

# Multiple behaviors for turning performance of Pacific Bluefin Tuna (*Thunnus orientalis*)

Abigail M. Downs<sup>1</sup>, Allison Kolpas<sup>2</sup>, Barbara A. Block<sup>3</sup>, and Frank E. Fish<sup>1,\*</sup>

<sup>1</sup>Department of Biology, West Chester University, West Chester, PA 19383, USA

<sup>2</sup>Department of Mathematics, West Chester University, West Chester, PA 19383, USA

<sup>3</sup>Department of Biology, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93905, USA

\* Author for correspondence (ffish@wcupa.edu)

Address: Department of Biology, West Chester University, West Chester, PA 19383, USA

Phone: 610-436-2460

**Keywords:** maneuverability, agility, *Thunnus orientalis*, ratchet turn, swimming

## Abstract

Tunas are known for exceptional swimming speeds due to their thunniform, lift-based propulsion, large muscle mass, and rigid fusiform body. A rigid body should restrict maneuverability in 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 video recorded 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 turn, where the tuna uses the caudal fin as a rudder, 2) powered turn, where the animal uses continuous near symmetrical strokes of the caudal fin through the turn, and 3) ratchet turn, 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  $302 \text{ deg s}^{-1}$ . During the ratchet turn, the rostrum exhibited a minimum global  $0.38L$  turn radius. The local turn radii were only 18.6% of the global ratchet turn. The minimum turn radii ranged from  $0.4L$  to  $1.7L$ . Compared to 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.

## Summary Statement

Despite generally rigid bodies, bluefin tuna are capable of maneuvering with high agility by using various turning behaviors, with a flexible tail and caudal peduncle.

## 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; 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 maneuverability and stability (Webb, 1984; Weihs, 1989, 1993, 2002; Taylor, 1989, Fish, 2002). Animals with a morphology associated for 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).

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 (Harris, 1936; Fish, 2002; Parson *et al.* 2011). Both the radius and the rotational rate are incorporated in an organism's turning performance. Turning performance has been studied on various species of 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). This study focuses on body flexibility. The antithesis of flexibility is rigidity. Rigidity 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 Nicastro, 2003; Rivera *et al.*, 2006; Parson *et al.*, 2011; Fish and Lauder, 2017). Rigidity of a swimmer can limit the rate of turning.

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 to 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 to other swimming modes, lateral oscillations at the rostrum of tunas have been shown to be 1.3 to 2 times greater by nonscombrid fishes despite previous observations (Dowis et al., 2003; Di Santo et al., 2021). 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). 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. Because of the relatively small size, these prey species exhibit greater agility and maneuverability than the tuna (Howland, 1974; Josse, *et al.*, 1998; Clark et al., 2016).

Although high swimming speeds and endurance are important, the ability to change direction at high speeds is necessary for the bluefin 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. The large muscle mass that actuates the caudal fin is concentrated anteriorly, acting as a large inertial mass and 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 (L) for yellowfin tuna was 0.47L with an average turning velocity of  $0.71\text{ m s}^{-1}$ . 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. 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 limitations from body rigidity by using a variety of behavioral methods to execute tight, quick maneuvers. The purpose of this study is to 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, 1944) were made at the Hopkins Marine Station of Stanford University. Tuna swam continuously in a 12.2 m diameter, 110,000 liter tank with an 2.4 m depth with a grid of 1 m squares painted on the bottom of the tank. The approximate body length of tuna swimming near the bottom of the tank. was 1.37 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  $\text{s}^{-1}$  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, 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 videos were analyzed frame-by-frame using Tracker Software (<https://physlets.org/tracker/>; Ver. 5.1.3). Because of the imprecision in determining absolute measures using the bottom grid as a scale due to the unknown swimming depth of each fish, a

relative measure of body length ( $L$ ) specific for the individual tuna were 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 fin, and the caudal fin refers to the 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 ( $\omega$ ;  $\text{deg s}^{-1}$ ) and turn radius ( $r$ ;  $L$ ). Swimming velocity ( $U$ ;  $L \text{ s}^{-1}$ ),  $\omega$ , 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 ten ratchet turns (see below). These ten 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 (Ver. 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 Tracker (Ver. 5.1.3) by drawing a straight line down the mid line 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 R Studio (Ver. 1.2.5019). Variation about means was expressed as + one standard deviation (SD). 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, ten 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 (Ver. 4.5.0). Data are available in the institutional data repository ([http://digitalcommons.wcupa.edu/bio\\_data/5](http://digitalcommons.wcupa.edu/bio_data/5)).

## 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 (S1) 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  $\omega$  observed for the glide turn was  $159.53 \text{ deg s}^{-1}$ . The minimum turn radius for the glide turn was  $0.7L$ . The mean  $\omega$  of the glide turn was  $99 \pm 52 \text{ deg s}^{-1}$ , while the mean  $r$  of the glide turn was  $2.6 \pm 1.0L$ . The mean extreme 20% calculated for  $r$  was  $0.9 \pm 0.2 L$ , and the mean extreme 20% of  $\omega$  was  $158 \pm 19 \text{ deg s}^{-1}$ .

The powered turn (S2) 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  $\omega$  of the powered turn was  $219 \text{ deg s}^{-1}$  and the minimum  $r$  was  $0.6L$ . The mean  $\omega$  observed was  $103 \pm 66 \text{ deg s}^{-1}$ , while the mean  $r$  was  $1.3 \pm 0.5 L$ . The mean extreme 20% calculated for  $r$  showed a radius of  $0.7 \pm 0.1L$  and the mean extreme 20% of the  $\omega$  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 (S3) 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 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  $\omega$  observed during the global ratchet turn was  $187 \text{ deg s}^{-1}$  and the minimum  $r$  was  $0.5L$ . The mean global  $\omega$  was  $104 \pm 36 \text{ deg s}^{-1}$ . The mean global  $r$  was  $1.1 \pm 0.6L$ . The mean extreme 20% of  $r$  and  $\omega$  for the global ratchet turn was  $0.6 \pm 0.2L$  and  $155 \pm 62 \text{ deg s}^{-1}$ , respectively. The mean  $\omega$  of the local ratchet turn was  $463 \pm 185 \text{ deg s}^{-1}$ , about 4 times faster than the global  $\omega$ . The mean  $r$  of the local ratchet turn was  $0.3 \pm 0.2L$ . (Fig. 3). The mean extreme 20% calculated for the local  $r$  was  $0.2 \pm 0.0L$  and the mean extreme 20% calculated for the local  $\omega$  was  $738 \pm 164 \text{ deg s}^{-1}$ .

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 ( $\text{deg s}^{-1}$ ) and radius ( $L$ ) 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).  $\omega$  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  $104 \text{ deg s}^{-1}$  and the smallest mean  $r$  was observed in



the ratchet turn at 1.1L. When the peduncle was tracked the fastest mean  $\omega$  observed was the glide turn at 162 deg s<sup>-1</sup> and the smallest mean  $r$  was for the ratchet turn at 1.0L. When the tail was tracked the fastest mean  $\omega$  observed was the glide turn at 123 deg s<sup>-1</sup> and the smallest mean  $r$  was the ratchet turn at 1.1L. 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  $\omega$  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  $\omega$  compared to  $r$  of the global turn for all three of the turn types followed a curvilinear trend (Fig. 4). The trends for each of the turning maneuvers was found to be significant at the  $P < 0.01$ . As  $\omega$  decreased,  $r$  increased indicating that a faster turn will complete a tighter turn. This trend was consistent with previously reported turning performance (Fish and Nicastrò, 2003; Parson et al., 2011). The increase in  $\omega$  with decreasing  $r$  because the tuna with smaller radius turns would move through a larger angular displacement for a given time compared to larger radius turns.

