 l) at the Field Museum of Natural History in Chicago, IL, USA. *Dasyatis americana*, *D. sabina*, *D. say*, *Raja eglanteria*, *Gymnura micrura* and *Rhinoptera bonasus* were maintained in outdoor holding tanks

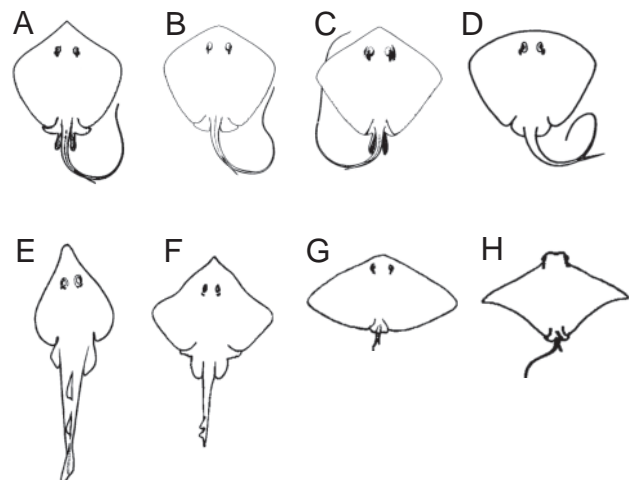


Fig. 1. Line drawings of the eight batoid species in this study. (A) *Dasyatis sabina* (Lesueur), (B) *Dasyatis say* (Lesueur), (C) *Dasyatis americana* Hildebrand and Schroeder, (D) *Dasyatis violacea* (Bonaparte), (E) *Rhinobatos lentiginosus* (Garman), (F) *Raja eglanteria* Bosc, (G) *Gymnura micrura* (Bloch and Schneider) and (H) *Rhinoptera bonasus* (Mitchill). Line drawings are modified from previous publications (Bigelow and Schroeder, 1953; Eschmeyer et al., 1983; Nelson, 1994).

Table 1. Data for the batoid species used in this study including sample size, degrees of freedom, mean morphometric data and capture locality and methods

Species	N	d.f.	Disc length (cm)	Disc width (cm)	Capture location/method
<i>Dasyatis americana</i>	8	39	27.7±7.0	30.7±8.8	NC; hook and line; donated*
<i>Dasyatis sabina</i>	9	47	20.9±4.2	22.1±3.9	NC; beach seining, hook and line
<i>Dasyatis say</i>	3	11	23.3±7.9	26.0±8.2	NC; otter trawl
<i>Dasyatis violacea</i>	3	8	55.0±13.5	71.7±17.6	Monterey and Steinhart aquariums
<i>Rhinobatos lentiginosus</i>	5	15	13.2±3.3	10.4±2.3	Purchased from wholesaler
<i>Raja eglanteria</i>	6	21	22.0±2.6	26.7±3.0	NC; otter trawl, hook and line
<i>Gymnura micrura</i>	3	15	16.0±0.5	28.9±1.0	NC; otter trawl
<i>Rhinoptera bonasus</i>	6	40	28.7±2.0	46.4±2.6	NC; otter trawl

NC, Beaufort, North Carolina.

*Five individuals donated by the National Aquarium in Baltimore.

N, sample size; d.f., degrees of freedom.

Values are means ± S.D.

with flow-through sea water and were studied in a flow tank (working area of 229 cm×61 cm×61 cm; 850 l) at the Duke University Marine Laboratory in Beaufort, NC, USA. Five of the six *Rhinoptera bonasus* individuals were studied from swimming sequences filmed by C. Heine at Duke University Marine Laboratory. Batoid specimens used in the present study are deposited at the Field Museum of Natural History, with the exception of C. Heine's *Rhinoptera bonasus* individuals.

Nine *Dasyatis violacea* individuals were filmed under water in a holding tank at the Monterey Bay Aquarium (MBA) in Monterey, CA, USA. Three individuals were filmed in a roundabout tank with a current of 1 knot (55 cm s⁻¹) at the Steinhart Aquarium in San Francisco, CA, USA. The data presented in this paper for *D. violacea* were analyzed from the Steinhart Aquarium rays because of the similarity between swimming speeds or flow speeds in the roundabout tank and the flow tanks used for the other species. Video recordings of rays from MBA were studied to assess swimming behavior qualitatively in this species, and MBA individuals were within the size range of the Steinhart aquarium individuals. *D. violacea* individuals were filmed at 60 frames s⁻¹ using a video camera outside the roundabout tank (at Steinhart Aquarium). The flow speed of the water in the tank (55 cm s⁻¹) and the sizes of the individuals were known, so the forward velocity could be determined for each individual. Three different velocities for each of the three individuals (ranging between 1 and 3 *DL* s⁻¹, where *DL* is disc length) were digitized for five fin beats at each speed. Kinematic variables were calculated using the same methods as for the other species. The disc lengths of the rays were used for scale to calculate kinematic variables and swimming velocities for each individual.

Lateral-view video recordings captured swimming events as the rays swam over a range of speeds in the flow tanks (1–3 *DL* s⁻¹). Rays were filmed during steady forward swimming. A Sony TR940 Hi8 video camera, output to a Panasonic AG-1970 tape deck, recorded images at a shutter speed of 1/1000 s and frame rate of 60 images s⁻¹. Red aluminum clip markers were placed along the edge of the

visible pectoral fin to assist in digitizing homologous points in each frame (Rosenberger and Westneat, 1999). Fin clips could not be placed on *Dasyatis violacea* individuals, so the fin tip at the widest portion of the fin (visible in all frames) was used for calculating the kinematic variables of frequency and amplitude. A Panasonic AG-1970 tape deck was used to play back video recordings for digitization (five fin beats per individual at each swimming speed). A TelevEyes/Pro video scan converter with Genlock superimposed the video and computer images onto a Sony PVM-1340 monitor. A custom-designed digitizing program, developed by J. Walker, was used to record digitized points from the lateral view and to measure the *x* and *y* coordinates of each point along the fin. Coordinate data were exported to Microsoft Excel '98 for calculation of the kinematic variables. Only sequences in which the rays were in the middle of the tank were used for digitizing to decrease the effect of boundary layers.

The following kinematic variables (defined below) were calculated for each individual at all the recorded swimming speeds: fin-beat frequency, mid-disc amplitude of the fin, propulsive wavespeed, number of waves present along the fin, phase velocity and stride length. Fin-beat frequency (*f*) was determined as the number of fin-beat cycles per second. The mid-disc fin amplitude was calculated as half the dorsoventral displacement of the widest portion of the fin and was standardized by disc width (proportion of disc width). Propulsive wavespeed (*c*) was calculated as the distance the wave traveled in the middle one-third of the fin divided by the time taken for it to move that distance. Wavespeed was standardized by disc length for each individual to facilitate comparison among species of different sizes. Amplitude and wavespeed were standardized using different disc measures as relevant to the kinematic variables. Wavespeed quantifies movement down the fin length, so disc length is more appropriate. Dividing by disc width for values of amplitude is preferred for maintaining equivalent angular displacement regardless of fin width. The number of waves present on the fin was calculated by dividing the length of the fin base

(distance from snout to posterior disc margin) by the wavelength. The fin base differs in batoid species, depending on whether structures such as a rostral cartilage or cephalic lobes are present anterior to the neurocranium. *Rhinobatos lentiginosus* and *Raja eglanteria* have rostral cartilages anterior to the neurocranium, and *Rhinoptera bonasus* has cephalic lobes (Miyake et al., 1992) making the fin base shorter than the disc length, which affects how the fin base is quantified. Other stingrays (*Dasyatis* species and *Gymnura micrura*) have fin radials extending to the anteriormost portion of the disc, making the fin base equal to the disc length. Fin base length was measured as the length between the anterior fin radial extension and posterior fin margin for all batoids. Phase velocity (U/c) was determined as the ratio of forward swimming speed (U) to propulsive wavespeed (c). Stride length (U/f) was calculated by dividing forward swimming

speed (U) by fin-beat frequency (f), and is the distance a fish travels in one oscillatory cycle.

Statistical analyses

All kinematic variables were regressed against swimming speed (DLs^{-1}) to test for significant trends. Individual differences within each species were tested using a nested analysis of variance (ANOVA). Species variability in kinematic variables was noteworthy, so the significance of interspecies variation was tested using analysis of covariance (ANCOVA). In this model, the association between a kinematic variable and velocity is compared among species to test for differences in slope and intercept. Although intraspecific variation was significant, species effects were significant for all kinematic variables. *Post-hoc* tests of significant differences between particular species pairs were

