

RESEARCH ARTICLE

Multiple behaviors for turning performance of Pacific bluefin tuna (*Thunnus orientalis*)

Abigail M. Downs¹, Allison Kolpas², Barbara A. Block³ and Frank E. Fish^{1,*}

ABSTRACT

Tuna are known for exceptional swimming speeds, which are possible because of their thunniform lift-based propulsion, large muscle mass and rigid fusiform body. A rigid body should restrict maneuverability with regard to turn radius and turn rate. To test if turning maneuvers by the Pacific bluefin tuna (*Thunnus orientalis*) are constrained by rigidity, captive animals were videorecorded overhead as the animals routinely swam around a large circular tank or during feeding bouts. Turning performance was classified into three different types: (1) glide turns, where the tuna uses the caudal fin as a rudder; (2) powered turns, where the animal uses continuous near symmetrical strokes of the caudal fin through the turn; and (3) ratchet turns, where the overall global turn is completed by a series of small local turns by asymmetrical strokes of the caudal fin. Individual points of the rostrum, peduncle and tip of the caudal fin were tracked and analyzed. Frame-by-frame analysis showed that the ratchet turn had the fastest turn rate for all points with a maximum of 302 deg s⁻¹. During the ratchet turn, the rostrum exhibited a minimum global 0.38 body length turn radius. The local turn radii were only 18.6% of the global ratchet turn. The minimum turn radii ranged from 0.4 to 1.7 body lengths. Compared with the performance of other swimmers, the increased flexion of the peduncle and tail and the mechanics of turning behaviors used by tuna overcomes any constraints to turning performance from the rigidity of the anterior body morphology.

KEY WORDS: Maneuverability, Agility, *Thunnus orientalis*, Ratchet turn, Swimming

INTRODUCTION

Animals have enhanced maneuverability while maintaining controlled stability through various morphological and behavioral adaptations. Stability is defined as a steady movement along an expected trajectory, while changes in rate of movement and changes in trajectory characterize maneuverability (Fish, 2002; Webb, 2004, 2006). Maneuverability enhances turning performance of marine animals at the expense of energy, whereas stability reduces the energetic cost of locomotion (Schakman et al., 2020). The morphology of an animal defines its locomotor performance and

dictates its maneuverability and stability (Webb, 1984; Weihs, 1989, 1993, 2002; Taylor, 1989; Fish, 2002). Animals with a morphology associated with high speed swimming are in general much less maneuverable than species that forage by stalking and lunging or live in complex environments (Webb, 1984; Weihs, 1993; Fish, 2002).


Turning performance has been studied in various species of aquatic animals, with many morphological attributes correlating with a high turning performance (Segre et al., 2019). Three main morphological characteristics have proved to be important for turning performance: body shape, the position and mobility of propulsors and control surfaces, and body flexibility (Rivera et al., 2006). In this study, we focus on body flexibility. A flexible body offers greater turning performance by allowing an animal to turn around a smaller radius of curvature and by increasing the rotational rate (Harris, 1936; Fish, 2002; Parson et al., 2011). The antithesis of flexibility is rigidity, which is the inability to bend and can limit turning performance without the use of additional mobile control surfaces or propulsors (Walker, 2000; Fish, 2002; Fish and Nicasastro, 2003; Rivera et al., 2006; Parson et al., 2011; Fish and Lauder, 2017).

Bluefin tuna (*Thunnus* sp.) of the family Scombridae (tribe Thunnini) are high-speed, pelagic swimmers with relatively inflexible bodies that foster low drag (Walters and Fierstine, 1964; Magnuson, 1978; Katz et al., 2001; Sepulveda et al., 2003). Bluefin tuna have a streamlined body shape with a large muscle mass in the anterior portion of their body, tapered wing-like pectoral fins and relatively low body flexibility compared with other fishes (Magnuson, 1978). These morphological features are all indicative of a constrained turning performance. Turning performance is categorized by two qualities; agility and maneuverability. Agility is the speed of reorientation, which can be defined as turning rate; whereas maneuverability is the minimum radius of the turning path (Walker, 2000). Bluefin tuna swim using lift-based propulsion with a stiff, high-aspect ratio lunate caudal fin that acts like an oscillating hydrofoil with the oscillatory movements are confined to the tail and caudal peduncle (Nursall, 1956; Lighthill, 1969; Webb, 1975; Lindsey, 1978; Graham and Dickson, 2004). This form of propulsion and the accompanying morphology have defined the thunniform swimming mode (Breder, 1926; Webb, 1975; Lindsey, 1978; Dowis et al., 2003; Sepulveda et al., 2003; Di Santo et al., 2021). Compared with other swimming modes, lateral oscillations at the rostrum of tunas have been shown to be 1.3- to 2-times greater than that in nonscombrid fishes despite previous observations (Dowis et al., 2003; Di Santo et al., 2021).

Scombrid fishes swim constantly and make extensive trans-oceanic migrations (Block et al., 2001; Stokesbury et al., 2004; Clark et al., 2013). Bluefin tuna are powerful predators that feed on small, schooling fish and squid. Because of their relatively small size, these prey species exhibit greater agility and maneuverability than the tuna (Howland, 1974; Josse et al., 1998; Clark et al., 2013). Although high swimming speeds and endurance are important, the ability to change direction at high speeds is necessary for the bluefin

¹Department of Biology, West Chester University, West Chester, PA 19383, USA. ²Department of Mathematics, West Chester University, West Chester, PA 19383, USA. ³Department of Biology, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93905, USA.

*Author for correspondence (ffish@wcupa.edu)

 A.M.D., 0000-0003-4668-9539; A.K., 0000-0003-0551-6957; B.A.B., 0000-0002-7486-3189; F.E.F., 0000-0001-5973-3282

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0>), which permits unrestricted use, distribution and reproduction in any medium provided that the original work is properly attributed.

tuna to capture their smaller, more elusive prey (Howland, 1974). The structure of the body, however, is indicative of a design that enhances stability over maneuverability. A large anterior muscle mass inserts on the caudal peduncle through elongate lateral tendons to power propulsive movements (Fierstine and Walters, 1968; Donley and Dickson, 2000; Graham and Dickson, 2004; Shadwick, 2005; Shadwick and Syme, 2008) and these muscles act as a large inertial mass, making the anterior body stiff. This morphology helps to reduce the pressure drag on the body (Lighthill, 1969; Webb, 1975). The caudal peduncle exhibits ‘narrow necking’ and possesses lateral keels, both of which reduce drag and lateral recoil from the oscillations of the caudal fin (Lighthill, 1969). The bluefin tuna and other scombrids have an array of large median fins (e.g. dorsal, anal), smaller median finlets and elongate pectoral fins that further stabilize the body (Magnuson, 1970, 1978; Nauen and Lauder, 2001). A musculo-vascular complex can erect the median dorsal fins of bluefin tuna (Pavlov et al., 2017). The first dorsal fin can be folded into a slot when not needed to control stability and maneuverability (Fish and Lauder, 2017). Blake et al. (1995) measured turning radius and turning rate in yellowfin tuna (*Thunnus albacares*). The average turning radius relative to body length (BL) for yellowfin tuna was 0.47 BL with an average turning velocity of 0.71 m s^{-1} . Such turning performance is below that of more flexible-bodied fishes (Fish and Nicastro, 2003).

Despite all the structural and morphological limitations to body flexibility, tuna consistently exhibit the ability to capture their more elusive prey. The ability to swim at high speeds and maneuver through the water with a rigid body presents a conundrum in understanding the locomotor performance of this aquatic predator. In this study, it is hypothesized that the bluefin tuna overcomes the limitations of body rigidity by using a variety of behavioral methods to execute tight, quick maneuvers. Here, we record and quantify swimming behaviors used by the Pacific bluefin tuna to determine whether turning performance is better than that expected based on their relatively rigid body.

MATERIALS AND METHODS

Video recordings of 13 captive Pacific bluefin tuna [*Thunnus orientalis* (Temminck and Schlegel 1844)] were made at the Hopkins Marine Station of Stanford University. Tuna swam continuously in a 9.1 m diameter, 110,000 liter tank with a 1.8 m depth and a grid of 1 m squares painted on the bottom of the tank. The approximate body length was estimated when tuna were swimming near the bottom of the tank at $\sim 1.37 \text{ m}$, although individual animals could not be accurately measured. The filtration system did not generate a current in the tank. Videos were recorded at 60 frames s^{-1} with a Canon EOS 5D Mark III from a catwalk directly above the center of the tank at a height of approximately 3 m above the surface of the water. The camera was clamped to the catwalk for stabilization. Recordings were taken during feeding bouts and non-feeding bouts to ensure maximum performance as well as routine swimming were recorded, respectively. The turns were all in the horizontal plane. The research was approved by the West Chester University Institutional Animal Care and Use Committee (Fish 201801). All IACUC and APLAC permissions were available on bluefin tunas from Stanford University.