The angle of the peduncle was measured throughout each turn to determine whether peduncle angle affected  $\omega$  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 to  $\omega$  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 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. 5).



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  $\omega$  between the global ratchet turn and the powered turn did not significantly differ ( $p = 0.971$ ). The  $\omega$  between the local ratchet and powered turn ( $p < 0.001$ ) were significantly different.  $\omega$  of the local ratchet and global ratchet turn ( $p < 0.001$ ) were significantly different (Fig. 6).

The  $a_{cg}$  of the fish during each type of turn significantly differed from each another ( $F = 226.1$ ,  $p < 0.001$ ). The global ratchet turn and the powered turn did not significantly differ ( $p = 0.977$ ). The local ratchet and the powered turn and the local ratchet and global ratchet turn were significantly different at  $p < 0.001$  (Fig. 7).

## 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  $\omega$ . 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  $\omega$  observed was  $160 \text{ deg s}^{-1}$  and the minimum  $r$  was  $0.7 L$ . The powered turn, an active turn, was viewed more during routine swimming rather than during feeding bouts. The maximum  $\omega$  of the powered turn was faster than gliding turns at  $219 \text{ deg s}^{-1}$  with a larger minimum turn radius of  $0.6L$ . The ratchet turn, a maneuver previously undocumented, used quick asymmetrical strokes of the tail to complete a tight radius turn. The maximum  $\omega$  of the ratchet turn was  $187 \text{ deg s}^{-1}$  and the minimum  $r$  was  $0.5L$ . 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  $\omega$  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 is comprised of muscle fibers packed into myomeres and attached to a horizontal septum (Fierstine and Walters, 1968; Gemballa et al., 2003). 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, 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). These 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; Knowler, *et al.*, 1999; Shadwick *et al.*, 1999; Westneat and Wainwright, 2001; Long, 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 *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.

The large anterior muscle mass in tuna that supplies the large force production makes the body wider compared to other fishes. This increase in the body width helps to streamline the body, 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 increases 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 haemal 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 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  $r$  and  $\omega$  without looking at different strategic methods to enhance turning performance. Blake *et al.* (1995) found that  $r$  compared to body size of the yellowfin tuna was large compared to other fish. The mean  $r$  of the yellowfin tuna was  $0.47L$ . In the present study, the local ratchet turn of the bluefin tuna allowed the tuna to have a mean  $r$  of  $0.2L$ . The  $\omega$  of the bluefin tuna when using the three different turning behaviors allowed the fish to have a greater turning performance relative to its body size compared to the yellowfin tuna (Figure 6). The yellowfin tuna in the study by Blake *et al.* (1995) had a mean  $\omega$  that was 66.8 % slower than  $\omega$  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  $1.18 \text{ m s}^{-1}$  to  $1.89 \text{ m s}^{-1}$ . The present study found that the velocity of an animal during the three different turning maneuvers ranged from  $1.42 L \text{ s}^{-1}$  to  $4.00 L \text{ s}^{-1}$ . The mean turning angle of a schooling bluefin tuna was  $23.3 \pm 2.7 \text{ deg}$ . 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 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 collection of a food source thrown into their tank. The different turning maneuvers displayed by the tuna in the present study can 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 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 Nicastrò, 2003; Rivera *et al.*, 2006; Parson *et al.*, 2011). Rigidity of a swimmer can limit the rate of turning. Figure 9 compares turning performance among different species relative to their body size. The black line extending from the smallest (whirligig beetle), a small aquatic insect and largest (USS Albacore), an experimental naval submarine, aquatic rigid bodies. 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  $\omega$  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  $\text{deg s}^{-1}$  higher on the graph than the yellowfin tuna and 50-650  $\text{deg s}^{-1}$  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 give the bluefin tuna the ability 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 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  $\omega$  of the boxfish ranged between 76.1-147.0  $\text{deg s}^{-1}$ , while the turn radii ranged from 0.0005 to 0.11L. 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  $\omega$  across the four different turning maneuvers (local ratchet, global ratchet, powered, and glide). The  $r$  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), crocodilians, penguins, cetaceans, and sea lions will have increased turning performance due to their flexible body designs (Fig. 9). 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 due to their small body size, flexible bodies, and use of multiple fins. The  $r$  ranged from  $0.06 - 0.09L$  and  $\omega$  ranged from  $425.6 - 7300 \text{ deg s}^{-1}$  among 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 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  $0.38L$ . 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  $0.22L$  (Fish, 2002). The California sea lion (*Zalophus californianus*) has maximum turning rate of  $690 \text{ deg s}^{-1}$  (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 turning maneuvers 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. 8). Furthermore,  $\omega$  for the bluefin tuna was 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  $21 \text{ deg}$  with a maximum of  $62 \text{ deg}$ . Although the angle the peduncle could bend showed no correlation with  $\omega$  or  $r$ , the extreme flexure of the peduncle allowed the tuna to compensate for its generally rigid body and perform turns equivalent with 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 (*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 9 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 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, 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 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, et al., 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, 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 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 would like to thank 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 forms part of a MSc thesis by the lead author Abigail Downs (West Chester University of Pennsylvania, 2020).

## Competing Interests

The authors declare no competing or financial interests



## Author Contributions

A.M.D. was the primary author, collected all data from videos, and performed statistical analysis. A.K. and A.M.D. performed the mathematical manipulation of data. B.A.B. arranged the logistics and maintenance of tuna. F.E.F. obtained funding for the study and was involved in writing the manuscript for publication.

## Funding

The work was supported by a grant from the Multidisciplinary University Research Initiative of the Office of Naval Research [N000141410533]

## References

- Au, D. W. K. and Pitman, R. L. (1986). Seabird associations with dolphins and tuna in the Eastern Tropical Pacific. *Condor* **88**, 304–317.
- Aleyev, Yu. G. (1977). *Nekton*. Junk: The Hague.
- Blake, R. W., Chatters, L. M. and Domenici, P. (1995). Turning radius of yellowfin tuna (*Thunnus albacores*) in unsteady swimming manoeuvres. *J. Fish. Biol.* **46**, 536–538.
- 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. and Fudge, D. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* **293**, 1310–1314.
- 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
- Breder, C. M., Jr. (1926). The locomotion of fishes. *Zoologica* **4**, 159–297.
- 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.

- 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.
- Dill, L. M. (1983) Adaptive flexibility in the foraging behaviour of fishes. *Can. J. Fish. Aquat. Sci.* **40**, 398–408
- 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.* **118**, e2113206118.
- 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.
- Donley, J. M., Sepulveda, C. A., Konstantinidis, P., Gembella, S. and Shadwick, R. E. (2002). Convergent evolution in mechanical design of lamnid sharks and tunas. *Nature* **429**, 61-65.
- Domenici, P. (2001) The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comp. Biochem. Physiol. A* **131**, 169-182.
- 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.
- 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.
- Fierstine, H. L. and Walters, V. (1968). Studies of locomotion and anatomy of scombrid fishes. *Mem. S. Calif. Acad. Sci.* **6**, 1-31.
- Fish, F. E. (2002). Balancing requirements for stability and maneuverability in cetaceans, *Integr. Comp. Biol.* **42**, 85–93.
- 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.

