

KINEMATICS AND CRITICAL SWIMMING SPEED OF JUVENILE SCALLOPED HAMMERHEAD SHARKS

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Summary

Kinematics and critical swimming speed (U_{crit}) of juvenile scalloped hammerhead sharks *Sphyrna lewini* were measured in a Brett-type flume (635 l). Kinematic parameters were also measured in sharks swimming in a large pond for comparison with those of sharks swimming in the flume. Sharks in the flume exhibited a mean U_{crit} of $65 \pm 11 \text{ cm s}^{-1}$ (\pm S.D.) or 1.17 ± 0.21 body lengths per second ($L s^{-1}$), which are similar to values for other species of sharks. In both the flume and pond, tailbeat frequency (TBF) and stride length (L_S) increased linearly with increases in relative swimming speed (U_{rel} =body lengths traveled per second). In the flume, tailbeat amplitude (TBA) decreased with increasing speed whereas TBA did

not change with speed in the pond. Differences in TBF and L_S between sharks swimming in the flume and the pond decreased with increases in U_{rel} . Sharks swimming at slow speeds (e.g. $0.55 L s^{-1}$) in the pond had L_S 19% longer and TBF 21% lower than sharks in the flume at the same U_{rel} . This implies that sharks in the flume expended more energy while swimming at comparable velocities. Comparative measurements of swimming kinematics from sharks in the pond can be used to correct for effects of the flume on shark swimming kinematics and energetics.

Key words: hammerhead shark, swimming, critical speed, flume, *Sphyrna lewini*.

Introduction

A large number of studies have examined the swimming performance and kinematics of teleosts (e.g. Brett, 1964; Hunter and Zweifel, 1971; Dewar and Graham, 1994). Fewer studies have focused on elasmobranchs (e.g. Webb and Keyes, 1982; Graham *et al.* 1990; Parsons, 1990). Also, while most studies of swimming performance and kinematics have been conducted either in flumes, annular tanks (Graham *et al.* 1990; Magnuson, 1978; Parsons, 1990) or large pools (Webb and Keyes, 1982; Weihs *et al.* 1981), none has yet compared the kinematics of the same species in a flume and in a large pond, pool or annular tank. It is not well understood how flumes affect the swimming kinematics and energetics of a particular fish, and since most information regarding active metabolism in fishes is derived from flume studies, field comparisons of kinematics may provide a way of correcting for possible flume effects.

Kaneohe Bay, Oahu, Hawaii, is a pupping and nursery ground for the scalloped hammerhead shark *Sphyrna lewini*, and hammerhead shark pups are the most abundant top-level predator in the bay (Clarke, 1971). A telemetry study conducted by Holland *et al.* (1992, 1993) demonstrated that hammerhead shark pups in Kaneohe Bay form loose schools, swimming just above the substratum during the day, and disperse at night to forage around the bases of the patch reefs.

These data, along with observations of hammerhead sharks in tanks and large ponds, indicate that they are obligate swimmers. Since these sharks are continuously active, knowledge of their swimming behavior is especially important to understanding their energetics.

In the present study, the kinematics and critical swimming speed (maximum aerobically sustainable swimming speed, U_{crit}) of juvenile scalloped hammerhead sharks *Sphyrna lewini* were measured using a large flume-respirometer, and the results were compared with studies of other sharks (Graham *et al.* 1990; Scharold *et al.* 1989; Gruber, 1992). In order to determine whether the flume affected swimming performance, the kinematics of hammerhead sharks in the flume were compared with those of sharks of the same size, free-swimming in a large pond.

Materials and methods

Juvenile scalloped hammerhead sharks *Sphyrna lewini* (Griffith and Smith) were collected from Kaneohe Bay using hand lines with barbless hooks. Sharks were immediately transported to the laboratory and placed in a 4 m diameter pool with flow-through sea water. Sharks were fed squid, and usually accepted food within 24 h of capture.

