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BRIEF COMMUNICATION

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Swimming kinematics of the Caribbean reef shark, *Carcharhinus perezi*

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Abstract

The Caribbean reef shark, *Carcharhinus perezi*, is known to rest on the substrate, a behaviour not documented in any of its congeners. We quantified the swimming kinematics of *C. perezi* in the wild and found that the head yawed at a frequency 15% greater than the tail beat, but that the amplitude of the tail exceeded the head yaw by approximately 80% across the range of velocities measured. We found that *C. perezi* velocity, head yaw frequency, and tailbeat frequency were all less than its obligate ram ventilating congener *C. limbatus*.

KEYWORDS
Bahamas, Carcharhinidae, elasmobranch, tailbeat frequency, volitional

The Caribbean reef shark, *Carcharhinus perezi* (Poey, 1876), is a medium-sized shark with a maximum total length of at least 249 cm (Castro, 2011). It is the most common Caribbean reef shark species (Compagno, 1984) and ranges from south-east Florida, throughout the Caribbean and south to Brazil (Castro, 2011). It inhabits continental and insular shelves, often near drop-offs along the edge of the reef (Castro, 2011). This species is hand-fed by dive tourism operators and is frequently encountered by divers, even without being enticed by food (Castro, 2011; Maljkovic & Cote, 2011). Although typically solitary or in small groups, this species can aggregate in large numbers in the presence of dive feeding operations (Castro, 2011).

Despite its abundance and ubiquity throughout the Caribbean, even basic information on its biology is lacking (Castro, 2011). One unique feature about its biology is that *C. perezi* has been documented to stop swimming and lay motionless on the seafloor (Clark, 1975; Randall, 1968). This cessation of swimming is not documented in any of the other 34 species in the genus. By comparing the swimming kinematics of *C. perezi* with its obligate ram ventilating congeners, we can begin to understand the impacts of ventilation mode on locomotion in large, free-swimming sharks in the wild.

To accomplish this goal, we obtained recorded video footage on 23 March 2016 at Tiger Beach, Bahamas (approximately 27.2501°N, 82.5343°W), a popular shark diving location off the north-west corner of Grand Bahama Island, The Bahamas. This is outside of the mating season for this species (Castro, 2011). A GoPro Hero 4 camera was affixed to a dive weight and placed on the seafloor at a depth of approximately 8 m with the camera aimed upwards. The position of the camera allowed the ventral surface of the sharks to be silhouetted against the surface. The camera recorded video at 1920 × 1080 pixel resolution and 30 fps using the linear field of view setting to minimize the distortion inherent in wide-angle lenses. The camera recorded continuously for 52 min and 10 s. During that time approximately three dozen individual *C. perezi* were present and milling around the dive boat between midwater and the surface, where they were attracted by odour and occasionally fed on fish scraps broadcast from the boat onto the water surface. Data collection consisted solely of placing a video camera on the seafloor to record sharks in the wild and no experimental manipulation was applied so an animal care protocol was deemed to be unnecessary. The video footage was analysed to meet the following criteria: *C. perezi* individuals were swimming in a straight line for at least three tailbeats and the shark remained at approximately the same depth. Based on these criteria, we identified 14 clips of video for analysis.

We used Loggerpro 3.10.1 (Vernier Software & Technology) to track movement of four anatomical landmarks along the ventral surface of each shark. The landmarks chosen for analysis were (a) the tip of the rostrum, (b) the midpoint between the trailing edge of the pectoral fins, (c) the midpoint between the trailing edge of the pelvic fins and (d) the caudal peduncle (Figure 1a). We tracked each point for every frame over the duration of the video clip. Positional (x, y) coordinates were produced for each point tracked. We standardized all measurements to animal body length (total length from the tip of the