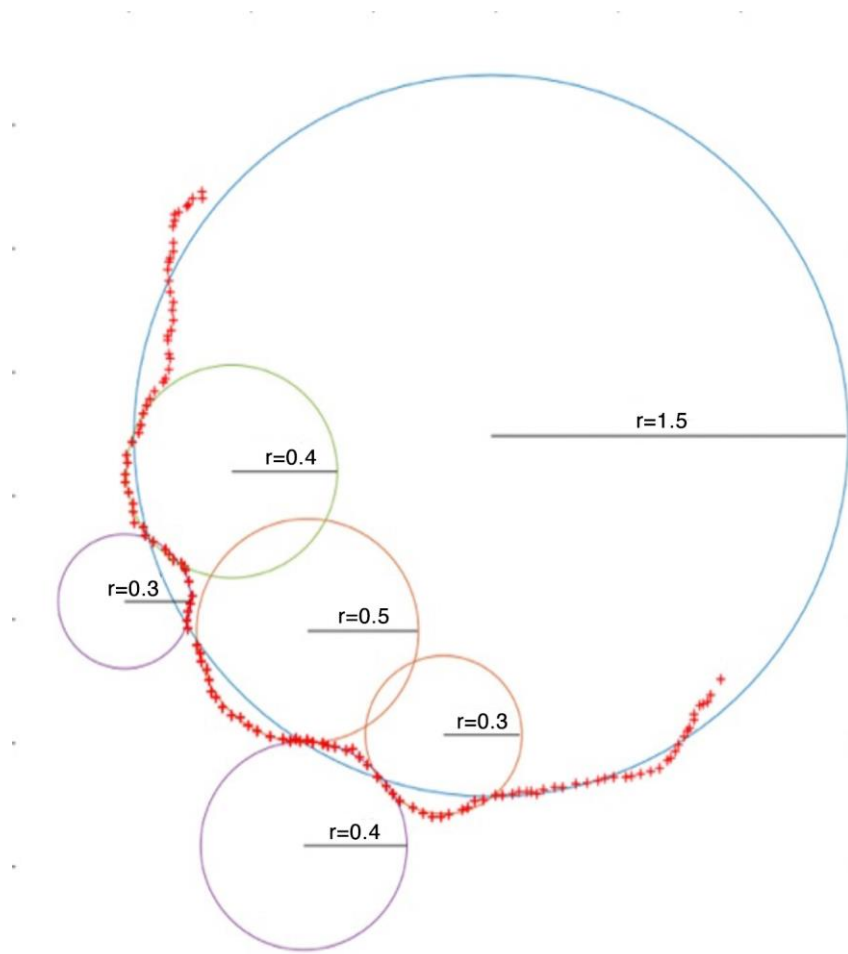
- Fish, F. E., Hurley, J. and Costa, D.P. (2003) Maneuverability by the sea lion *Zalophus californianus*: turning performance by an unstable body design. *J. Exp. Biol.* **206**, 667-674.
- Fish, F. E. and Nicastro, A. J. (2003). Aquatic turning performance by the whirligig beetle: constraints on maneuverability by a rigid biological system. *J. Exp. Biol.* **206**, 1649-1656.
- Fish, F. E. and Lauder, G. V. (2017). Control surfaces of aquatic vertebrates in relation to swimming modes. *J. Exp. Biol.* **220**, 4351-4363.
- 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.
- Graham, J. B. and Dickson, K. A. (2004). Tuna comparative physiology. *J. Exp. Biol.* **207**, 4015-4024.
- 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
- 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.
- 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.
- 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). *Journal of Experimental Biology* **13**, 476-493.
- Howland, H. C. (1974). Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**: 333-350.
- Kramer, E. (1960). Zur Form und Funktion des locomotion Apparates der Fishche. *Z. Wiss Zool.* **163**, 1-36.
- Katz, S. L., Syme, D. A. and Shadwick, R. E. (2001). Enhanced power in yellowfin tuna. *Nature* **410**, 770-771.
- 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. Ichthy.* **25**, 757-761.

- Lindsey, C. C. (1978). Form, function, and locomotory habits in fish. In *Fish Physiology: Locomotion*, Vol. 7 (eds. WS Hoar, DJ Randall), pp. 1-100. New York: Academic Press.
- Lighthill, J. (1969). Hydrodynamics of aquatic animal propulsion — a survey. *Ann. Rev. Fluid Mech.* **1**, 413–446.
- 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.
- Magnuson, J. J. (1970). Hydrostatic equilibrium of *Euthynnus affinis*, a pelagic teleost with a gas bladder. *Copeia* **1970**, 56-85.
- Magnuson, J. J. (1978). Locomotion by scombrid fishes: hydrodynamics, morphology and behaviour. In *Fish Physiology*, vol. 7 (eds. 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. *Mar. Mamm. Sci.* **20**, 498-509.
- Morales, J.M. and Ellner, S. P. (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behaviour. *Ecology* **83**, 2240–2247.
- 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.
- 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.
- Nursall, J. R. (1956). The lateral musculature and the swimming fish. *Proc. Zool. Soc. Lond.* **126**, 127-143.
- Nursall, J. R. (1958). The caudal fin as a hydrofoil. *Evolution* **12**: 116-120.
- Parry, D. A. (1949a). The swimming of whales and the discussion of Gray's paradox. *J. Exp. Biol.* **26**, 24-34.
- Parry, D.A. (1949b). The anatomical basis of swimming in whales. *Proc. Zool. Soc. Lond.* **119**, 49-60.

- 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.
- Randall, J. E. (1972). The Hawaiian trunkfishes of the Genus *Ostracion*. *Copeia* **1972**, 756–768.
- 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.
- 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.
- Shadwick, R.E. (2005). How tunas and lamnid sharks swim: an evolutionary convergence. *Am. Sci.* **93**, 524-531.
- Shadwick, R. E., Katz, S. L., Korsmeyer, K. E., Knowler, 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.
- 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.
- Shadwick, R. E. and Syme, D. A. (2008). Thunniform swimming: muscle dynamics and mechanical power production of aerobic fibers in yellowfin tuna (*Thunnus albacares*). *J. Exp. Biol.* **211**, 1603-1611.
- Stokesbury, M. J., Teo, S. L., 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.
- 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.
- Triantafyllou, M. S. (2017). Tuna fin hydraulics inspire aquatic robotics. *Science* **357**, 251-252.
- Tyler, J. C. (1980). Osteology, phylogeny and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). NOAA Technical Report NMFS Circular 434.

