

Swimming performance studies on the eastern Pacific bonito *Sarda chiliensis*, a close relative of the tunas (family Scombridae)

II. Kinematics

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Summary

The swimming kinematics of the eastern Pacific bonito *Sarda chiliensis* at a range of sustained speeds were analyzed to test the hypothesis that the bonito's swimming mode differs from the thunniform locomotor mode of tunas. Eight bonito (fork length FL 47.5 ± 2.1 cm, mass 1.25 ± 0.15 kg) (mean \pm s.d.) swam at speeds of 50 – 130 cm s^{-1} at $18 \pm 2^\circ\text{C}$ in the same temperature-controlled water tunnel that was used in previous studies of tunas. Kinematics variables, quantified from 60 Hz video recordings and analyzed using a computerized, two-dimensional motion analysis system, were compared with published data for similar sized tunas at comparable speeds. Bonito tailbeat frequency, tailbeat amplitude and stride length all increased significantly with speed. Neither yaw ($6.0 \pm 0.6\%$ FL) nor propulsive wavelength ($120 \pm 65\%$ fish total length) varied with speed, and there were no mass or body-length effects on the kinematics variables for the size range of bonitos used. Relative to similar sized yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas at similar speeds, the bonito has a lower tailbeat frequency, a higher yaw and a greater stride

length. The lateral displacement and bending angle of each intervertebral joint during a complete tailbeat cycle were determined for the bonito at a swimming speed of 90 cm s^{-1} . The pattern of mean maximum lateral displacement (z_{max}) and mean maximum bending angle (β_{max}) along the body in the bonito differed from that of both chub mackerel *Scomber japonicus* and kawakawa tuna *Euthynnus affinis*; z_{max} was highest in the bonito. This study verifies that *S. chiliensis* is a carangiform swimmer and supports the hypothesis that the thunniform locomotor mode is a derived tuna characteristic associated with changes in this group's myotomal architecture. The finding that yaw and z_{max} were greater in the bonito than in both mackerels and tunas suggests that swimming kinematics in the bonito is not intermediate between that of tunas and mackerels, as would be predicted on the basis of morphological characteristics.

Key words: locomotion, swimming, kinematics, Scombridae, eastern Pacific bonito, *Sarda chiliensis*, thunniform, carangiform, tuna.

Introduction

Tunas (family Scombridae, tribe Thunnini) are the only teleost fishes known to conserve metabolically derived heat to maintain the temperature of the slow-twitch myotomal locomotor muscle (red muscle, RM) elevated above ambient water temperature (Carey et al., 1971; Graham, 1973; Block, 1991). In addition, tuna RM is in a more anterior and medial position (closer to the vertebral column) than it is in other teleosts (Kishinouye, 1923; Graham et al., 1983; Ellerby et al., 2000; Graham and Dickson, 2000). Because this will reduce conductive heat loss from the RM across the body surface, the 'internalization' of RM was hypothesized to have been a precursor to the evolution of regional endothermy in the tunas (Block et al., 1993; Block and Finnerty, 1994; Westneat and Wainwright, 2001).

Swimming in tunas has been classified as thunniform locomotion, characterized by minimal lateral undulation of most of the body and thrust generation by rapid oscillations of the high-aspect-ratio caudal fin (Fierstine and Walters, 1968; Lighthill, 1970; Webb, 1975; Lindsey, 1978). Many morphological specializations of tunas are associated with thunniform swimming. These include the anterior–medial RM, streamlined body shape, elongated myotomes, RM–tendon–skeleton connections, and narrow-necking of the caudal peduncle (Fierstine and Walters, 1968; Lighthill, 1969, 1970; Webb, 1975; Magnuson, 1978; Ellerby et al., 2000; Graham and Dickson, 2000; Westneat and Wainwright, 2001). It has been proposed that the RM position in tunas evolved to enhance swimming performance by affecting the mechanical

transfer of muscle contractile force to the backbone and caudal propeller (Westneat et al., 1993; Ellerby et al., 2000; Graham and Dickson, 2000). The transition to thunniform locomotion was hypothesized to have occurred prior to the evolution of endothermy, in response to changing oceanographic conditions (Graham and Dickson, 2000).

Testing and distinguishing among these hypotheses requires knowledge of the tunas' sister groups and mapping morphological characteristics onto a scombrid phylogeny (Block and Finnerty, 1994; Graham and Dickson, 2000). The Scombridae is composed of a monotypic subgroup (the butterfly mackerel *Gasterochisma melampus*) and four tribes: Scombrini (mackerels), Scomberomorini (Spanish mackerels), Sardini (bonitos) and Thunnini (tunas) (Collette, 1978; Collette et al., 2001). According to phylogenies based on both morphological and gene-sequence data, the 15 species of tunas form a derived, monophyletic clade, and their closest relatives are the bonitos (Collette, 1978; Block et al., 1993; Finnerty and Block, 1995; Carpenter et al., 1995; Graham and Dickson, 2000; Collette et al., 2001). Because of this sister-taxon relationship, examination of the bonitos is essential for determining the sequence of character state changes that led to the specializations of the tunas. This study quantifies swimming kinematics in the eastern Pacific bonito *Sarda chiliensis* so that the trait of thunniform locomotion can be mapped precisely onto the scombrid phylogeny.

Studies of scombrid swimming kinematics have focused primarily on mackerels and tunas (Gray, 1933; Fierstine and Walters, 1968; Magnuson, 1970; Videler and Hess, 1984; Dewar and Graham, 1994b; Shadwick et al., 1998; Knower et al., 1999; Gibb et al., 1999; Donley and Dickson, 2000; Nauen and Lauder, 2000; Dickson et al., 2002). Donley and Dickson (2000) distinguished the kinematics of juvenile chub mackerel *Scomber japonicus* and kawakawa tuna *Euthynnus affinis*, and emphasized the importance of comparing similar-sized fish at comparable speeds. They found that, at the same speeds, the tuna swam with higher tailbeat frequencies, lower tailbeat amplitudes, lower stride lengths and less lateral displacement along most of the body, than did the chub mackerel.

