



# Faster is not always better: Turning performance trade-offs in the inshore squids *Doryteuthis pealeii* and *Illex illecebrosus*

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## ABSTRACT

Jet-propelled swimmers move differently than fin and flipper-based locomotors, relying heavily on directed, pulsed flows to effect maneuvers and turns. Despite a unique propulsive system involving both fins and a jet, little is currently known about the turning performance of most squids. In this study, the maneuverability of two morphologically and ecologically different squids, the shortfin squid, *Illex illecebrosus*, and longfin squid, *Doryteuthis pealeii*, was studied using kinematic tracking approaches. We recorded 128 spontaneous turns using a multi-camera system, tracked several landmarks on the squids, and calculated a range of kinematic parameters, including angular velocity and length-specific turning radius along the yaw axis for all turns. *Illex illecebrosus* completed faster but broader turns than *D. pealeii*. *Doryteuthis pealeii* relied more heavily on its fins for turning, with higher fin flap frequencies and amplitudes than *I. illecebrosus*. Both species were able to complete tighter turns when oriented arms-first versus tail-first, and *I. illecebrosus* curled its arms more in the arms-first mode, which likely increased angular velocity through a reduction in moment of inertia. The results of this study indicate that the jet, fins, and arms of squids all play important roles in turning performance, and there is a trade-off in squids between maximizing angular velocity and minimizing turning radius.

**Summary:** A kinematic analysis of maneuverability and agility of two inshore squid species: *Doryteuthis pealeii* and *Illex illecebrosus*.

## 1. Introduction

Investigations of animal swimming abilities are widespread (Blake et al., 1995; Blake and Chan, 2006; Dabiri et al., 2020; Drucker and Lauder, 2001a, 2001b; Fountain, 1904; Gray, 1933; Parson et al., 2011; Porter et al., 2011; Rivera et al., 2006; Robinson, 1893; Russell and Steven, 1930; Verrill, 1874). In the marine environment, maneuverability (the ability to turn tightly) and agility (the ability to turn quickly) are critical for predator avoidance, prey capture, movement in complex environments, and even communication (Arnold, 1962; Bartol et al., 2001b; Foyle and O'Dor, 1988; Hanlon et al., 2018; Hanlon et al., 1983; Hanlon and Messenger, 1996; Jastrebsky et al., 2017; Jastrebsky et al., 2016; Messenger, 1968). There is growing interest in turning performance of soft-bodied animals that must rely on directed jets as opposed to fins or flippers, such as jellyfishes, siphonophores, and squids (Bartol et al., 2022; Dabiri et al., 2020; Gemmell et al., 2015; Jastrebsky et al., 2016; Sutherland et al., 2019a).

Described as a three step process, jellyfish turning involves a torque

maximizing phase, a moment of inertia minimizing phase, and a final braking phase (Costello et al., 2021; Dabiri et al., 2020). Jellies use a stiffened inner margin of their bell to produce a strong pivot point around which they turn; coupled with enhanced outer margin bending and asynchronous contractions, jellies can produce turns up to  $\sim 400$  deg.  $s^{-1}$  (Dabiri et al., 2020; Petie et al., 2011). In contrast, siphonophores rely on division of labor to complete complex maneuvers. Younger nectophores positioned close to the apex of the colony and oriented at an angle produce significant torque, as their position represents the moment lever extremes in the colony. Older nectophores positioned farther from the apex produce the forward momentum (Costello et al., 2015; Sutherland et al., 2019b). This strategy allows the siphonophore *Nanomia bijuga* to complete turns of  $215 \pm 90$  deg.  $s^{-1}$  (average maximum angular velocity) with a length-specific turning radius of  $0.15 \pm 0.10$  (Sutherland et al., 2019a).

The >800 species of cephalopods have more complex neurocircuitry and morphologies than other jet-propelled invertebrates. Squids, in particular, are incredibly diverse, with slow-moving pelagic forms, such

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as glass squid (Cranchiids) to fast swimming cruisers like the flying squid (Ommastrephids) that can reach rectilinear speeds of  $11.2 \text{ m s}^{-1}$  and even glide in air (Clarke, 1962; Clarke et al., 1979; Hendrickson, 2004; Maciá et al., 2004; Muramatsu et al., 2013; Nigmatullin and Arkhipkin, 1998; O'Dor et al., 2013; O'Dor, 2013; O'Dor, 2002; O'Dor, 1988; O'Dor and Webber, 1991; Stewart et al., 2012; Webber et al., 2000). The ability to use two forms of propulsion (jet and fins) in tandem or alone set squids and cuttlefishes apart from other jet-propelled swimmers. Using this dual mode system, squids and cuttlefishes can hover, turn tightly, ascend vertically, and even swim forward or backward. This ability to swim forward (oriented arms-first) as well as backward (oriented tail-first) is especially important for hunting because squids and cuttlefishes often use both swimming directions during prey approach, strike, and recoil (Foyle and O'Dor, 1988; Jastrebsky et al., 2017; Kier, 1982; Kier and Van Leeuwen, 1997; Messenger, 1968; Nicol and O'Dor, 1985). The tapered mantle tip together with a streamlined body reduces drag when swimming tail-first, making this orientation more desirable for fast swimming or long-distance travel. However, some squids can also achieve a streamlined shape by holding their arms in a conical configuration while swimming arms-first (Anderson and DeMont, 2005; Bartol et al., 2022; Bartol et al., 2001a; Bartol et al., 2001b), although this likely has an associated muscular cost.

Switching swimming directions is facilitated by the flexible funnel of cephalopods. The funnel, which includes longitudinal, circular, and radial muscles as well as the funnel retractor muscles, can be pointed in any direction underneath the animal for directed jetting (Kier and Thompson, 2003). This allows for jets to be generated at any angle under the animal, leading to propulsion in forward, backward, upward, and sideways directions. In addition, fins can oscillate and/or undulate for propulsion, complementing the vectored jet. Squids and cuttlefishes fin morphologies vary greatly with fins of many shapes, sizes, and thicknesses, from thin skirt-like fins to large rhomboidal or lobate fins (Hanlon et al., 2018; Hoar et al., 1994; O'Dor et al., 1995). Many inshore squids decrease fin use with speed, often curling their fins around the mantle at the highest swimming speeds (O'Dor, 1988; Hoar et al., 1994; Bartol et al., 2001b). *Doryteuthis pealeii* (formerly *Loligo pealeii*) demonstrate two fin gaits: a slow-speed gait characterized by undulation and flapping and a fast-speed gait characterized by flapping motion and periods of fin inactivity whereby the fins curl around the mantle (Anderson and DeMont, 2005). *Lolliguncula brevis* exhibits similar fin transitions with speed (Bartol et al., 2001a, 2001b), while also employing more wavelike fin movements during arms-first swimming compared to tail-first swimming (Bartol et al., 2018). Based on hydrodynamic signatures, four distinct fin modes occur in *L. brevis* during tail-first swimming: fin mode I where a single vortex is shed on the downstroke, fin mode II where undulatory movements create a linked chain of vortices, fin mode III in which a vortex is shed on each downstroke and upstroke, and fin mode IV where linked double vortices are produced. Only fin modes II and III occur during arms-first swimming (Stewart et al., 2010).

Little is known quantitatively about the turning dynamics and kinematics of most species of cephalopods. Foyle and O'Dor (1988) reported average angular velocities of  $67\text{--}139 \text{ deg. s}^{-1}$  for the shortfin squid, *Illex illecebrosus*, during hunting, and maximum angular velocities of  $300 \text{ deg. s}^{-1}$ . During hunting, dwarf cuttlefish, *Sepia bandensis*, turn at angular velocities  $\sim 110\text{--}120 \text{ deg. s}^{-1}$  (Messenger, 1968). In a more recent study, Jastrebsky et al. (2016) found *S. bandensis* have average angular velocities of  $55 \text{ deg. s}^{-1}$  and mean maximum angular velocities of  $160 \text{ deg. s}^{-1}$  along the yaw axis, with some cuttlefish reaching angular velocities as high as  $485 \text{ deg. s}^{-1}$ . Squid *Lolliguncula brevis* exceeds *S. bandensis* in agility, exhibiting higher mean angular velocities ( $110.3 \text{ deg. s}^{-1}$ ), but it is less maneuverable, with minimum length-specific turning radii that are twice as large (Jastrebsky et al., 2016). Average minimum length-specific turning radii for both *L. brevis* and *S. bandensis* ( $3.4 \times 10^{-3}$  and  $1.2 \times 10^{-3}$ , respectively) are among the lowest values

reported for any aquatic animal (Jastrebsky et al., 2016). Recent 3D velocimetry studies have shown that the jet plays a greater role in turning than the fins, and orientation can affect jet flow dynamics in the squids *L. brevis*, *D. pealeii*, and *I. illecebrosus* (Bartol et al., 2022, 2023).