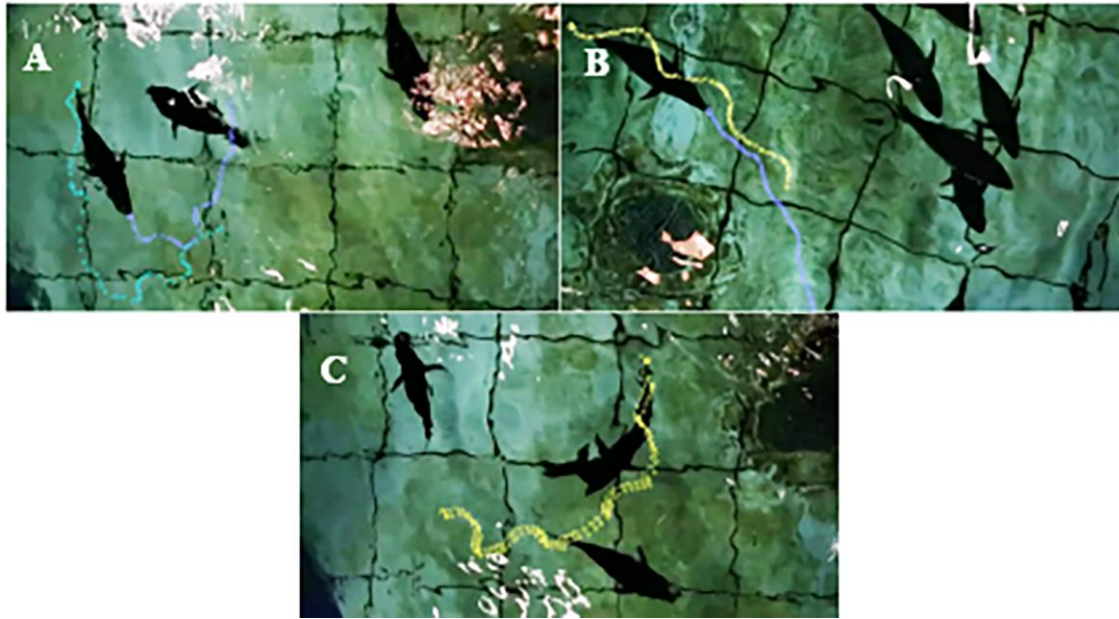
- Walker, J. (2000). Does a rigid body limit maneuverability? *J. Exp. Biol.* **203**, 3391-3396.
- Walters, V. and Fierstine, H. L. (1964). Measurements of swimming speed of yellowfin tuna and wahoo. *Nature* **202**, 208-209.
- Wang, J., Wainwright, D. K., Lindengren, R. E., Lauder, G. V. and Dong, H. (2020). Tuna locomotion: a computational hydrodynamic analysis of finlet function. *J. Roy. Soc. Interface* **17**, 20190590.
- 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.
- Webb, P. W. (1984). Form and function in fish swimming. *Sci. Am.* **251**, 72- 82.
- Webb, P. W. (2004). Maneuverability-General Issues. *J. Oceanic Eng.* **29**, 547-555.
- Webb, P. W. (2006). Stability and maneuverability. In *Fish Physiology; Fish Biomechanics, Vol. 23* (eds. R. E. Shadwick and G. V. Lauder), pp. 281-332. Amsterdam: Academic Press.
- Weihs, D. (1989). Design features and mechanics of axial locomotion in fish. *Am. Zool.* **29**, 151-160.
- Weihs, D. (1993). Stability of aquatic animal locomotion. *Cont. Math.* **141**, 443-461.
- Weihs, D. (2002). Stability versus maneuverability in aquatic locomotion. *Integr. Comp. Biol.* **42**, 127-134.
- Westneat, M. W. and Wainwright, S. A. (2001). Mechanical design for swimming: muscle, tendon, and bone. In *Tuna: Physiology, Ecology and Evolution* (eds. B. Block and D. Stevens), pp.271-311. San Diego: Academic Press.

## Figures and Tables

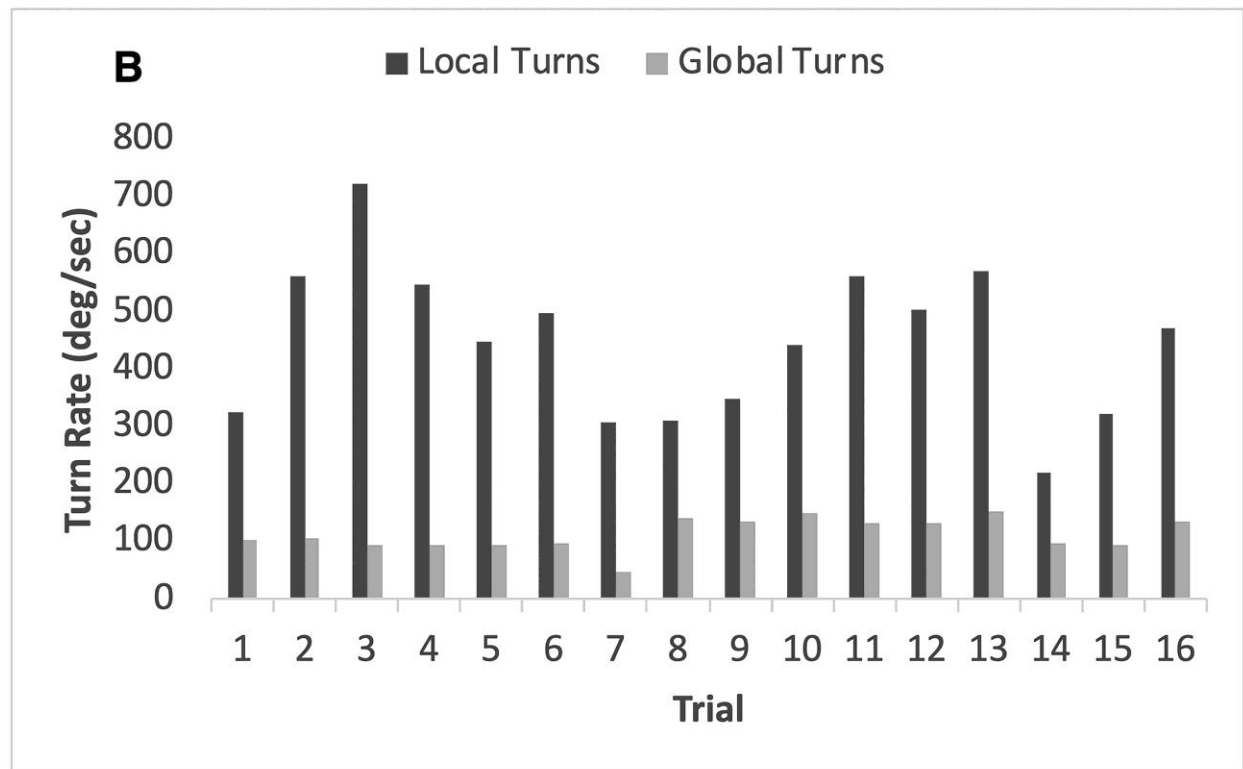
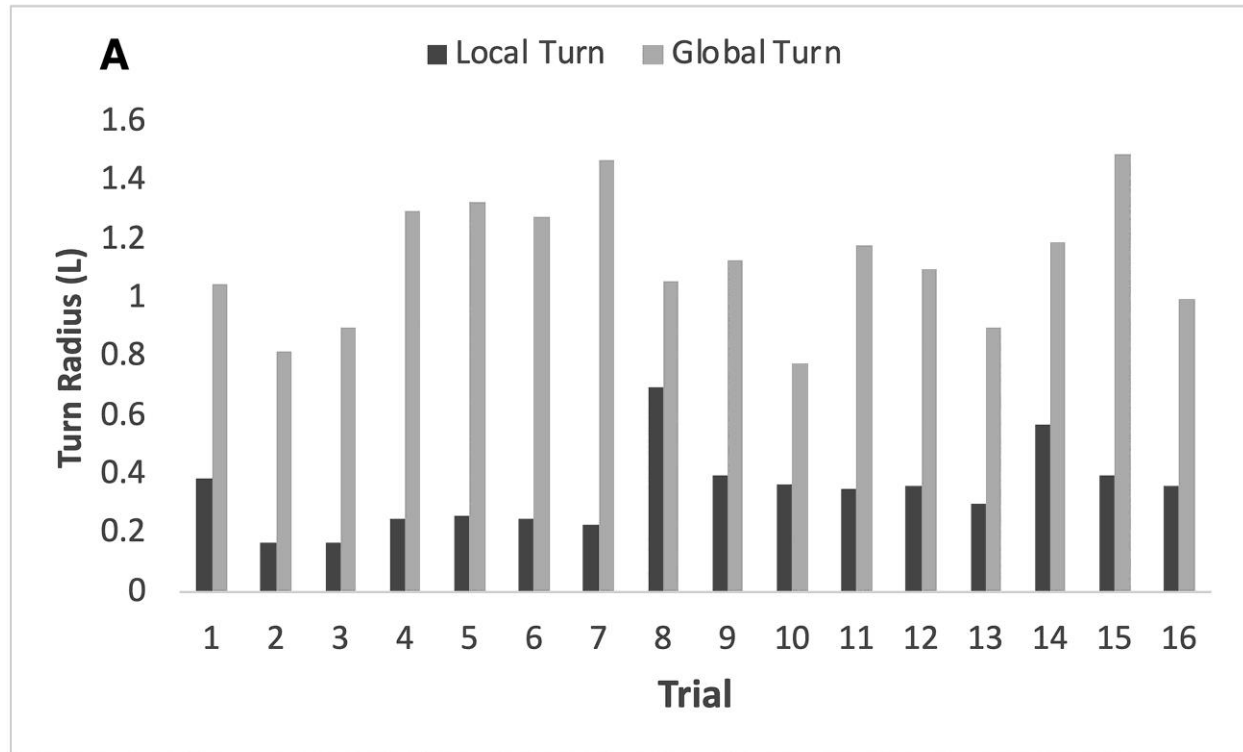


