

SWIMMING KINEMATICS OF JUVENILE KAWAKAWA TUNA (*EUTHYNNUS AFFINIS*) AND CHUB MACKEREL (*SCOMBER JAPONICUS*)

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Summary

The swimming kinematics of two active pelagic fishes from the family Scombridae were compared to test the hypothesis that the kawakawa tuna (*Euthynnus affinis*) uses the thunniform mode of locomotion, in which the body is held more rigid and undergoes less lateral movement in comparison with the chub mackerel (*Scomber japonicus*), which uses the carangiform swimming mode. This study, the first quantitative kinematic comparison of size-matched scombrids, confirmed significantly different swimming kinematics in the two species. Ten kawakawa (15.1–25.5 cm fork length, *FL*) and eight chub mackerel (14.0–23.4 cm *FL*), all juveniles, were videotaped at 120 Hz while swimming at several speeds up to their maximum sustained speed at 24 °C. Computerized motion analysis was used to digitize specific points on the body in sequential video frames, and kinematic variables were quantified from the progression of the points over time. At a given speed, kawakawa displayed a significantly greater tailbeat frequency, but lower stride length, tailbeat amplitude and

propulsive wavelength, than chub mackerel when size effects were accounted for. Midline curvatures subdivided on the basis of X-rays into individual vertebral elements were used to quantify axial bending in a subset of the fish studied. Maximum intervertebral lateral displacement and intervertebral flexion angles were significantly lower along most of the body in kawakawa than in chub mackerel, indicating that the kawakawa undergoes less axial flexion than does the chub mackerel, resulting in lower tailbeat amplitudes. However, lateral movement at the tip of the snout, or yaw, did not differ significantly interspecifically. Despite these differences, the net cost of transport was the same in the two species, and the total cost was higher in the kawakawa, indicating that the tuna juveniles are not more efficient swimmers.

Key words: locomotion, swimming, kinematics, Scombridae, chub mackerel, *Scomber japonicus*, juvenile, kawakawa tuna, *Euthynnus affinis*, thunniform, carangiform.

Introduction

In a revision of the original classification system of Breder (1926), Webb (1975) proposed that all possible patterns of body–caudal fin propulsion in fishes can be identified as one of four distinct swimming modes: anguilliform, subcarangiform, carangiform and thunniform. The thunniform mode, documented only in the tunas (Fierstine and Walters, 1968; Dewar and Graham, 1994), is believed to be the most efficient because of the small amount of lateral undulation along the body, which minimizes frictional drag (Webb, 1975). Tunas are streamlined, with a tear-drop-shaped body, a narrow caudal peduncle with lateral keels and a rigid, high-aspect-ratio caudal fin that oscillates rapidly to generate lift-based propulsive force. All these properties are considered to increase locomotor efficiency (Lighthill, 1970, 1975; Lindsey, 1978; Magnuson, 1978; Blake, 1983; Webb, 1975, 1998). However, the hypothesis that thunniform locomotion is the most efficient mode of body–caudal fin propulsion has not been tested empirically in swimming fishes.

Tunas are the most derived members of the family Scombridae, comprising a monophyletic group (tribe

Thunnini) with several unique characteristics (Collette, 1978; Block et al., 1993; Carpenter et al., 1995; Graham and Dickson, 2000). The only other scombrid fishes whose swimming mode has been characterized are the mackerels (tribe Scombrini), which have been classified as carangiform swimmers (Gray, 1933; Lindsey, 1978; Videler and Hess, 1984; Shadwick et al., 1998). Bonitos (tribe Sardini), the sister group to the tunas, have been described as carangiform swimmers ‘verging on the thunniform’ (Lindsey, 1978, p. 20), but the only kinematic data we could find on bonitos (Pyatetskiy, 1970; Altringham and Block, 1997) do not provide the information needed to determine swimming mode.

The length of the propulsive wave that travels down the body during steady swimming and the percentage of the body that undergoes lateral undulatory movements are the two criteria that have been used to distinguish the four modes of body–caudal fin locomotion (Webb, 1975; Lindsey, 1978; Videler, 1993). Gray (1933) indicated that propulsive wavelengths are slightly greater than body length in carangiform swimmers, with the exception of the Atlantic

mackerel *Scomber scombrus*, with a propulsive wavelength of 93% of body length (%L), and thunniform swimmers display propulsive wavelengths of 100–200%L (Lindsey, 1978). Lateral undulations confined to the posterior 30% of the body characterize carangiform locomotion, whereas thunniform swimmers have significant lateral movements confined to the peduncle and tail region (less than 30% of the body) (Kishinouye, 1923; Fierstine and Walters, 1968; Webb, 1975; Dewar and Graham, 1994). However, empirical data for scombrid fishes show that these criteria do not clearly and consistently distinguish the carangiform and thunniform modes.

The first descriptions of tuna swimming kinematics, which served as the basis by which thunniform locomotion was defined, were in the kawakawa (*Euthynnus affinis*) by Fierstine and Walters (1968) and Magnuson (1970). The propulsive wavelengths observed in kawakawa were between 100%L and 200%L, but the percentage of the body that undergoes lateral undulatory movements was not quantified (Fierstine and Walters, 1968). Those two studies were limited by the use of body-outline tracings for frame-by-frame analyses and because the fish swam in large circular tanks, making it difficult to measure swimming speeds accurately and to control the direction of travel. More recent studies of mackerel swimming between two points in a large tank (Videler and Hess, 1984) or of tuna and mackerel swimming steadily in a flow tank with an induced current (Dewar and Graham, 1994; Knower, 1998; Shadwick et al., 1998, 1999) have used computerized digitizing systems to obtain accurate body outlines and to quantify swimming movements. The mean propulsive wavelength was 98%L (range 78–106%) in Atlantic mackerel *S. scombrus* (Videler and Hess, 1984), and computer-generated midline curvatures in both *S. scombrus* and the chub mackerel *S. japonicus* show significant lateral undulations confined to the posterior third of the body (Videler and Hess, 1984; Shadwick et al., 1998), consistent with the general description of carangiform locomotion. In yellowfin tuna (*Thunnus albacares*), Dewar and Graham (1994) reported propulsive wavelengths of 123–129% of fork length (FL), within the range for thunniform locomotion. However, Knower (1998) reported propulsive wavelengths of only 103% and 97%FL in yellowfin and skipjack (*Katsuwonus pelamis*) tuna, respectively. Dewar and Graham (1994) also reported significant yaw (lateral undulation of the anterior of the fish) and found no position along the body that did not oscillate laterally. Thus, although all these studies have provided valuable information about the kinematics of scombrid fishes, they have not led to a quantitative characterization or a clear separation between the carangiform and thunniform swimming modes.