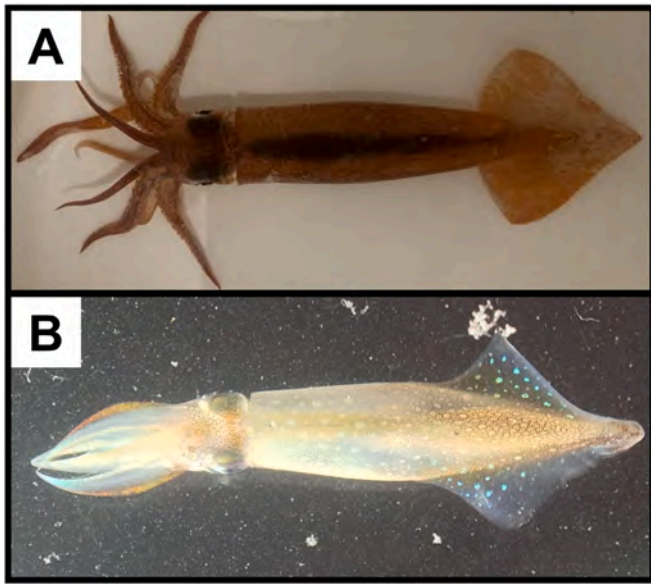
The longfin squid, *Doryteuthis pealeii*, and shortfin squid, *Illex illecebrosus*, differ ecologically, morphologically, and behaviorally, and they likely employ disparate turning strategies. Both *D. pealeii* and *I. illecebrosus* frequent neritic waters, but *D. pealeii* has a more southern distribution, residing in waters as far south as the Gulf of Venezuela, and does not venture as far offshore as *I. illecebrosus* (Black et al., 1987; Brodziak and Hendrickson, 1999; Coelho et al., 1994; Dawe et al., 1981; Hendrickson, 2004; Squires, 1967). While both species are negatively buoyant, *I. illecebrosus* is more streamlined, smaller, and has narrower fins than *D. pealeii*. *Doryteuthis pealeii* grows to  $\sim 50 \text{ cm}$  dorsal mantle length (DML), while *I. illecebrosus* reaches a maximum length of only  $\sim 35 \text{ cm}$  DML. Weights of smaller *D. pealeii* and *I. illecebrosus* are very similar, with *I. illecebrosus* beginning to outweigh *D. pealeii* at around  $20 \text{ cm}$  DML (Lange and Johnson, 1981). *Doryteuthis pealeii* fins extend  $\sim 50\%$  down the mantle and are rounded with low aspect ratios, whereas *I. illecebrosus* fins extend  $\sim 25\text{--}30\%$  down the mantle and are triangular in shape with high aspect ratios. Triangular, high-aspect ratio fins are thought to be more useful for lift and gliding than maneuverability (Jereb and Roper, 2010; Jereb and Roper, 2005; Roper et al., 1984). In addition, these flexible, dorsally-positioned, triangular fins can be used effectively as rudders, whereas the longer, thinner, lower aspect ratio fins of *D. pealeii* are generally not used for this purpose (Hoar et al., 1994). Finally, *I. illecebrosus* is a faster rectilinear swimmer than *D. pealeii* (O'Dor and Webber, 1991; Webber and O'Dor, 1985). To date, little is known about the turning performance of either of these squids (but see Bartol et al., (2023) for a wake-based analysis of turning).

In this study, we examined the kinematics of turns in *D. pealeii* and *I. illecebrosus*, with the goal of quantifying key metrics like turning radius, angular velocity, fin and jet frequency, and arm angles. Our objectives were to investigate whether turning capabilities differ according to species (*D. pealeii* vs *I. illecebrosus*) and swimming direction (arms-first vs tail-first). We hypothesized that *I. illecebrosus* will exhibit higher angular velocities but larger turning radii than *D. pealeii* due to its faster swimming speeds and more streamlined shape. In addition, we predicted that turns that are oriented arms-first will have smaller length-specific turning radii but be slower (lower angular velocities) than tail-first turns. This prediction was based on tight turns being reported for arms-first swimming when approaching prey (Jastrebsky et al., 2017) and overall lower swimming speeds observed for arms-first swimming relative to tail-first swimming (Bartol et al., 2001a, 2016). Indeed, we expected to observe a tradeoff between tighter and faster turns, a pattern seen in other taxa (Fish and Nicastro, 2003; Sutherland et al., 2019b; Walker, 2000). We also hypothesized that tighter turns would correlate with greater fin activity, as fin motions presumably play important roles in complementing the jet to achieve low length-specific turning radii.

## 2. Methods

### 2.1. Study species

In this study, 7 *Illex illecebrosus* (Lesueur 1821, Fig. 1A), and 29 *Doryteuthis pealeii* (Lesueur 1821, Fig. 1B) were used. Total length (TL) of *D. pealeii* ranged from  $10.8$  to  $28.0 \text{ cm}$ , with a mean  $\pm$  s.e.m. =  $16.4 \pm 0.7 \text{ cm}$ ; TL for *I. illecebrosus* ranged from  $15.1$  to  $19.3 \text{ cm}$ , with a mean of  $17.4 \pm 0.6 \text{ cm}$ . Squids were caught by jig or cast net in Boothbay Harbor, ME. Squids were kept in a flow-through race-way system (32 ppt and  $18 \text{ }^\circ\text{C}$ ) at the University of Maine's Darling Marine Center (DMC) in Walpole, ME, and fed a diet of live baitfish caught by seine net (*Luxilus* spp., *Notropis* spp., *Pimephales* spp., and *Semotilus* spp.). Individuals were easily distinguishable by TL and/or by body markings.



**Fig. 1.** Photos of squid species studied. (A) *Illex illecebrosus*. (B) *Doryteuthis pealeii*. Both squids are oriented with arms on the left and tip of the mantle (tail) on the right. Not to scale.

## 2.2. Data collection

All experiments were performed at the DMC. Squids were placed in a plexiglass experimental chamber (64 cm × 64 cm × 64 cm) filled with aerated and filtered saltwater (32 ppt and 18 °C). The chamber was illuminated using a series of halogen lights with spectral filters to produce red (>620 nm) wavelengths. One Dalsa Falcon camera (Teledyne Dalsa, Inc., Waterloo, ON, Canada; 1400 × 1200 pixels, 100 frames s<sup>-1</sup>) was positioned dorsally, and two other Falcons were positioned laterally. The cameras were outfitted with lenses ranging from 9 to 25 mm. Squids were recorded in ~1 min sessions (18,000 total frames) using IO industries DVR Express Core2 processor (London, ON, Canada). Squids swam freely in the experimental tank, turning spontaneously. To avoid collisions with tank walls, squids often switched swimming direction, i. e., arms-first to tail-first or vice versa. Each animal was recorded for no

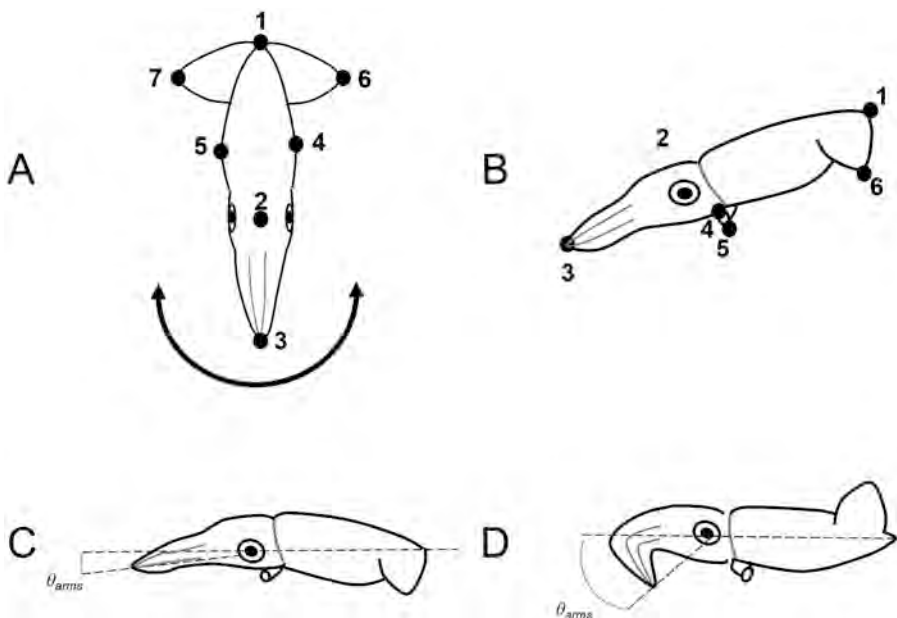
more than three hours at a time to avoid exhaustion. Squids were then returned to the holding tank after data collection.