Some kinematics data have been reported for bonitos, but comparisons with tunas and mackerels led to conflicting conclusions. The relationship between tailbeat frequency and speed for a 16 cm total length (*TL*) Atlantic bonito *Sarda sarda* derived from data in Pyatetskiy (1970) was similar to that of similar sized (14.8 and 16.7 cm *TL*) chub mackerel, but lower than that of a 16.2 cm *TL* kawakawa tuna (Donley, 1999; Donley and Dickson, 2000). In contrast, Altringham and Block (1997) reported similar tailbeat frequencies in *S. chiliensis* and yellowfin tuna *Thunnus albacares* swimming in a large, cylindrical tank, but swimming speed and fish size, which both affect tailbeat frequency, varied interspecifically. Block (personal observation, cited in Block and Finnerty, 1994) indicated that the Atlantic bonito swims in a more 'stiff-bodied' (tuna-like) fashion than mackerels do.

The most comprehensive study to date of bonito swimming (Ellerby et al., 2000) used sonomicrometry and

electromyography to measure RM strain and activity patterns, which have been correlated with swimming mode (Wardle et al., 1995; Altringham and Ellerby, 1999; Knower et al., 1999; Altringham and Shadwick, 2001), at several positions along the body in *S. chiliensis* (60–71 cm fork length, *FL*). Muscle activity patterns in the bonito were found to be more similar to those of tunas than to those of mackerels. On the other hand, based on the extent of maximum lateral displacement of five points along the dorsal midline measured from videotapes of bonito swimming steadily in a large, open tank, Ellerby et al. (2000) concluded that the bonito swims in the carangiform mode like the mackerel. They found lateral displacement of the bonito to be similar to that of the Atlantic mackerel (*Scomber scombrus*, 30–34 cm *TL*) from Videler and Hess (1984) and greater than that of a 44 cm *FL* yellowfin tuna derived from Dewar and Graham (1994b).

From the existing data, it is not possible to determine unequivocally if the swimming mode of bonitos is more similar to that of mackerels or tunas, or if it is intermediate between the two. Therefore, thunniform locomotion cannot be mapped onto the scombrid phylogeny at a specific position to determine if that trait evolved before or after the divergence of the tunas and bonitos. Furthermore, because most kinematic variables vary with swimming speed or fish size, it is important that interspecific comparisons are made at the same speeds in similar sized individuals. Thus, the objective of the present study was to quantify the swimming kinematics of the eastern Pacific bonito at a range of controlled speeds, and then to compare the bonito to tunas of similar size that have been swum at similar speeds in the same respirometer (Dewar and Graham, 1994b; Knower, 1998; Knower et al., 1999) and to intervertebral lateral displacement and bending angle data for chub mackerel and kawakawa tuna (Donley and Dickson, 2000).

Materials and methods

Swimming kinematics

This study utilized the same bonito *Sarda chiliensis* Cuvier as in the companion energetics study (Sepulveda et al., 2003), which describes the procedures for fish collection, handling and metabolic measurements in a large, temperature-controlled, swimming tunnel respirometer. After oxygen consumption rates were measured at a series of swimming speeds (experiments lasting up to 16 h), the fish was allowed to swim steadily at a low speed for at least 15 min before video analysis was initiated. The dorsal view of the fish was then videotaped at 60 Hz, using a JVC super VHS camcorder (model GR-SXM520; Fry's Electronics, Anaheim, CA, USA) mounted directly over the respirometer working section, for 2–15 min at each speed, from 50 cm s⁻¹ to 130 cm s⁻¹ in increments of 10 cm s⁻¹. All fish did not swim at all of the speeds. During videotaping, respirometer water temperature was maintained at 18±2°C, the temperature at which the bonitos were acclimated in the laboratory prior to experimentation.

A Motus 3.2 motion analysis system (Peak Performance Technologies, Inc., Englewood, CO, USA) was used to analyze videotaped segments that met the following criteria: (i) the fish was positioned in the middle of the chamber, away from the walls and bottom, (ii) the fish was swimming steadily through at least seven complete tailbeat cycles, and did not move forward or backward in the chamber, and (iii) both the head and tail of the fish were in the field of view. Two points, the tip of the upper lobe of the tail and the tip of the snout, were followed through time by digitizing sequential video frames for 7–14 complete tail beats at each swimming speed. Using the measured total length of the fish, a scaling factor was calculated for each video segment so that pixels could be converted to centimeters.

Using methods described in Donley and Dickson (2000), kinematic variables were quantified for each bonito at each test speed. Tailbeat frequency (in Hz) was calculated by following the tip of the tail through time and dividing the number of consecutive tail beats by the amount of time, in seconds, that it took to complete those tail beats. Tailbeat amplitude (cm) and yaw (cm) were determined by measuring the distance between the lateral-most positions of the tip of the tail and of the tip of the snout, respectively, during a complete tailbeat cycle (the excursion of the tail from one side of the body to the other and back again). Mean tailbeat amplitude and yaw values were computed at each speed for each fish. Stride length, the distance (cm) that the fish moves forward in each tailbeat cycle, was calculated by dividing swimming speed by tailbeat frequency. Relative values (as %*FL*) of tailbeat amplitude, yaw and stride length were also determined. The propulsive wavelength (the length of the wave of undulation that travels down the body of the fish from snout to tail tip during swimming) was obtained by dividing propulsive wave velocity by the corresponding tailbeat frequency. Propulsive wave velocity was determined from the amount of time (s) between the peaks in lateral displacement at the tip of the snout and the tip of the tail; then the *TL* (cm) of each individual (the distance between the two points) was divided by the mean progression time in order to obtain the propulsive wave velocity in cm s^{-1} at each speed. Propulsive wavelength was measured in both cm and as a percentage of *TL* (%*TL*). Based on the known size of the field of view that was videotaped and the resolution of 400 horizontal lines for super VHS, the spatial resolution of the measurements was 0.125–0.183 cm, which is equivalent to ranges of 0.25–0.41%*FL* and 0.23–0.38%*TL*. Depending on tailbeat frequency, there were 18–40 video fields per tail beat.