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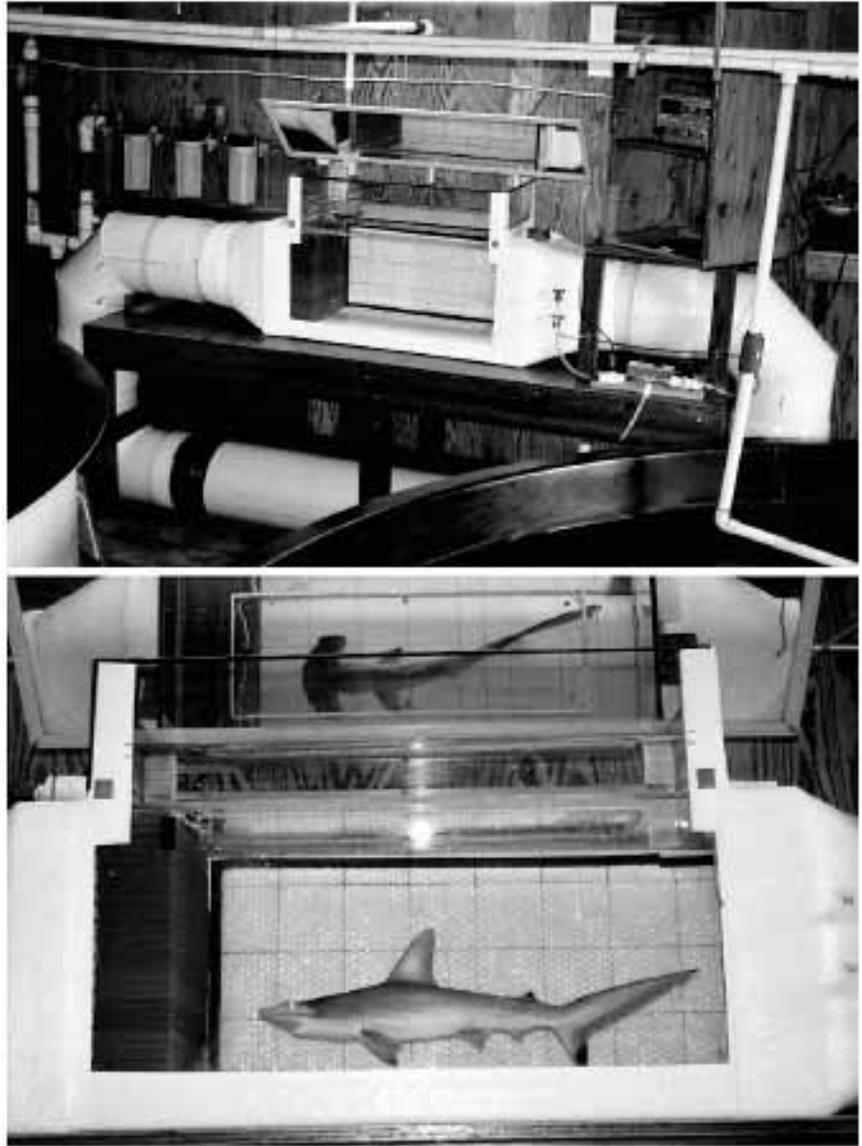


Fig. 1. A Brett-style flume-respirometer (volume 6351) used to swim juvenile scalloped hammerhead sharks. Grid marks on the back wall and bottom of the swimming chamber are 10 cm \times 10 cm. The shark in the lower photograph is 62 cm total length.

Measurements of kinematics and U_{crit} were made from sharks exercised in a 6351 Brett-type recirculating flume-respirometer (Fig. 1) housed at the Hawaii Institute of Marine Biology, Oahu, Hawaii. Water was moved through a vertically standing loop of 30.5 cm diameter polyvinylchloride (PVC) pipe by a 12 V trolling motor suspended in the lower portion of the loop. The swimming chamber was 100 cm long \times 40 cm wide \times 40 cm high and was constructed of 1 cm thick clear acrylic. A fine mesh (1.5 mm²) stainless-steel screen and two walls of flow straighteners were placed in front of the chamber. The first wall of flow straighteners consisted of 2.5 cm diameter PVC pipes with longer pipes located in the center of the wall to increase the skin resistance and slow down the faster moving water in the middle. The second wall (located 3 cm downstream) consisted of a 10 cm thick wall of 1 cm diameter straws. Dye tests revealed turbulence and eddies in the corners of the swimming chamber, but the movement of water in the center section was rectilinear. Water velocity was measured

and calibrated by timing the movement of dye injected into the center of the swimming chamber.