All videos were analyzed frame-by-frame using Tracker Software (<https://physlets.org/tracker/>; v. 5.1.3). Because of the imprecision in determining absolute measures using the bottom grid as a scale owing to the unknown swimming depth of each fish, a relative measure of body length (BL) specific for the individual tuna was used. The tuna swam circularly in the tank, although the direction of

travel was inconsistent so that any current produced by the fishes was unknown. Kinematics of the tip of the rostrum, peduncle and tip of the caudal fin were analyzed to follow the trajectory of each of the points. The rostrum refers to the stiff snout of the tuna, the peduncle refers to the insertion point of the caudal or tail fin of the tuna. Turns were classified based on the movements of the caudal fin through the turn. A custom MATLAB code was used to filter the trajectory of the digitized points to remove any observer error due to hand digitizing and distortion of the surface of the water. A circle of best fit was produced for each turn (Fig. 1), while calculating angular velocity or turn rate (ω ; deg s^{-1}) and turn radius (r ; BL). Swimming velocity (U ; BL s^{-1}), ω and r for all three points on the fish were calculated. The extreme 20% for all three parameters was calculated to compare maximum turning performance among the different turning maneuvers. Choice of the extreme 20% of values was considered arbitrary for comparison of turning performance but was used previously for comparisons (Webb, 1983; Gerstner, 1999; Fish and Nicastro, 2003; Fish et al., 2018).

Although it would have been appropriate to track the position of the center of gravity (CG) of the tuna to analyze the kinematics of turning, it was not possible to mark the position of CG on the fish. As the anterior body of the tuna was stiff and did not exhibit flexure, the rostrum was used as a proxy for CG as rostrum and CG would be turning at the same rate and trajectory (Fish et al., 2018).

Angle of attack of the caudal fin was measured for 10 ratchet turns (see below). These 10 videos were selected because of minimal distortion from the water. A screenshot of the swimming path was taken in Tracker and then analyzed in Fiji (v. 1.0). Angle of attack was measured as the angle between the trajectory of the caudal fin and the cord length, which was a line between the caudal fin tip and the peduncle (Fish et al., 1988). Angle of the peduncle during the different turning maneuvers was measured frame by frame in

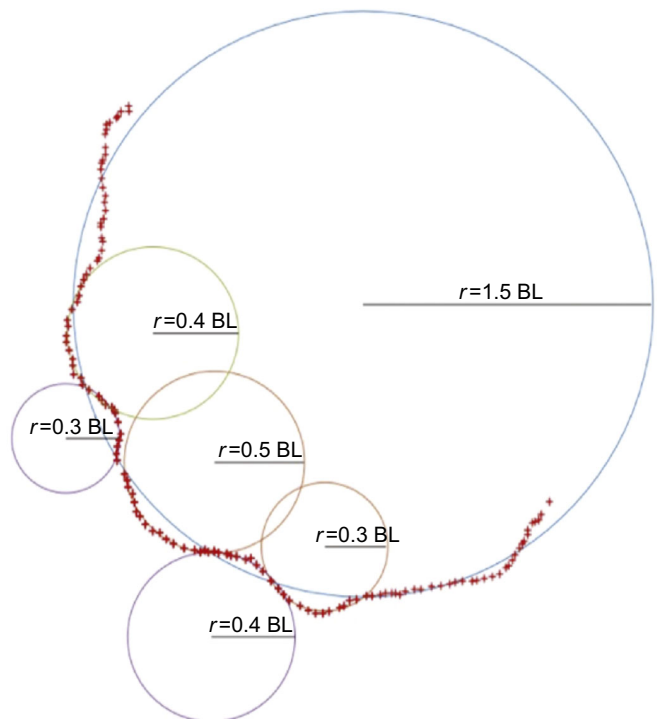


Fig. 1. Circle of best fit for a ratchet turn. The large blue circle represents the global ratchet turn while the smaller circles represent the local ratchet turns within the global turn. BL, body length.

Tracker (v. 5.1.3) by drawing a straight line down the midline of the body and then drawing a straight line through the peduncle and caudal fin. The angle was measured from the intersection of the two lines. Twenty videos were chosen based on clarity and minimal distortion from water. The average of the peduncle angle throughout the turn was taken to accurately represent the overall angle during a turn.

Statistics

All statistics were run in RStudio (v. 1.2.5019; <https://posit.co/>). Variation about means was expressed as ± 1 s.d. An ANOVA was run to accurately compare the radius and turn rate of each classified turn (see Results). A Tukey test was used to determine the differences between each type of turn. Because individuals could not be identified, the degrees of freedom were based on the 13 bluefin tuna in the tank. For the ratchet and powered turns, 25 videos were selected of each to be analyzed based on visibility (minimal wave distortion), and maximal performance. For the glide turns, 10 videos were selected to be analyzed based on the same criteria. The powered and ratchet turn were more frequently used by the fish leading to a larger sample of turn sequences. A regression was performed to compare the global turn rate of the three turns to the global turn radius. Degrees of freedom for the regression were also based on the 13 fish in the tank. Regression equations and correlation coefficients (R) were computed using Kaleidagraph software (v. 4.5.0; <https://www.synergy.com/>). Data are available in the institutional data repository at http://digitalcommons.wcupa.edu/bio_data/7.

RESULTS

Video analysis showed three different turning maneuvers that were used by the bluefin tuna while exercising yawing (lateral) turns (Fig. 2). These turns were categorized as (1) glide turn, (2) powered

turn and (3) ratchet turn. Behavioral observations were used to classify these turns. It is unknown if the pectoral fins of the tuna were fully abducted at all times when observed and whether their pitch was changing.

The glide turn (Movie 1) was characterized as using one large stroke of the caudal fin and then the fish glided passively through the remainder of the turn. In the glide turn, the caudal fin was used as a rudder, using one half stroke of the tail to complete the overall turn. The tail beat occurred to the outside of the overall turn (Fig. 2A). The maximum ω observed for the glide turn was $159.53 \text{ deg s}^{-1}$. The minimum turn radius for the glide turn was 0.7 BL. The mean ω of the glide turn was $99 \pm 52 \text{ deg s}^{-1}$, while the mean r of the glide turn was $2.6 \pm 1.0 \text{ BL}$. The mean extreme 20% calculated for r was $0.9 \pm 0.2 \text{ BL}$, and the mean extreme 20% of ω was $158 \pm 19 \text{ deg s}^{-1}$.

The powered turn (Movie 2) was characterized by continuous, nearly symmetrical strokes of the tail to actively swim through the turn. The powered turn was mainly viewed during routine swimming. The maximum ω of the powered turn was 219 deg s^{-1} and the minimum r was 0.6 BL. The mean ω observed was $103 \pm 66 \text{ deg s}^{-1}$, while the mean r was $1.3 \pm 0.5 \text{ BL}$. The mean extreme 20% calculated for r showed a radius of $0.7 \pm 0.1 \text{ BL}$ and the mean extreme 20% of the ω was $145 \pm 22 \text{ deg s}^{-1}$. A larger r was expected because the fish was using the powered turn during routine swimming bouts, without making tight turns to capture food.

The ratchet turn (Movie 3) by the tuna was similar to the motion of a ratchet tool. The ratcheting motion used a series of asymmetrical strokes to produce multiple small radius turns that additively generated a large radius turn. Like the powered turns, the ratchet turns are categorized as active turns as they both required multiple strokes of the caudal fin. In the ratchet turn, the tuna rotated around its CG with multiple asymmetrical strokes of the caudal fin. The tail beat towards the outside of the overall turn (Fig. 2C). The

