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Novel Mechanism for Turning Performance in Bluefin Tuna

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Abstract

Scombrid fishes can attain exceptional swimming speeds due to their thunniform, lift-based propulsion, large muscle mass, and fusiform body shape. A rigid body restricts maneuverability for aquatic organisms. To test if turning maneuvers by the rigid-bodied Pacific bluefin tuna (*Thunnus orientalis*) are constrained, captive animals were video recorded from above as the animals routinely swam around a large circular tank or during feeding bouts. The turning performance was classified into three different types of turns: 1) glide turn, where the tuna uses the caudal fin as a rudder to passively move through the turn, 2) powered turn, where the animal uses continuous symmetrical strokes of the caudal fin to propel itself through the turn, and 3) ratchet turn, where the overall global turn is completed by a series of small local turns by asymmetrical stokes of the caudal fin. Individual points of the rostrum, peduncle, and tip of the caudal fin were tracked and analyzed using Tracker software. Frame-by-frame analysis showed that of the global turns, the ratchet turn had the fastest turn rate at all three points tracked, with a maximum of 301.76 deg s^{-1}. During the ratchet turn, the peduncle exhibited a minimum global turn radius of 0.37m. However, the local turn radii were only 18.58% of the global ratchet turn. The minimum turn radii ranged from 0.38 m to 1.62m as a proportion of body length. Compared to the performance of other swimmers, the flexibility of the tail and mechanisms used by tuna does constrain turning performance.

Keywords: maneuverability, ratchet turn, powered turn, glide turn, local, global

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Introduction

Animals have enhanced maneuverability while maintaining controlled stability through different morphological adaptations as well as various behavioral adaptations. Stability is defined as a steady movement along an expected trajectory, while maneuverability is categorized by changes in rate of movement and/or trajectory (Fish, 2002, Webb, 2004, 2006; Fish et al., 2002). Maneuverability enhances turning performance of marine animals at the expense of energy, whereas stability reduces the energetic cost of locomotion (Fish et al., 2002; Schakmann et al., 2020). The morphology of an animal defines its locomotor performance and dictates its maneuvering and stabilizing performance (Webb, 1984; Weihs, 1989, 1993, 2002; Taylor, 1989, Fish, 2002). Animals with a morphology associated with high speed, steady state swimming are much less maneuverable than species that forage by stalking and lunging, or that live in complex environments (Webb, 1984; Weihs, 1993).

A flexible body is preferred for greater turning performance by allowing the animal to turn around a smaller radius of curvature, and by increasing rotational rate (Parson *et al.* 2011). 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. Turning performance has been studied on various aquatic animals with many morphological attributes being correlated to a high turning performance (Segre, *et al.,* 2018). Three main morphological characteristics have stood out: body shape, the position and mobility of propulsors and control surfaces, and body flexibility (Rivera, *et al.* 2006).

Bluefin tuna (*Thunnus* sp.) of the family Scombridae are high-speed periodic, pelagic swimmers with a relatively inflexible body that fosters low drag (Walters and Fierstine, 1964;

Magnuson, 1978; Katz et al., 2001). Bluefin tuna swim using lift-based propulsion with a stiff, high-aspect ratio lunate caudal fin that acts like an oscillating hydrofoil, and the oscillatory movements are confined to the caudal peduncle (Nursall, 1956; Lighthill, 1969; Webb, 1975; Lindsey, 1978; Graham and Dickson, 2004). This form of propulsion is referred to as the thunniform swimming mode (Breder, 1926; Webb, 1975; Lindsey, 1978). The caudal peduncle exhibits "narrow necking" and possesses lateral keels, both of which reduce drag and lateral recoil due to the oscillation of the caudal hydrofoil (Lighthill, 1969).

Scombrids have a streamlined body shape with a large muscle mass in the anterior portion of their body that inserts on the caudal peduncle through elongate lateral tendons (Fierstine and Walters, 1968; Graham and Dickson, 2004; Shadwick, 2005; Shadwick and Syme, 2008). This morphology helps to reduce the pressure drag on the body (Lighthill, 1969; Webb, 1975) but makes the thick anterior body stiff. Additionally, the bluefin tuna and other scombrids have an array of large median fins (e.g., dorsal, anal), smaller median finlets, and small, inflexible 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) and the first dorsal fin can be folded into a slot when not needed to control stability and maneuverability (Fish and Lauder, 2017). Together, these morphological features are all indicative of a powerful, stable body design but at the expense of a constrained turning performance.

Scombrid fishes swim constantly and make extensive trans-oceanic migrations (Block et al., 2001; Stokesbury et al., 2004; Clark et al., 2016). Bluefin tuna are powerful predators that feed on small, schooling fish and squid that, because of their relatively small size, exhibit greater agility and maneuverability than the tuna (Howland, 1974; Josse, *et al.,* 1998; Clark et al., 2016).