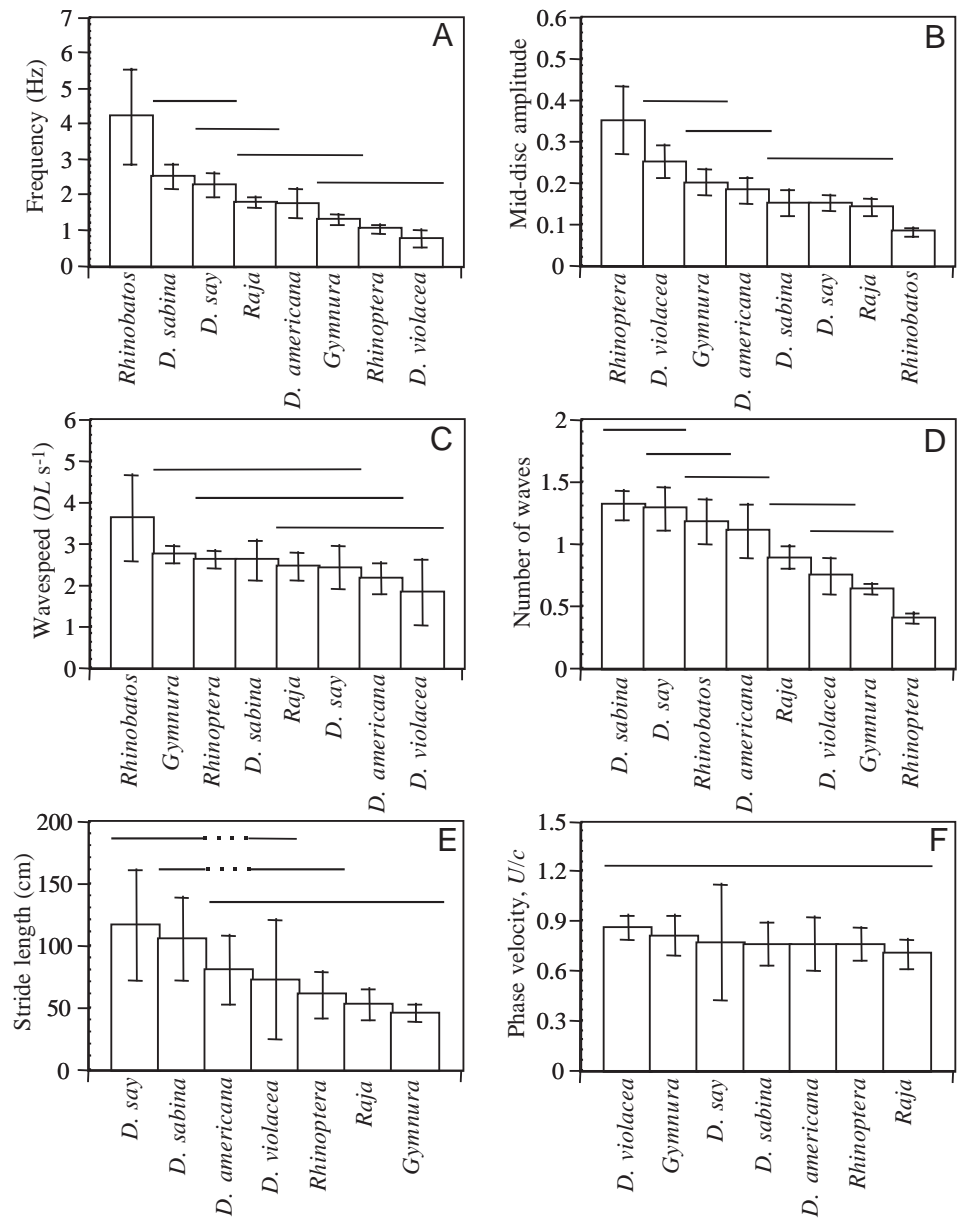


Fig. 2. Mean values of kinematic variables for all batoid species. (A) Frequency, (B) mid-disc amplitude, (C) wavespeed, (D) number of waves along the fin, (E) stride length and (F) phase velocity. Lines above the columns indicate species that are not significantly different from each other on the basis of Tukey-Kramer tests ($P < 0.01$). *Dasyatis americana* ($N=8$); *D. sabina* ($N=9$); *D. say* ($N=3$); *D. violacea* ($N=3$); *Gymnura micrura* ($N=3$); *Raja eglanteria* ($N=6$); *Rhinobatos lentiginosus* ($N=5$); *Rhinoptera bonasus* ($N=6$). Error bars represent the standard deviation from mean. DL , disc length; U , swimming speed; c , propulsive wavespeed.

tested using Tukey–Kramer tests ($P < 0.01$). Mean kinematic values across all velocities were used for the Tukey–Kramer tests. All analyses were performed using JMP 3.1 (SAS Institute). P -values were corrected using the sequential Bonferroni method (Rice, 1989) to evaluate significance.

Results

Kinematics: interspecific variation in swimming behavior

Batoid species differ significantly from each other in their mean kinematic variables (Fig. 2). *Rhinobatos lentiginosus* has a significantly higher frequency (4.2 Hz) and *Rhinoptera bonasus* and *Dasyatis violacea* have the lowest frequencies (1.04 and 0.78 Hz, respectively) among the batoid species (Fig. 2A; Table 2). Amplitude varies significantly among batoid species in that *Rhinoptera bonasus* (0.35) has the highest amplitude and *Rhinobatos lentiginosus* (0.08) has the lowest amplitude (Fig. 2B; Table 2). *Rhinoptera bonasus* and *Rhinobatos lentiginosus* differ significantly in amplitude from all other species (Fig. 2B). *Rhinobatos lentiginosus* has a significantly higher wavespeed (3.61 DL s^{-1}) than the other batoids (Fig. 2C; Table 2). The other batoids do not differ greatly from each other in wavespeed (Fig. 2C; Table 2). *Rhinoptera bonasus* has a significantly lower wave number (0.40) than other batoid species (Fig. 2D; Table 2), and *D. sabina* (1.31) and *D. say* (1.28) have the highest wave number (Fig. 2D). Stride length is highest in *D. say* and *D. sabina* and lowest in *Gymnura micrura* (Fig. 2E; Table 2). Phase velocity does not differ significantly among batoid species (Fig. 2F).

Three extremes in batoid locomotion are evident: axial-based undulation, pectoral fin undulation and pectoral fin oscillation. *Rhinobatos lentiginosus* swims primarily by using its thick tail (Fig. 3); however, this species also utilizes pectoral fin undulation to some extent (Fig. 4A). The tail is used for steady forward swimming, with the pectoral fins additionally activated for accelerating and maneuvering in the water. Pectoral fin activity is not steady and only lasts for very short periods. *Rhinobatos lentiginosus* individuals were never observed to use the pectoral fins alone for propulsion. When the pectoral fins are activated, fin-beat frequency is significantly higher compared with other batoids studied (Fig. 2A) and amplitude is significantly lower (Fig. 2B). In *Rhinobatos lentiginosus*, the wave begins to form on the pectoral fin just behind the eye. The wave moves very quickly down the fin, and there is an average of 1.2 waves present at any time (Table 2). Tail-beat frequency ranges between 1.3 and 2.0 Hz and increases linearly with increasing velocity.

Raja eglanteria, *Dasyatis violacea*, *Gymnura micrura* and *Rhinoptera bonasus* have less than one wave present on their fins, and are therefore not classified as undulatory pectoral fin propulsors (see Webb, 1994; Webb, 1998). *Raja eglanteria* (Fig. 4B) exhibits a more undulatory behavior during pectoral fin locomotion than the other three species by having slightly fewer than one wave on the fin, making it more of an intermediate undulator. As in *Rhinobatos lentiginosus*, the wave begins at the level of the eye in *Raja eglanteria* and is

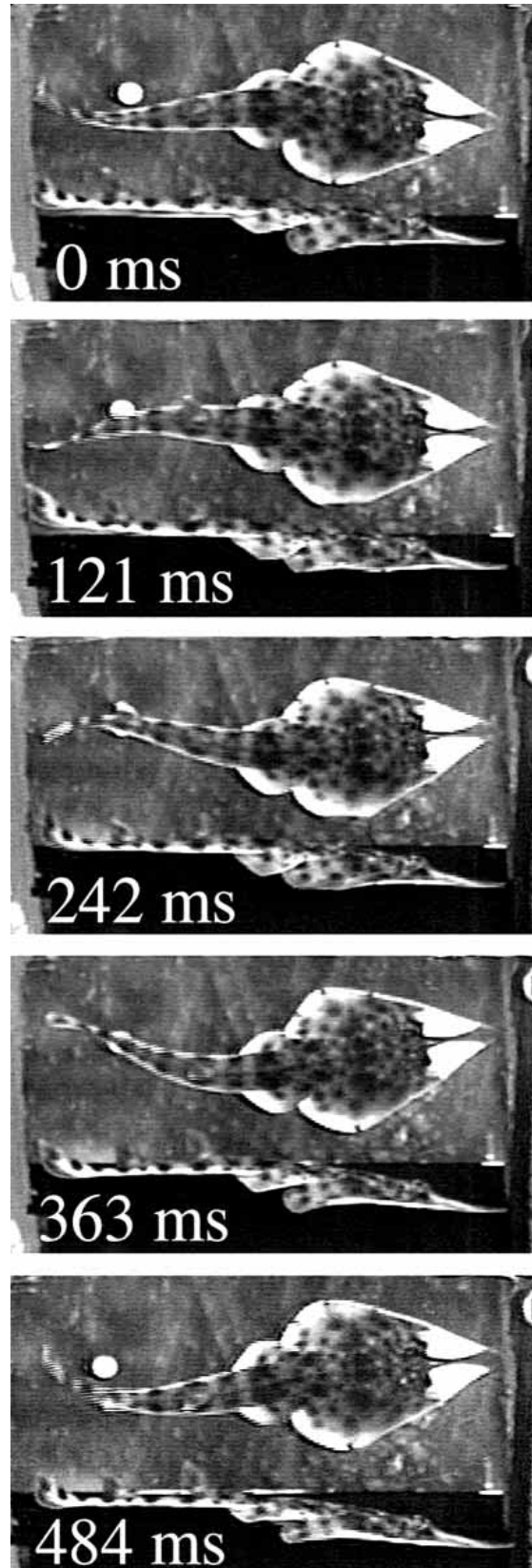


Fig. 3. Successive lateral and dorsal video images of *Rhinobatos lentiginosus* swimming in a flow tank at $\text{DLs}^{-1}=1$. The dorsal view, at the top of each frame, is a reflected mirror view. *R. lentiginosus* swims primarily with its thick tail. Anterior is to the right.