More recently, Knower et al. (1999) proposed different criteria, based on electromyographic (EMG) patterns along the length of the body during steady swimming, to separate the body-caudal fin swimming modes. In comparing patterns for representative anguilliform, subcarangiform, carangiform and thunniform swimmers, including the Atlantic mackerel and

yellowfin and skipjack tunas, Knower et al. (1999) found less overlap in slow, oxidative (red) muscle fiber activation on the two sides of the body in the swimming modes characterized by less lateral movement, with the least overlap found in the yellowfin tuna. In the tunas, red muscle EMG bursts begin later in the tailbeat cycle and EMG offsets coincide more closely with the time of peak force production. Shadwick et al. (1999) also showed that shortening of the red muscle in the skipjack tuna correlates with body bending at more posterior regions of the body and not with local body bending, as it does in all other fishes that have been studied, including the chub mackerel (Shadwick et al., 1998). This difference has been attributed to the unique axial, anterior position of the red muscle in tunas, the elongated shape of tunas' myotomes and differences in the tendons that transfer force from the red muscle to the axial skeleton and caudal fin (Fierstine and Walters, 1968; Westneat et al., 1993; Knower et al., 1999; Graham and Dickson, 2000). All these characteristics are expected to result in differences in swimming kinematics and increased swimming efficiency in tunas. What is needed to test these predictions are simultaneous measurements of the kinematics and energetics of size-matched individuals of closely related species representing the carangiform and thunniform swimming modes.

We examined the kinematics of similar-sized individuals of two members of the family Scombridae, one categorized as a thunniform swimmer (kawakawa tuna, *Euthynnus affinis*) and one as a carangiform swimmer (chub mackerel, *Scomber japonicus*). We hypothesized that the locomotor characteristics of *E. affinis* differ from those of *S. japonicus*, with *E. affinis* exhibiting less lateral displacement along the body. The methods of Jayne and Lauder (1995) were used to quantify body midline bending during steady swimming and to correlate body bending with vertebral morphology, which has not been performed previously with scombrids. Furthermore, by combining the kinematic data with metabolic cost of transport values measured in the same individuals used in the present study (Sepulveda and Dickson, 2000), we have tested the hypothesis that tunas are more efficient swimmers than are mackerels.

Materials and methods

Fish, *Euthynnus affinis* (Cantor, 1849) and *Scomber japonicus* (Houttuyn, 1782), were collected and maintained as described in Sepulveda and Dickson (2000). Following respirometry studies that measured maximal sustained swimming speed and metabolic rate (\dot{V}_{O_2}) at each speed up to that maximum (Sepulveda and Dickson, 2000), each fish was allowed to swim at a low speed for at least 15 min before video analysis was performed to quantify swimming kinematics. These experiments were conducted in a Brett-type temperature-controlled swimming tunnel containing a total volume of 35 l. Individual fish were held within a chamber 13.5 cm×13.5 cm×50.8 cm and were forced to swim against water currents of known velocities. Because \dot{V}_{O_2} , maximal sustained speed and kinematic variables were all measured on the same

individuals, the swimming tunnel had to have a volume small enough to allow a significant reduction in oxygen concentration within a 10 to 15 min period at each swimming speed. Corrections for solid-blocking effects were not necessary because the cross-sectional area of each individual was less than 10% of the cross-sectional area of the chamber (Brett, 1964; Webb, 1971). However, wall effects may have affected the kinematics relative to fish swimming in nature. Because this effect should be similar for both species, the interspecific comparisons that are the focus of the present study should not be compromised. Furthermore, most recent studies of scombrid locomotor kinematics have used swimming tunnels with similar dimensions relative to the size range of fish studied. For example, the respirometer used by Shadwick et al. (1998) to study *S. japonicus* 22–29 cm in total length (*TL*) and 110–185 g had a working section of 14.5 cm×14.5 cm×47 cm.

Video analysis

Fish held at 24 °C were videotaped at 120 Hz using a Peak Performance Technologies high-speed video camera (model TM640). The camera was positioned in front of a mirror mounted at 45° above the lid of the working section of the respirometer to obtain a dorsal view of the fish. Video recordings were made onto Maxell Professional SVHS tapes over a 2 to 10 min period at each speed at which the fish swam during its \dot{V}_{O_2} measurements. The speeds at which the fish were videotaped ranged from the lowest speed of 37–40 cm s⁻¹ to each individual's maximum sustainable speed, in increments of 7.5 cm s⁻¹ or 10 cm s⁻¹. A total of ten kawakawa (15.1–25.5 cm *FL*, 43–265 g) and eight chub mackerel (14.0–23.4 cm *FL*, 26–147 g) were analyzed; all individuals were juveniles.

All speeds on each video tape were analyzed using a Peak Performance Technologies two-dimensional motion-analysis system. Video segments in which the fish was swimming steadily through 8–10 complete tail beats and was positioned in the center of the chamber, away from the walls and bottom of the chamber, were selected for analysis. Six points along the dorsal midline of each fish were digitized in sequential video fields through 8–10 complete tail beats at each speed. The six digitized points were chosen by pinpointing landmarks on the dorsal surface of the fish that are easily observed in both species in sequential video fields: the tip of the snout, the point along the dorsal midline between both the anterior and the posterior insertion points of the eyes, the midpoint between the anterior insertions of the pectoral fins, the caudal peduncle and the tip of the upper lobe of the caudal fin (Fig. 1). A 5 cm square grid on the bottom of the flow chamber was used to calculate a scaling factor in each video tape. The kinematic variables were calculated for each speed by analyzing the progression of these digitized points through time.

Kinematic variables

All kinematic variables were calculated at each speed for each individual of both species. Tailbeat frequency was calculated

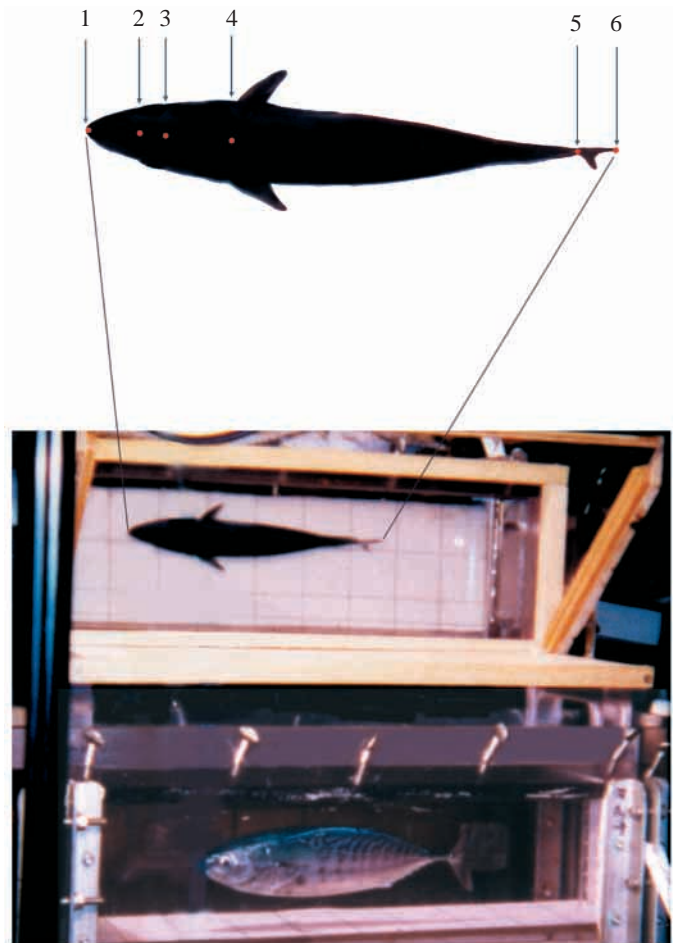


Fig. 1. A kawakawa (25.5 cm *FL*, the largest individual studied) swimming in the respirometer, viewed simultaneously from the side and in dorsal view from the 45° mirror placed on top of the respirometer. In sequential video fields at each swimming speed, six identifiable points along the fish's dorsal midline were digitized: 1, the tip of the snout; 2, the anterior insertion point of the eye; 3, the posterior insertion point of the eye; 4, the anterior insertion point of the dorsal fin; 5, the base of the caudal peduncle; 6, the tip of the upper lobe of the caudal fin. *FL*, fork length.