Although fast, steady swimming speeds and endurance are important, the ability to change direction at high speeds is necessary for the bluefin tuna to capture their smaller prey. However, the structure of the body indicates a design that enhances stability over maneuverability. Blake *et al.* (1995) measured turning radius and turning rate in yellowfin tuna (*Thunnus albacares).* The average turning radius relative to body length (L) for yellowfin tuna was 0.47 L with an average turning velocity of 0.71 m s^{-1}. Such turning performance was below that of more flexible-bodied fishes (Fish and Nicastro, 2003).

Despite all of the structural and morphological limitations to body flexibility, tuna consistently exhibit the ability to capture their more elusive prey. This suggests that bluefins combat their morphological restrictions with strategic modes of prey capture, but the ability to swim at high speeds and maneuver through the water with a rigid body presents a conundrum to an understanding of the locomotor performance of this aquatic predator. In this study, it is hypothesized that the bluefin tuna compensates for body rigidity by using a variety of behavioral methods to execute tight, quick maneuvers. The purpose of this study is to determine swimming mechanisms and turning behaviors that can potentially enhance turning performance in bluefin tuna.

Materials and Methods

Video recordings of captive Pacific bluefin tuna (*Thunnus orientalis*) were made at the Hopkins Marine Station of Stanford University. Tuna swam steadily in a 12.2 m diameter, 110,000 liter tank with an 2.4 m depth. Videos were recorded at 60 frames s^{-1} with a Canon EOS 5D Mark III manufactured in Japan from a catwalk directly above the center of the tank. 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, respectively. The turns used for analyses were all executed in the horizontal plane.

All videos were analyzed frame-by-frame using Tracker Software (https://physlets.org/tracker/; Ver. 5.1.3). The videos were scaled using a 1 m square grid at the bottom of the tank. The tip of the rostrum, peduncle, and tip of the caudal fin were digitized to follow the trajectory of each of the points. Turns were classified based on the movements of the caudal fin through the turn. A custom MatLab (Ver. 7.10) code written by Allison Kolpas was used to filter the trajectory of the digitized points to remove any observer error due to hand digitizing. A circle of best fit was produced for each global turn while calculating turn rate and radius (Figure 1). Multiple fit circles were calculated for turns made up of multiple miniature turns. (see Results). For each of the three points on the fish, turn rate, turn radius, and swimming velocity (U; m $^{s-1}$) were also calculated. The extreme 20% for all three parameters was calculated to compare maximum turning performance among the different turning maneuvers (Webb, 1983; Gerstner, 1999; Fish and Nicastro, 2003).

Centripetal acceleration in relation to the gravitational acceleration (g; 9.8 m s^{-2}) was computed as:

$$a_c = (U^2/r)/g \tag{1}$$
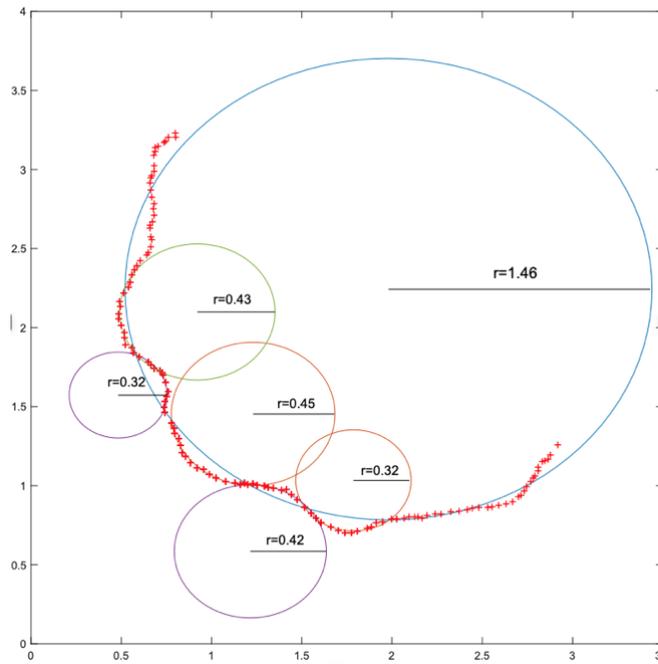
Figure 1. Circle of best fit for a ratchet turn. The large circle represents the global ratchet turn while the smaller circles represent the local ratchet turns within the global turn.

Angle of attack of the caudal fin was measured for a selected number (10) turns consisting of multiple miniature turns (later referred to as ratchet turns, see Results). These ten videos were selected because of minimal distortion from the water. A screenshot of the swimming path was taken in Tracker and the angle of attack was measured using the tracked points of the peduncle and tip of the tail in Fiji (Ver. 2.1.0) according to Fish, et al. (1988).

