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SYMPOSIUM

Not So Fast: Swimming Behavior of Sailfish during Predator–Prey Interactions using High-Speed Video and Accelerometry

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Synopsis Billfishes are considered among the fastest swimmers in the oceans. Despite early estimates of extremely high speeds, more recent work showed that these predators (e.g., blue marlin) spend most of their time swimming slowly, rarely exceeding $2 \, \mathrm{m \, s^{-1}}$. Predator–prey interactions provide a context within which one may expect maximal speeds both by predators and prey. Beyond speed, however, an important component determining the outcome of predator–prey encounters is unsteady swimming (i.e., turning and accelerating). Although large predators are faster than their small prey, the latter show higher performance in unsteady swimming. To contrast the evading behaviors of their highly maneuverable prey, sailfish and other large aquatic predators possess morphological adaptations, such as elongated bills, which can be moved more rapidly than the whole body itself, facilitating capture of the prey. Therefore, it is an open question whether such supposedly very fast swimmers do use high-speed bursts when feeding on evasive prey, in addition to using their bill for slashing prey. Here, we measured the swimming behavior of sailfish by using high-frequency accelerometry and high-speed video observations during predator–prey interactions. These measurements allowed analyses of tail beat frequencies to estimate swimming speeds. Our results suggest that sailfish burst at speeds of about $7 \, \mathrm{m \, s^{-1}}$ and do not exceed swimming speeds of $10 \, \mathrm{m \, s^{-1}}$ during predator–prey interactions. These speeds are much lower than previous estimates. In addition, the oscillations of the bill during swimming with, and without, extension of the dorsal fin (i.e., the sail) were measured. We suggest that extension of the dorsal fin may allow sailfish to improve the control of the bill and minimize its yaw, hence preventing disturbance of the prey. Therefore, sailfish, like other large predators, may rely mainly on accuracy of movement and the use of the extensions of their bodies, rather than resorting to top speeds when hunting evasive prey.

Introduction

Billfishes are considered among the fastest fish in the ocean (Videler 1993). Despite early estimates suggesting that sailfish, *Istiophorus platypterus* (*sensu* [Collette et al. 2006]), can swim as fast as $30 \, \mathrm{m \, s^{-1}}$ (Lane 1941), more recent work on other billfishes (blue marlin, *Makaira nigricans*) showed that these predators spend most of their time

swimming slowly (Block et al. 1992; Hoolihan 2005). Blue marlin swam most often at speeds slower than $1.2 \, m \, s^{-1}$ (97% of the time), only occasionally reaching speeds of approximately $2 \, m \, s^{-1}$ (Block et al. 1992). Block et al. (1992) stated that although blue marlin have been recorded to strike a bait trolled at $8 \, m \, s^{-1}$, these high speeds were never observed during 160 h of observations. Furthermore, theoretical work suggests that the maximum speeds attainable by marine fishes and cetaceans are limited to $10–15 \, m \, s^{-1}$ at shallow depths, due to cavitation problems arising at higher speeds (Iosilevskii and Weihs 2008). Therefore, two unresolved questions are: how fast can billfish swim and in which context are high speeds used?

Predator–prey interactions provide a context within which one may expect maximal speeds both by predators and by prey. Unsteady swimming is typically used by fish and other aquatic vertebrates during such interactions and it can be defined as a swimming behavior that implies changes in the direction and/or the speed of locomotion (Blake 1983; Videler 1993). Because large fish are faster than small fish (Domenici 2001; Vogel 2008), they are expected to eventually catch small fish if both predator and prey are swimming in a straight line. However, prey frequently perform maneuvers and accelerations when under attack. In addition to providing some degree of unpredictability (Jones et al. 2011), this behavior may be advantageous to the prey because previous kinematic work, carried out on various species by stimulating escapes or attacks, shows that small fish exhibit higher performance than large fish in unsteady swimming (Domenici 2001; Vogel 2008). Some large aquatic predators possess morphological adaptations such as elongated bills or tails that can be maneuvered effectively, thus allowing them to overcome their potential disadvantage in unsteady swimming performance when attacking their evasive smaller prey. These extensions of the body can be moved more rapidly than the whole body itself, thereby facilitating prey capture (Domenici et al. 2000, 2014; Oliver et al. 2013). It is therefore possible that predators, like billfishes, that possess such weapons may not resort to using extremely high speeds during predator–prey interactions. The sailfish is an example of a predator that uses its bill for capturing prey (Domenici et al. 2014). Thus, it provides the context to test if speeds as high as those estimated in previous work (Lane 1941) are used by a predator that possesses body weapons. In addition, sailfish possess the largest dorsal fin of all billfishes (i.e., the sail), which is extended during, and immediately prior to, slashing

maneuvers through the school of prey (Domenici et al. 2014). Domenici et al. (2014) suggest that extension of the dorsal fin may increase control of the bill, although it is not known whether it may also serve other purposes.