## 2.3. Data analysis

Videoed turns by squids were identified as either arms-first (arms at the leading edge of the turn), or tail-first (posterior tip of the mantle at the leading edge of the turn). Sections of video were selected according to the following criteria: (1) the animal needed to be completely visible in both the dorsal view and one of the side views; (2) the animal needed to be away from tank walls; and (3) total angular displacement had to be >10 deg. Frame-by-frame body tracking was performed using DLTdv digitizing software for turns along the yaw axis (Hedrick, 2008). The digitized points in the dorsal perspective included the (1) tail tip, (2) equidistant point between eyes, (3) most extended arm tip, (4) left side of the mantle (region of maximum amplitude), (5) right side of the mantle, (6) left fin tip, and (7) right fin tip (Fig. 2A). Digitized points in the lateral views included the (1) tail tip, (2) eye, (3) arm tip, (4) dorsal funnel edge, (5) ventral funnel edge, and (6) fin tip (Fig. 2B). Points were then smoothed with an in-house MATLAB routine using the Cross-Validation Criterion with a smoothing parameter within 0.1% (Walker, 1998). These tracked points were used to calculate the mean radius of the turn ( $R_{mean}$ ), the minimum radius of the turn ( $R_{min}$ ), maximum angular velocity during the turn ( $\omega_{max}$ ), mean angular velocity throughout the turn ( $\omega_{mean}$ ), degree of arm curling (measured by the vertical angular deviation from the mantle, Fig. 2C,D) ( $\theta_{arms}$ ), and total angular displacement of the animal during the turn ( $\theta_{total}$ ). These calculations were done using a two-segment approach (one segment from tail tip to the center of the eyes, one segment from eye center to arm tip) similar to the one described in Jastrebsky et al. (2016). Center of Rotation (COR) was defined as the point in the dorsal view that moved the least during the turn, and COR is generalized in such a way that the points do not need to fall on the body segments themselves, but instead can fall on an angle with respect to those segments. The radius of the turn ( $R$ ) was determined using:

$$\frac{1}{R} = \frac{z'}{[1 + (z')^2]^{3/2}} \quad (1)$$

where  $z' = dz/dx = \dot{z}/\dot{x}$ ,  $z'' = d^2z/dx^2 = (\ddot{x}\dot{z} - \dot{x}\ddot{z})/\dot{x}^3$ ,  $x$  and  $z$  are the coordinates of the COR in the dorsal view,  $t$  is time, the over dot



**Fig. 2.** Illustration of points tracked for kinematic measurements in both dorsal and lateral views. (A) For dorsal views, (1) tail tip, (2) point equidistant between eyes, (3) arm tip, (4) left side of mantle, (5) right side of mantle, (6) left fin tip, and (7) right fin tip were digitized. Turning in the yaw plane was measured as depicted by the arrow. (B) For lateral views, (1) tail tip, (2) eye, (3) arm tip, (4) funnel edge closest to the body, (5) funnel edge away from body, and (6) fin tip were digitized. (C, D) Illustration of degree of arm curling ( $\theta_{arms}$ ) with a representative small  $\theta_{arms}$  (C) and large  $\theta_{arms}$  (D).

represents time differentiation, and the derivatives were evaluated using fourth-order accurate finite difference equations. To control for outliers and errors in tracking, the top 10% of values of angular velocity were removed before reporting  $\omega_{max}$ ; for R, the bottom 10% were removed to determine  $R_{min}$ . R values were then normalized by animal total length, and  $(R/L)_{mean}$ , the average of all COR radii comprising the turning path, and  $(R/L)_{min}$ , the lowest R/L after the bottom 10% of R were removed, were calculated. Data greater than four standard deviations from the mean were considered outliers and removed, resulting in 3  $\omega_{max}$  and 2  $R_{min}$  data points (<5% of the data) being removed before analysis.

Fin beats for the inside and outside fins were identified visually (using both lateral and dorsal camera perspectives), with one full up-stroke and downstroke constituting a fin beat. The “inside” fin was the fin closest to the center of the turn; the “outside” fin was the fin farthest from the center of the turn. The number of fin beats was then divided by the total time of the turn to determine  $F_{in}$  (frequency of inside fin),  $F_{out}$  (frequency of outside fin), and  $F_{ave}$  (mean of  $F_{in}$  and  $F_{out}$ ). A paired t-test comparing the frequencies of  $F_{in}$  and  $F_{out}$  was insignificant ( $T_{1,127} = 1.2675, p = 0.2073$ ), thus all statistics were performed on  $F_{ave}$ . Mantle contraction frequency ( $F_{mantle}$ ) was determined visually by counting the contractions of the funnel and dividing that by the time of the turn. Fin amplitude ( $A_{fin}$ ) was calculated by dividing the maximum range of the fin beats during the turn (determined from lateral footage using either the inside or outside fin depending on which had greater amplitude) by the animal’s length.

2.4. Statistical analysis

A two-way mixed model MANOVA was used to examine the effect of species and swimming direction on turning parameters (IBM SPSS v. 28.0.0.0). The turning parameters (dependent variables) were  $(R/L)_{mean}$ ,  $(R/L)_{min}$ ,  $\omega_{max}$ ,  $\omega_{mean}$ ,  $\theta_{arms}$ ,  $\theta_{total}$ ,  $F_{mantle}$ ,  $F_{ave}$ , and  $A_{fin}$ . The Pillai–Bartlett statistic was used for determining significance, as recommended for unequal group sizes by Hand and Taylor (1987).  $(R/L)_{mean}$ ,  $(R/L)_{min}$ ,  $\omega_{max}$ , and  $\omega_{mean}$  data were  $\log_{10}$  transformed to meet assumptions of normality.  $\theta_{total}$  was square root transformed, and  $\theta_{arms}$  was cube root transformed to fit a normal distribution.  $F_{ave}$  was transformed to near normal values using the Tukey’s Ladder transformation, with a resulting lambda value of 0.95 (Tukey, 1977). ANOVAs were used following MANOVA significance to determine which variables were significant. Linear regressions were computed in R using untransformed data using an equation of  $y \propto x$ . Significance was defined at  $p$ -values  $\leq 0.05$ .

3. Results

A total of 128 turns (74 turns involving *Doryteuthis pealeii* and 54 turns with *Illex illecebrosus*) were analyzed for this study. Both species (MANOVA,  $F_{9,116} = 11.340, p < 0.001$ ) and swimming direction (MANOVA,  $F_{9,116} = 2.682, p = 0.007$ ) were significant. A species  $\times$  swimming direction interaction approached significance and warranted further investigation (MANOVA,  $F_{9,116} = 1.987, p = 0.074$ ). The interaction derived from *I. illecebrosus* having greater  $\theta_{arms}$  during arms-first turns than tail-first turns while *D. pealeii* showed no difference between swimming directions (Fig. 3). See Table 1 for a summary of statistical results.

3.1. Species comparison

Of the 74 turns recorded for *D. pealeii*, 47.44% were oriented arms-first, and 52.56% were oriented tail-first (Fig. 4). Due to the fewer number of *I. illecebrosus* individuals, only 54 turns were analyzed. Of those, 50.91% were oriented arms-first, and 49.09% were oriented tail-first (Fig. 4). The total angular displacement for *D. pealeii* turns ranged from 11.08 to 142.98 deg., with an average displacement of  $52.45 \pm 3.74$  deg. (mean  $\pm$  s.e.m. reported). The angular displacement of

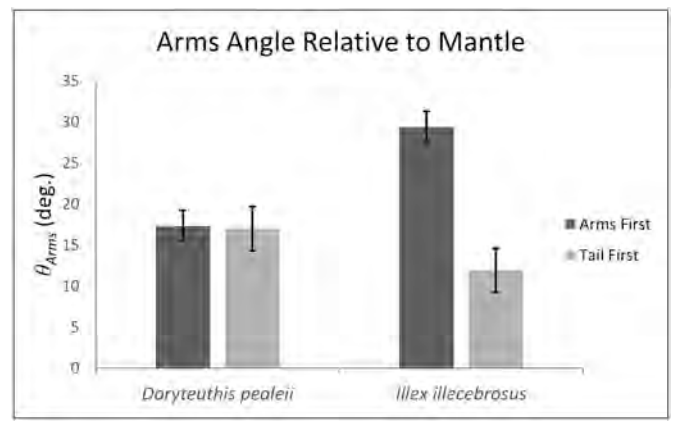


Fig. 3. Arm curling ( $\theta_{arms}$ ) for *Illex illecebrosus* and *Doryteuthis pealeii* in the arms-first and tail-first swimming directions. Error bars shown are standard error of the mean.

Table 1

Statistical results from ANOVAs performed following significant MANOVA tests. Asterisks denote significance.