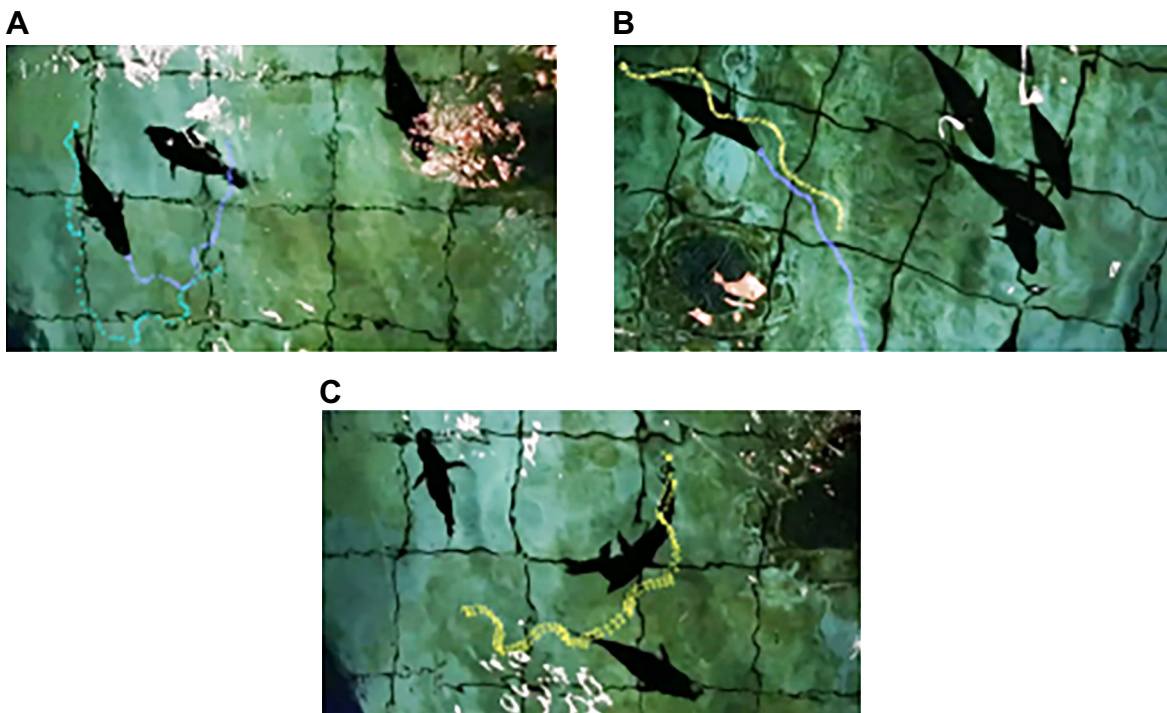


Fig. 2. The three different turning maneuvers utilized by Pacific bluefin tuna during feeding bouts. (A) The rostrum and tip of the tail tracked during one frame of a glide turn. The blue line represents the trail of the rostrum and the green line represents the trail of the tip of the tail. (B) The rostrum and tip of the tail tracked during one frame of a powered turn. The blue line represents the trail of the rostrum and the yellow line represents the trail of the tip of the tail. (C) The tip of the tail tracked during one frame of a ratchet turn (yellow line).

ratchet turn can be broken up into an overall global turn composed of a series of smaller local turns. The local turns were differentiated from the global turn to show the difference between the overall effect of the turn and the individual actions. The maximum ω observed during the global ratchet turn was 187 deg s^{-1} and the minimum r was 0.5 BL. The mean global ω was $104 \pm 36 \text{ deg s}^{-1}$. The mean global r was $1.1 \pm 0.6 \text{ BL}$. The mean extreme 20% of r and ω for the global ratchet turn was $0.6 \pm 0.2 \text{ BL}$ and $155 \pm 62 \text{ deg s}^{-1}$, respectively. The mean ω of the local ratchet turn was $463 \pm 185 \text{ deg s}^{-1}$, about 4 times faster than the global ω . The mean r of the local ratchet turn was $0.3 \pm 0.2 \text{ BL}$ (Fig. 3). The mean extreme 20% calculated for the local r was $0.2 \pm 0.0 \text{ BL}$ and the mean extreme 20% calculated for the local ω was $738 \pm 164 \text{ deg s}^{-1}$.

Ten videos of ratchet turns were selected to analyze the angle of attack. Table 1 shows the mean angle of attack of each global ratchet turn with the turn rate (deg s^{-1}) and radius (BL) of the turn. Means for angles of attack ranged from 16 to 41 deg. Besides tracking the peduncle, the sequential positions of the rostrum and tail were also recorded for comparison amongst the three different points (rostrum, peduncle, tail) (Table 2). ω and r of the global turns was calculated at the three different positions. Trends changed slightly depending on which point of the body was tracked. When the rostrum was tracked, the fastest mean turn rate was that of the ratchet turn at 104 deg s^{-1} and the smallest mean r was observed in the ratchet turn at 1.1 BL. When the peduncle was tracked, the fastest mean ω observed was the glide turn at 162 deg s^{-1} and the smallest mean r was for the ratchet turn at 1.0 BL. When the tail was tracked,

Table 1. Mean (\pm s.d.) angles of attack to individual turn radius and turn rate for 10 global ratchet turns

Video ID	Mean angle of attack (deg)	Turn rate (deg s^{-1})	Radius (BL)
9M2A0948-1	32 ± 18	110	1.1
9M2A0949-1	32 ± 20	115	0.9
9M2A0955-1	26 ± 12	77	1.4
9M2A0956-1	30 ± 12	81	1.3
9M2A0966-1	22 ± 10	136	1.1
9M2A0966-2	41 ± 5	114	1.2
9M2A0968-1	30 ± 5	148	0.8
9M2A0969-1	22 ± 6	110	1.2
9M2A0974-1	16 ± 7	148	0.9
9M2A0972-1	24 ± 7	82	1.2

the mean ω observed was the glide turn at 123 deg s^{-1} and the smallest mean r was the ratchet turn at 1.1 BL. It was expected that the glide turn would have the fastest turn rates in the posterior region of the body because the peduncle can be flexed to a greater degree than when the fish is actively swimming. This flexion cants the caudal fin at a high angle of attack creating a larger turning force to propel the tuna through the turn. It is hypothesized that when tracking the rostrum, the fastest ω was observed during the ratchet turn because the multiple strokes of the tail allowed for greater thrust production and therefore turned the anterior of the fish faster. The kinematics on the peduncle were used for the purpose of this study because of their importance for thrust production.

The ω compared to r of the global turn for all three of the turn types followed a curvilinear trend (Fig. 4A). The trend for each of the turning maneuvers was found to be significant at $P < 0.01$: as ω decreased, r increased, indicating that a faster turn will complete a tighter turn. This trend was consistent with previously reported turning performance (Fish and Nicastro, 2003; Parson et al., 2011). The increase in ω with decreasing r can be explained by the fact that the tuna with smaller radius turns would move through a larger angular displacement for a given time compared with larger radius turns.

The angle of the peduncle was measured throughout each turn to determine whether peduncle angle affected ω and/or r of the turns. With a greater degree of bending at the peduncle, the fish can potentially produce an increased turning force effectively reducing the turn radius in a short time period, and therefore generate a faster turn rate. However, when compared with ω and r , there was no correlation between angle of peduncle and either variable. The maximum angle of the peduncle observed was 62 deg. This degree of flexion demonstrates significant flexibility in the posterior region of the tuna's body than previously observed.

The r of the three turning behaviors differed statistically (ANOVA, $F=165.5$, $P < 0.001$). The r of the global ratchet turn and the global powered turn were not significantly different from

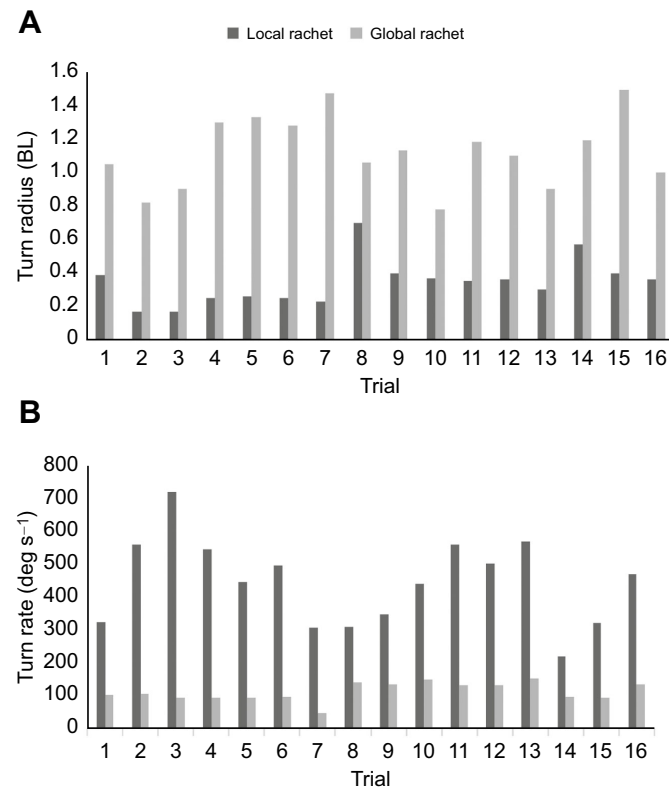


Fig. 3. Comparison between turn radius and turn rate of global and local ratchet turns of Pacific bluefin tuna. (A) Turn radius (BL) and (B) turn rate (deg s^{-1}). Sixteen bluefin tuna turning trials were analyzed to determine turn radius and turn rate. These 16 turns were chosen out of nearly 100 turns due to clarity of the video. Fish were recorded swimming in the tank on 10 separate occasions.