Angle of the peduncle during the different turning maneuvers was measured frame-by-frame in Tracker by drawing a line down the mid line of the body and then drawing a line through the peduncle and caudal fin. The angle between the two lines was then measured. 20 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 R Studio (Ver. 1.2.5019). An ANOVA was run to accurately compare the radius and turn rate of each classified turn (see Results). Data was log transformed due to abnormal distribution in the original data set. A Tukey test was used to determine the differences between each type of turn. There were 13 bluefin tuna in the tank during each video recording. Because individuals could not be identified, all degrees of freedom were based on the 13 fish. For two of the classified turns (ratchet and powered turns), 25 videos were selected of each to be analyzed based on visibility (minimal wave distortion), and maximal performance. For the remaining turn (glide turns), 10 videos were selected to be analyzed based on the same criteria. See results for descriptions of each classified turn. The powered and ratchet turn were more frequently used by the fish leading to a larger sample of turn sequences. Regression equations and correlation coefficients were computed using Kaleidagraph software (Ver. 4.5.0). 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.

Results

Video analysis showed three different turning maneuvers that were used by the bluefin tuna while exercising yawing turns (Figure 2). These turns were categorized as (1) glide turn, (2) powered turn, and (3) ratchet turn.
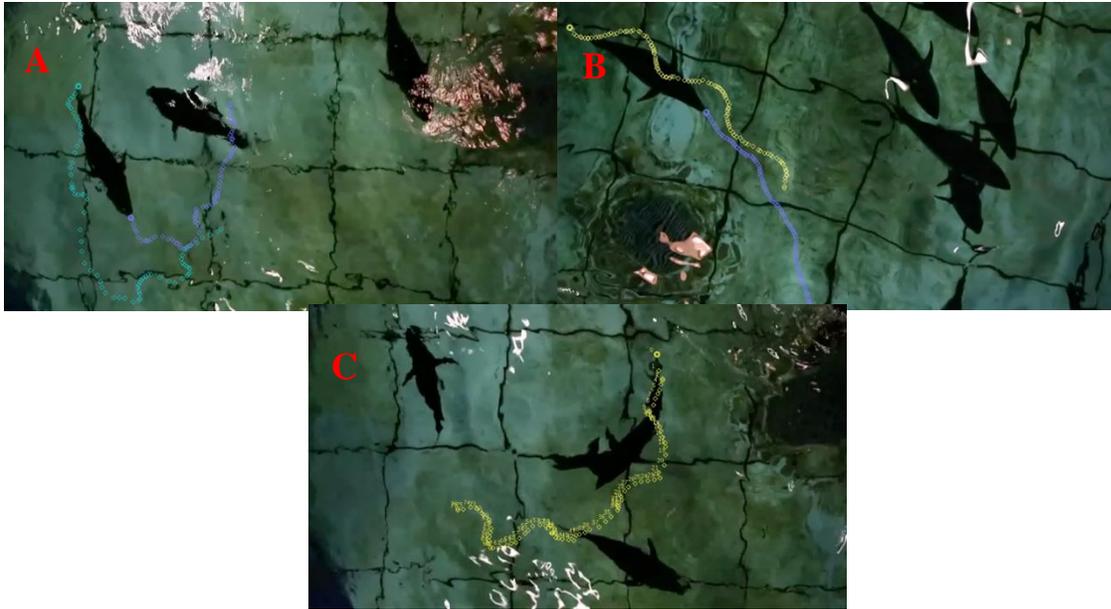
Figure 2. Visual representation of the three different turning maneuvers utilized by bluefin tuna during feeding bouts. A) the rostrum (blue) and the tip of the tail (green) being tracked during a glide turn, B) the rostrum (blue) and the tip of the tail (yellow) during a powered turn, C) the tip of the tail (yellow) being tracked during a ratchet turn.

The glide turn was characterized as using one large stroke of the caudal fin and then the fish glided passively through the remainder of the turn. The glide turn used the caudal fin 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 (Figure 2A). The maximum turn rate observed for the glide turn was 247.59 deg s^{-1}. The minimum turn radius for the glide turn was 0.50 m. The mean turn rate of the glide turn was 161.87 +/- 60.23 deg s^{-1}, while the mean turning radius of the glide turn was 1.08 +/-

0.45 m. The mean extreme 20% calculated for turn radius was 0.57 +/- 0.11 m, and the mean extreme 20% of turn rate was 233.33 +/- 20.16 deg s^{-1}.

The powered turn was characterized by the use of continuous, nearly symmetrical, strokes of the tail to actively swim through the turn. The powered turn was mainly viewed during routine swimming. The maximum turn rate of the powered turn was 208.53 deg s^{-1} and the minimum turn radius was 0.73 m. The mean turn rate observed was 103.73 +/- 42.13 deg s^{-1}, while the mean turn radius was 1.41 +/- 0.61 m. The mean extreme 20% calculated for turn radius showed a radius of 0.80 +/- 0.08 m and the mean extreme 20% of the turn rate was 166.92 +/- 24.77 deg s^{-1}. A larger turn radius was expected because the fish was using the powered turn during routine swimming bouts, without making tight turns to capture food.