from the two-dimensional display of the progression of the tip of the tail over time by dividing the number of consecutive tailbeat cycles by the time, in seconds, taken for the completion of those beats. One tailbeat cycle is defined as the excursion of the tail from one side of the body to the other and back again. Using the same two-dimensional display, tailbeat amplitude, the distance between the lateral-most positions of the tip of the tail during one complete tailbeat cycle, was calculated by measuring the height of each symmetrical tail beat in pixels. These values were then converted to centimeters by dividing by the scaling factor (pixels cm⁻¹) calculated prior to digitizing. Because of a degree of body curvature throughout the tailbeat cycle, it was not possible to use the video tapes to obtain accurate estimates of each fish's length in pixels. Because the fish were swimming in the center of the chamber, the calculated tailbeat amplitudes overestimated the actual tailbeat amplitudes by 0.5–2.0%. The

mean tailbeat frequency and tailbeat amplitude at each speed were used in statistical analyses. Stride length (l), measured in cm tailbeat^{-1} , is the distance a fish travels forward with each tail beat. To calculate l , speed was divided by mean tailbeat frequency.

Propulsive wave velocity (C), the speed of the wave of undulation that travels down the length of the body from snout to the tail during swimming, was calculated by first overlaying the two-dimensional displays showing the lateral displacement through time of the digitized points at the tip of the snout and the tip of the tail and then measuring the time (in seconds) between the peaks in lateral displacement at the two points (Dewar and Graham, 1994). This represents the time required for the wave of undulation to pass from anterior to posterior between the two points on the fish [a distance equal to fish total length (TL)]. Measurements were repeated 7–10 times for each individual at each speed to calculate a mean progression time. The TL (cm) of each individual (the distance between the two points) was divided by the mean progression time to obtain the propulsive wave velocity (C ; in cm s^{-1}) at each speed for each individual. Propulsive wavelength (λ) was calculated by dividing C by mean tailbeat frequency.

Body bending analysis

The body bending analysis entailed comparing the intervertebral lateral displacement and bending angle at each intervertebral joint along the entire length of the axial skeletons of kawakawa tuna and chub mackerel (see Jayne and Lauder, 1995). Three individuals of each species were used, three size-matched pairs that were videotaped at similar speeds: 15.1 and 14.0, 21.2 and 21.0, and 23.4 and 24.0 cm FL for kawakawa and chub mackerel, respectively. Each individual was redigitized swimming at one low and one high speed. Thirty-two approximately equally spaced points along the dorsal outline were digitized in sequential video fields through one complete tail beat, for each individual at each of the two speeds, using the Peak Performance Technologies analysis system.

To calculate the relative positions of the vertebral joints, the lateral view of each individual was X-ray photographed at the University of California, Irvine (UCI). The lengths of the skull and each vertebra were determined from the X-rays using a Measurement TV program in Dr George Lauder's laboratory at UCI to digitize points at the tip of the snout, the posterior edge of the neurocranium and all intervertebral joints up to and including the posterior tip of the hypural plate. An additional segment was added to the digitized midline corresponding to the length between the posterior edge of the hypural plate and the tip of the tail. Because of the difference in the number of vertebrae between the two species (39 in kawakawa compared with 31 in chub mackerel), the positions of each joint along the body were converted to a percentage of total length ($\%TL$), which is the length from the tip of the snout to the posterior tip of the tail.

The dorsal outline point-coordinate data were converted to complete curves using a cubic spline function as described by

Jayne and Lauder (1995). A computer algorithm was then used to calculate a dorsal midline for each video field from the dorsal outlines. Each calculated midline was then divided into segments that represent the various skeletal elements, using the relative lengths of each vertebral element. This was carried out for all fields comprising a full tailbeat cycle for each of the six fish swimming at both speeds. Intervertebral lateral displacement and intervertebral bending angle were then calculated using an Excel macro written by Jayne and Lauder (1995).

Maximum intervertebral lateral displacement (D) was determined for each of the joints along the axial skeleton. For statistical analysis, lateral displacement was converted to units of relative length ($\%TL$), and the mean maximum lateral displacements at specific positions along the body (as $\%TL$) for each species were compared. Lateral displacements are calculated from the midline; thus, the maximum lateral displacement at the tip of the tail is equivalent to half the tailbeat amplitude as defined above, and twice the maximum lateral displacement at the tip of the snout is equivalent to yaw.

The angle of bending between vertebral elements (β) was determined for each joint along the axial skeleton, beginning with the joint between the posterior edge of the neurocranium and the first vertebra and ending at the joint between the last caudal vertebra and the anterior edge of the hypural plate. The angle calculated is that angle subtended to the position of the adjacent anterior skeletal segment at the same point in time. For statistical analysis, the maximum angle at each intervertebral joint was determined, and mean maximum angles at specific positions along the body (as $\%TL$) for each species were compared.

Statistical analyses

Because speed and size covary and both may have an effect on each kinematic variable, it was necessary to use a multivariate analysis to quantify the effects of speed and size and to assess their relative influences on each kinematic variable. We addressed the question of whether there was a significant difference between chub mackerel and kawakawa in the relationship between speed and each kinematic variable when size has been accounted for. In most published kinematic studies, it has been common practice to account for differences in size between individuals by dividing the kinematic variable by a unit of length or testing the significance of a regression of a kinematic variable *versus* speed expressed in body lengths s^{-1} rather than cm s^{-1} . Those methods of adjusting for fish size assume that size has a linear effect on the kinematic variable and on speed. However, the effect of size may not be linear; in this case, this assumption is incorrect because it introduces a different size effect to the data (Hunter and Zweifel, 1971; Packard and Boardman, 1999). Therefore, we have used the more accurate and appropriate method of accounting for both size and speed effects by using a multiple regression analysis.

Statistical analyses were performed with Minitab (version 10.5) and SAS (version 6.12). Using Minitab, it was determined

that the kinematic data were normally distributed and did not therefore require transformation prior to analysis. A statistical model was then created for each kinematic variable in SAS using a repeated-measures multiple regression analysis. Each multiple regression equation represents a plane in three-dimensional space, and takes the form $y = \gamma_0 + \gamma_1 x_1 + \gamma_2 x_2 + \gamma_3 x_1 x_2$, where y is the kinematic variable, x_1 , x_2 and $x_1 x_2$ are explanatory variables for speed, fork length and a speed \times fork length interaction, and the γ values are numerical coefficients that represent the magnitude of the effect of each variable. The statistical program tests if each γ value is significantly different from zero ($P=0.05$). If not, then the corresponding variable makes no significant contribution to the relationship, and the variable is dropped from the model and a new regression is calculated. The final models used to describe the actual fish kinematics were derived through this backwards step-wise reduction process in which insignificant terms were dropped from the model one by one until only significant terms remained.