Table 2. Mean (\pm s.d.) turn rate and turn radius for global turns measured at the rostrum, peduncle and tip of the tail during the three different turns observed ($n=25$)

Body point	Turn parameter	Glide	Powered	Ratchet
Rostrum	Turn rate (deg s^{-1})	99 ± 3	103 ± 6	104 ± 5
	Turn radius (BL)	2.6 ± 0.8	1.3 ± 0.4	1.1 ± 0.5
Peduncle	Turn rate (deg s^{-1})	162 ± 6	104 ± 5	122 ± 5
	Turn radius (BL)	1.2 ± 0.4	1.5 ± 0.6	1.0 ± 0.3
Tail	Turn rate (deg s^{-1})	123 ± 5	100 ± 100	119 ± 7
	Turn radius (BL)	1.7 ± 0.5	1.6 ± 0.7	1.1 ± 0.6

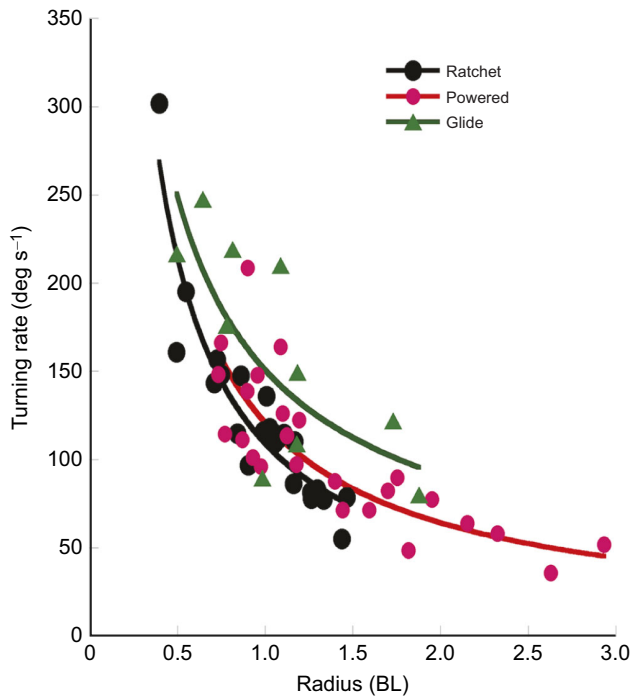


Fig. 4. Regressions comparing the turning rates of the global turns of the ratchet, powered and glide turns. 56 turns were analyzed and selected from nearly 100 turns owing to clarity. Fish were recorded swimming in the tank on 10 separate occasions. The regression equations for each line are $\omega=109 r^{-0.97}$ for ratchet turns ($R=0.9$), $\omega=121 r^{-0.91}$ for powered turns ($R=0.8$) and $\omega=151 r^{-0.73}$ for glide turns ($R=0.7$).

one another ($P=0.511$), with the powered turn having a larger r . The local ratchet turn significantly differed from the powered turn ($P<0.001$) and the global ratchet turn ($P<0.001$) (Fig. 5A).

The result of the ANOVA testing statistical difference between turn rates indicated that the turn rates of the three turns statistically differed ($F=225.9$, $P<0.001$). The ω between the global ratchet turn and the powered turn did not significantly differ ($P=0.971$). The ω between the local ratchet and powered turn ($P<0.001$) were significantly different as was ω between the local ratchet and global ratchet turn ($P<0.001$) (Fig. 5B). The g force on the fish significantly differed during each type of turn ($F=226.1$, $P<0.001$). The global ratchet turn and the powered turn were not significantly different ($P=0.977$); however, the local ratchet and the powered turn and the local ratchet and global ratchet turn were significantly different at $P<0.001$ (Fig. 5C).

DISCUSSION

Bluefin tuna turning

Pacific bluefin tuna exhibited three different turning maneuvers to yaw and change the trajectory of their motion. The glide turn, the powered turn, and the ratchet turn all allowed for a rapid and tight turning performance for the tuna as a rigid-bodied animal. The glide turn, where the caudal fin acted as a boat rudder, was a passive turn with a quick ω . The glide turn was classified as a passive turn as the tail not actively moving through the turn as opposed to actively oscillating throughout the turn. The maximum ω observed was 160 deg s^{-1} and the minimum r was 0.7 BL . The powered turn, an active turn, was viewed more during routine swimming rather than during feeding bouts. The maximum ω of the powered turn was faster than gliding turns at 219 deg s^{-1} with a larger minimum turn radius of 0.6 BL . The ratchet turn, a maneuver previously

undocumented, used quick asymmetrical strokes of the tail to complete a tight radius turn. The maximum ω of the ratchet turn was 302 deg s^{-1} and the minimum r was 0.4 BL . The local elements of the global ratchet turn minimized the radius of the global turn, but the fast strokes of the caudal fin during the local turns allowed for a relatively high ω of the collective global turn. Other fins, such as the dorsal fin and pectoral fins, are utilized in turning maneuvers but cannot be observed.

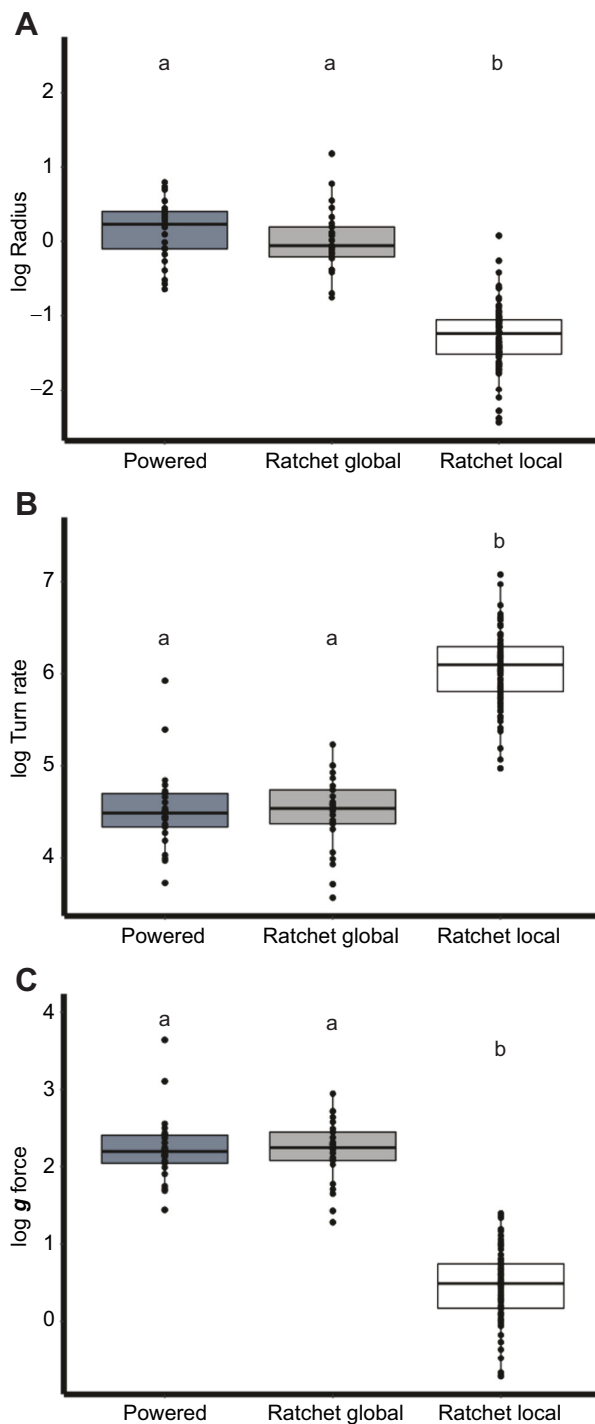
Like many other fishes, the anterior muscle mass of tunas comprises muscle fibers packed into myomeres and attached to a horizontal septum (Fierstine and Walters, 1968; Gemballa et al., 2003; Lear et al., 2020). A specialization of tunas is that each myomere is separated by an individual myoseptum, which conjugate to form tendons in the peduncle region of the fish (Fierstine and Walters, 1968). The posterior oblique tendons originate from connective tissue fibers of the myosepta (Kafuku, 1950; Fierstine and Walters, 1968). A large, superficial tendon known as the great lateral tendon, spans from the caudal vertebrae through the peduncle and into the caudal fin rays (Fierstine and Walters, 1968). A third tendon set, the paired lateral tendons, lie medial to the great lateral tendon and insert at the beginning of the fin rays (Kishinouye, 1923; Fierstine and Walters, 1968; Shadwick et al., 2002).