The ratchet turn 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 center of mass with multiple asymmetrical strokes of the caudal fin. The tail beat towards the outside of the overall turn (Figure 2C). The ratchet turn can be broken up into an overall global turn composed of a series of smaller local turns. The maximum turn rate observed during the global ratchet turn was 301.76 deg s^{-1} and the minimum turn radius was 0.37m. The mean global turn rate was 121.96 +/- 49.34 deg s^{-1}. The mean global turn radius was 0.99 +/- 0.28 m. The mean extreme 20% of the turn radius and turn rate for the global ratchet turn was 0.57 +/- 0.14 m and 192.44 +/-63.67 deg s^{-1}, respectively. The mean turn rate of the local ratchet turn was 462.63 +/- 185.35 deg s^{-1}, about 4 times faster than the global turn rate. The mean radius of the local ratchet turn was 0.30 +/- 0.15 m. (Figure 3). The mean extreme 20%

calculated for the local turn radius was 0.16 +/- 0.04 m and the mean extreme 20% calculated for the local turn rate was 738.01 +/- 164.08 deg s^{-1}.
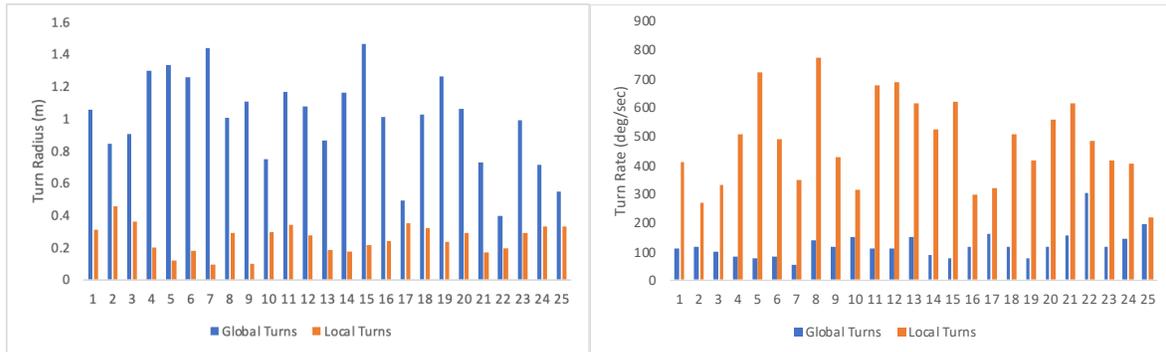
Figure 3. Comparing turn radius and tun rate between the global and local ratchet turns. Turn radius of the global turns is nearly 7x higher than that of the local turns in some cases, while turn rate of the global turns is nearly an eighth of that observed in the local turns in some cases.

Ten videos of ratchet turns were selected to analyze the angle of attack. Table 1 exhibits the mean angle of attack of each global ratchet turn with the turn rate (deg s^{-1}) and radius (m) of said turn. Means for angles of attack ranged from 16.08 to 40.82 deg.

Table 1. Mean angle of attack, turn rate, and turn radius of each global ratchet turn.

Video	Mean Angle of Attack (deg)	Turn Rate (deg/s)	Radius(m)
9M2A0948-1	32.29 +/- 18.00	109.67	1.06
9M2A0949-1	31.77 +/- 20.07	114.65	0.84
9M2A0955-1	25.81 +/- 11.62	77.36	1.33
9M2A0956-1	29.73 +/- 11.89	81.33	1.26
9M2A0966-1	21.63 +/- 10.35	135.99	1.01
9M2A0966-2	40.82 +/- 5.36	114.4	1.11
9M2A0968-1	30.01 +/- 5.25	147.96	0.75
9M2A0969-1	21.6 +/- 6.39	110.3	1.17
9M2A0974-1	16.08 +/- 6.89	147.67	0.86
9M2A0972-1	24.31 +/- 7.24	81.8	1.12

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). Turn rate and turn radius of the global turns were 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 104.01 deg/$^{s-1}$ and the smallest mean turn radius was observed in the ratchet turn at 1.08 m. When the peduncle was tracked the fastest mean turn rate observed was the glide turn at 161.87 deg/$^{s-1}$ and the smallest mean turn radius observed was that of the ratchet turn at 0.99 m. When the tail was tracked the fastest mean turn rate observed was the glide turn at 123.14 deg/$^{s-1}$ and the smallest mean turn radius was the ratchet turn at 1.05 m. It was expected that the glide turn would have the fastest turn rates in the posterior region of the body, because it is a passive turn. It is hypothesized that when tracking the rostrum the fastest turn rate 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 the ability for thrust production via the peduncle region.

Table 2. Comparison of mean global turn rates and turn radii of the three points tracked on the bluefin tuna among the three different turn types.