**Fig. 1.** Circle of best fit for a ratchet turn. The large circle represents the global ratchet turn while the smaller circles represent the local ratchet turns within the global turn. The units for the turn radius ( $r$ ) are in body lengths (L).

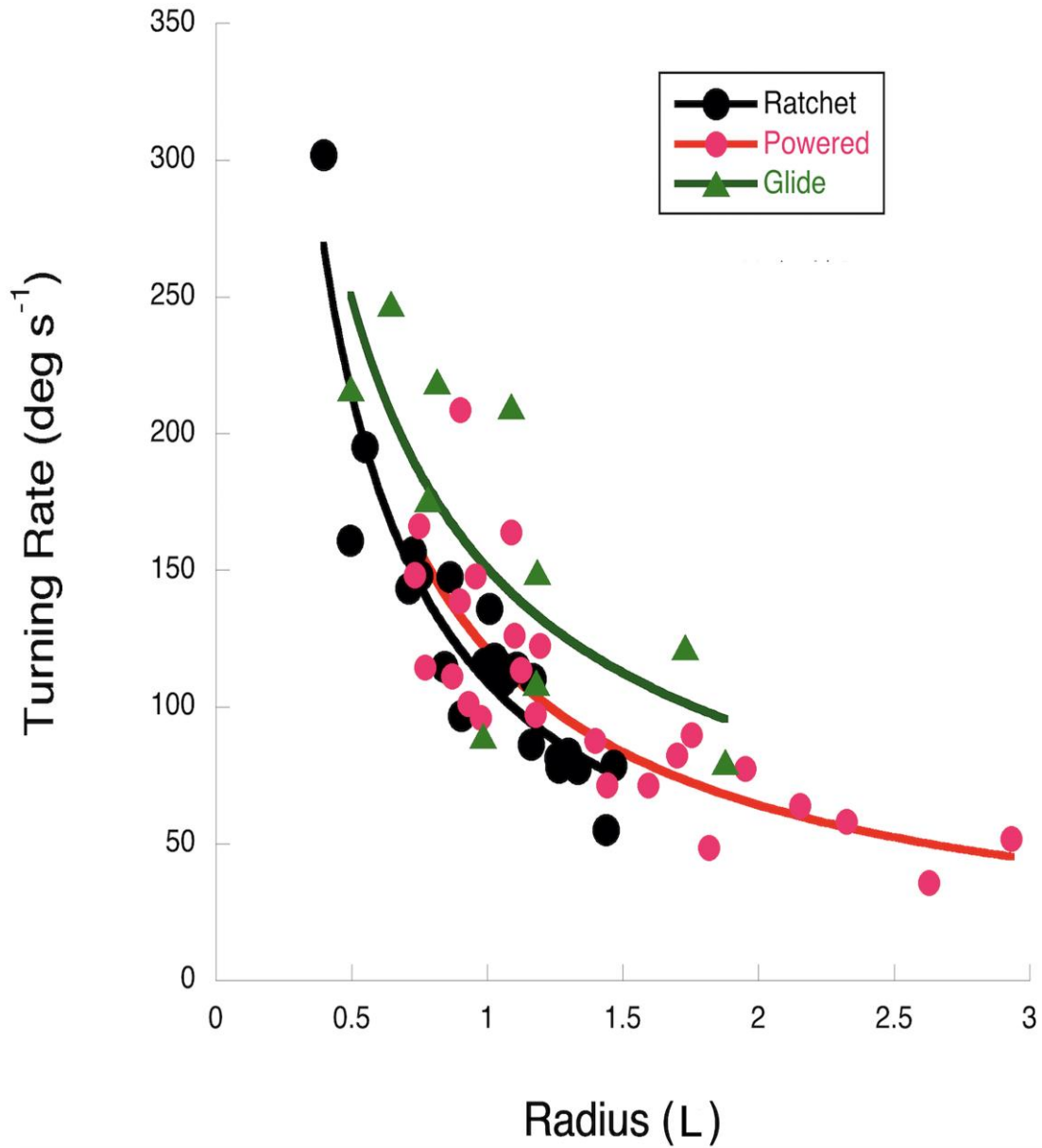




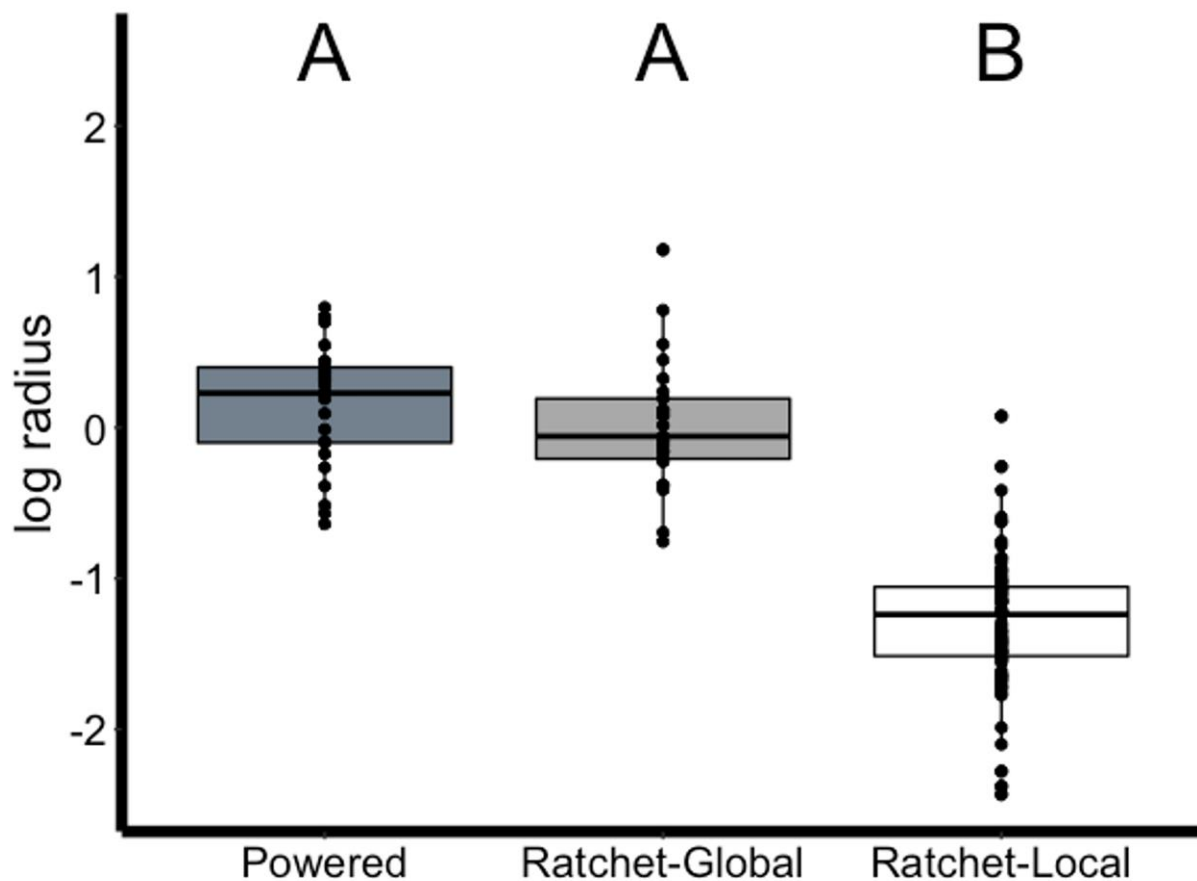
**Fig. 2.** Visual representation of the three different turning maneuvers utilized by bluefin tuna during feeding bouts. Image A shows the rostrum and the tip of the tail being tracked during one frame of a glide turn, Image B shows the rostrum and the tip of the tail being tracked during one frame of a powered turn, Image C shows the tip of the tail being tracked during one frame of a ratchet