The tendons of the myosepta that form the dorsal and ventral anterior cones between the red muscle fibers are weakly developed in tunas (Westneat and Wainwright, 2001; Long et al., 2002). These weakly developed tendons within the myosepta uncouple the red muscle from the local body, allowing for more bending in the posterior region of the body and greater opportunity to produce mechanical work via the posterior oblique and great lateral tendons (Westneat et al., 1993; Knower et al., 1999; Shadwick et al., 1999; Westneat and Wainwright, 2001; Long et al., 2002). Forces generated by the large muscle mass in the anterior region of the body are transferred via the tendon complex into the caudal fin of the tuna (Westneat and Wainwright, 2001; Shadwick, 2005). This force transfer can explain the high turn rates exhibited in bluefin tuna while still maintaining a degree of flexibility in the peduncle through the elastic tendons.

The large anterior muscle mass in tuna that supplies the large force production makes the body wider compared with other fishes. This increase in the body width helps to streamline the body and reduces anterior yaw from recoil forces from oscillations of the tail, but stiffens the anterior body (Magnuson, 1970, 1978; Webb, 1975; Dowis et al., 2003). Despite the thickened body, the kinematics patterns displayed by tuna have similarity with other more flexible-bodied fishes using body-caudal fin swimming (Di Santo et al., 2021). However, narrow necking in the peduncle and the double joint of the caudal vertebrae increase flexibility in the peduncle and at the base of the caudal fin in tuna (Fierstine and Walters, 1968; Shadwick et al., 2002). The double joint is associated with the two vertebrae in the caudal fin complex which are short and have reduced zygapophyses (Fierstine and Walters, 1968). The depressed neural and hemal spines of the vertebrae in the peduncle are associated with the lateral keels (Fierstine and Walters, 1968). The keels provide increased leverage to transfer force by tendons originating from the anterior musculature (Shadwick et al., 2002; Donley et al., 2004). The structure of the peduncle and caudal fin complex provides flexibility for tuna with the ability generate the torque required for turning.

Comparison with turning in other tuna species

Blake et al. (1995) studied yellowfin tuna to determine whether specializations for steady swimming would affect the turning



performance of the fish. Blake et al. (1995) filmed yellowfin tuna (*T. albacares*) from above as the fish swam around a circular tank. Food was periodically thrown into the tank to encourage maneuvers. Blake's study looked strictly at r and ω without looking at different strategic methods to enhance turning performance. Blake et al. (1995) found that r compared with body size of the yellowfin tuna was large compared with r in other fish. The mean r of the yellowfin tuna was 0.47 BL. In the present study, the local ratchet turn of the bluefin tuna allowed the tuna to have a mean r of 0.2 BL. The ω of the bluefin tuna when using the three different turning behaviors

Fig. 5. Effect of a powered turn and global and local ratchet turns on the radius, turn rate and g force of the turn. (A) Box plots representing the distribution of the data for radius (BL) of the turn. Global ratchet compared with powered, $P=0.51$; local ratchet compared with powered, $P<0.001$; global ratchet compared with local ratchet, $P<0.001$. (B) Turn rate (deg s^{-1}). Global ratchet compared with powered, $P=0.98$; local ratchet compared with powered, $P<0.001$; global ratchet compared with ratchet-local, $P<0.001$. (C) g force of the turn. Global ratchet compared with powered, $P=0.98$; local ratchet compared with powered, $P<0.001$; global ratchet compared with ratchet-local, $P<0.001$. Each point is represented by a dot on the graph with mean indicated by the horizontal bar and 25–75% of the points are represented by the box. Outliers fall off the vertical line in the center of the box. Based on a one-way ANOVA analysis, boxplots with same label (a) show no statistical difference, while boxplots with a differing label (b) show a statistical difference from those boxplots labeled with a.

allowed the fish to have a greater turning performance relative to its body size compared with the yellowfin tuna (Fig. 5B). The yellowfin tuna in the study by Blake et al. (1995) had a mean ω that was 66.8% slower than ω for the bluefin tuna.

Newlands et al. (2004) examined different techniques for adaptive search behavior in Atlantic bluefin tuna (*Thunnus thynnus*) using ultrasonic telemetry. Newlands et al. (2004) found that the velocity of a bluefin tuna traveling in schools ranged from 1.18 to 1.89 m s^{-1} . The present study found that the velocity of an animal during the three different turning maneuvers ranged from 1.42 to 4.00 BL s^{-1} . The mean turning angle of a schooling bluefin tuna was 23.3 ± 2.7 deg. The turning angle for Pacific bluefin tuna for each of the three turning maneuvers was found to be 72.8% greater than the mean reported by Newlands et al. (2004). The difference may be due to the different conditions in which the two species were measured. The Atlantic bluefin tuna were examined with respect to movement of a school, whereas the Pacific bluefin tuna were examined as individuals rapidly turned to optimize collection of a food source thrown into their tank. The different turning maneuvers displayed by the tuna in the present study would be beneficial for tuna in the wild when chasing prey because of the potential to turn at greater angles while maintaining a faster speed.

Comparison of bluefin tuna with other animals

Rigidity, defined as the inability to be bent or be forced out of shape, plays an important role in understanding stability and maneuverability (Walker, 2000; Fish, 2002; Fish and Nicastro, 2003; Maresh et al., 2004; Rivera et al., 2006; Parson et al., 2011; Segre et al., 2019). Rigidity of a swimmer can limit the rate of turning. Fig. 6 compares turning performance among different species relative to their body size, with the black line extending from the small whirligig beetle (an aquatic insect) to the USS *Albacore*, an experimental naval submarine. The line separates the turning performance between flexible and rigid-bodied animals. Flexible-bodied animals are concentrated above the line and rigid-bodied swimmers have turning rates for their body size below the line. The ω of the three turning maneuvers of the bluefin tuna with a rigid anterior body are all above the line. The local ratchet turn is approximately 50–100 deg s^{-1} higher on the graph than the yellowfin tuna and 50–650 deg s^{-1} higher than cetaceans. The yellowfin tuna had a smaller body size than the bluefin tuna in this study, while the cetaceans had a more flexible body than the bluefin tuna (Fish, 2002). This indicates that the flexible peduncle and rapid strokes of the caudal fin enable the bluefin tuna to turn quickly relative to its body size to overcome the rigidity of its body (see Foraging techniques and turning).

Rigid bodies are expected to severely limit turning performance. Walker (2000) examined a single spotted boxfish (*Ostracion meleagris*) to determine how a rigid body limits turning

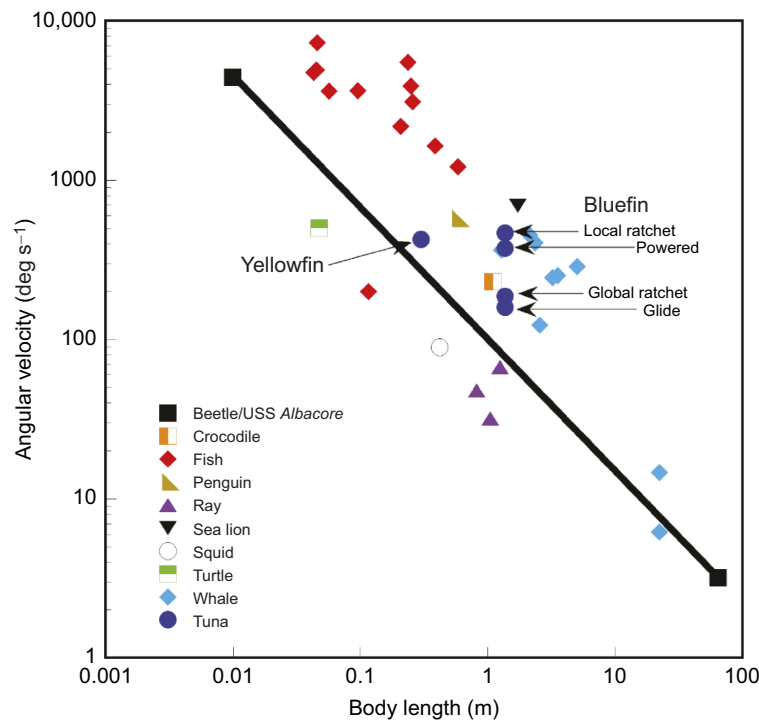


Fig. 6. Comparison of turning performance amongst different species. The turning rate is shown as a function of the body length. The black line indicates the two extremes of two rigid bodies: the whirligig beetle and the submarine USS *Albacore*. The three turning maneuvers as well as the local elements of the ratchet turn are represented by the dark blue circles and fall to the right of the black line.

performance. Boxfishes have thickened scales that are modified into bony plates that encompass their bodies (Randall, 1972; Tyler, 1980; Walker, 2000). This thickened carapace makes it impossible for the boxfish to flex its body anterior to the caudal peduncle. The ω of the boxfish ranged between 76.1 and 147.0 deg s⁻¹, while the turn radii ranged from 0.0005 to 0.11 BL. The relatively small r was performed using the actions of the multiple fins located about the body in order to compensate for the restriction of the rigid body. In comparison, the turn rate of the bluefin tuna displayed a greater range and higher maximum ω across the four different turning maneuvers (local ratchet, global ratchet, powered and glide). The r values for the tuna were greater for its size than the boxfish owing to the limited mobility of the tuna's fins. With the exception of the caudal fin, the fins of the tuna act as passive control surfaces (Magnuson, 1970, 1978; Fish and Lauder, 2017).