		Glide	Powered	Ratchet
Rostrum	Turn Rate(deg/s)	99.33	102.91	104.01
	Turn Radius(m)	2.46	1.25	1.08
Peduncle	Turn Rate(deg/s)	161.87	103.73	121.96
	Turn Radius(m)	1.08	1.41	0.99
Tail	Turn Rate(deg/s)	123.14	99.83	118.88
	Turn Radius(m)	1.67	1.53	1.05

The turn rate compared to turn radius of the global turn for all three of the turn types followed a curvilinear trend (Figure 4). The trends for each of the turning maneuvers was found to be significant at the $P < 0.01$. As turning rate decreased, turn radius increased indicating that a faster turn will complete a tighter turn.
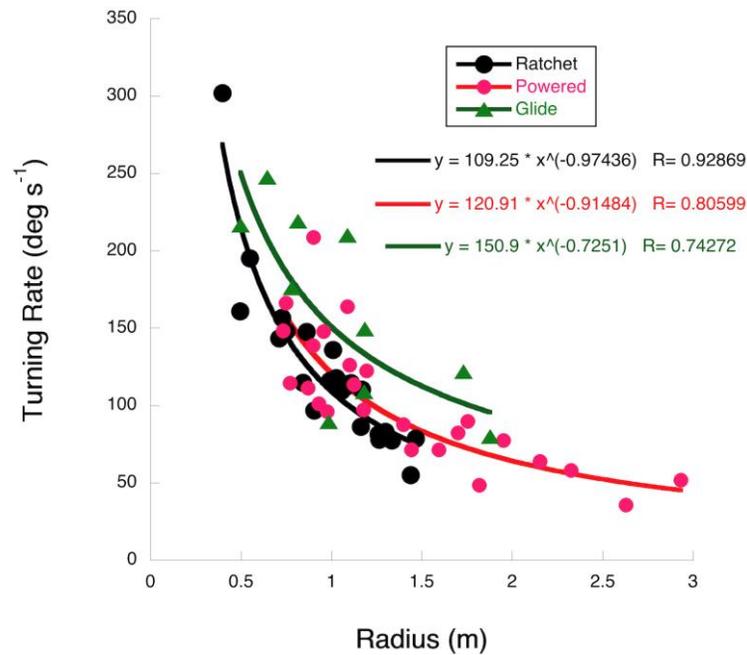
Figure 4. Regression comparing the turning rate of the global turns of the ratchet, powered, and glide turns.

The angle of the peduncle was measured throughout each turn to determine whether peduncle angle affected turn rate and/or turn radius. Having a greater angle of peduncle could lead to a greater production of thrust and therefore faster turn rates. However, when compared to turn rate and turn radius, there was no correlation between angle of peduncle and either variable (Figure 5). The maximum angle of the peduncle observed was 61.97 deg. This degree of flexion shows much greater flexibility in the posterior region of the tuna's body than previously observed.
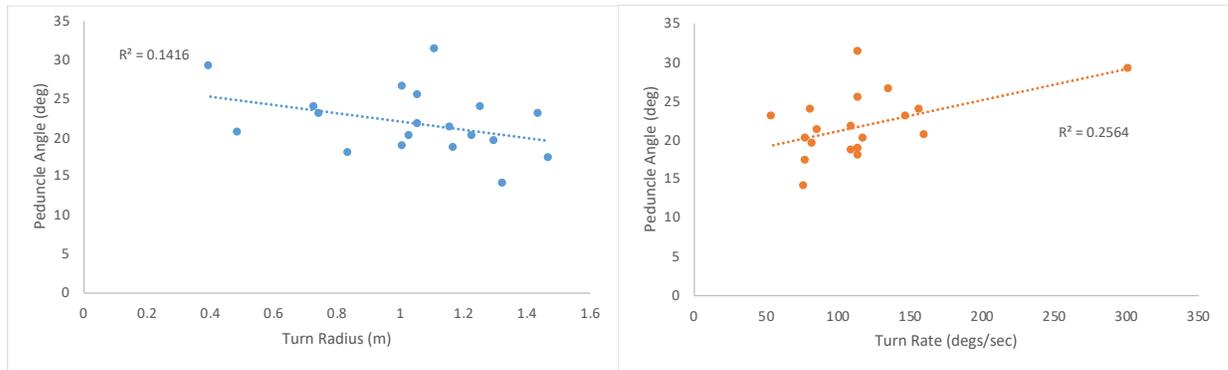
Figure 5. Comparison between mean peduncle angle and turn radius during a global turn and mean peduncle angle and turn rate during a global turn. (N = 20 turns)