Table 2. Statistical significance of least-squares regressions with F-tests of kinematic data across all swimming speeds within species of batoids, where y is a measurement from the Variable column and x is swimming speed

Variable/Species	Mean	S.D.	Range		Regression	r^2	F ratio	P
			Minimum	Maximum				
Fin-beat frequency (Hz)								
<i>Dasyatis sabina</i>	2.51	0.36	1.91	3.41	$y=0.57x+1.4$	0.53	51.3	<0.0001*
<i>Dasyatis say</i>	2.27	0.35	1.83	2.88	$y=0.27x+1.6$	0.59	25.7	<0.0001*
<i>Dasyatis americana</i>	1.74	0.42	1.09	2.54	$y=0.63x+0.7$	0.62	60.9	<0.0001*
<i>Dasyatis violacea</i>	0.78	0.24	0.48	1.33	$y=0.27x+0.3$	0.98	364.9	<0.0001*
<i>Rhinobatos lentiginosus</i>	4.20	1.34	2.40	6.67	$y=0.64x+3.1$	0.27	5.3	0.038
<i>Raja eglanteria</i>	1.78	0.16	1.38	2.07	$y=0.21x+1.5$	0.10	2.7	0.115
<i>Gymnura micrura</i>	1.29	0.14	1.06	1.50	$y=-0.14x+1.6$	0.15	2.5	0.136
<i>Rhinoptera bonasus</i>	1.04	0.12	0.83	1.28	$y=0.07x+0.9$	0.10	4.2	0.047
Mid-disc amplitude (proportion of disc width)								
<i>Dasyatis sabina</i>	0.15	0.03	0.09	0.20	$y=0.001x+0.2$	0.01	0.01	0.923
<i>Dasyatis say</i>	0.15	0.02	0.12	0.17	$y=-0.001x+0.1$	0.00	0.01	0.991
<i>Dasyatis americana</i>	0.18	0.03	0.14	0.24	$y=0.004x+0.2$	0.01	0.3	0.566
<i>Dasyatis violacea</i>	0.25	0.04	0.20	0.32	$y=0.01x+0.2$	0.35	3.7	0.095
<i>Rhinobatos lentiginosus</i>	0.08	0.01	0.05	0.11	$y=0.001x+0.1$	0.01	0.02	0.901
<i>Raja eglanteria</i>	0.14	0.02	0.09	0.18	$y=0.04x+0.1$	0.15	4.5	0.045
<i>Gymnura micrura</i>	0.20	0.03	0.16	0.26	$y=0.01x+0.2$	0.02	0.2	0.635
<i>Rhinoptera bonasus</i>	0.35	0.08	0.21	0.46	$y=0.03x+0.3$	0.04	1.1	0.309
Wavespeed (proportion of disc length)								
<i>Dasyatis sabina</i>	2.59	0.46	1.65	3.46	$y=0.59x+1.4$	0.39	29.8	<0.0001*
<i>Dasyatis say</i>	2.41	0.52	1.50	3.16	$y=0.22x+1.9$	0.17	3.8	0.068
<i>Dasyatis americana</i>	2.15	0.38	1.33	3.06	$y=0.45x+1.4$	0.37	22.7	<0.0001*
<i>Dasyatis violacea</i>	1.82	0.78	1.00	3.43	$y=0.85x+0.4$	0.97	193.7	<0.0001*
<i>Rhinobatos lentiginosus</i>	3.61	1.05	2.03	5.83	$y=0.08x+3.5$	0.01	0.1	0.752
<i>Raja eglanteria</i>	2.44	0.35	1.66	2.92	$y=1.07x+1.1$	0.58	33.2	<0.0001*
<i>Gymnura micrura</i>	2.73	0.21	2.26	3.14	$y=0.30x+2.1$	0.29	5.8	0.031
<i>Rhinoptera bonasus</i>	2.62	0.20	2.34	2.95	$y=0.39x+1.9$	0.69	31.0	<0.0001*
Wave number								
<i>Dasyatis sabina</i>	1.31	0.12	1.08	1.56	$y=-0.12x+1.6$	0.19	10.9	0.002*
<i>Dasyatis say</i>	1.28	0.18	0.93	1.65	$y=-0.02x+1.3$	0.01	0.2	0.644
<i>Dasyatis americana</i>	1.10	0.21	0.77	1.43	$y=-0.14x+0.9$	0.12	5.1	0.029*
<i>Dasyatis violacea</i>	0.74	0.15	0.57	0.92	$y=-0.10x+0.9$	0.33	3.4	0.107
<i>Rhinobatos lentiginosus</i>	1.17	0.18	0.92	1.44	$y=-0.14x+0.9$	0.76	45.1	<0.0001*
<i>Raja eglanteria</i>	0.89	0.09	0.78	1.08	$y=-0.21x+1.2$	0.34	12.6	0.002*
<i>Gymnura micrura</i>	0.63	0.04	0.57	0.74	$y=-0.07x+0.8$	0.32	6.5	0.023*
<i>Rhinoptera bonasus</i>	0.40	0.04	0.34	0.46	$y=-0.02x+0.4$	0.06	0.9	0.370
Stride length (cm)								
<i>Dasyatis sabina</i>	104.90	33.71	53.33	221.59	$y=66.3x-25.0$	0.75	137.2	<0.0001*
<i>Dasyatis say</i>	116.53	44.51	43.90	201.92	$y=42.7x+16.4$	0.90	170.3	<0.0001*
<i>Dasyatis americana</i>	79.87	28.02	41.67	144.19	$y=51.0x-8.5$	0.91	393.6	<0.0001*
<i>Dasyatis violacea</i>	72.21	48.29	24.72	197.47	$y=54.5x-19.5$	0.95	133.6	<0.0001*
<i>Raja eglanteria</i>	51.83	12.61	24.88	70.25	$y=45.2x-6.9$	0.81	99.3	<0.0001*
<i>Gymnura micrura</i>	45.16	7.45	32.61	56.87	$y=14.0x+14.0$	0.51	14.7	0.002*
<i>Rhinoptera bonasus</i>	60.18	18.58	27.27	100.62	$y=32.0x-3.6$	0.99	804.5	<0.0001*
Phase velocity								
<i>Dasyatis sabina</i>	0.76	0.13	0.46	0.97	$y=0.18x+0.4$	0.43	31.3	<0.0001*
<i>Dasyatis say</i>	0.77	0.35	0.34	0.98	$y=0.23x+0.3$	0.87	62.3	<0.0001*
<i>Dasyatis americana</i>	0.76	0.16	0.42	0.98	$y=0.24x+0.4$	0.56	41.6	<0.0001*
<i>Dasyatis violacea</i>	0.86	0.07	0.73	0.96	$y=0.06x+0.8$	0.19	1.5	0.273
<i>Raja eglanteria</i>	0.70	0.09	0.55	0.92	$y=0.23x+0.4$	0.43	18.2	<0.0001*
<i>Gymnura micrura</i>	0.81	0.12	0.62	0.98	$y=0.27x+0.2$	0.79	47.8	<0.0001*
<i>Rhinoptera bonasus</i>	0.76	0.10	0.58	0.96	$y=0.34x+0.2$	0.92	132.6	<0.0001*

* $P < 0.05$, sequential Bonferroni-corrected.

propagated posteriorly along the fin. Fin-beat frequency is moderate (Fig. 2A; Table 2) and fin amplitude is relatively low in *Raja eglanteria* compared with the other batoids (Fig. 2B;

Table 2). *Raja eglanteria* is not an active swimmer, and individuals did not swim above velocities of $2 DL s^{-1}$ during the kinematic experiments.

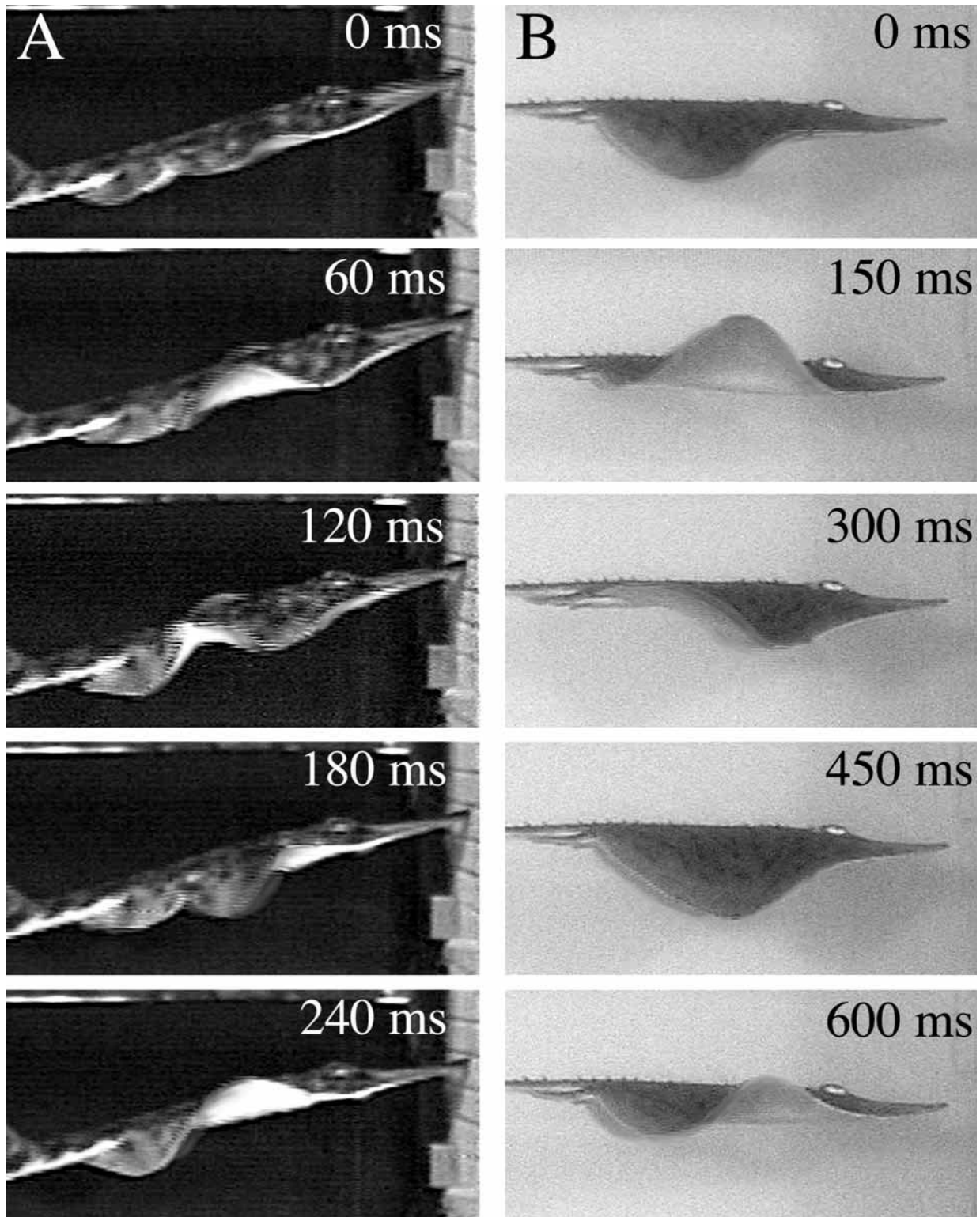


Fig. 4. Successive lateral video images of (A) *Rhinobatos lentiginosus* and (B) *Raja eglanteria* swimming in flow tanks at $DL s^{-1}=2$. *Rhinobatos lentiginosus* occasionally supplements tail swimming with short undulatory bursts of pectoral fin locomotion to help accelerate and maneuver in the water. *Raja eglanteria* swims by passing undulatory waves down the pectoral fins. Anterior is to the right.