Critical swimming speed

Critical swimming speeds of 11 hammerhead sharks were measured using methods described by Graham *et al.* (1990). Attempts to acclimate the shark pups in the flume overnight were unsuccessful and resulted in high mortality. Consequently, sharks were placed in the swimming section of the flume at a starting velocity of 26 cm s⁻¹ (approximately 0.5 L s⁻¹; the slowest velocity the sharks would maintain) and, after 30 min at the initial speed, the water velocity was increased by 10 cm s⁻¹ increments every 30 min until the sharks became exhausted and could no longer maintain their position in the flume. The 30 min swimming duration and 10 cm s⁻¹ velocity increment were selected in order to make direct comparisons with sharks studied by Graham *et al.* (1990).

Critical swimming speed was determined using an equation described by Brett (1964):

$$U_{\text{crit}} = U_f + [(T_f/T_i)U_i], \quad (1)$$

where U_f is the highest speed that the shark is able to maintain for the entire 30 min period, T_f is the time (<30 min) the shark was able to swim at the final (next highest) speed, T_i is the time interval (30 min) and U_i is the speed increment by which the velocity was increased (10 cm s^{-1}). Water temperature (to $24 \pm 2 \text{ }^\circ\text{C}$) and oxygen concentration (to $5.81 \pm 0.59 \text{ mg l}^{-1}$) were monitored throughout each run using a YSI oxygen meter with a BOD oxygen probe. No solid blocking correction was applied since the hammerhead sharks in this study only occupied approximately 2% (<10%) of the cross-sectional area of the swimming chamber of the flume (Webb, 1971).

Kinematics

Sharks were videotaped (at 30 frames s^{-1}) at each swimming speed in both dorsal and lateral views and kinematics were determined using frame-by-frame analysis. Tailbeat amplitude was determined by measuring the maximum distance that the tip of the shark's tail moved from one lateral extent to the other. Tailbeat frequency was determined by counting the number of complete tailbeat cycles in 1 min. Stride length (defined as the distance the shark traveled per tail beat) was calculated as:

$$L_S = U/TBF, \quad (2)$$

where L_S is stride length (in cm), U is swimming velocity (in cm s^{-1}) and TBF is tailbeat frequency (in beats s^{-1}) (Videler and Wardle, 1991). Each parameter was measured up to 30 times over the course of each 30 min test period. The means for each period were used for analysis. Only recordings from sharks exhibiting steady swimming in the center of the flume were used for analysis.

Nine shark pups were collected from the bay and placed in a large seawater pond ($40 \text{ m} \times 30 \text{ m}$; mean depth 1 m).

Individuals were videotaped using a camera suspended 3 m above the water surface as they cruised over a $2 \text{ m} \times 2 \text{ m}$ grid placed on the sand. Data were recorded only if the sharks were swimming in a straight path for at least 3 m before crossing the grid and at a constant speed (determined by monitoring TBF) and depth. To determine more precisely whether sharks were swimming at a constant speed, detailed video analyses were used to quantify the sharks course and velocity across the grid. A shark was determined to be swimming at a constant speed if it moved at a constant distance per video frame over the course of the grid. Tailbeat amplitude, tailbeat frequency, swimming velocity and stride length were determined from analysis of video tapes.

Only data points which were within the same range of swimming speeds were used to compare kinematics between the flume and the pond.

Values are presented as means \pm S.D. (unless stated otherwise).

Results

Critical swimming speed

Sharks exhibited a mean U_{crit} of $65 \pm 11 \text{ cm s}^{-1}$ or $1.17 \pm 0.21 \text{ L s}^{-1}$ (\pm S.D.) (Table 1). Water temperature and dissolved oxygen concentration from U_{crit} experiments are also included in Table 1. No correlation was found between water temperature and U_{crit} ($r=0.15$) or between O_2 concentration and U_{crit} ($r=0.065$).