To test for significant interspecific differences, each multiple regression equation for chub mackerel was used as a baseline with which the corresponding regression for kawakawa was compared. If there are significant interspecific differences in the slopes in either or both the x_1 and x_2 dimensions, then these differences are best described by two separate planes with different orientations in three-dimensional space. If there is no difference in the slope in either the x_1 or x_2 dimension but the y -intercepts (γ_0 values) are significantly different, then the species differences are best represented by two parallel planes, one above the other in three-dimensional space. Each kinematic variable was tested for the effects of species, speed and fish size in terms of both mass and length. Interaction terms

were created in Minitab and included interactions of species with speed, mass and fork length and of speed with mass and fork length.

The body bending data were subjected to analysis of variance (ANOVA) using SuperANOVA (version 1.11). A three-way ANOVA was performed on the maximum intervertebral lateral displacement and maximum intervertebral bending angle data for each species to determine whether there were any significant effects of position, species, speed or position \times species interactions. In all statistical analyses, a significance level of $P=0.05$ was used.

Results

Kinematics

Several swimming kinematic variables were compared between *E. affinis* and *S. japonicus* to characterize their respective swimming modes. The multiple regression equations for each kinematic variable described by the final statistical models are shown in Table 1. Whenever both size and speed effects were significant, the maximum and minimum values for both size and speed were used to solve the equation for the four corners of a plane, which was then plotted, along with the data for all individuals, in three-dimensional space in which the x_1 , x_2 and y axes are speed, fork length and the kinematic variable, respectively. When a kinematic variable varied with only speed or size, two-dimensional plots were used.

Tailbeat frequency

Speed effects

When the effects of fish size were accounted for, tailbeat

Table 1. The equations for the three-dimensional planes representing the final models of the repeated-measures multiple regression analysis for each kinematic variable (see text for details)

Kinematic variable, y	Species	Multiple regression equation
Tailbeat frequency (Hz)	<i>Scomber japonicus</i>	$y = (4.18 \pm 0.84) + (0.050 \pm 0.002)U + (-0.118 \pm 0.041)FL$
	<i>Euthynnus affinis</i>	$y = (7.66 \pm 1.89) + (0.050 \pm 0.002)U + (-0.251 \pm 0.094)FL$
Tailbeat amplitude (cm)	<i>S. japonicus</i>	$y = (-0.060 \pm 0.528)^* + (0.010 \pm 0.002)U + (0.137 \pm 0.026)FL$
	<i>E. affinis</i>	$y = (-0.060 \pm 0.528)^* + (-0.002 \pm 0.004)^*U + (0.137 \pm 0.026)FL$
Tailbeat amplitude (%FL)	<i>S. japonicus</i>	$y = (13.46 \pm 0.48) + (0.052 \pm 0.008)U$
	<i>E. affinis</i>	$y = (13.46 \pm 0.48) + (-0.008 \pm 0.001)U$
Stride length, l (cm)	<i>S. japonicus</i>	$y = (-1.82 \pm 1.36) + (0.086 \pm 0.006)U + (0.462 \pm 0.066)FL$
	<i>E. affinis</i>	$y = (-3.69 \pm 1.75) + (0.086 \pm 0.006)U + (0.462 \pm 0.066)FL$
Stride length, l (%FL)	<i>S. japonicus</i>	$y = (73.92 \pm 10.12) + (0.413 \pm 0.028)U + (-1.782 \pm 0.500)FL$
	<i>E. affinis</i>	$y = (19.99 \pm 2.62) + (0.413 \pm 0.028)U + (0.395 \pm 0.136)FL$
Propulsive wavelength, λ (cm)	<i>S. japonicus</i>	$y = (-7.93 \pm 4.31)^* + (1.745 \pm 0.269)FL + (-0.0438 \pm 0.0131)M$
	<i>E. affinis</i>	$y = (-9.90 \pm 5.03) + (1.745 \pm 0.269)FL + (-0.0438 \pm 0.0131)M$
Propulsive wavelength, λ (%TL)	<i>S. japonicus</i>	$y = (24.70 \pm 22.95)^* + (6.524 \pm 1.684)FL + (-0.532 \pm 0.129)M$
	<i>E. affinis</i>	$y = (24.70 \pm 22.95)^* + (4.711 \pm 1.318)FL + (-0.213 \pm 0.045)M$

In each equation, means \pm S.E.M. are given for each coefficient, speed (U) is in cm s^{-1} , fork length (FL) is in cm, mass (M) is in g. An asterisk indicates a coefficient that is not significantly different from zero ($P > 0.05$). TL , total length.

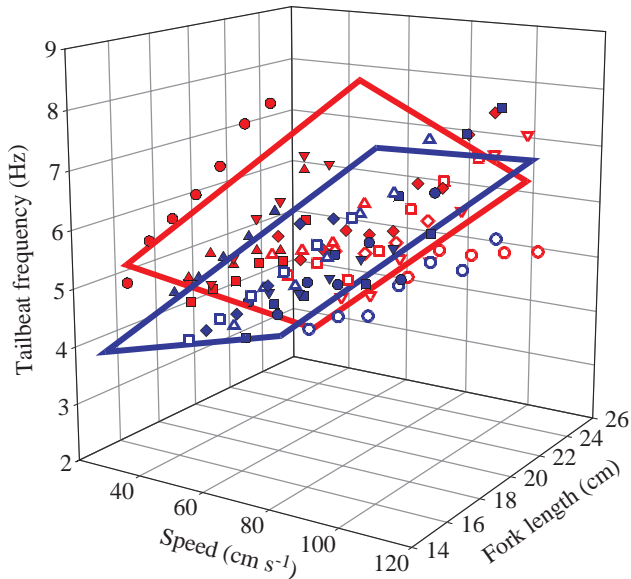


Fig. 2. The dependence of tailbeat frequency on both swimming speed and fish fork length in kawakawa (red plane and red symbols) and chub mackerel (blue plane and blue symbols). Each symbol indicates the tailbeat frequency *versus* speed data for an individual. The maximum and minimum values of speed and fork length were used to solve the multiple regression equations (Table 1) for the four corners of each plane. At a given size, the kawakawa uses a significantly greater tailbeat frequency than does the chub mackerel to swim at a given speed. The increase with speed is similar in the two species, but tailbeat frequency decreases more with fork length in the kawakawa than it does in the chub mackerel.

frequency increased significantly with speed in both species ($P=0.0001$) (Fig. 2). There was no significant difference between the slopes of the regressions of tailbeat frequency *versus* speed for kawakawa and chub mackerel (Table 1).

Size effects

When the effects of speed were accounted for, there was a significant effect of fork length on tailbeat frequency ($P=0.0055$); at the same speed, smaller individuals had higher tailbeat frequencies than did larger individuals. The pattern of decrease in tailbeat frequency with length was significantly different between the two species ($P=0.0135$). With a given increase in *FL*, tailbeat frequency decreased more in kawakawa than it did in chub mackerel. When the effects of speed and *FL* were accounted for, mass had no significant effect on tailbeat frequency.