The four *Dasyatis* species (*D. americana*, *D. sabina*, *D. say* and *D. violacea*), *Rhinoptera bonasus* and *Gymnura micrura* propel themselves through the water strictly with their pectoral fins. *Rhinobatos lentiginosus* (Fig. 4A), *D. sabina* (Fig. 5A) and *D. say* exhibit the most undulatory pectoral locomotion among the eight species in this study, having the highest number of waves on their fins (Fig. 2D). *D. americana* has just over one wave on the fins, making it undulatory, but to a lesser extent than *D. sabina*, *D. say* and *Rhinobatos lentiginosus*.

The wave begins approximately at the level of the eye and propagates posteriorly in the four *Dasyatis* species. *D. violacea* exhibits a more oscillatory-based swimming behavior than the other *Dasyatis* species and has 0.7 waves on the fin. Fin-beat frequency is low (Fig. 2A) and fin amplitude is relatively high (Fig. 2B) in *D. violacea*.

Gymnura micrura (Fig. 5B) uses fin movements that are intermediate between undulatory and oscillatory locomotion. *Gymnura micrura* was observed using two different swimming

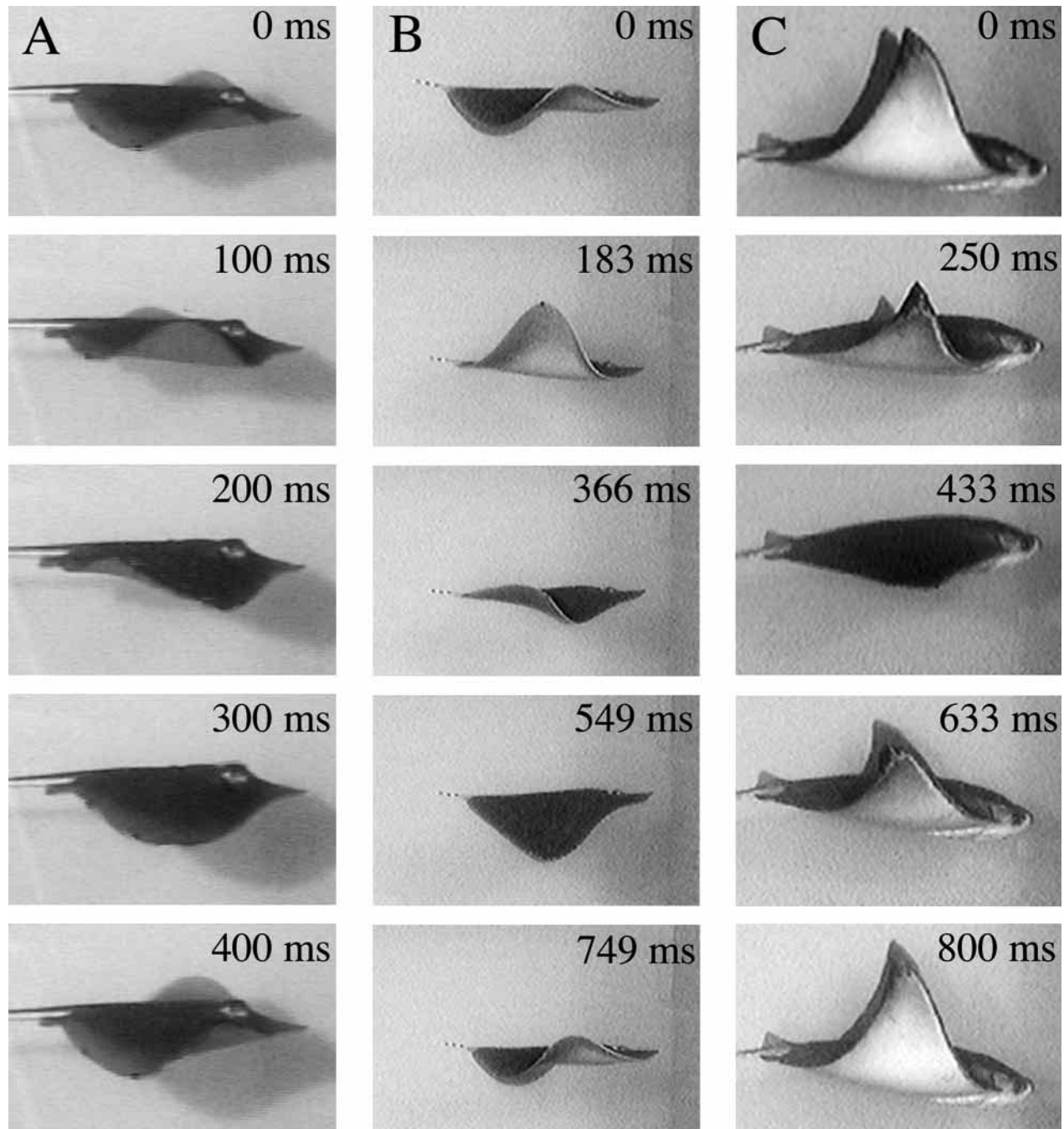


Fig. 5. Successive lateral video images of (A) *Dasyatis sabina*, (B) *Gymnura micrura* and (C) *Rhinoptera bonasus* swimming in a flow tank at $DLs^{-1}=2$. *D. sabina* swims by propagating waves down the pectoral fins from anterior to posterior. *G. micrura* is an intermediate species between undulation and oscillation. *R. bonasus* swims by oscillating the pectoral fins up and down. Anterior is to the right.

behaviors. During slow swimming along the bottom of the tanks and during maneuvering, multiple low-amplitude waves were passed down the distal edges of the fin (undulatory mode). When swimming in the water column, locomotion in *Gymnura micrura* was always more oscillatory. The data for *Gymnura micrura* presented in this paper are from sequences of the individuals using more oscillatory-based locomotion in the water column. Fin-beat frequency is relatively low

(Fig. 2A) and amplitude is moderately high (Fig. 2B) in *Gymnura micrura*.

Rhinoptera bonasus exhibits the oscillatory extreme of pectoral locomotion, with less than half a wave present on the fins (Fig. 5C). The fins move up and down in a flapping motion analogous to flight in birds. The fins do not extend below the ventral body axis during the downstroke in *Rhinoptera bonasus*. Fin-beat frequency is much lower than all the other