The lateral displacement and bending angle of each intervertebral joint during the tailbeat cycle were determined using the techniques of Jayne and Lauder (1995) and Donley and Dickson (2000). With the Peak Performance Motus system, 32 points approximately equally spaced around the dorsal outline of each individual were digitized in consecutive frames for one complete tailbeat cycle at a swimming speed of 90 cm s^{-1} (relative speeds of 1.63–1.85 *TL s}^{-1}), a speed at which all bonito swam. The points were converted into*

complete curves using a cubic spline function, and a midline was calculated for each frame (Jayne and Lauder, 1995). Lateral view X-rays were taken of each individual, and the lengths of the skull, each vertebra, and the hypural plate were measured with digital calipers. Each midline was divided into segments representing the measured skeletal elements, and the position in each frame of each intervertebral joint and of the snout and tail tip were calculated. Using a Microsoft Excel macro written by Jayne and Lauder (1995), the lateral displacement (z , using the terminology of Jayne and Lauder, 1995) and angle of flexion (β) of each intervertebral joint throughout the tailbeat cycle were calculated. Then, maximum lateral displacement (z_{max}) and maximum bending angle (β_{max}) during the tail beat were determined for each joint along the body for each bonito. Mean z_{max} and β_{max} values for each intervertebral joint for the eight bonito studied were compared with data for all intervertebral joints in the chub mackerel and kawakawa tuna studied by Donley and Dickson (2000) at speeds of 75–100 cm s^{-1} . For these comparisons, the maximum lateral displacement of each joint, measured in cm, was converted to relative fish length (%*TL*), and the position along the body of each intervertebral joint was expressed as %*TL*. The z_{max} at 0%*TL* is one-half of yaw, and z_{max} at 100%*TL* is one-half of tailbeat amplitude, as defined above.

Statistical analysis

The bonito kinematic variables were assessed for significant effects of swimming speed (cm s^{-1}) and fish size (mass in g and length in cm) and for significant interactions between these factors. Minitab (version 13.1) was used to create the data file, calculate interaction terms and test for normality. SAS (version 8.2) was used to perform repeated-measures multiple regression analyses on tailbeat frequency (in Hz), tailbeat amplitude, yaw and stride length (in both cm and %*FL*), propulsive wavelength (in cm and %*TL*), and on z_{max} (in %*TL*) and β_{max} (in degrees). The initial statistical models for tailbeat frequency, tailbeat amplitude, yaw, stride length and propulsive wavelength included the main effects of speed, mass and *FL*, as well as all possible interaction terms. The models for z_{max} and β_{max} included mass, fish total length, position along the body, and all possible interactions, but did not include swimming speed because only one speed was used. For each variable, the full model was subjected to a backward stepwise reduction to fit the best model to the data; each non-significant term was dropped until a final model that included all significant terms was obtained.

We then determined if tailbeat frequency (in Hz), tailbeat amplitude, yaw and stride length (all expressed as %*FL*), and propulsive wavelength (in %*TL*) in the bonito differed significantly from published data for two species of tuna (*Thunnus albacares* and skipjack *Katsuwonus pelamis*). Because there was limited access to the raw data for the tunas, two-sample *t*-tests (Dixon and Massey, 1969) were used to detect significant interspecific differences in mean values or in the slopes and *y*-intercepts of linear regressions reported in the literature.

We tested for significant interspecific differences in mean maximum lateral displacement of the body midline and mean maximum flexion angles, at all intervertebral joints along the body, between the bonito and the chub mackerel and kawakawa tuna from Donley and Dickson (2000). Repeated-measures multiple regression analyses were run in SAS to determine if there were any significant effects of position along the body (%*TL*), species, or position \times species on z_{\max} and β_{\max} . The position term was squared in order to incorporate curvature into the equation for a more accurate model of the data, but the coefficients of the squared terms were not interpreted. Significant interspecific differences are indicated as significant terms in the final regression model, after a backward stepwise reduction process was completed. A significance level of $P=0.05$ was used in all statistical analyses.

Results

Swimming kinematics of the eastern Pacific bonito

A total of eight bonito were analyzed, $FL=47.5\pm 2.1$ cm, range 45.0–50.5 cm *FL*, mass 1.25 ± 0.15 kg (means \pm s.d.). When the effects of fish size were accounted for, tailbeat frequency increased significantly with speed ($P<0.0001$) in the bonito (Fig. 1). When the effects of speed were accounted for, there was no significant effect of fish length or mass on tailbeat frequency. The range of tailbeat frequencies was 1.5–3.2 Hz.

Tailbeat amplitude, yaw and stride length were assessed for size and speed effects using the absolute values in cm, as well as relative values (%*FL*). When the effects of fish size were accounted for, both tailbeat amplitude and stride length increased significantly with swimming speed (Figs 2 and 3), but yaw did not vary significantly with speed. When the effects of speed were accounted for, there were no significant effects of *FL* or mass on tailbeat amplitude, yaw or stride length. When these three kinematics variables were expressed as %*FL*, no significant size effects were detected. Tailbeat amplitude ranged from 16 to 24%*FL*, and the range of stride length was 62–91%*FL*. The yaw for the bonito ranged from 5.2 to 6.9%*FL* ($6.0\pm 0.6\% *FL*, mean \pm s.d.).$

Propulsive wavelength (in cm and in %*TL*) did not vary significantly with fish size or with swimming speed ($P=0.065$) in the bonito. Thus, a mean for each individual and a grand mean for all eight fish were calculated. The propulsive wavelength was 110–129%*TL* ($120\pm 6\% *TL*, mean \pm s.d.).$

Both mean maximum intervertebral lateral displacement (z_{\max}) and mean maximum intervertebral bending angles (β_{\max}) varied significantly with position along the body ($P<0.0001$) in the bonito (Figs 4 and 5). Minimum mean z_{\max} occurred at 30%*TL* (the joint between vertebrae 11 and 12) and maximum z_{\max} occurred at the tail tip. Minimum mean β_{\max} occurred at 18%*TL* (the joint between the first and second vertebrae) and maximum mean β_{\max} was at the joint between the last vertebra and the hypural plate (92%*TL*). There were no significant effects of fish mass or length on bonito z_{\max} or β_{\max} .