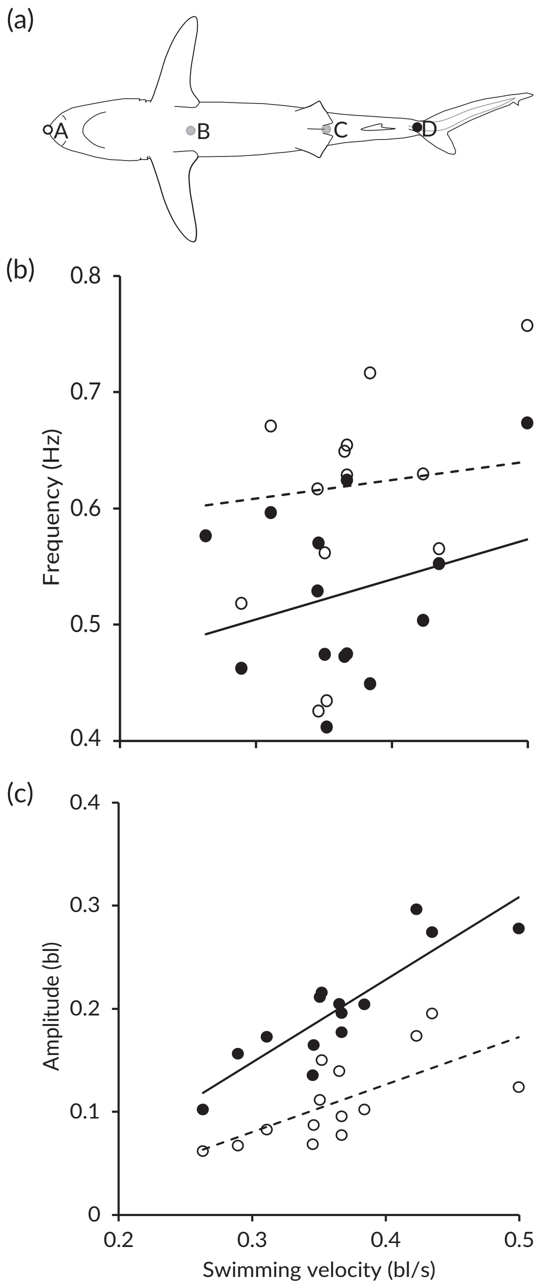

FIGURE 1 (a) Illustration of a shark showing the four points that were tracked along the ventral midline: A, tip of the rostrum; B, midpoint between the insertion of the pectoral fins; C, midpoint between the insertion of the pelvic fins; D, caudal peduncle. (b) Neither tailbeat frequency (filled circles) nor head yaw frequency (open circles) showed a significant correlation with swimming velocity in adult *C. perezi*. The large variance resulted in poor predictability for both parameters. (c) Tailbeat amplitude (filled circles) and head yaw amplitude (open circles) both showed a significant positive correlation with swimming velocity in adult *C. perezi*

rostrum to the tip of the caudal fin dorsal lobe) to account for variations attributed to animal size and distance from the camera.

We defined swimming velocity as the displacement of the pectoral region (Figure 1a, point B) over time between frames (33 ms), averaged for all frames within each clip, and expressed this metric as body lengths per second (bl s^{-1}) (Porter *et al*., 2020). Tailbeat frequency (Hz) was quantified as the time required for the caudal peduncle (Figure 1a, point D) to complete one full lateral excursion from one side of the body to the other and return to the starting position. Tailbeat amplitude was defined as the total peak-to-peak distance between lateral excursions of the caudal peduncle (Figure 1a point D) and was expressed in body lengths (bl). We used the same definitions to calculate head yaw frequency and amplitude from the tip of the rostrum (Figure 1a, point A). Strouhal number (*St*) was used to quantify swimming efficiency and was calculated as $St = AF/V$, where is A is the tailbeat amplitude (bl), F is the tailbeat frequency (Hz) and V is the swimming velocity of the animal (bl s^{-1}) (Rohr & Fish, 2004). The range and mean of the swimming kinematic variables are reported in Table 1.

Neither head yaw frequency nor tailbeat frequency displayed a significant relationship with velocity (head yaw frequency $y = 0.1582x + 0.5611$, $R^2 = 0.007$, regression ANOVA $F = 0.085$, $P = 0.776$; tailbeat frequency $y = 0.3458x + 0.4006$, $R^2 = 0.077$, regression ANOVA $F = 0.995$, $P = 0.338$) (Figure 1b). The mean head yaw frequency (0.619 ± 0.113[s.d.] Hz) was significantly greater than the mean tailbeat frequency (0.526 ± 0.075[s.d.] Hz) (ANOVA $F = 6.45$, $P = 0.017$).

In contrast, both head yaw amplitude and tailbeat amplitude showed a significant positive regression with increasing velocity (head yaw amplitude $y = 0.4612x - 0.0579$, $R^2 = 0.443$, regression ANOVA $F = 9.543$, $P = 0.009$; tailbeat amplitude $y = 0.8036x - 0.0932$, $R^2 = 0.765$, regression ANOVA $F = 39.091$, $P < 0.001$) (Figure 1c). An analysis of covariance, with swimming velocity as the covariate, revealed that tailbeat amplitude was significantly greater than head yaw amplitude (ANCOVA $F = 23.476$, $P < 0.001$) across the range of velocities.

This study is only the second study to directly quantify the swimming kinematics in volitionally swimming sharks in the wild. A previous study quantified the swimming kinematics of a similar sized and co-occurring congener, *C. limbatus* (Porter *et al*., 2020). That study employed similar point tracking techniques to quantify the kinematics and the similar methodologies allow the values from that study for *C. limbatus* to be directly compared to the values in this study for *C. perezi* (Table 1).