Kinematics

Sharks exercised in the flume (mean total length $57.3 \pm 3.2 \text{ cm}$) were the same size as those observed in the pond ($59.8 \pm 3.4 \text{ cm}$) (Student's t -test: $t=1.75$, d.f.=16, $P=0.1$). Sharks observed in the pond swam at a variety of speeds, ranging from 31 to 102 cm s^{-1} (0.56 – 1.68 L s^{-1}) (mean $60 \pm 18 \text{ cm s}^{-1}$ or $1.00 \pm 0.28 \text{ L s}^{-1}$). Over the range of speeds used for kinematic

Table 1. Critical swimming speed experiment data

Total length (cm)	Wet mass (kg)	Water temperature ($^\circ\text{C}$)	Dissolved O_2 concentration (mg l^{-1})	U_{crit} (cm s^{-1})	U_{crit} (L s^{-1})
52	0.614	26.5–27.0	5.17–4.49	47.6	0.91
59	0.684	24.5–25.0	5.56–5.02	56.2	0.95
52	0.511	23.1–23.6	5.62–5.07	56.6	1.09
53	0.551	22.8–23.6	6.37–5.52	67.4	1.26
53*	0.551	22.5–22.8	5.99–5.60	57.5	1.07
60	0.699	22.8–23.8	6.06–5.06	83.1	1.38
54	0.550	22.8–23.2	5.70–5.15	63.2	1.16
56	0.675	21.6–21.9	6.91–6.05	73.7	1.31
58	0.725	22.3–22.6	6.91–6.43	57.4	0.99
58	0.650	23.3–23.7	7.02–6.42	56.8	0.98
54	0.548	24.6–25.3	6.38–5.46	76.8	1.42
52	0.548	26.2–28.6	6.50–5.65	80.0	1.55

* represents replicate run on the same shark.

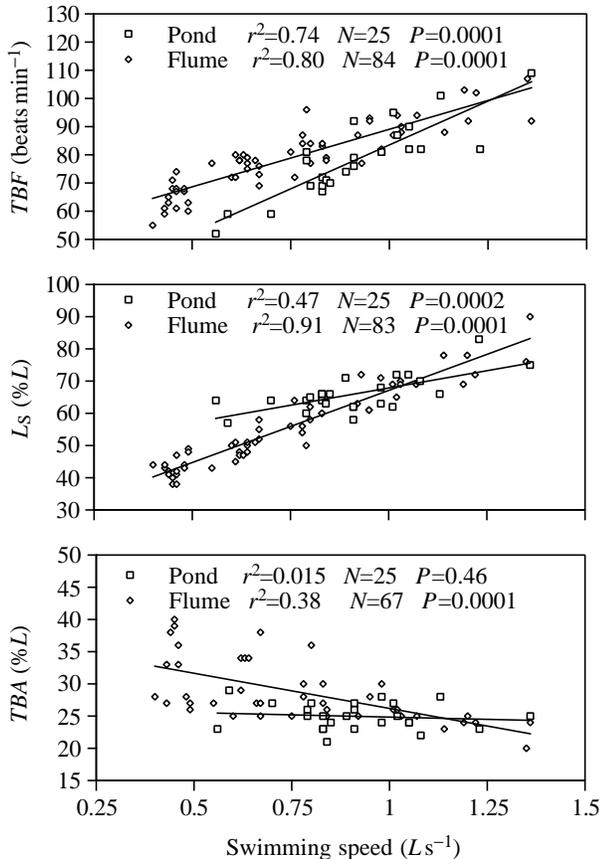


Fig. 2. Kinematic parameters of juvenile scalloped hammerhead sharks observed in the flume and the pond over a range of swimming speeds given in body lengths per second ($L s^{-1}$). TBF , tailbeat frequency in beats min^{-1} ; L_S , stride length as a percentage of the shark's total length (% L); TBA , tailbeat amplitude as a percentage of the shark's total length (% L).

comparisons between the flume and pond sharks ($35\text{--}73\text{ cm s}^{-1}$ or $0.62\text{--}1.36 L s^{-1}$), both groups exhibited similar anguilliform-to-subcarangiform swimming movements.

At speeds up to $1 L s^{-1}$, sharks in the pond had lower mean TBF , longer L_S and shorter TBA values than sharks in the flume at the same U_{rel} (Fig. 2). TBF and L_S of sharks increased linearly with increases in U_{rel} in both the flume and the pond. Whereas TBA of sharks in the flume decreased as U_{rel} increased, no relationship was found between TBA and U_{rel} for sharks observed in the pond (Fig. 2).