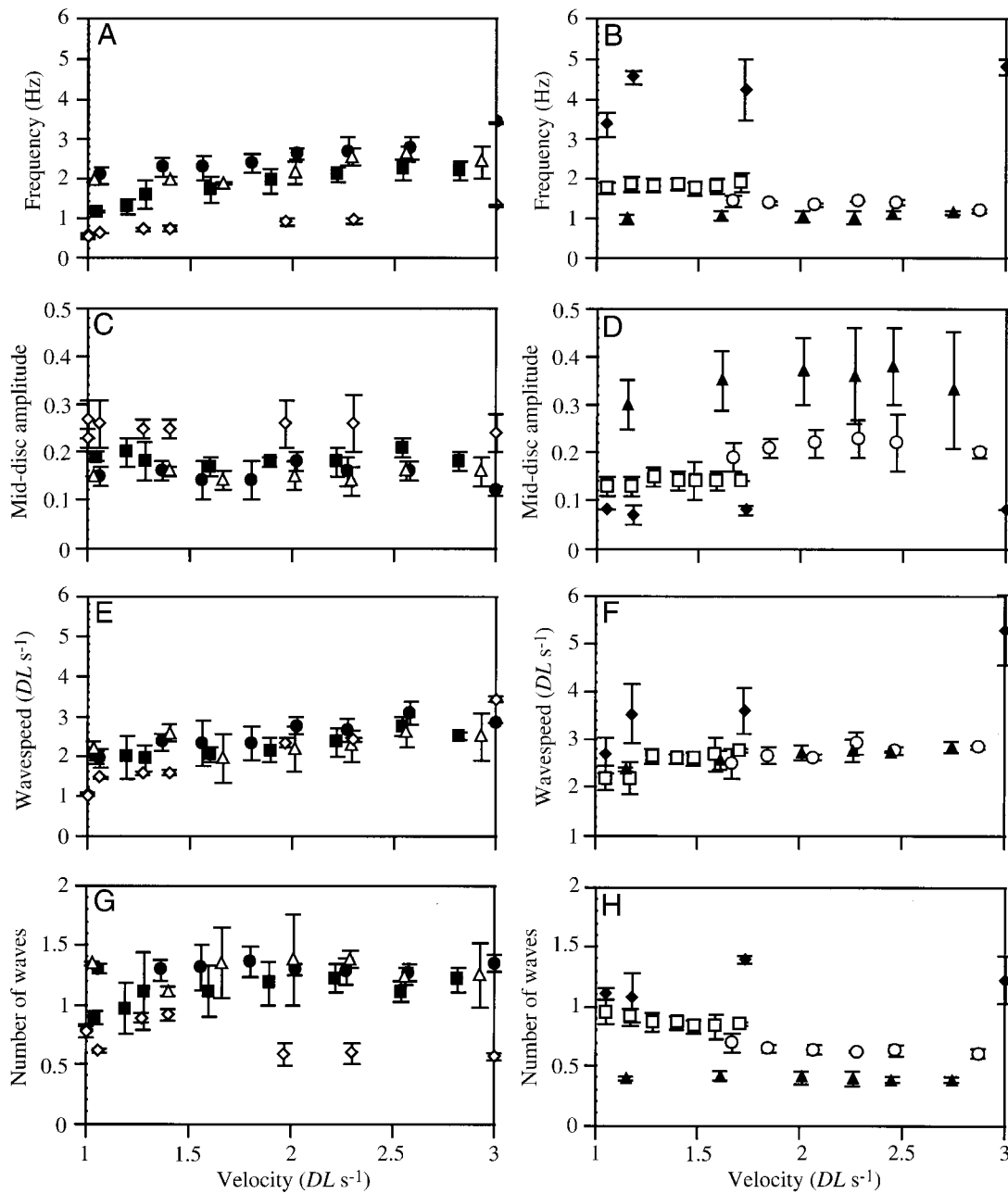


Fig. 6. Variation in kinematic variables with swimming velocity. Graphs down the left-hand side include the *Dasyatis* species; graphs down the right-hand side include the remaining four batoid species. Fin-beat frequency for (A) four *Dasyatis* species and (B) four batoids. Mid-disc amplitude for (C) four *Dasyatis* species and (D) four batoids. Wavespeed for (E) four *Dasyatis* species and (F) four batoids. Wave number for (G) four *Dasyatis* species and (H) four batoids. Symbols represent mean values of each species at each speed: ■, *Dasyatis americana* (N=8); ●, *Dasyatis sabina* (N=9); △, *Dasyatis say* (N=3); ◇, *Dasyatis violacea* (N=3); □, *Raja eglanteria* (N=6); ○, *Gymnura micrura* (N=3); ▲, *Rhinoptera bonasus* (N=6); ◆, *Rhinobatos lentiginosus* (N=5). Error bars represent the standard deviation from mean. DL, disc length.

Table 3. *F ratios from analyses of covariance examining species effects of kinematic variables*

Variable	Velocity	Species	Velocity×species
Fin-beat frequency (Hz)	34.8*	7.3*	8.8*
Mid-disc amplitude	3.6	6.6*	0.7
Wavespeed ($DL\ s^{-1}$)	43.4*	13.3*	3.7*
Number of waves	1.7	12.8*	6.7*
Stride length (cm)	83.5*	9.1*	5.9*
Phase velocity, U/c	104.8*	13.3*	9.7*

*Significant ($P < 0.05$), sequential Bonferroni-corrected.
 DL , disc length; U , swimming speed; c , propulsive wavespeed.

batoids except *Dasyatis violacea* (Fig. 2A), while the amplitude is significantly higher (Fig. 2B).

Kinematics: trends with velocity

The eight batoid species share some general trends in variation of kinematic variables with velocity, but there are key locomotor differences among them (Tables 2, 3). Fin-beat frequency increases significantly with increasing velocity for all *Dasyatis* species (Fig. 6A; Table 2), but remains constant with increasing velocity for the other four species of batoids (Fig. 6B; Table 2). Disc-width-specific amplitude remains constant with changing velocity for all species (Fig. 6C,D; Tables 2, 3). Propulsive wavespeed (in the central region of the fin) increases significantly with increasing speed for all species of *Dasyatis* except *D. say* (Fig. 6E; Table 2) and

increases for *Raja eglanteria* and *Rhinoptera bonasus* (Fig. 6F; Table 2). The number of waves present on the fin (Fig. 6G,H; Tables 2, 3) remains constant with velocity for *D. say*, *D. violacea* and *Rhinoptera bonasus* and decreases significantly with increasing speed for *D. sabina*, *D. americana*, *Rhinobatos lentiginosus*, *Raja eglanteria* and *Gymnura micrura*. Because *Rhinobatos lentiginosus* uses its tail for primary propulsion, it is not included in the graphs for stride length and phase velocity. All species increase stride length significantly with velocity (Fig. 7A,B; Table 2). All batoid species, except *D. violacea*, increase phase velocity significantly with increasing speed (Fig. 7C,D; Table 2). Phase velocity averages between 0.7 and 0.86 for the batoid species.

Discussion

General locomotor behavior

The eight batoid species in this study use different locomotor modes to propel themselves forward through the water. At one extreme is *Rhinobatos lentiginosus*, which uses a combination of axial-based and pectoral-fin-based undulation (Figs 3, 4A); the other seven species use their pectoral fins for swimming through the water. *Rhinobatos lentiginosus* swims in a manner similar to that of typical sharks (Thomson and Simanek, 1977; Webb and Keyes, 1982; Ferry and Lauder, 1996; Lowe, 1996; Wilga and Lauder, 2000) and other basal batoids, such as sawfishes (L. J. Rosenberger, personal observation) and electric rays (Roberts, 1969), that primarily use their thick tails to swim through the water. Wilga and Lauder (2000) found that

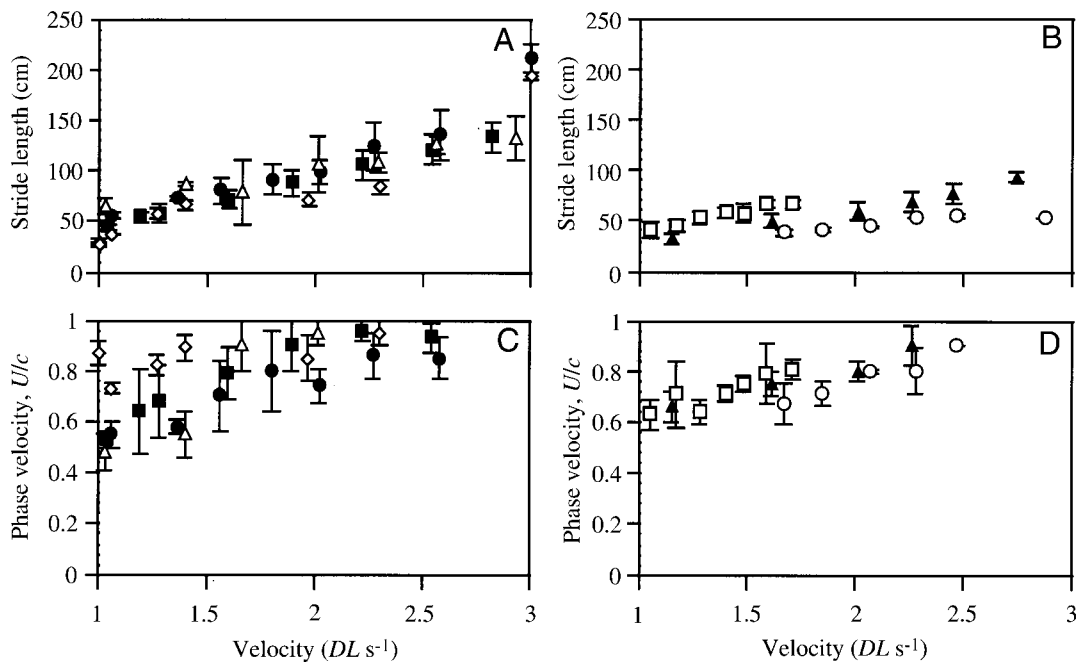


Fig. 7. Variation in kinematic variables with swimming velocity. Stride length for (A) four *Dasyatis* species and (B) three batoid species. Phase velocity for (C) four *Dasyatis* species and (D) three batoid species. Symbols represent mean values of each species at each speed: ■, *Dasyatis americana* ($N=8$); ●, *Dasyatis sabina* ($N=9$); △, *Dasyatis say* ($N=3$); ◇, *Dasyatis violacea* ($N=3$); □, *Raja eglanteria* ($N=6$); ○, *Gymnura micrura* ($N=3$); ▲, *Rhinoptera bonasus* ($N=6$). Error bars represent the standard deviation from mean. DL , disc length; U , swimming speed; c , propulsive wavespeed.

leopard sharks, *Triakis semifasciata*, angle their bodies upwards when swimming steadily in the flow tank to generate lift on the body. *Rhinobatos lentiginosus* also swims at a positive angle when swimming forward, although it is able to maintain a horizontal body position at times. In contrast, other batoid species that use only pectoral-fin-based locomotion maintain fairly horizontal body positions during steady forward swimming. *Rhinobatos lentiginosus* differs from other batoid species studied to date in that it uses the pectoral fins in conjunction with tail-based swimming when it moves up and down in the water column and accelerates. *Rhinobatos lentiginosus* has values of frequency and wavespeed that are much higher and values of amplitude that are much lower than for any other batoid species studied to date. High frequency and wavespeed potentially generate the additional thrust needed to swim. A wave number of 1.2 places *Rhinobatos lentiginosus* within the undulatory locomotor category. The other seven species that use their pectoral fins for swimming vary greatly in their kinematic behavior, with differences in fin-beat frequency, fin amplitude and the degree of undulation present on the fin.

The *Dasyatis* species discussed here are surprisingly variable in their overall swimming behavior. Wave number, which indicates the degree of undulation on the fin, varies greatly among the species. *Dasyatis sabina* and *D. say* do not differ significantly from each other in their kinematic variables (Table 2). They, together with *Rhinobatos lentiginosus*, are the most undulatory of the eight species in this study. By comparison, *Taeniura lymma* averaged 1.4 waves on the fin (Rosenberger and Westneat, 1999), a value that does not differ significantly from those for *Rhinobatos lentiginosus*, *D. say* and *D. sabina*. *D. americana* is slightly less undulatory than *D. sabina* and *D. say*, with an average of 1.1 waves on the fins, and *D. violacea* is intermediate between undulation and oscillation, with 0.74 waves on the fin. Frequency and wave number are significantly lower and amplitude is higher in *D. violacea* than the other *Dasyatis* species. Within the *Dasyatis* species, there is a trade-off between frequency/wave number and amplitude, with *D. violacea* having the lowest frequency and wave number and the highest amplitude and *D. sabina* having the highest frequency and wave number and one of the lowest amplitudes (Fig. 6A,C). This was found to be true within individuals of *Taeniura lymma* (Rosenberger and Westneat, 1999) and among the batoid species in this study as well.