turn. In Image A, the blue line represents the trail of the rostrum and the green line represents the trail of the tip of the tail. In Image B, the blue line represents the trail of the rostrum and the yellow line represents the trail of the tip of the tail. In Image C, the yellow line represents the trail of the tip of the tail.



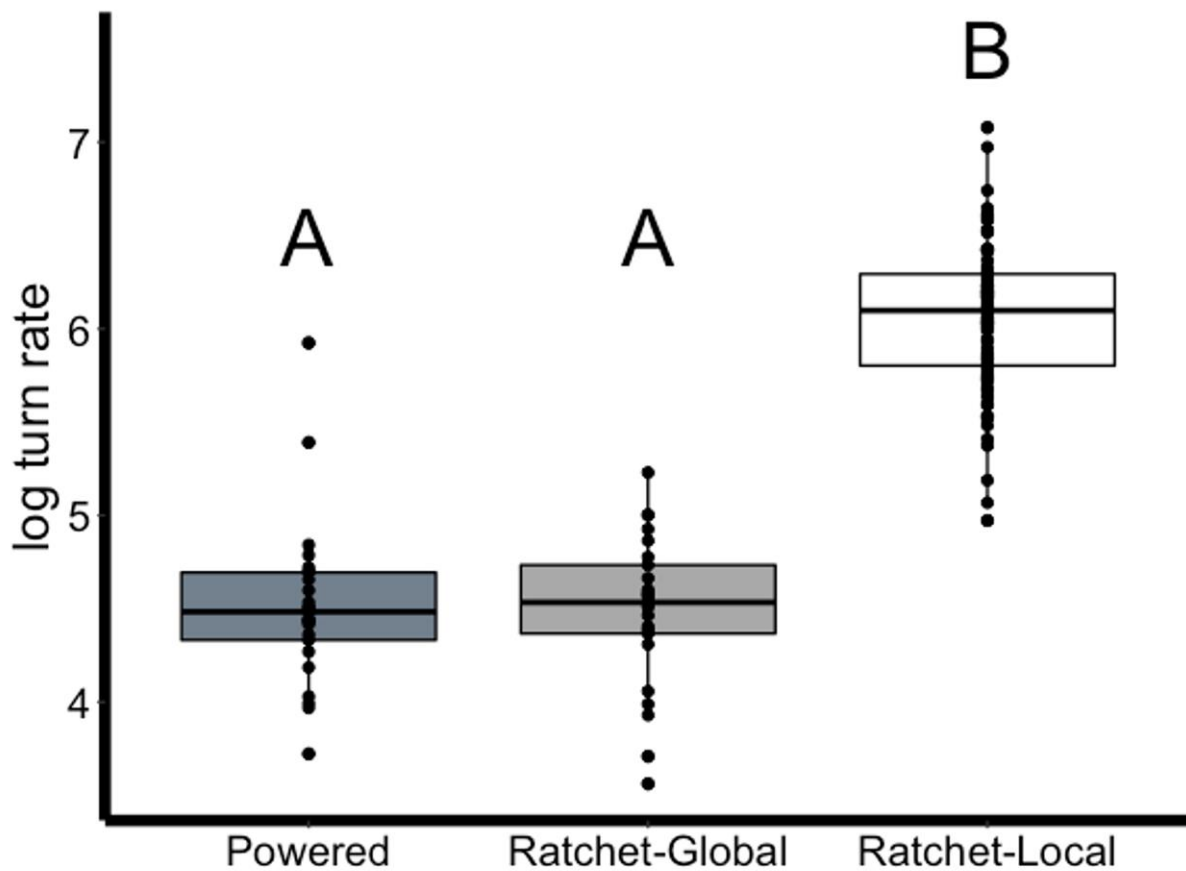
**Fig. 3.** Comparison between (A) turn radius (L) and (B) turn rate ( $\text{deg s}^{-1}$ ) of the global ratchet turn and local ratchet turn. Sixteen bluefin tuna turning trials were analyzed to determine turn radius and turn rate. These 16 turns were chosen out of nearly 100 turns due to clarity of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