Highly maneuverable animals such as many fishes (exception of boxfish), crocodylians, penguins, cetaceans and sea lions will have increased turning performance owing to their flexible body designs (Fig. 6). Generally, the small, flexible-bodied fishes display the fastest turning performance. Coral reef fish were shown to exhibit small turn radii and exceptional turning rates relative to body length owing to their small body size, flexible bodies, and use of multiple fins. The r ranged from 0.06 to 0.09 BL and ω ranged from 425.6 to 7300 deg s⁻¹ in various coral reef fishes (Gerstner, 1999). These reef fishes used their median, paired and caudal fins, and body flexibility to accomplish small radius turns, unlike the tuna, which is limited to the use of only its peduncle and caudal fin. Larger swimmers such as cetaceans and the sea lion have greater turning performance for their respective body sizes. The minimum turn radius of the bluefin tuna was 0.38 BL. For other swimmers of the same order of magnitude of body size of the tuna, the minimum r was smaller. An examination of multiple species of cetaceans showed the minimum r of 0.22 BL (Fish, 2002). The California sea lion (*Zalophus californianus*) has maximum turning rate of 690 deg s⁻¹. The high turning performance is most likely due to increased body flexibility. Flexibility in the body of the California

sea lion allows these pinnipeds to make quick turning maneuvers within their environment (Fish, 2002; Fish et al., 2003). Bending of the body and neck is an important component to turning (Aleyev, 1977; Godfrey, 1985; Fish et al., 2003). The flexible neck and body of the sea lion allow it to hyperextend its spine and touch its nose to its pelvic flippers (Riedman, 1990; Fish et al., 2003) and this exaggerated dorsal bending is used in the turning maneuvers (Godfrey, 1985; Fish et al., 2003).

Despite restrictions due to the rigid body of the bluefin tuna, it demonstrated greater turn rates for its size compared with the yellowfin tuna (Fig. 8). Furthermore, ω for the bluefin tuna was in line with trends displayed by more flexible-bodied swimmers. The tuna was thus able to compensate for its stiff body by increased flexibility of the peduncle. Through an active turn, the peduncle bent at a mean of 21 deg with a maximum of 62 deg. Although the angle the peduncle could bend showed no correlation with ω or r , the extreme flexure of the peduncle allowed the tuna to compensate for its generally rigid body and perform turns equivalent to the turning performance of flexible-bodied swimmers.

Foraging techniques and turning

Many fishes will modify their foraging habits to increase their feeding rates (Dill, 1983; Bonsall et al., 2002; Morales and Ellner, 2002; Newlands et al., 2004). Newlands et al. (2004) identified two different search strategies used by the bluefin tuna while foraging, including klinokinesis (regulation of turning) and orthokinesis (speed). Atlantic bluefin tuna typically feed on much smaller prey, such as sand lance, anchovy, squid, and krill (Karakulak et al., 2009; Butler et al., 2010; Logan, et al., 2011; Rohit et al., 2010; Golet et al., 2015). The immense difference in size between predator and prey allow the prey to be more maneuverable than the tuna, theoretically making it difficult for the more rigid-bodied tuna to turn and acquire the prey species (Howland, 1974). Fig. 6 shows that small fishes display much higher angular velocities than the bluefin tuna; however, squid have a much weaker turning performance than that of the tuna. Although the different turning maneuvers do not put

the turning performance of tuna above small schooling fishes, these movements along with other predatory tactics increase the tuna's ability to capture prey.

In any predator-prey pursuit, it can be assumed that the predator is chasing the prey in a straight line and moving at maximum velocities, but also frequently turning with minimal turning radii to increase maneuverability (Howland, 1974). However, it was found that prey can safely and effectively trade velocity for a smaller turning radius to escape a predator. The speed of a large fish is inversely proportional to its turning angle, posing a problem for massive animals, like the bluefin tuna, to keep up with the path of their smaller, highly elusive prey (Domenici, 2001).

The high stiffness of the anterior body requires tuna to use strategies to overcome any maneuvering liability to capture elusive prey. While studying seabird interactions with dolphins and tuna, Au and Pitman (1986) found that yellowfin tuna often feed on medium-sized schools near the surface. Hunting in schools and bringing their prey to the surface is a tactical strategy to cluster and tightly pack their prey in a confined space, rather than relying solely on speed or out-maneuvering single prey in the open ocean. By herding their prey toward the surface of the water in a concentrated bait ball, gannets and dolphins in association with tuna limit the space of available to the schooling fish and thus reduce the need for high maneuverability (Davoren, et al., 2010). Edwards (1992) found that bluefin tuna will 'piggyback' off dolphins and allow the dolphins to herd schooling fish that the tuna consume. Bluefin tuna will attack the middle of the bait ball, completely destroying the integrity of the ball (Clua and Grosvalet, 2001). As the tuna make approximately two to three passes through the bait ball, the dolphins swim around the surrounding areas, forcing the broken bait ball back together. The tuna attack from the bottom of the bait ball, as dolphins circle and aerial predators (varieties of bird species) attack from the surface. The attacking tuna make four to five additional passes through the bait ball before the hunt by all predators is completed (Clua and Grosvalet, 2001). Although preying on bait balls does not require a high rate of turning by tuna to capture their prey, utilizing the different turning maneuvers allows the tuna to extend the performance envelope when foraging.

Conclusions

The bluefin tuna employs various turning behaviors to increase its maneuverability. This study observed and analyzed three types of turning maneuvers/behaviors – the glide turn, powered turn and ratchet turn – that enable the Pacific bluefin tuna to exhibit higher turning performance than has been previously measured in yellowfin tuna (Blake et al., 1995). Despite morphological adaptations for efficient continuous swimming, including a relatively rigid anterior body, the use of the caudal fin complex to power relatively rapid and tight turns results in turning performance similar to that of other more flexible-bodied teleost fishes. The turning maneuvers should allow the Pacific bluefin tuna to capture more maneuverable prey in its epipelagic habitat.

Acknowledgements

We acknowledge the support and assistance of members of the West Chester University Liquid Life Laboratory, including Danielle Adams, Kaitlyn Cardenas, Sarah Kerr, Ariel Leahy and Katherine Riordan. In addition, we thank the anonymous reviewers for their help and suggestions on the manuscript. We are grateful to Hilary Bart-Smith and Robert Brizzolara for financial support from the Office of Naval Research. Some of the results and discussion in the paper form part of an MSc thesis by the lead author Abigail Downs (West Chester University of Pennsylvania, 2020). We thank the Tuna Research and Conservation Staff, and Monterey Bay Aquarium for helping to maintain the tunas for this study.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.M.D., F.E.F.; Methodology: A.M.D., A.K.; Software: A.K.; Validation: A.M.D., F.E.F.; Formal analysis: A.M.D., A.K.; Resources: B.A.B., F.E.F.; Data curation: A.M.D.; Writing - original draft: A.M.D.; Writing - review & editing: A.M.D., A.K., B.A.B., F.E.F.; Supervision: F.E.F.; Project administration: F.E.F.; Funding acquisition: F.E.F.

Funding

The work was supported by a grant from the Multidisciplinary University Research Initiative of the Office of Naval Research [N000141410533]. Funding for the holding and maintenance of tunas was from the Monterey Bay Aquarium TAG A GIANT and Stanford University. Open Access funding provided by West Chester University. Deposited in PMC for immediate release.