Turning performance of multiple species was compared and the three different turning maneuvers were analyzed as well to determine how well they enhanced bluefin's turning performance (Figure 6). The three turning maneuvers, as well as the local elements of the ratchet turn, place the bluefin tuna, to the right of the graph indicating enhanced turning performance compared to beetles, crocodiles, fish, penguins, rays, squid, and turtles when utilizing the different maneuvers.
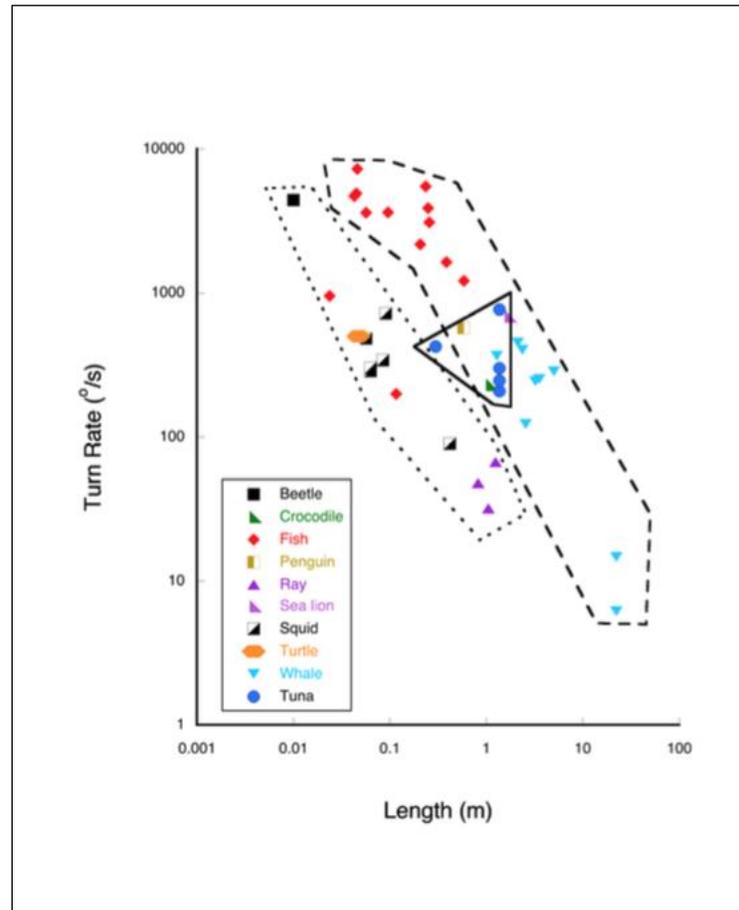
Figure 6. Comparison of turning performance amongst different species. The three turning maneuvers as well as the local elements of the ratchet turn are represented by the blue circles encased by the outlined triangle and fall to the right of the graph. The yellowfin tuna is indicated by the furthest left blue circle in the triangle.

The result of an ANOVA indicated that the radii of the three turning behaviors were statistically different (F = 192.2, $p < 0.001$). The radius of the global ratchet turn and the global powered turn significantly differed from one another ($p=0.014$), with the powered turn having a larger radius. Expectantly, the local ratchet turn significantly differed from the powered turn ($p < 0.001$) and the global rachet turn ($p < 0.001$) (Figure 7).

Figure 7. ANOVA analysis comparing the radius of the powered turn, global ratchet turn, and local ratchet turn (p < 0.001). Each point is represented by a dot on the graph with mean indicated by the horizontal bar and the 25%-75% of the points represented by the colored box. Outliers fall off the vertical line in the center of the box.

The result of the ANOVA testing statistical difference between turn rates indicated that the turn rates of the three turns statistically differed (F = 182.9, $p < 0.001$). The turn rate between the global ratchet turn and the powered turn did not significantly differ ($p = 0.933$). The turn rate between the local ratchet and powered turn ($p<0.001$) were significantly different. Turn rate of the local ratchet and global ratchet turn ($p<0.001$) were significantly different (Figure 8).
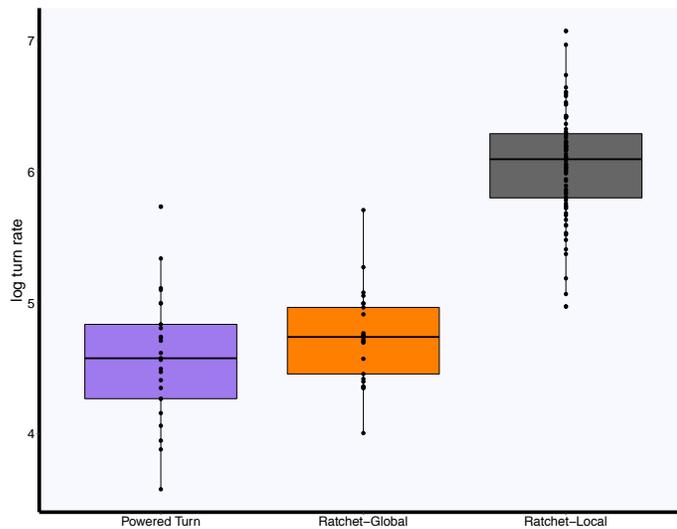
Figure 8. ANOVA analysis comparing the turn rate of the powered turn, global ratchet turn, and local ratchet turn (p < 0.001). Each point is represented by a dot on the graph with mean indicated by the horizontal bar and the 25%-75% of the points represented by the colored box. Outliers fall off the vertical line in the center of the box.