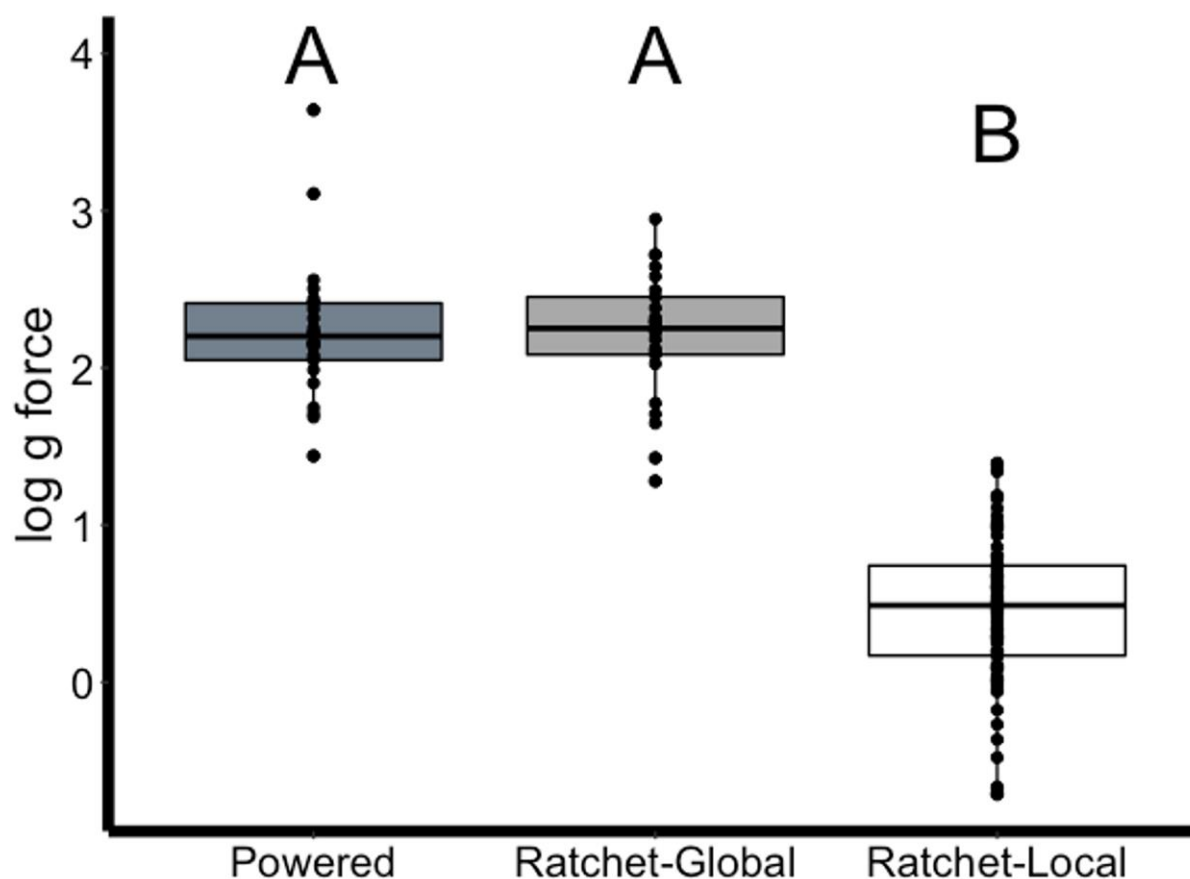
**Fig. 4.** Regressions comparing the turning rates of the global turns of the ratchet, powered, and glide turns of Pacific Bluefin tuna. 56 turns were analyzed and chosen out of nearly 100 turns due to clarity. Fish were recorded swimming in the tank on 10 separate occasions. The regression equations 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).



**Fig. 5.** Box plots representing the distribution of the data comparing the effect of a powered turn, global ratchet turn, and local ratchet turn on the radius of the turn. 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. Ratchet-global compared to powered  $P=0.51$ . Ratchet-local compared to powered  $P<0.001$ . Ratchet-global compared to ratchet-local  $P<0.001$ . 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.

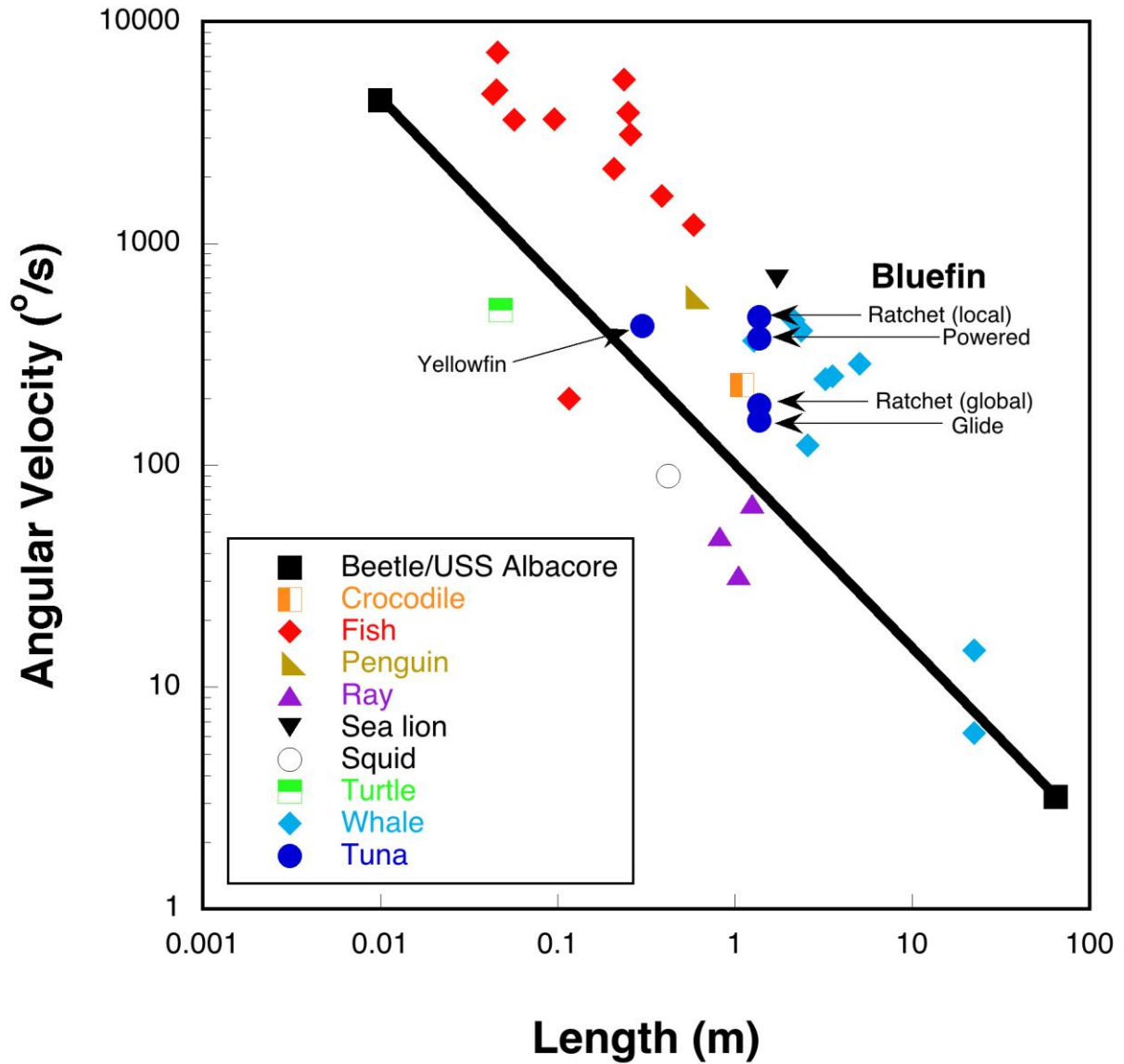


**Fig. 6.** Box plots representing the distribution of the data comparing the effect of a powered turn, global ratchet turn, and local ratchet turn on the g force of the turn. Each point is represented by a dot on the graph with mean indicated by the horizontal bar and the 25%-75% of the points represented by the colored box. Outliers fall off the vertical line in the center of the box. Ratchet-global compared to powered  $P=0.98$ . Ratchet-local compared to powered  $P<0.001$ . Ratchet-global compared to ratchet-local  $P<0.001$ . 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.