To investigate the possibility that high swimming speeds are used by sailfish during predator–prey interactions, we quantified their swimming behavior while hunting, using two different methods: high-speed video recording and high-frequency accelerometers. For both methods, we measured sailfish's tail-beat frequencies (TBFs) from which we estimated swimming speeds during bursting and cruising. We then compared the observed swimming performance with values previously reported, based on the motion of the bill during slashing of the prey (Domenici et al. 2014), in order to provide a basis for discussing the feeding strategies in billfishes. To investigate the potential role of the dorsal fin in minimizing disturbance of the prey by the bill, we measured oscillations of the bill while sailfish were actively swimming with, or without, extension of their dorsal fin.

Material and methods

Swimming behavior of sailfish (*I. platypterus*) was investigated using two methods: high-speed video observations and tri-axial accelerometry. Observations were obtained 30–70 km offshore from Cancun, Mexico (21 28.3–41.15 N, 86 38.41–41.30 W), between 10.00 and 16.00 h during the months of January–February (2012–2014, 6 days per year, 18 days in total).

High-speed video observations of sailfish swimming during predation events

High-speed video footage was collected while sailfish were in the proximity of, or attacking, schools of adult sardines (*Sardinella aurita*). Observations were carried out near the surface (animals 0–5 m deep; depth of the water 30–40 m) under calm sea conditions. Sailfish–sardine interactions were located by tracking avian predators (frigate birds, *Fregata magnificens*, and pelicans, *Pelecanus occidentalis*) that were observed feeding on schools of sardines near the surface of the water. Upon locating a prey school, snorkelers entered the water and filmed the swimming behavior of sailfish from above, using hand-held cameras (Casio EX-FH100 high-speed cameras filming at 240 fps). We collected 122 min of video of sailfish–sardine interactions. Sailfish TBF was measured when sailfish were cruising at a steady motion with no apparent accelerations or while

bursting (defined as a sudden increase in speed). These events occurred while sailfish (groups 6–40 individuals) were surrounding a school of sardines (groups 10–1000+). The number of individual prey and predators was estimated visually based on video images. During both cruising and bursting, sailfish swam with their dorsal and pelvic fins retracted. Fin extension occurred only during, or immediately prior to, slashing maneuvers through the school of prey. Estimates of speed were obtained according to the following formula (Videler 1993):

$$U = BL \times S \times TBF, \tag{1}$$

where U is the swimming speed in $m\,s^{-1}$, BL is the body length (m), S is the stride length (proportion of BL), defined as the distance covered per tail beat, and TBF (Hz) is the tail beat frequency. Body length was based on the length of adult sailfish, excluding the bill (~150 cm [Domenici et al. 2014]). The stride length was measured during 6 days in February 2015 (in the same location where the high-speed videos were recorded) by using a Dual-Frequency Identification Sonar (Diver-Held DIDSON, Sound Metrics Corp.), operated at 1.1/1.8 MHz. The DIDSON recorded position and size of sailfish at a sampling rate of 6–7 Hz, within a range of 20 m. The fine spatial resolution provided by the DIDSON (Boswell et al. 2008; Handegard et al. 2012) allowed empirical estimates of stride length, expressed in body lengths within a single tail-beat cycle.

To investigate the potential role of the dorsal fin in reducing oscillations of the bill, we analyzed two video sequences in which sailfish were actively swimming in a straight line directly below the camera (one with and one without extension of the dorsal and pelvic fins). The sequence with no extension of the fin was selected from the cruising sequences analyzed for TBF, while the sequence with extension of the fin was an additional sequence that was not included in the TBF analysis. To qualitatively test whether the extension of the dorsal and pelvic fins minimizes the bill's angle of yaw during active swimming, we measured (1) the angle of the bill relative to the direction of motion of the fish (yaw angle), and (2) the angle of the tail relative to the direction of motion of the fish. Angles of yaw were determined by digitizing two points along the bill for each frame (WinAnalyze motion-analysis software, v. 1.9 2D; Mikromak Service Brinkmann, Berlin, Germany). The yaw-angle corresponds to the angle between the line passing through these two points and the line representing the swimming direction of the