Species effects

Because both speed and size had a significant effect on tailbeat frequency, the data sets of the two species were represented as planes in three-dimensional space (Fig. 2). The *y*-intercepts for the two species differed significantly ($P=0.0014$), with the plane for *E. affinis* being above that for *S. japonicus*, indicating that tailbeat frequency was greater in kawakawa than in chub mackerel when speed and size effects

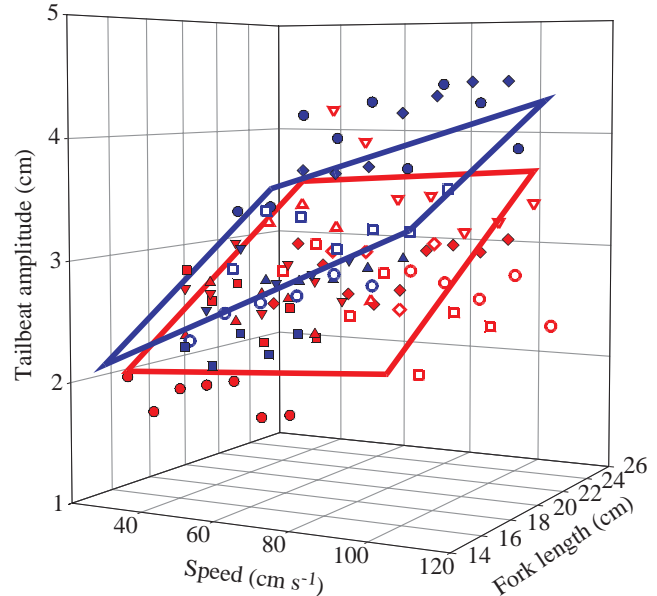


Fig. 3. The dependence of tailbeat amplitude on both swimming speed and fish fork length in kawakawa (red plane and red symbols) and chub mackerel (blue plane and blue symbols). Each symbol indicates the tailbeat amplitude *versus* speed data for an individual. The maximum and minimum values of speed and fork length were used to solve the multiple regression equations (Table 1) for the four corners of each plane. The *y*-intercepts of the two planes are similar, and the effects of fork length on tailbeat amplitude are similar in both species. However, tailbeat amplitude does not vary significantly with speed in the kawakawa, but increases with speed in the chub mackerel; thus, the two species have similar tailbeat amplitudes at low speeds, but tailbeat amplitude is greater in the chub mackerel at the higher speeds.

are accounted for. Although both speed and size had an effect on tailbeat frequency in both species, the size effects were not as great in *E. affinis*, whereas speed effects were the same in both species (Fig. 2). Mean tailbeat frequency in the kawakawa and the chub mackerel were, respectively, 4.57 and 3.82 tailbeat cycles s^{-1} (Hz) at the lowest swimming speeds (approximately 40 $cm s^{-1}$) and 7.03 and 6.57 Hz at the highest swimming speeds (approximately 80–100 $cm s^{-1}$).

Tailbeat amplitude

Speed effects

Tailbeat amplitude, measured both in centimeters and as a percentage of fish fork length (%*FL*), increased significantly with speed in the chub mackerel ($P=0.0001$), but not in the kawakawa (Table 1).

Size effects

When the effects of speed were accounted for, tailbeat amplitude (in cm) increased with *FL* in both species (Fig. 3). There was no significant effect of mass on tailbeat amplitude when *FL* effects were accounted for. To attempt to remove size effects, as other investigators have done, tailbeat amplitude was converted into relative units (%*FL*). There was no

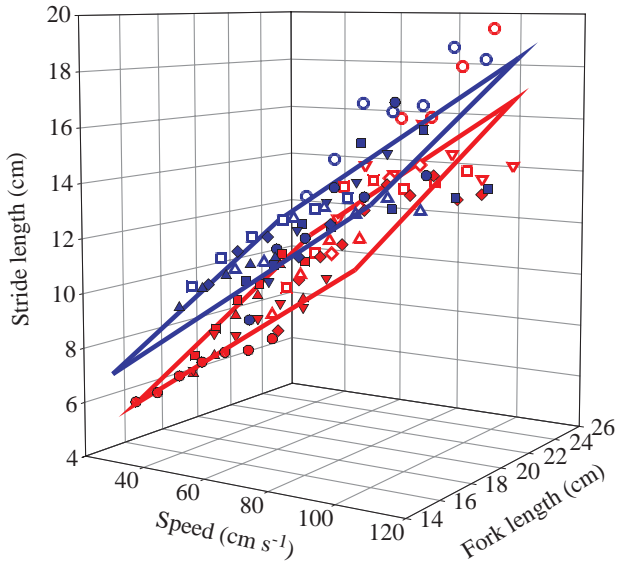


Fig. 4. The dependence of stride length on both swimming speed and fish fork length in kawakawa (red plane and red symbols) and chub mackerel (blue plane and blue symbols). Each symbol indicates the stride length *versus* speed data for an individual. The maximum and minimum values of speed and fork length were used to solve the multiple regression equations (Table 1) for the four corners of each plane. At a given size and speed, the chub mackerel has a significantly greater stride length than does the kawakawa. The increase in stride length with both fork length and speed is similar in the two species.

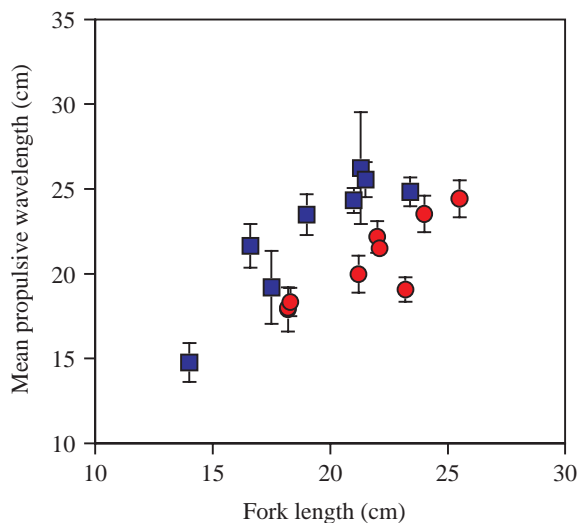


Fig. 5. Mean propulsive wavelength *versus* fork length in kawakawa (red circles; $N=9$) and chub mackerel (blue squares; $N=8$). Because there was no significant effect of speed on propulsive wavelength, the mean of the propulsive wavelengths at all swimming speeds was calculated for each individual. Error bars represent ± 1 s.d. Mean propulsive wavelength is significantly greater in the chub mackerel than in the kawakawa when the effects of size are accounted for.

significant effect of size on tailbeat amplitude when expressed as %FL (Table 1), indicating that using tailbeat amplitude in relative units of fish length was an appropriate adjustment for size differences.