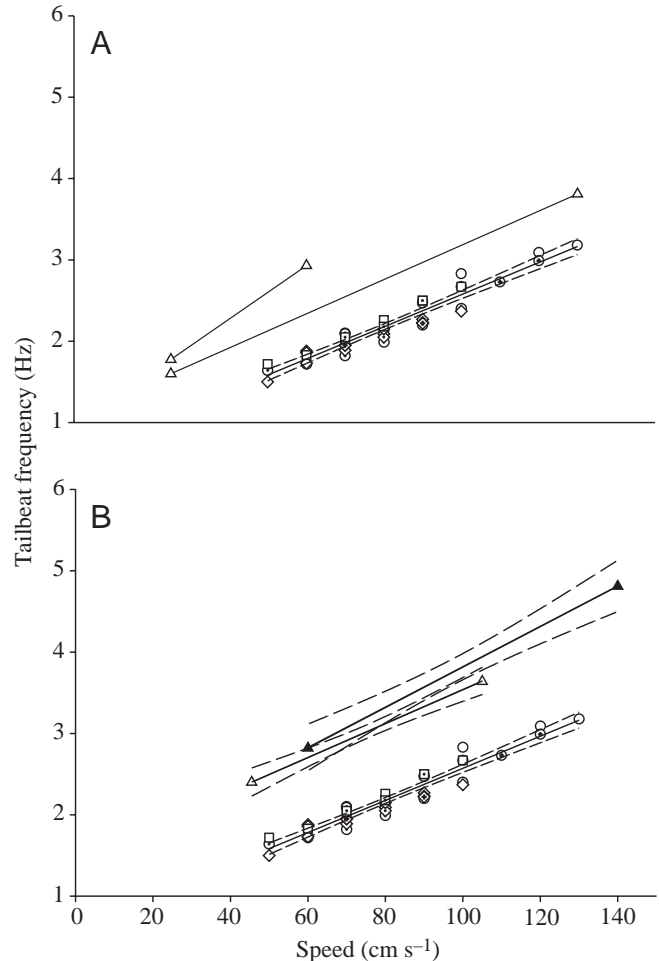


Fig. 1. Relationship between tailbeat frequency and swimming speed for *Sarda chiliensis* (each symbol denotes one individual) compared with (A) 42 cm and 53 cm yellowfin tuna *Thunnus albacares* (open triangles) (Dewar and Graham, 1994b) and (B) 40–44 cm yellowfin (open triangles) and 38–41 cm skipjack tuna *Katsuwonus pelamis* (solid triangles) (Knower et al., 1999). Best-fit regression equation (regression coefficients \pm s.d.) for the bonito data: tailbeat frequency = $0.017\pm 0.002 \times \text{speed} + 0.75\pm 0.15$ ($N=8$). Broken lines are 95% confidence intervals of the regressions.

Interspecific comparisons

Significant effects of fish size were not detected for any of the kinematics variables measured in the present study, most likely due to the small size range of the bonito studied. Therefore, interspecific comparisons were made using the mean values of yaw, propulsive wavelength, and z_{\max} and β_{\max} at different positions along the body, and the regressions of the other kinematics variables versus swimming speed for the bonito. In these comparisons, we have assumed that temperature differences among the studies compared (with reported temperatures ranging from 18°C to 28°C) do not contribute significantly to differences in tailbeat frequency, tailbeat amplitude, yaw and stride length. This assumption is based on a number of studies that have found little to no effect of temperature on these kinematics variables when fish are

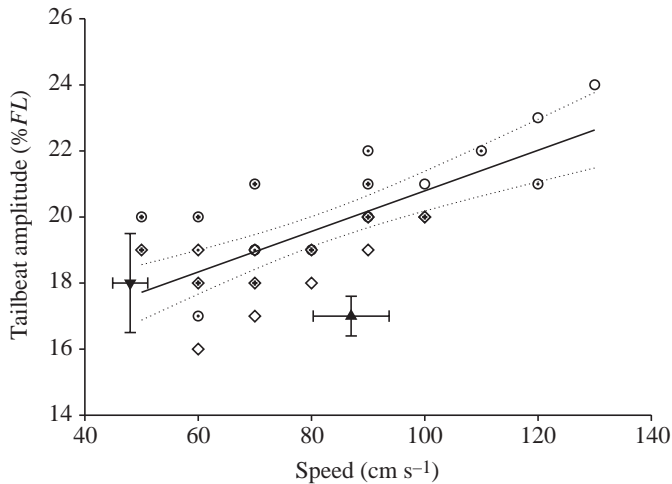


Fig. 2. Tailbeat amplitude as a function of swimming speed for *Sarda chiliensis* (each symbol denotes one individual) and two sizes of yellowfin tuna, *Thunnus albacares* (inverted solid triangle for 42 cm and upright solid triangle for 48 cm) from Dewar and Graham (1994b). The solid line is the best-fit regression equation (regression coefficients \pm s.d.) for the bonito: tailbeat amplitude = $0.06 \pm 0.01 \times$ speed + 14.0 ± 0.95 ($N=8$). Dotted lines represent 95% confidence intervals of the regression. *FL*, fork length.

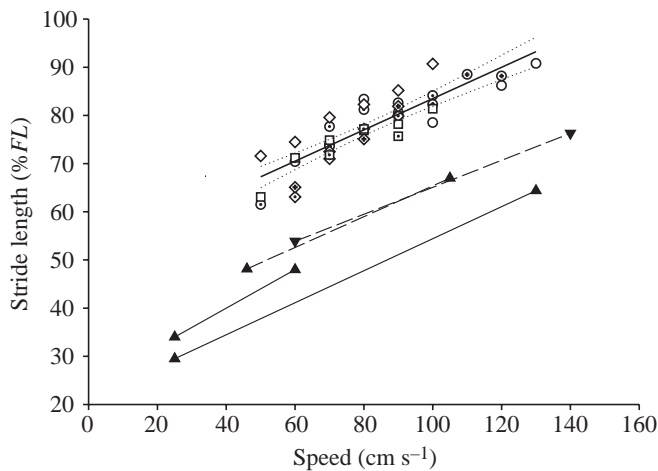


Fig. 3. Stride length versus swimming speed for *Sarda chiliensis* (each symbol denotes one individual) and two species of tuna, yellowfin *Thunnus albacares* (upright solid triangles) and skipjack *Katsuwonus pelamis* (inverted solid triangles). Tuna data represented by solid lines are from Dewar and Graham (1994b) and by broken lines from Knowler (1998). Best-fit regression equation (regression coefficients \pm s.d.) for the bonito: stride length = $0.32 \pm 0.08 \times$ speed + 51.15 ± 6.98 ($N=8$). Dotted lines are the 95% confidence intervals of this regression.