The centripetal acceleration (g) of the fish during each type of turn significantly differed from each another (F = 108, $p < 0.001$). The global ratchet turn and the powered turn were significantly different with p=0.027. The local ratchet and the powered turn and the local ratchet and global ratchet turn were significantly different at p<0.001 (Figure 9).
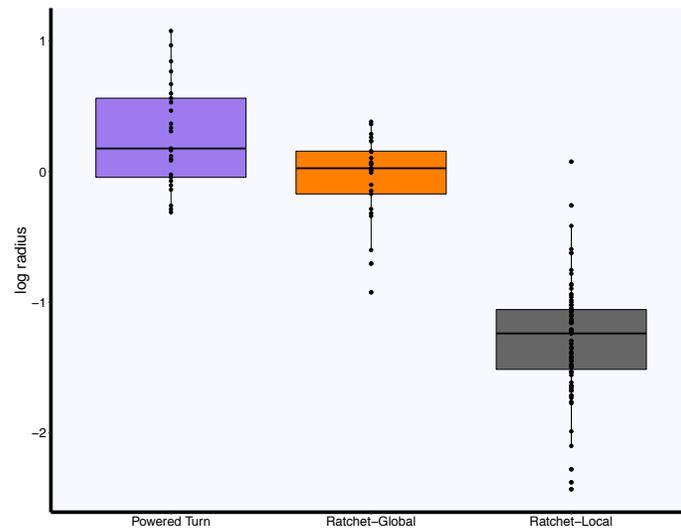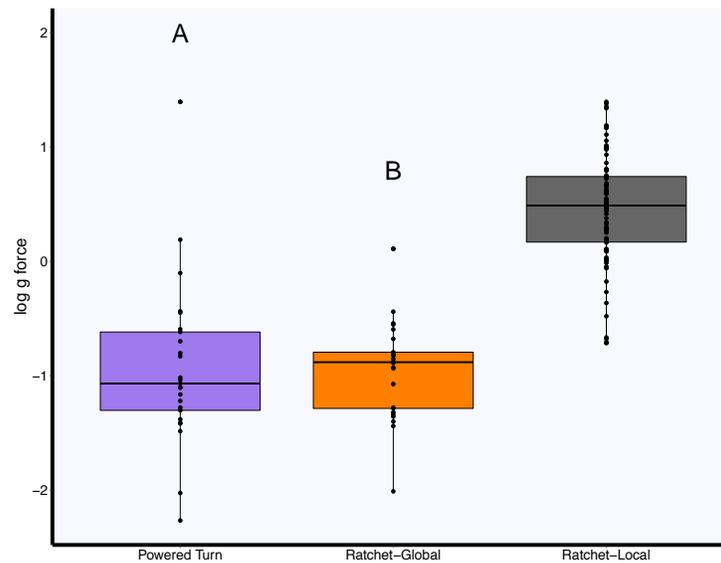
Figure 9. ANOVA comparing the g force between the powered turn, global ratchet turn, and local ratchet turn (p < 0.001). Each point is represented by a dot on the graph with mean indicated by the horizontal bar and the 25%-75% of the points represented by the box. Outliers fall off the vertical line in the center of the box.

Discussion

Bluefin Tuna Turning

Bluefin tunas 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 turn rate. The maximum turn rate observed was 247.59 deg s [-1] and the minimum turn radius was 0.50 m. The powered turn, an active turn, was viewed more during routine swimming rather than during feeding bouts. The maximum turn rate of the powered turn was slower than gliding turns at 208.53 deg s [-1] with

a larger minimum turn radius of 0.73 m. The ratchet turn, a maneuver previously undocumented, used quick asymmetrical strokes of the tail to complete a tight radius turn. The maximum turn rate of the ratchet turn was 301.76 deg s^{-1} and the minimum turn radius was 0.37 m. The local elements of the 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 high turn rate of the collective global turn.

Like many other fishes, the anterior muscle mass of scombrids is comprised of muscle fibers packed into myomeres and attached to a horizontal septum (Fierstine and Walters, 1968). A specialization of scombrids 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, lay medial to the great lateral tendon and insert at the beginning of the fin rays (Kishinouye, 1923; Fierstine and Walters, 1968; Shadwick, 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). It is predicted that having those weakly developed tendons within the myosepta uncouples 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, 2002).

It can be assumed that 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 *et al.*, 2003; Westneat and Wainwright, 2001; Shadwick, 2003). 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.

Comparison to Other Tuna Turning

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 (*Thunnus 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 turn radius and turn rate without looking at different strategic methods to enhance turning performance. Blake *et al.* (1995) found that the mean turning radius compared to body size of the yellowfin tuna was large compared to other fish. The mean turning radius of the yellowfin tuna was large (0.47 m +/- 0.18). In the present study, the local ratchet turn of the bluefin tuna allowed the tuna to have a mean turn radius of 0.15 body lengths. Additionally, the yellowfin tuna in the study by Blake *et al.* (1995) had a mean turning rate that was 66.8% slower than the turn rate for the bluefin tuna in this study. Thus both the turn radius and the turn rate of the bluefins when using the three different turning mechanisms allowed the fish to have a greater turning performance relative to its body size compared to the yellowfin tuna (Figure 6).

Newlands, *et al.* (2004) examined different techniques for adaptive search behavior in Atlantic bluefin tuna (*Thunnus thynnus*). They found that the velocity of Atlantic bluefin tuna traveling in schools ranged from 1.18 m s^{-1} to 1.89 m s^{-1}. The current study found that the

velocity of a Pacific bluefin tuna during the three different turning maneuvers ranged from 1.37 m s^{-1} to 3.86 m s^{-1}. Additionally, the mean turning angle of a schooling bluefin tuna in the current study was 23.3 +/- 2.71 deg, 72.8 % greater than the mean reported by Newlands *et al*. (2004) for Atlantic bluefin. The difference may have been due to the 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 capture of a food source thrown into their tank. For any scombrid, these high performance turning maneuvers would be beneficial when chasing small, maneuverable prey because of the potential to turn at greater angles while maintaining a faster speed.