Species effects

Differences in the data sets of the two species are best represented in three-dimensional space (Fig. 3). The y-intercepts of the two planes are similar, and the effects of FL on tailbeat amplitude (cm) are similar in the two species, but the effect of speed on tailbeat amplitude differs interspecifically ($P=0.0001$). As speed increased, the relationship between tailbeat amplitude and speed for the two species diverged, with *E. affinis* having lower amplitudes than *S. japonicus* at high speeds (Fig. 3). This is because

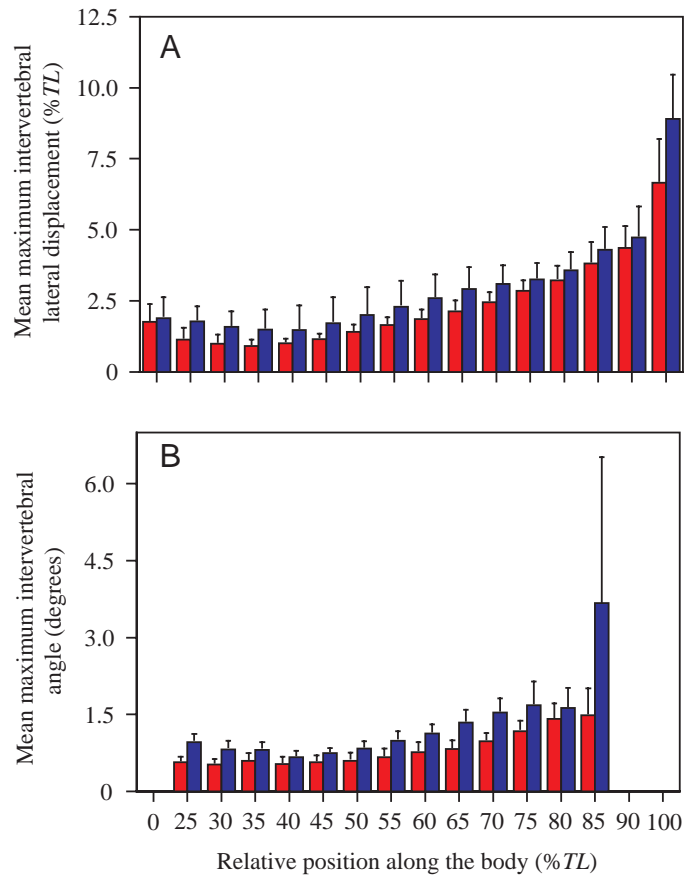


Fig. 6. Mean maximum intervertebral lateral displacement (A) and mean maximum intervertebral bending angle (B) *versus* position along the body (%TL) in kawakawa (red) and chub mackerel (blue). In both species, there was no significant effect of swimming speed on either variable, but there were significant effects of body position and species. Minimum lateral displacement occurred at approximately 35–40%TL and minimum bending occurred at approximately 40%TL in both species. Both maximum intervertebral lateral displacement and maximum intervertebral bending angle were significantly greater in the chub mackerel than in the kawakawa. Values are means \pm s.d. ($N=3$). TL, total length.

tailbeat amplitude did not vary significantly with speed in the kawakawa, but increased with speed in the chub mackerel (Table 1). Maximum tailbeat amplitude ranged from 12 to 14.5%*FL* in kawakawa and from 14 to 20.5%*FL* in chub mackerel.

Stride length

Speed effects

When size effects were accounted for, stride length *l* increased significantly with speed ($P=0.0001$). There was no significant difference in the slopes of the regressions of *l* versus speed for the two species (Table 1).

Size effects

When speed effects were accounted for, both species showed a significant increase in *l* (in cm) with fish fork length ($P=0.0001$). There was no significant difference in the slopes of the regressions of *l* versus *FL* for the two species. There was no significant effect of mass on *l* when *FL* effects were accounted for (Table 1). Because other studies have used relative stride lengths, we also analyzed stride length converted to %*FL*. However, a significant effect of *FL* was evident (Table 1), indicating that the effects of *FL* were not removed by using relative *l* values.

Species effects

The *l* data are represented as two parallel planes in three-dimensional space, with the plane for *S. japonicus* being higher than that for *E. affinis* (Fig. 4). The *y*-intercepts of the planes differ, but the slopes in both the x_1 and x_2 dimensions are equal for the two species. Thus, stride lengths increase similarly with speed and with *FL* in *E. affinis* and *S. japonicus* but, at a given speed and size, the length of each stride is significantly lower in *E. affinis* ($P=0.0001$).

Propulsive wavelength

Speed effects

When size effects were accounted for, there was no significant relationship between propulsive wavelength λ (cm) and speed.

Size effects

When speed effects were accounted for, both mass and fork length had a significant effect on λ (Table 1). As *FL* increased, there was a significant increase in λ ($P=0.0001$). When the effects of *FL* were taken into account, there was a significant decrease in λ with mass ($P=0.0013$). Thus, if a three-dimensional plane were to be drawn, unlike those for the other variables, the two *x* values would be mass and *FL*, with no speed axis (Table 1).

Propulsive wavelength as a percentage of body length is one of the criteria used to determine swimming mode. Thus, the statistical analyses included an assessment of λ expressed as a percentage of fish total length (%*TL*). However, this size adjustment in λ did not completely account for differences in size, as indicated by the presence of significant size effects in the final models for both λ (cm) and λ (%*TL*) (Table 1).

Species effects

There was a significant effect of size, but not speed, on propulsive wavelength, so differences between species were represented by plotting mean λ versus *FL* (Fig. 5). When the effects of fish size are accounted for, the propulsive wavelengths (cm) of *E. affinis* were significantly lower than they were for *S. japonicus* ($P=0.0081$). Mean relative propulsive wavelengths ranged from 89 to 96%*TL* in kawakawa and from 98% to 120%*TL* in chub mackerel. These propulsive wavelengths were then translated into the number of propulsive waves on the body: 1.04–1.12 in the kawakawa and 0.84–1.02 in the chub mackerel.

Body bending

Body bending analysis was performed on three size-matched individuals of each species swimming at one low and one high speed. Intervertebral lateral displacement and intervertebral bending angle at each joint along the axial skeleton were determined. Each of these variables was assessed separately for the effects of species, position along the body, speed and species \times position and species \times speed interactions using a three-way ANOVA in SuperANOVA (version 1.11). Position along the body was represented in relative units, or percentage of total length (%*TL*).

Intervertebral lateral displacement

Speed effects. There was no significant effect of swimming speed on maximum lateral displacements in either species.

Position effects. Intervertebral lateral displacement *D* varied significantly with axial position ($P=0.0001$), but the pattern of maximum lateral displacement with position along the body was similar in both species (Fig. 6A). Minimum lateral amplitudes occurred at 35–40%*TL* in both species, and maximum *D* occurred at the tip of the caudal fin (100%*TL*).

Species effects. Mean maximum lateral displacements were significantly greater in the chub mackerel than in the kawakawa ($P=0.0001$) (Fig. 6A).

To determine whether there are interspecific differences in yaw, twice the mean maximum lateral displacement at the tip of the snout (0%*TL*) for the two species was compared using a two-tailed *t*-test. There was no significant effect of speed on the yaw values within each species ($P>0.30$), so values for both low and high speeds were grouped together in the analysis. Mean yaw was $3.5\pm 1.2\%$ *TL* in the kawakawa and $3.8\pm 1.5\%$ *TL* (means \pm s.d.) in the chub mackerel; these values do not differ significantly ($P=0.684$).