fish. The direction of swimming was determined as the line joining two points, both positioned along the midline of the fish at 0.35 BL from the tip of the head, one at the beginning and the other one at the end of the sequence analyzed (approximately one tail-beat cycle). Motion of the bill to the right and the left of the swimming direction (0°) are represented by positive and negative angular values, respectively. Because the bill is a rigid structure, any two points along the bill were used since different pairs of points would yield the same angle of yaw. The angle of the tail was determined by marking two points along the tail using natural blue marks on the body, one just anterior of the caudal peduncle and another approximately one-tenth of the body length in front of the first point. The angle of the tail was determined as the angle between the line passing through these two points and the line representing the swimming direction of the fish. Motion of the tail to the left and the right of the swimming direction (0°) are represented by positive and negative angular values, respectively.

Tri-axial accelerometry on free-swimming sailfish

Accelerometer and gyroscope data loggers ($30 \times 12 \times 12$ mm, mass in air = 7 g; LP-BLKU02, Biologging Solutions Inc., Kyoto, Japan) were attached to sailfish ($n = 3$, total length: 196–220 cm) caught by professional fishermen in areas where we observed predator–prey interactions. The principle of reduction was applied by using the minimum number of individuals ($n = 3$) to obtain a mean value. The principle of refinement was applied to reduce to an absolute minimum the pain, distress, or suffering of the fish. This was accomplished by exposing each individual to the air for a minimal amount of time (less than 45 s) and by placing the accelerometer using a non-invasive procedure by means of a time-release strap secured onto a hard surface (the bill), thus minimizing disturbance to the fish's body. After release in the water, no sign of distress or irregular swimming was observed by a team member who entered the water and swam at the surface above the sailfish until the latter was out of sight. Recording was set for 23–34 min post-release, after which the accelerometer detached from the sailfish using an automated release mechanism (BLS-Band, Biologging Solutions Inc.) which is similar to mechanisms used in other studies (Watanabe et al. 2004). To allow recovery of tags, accelerometers included a built-in VHF transmitter that could be located using a boat-operated VHF-receiver with a directional Yagi-antenna. Acceleration data were analyzed on Igor Pro (WaveMetrics Inc., Lake Oswego, OR).

A tri-axial accelerometer and gyroscope measured the acceleration ($\pm16\,g$) and angular velocity ($\pm6000\,\deg\,s^{-1}$) at 200 Hz. For the purposes of this study, only acceleration data were used during analyses. Dynamic (caused by the oscillation of the bill) and static (caused by the change in gravity) accelerations were recorded simultaneously and were separated into discrete components during analyses by running a 3-s moving average on the acceleration data (Shepard et al. 2008). Dynamic acceleration was used to determine TBF and linear acceleration. The frequency of the lateral movement of the bill was considered to match the TBF based on video observations. This is in agreement with previous work, which demonstrated that the lateral acceleration of the oscillations of the anterior body has the same frequency as the tail-beat (Xiong and Lauder 2014). TBF was determined by applying a Wavelet analysis (Min cycle $= 0.1$ s, Max cycle $= 1.0$ s) (Sakamoto et al. 2009) to the lateral acceleration at 1 s intervals. The dominant frequency obtained for each interval was considered as a TBF event. Subsequently, TBF was used to estimate speeds based on Equation (1), in which body lengths were based on the total lengths of the three specimens used for accelerometry, minus the length of the bill, calculated as a fixed proportion of total length (Domenici et al. 2014). Linear acceleration was also obtained, both as total acceleration (scalar value of the vector summation of *x surge*, *y sway*, and *z heave* components) and as forward acceleration (*x surge* component). While forward acceleration is relevant because it is in the direction of swimming, and predatory bursts typically involve swimming in a straight line, total acceleration is relevant for comparison with previous work, which is mainly based on acceleration using at least *x* (surge) and *y* (sway) components (Domenici and Blake 1997).

Statistics

A two-way ANOVA was used to test the effect of recording methods (i.e., high-speed videos versus accelerometry) and swimming mode (i.e., cruising versus bursting) on swimming speed.