acclimated to the measurement temperature and comparisons are made at a given speed (for a review, see Dickson et al., 2002). Temperature does affect swimming performance in fishes, primarily through changes in water viscosity that significantly impact swimming at low Reynolds numbers

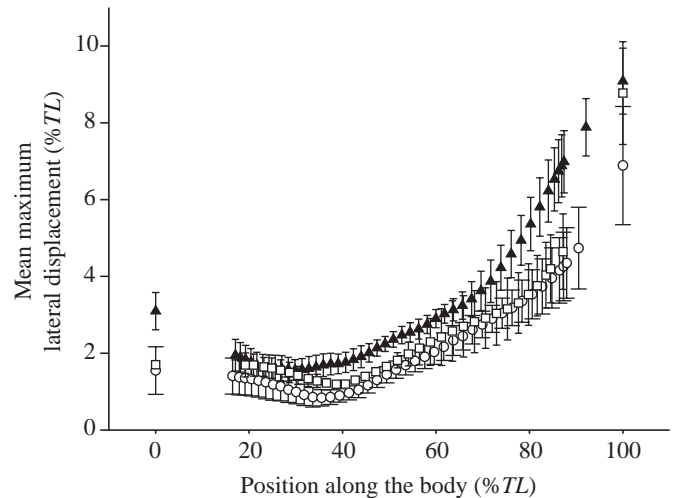


Fig. 4. Maximum lateral displacement (means \pm s.d.) at each intervertebral joint as a function of relative position along the body for *Sarda chiliensis* (solid triangles), kawakawa tuna *Euthynnus affinis* (open circles) and chub mackerel *Scomber japonicus* (open squares). Tuna and mackerel data are from Donley and Dickson (2000).

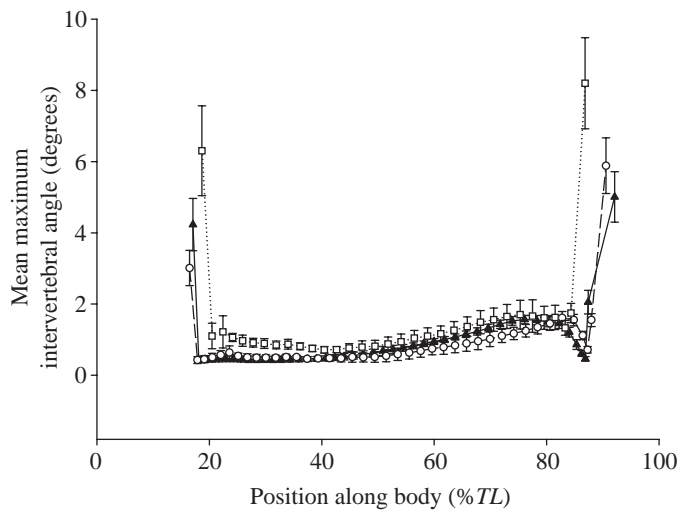


Fig. 5. Maximum bending angle (means \pm s.d.) at each intervertebral joint as a function of relative position along the body for *Sarda chiliensis* (solid triangles), kawakawa tuna *Euthynnus affinis* (open circles) and chub mackerel *Scomber japonicus* (open squares). Tuna and mackerel data are from Donley and Dickson (2000).

(Fuiman and Batty, 1997; Johnson et al., 1998) and by affecting muscle power output and patterns of muscle fiber recruitment, leading to higher maximum sustainable speeds at higher temperatures (e.g. Rome and Swank, 1992; Altringham and Block, 1997; Rome et al., 2000).

Tailbeat frequency increased significantly with speed in both yellowfin and skipjack tunas (Dewar and Graham, 1994b; Knowler 1998; Knowler et al., 1999), as it did in the bonito (Fig. 1). The slopes of the tailbeat frequency versus speed

Table-1. Comparative data for yaw and propulsive wavelength (as a percentage of fish length) in scombrid fishes

Species	Yaw		PWL		PWL range		Fish length (cm)		Speed (cm s ⁻¹)	Speed range (body lengths s ⁻¹)		References
	%FL	%TL	%FL	%TL	%FL	%TL	FL	TL		FL s ⁻¹	TL s ⁻¹	
Tunas												
Yellowfin tuna <i>Thunnus albacares</i>	4.3±0.38		124±9				42±1.6		47±9.8	~1.1		1
Yellowfin tuna <i>Thunnus albacares</i>	2.8±0.15		123±17				48±2.2		92±3.3	~1.9		1
Yellowfin tuna <i>Thunnus albacares</i>			103				40–44		46–105	1.1–2.7		2
Skipjack tuna <i>Katsuwonus pelamis</i>			97				38–41		60–140	1.5–3.7		2
Kawakawa tuna <i>Euthynnus affinis</i>		3.5±1.2	96±2	93±1		89–96	15.1–25.5 (21.4±2.7)	16.0–27.1	30–120	1.6–5.0		3
Bonito												
Eastern Pacific bonito <i>Sarda chiliensis</i>	6.0±0.6	5.6±0.6	128±2	120±2	118–134	110–129	45.0–50.5	49.0–55.0	50–140	1.0–2.9	1.0–2.7	4
Eastern Pacific bonito <i>Sarda chiliensis</i>		5.0±1		113±6			60–71					5
Mackerels												
Atlantic mackerel <i>Scomber scombrus</i>		3.0–3.6		89		78–106		30–34	129–381		3.9–11.2	6
Chub mackerel <i>Scomber japonicus</i>		3.8±1.5	116±4	109±3	97–144	98–119	14.0–23.4 (20.3±3.4)	14.8–25.3	30–110	1.4–5.9		3
Chub mackerel <i>Scomber japonicus</i>		2.2±0.4	106±2	98±2	89–124	84–105	15.6–26.3 (20.9±4.0)		30–105	1.4–4.8		7

Values are means ± S.D. or range (N.B. PWL values are means ± S.E.M.).