The mean swimming velocity of *C. limbatus* was approximately double the mean velocity found for *C. perezi*. These data are taken from volitionally swimming sharks and likely represent a limited range of velocities which the sharks are capable of achieving. The large differences in swimming velocity may reflect behavioural differences in the animals at the time of filming. The *C. limbatus* individuals were swimming along the coast during their annual migration (Kajiura & Tellman, 2016), whereas the *C. perezi* were filmed around a dive boat that was chumming to attract sharks. As a result, the *C. perezi* may have been swimming more slowly to maintain proximity to the food odour. In contrast to the obligate ram ventilating and faster swimming *C. limbatus*, the metabolic demands of the slower swimming *C. perezi* might not require as much water flow over the gills, which may explain its ability to rest on the bottom (Clark, 1975; Randall, 1968). Despite the dramatic difference in swimming velocities, the Strouhal

TABLE 1 Swimming kinematic variables for *C. perezi* and *C. limbatus*. Values for *C. limbatus* are from Porter *et al.*, 2020

Kinematic variable	*C. perezi* Minimum	*C. perezi* Maximum	*C. perezi* Mean ± SD	*C. limbatus* Mean ± SD
Velocity (bl s^{-1})	0.263	0.500	0.36 ± 0.060	0.75 ± 0.18
Strouhal	0.207	0.375	0.28 ± 0.050	0.25 ± 0.01
Head yaw frequency (Hz)	0.426	0.832	0.62 ± 0.113	1.23 ± 0.37
Tailbeat frequency (Hz)	0.412	0.673	0.53 ± 0.075	0.82 ± 0.24
Head yaw amplitude (bl)	0.062	0.196	0.11 ± 0.042	0.13 ± 0.03
Tailbeat amplitude (bl)	0.102	0.297	0.20 ± 0.056	0.26 ± 0.08

number was similar for both species and falls within the range of optimal thrust and efficient swimming (Rohr & Fish, 2004; Triantafyllou *et al.*, 1991, 1993). This would suggest that these carcharhinid sharks swim efficiently over a range of velocities.

As with swimming velocity, the head yaw frequency of *C. limbatus* was double that of *C. perezi* and the tailbeat frequency of *C. limbatus* was about 65% greater than that of *C. perezi*. The greater head yaw and tailbeat frequencies of *C. limbatus* likely contribute to its faster swimming velocity compared to *C. perezi*. Despite the differences in frequency, the amplitude of head yaw and tailbeat were similar between the species. This suggests that frequency, rather than amplitude, might be a more important contributor to velocity for sharks in this genus. A previous study demonstrated that tailbeat frequency increased with velocity, whereas tailbeat amplitude decreased for the congeneric *C. melanopterus* in aquaria (Webb & Keyes, 1982). This differs from the present study for sharks in the wild, which found that amplitude increased significantly with velocity whereas frequency did not. Differences in fin morphology may account for differences in swimming kinematics and the physical constraints of the captive environment may have contributed to the smaller tailbeat amplitude for *C. melanopterus*.

The head yaw and tailbeat frequencies did not change significantly across a range of velocities. This might be attributable to the poor fit of the regressions, which showed a significant amount of variance across a range of swimming velocities (Figure 1b). In contrast, head yaw and tailbeat amplitudes did show a significant positive correlation with velocity (Figure 1c). The strong correlation for amplitude, but not for frequency, suggests that the frequency is genuinely more variable and a larger sample size over a range of velocities might be needed to establish a correlation. Another explanation for the lack of correlation between tailbeat frequency and velocity might be that the sharks were encountering different ambient current flow velocities. Sharks swimming with the prevailing current could achieve a greater groundspeed with a lower tailbeat frequency than sharks swimming against the flow (Papastamatiou *et al.*, 2021). We were unable to assess current velocity from the video and were thus unable to determine how much it contributed to the high variability seen in the data.

This study also found significant differences between the oscillation frequencies at the anterior and posterior regions of the shark. The mean head yaw frequency is about 15% faster than the tailbeat frequency, and the mean tailbeat amplitude is about double the head yaw amplitude. Differences in anterior and posterior oscillation frequency have been documented in other shark species, including the blacktip shark, *C. limbatus* (Porter *et al.*, 2020), and the scalloped hammerhead shark, *Sphyrna lewini*, and bonnethead shark, *Sphyrna tiburo* (Hoffmann *et al.*, 2017). Other studies have used animal-borne accelerometers to derive tailbeat frequency in wild sharks (Nakamura *et al.*, 2011; Watanabe *et al.*, 2019; Whitney *et al.*, 2016). In those studies, the accelerometer is affixed to the first dorsal fin and whole-body acceleration is used as a proxy to calculate tailbeat frequency. As a result, accelerometer-based studies cannot distinguish fine-scale differences in movements that may occur between the anterior and posterior body regions, such as the head yaw and tailbeat measurements presented here.

There are recognized limitations to the methods used to collect the footage analysed in this study. Because we could not distinguish individuals in the video, there is a possibility that some individuals were analysed more than once, leading to pseudoreplication. However, the number of individuals present was approximately three times greater than the number of individuals analysed so it is possible that each video clip represents a different individual. In addition, the video footage was collected by aiming the camera toward the brightly lit surface, which resulted in the sharks being imaged as silhouettes. As a result, we were unable to distinguish the presence of claspers, and were thus unable to determine the proportion of males and females analysed. Despite these limitations, the data collected provide insight into the volitional swimming kinematics of sharks in the wild.

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AUTHOR CONTRIBUTIONS

S.M.K. conceived the study, recorded the footage, supervised the students and wrote the manuscript. J.C.L. collected the data and helped with the analysis. B.T.R. helped with the analysis and wrote the manuscript. M.E.P. conceived the analysis and wrote the manuscript.

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