Data availability

Data are available from the West Chester University institutional data repository at http://digitalcommons.wcupa.edu/bio_data/7

References

- Aleyev, Y. G. (1977). *Nekton*. Junk: The Hague.
- Au, D. W. K. and Pitman, R. L. (1986). Seabird interactions with dolphins and tuna in the Eastern Tropical Pacific. *Condor* **88**, 304-317. doi:10.2307/1368877
- Blake, R. W., Chatters, L. M. and Domenici, P. (1995). Turning radius of yellowfin tuna (*Thunnus albacares*) in unsteady swimming manoeuvres. *J. Fish. Biol.* **46**, 536-538. doi:10.1111/j.1095-8649.1995.tb05994.x
- Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L., Seitz, A., Walli, A. et al. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* **293**, 1310-1314. doi:10.1126/science.1061197
- Bonsall, M. B., French, D. R. and Hassell, M. P. (2002). Metapopulation structures affect persistence of predator-prey interactions. *J. Anim. Ecol.* **71**, 1075-1084. doi:10.1046/j.1365-2656.2002.00670.x
- Breder, C. M., Jr. (1926). The locomotion of fishes. *Zoologica* **4**, 159-297. doi:10.5962/p.203769
- Butler, C. M., Rudershausen, P. J. and Buckel, J. A. (2010). Feeding ecology of Atlantic bluefin tuna (*Thunnus thynnus*) in North Carolina: diet, daily ration, and consumption of Atlantic menhaden (*Brevoortia tyrannus*). *Fish. Bull.* **108**, 56-69.
- Clark, T. D., Farwell, C. J., Rodriguez, L. E., Brandt, W. T. and Block, B. A. (2013). Heart rate responses to temperature in free-swimming Pacific bluefin tuna (*Thunnus orientalis*). *J. Exp. Biol.* **216**, 3208-3214. doi:10.1242/jeb.086546
- Clua, É. and Grosvalet, F. (2001). Mixed-species feeding aggregation of dolphins, large tunas and seabirds in the Azores. *Aquat. Living Resour.* **14**, 11-18.
- Davoren, G. K., Garthe, S., Montevecchi, W. A. and Benvenuti, S. (2010). Influence of prey behaviour and other predators on the foraging activities of a marine avian predator in a Low Arctic ecosystem. *Mar. Ecol. Prog. Ser.* **404**, 275-287. doi:10.3354/meps08370
- Di Santo, V., Goerig, E., Wainwright, D. K., Akanyeti, O., Liao, J. C., Castro-Santos, T. and Lauder, G. V. (2021). Convergence of undulatory swimming kinematics across a diversity of fishes. *Proc. Nat. Acad. Sci. USA* **118**, e2113206118. doi:10.1073/pnas.2113206118
- Dill, L. M. (1983). Adaptive flexibility in the foraging behavior of fishes. *Can. J. Fish. Aquat. Sci.* **40**, 398-408. doi:10.1139/f83-058
- Domenici, P. (2001). The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comp. Biochem. Physiol. A* **131**, 169-182. doi:10.1016/S1095-6433(01)00465-2
- Donley, J. M. and Dickson, K. A. (2000). Swimming kinematics of juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). *J. Exp. Biol.* **203**, 3103-3116. doi:10.1242/jeb.203.20.3103
- Donley, J. M., Sepulveda, C. A., Konstantinidis, P., Gembella, S. and Shadwick, R. E. (2004). Convergent evolution in mechanical design of lamnid sharks and tunas. *Nature* **429**, 61-65. doi:10.1038/nature02435
- Dowis, H. J., Sepulveda, C. A., Graham, J. B. and Dickson, K. A. (2003). Swimming performance studies on the eastern Pacific bonito (*Sarda chiliensis*), a close relative of the tunas (Family Scombridae). II. Kinematics. *J. Exp. Biol.* **206**, 2749-2758. doi:10.1242/jeb.00496
- Edwards, E. F. (1992). Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: a basis for the bond. *Nat. Mar. Fish. Serv.* **90**, 678-690.
- Fierstein, H. L. and Walters, V. (1968). Studies in locomotion and anatomy of scombrid fishes. *Mem. S. Calif. Acad. Sci.* **6**, 1-31. doi:10.5962/bhl.title.146943
- Fish, F. E. (2002). Balancing requirements for stability and maneuverability in cetaceans. *Integr. Comp. Biol.* **42**, 85-93. doi:10.1093/icb/42.1.85
- Fish, F. E. and Lauder, G. V. (2017). Control surfaces of aquatic vertebrates: active and passive design and function. *J. Exp. Biol.* **220**, 4351-4363. doi:10.1242/jeb.149617