Variable	Turning Metric	DF	F	P	
Species	Average length-specific turning radius ( $R/L_{mean}$ )	1,124	8.978	0.003**	
	Minimum length-specific turning radius ( $R/L_{min}$ )	1,124	5.207	0.024*	
	Average angular velocity ( $\omega_{mean}$ )	1,124	7.562	0.007**	
	Maximum angular velocity ( $\omega_{max}$ )	1,124	12.913	<0.001**	
	Average fin flap frequency ( $F_{ave}$ )	1,124	92.599	<0.001**	
	Average fin flap amplitude ( $A_{fin}$ )	1,124	3.891	0.051	
	Average mantle contraction frequency ( $F_{mantle}$ )	1,124	0.006	0.936	
	Swim Direction	Average length-specific turning radius ( $R/L_{mean}$ )	1,124	5.730	0.018*
		Minimum length-specific turning radius ( $R/L_{min}$ )	1,124	0.742	0.391
		Average angular velocity ( $\omega_{mean}$ )	1,124	0.189	0.664
Maximum angular velocity ( $\omega_{max}$ )		1,124	0.639	0.426	
Average fin flap frequency ( $F_{ave}$ )		1,124	0.001	0.980	
Average fin flap amplitude ( $A_{fin}$ )		1,124	0.084	0.772	
Average mantle contraction frequency ( $F_{mantle}$ )		1,124	0.299	0.585	

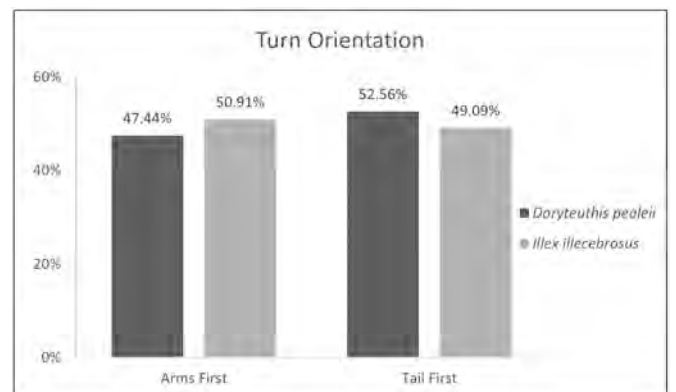


Fig. 4. Demographics of swimming directions. Percentages of arms-first and tail-first swimming directions for *Doryteuthis pealeii* and *Illex illecebrosus*.

*I. illecebrosus* ranged from 18.88 to 96.01 deg. and averaged  $52.02 \pm 2.50$  deg.

The mean radius ( $R_{mean}$ ) of all turns performed by *D. pealeii* was  $2.73 \pm 0.14$  cm, with a range of 0.78–8.50 cm, and a minimum R across all

turns of 0.016 cm. When the radii of the turns were standardized by the body length of the squid, average length-specific turning radius of the turns  $[(R/L)_{mean}]$  was  $0.16 \pm 0.009$  and the average minimum length-specific turning radius during turns  $[(R/L)_{min}]$  was  $0.0097 \pm 0.0011$ . The mean radius ( $R_{mean}$ ) for *I. illecebrosus* turns was  $3.42 \pm 0.17$  cm, with a range of 0.84–7.02 cm and a minimum  $R$  across all turns of 0.017 cm. When standardized for the length of the animal,  $(R/L)_{mean}$  was  $0.20 \pm 0.011$ .  $(R/L)_{min}$  was  $0.012 \pm 0.0014$ . Both  $(R/L)_{mean}$  (ANOVA,  $F_{1,124} = 8.978, p = 0.003$ ) and  $(R/L)_{min}$  (ANOVA,  $F_{1,124} = 5.207, p = 0.024$ ) were significantly larger for *I. illecebrosus* than *D. pealeii* (Fig. 5A,B).

*Illex illecebrosus* achieved higher average angular velocity ( $\omega_{mean}$ ; ANOVA,  $F_{1,124} = 7.562, p = 0.007$ ) and maximum angular velocity ( $\omega_{max}$ ; ANOVA,  $F_{1,124} = 12.913, p < 0.001$ ) during turns than *D. pealeii* (Fig. 5C,D). The mean angular velocity for *I. illecebrosus* was  $46.52 \pm 2.87$  deg.  $s^{-1}$  (range: 9.29–101.28 deg.  $s^{-1}$ ) and mean  $\omega_{max}$  was  $108.73$

$\pm 6.59$  deg.  $s^{-1}$ , with the highest  $\omega_{max} = 255.66$  deg.  $s^{-1}$ . For *D. pealeii*,  $\omega_{mean}$  was  $37.66 \pm 2.61$  deg.  $s^{-1}$  (range: 6.97–110.07 deg.  $s^{-1}$ ) and mean  $\omega_{max}$  was  $82.36 \pm 5.50$  deg.  $s^{-1}$ , with the highest  $\omega_{max} = 269.23$  deg.  $s^{-1}$ .

*Doryteuthis pealeii* demonstrated higher average fin flap frequency ( $F_{ave}$ ) than *I. illecebrosus* (ANOVA,  $F_{1,124} = 92.599, p < 0.001$ ).  $F_{ave}$  for *D. pealeii* and *I. illecebrosus* were  $2.25 \pm 0.10$  Hz and  $0.79 \pm 0.11$  Hz, respectively (Fig. 5E). There was also a near significant difference in average fin flap amplitude ( $A_{fin}$ ) between species, with *D. pealeii* moving their fins over a larger relative distance ( $A_{fin} = 0.179 \pm 0.006$ ) than *I. illecebrosus* ( $A_{fin} = 0.160 \pm 0.007$ ; Fig. 5F). There was no significant difference between species in average mantle contraction frequency ( $F_{mantle}$ ; *D. pealeii*  $F_{mantle} = 1.75 \pm 0.10$  Hz, *I. illecebrosus*  $F_{mantle} = 1.67 \pm 0.07$  Hz). As mentioned earlier, there was a strong trend showing

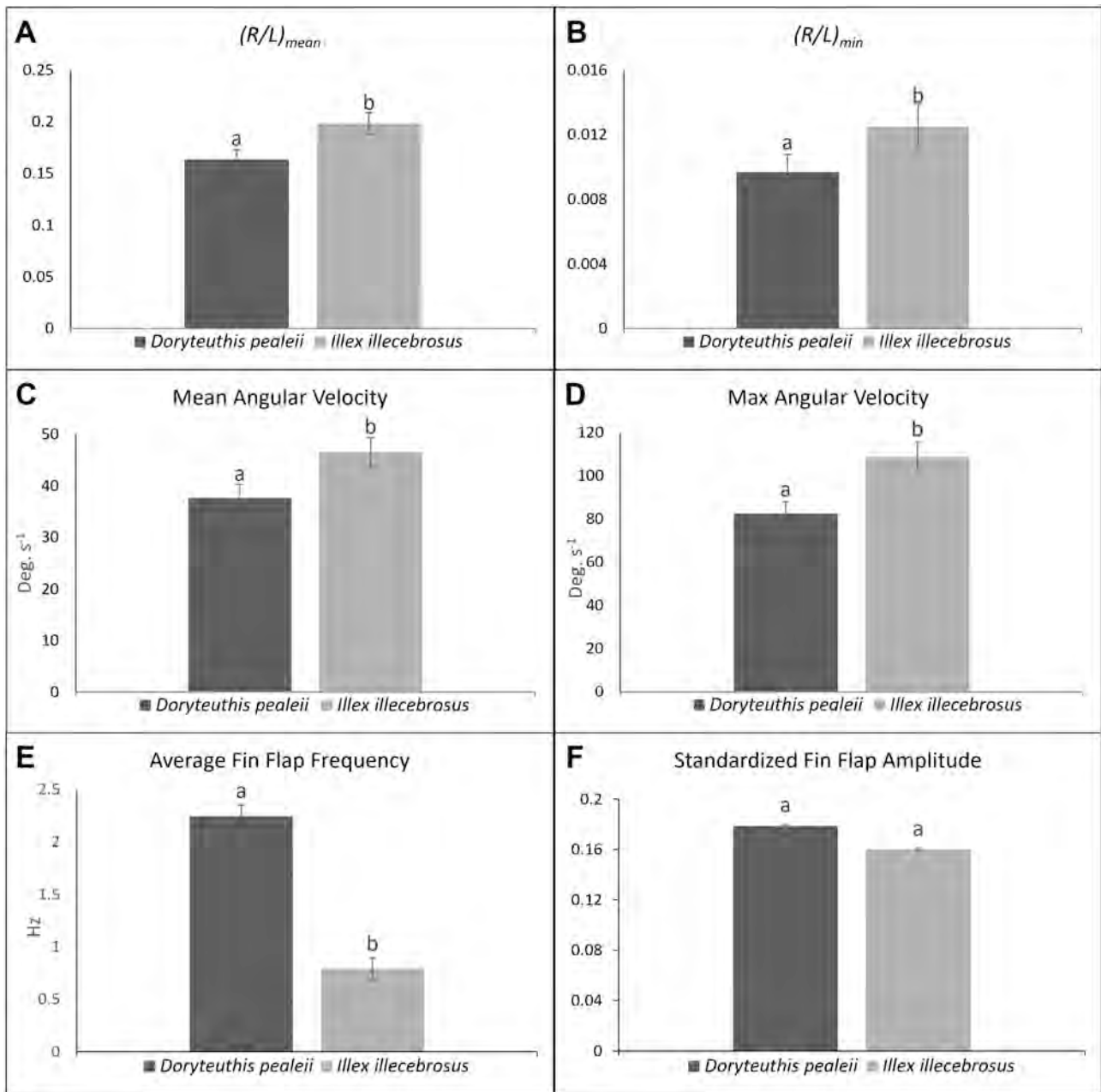


Fig. 5. Kinematic measures for *Doryteuthis pealeii* and *Illex illecebrosus*. (A) Average length-specific turning radius  $(R/L)_{mean}$ , (B) minimum length-specific turning radius  $(R/L)_{min}$ , (C) average angular velocity ( $\omega_{mean}$ ), (D) maximum angular velocity ( $\omega_{max}$ ), (E) average fin flap frequency of both fins ( $F_{ave}$ ), and (F) standardized fin flap amplitude ( $A_{fin}$ ) for *D. pealeii* and *I. illecebrosus*. Different letters denote significant differences; error bars shown are standard error of the mean.