The differences in swimming behavior seen among *Dasyatis* species can be associated to a certain extent with how they live. *Dasyatis sabina*, *D. say* and *D. americana* swim using undulatory locomotion and have a high fin-beat frequency and low amplitude, which is potentially more suited to their benthic lifestyle, allowing high maneuverability for turning quickly, moving backwards and swimming at fairly slow velocities. In contrast, *D. violacea* lives a primarily pelagic lifestyle and has a more oscillatory mode of pectoral locomotion, with lower frequency and higher amplitude, than the other *Dasyatis* species; however, it is considered here to be an intermediate

form. Oscillatory locomotion generates lift, potentially making swimming in the water column more efficient for *D. violacea*. *D. americana* is intermediate in values of frequency, amplitude and wave number among the four *Dasyatis* species and, although it is considered a benthic species, it has a more active lifestyle than *D. sabina* and *D. say*. Having a lower wave number makes the wave on the fin less undulatory, which may be better for quick escapes and distance swimming.

Raja eglanteria borders on intermediate/undulatory fin behavior with a mean of 0.9 waves (Table 2). Daniel (1988) estimated a wave number of 1.5 for his individuals of *R. eglanteria*, which is much higher than was found in the present study. The difference between the two measurements probably has to do with how wave number was determined. He does not give his calculation for wave number, so his value may be estimated from video recordings rather than measured directly (Daniel, 1988). *Raja eglanteria* has a higher wave number at lower speeds, with values just over 1, so it becomes less undulatory as it swims faster. Fin-beat frequency is intermediate compared with the other batoids in the study and is very close in value to that of *Dasyatis americana*. Amplitude is lower in *Raja eglanteria* than in all batoids except *Rhinobatos lentiginosus*. *Raja eglanteria* did not perform as well in the flow tank as the stingrays and did not swim above a velocity of $2DLs^{-1}$. Koester and Spirito (1999) presented data suggesting that primary propulsion in the little skate *Leucoraja erinacea* is performed using the pelvic fins to punt, or 'skate', along the bottom and that pectoral fins are used mainly for swimming over vegetation and other obstacles and for making quick escapes. This might help explain the generally poor swimming performance of the individuals of *Raja eglanteria* examined, if they too, use a more pelvic-based locomotor behavior in general.

Both *Rhinoptera bonasus* and *Gymnura micrura* use a more oscillatory-based behavior when swimming in the water column; *Rhinoptera bonasus* has the most oscillatory behavior of all eight species (Fig. 5C). *Rhinoptera bonasus* swims using broad up- and downstrokes with less than half a wave present on the fins, which can be considered a form of underwater flight. Frequency is quite low, and amplitude is the highest among the eight species in this study. *Rhinoptera bonasus* also exhibits a unique kinematic behavior in fin amplitude compared with other stingrays. During the downstroke, the fins do not extend below the ventral body axis (Fig. 5C), resulting in a fin amplitude that is not as large as one might expect on the basis of the extremely elongated fins. Although this species is found mostly in the water column, it is tied to the bottom for feeding on molluscs and crustaceans (Bigelow and Schroeder, 1953). A possible advantage of avoiding a ventral displacement during the downstroke is to utilize the ventral lateral line canals fully to detect prey better in the substratum. The other species in this study, with the exception of *Dasyatis violacea*, are also tied to the bottom for feeding. They use undulatory locomotion, which does not yield the same degree of substratum disturbance that a full downstroke of oscillatory locomotion produces. Species that are truly pelagic, such as

mobulid and manta rays, exhibit a full downstroke during swimming (Klausewitz, 1964).

Gymnura micrura is the second most oscillatory species in this study, with an average of 0.6 waves on the fin (Table 2). *Gymnura micrura* modifies its swimming behavior on the basis of proximity to the substratum. Small-amplitude undulations of the fin are used when swimming along the bottom, presumably to keep the benthos undisturbed and to allow prey to be detected by the ventral lateral line canals, as found in other stingray species that live on the bottom and use undulatory locomotion. When *Gymnura micrura* is swimming in the water column, a partial sinusoidal wave is propagated along the fin as in other stingrays, and there is a lag time before a new wave begins, producing less than one wave on the fin. Unlike *Rhinoptera bonasus*, the fins extend well below the body axis on the downstroke (Fig. 5B). The direction and speed of the fin movement suggest that the downstroke is probably the major power stroke for *Gymnura micrura* when using the more oscillatory behavior in the water column, at least at high speeds. At its highest swimming speed, *Gymnura micrura* uses a quick and powerful downstroke, with a 'pause' phase at peak upstroke. *Taeniura lymma* was also suggested to use the downstroke primarily as the powerstroke, on the basis of electromyographic data (Rosenberger and Westneat, 1999). In comparison, the bird wrasse (*Gomphosus varius*) was shown to use the upstroke as the power stroke (Walker and Westneat, 1997).

At times, both *Rhinoptera bonasus* and *Gymnura micrura* glided through the water flow keeping the pectoral fins slightly upturned and without movement. This gliding behavior has been observed in many individuals at aquariums throughout the country in addition to the rays in this study. The shape of their discs (Fig. 1) and the upturned fins may provide lift to the body, keeping these rays level and moving forward through the water column. Gliding behavior has also been observed in aquatic birds such as penguins (Clark and Bemis, 1979) at lower swimming speeds.

The major differences found in swimming behavior among batoid fishes can be correlated with their habitat and lifestyle. Batoids that use pectoral undulation (*Taeniura lymma*, *Dasyatis americana*, *D. sabina*, *D. say*, *Raja eglanteria*, *Rhinobatos lentiginosus*) are primarily benthic species that are mostly sedentary, but swim slowly along the bottom to find food. Pectoral oscillation is found in species that live mostly to completely pelagic lives in the water column such as in *D. violacea* and *Rhinoptera bonasus*. *Gymnura micrura*, which spends most of its time in the benthos, utilizes an undulatory behavior on the bottom, but switches to a more oscillatory-based mode when swimming in the water column. Although wavespeed does not differ greatly among batoid species, frequency and wavelength do differ significantly, yielding varying degrees of waviness on the pectoral fins. Undulatory and oscillatory pectoral locomotion in batoids is analogous to rowing (drag-based) and flapping (lift-based) pectoral locomotion in bony fishes, respectively. Undulatory and rowing-based swimmers are specialized for mechanically

efficient low-speed swimming, reduced drag from the body and fins, and a high level of control or maneuverability (Blake, 1983a; Blake, 1983b; Lighthill and Blake, 1990; Walker and Westneat, 2000). In contrast, oscillatory swimmers have a better lift performance (Daniel et al., 1992), are good at efficient steady cruising because of their higher thrust production (Chopra, 1974; Blake, 1983b; Cheng et al., 1991; Daniel et al., 1992) and are believed to be less maneuverable (Blake, 1983b).

Effects of velocity on swimming kinematics in batoid species

The batoid species in this study use different strategies for increasing swimming velocity, which is not surprising because of the extreme range of swimming behavior found in the group. Common kinematic variables that fishes and other aquatic animals modify to change swimming velocity include fin-beat frequency (Gibb et al., 1994; Arreola and Westneat, 1996; Drucker and Jensen, 1996; Gordon et al., 1996; Westneat, 1996; Walker and Westneat, 1997; Rosenberger and Westneat, 1999; Wilga and Lauder, 2000), amplitude (Curren et al., 1994; Fish, 1998), wave number (Rosenberger and Westneat, 1999) and wavespeed (Rosenberger and Westneat, 1999). Because *Rhinobatos lentiginosus* generates most of its propulsive thrust with the tail, it is not surprising that most kinematic variables of fin movement do not change significantly with velocity. *Rhinobatos lentiginosus* swims faster by increasing the tail-beat frequency, as in other tail-based propulsors such as typical sharks (Gray, 1968; Thomson and Simanek, 1977; Webb and Keyes, 1982; Scharold et al., 1989; Lowe, 1996; Wilga and Lauder, 2000), eels (Gillis, 1998), other fishes that use body and caudal fin undulation (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb et al., 1984; Videler, 1993; Dewar and Graham, 1994; Wardle et al., 1995; Webb, 1988) and cetaceans (Curren et al., 1994; Fish, 1998).

Although the four *Dasyatis* species differ somewhat in their general kinematic behavior, they share general trends in kinematic variables with velocity, as might be predicted by their shared common ancestry. Fin-beat frequency, wavespeed and stride length increase significantly with increasing velocity for all *Dasyatis* species, except wavespeed in *D. say*. Mid-disc amplitude remains constant for all *Dasyatis* species, and the number of waves along the fin remains constant with velocity for *D. say* and *D. violacea* and decreases in *D. americana* and *D. sabina*. Mid-disc amplitude is assumed to have little effect on swimming speed. Overall, these results are consistent with data from the blue-spot stingray *Taeniura lymma* (Rosenberger and Westneat, 1999). The five species of dasyatid stingrays examined to date (including *Taeniura lymma*) use similar strategies for increasing swimming speed by increasing fin-beat frequency and wavespeed. Fin-beat frequency and wavespeed are likely to be easier for the rays to modify than other kinematic variables because the onset times for muscle firing change over a range of swimming velocities (Rosenberger and Westneat, 1999). Phase velocity averaged between 0.76 and 0.86, which is within the range found for *T. lymma* (Rosenberger and Westneat, 1999) and is similar to the

value for the skate *Raja eglanteria* (Daniel, 1988; this study). Values of phase velocity below 1 indicate that fin or body waves are moving backwards at a faster speed than the forward speed of the fish, therefore generating thrust.