Results

Our video analysis showed TBF ranged from 1.2 to 2.55 Hz (mean $\pm$ SE $= 2.02 \pm 0.08$ Hz, $N = 12$) for cruising and 4.44 to 8.57 Hz (6.15 $\pm$ 0.42 Hz, $N = 10$) for bursting. The stride lengths estimated by the DIDSON ranged 0.603–0.871 body lengths (mean $\pm$ SE $= 0.74 \pm 0.08$ body lengths, $N = 14$). Based on TBF and stride-length data, the estimated
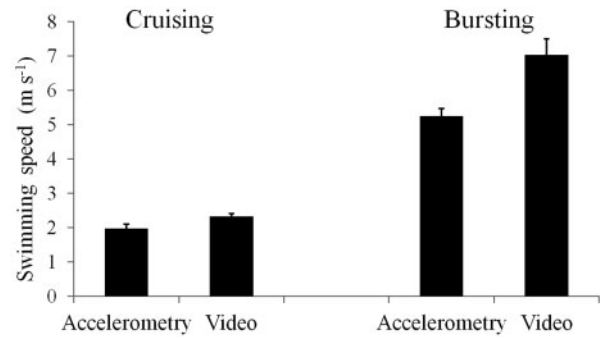

Fig. 1 Mean swimming speed ($\pm$SE) estimated from high-speed analysis of videos and accelerometry both for cruising (left) and bursting (right).

mean swimming speeds were 2.3 ± 0.1 and $7.02 \pm 0.48\,\mathrm{m\,s^{-1}}$ for cruising and bursting, respectively (Fig. 1 and Table 1). Additionally, the minimum and maximum estimated swimming speeds were 1.37 and $2.91\,\mathrm{m\,s^{-1}}$ for cruising and 5.06 and $9.77\,\mathrm{m\,s^{-1}}$ for bursting. Video recording also showed that the dorsal fin and the pelvic fins were extended in all cases when the sailfish was approaching the prey and had inserted the bill within the school of sardines (Fig. 2). Conversely, the fins were partially or fully retracted when the sailfish were not in the immediate proximity of the school of prey (Fig. 2). Two sequences of a sailfish swimming in a straight line and recorded from above were analyzed to determine the movement of the bill and its angles of yaw. In one sequence, the dorsal fin and the pelvic fins were extended, while in the other sequence they were retracted. These two sequences provide a qualitative view of the motion of the bill while the fish is actively swimming with, or without, its fins extended (Fig. 2). When the sailfish is swimming without the fins extended, the angle of the bill varies with a period similar to that of the tail, and the maximum angle of yaw is 7.10° (Fig. 2). In contrast, when the fins were extended, the angle of the bill varied by approximately 2° during a full cycle of the tail's beat, with a maximum angle of yaw of 0.98° (Fig. 2).

A typical accelerometer trace, wavelet analysis, and frequency distribution of the TBF are shown in Fig. 3. TBF data were split into categories of cruising and bursting, using 3 Hz as a cutting-off point based on the ranges of cruising and bursting observed during video analysis. Accelerometer measurements showed mean ($\pm$SE) TBF values of 1.54 ± 0.11 Hz ($N = 3$) for cruising and 4.15 ± 0.19 Hz ($N = 3$) for bursting. The value used for each fish is a mean value based on 35, 28, and 195 TBF bursting events and on 1989, 1345, and 1190 TBF cruising

Table 1 Mean, minimum, and maximum speed and TBF values measured with high-speed video and accelerometry

	High-speed video			Accelerometry		
	Mean $\pm$ SE	Minimum	Maximum	Mean $\pm$ SE	Minimum	Maximum
Bursting speed (m s^{-1})	7.02 $\pm$ 0.48	5.06	9.77	5.23 $\pm$ 0.24	3.99	8.19
Cruising speed (m s^{-1})	2.3 $\pm$ 0.1	1.37	2.91	1.95 $\pm$ 0.14	1.35	3.71
Bursting TBF (Hz)	6.15 $\pm$ 0.42	4.44	8.57	4.15 $\pm$ 0.19	3.16	6.49
Cruising TBF (Hz)	2.02 $\pm$ 0.08	1.2	2.55	1.54 $\pm$ 0.11	1.07	2.94