*I. illecebrosus* curled their arms to a greater degree during arms-first turning ( $\theta_{arms} = 29.36 \pm 4.09$  deg) than during tail-first turning ( $\theta_{arms} = 11.93 \pm 1.93$  deg). However, *D. pealeii* did not exhibit a difference between swimming directions (arms-first  $\theta_{arms} = 17.31 \pm 3.18$  deg., tail-first  $\theta_{arms} = 17.00 \pm 2.78$  deg).

### 3.2. Swimming direction comparison

Arms-first turns had significantly lower  $(R/L)_{mean}$  than tail-first turns, and a trend towards lower  $(R/L)_{min}$  (Fig. 6A,B). For arms-first turns,  $(R/L)_{mean}$  was  $0.162 \pm 0.008$  and  $(R/L)_{min}$  was  $9.81 \times 10^{-3} \pm 8.80 \times 10^{-4}$ . For tail-first turns,  $(R/L)_{mean}$  was  $0.194 \pm 0.012$  and  $(R/L)_{min}$  was  $1.19 \times 10^{-2} \pm 1.48 \times 10^{-3}$ . Arms-first turns had an average  $\omega_{mean}$  of  $41.90 \pm 2.81$  deg.  $s^{-1}$ , and  $\omega_{max}$  was  $87.39 \pm 4.92$  deg.  $s^{-1}$ , with a range of 21.91–196.27 deg.  $s^{-1}$ .  $\omega_{mean}$  for tail-first turns was  $40.90 \pm 2.78$  deg.  $s^{-1}$ , and  $\omega_{max}$  was  $99.58 \pm 7.16$  deg.  $s^{-1}$ , with a range from 15.01 to 269.23 deg.  $s^{-1}$ . No significant difference in  $\omega_{mean}$  or  $\omega_{max}$  between the turning swimming directions was detected (Fig. 6C,D).

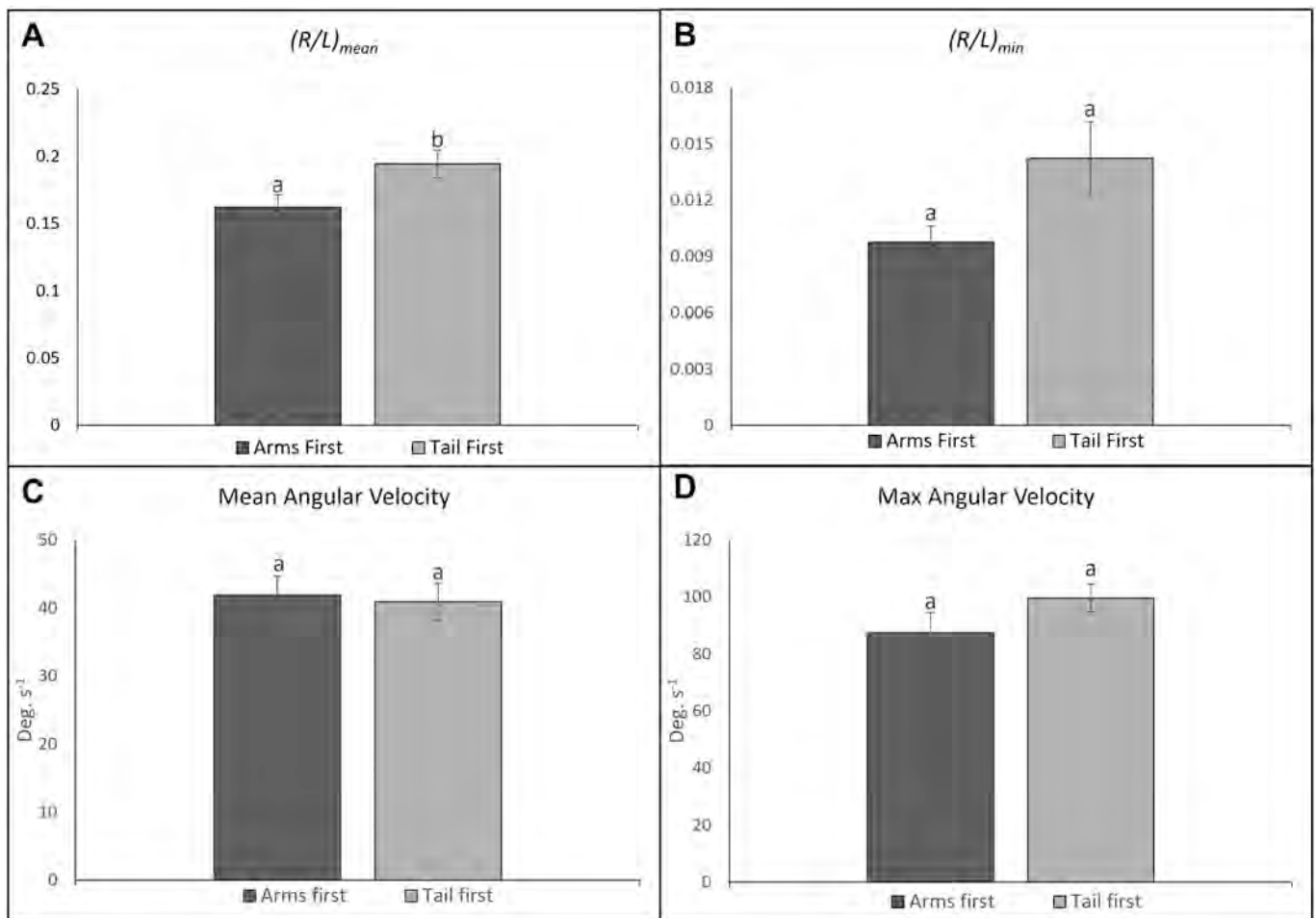
There was no significant difference in fin frequencies or amplitude between swimming directions, as well as no statistical difference in  $F_{mantle}$ . Squids turning arms-first had a  $A_{fin} = 0.172 \pm 0.006$  (range = 0.072–0.313),  $F_{ave} = 1.63 \pm 0.14$  Hz (range = 0–4.375 Hz), and  $F_{mantle} = 1.79 \pm 0.102$  Hz (range = 0.714–5 Hz). Squids turning tail-first had an  $A_{fin} = 0.170 \pm 0.007$  (range = 0.001–0.300),  $F_{ave} = 1.63 \pm 0.134$  Hz (range = 0–3.85 Hz), and  $F_{mantle} = 1.65 \pm 0.08$  Hz (range = 0.8–5 Hz).