Mean maximum lateral displacement at the tip of the tail was $6.7\pm 1.5\%$ *TL* in the kawakawa and $8.9\pm 1.6\%$ *TL* (means \pm s.d.) in the chub mackerel. These values are similar to half the tailbeat amplitude values for the same individuals.

Intervertebral bending angle

Speed effects. There was no significant effect of speed on mean maximum intervertebral bending angles in either species.

Position effects. Intervertebral bending angle β varied significantly with position along the body ($P=0.0001$). The

positions of minimum and maximum bending angle were similar for the two species, occurring at approximately 40% *TL* and 85% *TL*, respectively (Fig. 6B). However, β increased significantly more near the posterior end of the body in chub mackerel than it did in kawakawa (Fig. 6B), as indicated by a significant species \times position interaction term ($P=0.0448$).

Species effects. Mean maximum intervertebral angles ranged from 0.67 to 3.6° in chub mackerel and from 0.53 to 1.48° in kawakawa; there was a significant species effect, with greater angles in the chub mackerel ($P=0.0001$).

Discussion

The specific goal of this study was to create a more complete quantitative description of the swimming kinematics of two scombrid fishes to test the hypothesis that the kawakawa tuna uses a different locomotor mode from the chub mackerel, in which the body is held more rigid with less lateral undulation, and thus swims more efficiently. Taken together, the kinematic data show that the kawakawa does display less lateral movement of the body than does the chub mackerel while swimming at the same speeds. The most direct measures of body flexure, maximum intervertebral lateral displacement and bending angle, were significantly lower in the kawakawa than in the chub mackerel (Fig. 6). To maintain the same swimming speed, kawakawa beat their tails at a higher frequency than do chub mackerel but use lower tailbeat amplitudes and move a smaller distance per tail beat. However, despite less lateral movement in the kawakawa, the maximal sustainable speeds and net cost of transport did not differ significantly between the two species (Sepulveda and Dickson, 2000). Thus, we have not provided evidence that thunniform locomotion is more efficient than the carangiform swimming mode.

Kinematics and comparisons with previous studies

At sustainable speeds, most fishes that utilize body–caudal fin propulsion increase their swimming speed primarily by increasing tailbeat frequency. Previous research has documented linear increases in tailbeat frequency with speed in a number of teleost species, including scombrids (Magnuson and Prescott, 1966; Yuen, 1966; Pyatetskiy, 1970; Hunter and Zweifel, 1971; Webb, 1971; Magnuson, 1978; Videler and Hess, 1984; Fierstine and Walters, 1968; Dewar and Graham, 1994; Jayne and Lauder, 1995), as was found for both *E. affinis* and *S. japonicus* in the present study (Fig. 2). Tailbeat frequency also varied with fish length in the juvenile scombrids, with larger individuals having a lower tailbeat frequency than smaller individuals swimming at the same speed (Fig. 2), as has been shown in other teleosts (Bainbridge, 1958; Magnuson, 1963; Magnuson and Prescott, 1966; Yuen, 1966; Pyatetskiy, 1970; Hunter and Zweifel, 1971; Videler and Hess, 1984; Fierstine and Walters, 1968; Webb, 1975; Webb et al., 1984; Dewar and Graham, 1994).

The effect of speed on tailbeat amplitude differed between the two species; tailbeat amplitude increased significantly with speed in chub mackerel, but did not vary with speed in

kawakawa (Fig. 3; Table 1). The maximum amplitudes recorded in the present study (14.5% *FL* in kawakawa and 20.5% *FL* in chub mackerel) are consistent with the range of amplitudes recorded for yellowfin *Thunnus albacares* (Dewar and Graham, 1994) and bluefin *Thunnus thynnus* (Wardle et al., 1989) tunas, dace *Leuciscus leuciscus*, trout *Salmo irideus* and goldfish *Carassius auratus* (Bainbridge, 1958) and trout *Oncorhynchus mykiss* (Webb et al., 1984). However, the mean tailbeat amplitude values for similar-sized chub mackerel (approximately 23–26 cm *TL*) in the present study are consistently lower than those measured at similar speeds in a three-dimensional kinematic study by Gibb et al. (1999), possibly because of differences in the methods used in the two studies.

Relationships between tailbeat amplitude and speed from previous studies are less consistent than are trends in tailbeat frequency. Previous results in the three species studied by Bainbridge (1958), the jack mackerel *Trachurus symmetricus* (Hunter and Zweifel, 1971), and bluefish *Pomatomus saltatrix* and gray mullet *Mugil cephalus* (Pyatetskiy, 1970) indicated that tailbeat amplitude remains constant with changes in speed above a minimum steady swimming speed. In the chub mackerel in the study of Gibb et al. (1999), tailbeat amplitude increased significantly with speed. In previous studies of tunas, amplitudes did vary with speed in kawakawa (Fierstine and Walters, 1968), but did not change with speed in yellowfin (Dewar and Graham, 1994). Thus, the tailbeat amplitude *versus* speed relationships in the present study are generally consistent with previous studies, even though there was a great deal of variability in these data (Fig. 3).

At a given speed and size, relative stride length *l* was significantly lower in kawakawa than in chub mackerel (Fig. 4). Relative stride lengths observed at the highest swimming speeds ranged from 50 to 85% *TL* in kawakawa and from 60 to 85% *TL* in chub mackerel, both of which encompass the range predicted by Videler (1993) for maximum *l*. Stride lengths greater than 80% *TL* have also been reported for bluefin tuna (Wardle et al., 1989). However, because we found a significant effect of *FL* on *l*, comparisons among species based on relative *l* (as a percentage of fish length) may be misleading.

The significant increase in *l* with speed found in both kawakawa tuna and chub mackerel in the present study is consistent with stride length relationships observed in other teleost fishes, including scombrids (Fierstine and Walters, 1968; Hunter and Zweifel, 1971; Webb et al., 1984; Dewar and Graham, 1994). As swimming speed increases, the kawakawa and chub mackerel may recruit more red muscle fibers to power the tail beat, and this may result in an increase in the distance swum per tail beat. Alternatively, adjustments in swimming kinematics and in the angle of attack of the tail, which was not quantified in the present study, may alter *l*. By changing gait as speed increases, fish may also be able to vary *l* (Webb, 1998).

Videler (1993) suggested that fish may utilize their extended pectoral fins as a braking system while swimming at low speeds and, thereby, reduce their stride lengths at these speeds;

at higher swimming speeds, fish adduct their pectoral fins, resulting in an increase in stride length. Scombrids have also been observed to orient the body at an angle to the flow to generate lift at low speeds (He and Wardle, 1986), a behavior that may reduce l . However, the fish in the present study swam continuously with their pectoral fins adducted and appeared to orient the body parallel to the flow in all video sequences analyzed at all speeds studied. Thus, the increased stride length cannot be attributed to variations in the use of the pectoral fins, body 'tilting' or different gaits.