Notes: Mean, minimum, and maximum for high-speed video observation are based on $n = 10$ and 12 for bursting and cruising, respectively. Mean values for accelerometry are based on three individuals ($n = 3$) and minimum and maximum values are based on the total number of TBF events (258 TBF events for bursting and 4524 TBF events for cruising).
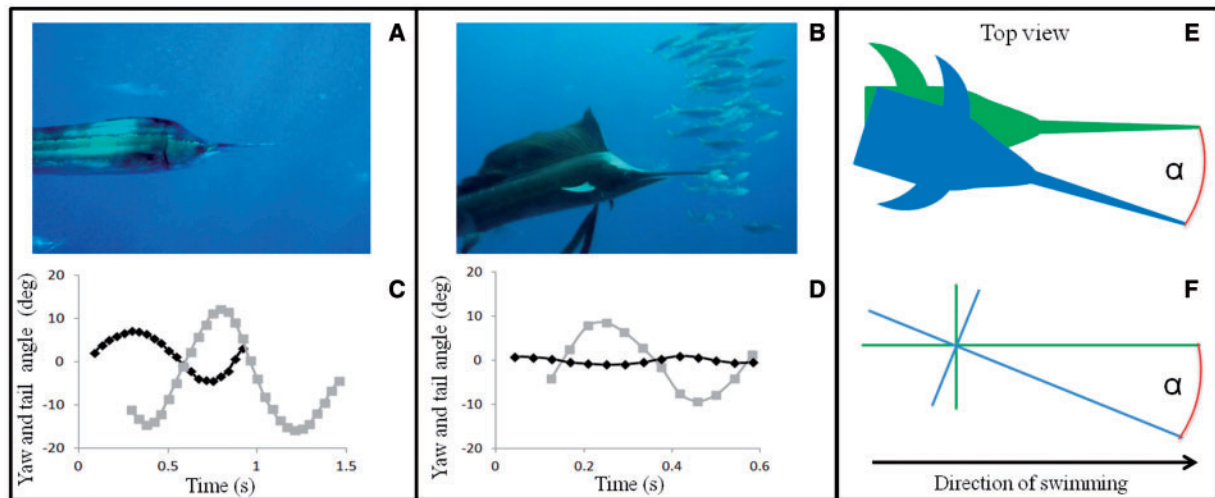

Fig. 2 (A) Sailfish keep their dorsal and pelvic fins retracted during swimming when not in the immediate proximity of their prey. (B) When swimming while their bill is inserted into a school of prey, sailfish keep their dorsal and pelvic fin extended. Lower panels show angle of the tail (gray line) and of yaw (black line) of sailfish actively swimming without (C) and with (D) the dorsal fin extended, based on video analysis of sequences recorded from above. The "zero" value represents the direction of swimming. Note that the data on the angle of yaw and of the tail angle have different durations because the bill and the tail were not always visible simultaneously during each sequence. The periods of oscillations of the tail and yaw are similar in each sequence, i.e., about 1.2 and 2.4 Hz in panels C and D, respectively. Videos were recorded at 240 fps. In the figure, 1 out of every 10 points is shown (i.e., 24 fps). (E) Methodology used to measure the angle of yaw (α) in sailfish drawn from top view. The two outlines indicate a sailfish positioned along the direction of swimming and at the maximum deflection to the right, respectively, and (F) Midlines of the sailfish based on the outlines in (E).

events for each of the three individuals, respectively. Based on these TBF values, estimated mean swimming speeds for sailfish were 1.95 ± 0.14 for cruising and 5.23 ± 0.24 m s^{-1} for bursting (Fig. 1 and Table 1). The minimum and maximum TBF values recorded with accelerometers, based on all TBF events pooled for the three tagged individuals (a total of 4524 TBF events for cruising and 258 TBF events for bursting) were 1.07 and 2.94 Hz for cruising and 3.16 and 6.49 Hz for bursting. These TBF values yielded minimum and maximum estimated speeds of 1.35 and 3.71 m s^{-1} for cruising and 3.99 and 8.19 m s^{-1} for bursting. Furthermore, total and forward acceleration during bursting showed maximum values ranging 5.29–31.75 m s^{-2} (mean 16.07 ± 8.02 m s^{-2}, $N = 3$)

and 1.62–6.29 m s^{-2} (mean 3.35 ± 1.48 m s^{-2}, $N = 3$), respectively.

The two-way ANOVA found a significant difference in speed between cruising and bursting within each recording method (High-speed video, $P < 0.001$; Accelerometry, $P < 0.01$). Within each swimming mode, speed was not significantly different when comparing the two methods (Burst, $P = 0.053$; Cruise, $P = 0.94$).