Raja eglanteria uses a different strategy to increase swimming speed from the other batoids studied. *Raja eglanteria*, a mostly undulatory species, decreases wave number significantly (Fig. 6H; Table 2) and increases wavespeed significantly (Fig. 6F; Table 2) to increase swimming velocity. These results are somewhat different from those found for undulatory stingrays in the family Dasyatidae. As discussed above, three of the four *Dasyatis* stingrays increase both frequency and wavespeed, keeping wave number and amplitude constant. *Taeniura lymma* (Rosenberger and Westneat, 1999) and *Dasyatis americana* increase frequency and wavespeed and decrease wave number, but hold amplitude constant. All these species fall more towards the undulatory extreme of the continuum, but differ in their relationships to each other. Skates and stingrays are thought to have evolved independently from different 'guitarfish-like' ancestors (McEachran et al., 1996) that probably used a combination of axial and pectoral locomotion similar to *Rhinobatos lentiginosus* in this study. If true, *Raja eglanteria* and its other skate relatives have evolved strict pectoral locomotion independently from the stingrays, which may help to explain the observed differences in strategies for increasing swimming velocity. Additional species of skates should be studied to determine whether they modify their swimming behavior in a similar manner to *Raja eglanteria* to test the independent origins hypothesis and to explore the potential diversity in behavior based on differences in disc shape found among skates.

Rhinoptera bonasus and *Gymnura micrura* use similar strategies to modify kinematic variables to increase swimming velocity that are different from those used by more undulatory rays. *Rhinoptera bonasus* significantly increases wavespeed to increase velocity (Fig. 6F; Table 2) rather than frequency, amplitude or wave number. In addition, Heine (1992) found that *Rhinoptera bonasus* increased the speed at which the distal fin tip moved through the water (fin-tip velocity), keeping frequency, amplitude and the angle of attack of the fin constant. *Gymnura micrura* significantly decreases wave number, but maintains other kinematic variables constant with speed increase (Fig. 6H; Table 2). *Gymnura micrura* also uses a similar strategy to *Rhinoptera bonasus* by increasing the velocity of fin-tip movement through the water to increase swimming speed. At the highest flow speeds, *Gymnura micrura* exhibits a pause phase between fin beats; the fins move down then quickly up, pause, then repeat the quick fin beat. Frequency remains constant, while fin-tip velocity increases with speed. These strategies are very different from those of the undulatory rays (Rosenberger and Westneat, 1999; present study) and other fishes with lift-based oscillatory locomotion such as pectoral fin flappers (Webb, 1973; Drucker and Jensen, 1996; Westneat, 1996; Walker and Westneat, 1997), tail oscillators (Webb and Keyes, 1982; Dewar and Graham, 1994;

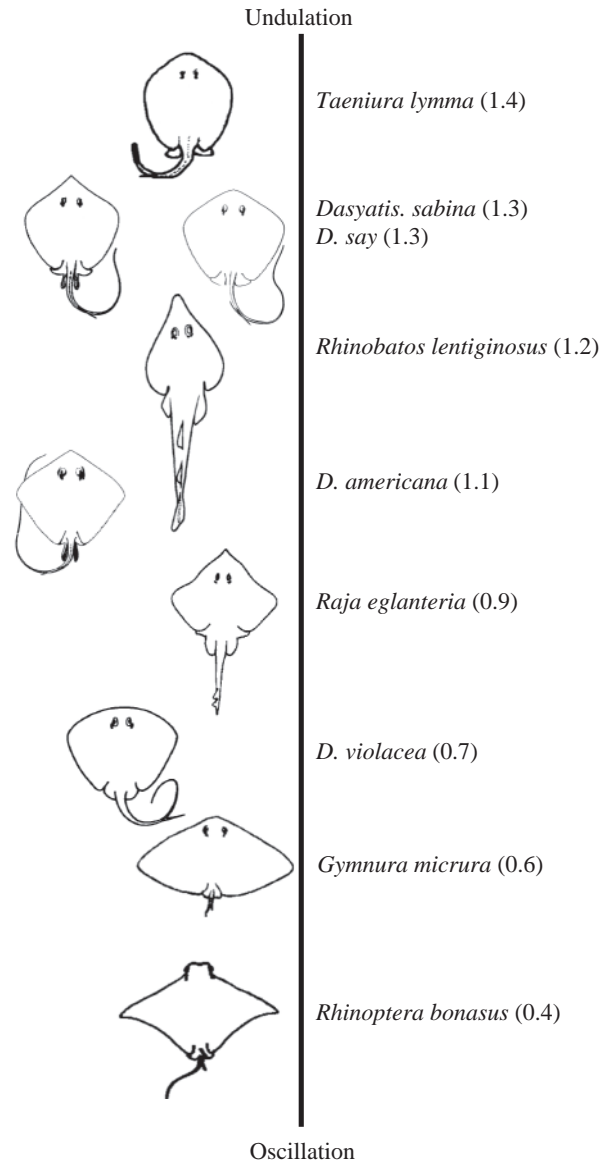


Fig. 8. Diagram illustrating the undulation-to-oscillation continuum for the nine batoid species studied to date. The mean wave number for each species is given in parentheses.

Lowe, 1996) and flapping aquatic birds (Clark and Bemis, 1979; Baudinette and Gill, 1985) that increase their frequency. *Gymnura micrura* and *Rhinoptera bonasus* belong to the same clade of stingrays, with *Gymnura micrura* as the most basal member of the group (Lovejoy, 1996; McEachran et al., 1996). The strategy of changing the fin-tip velocity to change swimming speed in both *Gymnura micrura* and *Rhinoptera bonasus* could be due to their shared ancestry, as is predicted for the *Dasyatis* species.

Pectoral locomotion in batoid fishes: the undulation/oscillation continuum

Batoid fishes show an amazing amount of diversity in their swimming behavior, including axial-based locomotion, a

combination of axial- and pectoral-fin-based locomotion and strict pectoral-fin-based locomotion that falls along a continuum between undulation and oscillation. This discussion focuses on nine batoid species (including *Taeniura lymma*; Rosenberger and Westneat, 1999) that fall at different points along a continuum between undulatory and oscillatory pectoral fin locomotion (Fig. 8). Traditionally, locomotor behavior in batoids has been divided into discrete categories (Breder, 1926; Lindsey, 1978; Webb, 1994; Webb, 1998) of undulation ('rajiform', more than one wave on the fin or body) and oscillation ('mobuliform', less than half a wave on the fin or body) on the basis of the number of waves present. Undulatory pectoral locomotion is the most common mode of swimming among the batoid fishes and is located at one extreme of the undulation/oscillation continuum. Five of the nine batoid species studied, including *Taeniura lymma*, *Dasyatis sabina*, *D. say*, *D. americana* and *Rhinobatos lentiginosus*, fall within the definition of undulation because they have more than one wave present (Fig. 8), although *D. americana* has a wave range that falls below the undulation 'boundary' (Table 2). A number of fishes have multiple waves on the body or fin (anguillids, gymnotoids, *Amia calva*), but the current category of 'undulation' does not provide an adequate distinction among the wave numbers that can occur in different fish species. *Rhinoptera bonasus* is the only species of the nine studied that exhibits oscillatory behavior as defined as having less than half a wave present on the fin. Mobulid rays (Klauewitz, 1964) and the other myliobatid stingrays, including bat rays (Heine, 1992) and eagle rays, also have oscillatory-based locomotion. Three of the nine batoid species (*Raja eglanteria*, *Dasyatis violacea* and *Gymnura micrura*) examined to date have between half and one wave on the body or fin (Fig. 8), making them intermediate in swimming mode.

Although locomotor behavior has traditionally been placed into discrete categories, there is a continuum of behavior among species of batoid (Fig. 8). The nine batoid species are mapped onto the undulation/oscillation continuum (Fig. 8) on the basis of wave number to emphasize the existence of a continuum in swimming behavior among these fishes. Discrete categories can be useful for quickly identifying a broadly defined swimming mode, but they do not reflect subtle differences in swimming behavior within and among species, and categories are not divided on the basis of biological relevance. Another problem is that some species, such as *Gymnura micrura*, modify their swimming behavior on the basis of where they are swimming in the water column. As discussed above, *Gymnura micrura* passes multiple waves along the fins when swimming slowly along the bottom, but switches to a more flapping behavior when swimming in the water column, suggesting that it should fit into both categories of undulation and oscillation. *Dasyatis americana* modifies its behavior with swimming speed, becoming less undulatory at higher swimming speeds. *Rhinobatos lentiginosus* uses both axial-based and pectoral-fin-based modes, making it difficult to categorize. While locomotor

categories such as 'carangiform', 'amiiform' and 'rajiform' continue to be useful for a quick description of a fish's general swimming behavior, the limitations to such a system should be considered. In short, diversity of locomotor behavior within and among species is hidden by broad, artificial categories, which have been erected subjectively and do not necessarily reflect biologically relevant behavioral differences among fishes. As additional locomotor behaviors among fish species are described in detail, it may be possible then to divide behaviors into categories on the basis of biomechanical relevance rather than only the number of waves present on the fins or body.

Batoid fishes use multiple modes of behavior to move through the water. The majority of batoid species, including skates, stingrays and the electric ray *Hypnos monopterygium* (Michael, 1993), use strict pectoral-fin-based locomotion. Only a few groups, such as the sawfishes and most electric rays (Roberts, 1969), use strict axial-based locomotion. The remaining species (guitarfishes and some electric rays) use a combination of the two. Previous and current research on swimming behavior has focused almost exclusively on pectoral-fin-based locomotion, making axial and combination locomotor behaviors ripe for study. This study provides a foundation of knowledge on the kinematic behavior of pectoral fin locomotion in several species of batoid that range from undulation to oscillation. The kinematic data presented here and previously pose questions for future study including how muscle behavior differs between undulatory and oscillatory species and how different species generate propulsive thrust. The extreme ecological and locomotor diversity in batoids provides an excellent opportunity to investigate the ecomorphology of locomotion in the group as well.