- Fish, F. E. and Nicastro, A. J.** (2003). Aquatic turning performance by the whirligig beetle: constraints on maneuverability by a rigid biological system. *J. Exp. Biol.* **206**, 1649-1656. doi:10.1242/jeb.00305
- Fish, F. E., Innes, S. and Ronald, K.** (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157-173. doi:10.1242/jeb.137.1.157
- Fish, F. E., Hurlley, J. and Costa, D. P.** (2003). Maneuverability by the sea lion *Zalophus californianus*: turning performance of an unstable body design. *J. Exp. Biol.* **206**, 667-674. doi:10.1242/jeb.00144
- Fish, F. E., Kolpas, A., Crossett, A., Dudas, M. A., Moored, K. W. and Bart-Smith, H.** (2018). Kinematics of swimming of the manta ray: three-dimensional analysis of open water maneuverability. *J. Exp. Biol.* **221**, jeb166041. doi:10.1242/jeb.166041
- Gemballa, S., Ebmeyer, L., Hagen, K., Hannich, T., Hoja, K., Rolf, M., Treiber, K., Vogel, F. and Weitbrecht, G.** (2003). Evolutionary transformations of myoseptal tendons in gnathostomes. *Proc. R. Soc. Lond. B* **270**, 1229-1235. doi:10.1098/rspb.2003.2345
- Gerstner, C. L.** (1999). Maneuverability of four species of coral-reef fish that differ in body and pectoral-fin morphology. *Can. J. Zool.* **77**, 1102-1110. doi:10.1139/z99-086
- Godfrey, S. J.** (1985). Additional observations of subaqueous locomotion in the California sea lion (*Zalophus californianus*). *Aqu. Mamm.* **11**, 53-57.
- Golet, W. J., Record, N. R., Lehuta, S., Lutcavage, M., Galuardi, B., Cooper, A. B. and Pershing, A. J.** (2015). The paradox of the pelagics: why bluefin tuna can go hungry in a sea of plenty. *Mar. Ecol. Prog. Ser.* **527**, 181-192. doi:10.3354/meps11260
- Graham, J. B. and Dickson, K. A.** (2004). Tuna comparative physiology. *J. Exp. Biol.* **207**, 4015-4024. doi:10.1242/jeb.01267
- Harris, J. E.** (1936). The role of the fins in the equilibrium of the swimming fish. I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchill). *J. Exp. Biol.* **13**, 476-493. doi:10.1242/jeb.13.4.476
- Howland, H. C.** (1974). Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333-350. doi:10.1016/0022-5193(74)90202-1
- Josse, E., Bach, P. and Dagorn, L.** (1998). Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* **371**, 61-69. doi:10.1023/A:1017065709190
- Kafuku, T.** (1950). Red muscles in fishes. I. Comparative anatomy of scombroid fishes of Japan. *Jap. J. Ichthy.* **1**, 89-100.
- Karakulak, F. S., Salman, A. and Oray, I. K.** (2009). Diet composition of bluefin tuna (*Thunnus thynnus* L. 1758) in the Eastern Mediterranean Sea, Turkey. *J. Appl. Ichthyol.* **25**, 757-761. doi:10.1111/j.1439-0426.2009.01298.x
- Katz, S. L., Syme, D. A. and Shadwick, R. E.** (2001). Enhanced power in yellowfin tuna. *Nature* **410**, 770-771. doi:10.1038/35071170
- Kishinouye, K.** (1923). Contributions to the comparative study of the so-called scombroid fishes. *Tokyo Imp. Univ. Col. Agr. J.* **8**, 293-475.
- Knower, T., Shadwick, R. E., Katz, S. L., Graham, J. B. and Wardle, C. S.** (1999). Red muscle activation patterns in yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas during steady swimming. *J. Exp. Biol.* **202**, 2127-2138. doi:10.1242/jeb.202.16.2127
- Lear, M. J. C., Millard, M., Gleiss, A. C., Dale, J., Dimitrov, M., Peiros, E. and Block, B.** (2020). Biomechanical analysis of the slow-twitch (red) muscle force transmission pathways in tunas. *Physiol. Biochem. Zool.* **93**, 185-198.
- Lighthill, M. J.** (1969). Hydromechanics of aquatic animal propulsion — a survey. *Ann. Rev. Fluid Mech.* **1**, 413-446. doi:10.1146/annurev.fl.01.010169.002213
- Lindsey, C. C.** (1978). Form, function, and locomotory habits in fish. In *Fish Physiology: Locomotion*, Vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 1-100. New York: Academic Press.
- Logan, J. M., Rodríguez-Marín, E., Goñi, N., Barreiro, S., Arrizabalaga, H., Golet, W. and Lutcavage, M.** (2011). Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. *Mar. Biol.* **158**, 73-85. doi:10.1007/s00227-010-1543-0
- Long, J. H., Adcock, B. and Root, R. G.** (2002). Force transmission via axial tendons in undulating fish: a dynamic analysis. *Comp. Biochem. Physiol. A* **133**, 911-929. doi:10.1016/S1095-6433(02)00211-8
- Magnuson, J. J.** (1970). Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost without a gas bladder. *Copeia* **1970**, 56-85. doi:10.2307/1441976
- Magnuson, J. J.** (1978). Locomotion by scombrid fishes: hydrodynamics, morphology and behaviour. In *Fish Physiology*, Vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 239-313. New York: Academic Press.
- Maresh, J. L., Fish, F. E., Nowacek, D. P., Nowacek, S. M. and Wells, R. S.** (2004). High performance turning capabilities during foraging by bottlenose dolphins (*Tursiops truncatus*). *Mar. Mamm. Sci.* **20**, 498-509. doi:10.1111/j.1748-7692.2004.tb01175.x
- Morales, J. M. and Ellner, S. P.** (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* **83**, 2240-2247. doi:10.1890/0012-9658(2002)083[2240:SUAMIH]2.0.CO;2
- Nauen, J. C. and Lauder, G. V.** (2001). Locomotion in scombrid fishes: visualization of flow around the caudal peduncle and finlets of the chub mackerel *Scomber japonicus*. *J. Exp. Biol.* **204**, 2251-2263. doi:10.1242/jeb.204.13.2251
- Newlands, N. K., Lutcavage, M. E. and Pitcher, T. J.** (2004). Analysis of foraging movements of Atlantic bluefin tuna (*Thunnus thynnus*): individuals switch between two modes of search behaviour. *Popul. Ecol.* **46**, 39-53. doi:10.1007/s10144-004-0169-9
- Nursall, J. R.** (1956). The lateral musculature and the swimming of fish. *Proc. Zool. Soc. Lond.* **126**, 127-143. doi:10.1111/j.1096-3642.1956.tb00429.x
- Parson, J., Fish, F. E. and Nicastro, A. J.** (2011). Turning performance in batoid rays: limitations of a rigid body. *J. Exp. Mar. Biol. Ecol.* **402**, 12-18. doi:10.1016/j.jembe.2011.03.010
- Pavlov, V., Rosental, B., Hansen, N. F., Beers, J. M., Parish, G., Rowbotham, I. and Block, B. A.** (2017). Hydraulic control of tuna fins: a role for the lymphatic system in vertebrate locomotion. *Science* **357**, 310-314. doi:10.1126/science.aak9607
- Randall, J. E.** (1972). The Hawaiian trunkfishes of the genus *Ostracion*. *Copeia* **1972**, 756-768. doi:10.2307/1442733
- Riedman, M.** (1990). *The Pinnipeds: Seals, Sea Lions, and Walruses*. Berkeley, CA: University of California Press.
- Rivera, G., Rivera, A. R., Dougherty, E. E. and Blob, R. W.** (2006). Aquatic turning performance of painted turtles (*Chrysemys picta*) and functional consequences of a rigid body design. *J. Exp. Biol.* **209**, 4203-4213. doi:10.1242/jeb.02488
- Rohit, P., Rao, G. S. and Ram Mohan, K.** (2010). Feeding strategies and diet composition of yellowfin tuna *Thunnus albacares* (Bonnaterre, 1788) caught along Andhra Pradesh, east coast of India. *Indian J. Fish.* **57**, 13-19.
- Schakman, M., Steffensen, J. F., Bushnell, P. G. and Korsmeyer, K. E.** (2020). Swimming in unsteady water flows: is turning in a changing flow an energetically expensive endeavor for fish? *J. Exp. Biol.* **223**, jeb212795. doi:10.1242/jeb.212795
- Segre, P. S., Cade, D. E., Calambokidis, J., Fish, F. E., Friedlaender, A. S., Potvin, J. and Goldbogen, J. A.** (2019). Body flexibility enhances maneuverability in the world's largest predator. *Integr. Comp. Biol.* **59**, 48-60. doi:10.1093/icb/icy121
- Sepulveda, C. A., Dickson, K. A. and Graham, J. B.** (2003). Swimming performance studies on the eastern Pacific bonito (*Sarda chiliensis*), a close relative of the tunas (Family Scombridae). I. Energetics. *J. Exp. Biol.* **206**, 2739-2748. doi:10.1242/jeb.00497
- Shadwick, R. E.** (2005). How tunas and lamnid sharks swim: an evolutionary convergence. *Am. Sci.* **93**, 524-531. doi:10.1511/2005.56.524
- Shadwick, R. E. and Syme, D. A.** (2008). Thunniform swimming: muscle dynamics and mechanical power production of aerobic fibres in yellowfin tuna (*Thunnus albacares*). *J. Exp. Biol.* **211**, 1603-1611. doi:10.1242/jeb.013250
- Shadwick, R. E., Katz, S. L., Korsmeyer, K. E., Knower, T. and Covell, J. W.** (1999). Muscle dynamics in skipjack tuna: timing of red muscle shortening in relation to activation and body curvature during steady swimming. *J. Exp. Biol.* **202**, 2139-2150. doi:10.1242/jeb.202.16.2139
- Shadwick, R. E., Rapoport, H. S. and Fenger, J. M.** (2002). Structure and function of tuna tail tendons. *Comp. Biochem. Physiol. A* **133**, 1109-1125. doi:10.1016/S1095-6433(02)00215-5
- Stokesbury, M. J. W., Teo, S. L. H., Seitz, A., O'Dor, R. K. and Block, B. A.** (2004). Movement of Atlantic bluefin tuna (*Thunnus thynnus*) as determined by satellite tagging experiments initiated off New England. *Can. J. Fish. Aqu. Sci.* **61**, 1976-1987. doi:10.1139/f04-130
- Taylor, M. E.** (1989). Locomotor adaptations by carnivores. In *Carnivore Behaviour, Ecology, and Evolution* (ed. J. L. Gittleman), pp. 382-409. Ithaca, NY: Cornell University Press.
- Tyler, J. C.** (1980). Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). *NOAA Technical Report NMFS Circular* **434**. doi:10.5962/bhl.title.63022
- Walker, J. A.** (2000). Does a rigid body limit maneuverability? *J. Exp. Biol.* **203**, 3391-3396. doi:10.1242/jeb.203.22.3391
- Walters, V. and Fierstine, H. L.** (1964). Measurements of swimming speeds of yellowfin tuna and wahoo. *Nature* **202**, 208-209. doi:10.1038/202208b0
- Webb, P. W.** (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Can.* **190**, 1-158.
- Webb, P. W.** (1983). Speed, acceleration and manoeuvrability of two teleost fishes. *J. Exp. Biol.* **102**, 115-122. doi:10.1242/jeb.102.1.115
- Webb, P. W.** (1984). Form and function in fish swimming. *Sci. Am.* **251**, 72-82. doi:10.1038/scientificamerican0784-72
- Webb, P. W.** (2004). Maneuverability-general issues. *J. Oceanic Eng.* **29**, 547-555. doi:10.1109/JOE.2004.833220
- Webb, P. W.** (2006). Stability and maneuverability. In *Fish Physiology: Fish Biomechanics*, Vol. 23 (ed. R. E. Shadwick and G. V. Lauder), pp. 281-332. Amsterdam: Academic Press.
- Weis, D.** (1989). Design features and mechanics of axial locomotion in fish. *Am. Zool.* **29**, 151-160. doi:10.1093/icb/29.1.151
- Weis, D.** (1993). Stability of aquatic animal locomotion. *Cont. Math.* **141**, 443-461. doi:10.1090/conm/141/19
- Weis, D.** (2002). Stability versus maneuverability in aquatic locomotion. *Integr. Comp. Biol.* **42**, 127-134. doi:10.1093/icb/42.1.127
- Westneat, M. W. and Wainwright, S. A.** (2001). Mechanical design for swimming: muscle, tendon, and bone. In *Tuna: Physiology, Ecology and Evolution* (ed. B. Block and D. Stevens), pp. 271-311. San Diego: Academic Press.
- Westneat, M. W., Hoese, W., Pell, C. A. and Wainwright, S. A.** (1993). The horizontal septum: mechanisms of force transfer in locomotion of scombrid fishes (Scombridae, Perciformes). *J. Morph.* **217**, 183-204. doi:10.1002/jmor.1052170207