Discussion

Our results based on both video analysis and accelerometry suggest that sailfish do not exceed swimming speeds of 10 m s^{-1} during interactions with
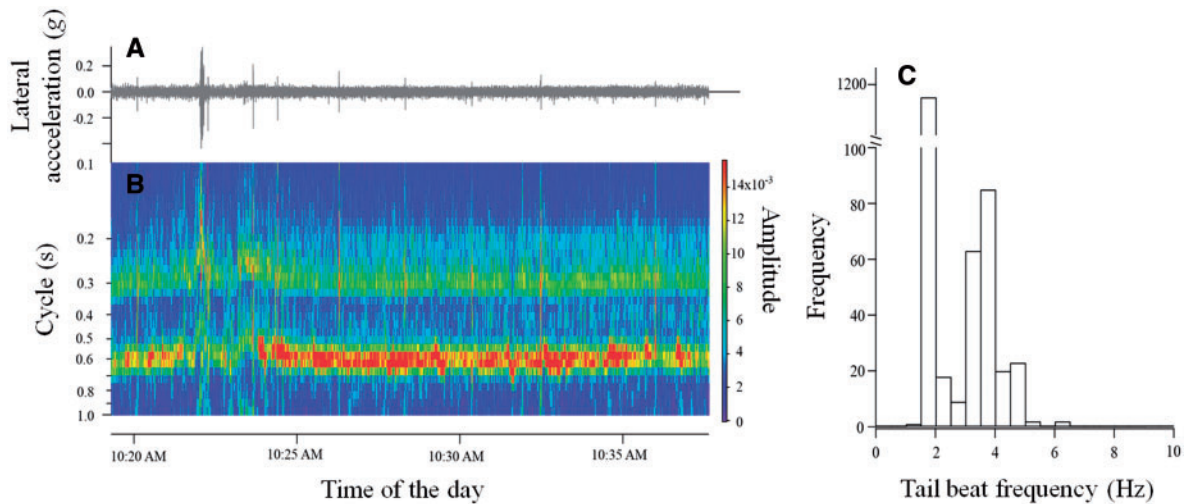
Fig. 3 Example of the wavelet analysis applied to lateral acceleration measured using accelerometry in one of the three tagged sailfish. (**A**) The lateral acceleration in g. (**B**) The TBF cycles in seconds and the color shows the amplitude of the frequency for every second. (**C**) The frequency-distribution of the TBF measured on the basis of A and B.

their prey. While these speeds are much lower than previous estimates ($30\,\mathrm{m\,s^{-1}}$) (Lane 1941), it is possible that such early values may have been affected by large errors. Similarly, we cannot rule out the possibility that sailfish can attain higher speeds than the ones we observed although such speeds may be rare events or achieved in contexts other than predator–prey interactions. In addition, large predators may not necessarily use their top speeds when hunting an evasive prey. Recent field work on cheetahs (*Acinonyx jubatus*), a terrestrial species known for its extreme top recorded speed ($29\,\mathrm{m\,s^{-1}}$) (Sharp 1997), found that this predator exhibited speeds mainly within the range of 10–$20\,\mathrm{m\,s^{-1}}$, with the mean top speed of $14.9\,\mathrm{m\,s^{-1}}$ (Wilson et al. 2013). These authors suggest that peak running speeds are unlikely to be used by cheetahs in the final stages of a hunt as these speeds would result in poor maneuverability, requiring as long as 6 s to perform a $180°$ turn (Wilson et al. 2013). In addition, high speeds are known to increase the reaction distance of prey (Dill 1974; Webb 1986); hence, maximum speeds do not necessarily result in increased capture success. Importantly, there is often a trade-off between speed and accuracy (Chittka et al. 2009) such that predators aiming at catching a highly maneuverable prey item might need to avoid maximal speeds in order to increase their motor accuracy.

Although we cannot be certain that the accelerometer data reported here were obtained during predator–prey interactions, the estimated speeds calculated from these data were within similar ranges as the video analysis (Table 1) and no significant difference

was found in either cruise or burst values when comparing the two methods. Therefore, it is likely that the values obtained with the two methods were measured during similar behavioral contexts. Moreover, a previous study investigating post-release behavioral changes in large pelagic fish indicated that sailfish regain normal behavior relatively quickly after release (Hoolihan et al. 2011). As found in marlin (Block et al. 1992), sailfish appear to use low-gear and high-gear gaits, most likely corresponding to the use of red aerobic muscle for swimming at low speeds and white anaerobic muscle for swimming at high speeds (Videler 1993; Shadwick and Gemballa 2006; Bernal et al. 2010; Marras et al. 2013). The mean cruising speed estimated here (both using accelerometry and high-speed video) is about $2\,\mathrm{m\,s^{-1}}$ which is higher than the mean speed previously recorded in other billfishes, which showed speeds more than $2\,\mathrm{m\,s^{-1}}$ only rarely (Block et al. 1992). Although sailfish were cruising at a steady speed, it is likely that the predator–prey context within which they were observed caused a high level of activity. It is possible that differences between our data and those of Block et al. (1992) may also be due both to methodological and to species-specific differences. In addition, work by Block et al. (1992) measured speed directly, while we estimated speed based on the frequency of tail beat. TBF is known to be a main determinant of speed in fish (Videler 1993). The dependency of speed from TBF is modulated by stride length which varies between 0.6 and 1 body lengths in pelagic fishes (Videler 1993). While variation in stride length is a potential source of error in our estimates

of speed, our data show that stride length only varied between 0.603 and 0.871 body lengths in sailfish; therefore, using a mean of 0.76 body lengths implies maximum potential errors ranging 14–21%.