There were significant differences in the slopes of TBF , L_S and TBA versus U_{rel} between sharks in the flume experiments and the pond. Tailbeat frequencies of sharks in the pond increased at a significantly faster rate than those in the flume at the same U_{rel} [General Linear Model (SAS, 1985): $F=8.72$, $P=0.0041$], whereas L_S increased at a slower rate (General Linear Model: $F=82.4$, $P=0.0001$) (Fig. 2). Tailbeat amplitude of sharks in the pond did not change significantly with increases in U_{rel} , whereas the TBA of sharks in flume experiments decreased at a significantly faster rate (General Linear Model: $F=17.4$, $P=0.0001$) (Fig. 2).

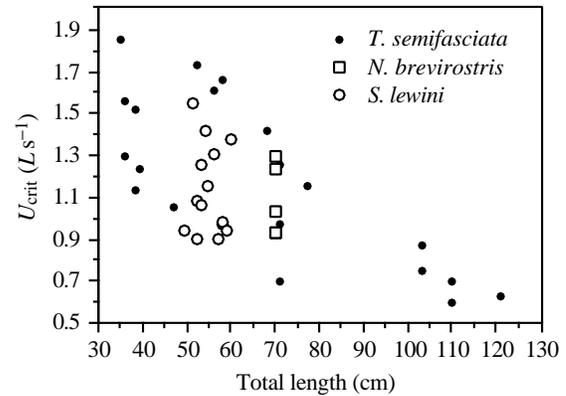


Fig. 3. Critical swimming speeds (U_{crit}) of *Triakis semifasciata*, *Negaprion brevirostris* and *Sphyrna lewini* of varying lengths. Data for *T. semifasciata* and *N. brevirostris* are from Graham *et al.* (1990).

At slow swimming speeds, sharks in the flume exhibited higher and more variable TBF s than sharks in the pond, and flume sharks had shorter L_S values than sharks observed in the pond (Fig. 2). Tailbeat amplitudes of sharks in the flume were 2–3 times more variable at slow speeds than at higher speeds and also varied more than those for sharks in the pond. Differences in TBF and L_S between flume sharks and pond sharks decreased with increases in U_{rel} , such that, at U_{crit} ($1.2 L s^{-1}$) these variables differed by only 3%.

Discussion

Critical swimming speed

Critical swimming speeds of juvenile hammerhead sharks were comparable with U_{crit} values for leopard sharks (*Triakis semifasciata*) and lemon sharks (*Negaprion brevirostris*) of similar lengths (Graham *et al.* 1990) (Fig. 3). U_{crit} is considered to be a measure of aerobically sustainable swimming capacity and slower, less active fishes are thought to have lower U_{crit} values than cruise-adapted species (Graham *et al.* 1990). According to Thomson and Simanek (1977), the leopard shark possesses adaptations characteristic of a slow-moving, demersal shark, whereas hammerhead and lemon sharks are morphologically better designed for cruising. Hammerhead sharks in this study, however, exhibited lower or equivalent U_{crit} values than similarly sized leopard sharks. Although it is possible that these results reflect the actual aerobically sustainable swimming speeds of the sharks tested, it is likely that the flume effects documented at slower speeds, or the stress of short acclimation times in the flume prior to experiments, may have resulted in more rapid fatigue and lower U_{crit} values. In addition, U_{crit} measurements of fishes in other studies have been found to vary depending on the different time or velocity increments used (Farlinger and Beamish, 1977). Thus, it is possible that the protocol used in the present study may have affected the U_{crit} of the sharks.

Kinematics

Swimming in the flume significantly affected hammerhead shark swimming kinematics, particularly at slow swimming speeds, compared with the more natural situation in the pond. Sharks in the pond cruising at slow speeds (e.g. $0.55 L s^{-1}$) exhibited L_S values 19% longer than sharks swimming in the flume at the same U_{rel} . In addition, pond sharks beat their tails 21% slower than sharks observed in the flume at the same U_{rel} ($0.55 L s^{-1}$) (Fig. 2). This suggests that sharks in the flume expended more energy, particularly while swimming at comparatively slow velocities.

It is unclear why sharks in the flume swam differently to those in the field. Videler (1993) suggested that the confined space, noise, or non-laminar flow conditions of a flume may stress fish and affect their swimming behavior. Although it is possible that the differences in swimming kinematics are the result of behavioral responses to swimming in a confined space, certain physical factors may also offer explanations for differences in swimming kinematics.