FL, fork length; TL, total length; PWL, propulsive wavelength.

¹Dewar and Graham (1994b); ²Knower (1998); ³Donley and Dickson (2000); ⁴This study; ⁵Ellerby et al. (2000); ⁶Videler and Hess (1984); ⁷Dickson et al. (2002).

relationships did not differ significantly ($P>0.25$) between the bonito and two groups of yellowfin tuna (FL 42±1.6 cm and 53±3.0 cm, means ± S.D.) (data from Dewar and Graham, 1994b) or between the bonito and 40–44 cm FL yellowfin tuna and 38–41 cm FL skipjack tuna (data from Knower et al., 1999). Because the slopes did not differ, comparisons were made between the y -intercepts of these lines. The intercepts of the tailbeat frequency *versus* speed relationships for the 42 cm and 53 cm yellowfin tuna groups did not differ significantly from that of the bonito ($P>0.25$) (Fig. 1A), but the intercepts for the 40–44 cm yellowfin and 38–41 cm skipjack tuna were significantly higher than for the bonito ($P<0.0005$) (Fig. 1B). Because the original data from Knower et al. (1999) were provided to us, 95% confidence intervals for the tailbeat frequency *versus* speed relationships were calculated and plotted (Fig. 1B). The lack of overlap of the 95% confidence intervals over the range of speeds studied suggests that the bonito swim at a given speed with significantly lower tailbeat frequencies than do similar sized yellowfin and skipjack tunas.

The only published data for tailbeat amplitudes and yaw at known speeds in tunas that are of comparable size to the bonito in the present study are from yellowfin tuna (Dewar and Graham, 1994b). Tailbeat amplitude did not vary significantly with speed in the yellowfin tuna, and the values (mean ± S.D.)

of Dewar and Graham (1994b) are compared with the bonito data plotted in Fig. 2. It appears that, at similar speeds, the tailbeat amplitude of the bonito does not differ significantly from that of one group of yellowfin (FL 42±1.6 cm, swimming at a speed of 40±2.8 cm s⁻¹; means ± S.D.) but is higher than that of the larger yellowfin (48±2.2 cm FL , swimming at 100±6.5 cm s⁻¹). The yaw for the bonito (6.0±0.6% FL , mean ± S.D.) is significantly greater ($P<0.001$) than the values for both the 42 cm (4.3±0.38% FL) and 48 cm (2.8±0.15% FL) yellowfin tuna groups (Table 1). A high yaw value (5% TL) was also observed for the eastern Pacific bonito by Ellerby et al. (2000).

Stride length increased significantly with speed in the yellowfin and skipjack tunas (Dewar and Graham, 1994b; Knower 1998), as it did in the bonito (Fig. 3). The slopes of the stride length *versus* speed relationships did not differ significantly ($P>0.25$) between the bonito and the two groups of yellowfin tuna from Dewar and Graham (1994b), or between the bonito and the yellowfin and skipjack tunas from Knower et al. (1999). The y -intercepts of the four tuna stride length *versus* speed regressions were significantly lower than that of the bonito ($P<0.001$). Thus, at a given speed, stride length is greater in the bonito than it is in similar-sized tunas (Fig. 3).

The range of values for relative propulsive wavelength (as

%*FL*) in the bonito (Table 1) overlapped with data for yellowfin tuna from Dewar and Graham (1994b) ($124 \pm 9\%$ *FL* and $123 \pm 17\%$ *FL* for 42 cm *FL* and 48 cm *FL* groups, respectively; means \pm S.E.M.), but were higher than values reported by Knower (1998) (103% *FL* in 40–44 cm *FL* yellowfin tuna and 97% *FL* in 38–41 cm *FL* skipjack tuna).

The patterns of mean maximum intervertebral lateral displacement (z_{\max}) and mean maximum bending angle (β_{\max}) at all intervertebral joints in the bonito were compared with data from juvenile kawakawa tuna and chub mackerel (Donley and Dickson, 2000), the only scombrid species that have been analyzed in this manner. Overall, mean z_{\max} was significantly higher in the bonito than in both the tuna ($P < 0.0001$) and the mackerel ($P = 0.032$). Lateral displacement at the snout and posterior to 40% *TL* is greater in the bonito than in the other two species (Fig. 4). The pattern of z_{\max} along the body differed between the bonito and the kawakawa tuna, as indicated by a significant tuna \times position interaction ($P = 0.0025$), but did not vary significantly between the bonito and the chub mackerel. The minimum mean z_{\max} occurred at 38% *TL* (between vertebrae 10 and 11) in the chub mackerel and at 41% *TL* (between vertebrae 15 and 16) in the kawakawa tuna, compared with 30% *TL* in the bonito; maximum mean z_{\max} occurred at the tip of the tail in all three species.

Mean maximum bending angles in the bonito differed significantly from those in both the kawakawa tuna ($P = 0.0016$) and the chub mackerel ($P = 0.032$), as did the pattern of β_{\max} versus position along the body, as indicated by significant species \times position interaction terms ($P < 0.0001$). The mackerel had higher bending angles than the bonito in the anterior third of the body, and the tuna had lower bending angles than the bonito at approximately 65–75% *TL* (Fig. 5). The position of minimum mean β_{\max} was 40% *TL* (between vertebrae 11 and 12) in the chub mackerel and 18% *TL* (between vertebrae 1 and 2) in both the kawakawa tuna and the bonito; maximum mean β_{\max} occurred at the intervertebral joint anterior to the hypural plate in all three species (at 87, 90 and 92% *TL* in the mackerel, tuna and bonito, respectively).