The use of high-speed video and accelerometry to assess TBF allows us to discuss the pros and cons of these two methodologies for studying swimming behavior in the field in relation to predator–prey interactions. While high-speed video analysis was used to determine TBF during foraging, such analysis was based on observations carried out in a single context (sailfish surrounding their prey) and using small sample sizes ($N = 10$ and 12 for bursting and cruising, respectively). Video observations were possible only when sailfish stayed in a small area while preying upon a school of sardines. High-speed video analysis did not allow us to test if sailfish may use high swimming speed during other contexts, for example during the approach to a group of prey from a distance. Accelerometry, on the other hand, although measured on three individuals only (to minimize fishing), was based on a large number of TBF events (258 and 4524 for bursting and cruising, respectively). However, accelerometry admittedly has the disadvantage that the specific context within which TBFs were measured is unknown. We can speculate that sailfish may have been in a predatory mode (hence either feeding or approaching a feeding patch) for at least part of the time, given that predator–prey interactions were occurring in the area. Therefore, the TBF values of bursting measured during accelerometry could potentially include attacks toward prey as well as approaches to groups of prey from hundreds of meters, or any other context within which bursts are used. Thus, in our opinion the two methods have different characteristics and complement each other when studying predator–prey interactions. Generally speaking, work on swimming behavior in contexts that involve large distances would be more suitable for accelerometry while high-speed video may be useful when studying swimming behavior in small (or enclosed) areas.

Interestingly, the mean burst speed was $7.02 \, \mathrm{m \, s^{-1}}$ (based on video), which is similar to the mean top speed (i.e., $6.2 \, \mathrm{m \, s^{-1}}$, also based on video) achieved by the tip of the bill during a slashing maneuver (Domenici et al. 2014). This speed is about 3.4 times faster than the maximum speed expected for the prey (Domenici et al. 2014). However, while during a powerful slash, the tip of the bill can achieve an acceleration as high as $131.6 \, \mathrm{m \, s^{-2}}$, data from accelerometry showed much lower values in the bursts of swimming sailfish, ranging from 2 to $6 \, \mathrm{m \, s^{-2}}$ (forward acceleration) and from 5 to $32 \, \mathrm{m \, s^{-2}}$ (total acceleration). Maximum values of acceleration in the literature are available only for smaller fish (5–63 cm in body length) and range from 16 to $151 \, \mathrm{m \, s^{-2}}$ (Domenici and Blake 1997). Since both acceleration and maneuverability are expected to decrease with the increasing size of fish (Webb and Debuffrenil 1990), the low values found in swimming sailfish are not surprising. However, the use of a weapon such as the bill allows sailfish to achieve much higher motor performances, with an acceleration comparable to the highest values recorded in swimming fish (Domenici and Blake 1997; Domenici et al. 2014), thereby compensating for the potential disadvantage of being about 10–15 times longer and therefore, less maneuverable than their prey.

Domenici et al. (2014) outlined the typical behavioral chain of events in sailfish's attacks. Sailfish first approach their schooling prey, and then insert their bill into the moving school. Typically, the prey do not react to the insertion of the bill, possibly because its thin profile makes it a stealthy object. During this phase, sailfish chase the prey, matching their speed (i.e., $1.17 \, \mathrm{m \, s^{-1}}$ [Domenici et al. 2014]) without overtaking them and with the dorsal and pelvic fin extended (see Fig. 2). With the bill located inside the prey school, sailfish move their bill to either (a) slash laterally (speed $6.2 \, \mathrm{m \, s^{-1}}$, acceleration $131.6 \, \mathrm{m \, s^{-2}}$) through the school and injure prey, or (b) tap on individual fish to destabilize and eventually capture a prey in 33% of the events. In this chain of events, it does not appear necessary for sailfish to obtain extreme swimming speeds while foraging. The rapid motion of the bill makes it difficult for prey to avoid its impact, overcoming any potential advantage in maneuverability by the prey. Indeed, accuracy of motion and control of the bill may be more important for slashing and tapping, than the swimming speed of the sailfish itself. The extension of the dorsal and pelvic fins during these motions may also serve to maximize "control surfaces" (Lauder and Drucker 2004) and therefore increase accuracy (Domenici et al. 2014). Furthermore, sailfish and other billfishes (e.g., marlin) swim with relatively large amplitudes, as the arrangement of the plates of the backbone permits a high degree of lateral flexion (Hebrank et al. 1990). While this flexibility may permit some degree of maneuverability during swimming and turning, large yaw-angles of the bill would increase hydrodynamic and visual disturbance and possibly induce an evasive reaction when the bill is inserted in the school of prey. Hence, it is possible that the extension of the dorsal fin may minimize this side motion, thereby minimizing disturbance of