### 3.3. Regressions

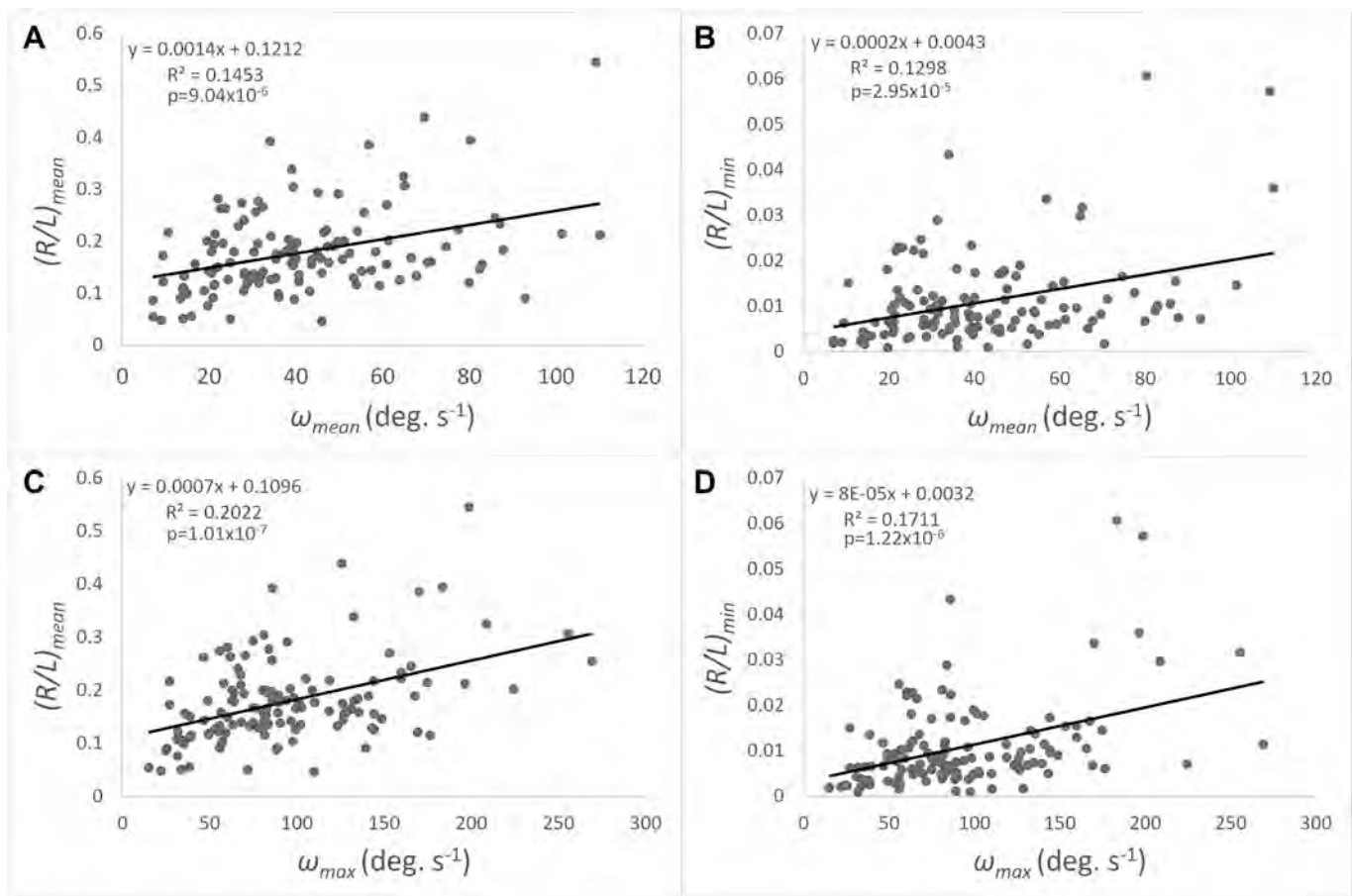
Linear regressions were computed using untransformed data. As average angular velocity increased, both average and minimum length-specific turning radius increased (Fig. 7A,B). Similarly, as maximum angular velocities increased, both average and minimum turning radius increased (Fig. 7C,D). As the frequency of fin beats increased, both average length-specific turning radius and maximum angular velocity decreased, although the regressions did not explain a high proportion of the variability given the low  $R^2$  values (Fig. 8A,B). As the frequency of fin beats increased, fin beat amplitude also increased, and as the average amplitude of fin beats increased, maximum turning velocity decreased (Fig. 8C,D). While *Doryteuthis pealeii* showed no such relationships (Fig. 9A,C), *Illex illecebrosus* showed a positive relationship between mantle contraction frequency and average angular velocity and a near significant positive trend between mantle contraction frequency and average length-specific turning radius (Fig. 9B,D).

### 4. Discussion

We found that *Illex illecebrosus* exhibited greater agility (faster turns) but less maneuverability (higher turning radii) than *Doryteuthis pealeii*. *Illex illecebrosus*' mean angular velocity was 20% greater than that recorded for *D. pealeii*, but *D. pealeii* achieved significantly lower  $(R/L)_{mean}$  and  $(R/L)_{min}$  (0.16 and 0.0097, respectively) than *I. illecebrosus* (0.20 and 0.012). These findings differ from Bartol et al. (2023), who did



**Fig. 6.** Analysis of kinematic measures by swimming direction. (A) Average length-specific turning radius  $(R/L)_{mean}$ , (B) minimum length-specific turning radius  $(R/L)_{min}$ , (C) average angular velocity  $(\omega_{mean})$ , and (D) maximum angular velocity  $(\omega_{max})$  for arms-first turns and tail-first turns. Different letters denote significant differences; error bars shown are standard error of the mean.

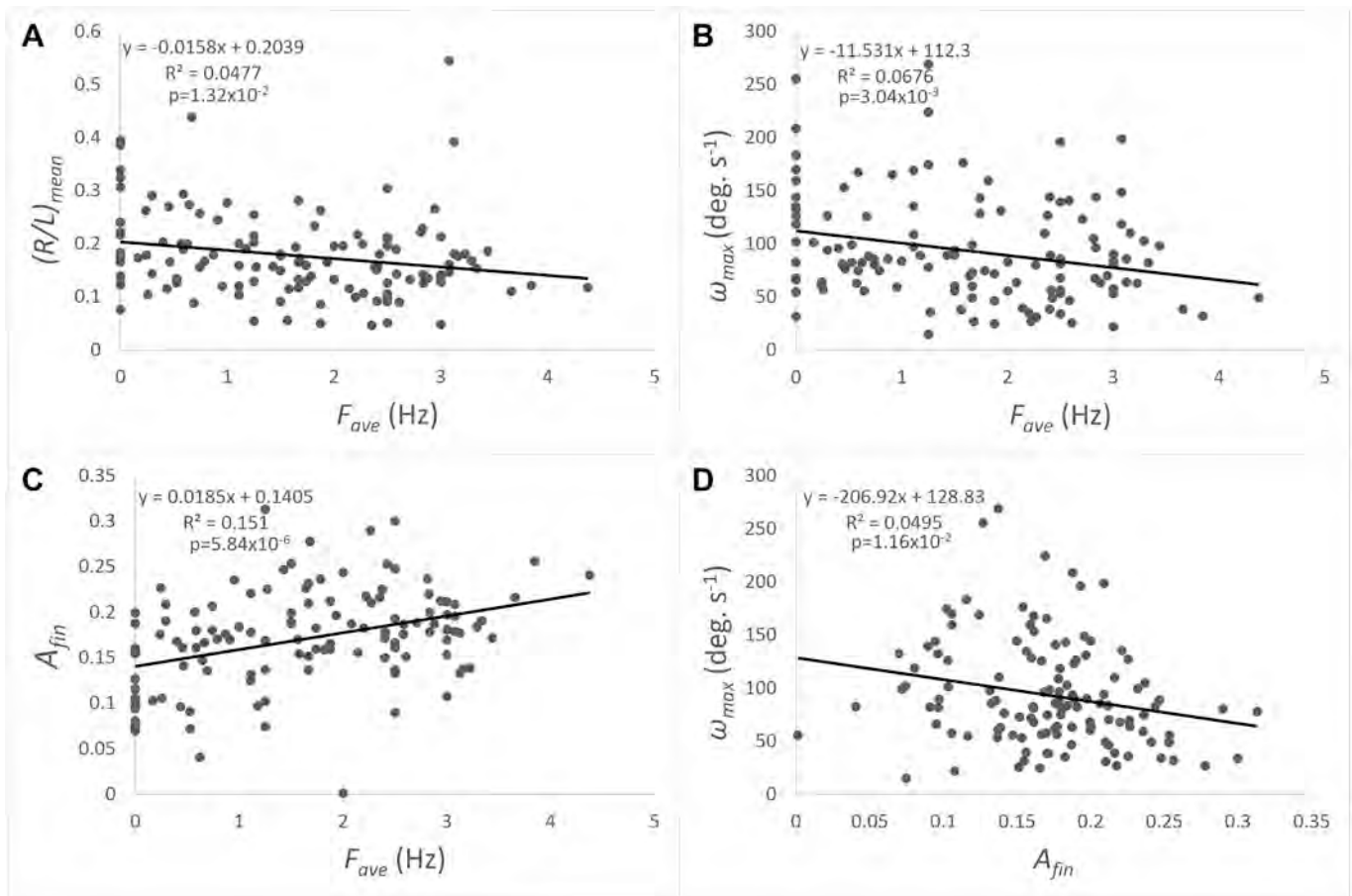


**Fig. 7.** Linear regressions of kinematic measures of turning for *Doryteuthis pealeii* and *Illex illecebrosus*. (A) Average angular velocity ( $\omega_{mean}$ ) and average length-specific turning radius  $[(R/L)_{mean}]$ , (B) average angular velocity ( $\omega_{mean}$ ) and minimum length-specific turning radius  $[(R/L)_{min}]$ , (C) maximum angular velocity ( $\omega_{max}$ ) and average length-specific turning radius  $[(R/L)_{mean}]$ , and (D) maximum angular velocity ( $\omega_{max}$ ) and minimum length-specific turning radius  $[(R/L)_{min}]$ . Regression equations, significance levels, and coefficients of determination are displayed in the top left of plots.