Discussion

The objective of this study was to characterize the swimming mode of the eastern Pacific bonito under controlled conditions (i.e. at a range of steady swimming speeds) and to compare specific kinematics variables between bonitos, tunas and mackerels. This study was designed to determine if the bonito utilizes a mode of locomotion similar to the thunniform mode used by tunas, in which minimal lateral displacement of the body occurs during steady swimming. Our analyses demonstrate that the swimming kinematics of the eastern Pacific bonito are significantly different from those of yellowfin and skipjack tunas. Relative to comparably sized tunas swimming at similar speeds, the bonito swims with a lower tailbeat frequency, greater yaw, higher stride length and a greater degree of lateral displacement along the body. These findings confirm the tentative conclusion from comparison of

tailbeat frequency versus speed relationships (Donley, 1999; Donley and Dickson, 2000) and the conclusion of Ellerby et al. (2000), based on midline lateral displacement data, that the bonitos use the carangiform locomotor mode, and supports the hypothesis that thunniform locomotion is an autapomorphy of the tunas, associated with the anterior and medial RM position.

Because the mackerels that have been studied are all less than 35 cm in length, we cannot compare tailbeat frequency, tailbeat amplitude or stride length data for similar sized mackerels and bonitos swimming at comparable speeds. However, interspecific comparisons of the variables that are apparently independent of fish size, yaw and z_{\max} expressed as a percentage of fish length, show that the bonito swims with significantly more lateral displacement along most of the body, including the snout, than do juvenile chub mackerel. Thus, swimming kinematics in the bonito may not be intermediate between that of tunas and mackerels, as would be predicted on the basis of morphological characteristics.

Swimming kinematics variables

Although we concluded that tailbeat frequency at a given speed is significantly lower in the bonito than it is in similar sized tunas, based on comparison with data for yellowfin and skipjack tunas from Knower et al. (1999), the relationships between tailbeat frequency and speed did not differ significantly between the bonito and the yellowfin tuna from Dewar and Graham (1994b). There was much greater variability in the Dewar and Graham (1994b) data than in that of Knower et al. (1999), which may be due to the methods that were used to record tailbeat frequency. Dewar and Graham (1994b) used visual observations and a stopwatch to determine the time required for a fish to complete 20 tail beats while swimming steadily, whereas Knower et al. (1999) used frame-by-frame analysis of video footage to calculate tailbeat frequency. The high variability may also be a consequence of the inclusion of lower swimming speeds by Dewar and Graham (1994b). If a fish swims at a speed that is below the minimum speed required for hydrostatic equilibrium (Magnuson, 1978), it may use sporadic swimming motions to maintain position, which can lead to high variability in kinematics data. Consequently, we believe that the values measured in Knower et al. (1999) are a more accurate representation of tuna tailbeat frequency at steady, sustainable speeds. However, it should be noted that the tunas used in Knower et al. (1999) all were smaller in *FL* than the bonito in the present study and thus would be expected to use higher tailbeat frequencies at a given speed than larger individuals. Because no size effects were observed in either study, it is not possible to extrapolate the data sets to a common fish size. When we compared the largest tuna (44 cm *FL* yellowfin) from Knower et al. (1999) and our smallest bonito (45 cm *FL*), tailbeat frequency was higher at a given speed in the tuna than in the bonito.

Because tailbeat frequencies were lower in the bonito, we expected that tailbeat amplitudes would be higher in the bonito compared to tunas. The bonito did swim at a given speed with a higher tailbeat amplitude than the 48 cm yellowfin, but there

was no difference between the bonito and 42 cm yellowfin (Fig. 2). In addition, the maximum lateral displacement of the tip of the tail (one-half of the tailbeat amplitude) was significantly greater in the bonito than in the juvenile tuna of Donley and Dickson (2000) when expressed as %*TL* (Fig. 4). Thus, the limited tailbeat amplitude data that are available provide some support for a difference in swimming mode between the bonito and tuna.

Stride length in the bonito was higher than the values reported for tunas by both Dewar and Graham (1994b) and Knowler et al. (1999), indicating that the bonito moves farther with each tailbeat. Altringham and Block (1997) also noted greater stride lengths in free-swimming bonito (42–47 cm *TL*) compared with larger yellowfin tuna (58–81 cm *TL*). These data further support the difference in swimming mode between tunas and the bonito.

Yaw, the result of anterior recoil forces generated by oscillation of the tail, is minimized in scombrid fishes by narrow necking of the caudal fin, a large muscle mass and a high body depth (Lighthill, 1969; Lindsey, 1978; Webb, 1978, 1998). Magnuson (1978) found that maximum body thickness (the average of maximum height and maximum width) for seven tuna species ranged between 20.8 and 23.5%*FL*, but was only 18.4%*FL* for *Sarda chiliensis* and 16.0%*FL* for *Scomber scombrus*. Decreased yaw has been used to distinguish thunniform locomotion from other swimming modes (Fierstine and Walters, 1968; Dewar and Graham, 1994b; Ellerby et al., 2000). In the present study, the bonito had significantly higher yaw than did similar sized yellowfin tuna at similar speeds, which supports the hypothesis that tunas utilize a different swimming mode than do bonitos. Because yaw (as a percentage of fish length) apparently does not vary significantly with fish size, we examined yaw values from a number of other scombrid fishes (Table 1) and also found yaw in the bonito to exceed that in kawakawa tuna and Atlantic and chub mackerels. This interspecific difference is reflected in the midline lateral displacement at the tip of the snout (one-half of yaw) (Fig. 4). Thus, although morphological characteristics indicate that yaw in the bonito would be intermediate between that in mackerels and tunas, yaw was highest in the bonito.

Propulsive wavelength values (as %*FL* or %*TL*) for tunas, mackerels and the eastern Pacific bonito overlap (Table 1), and no consistent pattern was detected. Propulsive wavelength has been used previously to categorize swimming mode, and should be greater for thunniform than for carangiform swimmers (Lindsey, 1978). However, Donley and Dickson (2000) found that propulsive wavelength as a percentage of body length was greater in the chub mackerel than in the kawakawa tuna, and varied with fish size. Although propulsive wavelength in scombrids is not known to vary with swimming speed, it does vary with temperature (Dewar and Graham, 1994b; Donley and Dickson, 2000; Dickson et al., 2002). Studies with other fish species indicate that propulsive wavelength varies with axial position (Blight, 1977) and within a given species (Long and Nipper, 1996) suggest that this variable should not be used as a criterion for distinguishing fish

swimming modes (see Long and Nipper, 1996; Donley and Dickson, 2000).