**Fig. 7.** Box plots representing the distribution of the data comparing the effect of a powered turn, global ratchet turn, and local ratchet turn on the g force of the turn. 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. Ratchet-global compared to powered  $P=0.98$ . Ratchet-local compared to powered  $P<0.001$ . Ratchet-global compared to ratchet-local  $P<0.001$ . 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.





**Fig. 8.** 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 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 blue circles and fall to the right of the black line.

**Table 1.** Comparison of mean (+SD) angles of attack to individual turn radius and turn rate for ten global ratchet turns.

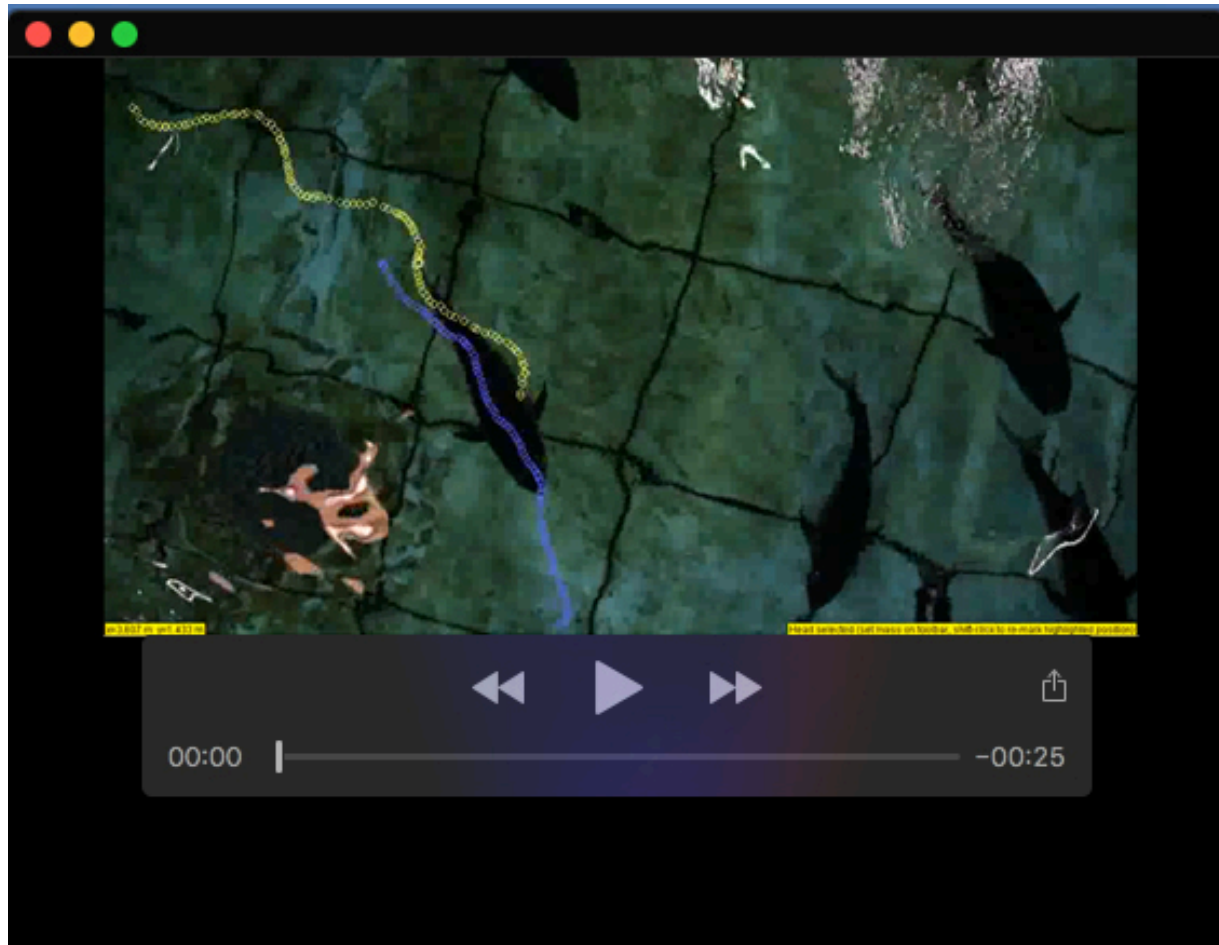
Video	Mean Angle of Attack (deg)	Turn rate (deg s <sup>-1</sup> )	Radius (L)
gM2A0948-1	32 + 18	110	1.1
gM2A0949-1	32 + 20	115	0.9
gM2A0955-1	26 + 12	77	1.4
gM2A0956-1	30 + 12	81	1.3
gM2A0966-1	22 + 10	136	1.1
gM2A0966-2	41 + 5	114	1.2
gM2A0968-1	30 + 5	148	0.8
gM2A0969-1	22 + 6	110	1.2
gM2A0974-1	16 + 7	148	0.9
gM2A0972-1	24 + 7	82	1.2

**Table 2.** Comparison of mean (+SD) turn rate and turn radius for global turns measured at the rostrum, peduncle and tip of the tail during the three different turns behaviors observed.

Body Point	Turn Parameter	Glide	Powered	Ratchet
Rostrum	Turn rate (deg s <sup>-1</sup> )	99	103	104
Rostrum	Turn radius (L)	2.6	1.3	1.1
Peduncle	Turn rate (deg s <sup>-1</sup> )	162	104	122
Peduncle	Turn radius (L)	1.2	1.5	1.0
Tail	Turn rate (deg s <sup>-1</sup> )	123	100	119
Tail	Turn radius (L)	1.7	1.6	1.1



**Movie 1.** Glide turn in which the caudal fin is used as a rudder. The blue diamonds and green diamonds show the sequential positions of rostrum and caudal fin through the turn, respectively.



**Movie 2.** Powered turn in which the tuna is using the caudal fin to move through the turn. The blue diamonds and yellow diamonds show the sequential positions of rostrum and caudal fin through the turn, respectively.



**Movie 3.** Ratchet turn in which the tuna moves the caudal fin is swept through multiple asymmetrical strokes to produce small turns, which are summed to produce a larger global turn. The red diamonds and little blue diamonds show the sequential positions of rostrum and caudal fin through the turn, respectively.