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References

- Arreola, V. I. and Westneat, M. W.** (1996). Mechanics of propulsion by multiple fins: kinematics of aquatic locomotion in the burrfish (*Chilomycterus schoepfi*). *Proc. R. Soc. Lond. B* **263**, 1689–1696.
- Bainbridge, R.** (1958). The speed of swimming of fish as related to size and to frequency and amplitude of the tail beat. *J. Exp. Biol.* **35**, 109–133.
- Baudinette, R. V. and Gill, P.** (1985). The energetics of flying and paddling in water: locomotion in penguins and ducks. *J. Comp. Physiol. B* **155**, 373–380.
- Bigelow, H. B. and Schroeder, W. C.** (1953). Sawfishes, guitarfishes, skates and rays. In *Fishes of the Western North Atlantic*. New Haven: Sears Foundation for Marine Research.
- Blake, R. W.** (1983a). Swimming in the electric eels and knifefishes. *Can. J. Zool.* **61**, 1432–1441.
- Blake, R. W.** (1983b). Median and paired fin propulsion. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 215–247. Praeger.
- Breder, C. M.** (1926). The locomotion of fishes. *Zoologica* **50**, 159–297.
- Campbell, B.** (1951). The locomotor behavior of spinal elasmobranchs with an analysis of stinging in *Urobatis*. *Copeia* **1951**, 277–284.
- Carvalho, M.** (1996). Higher-level elasmobranch phylogeny, basal squalians and paraphyly. In *Interrelationships of Fishes* (ed. M. Stiassny, L. Parenti and G. Johnson), pp. 35–62. New York: Academic Press.
- Cheng, J., Zhuang, L. and Tong, B.** (1991). Analysis of swimming three-dimensional waving plates. *J. Fluid Mech.* **232**, 341–355.
- Chopra, M. G.** (1974). Hydromechanics of lunata-tail swimming propulsion. *J. Fluid Mech.* **64**, 375–391.
- Clark, B. D. and Bemis, W.** (1979). Kinematics of swimming penguins at the Detroit Zoo. *J. Zool., Lond.* **188**, 411–428.
- Compagno, L. J. V.** (1999). Systematics and body form. In *Sharks, Skates and Rays: The Biology of Elasmobranch Fishes* (ed. W. C. Hamlett), pp. 1–42. Baltimore, MD: John Hopkins University Press.
- Curren, K. C., Bose, N. and Lien, J.** (1994). Swimming kinematics of a harbor porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*). *Mar. Mammal. Sci.* **10**, 485–492.
- Daniel, T. L.** (1988). Forward flapping flight from flexible fins. *Can. J. Zool.* **66**, 630–638.
- Daniel, T., Jordan, C. and Grunbaum, D.** (1992). Hydromechanics of swimming. In *Advances in Comparative and Environmental Physiology*, vol. 11, *Mechanics of Animal Locomotion* (ed. R. McN. Alexander), pp. 17–49. Berlin: Springer-Verlag.
- Dewar, H. and Graham, J. B.** (1994). Studies of tropical tuna swimming performance in a large water tunnel. *J. Exp. Biol.* **192**, 45–59.
- Drucker, E. G. and Jensen, J. S.** (1996). Pectoral fin locomotion in the striped surfperch. I. Kinematic effects of swimming speed and body size. *J. Exp. Biol.* **199**, 2235–2242.
- Eschmeyer, W. N., Herald, E. S. and Hamman, H.** (1983). *Pacific Coast Fishes*. Boston, MA: Houghton Mifflin Company.
- Ferry, L. A. and Lauder, G. V.** (1996). Heterocercal tail function in leopard sharks: a three-dimensional kinematic analysis of two models. *J. Exp. Biol.* **199**, 2253–2268.
- Fish, F. E.** (1998). Comparative kinematics and hydrodynamics of odontocete cetaceans: morphological and ecological correlates with swimming performance. *J. Exp. Biol.* **201**, 2867–2877.
- Gibb, A. C., Jayne, B. C. and Lauder, G. V.** (1994). Kinematics of pectoral fin locomotion in the bluegill sunfish *Lepomis macrochirus*. *J. Exp. Biol.* **189**, 133–161.
- Gillis, G. B.** (1998). Environmental effects on undulatory locomotion in the American eel *Anguilla rostrata*: kinematics in water and on land. *J. Exp. Biol.* **201**, 949–961.
- Gordon, M. S., Plaut, I. and Kim, D.** (1996). How puffers (Teleostei: Tetraodontidae) swim. *J. Fish Biol.* **49**, 319–328.
- Gray, J.** (1968). *Animal Locomotion*. New York: W. W. Norton & Co. Inc.
- Heine, C.** (1992). Mechanics of flapping fin locomotion in the cownose ray, *Rhinoptera bonasus* (Elasmobranchii: Myliobatidae). PhD dissertation, Duke University, Durham, NC, USA.
- Hunter, J. R. and Zweifel, J. R.** (1971). Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus* and other fishes. *Fish. Bull.* **69**, 253–266.
- Klausewitz, W.** (1964). Der Lokomotionsmodus der Flugelrochen (Myliobatoidei). *Zool. Anz.* **173**, 110–120.
- Klausewitz, W.** (1965). Die Bewegungsweise der Geigenrochen – aus Funktioneller und Stammesgeschichtlicher sicht. *Natur Museum* **95**, 97–108.
- Koester, D. M. and Spirito, C. P.** (1999). Pelvic fin locomotion in the skate, *Leucoraja erinacea*. *Am. Zool.* **39**, 55A.
- Lighthill, J. and Blake, R. W.** (1990). Biofluidynamics of balistiform and gymnotiform locomotion. Part 1. Biological background and analysis of elongated-body theory. *J. Fluid Mech.* **212**, 183–207.
- Lindsey, C. C.** (1978). Form, function and locomotory habits of fish. In *Fish Physiology*, vol. 7, *Locomotion* (ed. W. S. Hoar and D. J. Randall), pp. 1–100. New York: Academic Press.
- Lovejoy, N.** (1996). Systematics of myliobatoid elasmobranchs: With emphasis on the phylogeny and historical biogeography of neotropical freshwater stingrays (Potamotrygonidae: Rajiformes). *Zool. J. Linn. Soc.* **117**, 207–257.
- Lowe, C. G.** (1996). Kinematics and critical swimming speed of juvenile scalloped hammerhead sharks. *J. Exp. Biol.* **199**, 2605–2610.
- Magnan, A.** (1930). Les caracteristiques geometriques et physiques des poissons. Deuxieme partie. *Ann. Sci. Nat. Zool.* **13**, 134–269.
- Marey, E. J.** (1893). Des mouvements de natation de la raie. *C.R. Acad. Sci. Paris* **116**, 77–81.
- McEachran, J., Dunn, K. and Miyake, T.** (1996). Interrelationships of the batoid fishes (Chondrichthyes: Batoidea). In *Interrelationships of Fishes* (ed. M. Stiassny, L. Parenti and G. Johnson), pp. 63–84. New York: Academic Press.
- Michael, S. W.** (1993). *Reef Sharks and Rays of the World*. Monterey: Sea Challengers.
- Miyake, T. J. D., McEachran, P. J. and Hall, B. K.** (1992). Development and morphology of rostral cartilages in batoid fishes (Chondrichthyes: Batoidea), with comments on homology within vertebrates. *Biol. J. Linn. Soc.* **46**, 259–298.
- Nelson, J. S.** (1994). *Fishes of the World*. New York: John Wiley & Sons.
- Rice, W. R.** (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- Roberts, B. L.** (1969). The buoyancy and locomotory movements of electric rays. *J. Mar. Biol. Ass. UK* **49**, 621–640.
- Rosenberger, L. J. and Westneat, M. W.** (1999). Functional morphology of undulatory pectoral fin locomotion in the stingray *Taeniura lymma*. *J. Exp. Biol.* **202**, 3523–3539.
- Scharold, J., Lai, N. C., Lowell, W. R. and Graham, J. B.** (1989). Metabolic rate, heart rate and tailbeat frequency during sustained

- swimming in the leopard shark *Triakis semifasciata*. *Exp. Biol.* **48**, 223–230.
- Shirai, S.** (1996). Phylogenetic interrelationships of neoselachians (Chondrichthyes: Euselachii). In *Interrelationships of Fishes* (ed. M. Stiassny, L. Parenti and G. Johnson), pp. 9–34. New York: Academic Press.
- Thomson, K. S. and Simanek, D. E.** (1977). Body form and locomotion in sharks. *Am. Zool.* **17**, 343–354.
- Videler, J. J.** (1993). *Fish Swimming*. London: Chapman & Hall.
- Walker, J. A. and Westneat, M. W.** (1997). Labriform propulsion in fishes: kinematics of flapping aquatic flight in the bird wrasse *Gomphosus varius* (Labridae). *J. Exp. Biol.* **200**, 1549–1569.
- Walker, J. A. and Westneat, M. W.** (2000). Mechanical performance of aquatic rowing and flying. *Proc. R. Soc. Lond. B* **267**, 1875–1881.
- Wardle, C. S., Videler, J. J. and Altringham, J. D.** (1995). Tuning in to fish swimming: body form, swimming mode and muscle function. *J. Exp. Biol.* **198**, 1629–1636.
- Webb, P. W.** (1973). Kinematics of pectoral fin propulsion in *Cymatogaster aggregata*. *J. Exp. Biol.* **59**, 697–710.
- Webb, P. W.** (1988). Simple physical principles and vertebrate aquatic locomotion. *Am. Zool.* **28**, 709–725.
- Webb, P. W.** (1994). The biology of fish swimming. In *Mechanics and Physiology of Animal Swimming* (ed. L. Maddock, Q. Bone and J. M. V. Rayner), pp. 45–62. Cambridge: Cambridge University Press.
- Webb, P. W.** (1998). Swimming. In *The Physiology of Fishes*, second edition (ed. D. H. Evans), pp. 3–24. New York: CRC Press.
- Webb, P. W. and Keyes, R. S.** (1982). Swimming kinematics of sharks. *Fish. Bull.* **80**, 803–812.
- Webb, P. W., KostECKI, P. T. and Stevens, E. D.** (1984). The effect of size and swimming speed on locomotor kinematics of rainbow trout. *J. Exp. Biol.* **109**, 77–95.
- Westneat, M. W.** (1996). Functional morphology of aquatic flight in fishes: Mechanical modeling, kinematics and electromyography of labriform locomotion. *Am. Zool.* **36**, 582–598.
- Wilga, C. D. and Lauder, G. V.** (2000). Three-dimensional kinematics and wake structure of the pectoral fins during locomotion in leopard sharks, *Triakis semifasciata*. *J. Exp. Biol.* **203**, 2261–2278.