The intervertebral flexion angles were higher in the chub mackerel than in the bonito and in the kawakawa tuna (Fig. 5). These angles reflect intervertebral lateral displacement, the number of vertebrae and vertebral flexibility. The larger angles in the mackerel can be attributed primarily to the smaller number of vertebrae in the chub mackerel (31) relative to the kawakawa (39) and the bonito (44); when there are fewer intervertebral joints, larger angles are required as the body midline is displaced laterally a given distance. In all three species, low β_{\max} values were found for the intervertebral joints just anterior to the hypural plate, and β_{\max} values at this position were highest in the chub mackerel because the mackerel has one relatively large vertebra in this position, whereas the tuna and bonito have two or three much shorter vertebrae (Collette, 1978).

The interspecific differences in vertebral number may also contribute to differences in yaw and in the pattern of z_{\max} along the body. Videler (1985) suggested that a greater number of vertebrae would lead to a greater degree of lateral flexibility. This may explain why the bonito swims with greater lateral displacement than do the kawakawa tuna and chub mackerel (Fig. 4). However, if vertebral number was the only factor involved, lateral displacement would be lowest in the chub mackerel, which has the fewest vertebrae of the three species, but lateral displacement is lowest in the tuna (Fig. 4).

The lower z_{\max} and β_{\max} values observed in the tuna may result from specializations for axial stiffness and/or the anterior–medial RM position. Relative to other scombrids, tunas have enlarged neural and hemal spines, larger zygapophyses that link adjacent vertebrae, more epipleural ribs and more extensive branching of tendons as they insert onto the backbone within the horizontal septum, and bony caudal keels which are thought to stiffen the caudal region (Kishinouye, 1923; Fierstine and Walters, 1968; Collette, 1978; Hebrank, 1982; Westneat et al., 1993). Tunas also have a well developed vertical septum containing collagen fibers in a crossed-fiber array, and some tuna species possess bony projections (lattices; Kishinouye, 1923) that extend between their hemal spines that may stiffen the skeleton (Westneat and Wainwright, 2001). Furthermore, in the tunas *Euthynnus*, *Katsuwonus* and *Thunnus*, the first vertebra is partially or fully sutured to the skull (Collette, 1978). All of these characteristics may reduce axial flexibility, but their contribution to differences in swimming kinematics remains to be determined empirically.

Differences in swimming mode between mackerels, bonitos and tunas may also be related to the position of the RM, its pattern of activation, and how muscle contractile force is transferred to the skeleton to produce swimming movements. In bonitos and mackerels, the lateral RM is firmly attached to the skin and is connected to the backbone *via* posterior oblique tendons (POTs) within the horizontal septum that insert onto the backbone at higher angles than they do in tunas (Westneat et al., 1993; Graham and Dickson, 2000; Westneat and

Wainwright, 2001). Contraction of RM therefore results in localized bending in the chub mackerel (Shadwick et al., 1998) and most likely also in the eastern Pacific bonito (Ellerby et al., 2000; Altringham and Shadwick, 2001). In the tunas, little of the RM is firmly attached to the skin and the POTs are longer and insert onto the backbone at a lower angle (Westneat et al., 1993; Graham and Dickson, 2000). Tuna RM transfers contractile force further caudally, allowing RM contraction in tunas to be uncoupled from local bending (Knower et al., 1999; Shadwick et al., 1999; Altringham and Shadwick, 2001). Because of the POT morphology, muscle contractile force is also transferred caudally with a higher velocity ratio, but a lower mechanical advantage, in tunas compared with mackerels and bonitos (Westneat et al., 1993; Graham and Dickson, 2000), and this is reflected in the higher tailbeat frequencies and lower tailbeat amplitudes in tunas. Future studies are needed to test how differences in vertebral number, structures that affect axial stiffness, total muscle mass, RM position and connective tissue linkages between the locomotor muscle, skin and skeleton affect scombrid swimming kinematics.

Conclusions

The results of this kinematics study support the hypothesis that thunniform locomotion is a derived characteristic of the endothermic tunas associated with the anterior, medial position of the RM. The traits of anterior–medial RM, thunniform locomotion and endothermy all map onto the scombrid phylogeny after the divergence of the bonitos and tunas, and we cannot determine if the anterior–medial RM evolved initially for a less flexible swimming mode and secondarily as a way to conserve metabolically derived heat. However, when combined with the swimming energetics data for the bonito (Sepulveda et al., 2003), we have shown that an increase in energetic efficiency is apparently not associated with thunniform locomotion. Sepulveda et al. (2003) found that the net cost of transport during sustained swimming was similar in the eastern Pacific bonito and the yellowfin tuna studied by Dewar and Graham (1994a), but that total metabolic costs were higher in the tuna due to a higher standard metabolic rate. This corresponds with the results of similar size-matched comparisons of juvenile chub mackerel and kawakawa tuna (Donley and Dickson, 2000; Sepulveda and Dickson, 2000; Korsmeyer and Dewar, 2001). Thus, there is no evidence that increased swimming efficiency was the selective advantage leading to the evolution of the thunniform locomotor mode. It may be that the advantages of endothermy, not swimming efficiency, led to the evolution of the anterior–medial RM in tunas, because heat loss from RM across the body surface would be reduced. If so, thunniform locomotion may simply be a consequence of changes in the biomechanical linkages of the locomotor muscle with the backbone and caudal propeller necessitated by this RM position.

The next step in trying to determine at what point thunniform locomotion evolved within the family Scombridae will require making comparisons among the 15 tuna species.

Although it is assumed that all of the tunas use thunniform locomotion, swimming in many tuna species has not been studied. Efforts should be directed at describing the swimming mode of the most basal tuna, *Allothunnus fallai*. Although this species does not possess all of the circulatory specializations for endothermy that are found in the other tunas, its RM is located in an anterior, medial position and a small central heat exchanger is present (Graham and Dickson, 2000). Characterizing the swimming kinematics of this species and determining if it is able to elevate RM temperature will establish whether the anterior–medial RM evolved prior to the evolution of thunniform locomotion or prior to the evolution of endothermy.

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