the prey. Although based on a single observation (swimming sequences in which both caudal fin and bill are simultaneously visible from a top view are rare), it appears that when sailfish swim with their dorsal and pelvic fins extended, there is little variation in the angle of the bill, and the bill's yaw-angle is minimized (<1°). Conversely, sailfish swimming without extended fins show a yaw-angle of about 7°. This value is in line with the angle of yaw observed in other teleost fish (herring, 6.3°; cod, 3.4°; bream, 8.0°; goldfish, 7.4°; dace, 1.7°) (Rowe et al. 1993). Cartilaginous fishes, which swim with large undulations, show slightly higher yaw-angles; hammerhead and bonnethead sharks exhibited a yaw-angle of 8.45° and 7.8°, respectively, and lemon and blacknose sharks show 7.55° and 7.5°, respectively (calculated based on McComb et al. [2009]). In addition to minimizing anterior side-motions while the bill is inserted in the school of prey, it is possible that extended dorsal and pelvic fins may increase the accuracy of maneuvers of the bill, even in the later phases, such as tapping and slashing. Furthermore, slashing occurs through powerful bending of the body, hence extension of the sail may also serve to resist lateral forces in the opposite direction of the slash, thereby increasing the efficacy of the slash.

Webb and Debuffrenil (1990) suggested that, because small fish are more maneuverable than their large predators, as the difference in size between predator and prey increases, predators may resort to alternative feeding strategies that culminate in filter feeding, i.e., when the predator–prey size ratio is so large (i.e., 1000:1) that capture of prey occurs regardless of the evasive performance of the prey. When prey are small, but not small enough to be captured by filter feeding, predators may have difficulties in catching their prey using whole-body attacks because of their lower maneuverability. In these cases, other feeding strategies may be used, such as cooperative hunting, concentrating, disturbing, and disorienting prey by slapping and slashing them, followed by capture of the stunned or injured individuals (Webb and Debuffrenil 1990). This is the case, for example, for three large predators well known for their use of weapons when catching prey, i.e., sailfish (Domenici et al. 2014), killer whales (Domenici et al. 2000), and thresher sharks (Oliver et al. 2013). Although feeding strategies are affected by a number of other factors such as the type of habitat, behavior, and morphology both of the predator and their prey, it is possible that the predator–prey size-ratio may affect the generality of predatory behavior. Predator–prey size-ratios of the three species of

predators that use weapons are within the range 10:1 to 20:1 (sailfish, 12.6:1; killer whale, 13.5:1; thresher shark, 15.5:1, based on mean lengths from previous studies) (Domenici et al. 2000, 2014 and Oliver et al. 2013, respectively). As a comparison, piscivorous predators that use whole-body acceleration to capture their prey typically show predator–prey size-ratios mainly ranging from 2:1 to 10:1 (Scharf et al. 2000), although various species of sharks that also use whole-body acceleration for capturing prey are more than 10 times longer than their prey. Hence, while the species known to use a weapon show predator:prey ratios of about 12–15:1, not all predators with such a predator:prey size ratio use weapons to capture prey. At least in the case of some piscivorous predators, it is possible that a predator–prey size-ratio more than 10:1 but less than 100:1 implies such a disadvantage in term of unsteady swimming relative to the prey, such that feeding using whole-body acceleration becomes overtly difficult. At the same time, the prey is not small enough to be caught using filter feeding. It is perhaps in this range of predator–prey size-ratio (i.e., 10:1 to 100:1) that the use of weapons has evolved in some species as an effective strategy for foraging on schooling prey.

Further work combining field observations of swimming speeds employed during predator–prey interactions in the oceans, with scaling of locomotor performance based on kinematic and physiological measurements, could prove informative regarding the basic rules governing locomotor strategies for foraging and defense in predators and their prey.

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