not find statistical differences in angular velocity and turning radius between these species. However, one reason for this apparent discrepancy is that all turning sequences in Bartol et al. (2023) required accompanying laser-based 3D velocimetry data, which restricted the range and length of turns to those with prominent linkable flow elements within the sampling volume. Conversely, in the present study, no such restrictions were present; any turn meeting the three criteria mentioned earlier could be considered. The observed differences in agility and maneuverability in the present study may be due to disparities in how the arms, fins, and jet are used in the two species. While not significant, there was a strong trend suggesting that *I. illecebrosus* curled its arms more when turning arms-first than tail-first, but *D. pealeii* showed no difference in arm angle between swimming directions. The high level of arm bending ( $\sim 30$  deg. relative to mantle) by *I. illecebrosus* reduced the moment of inertia by bringing mass closer to the center of rotation (like ice skaters pulling arms in close to their bodies to spin faster), resulting in higher angular velocities. *Illex illecebrosus* also flapped its fins less often and with smaller amplitude than *D. pealeii*. In fact, *I. illecebrosus* rarely extended its fins beyond the height of the mantle (when viewed laterally), while *D. pealeii* extended its fins more significantly, nearly touching them together above and below the body. The increased use of fins during turning presumably aided *D. pealeii* in performing more controlled tighter turns than *I. illecebrosus*, as fin flows have been shown to contribute angular impulse along yaw, pitch, and roll axes (Bartol et al., 2022). In addition to greater fin activity to aid tight turning, fins that extend farther along the mantle, like those in *D. pealeii*, may allow for more control of turning (i.e., lower turning

radii) due to greater interaction with the fluid medium (more surface area) and more complex fin movements, such as multiple undulatory waves that are difficult to produce with a shorter fin (Jereb and Roper, 2005; Jereb and Roper, 2010; Roper et al., 1984). Indeed, we observed more undulatory fin movements in *D. pealeii* than *I. illecebrosus* during maneuvers. Reduced fin use requires greater reliance on the powerful jet, which should contribute to elevated angular velocities (Bartol et al., 2022). This hypothesis is supported by the observed positive relationship between mantle contraction frequency and average angular velocity for *I. illecebrosus* but not *D. pealeii*. Thus, in addition to increased arm curling, *I. illecebrosus*' heavy reliance on its jet likely contributed to its higher angular velocities.

We also found a positive relationship between  $R/L$  and  $\omega$ , a pattern seen in other taxa (Fish and Nicasastro, 2003; Walker, 2000). This relationship underscores the tradeoff between tight and fast turning: as turn speed increases, the ability to complete tighter turns is compromised because inertia increases. Turns of high angular velocity are often driven by long, powerful jet pulses (Bartol et al., 2022), and we observed greater  $R/L$  with higher jet frequency in *I. illecebrosus*. In contrast, we found that greater fin use (i.e., increased fin flap frequency and amplitude) tended to be more strongly related to slower and tighter turns. Due to muscle force limitations, fin use during rectilinear swimming generally decreases with speed, with the fins often curling along the body (O'Dor, 1988; Anderson and Grosenbaugh, 2005; Bartol et al., 2001a; Bartol et al., 2018; Stewart et al., 2010). However, during tight turning, where speed is of lower priority and fin power constraints are less problematic, fin use plays an important role both in effecting the turn



**Fig. 8.** Linear regression analysis of fin movements and various kinematic measures for *Illex illecebrosus* and *Doryteuthis pealeii*. Mean frequency of fin flaps ( $F_{ave}$ ) during turns and how it relates to (A) average length-specific turning radius [ $(R/L)_{mean}$ ], (B) maximum angular velocity during turning ( $\omega_{max}$ ), and (C) standardized fin flap amplitude ( $A_{fin}$ ). (D) The relationship between standardized fin flap amplitude ( $A_{fin}$ ) and maximum angular velocity ( $\omega_{max}$ ). Regression equations, significance levels, and coefficients of determination are displayed in the top left of plots.

and producing lift to counteract negative buoyancy (both *D. pealeii* and *I. illecebrosus* are negatively buoyant). Based on the results of this study, greater fin use facilitated slower but tighter (lower  $R/L$ ) turns and greater jet frequency aided faster (higher  $\omega$ ; in *I. illecebrosus*) but broader turns, highlighting the tradeoffs between  $R/L$  and  $\omega$ .

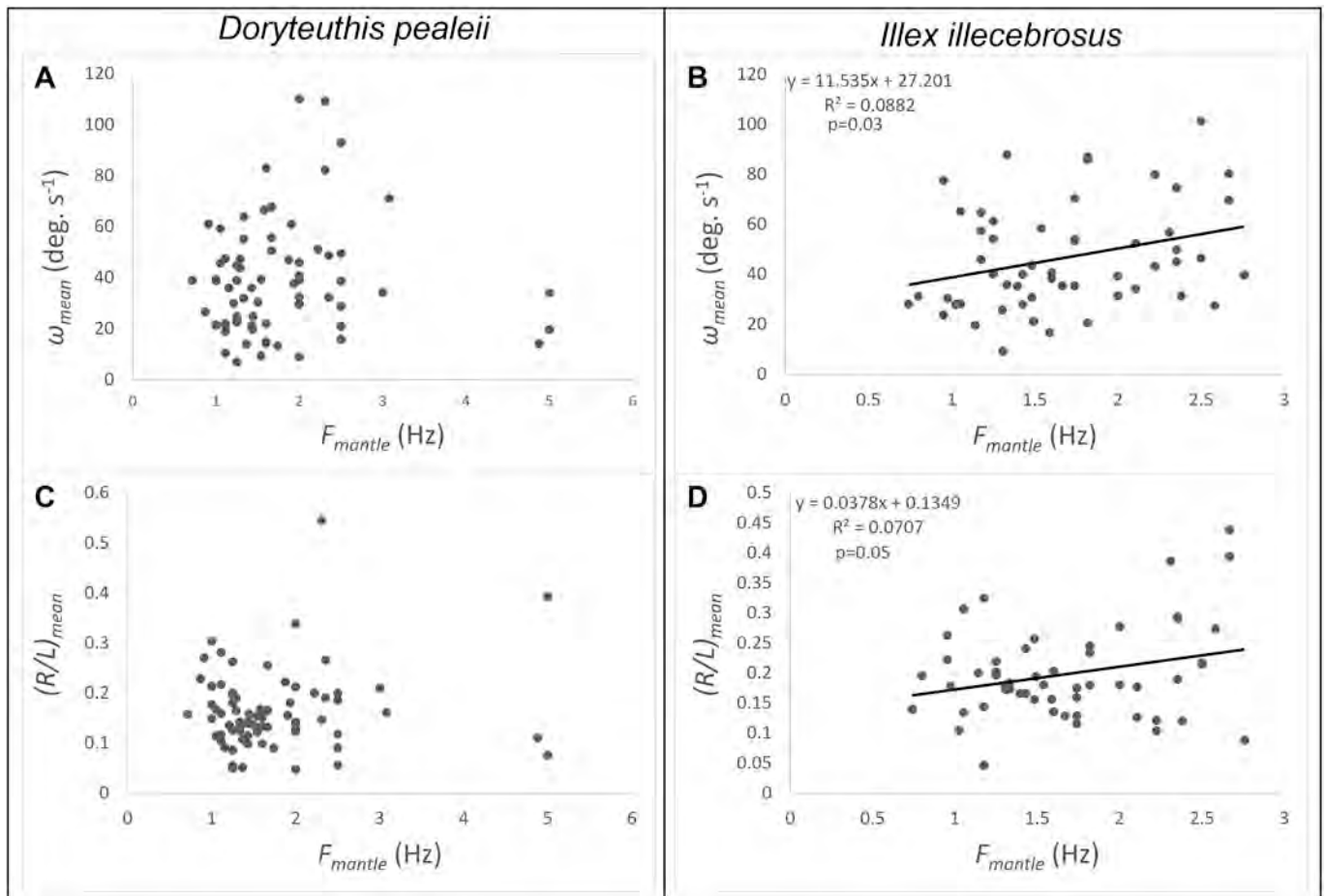
For both species, swimming direction had a significant effect on kinematic measures of turning. Arms-first turns were tighter and showed a trend towards lower maximum angular velocities. Bending of the funnel is a potential limiting factor for arms-first turning, as it requires greater shortening of radial muscles to prevent kinking/funnel constriction and ventral longitudinal muscles to maintain curvature (Bartol et al., 2016; Kier and Thompson, 2003). These muscle requirements can impart force restrictions on jet production, resulting in diminished angular velocities. Although muscle requirements associated with bending presumably limited angular velocity, they did not appear to reduce maneuverability given that tighter turns [lower  $(R/L)_{mean}$  and  $(R/L)_{min}$ ] were observed in the arms-first vs the tail-first swimming direction.

The arms-first swimming direction may confer advantages for tight turning, including improved visual perception, as the eyes are closer to the leading edge of the turn than during tail-first turning; improved steering, as forwardly positioned arms can bend in the direction of the turn; and better turn authority as posteriorly located fins can function as rudders. In addition, flow quantification has shown that inshore squids, such as *Lolliguncula brevis*, consistently produce shorter vortex ring flows in the arms-first mode relative to the tail-first mode (Bartol et al., 2022; Bartol et al., 2016). These short vortex rings provide more controlled impulse than longer jets, allowing for shorter turning radii.