Comparison of Bluefin Tuna to 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; Rivera *et al.,* 2006; Parson *et al.,* 2011). Rigidity of a swimmer can limit the rate of turning. Figure 6 compares turning performance among different species relative to their body size. The turn rate of the three turning maneuvers of the rigid-bodied bluefin tuna are all above the black line. The local ratchet turn is higher on the graph than the yellowfin tuna (about 50-100 deg s^{-1} higher) as well as cetaceans (ranging from 50-650 deg s^{-1} higher). The yellowfin tuna have a smaller body size than the bluefin, while the cetacean has a more flexible morphology than the bluefin. This indicates that the flexible peduncle and rapid strokes of the caudal fin give the bluefin tuna the ability to turn quickly relative to its body size to compensate for the rigid body.

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 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 undulate anteriorly to the caudal peduncle, like bluefin tuna. The turn rate of the boxfish ranged between 76.1-147.0 deg s^{-1}, while the turn radii ranged from 0.0005 to 0.11 L. The relatively small turn radii 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 turning rates across the four different turning maneuvers (local ratchet, global ratchet, powered, and glide). The turn radii for the tuna were greater 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 in the generation of lift (Magnuson, 1970, 1978; Fish and Lauder, 2017).

Highly maneuverable animals such as many fishes (exception of boxfish), crocodilians, penguins, cetaceans, and sea lions will have increased turning performance due to their flexible body designs. Figure 6 shows that fishes, crocodilians, penguins, sea lion, and cetaceans are situated to the right of the graph, indicating a maneuverable body in relation to body size.. Generally, the small, flexible-bodied fishes display the fastest turning performance. Coral reef fish, such as bluehead wrasse, ocean surgeonfish, beaugregory damselfish, and the foureye butterflyfish exhibit small turn radii and exceptional turning rates compared to body length due to their small body size and use of pectoral and medial flippers. The turn radius ranged from 0.06 – 0.09L between the four fish and the angular velocities ranged from 425.6 – 7300 deg s^{-1} Gerstner, 1999). These reef fish use their median, paired, caudal fins, and body flexibility to

accomplish such small radius turns, unlike the tuna, which is limited to only the use of 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 0.37 m with a relative turn radius of 0.27 L. For other swimmers of the same order of

magnitude as the tuna, the minimum turn radii were smaller. An examination of multiple species

of cetaceans showed the minimum turn radius of 0.22 L (Fish, 2002). The California sea lion

(*Zalophus californianus*) has maximum turning rate of 690 deg s^{-1} (Fish et al., 2002). 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 its

environment (Fish, 1997; 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). This exaggerated dorsal bending is used in the

preferred turning maneuver of the California sea lion (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 to the yellowfin tuna (Fig. 6). Furthermore, the turn rates for the

bluefin tuna were in line with trends displayed by more flexible-bodied swimmers. The tuna was

thus able to compensate for the stiff body by increased flexibility of the peduncle. Through an

active turn, the peduncle bent at a mean of 21.37 deg with a maximum of 61.97 deg. Although

the angle the peduncle angle was bent at shows no correlation to turn rate or turn radius, the

ability of the body to bend in that region shows flexibility previously undescribed for the tuna.

Foraging Techniques

Many fishes will modify their foraging habits to increase their feeding rates (Dill, 1983; Bonsall et al. 2002; Morales and Ellner 2002; Newlands 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 (*Thunnus thynnus)* typically feed on much smaller prey, such as sand lance, anchovy, squid, and krill (Karskulak et al., 2009; Butler et al., 2010; Logan, et al., 2010; 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). Figure 8 shows 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 their 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 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, 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 of dolphins and allow the dolphins to do the work of herding schooling fish that the tuna consume. Bluefin tuna will attack the middle of the bait ball, completely destroying the integrity of the ball (Clua, et al., 2001). As the tuna make approximately two to three passes through the bait ball, the dolphin swim around the surrounding areas, essentially 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, et al., 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 allow for the tuna to extend the performance envelope when foraging.

Conclusions

The bluefin tuna compensates for its relatively stiff body by employing various turning behaviors to increase its maneuverability. This study analyzed behavioral strategies in different turning maneuvers to enhance turning performance. The glide turn, powered turn, and ratchet turn enable the bluefin to exhibit higher turning performance than yellowfin tuna and many flexible-bodied animals. The various turning maneuvers observed for the bluefin tuna enhances

turn rate while minimizing turn radius. The three turning maneuvers of the bluefin tuna are important in expanding the capability of this predator in capturing more maneuverable prey as well as providing an understanding the tradeoffs between a stable and maneuverable body design.

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