One possibility is that flow conditions may have accounted for the kinematic differences at slow speeds and these effects may have lessened at higher velocities. Kinematic adjustments to stabilizing motions of sharks swimming at slow speeds in the flume may have been compounded by turbulence or eddies near the walls, and may have contributed to the differences between the pond and flume. In addition, the hammerhead sharks may have been more sensitive to flow conditions because of their flat wing-shaped head. Nakaya (1995) demonstrated that hammerhead sharks possess a unique hypaxial musculature which increases the range of dorso-ventral movement of their large, flat head, thus increasing the potential use of the head as a foil. The anterior placement of this foil-like head is thought to increase manoeuvrability, but decrease stability (Nakaya, 1995; Weihs, 1989). It is possible that this cephalofoil may have been sensitive to the more turbulent flow near the flume walls, making the shark less stable at slow speeds and resulting in decreased swimming performance.

It is also possible that wall effects or the proximity of the walls of the flume may have negatively affected the sharks' kinematics. Webb (1993) found that steelhead trout (*Oncorhynchus mykiss*) may benefit from the close proximity of flume walls; they maintain a constant speed and TBF , but decrease their TBA , thus utilizing a hydraulic advantage (vertical ground effect). This advantage was not observed for trout in unbounded flow. Webb (1993) also found the benefits of this vertical ground effect to be reduced as the trout were forced to swim faster. This is contrary to the findings from the present study, since hammerhead sharks in the flume (in flow bounded by walls) exhibited higher TBF and wider TBA values compared to sharks in the pond (in unbounded flow) at the same slow speeds. This indicates that the sharks in the flume, at slow speeds, had to generate more thrust to swim at the same comparable speed. Current theories suggest that wall effects have a positive influence on thrust, however, all of these

observations have been based on studies on teleost fishes with homocercal tails, not on sharks with heterocercal tails. It is possible that, at slow speeds, differences in tail shape, flexibility, and/or swimming behavior between the hammerhead sharks and trout may account for the differences in swimming kinematics in close proximity to walls. It is possible that flow conditions (turbulence and eddies) were significant enough to counter any positive wall effects, thus hindering forward thrust of sharks in the flume at slow speeds. The extent to which these variables affect the swimming energetics of different species is still unknown.

Interspecific variability in swimming kinematics may be more common in sharks than teleosts. Webb and Keyes (1982) suggested that the propulsive system may be more plastic in sharks than teleosts. Kinematic studies of several teleost species have shown that many bony fishes only vary TBF in order to increase forward thrust (Hunter and Zweifel, 1971; Aleyev, 1977; Dewar and Graham, 1994). Sharks, however, have been shown to change speed by varying TBF , TBA or body wavelength, and sharks of different body shapes may modulate different combinations of these variables to maximize their swimming efficiency (Webb and Keyes, 1982; Graham *et al.* 1990). This may provide an alternative for regulating thrust while maintaining stability at different speeds, since sharks lack the flexible median and paired fins used by teleosts. Hunter and Zweifel (1971) found that the TBF of a smoothhound shark (*Triakis henlei*) exercised in a flume increased linearly with increases in swimming speed, but that TBA remained the same ($0.2L$). In contrast, Webb and Keyes (1982) found the TBF of blacktip reef sharks (*Carcharhinus melanopterus*) in a large pool to increase linearly with increases in U_{rel} , but also found TBA , propulsive wavelength and L_S to simultaneously decrease. TBF of leopard sharks has been shown to reach a plateau at around U_{crit} in three different flume studies, while TBA was found to be highly variable but generally to decrease with increases in speed (Graham *et al.* 1990; Scharold *et al.* 1989; Gruber, 1992). Unlike leopard sharks, hammerhead sharks in the pond increased TBF linearly with increases in speed, with only a slight decrease in the rate of change after U_{crit} . In contrast to the blacktip sharks, L_S increased with increasing speed, while TBA ($0.24L$) remained unchanged for hammerhead sharks in the pond. Clearly, sharks of different body shapes may modulate different kinematic variables to increase swimming speed and improve locomotory efficiency.

Most of the information available regarding kinematics and active metabolism in bony fishes and sharks has been acquired from flume experiments. The present study provides some of the first empirical data quantifying the impact that a flume, such as the one used in the present study, may have on the kinematics of a shark. Although this study was not designed to examine factors that might affect swimming in a flume, these results do indicate that, whenever possible, field data should be acquired to provide a means of correcting for potential flume effects on swimming kinematics and energetics.

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