From an ecological perspective, tight arms-first turns and fast tail-first turns follow expectations. During prey capture where the squids must orient arms-first to see and capture their target, minute corrections in heading are required to intercept fast moving prey. Therefore, the ability to turn tightly is advantageous for prey interactions, as noted by Jastrebsky et al. (2017), who measured the kinematics of turns by squids that were associated with the capture of shrimp and fish. Tight turns are also important for navigating complex habitats and mating. Often during mating, squids must orient arms-first to allow male squids to deposit a spermatophore into or onto the female (Arnold, 1962; Hanlon et al., 1983; Hanlon and Messenger, 1996). This complex behavior requires arms-first swimming from both individuals, as well as precise body positioning. Conversely, escaping from predators and swimming in a group are behaviors that require fast tail-first turning. High speeds and quick changes in direction are useful strategies for avoiding a predator. In addition, *D. pealeii* and *I. illecebrosus* often form schools and shoals (Hanlon et al., 2018). To maintain position in these collective groups, squids must make quick angular adjustments often at high speeds while swimming predominantly in the tail-first swimming direction.

In comparison to other jet-propelled swimmers, both *I. illecebrosus* and *D. pealeii* demonstrate intermediate  $R/L$  values (Table 2). The lower  $R/L$  values in Jastrebsky et al. (2017) may be a product of squid being enticed to turn with prey items, resulting in more extreme turns, while the turns in our study were spontaneous and perhaps more reflective of routine movements during non-feeding behavior. Although  $(R/L)_{mean}$  for the squids in our study were similar to the common siphonophore, *N. bijuga*, our  $(R/L)_{min}$  was lower (Sutherland et al., 2019a, 2019b). This





**Fig. 9.** Linear regressions of mantle contraction frequency for *Doryteuthis pealeii* (A,C) and *Illex illecebrosus* (B,D). For *D. pealeii*, relationships between mean angular velocity ( $\omega_{mean}$ ) and mantle contraction frequency ( $F_{mantle}$ ) (A) and average length-specific turning radius [ $(R/L)_{mean}$ ] and mantle contraction frequency ( $F_{mantle}$ ) (C) were not significant. For *I. illecebrosus*, both average angular velocity ( $\omega_{mean}$ ) (B) and normalized mean radius of turns [ $(R/L)_{mean}$ ] (D) had significant relationships with mantle contraction frequency ( $F_{mantle}$ ). Regression equations, significance levels, and coefficients of determination are displayed in the top left of plots.

**Table 2**

Kinematic measurements from jet-propelled swimmers. Asterisks refer to measurements that were calculated from data provided in paper.

Species	$R/L_{mean}$	$R/L_{min}$	$\omega_{mean}$ (deg. s <sup>-1</sup> )	$\omega_{max}$ (deg. s <sup>-1</sup> )	Study
<i>Aurelia aurita</i> *	–	–	–	~400	Dabiri et al., 2020
<i>Doryteuthis pealeii</i>	0.16	0.0097	37.66	82.36	present study
<i>Illex illecebrosus</i>	0.20	0.012	46.52	108.73	present study
<i>Illex illecebrosus</i>	–	0.5	90	–	Foyle and O’Dor, 1988
<i>Lolliguncula brevis</i>	0.009	0.003	110.3	268.4	Jastrebsky et al., 2016
<i>Nanomia bijuga</i>	0.15	0.05	104	215	Sutherland et al., 2019b
<i>Sepia bandensis</i>	0.095	0.0012	54.8	160.2	Jastrebsky et al., 2016
<i>Sepia officinalis</i> *	–	–	~115	–	Messenger, 1968

finding together with the lower  $(R/L)_{min}$  reported for *S. bandensis* and *L. brevis* in prior studies suggest that cephalopods have the capacity to turn very tightly. The two squids considered in our study turned more slowly than other jet-propelled animals measured to date. This is likely a product of their larger size. For our study, *D. pealeii* and *I. illecebrosus* averaged approximately 16–17 cm in TL, whereas *L. brevis* and *S. bandensis* averaged ~9 cm and ~6 cm in TL, respectively (Jastrebsky et al., 2016). The common siphonophore, *Nanomia bijuga*, averaged ~1.6 cm in colony length (Sutherland et al., 2019a, 2019b), and the moon jelly, *Aurelia aurita*, ranged from 1.8 to 5.4 cm in bell diameter (Dabiri et al., 2020). Smaller animals generally have lower moments of inertia than larger animals because their mass is distributed closer to the axis of rotation, allowing them to achieve higher angular velocities, a trend seen both within and between many other taxa (Fish et al., 2018;

Fish and Holzman, 2019).

Compared to non-jetters, *I. illecebrosus* and *D. pealeii* are highly maneuverable. Relatively rigid yellowfin tuna (*Thunnus albacares*) have  $(R/L)_{mean} \sim 0.47$ , while the flexible California sea lion (*Zalophus californianus*) turns with an  $(R/L)_{min} \sim 0.13$  (Blake et al., 1995; Fish et al., 2003). Bottlenose dolphins (*Tursiops truncatus*), angelfish (*Pterophyllum eimekei*), and painted turtle (*Chrysemys picta*) all have  $(R/L)_{mean}$  more than double that of *I. illecebrosus* and *D. pealeii* (Blake et al., 1995; Maresh et al., 2004; Rivera et al., 2006). Conversely, only the leopard shark (*Triakis semifasciata*) and spotted boxfish (*Ostracion melegrisi*) have mean turning radii smaller than the squids examined in this paper (Porter et al., 2011; Walker, 2000). Therefore, the combination of a highly vectorable jet and muscular hydrostatic fins likely facilitates tight turning. Both *D. pealeii* and *I. illecebrosus* demonstrate an intermediate

level of agility, turning faster than some fish and most rays. However, other fish and marine mammals can execute turns with nearly double the angular velocity (Domenici and Blake, 1991; Fish et al., 2018; Mayerl et al., 2019; Parson et al., 2011; Rivera et al., 2006). These higher values likely reflect differences in body flexibility, whereby squids have hybrid architectures with rigid (mantle with gladius) and flexible (fins and arms) components while the higher performing fishes and marine mammals have more flexible axial elements to facilitate elevated turning rates (Fish et al., 2018).

#### 4.1. Concluding thoughts

This study represents the first comparative kinematic-focused turning study of two inshore squids, the shortfin squid, *Illex illecebrosus*, and longfin squid, *Doryteuthis pealeii*. We found that *D. pealeii* turned more tightly but more slowly than *I. illecebrosus*. High fin use likely contributed to *D. pealeii*'s lower length-specific turning radii, while greater arm curvature, particularly in the arms-first mode, and greater reliance on the powerful jet probably were major factors in *I. illecebrosus*' higher angular velocities. Turning swimming direction (i. e., arms-first or tail-first) played a role in maneuverability and agility, with arms-first turns having significantly lower length-specific radii and tail-first turns exhibiting a trend in higher maximum angular velocity. Tighter turns in the arms-first mode are advantageous for tracking prey and navigating complex habitats, while faster turns in the tail-first mode are useful for escape responses and quick adjustments in schools and shoals. While *I. illecebrosus* and *D. pealeii* have moderate angular velocities, their length-specific turning radii minima are lower than other non-cephalopod swimmers.

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#### CRediT authorship contribution statement

**Alissa M. Ganley:** Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Paul S. Krueger:** Conceptualization, Methodology, Software, Validation, Investigation, Resources, Writing – review & editing, Supervision. **Ian K. Bartol:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

#### Declaration of Competing Interest

No competing interests declared.

#### Data availability

Data used in this study may be requested by contacting the corresponding author.

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## List of Symbols

- $\omega_{mean}$ : average angular velocity of turn (deg. s<sup>-1</sup>)  
 $\omega_{max}$ : maximum angular velocity achieved during turn (deg. s<sup>-1</sup>)  
 $L$ : total length of squid, (cm)  
 $R_{mean}$ : average radius of turn (cm)  
 $R_{min}$ : minimum radius achieved during turn (cm)  
 $(R/L)_{mean}$ : average radius of a turn standardized by total length of squid (dimensionless)  
 $(R/L)_{min}$ : minimum radius achieved during turn standardized by total length of squid (dimensionless)  
 $\theta_{total}$ : total angular displacement of the turn (deg.)  
 $\theta_{arms}$ : degree of arm curling (deg.)  
COR: center of rotation  
 $TL$ : total length of squid (cm)  
 $DML$ : dorsal mantle length of squid (cm)  
 $F_{in}$ : frequency of fin beats for inside fin (Hz)  
 $F_{mantle}$ : frequency of mantle contractions (Hz)  
 $F_{out}$ : frequency of fin beats for outside fin (Hz)  
 $F_{ave}$ : average frequency of fin beats between both fins (Hz)  
 $A_{fin}$ : maximum range of amplitude of fin beats standardized by animal length (dimensionless)