In previous studies, propulsive wavelength (λ) has been used to classify swimming mode (see Introduction). On the basis of characterizations of thunniform and carangiform swimming, the kawakawa was predicted to have higher λ values than the chub mackerel. However, the opposite was found to be true (Fig. 5). This may be due to the greater number of vertebrae in the kawakawa, because λ during steady swimming has been hypothesized to be inversely proportional to vertebral number (see Videler, 1985; Jayne and Lauder, 1995; Long and Nipper, 1996). When size effects were taken into account, there was no significant relationship between λ and speed in either kawakawa or chub mackerel. This result confirms the propulsive wavelength trends seen in some studies (Webb et al., 1984), but is not consistent with others (Jayne and Lauder, 1995). However, there were significant effects on λ of mass and fork length, measured both in absolute terms (in cm) and as a percentage of total length, in both species in the present study. Thus, differences in size were not correctly accounted for by dividing by fish length. This implies that many previous comparisons of propulsive wavelengths among species and in fish of different sizes are confounded by mass and length effects and cannot accurately be made by expressing λ as a percentage of fish length. Furthermore, other studies have shown λ to vary with axial position (Blight, 1977) and within a fish species (Long and Nipper, 1996). Thus, it is unclear whether propulsive wavelength can or should be used as a criterion for distinguishing swimming modes in fishes (see also Long and Nipper, 1996). Instead, the body bending characteristics were focused on, because they are more direct measures of body flexure.

Body bending

Many previous kinematic studies of fish bending patterns have quantified body midline curvature but have not analyzed bending along the axial skeleton at each intervertebral joint. The latter is more meaningful because it relates body bending to the morphological characteristics of the fish that allow bending. Prior to the present study, such studies had been completed on anguilliform and subcarangiform swimmers (Jayne and Lauder, 1995; Gillis, 1998; Lauder, 2000), but not on carangiform or thunniform swimmers. We have shown that this type of analysis can distinguish the swimming patterns of the kawakawa and chub mackerel (Fig. 6). Both maximum intervertebral lateral displacement and maximum intervertebral bending angle were significantly lower in the kawakawa than in the chub mackerel, supporting the

hypothesis that the kawakawa is a more stiff-bodied swimmer than is the chub mackerel.

There was no significant relationship between speed and maximum intervertebral lateral displacement or bending angle in either kawakawa or chub mackerel, but body bending characteristics did vary with vertebral position. The position of both minimum lateral displacement and minimum intervertebral angle occurred at approximately 35–40% TL in both species. These data are consistent with previous studies of other teleosts, in which the position of minimum lateral displacement occurred posterior to the neurocranium at the center of mass, with amplitudes increasing from that point caudally (Videler and Hess, 1984; Dewar and Graham, 1994; Jayne and Lauder, 1995; Shadwick et al., 1998). Maximum lateral displacement occurred at the tail tip (Fig. 6A), but maximum intervertebral bending angle occurred just anterior to the caudal fin (Fig. 6B). The relationship between bending angle and body position differed between the two species. In the middle and posterior regions of the body, the angles were higher in chub mackerel than in kawakawa. The greater bending angles caused the greater lateral displacement and tailbeat amplitudes in the chub mackerel.

The intervertebral lateral displacement data allowed us to estimate yaw, or twice the maximum lateral displacement that occurs at the tip of the snout. On the basis of the predicted differences between thunniform and carangiform locomotion, thunniform swimmers should display less yaw because the anterior of the body should be held more rigid. However, a significant amount of yaw (2.3–5% FL) was found in a kinematic study of yellowfin tuna (Dewar and Graham, 1994). That range encompasses the values of 3.0–3.6% of body length in Atlantic mackerel *Scomber scombus* reported by Videler and Hess (1984). In the present study, yaw values for both species fell within the range for yellowfin tuna, and yaw did not differ significantly between the kawakawa and the chub mackerel ($3.5 \pm 1.2\% TL$ and $3.8 \pm 1.5\% TL$, respectively; means \pm S.D.). Thus, any contributions to drag made by the side-to-side movements of the snout should be similar in the two species.

Because neither intervertebral lateral displacement nor intervertebral bending angle varied significantly with speed in either kawakawa or chub mackerel, but did differ between the two species, the properties that determine the degree of axial lateral flexion must vary interspecifically and with position along the body in both species, but remain constant with changes in swimming speed. This suggests that morphological properties, such as the degree of articulation between adjacent vertebrae, the number, length and diameter of vertebrae, characteristics of the intervertebral joints, red muscle placement and/or the placement and strength of tendon attachments to the axial skeleton, are important determinants of intervertebral flexion. These characteristics will not change with swimming speed but may vary along the length of the body and are known to vary between tunas and mackerels (Collette, 1978; Graham et al., 1983; Westneat et al., 1993; Graham and Dickson, 2000).

Videler (1985) suggested that the bony appendages between vertebrae (pre- and post-zygapophyses) did not restrict lateral flexion, but rather that the nature of the intervertebral joints (the tightness of collagenous connection and the cross-sectional diameter of vertebrae) determined lateral flexibility in the Atlantic mackerel (*Scomber scombrus*). The diameters of the vertebrae in *S. scombrus* are very similar down the length of the body up to the twenty-fourth vertebra and then decrease caudally. This observation led Videler (1985) to suggest that mackerel have limited flexibility throughout much of their body, but increased flexibility near the peduncle, which is reflected both in the midline curvatures reported for this species and in the body bending data in the present study (Fig. 6). However, other studies have suggested that the zygapophyses are important determinants of lateral flexion (see below). Furthermore, the distribution of the myotomal muscle may also affect lateral displacement.

Differences in lateral bending properties with position along the body were also seen in Hebrank's (1982) study of the mechanical properties of isolated backbones of the skipjack tuna *Katsuwonus pelamis*, a species similar in body shape and vertebral number (40–41) to the kawakawa (Kishinouye, 1923; Godsil and Byers, 1944; Fierstine and Walters, 1968). Hebrank (1982) found three distinct regions of differing flexibility along the axial skeleton of skipjack tuna. All intervertebral joints along the body from the cranium to the intervertebral joint anterior to the thirty-fourth vertebra were similar in their bending properties. There was significantly less flexibility in the intervertebral joints between vertebrae 34, 35 and 36. Hebrank (1982) attributed this limited flexibility to the presence of the bony processes on those vertebrae that form the caudal keel (located at approximately 81–88% TL in *K. pelamis*). The intervertebral joints posterior to the keel within the caudal fin complex had greater flexibility, suggesting that the majority of thrust-producing lateral movements were restricted to the tail region in skipjack (Hebrank, 1982). A similar morphology has been described in the little tunny *Euthynnus alletteratus* (Nursall, 1956) and in *E. affinis*, in which the keel is on vertebrae 33, 34 and 35 (Godsil, 1954; see X-ray photograph in Fig. 7). Magnuson (1970) reported that the peduncular vertebrae of *E. affinis* are fused, the vertebrae anterior to the prepeduncular joint have long interlocking zygapophyses that would restrict lateral flexion and that vertebrae 30, 31 and 32, which form the two joints immediately anterior to the caudal keel, have poorly developed zygapophyses which would allow more lateral bending at these joints.

The pattern of less flexibility at the caudal keel relative to intervertebral joints located more anteriorly and posteriorly is consistent with the 'double-jointed' system described by Fierstine and Walters (1968), which has been suggested to be a characteristic of the unique thunniform locomotor mode of tunas (Fierstine and Walters, 1968; Dewar and Graham, 1994). However, the intervertebral angle data for the kawakawa in the present study do not support this view. In contrast to what would be predicted from Hebrank (1982), the bending angles

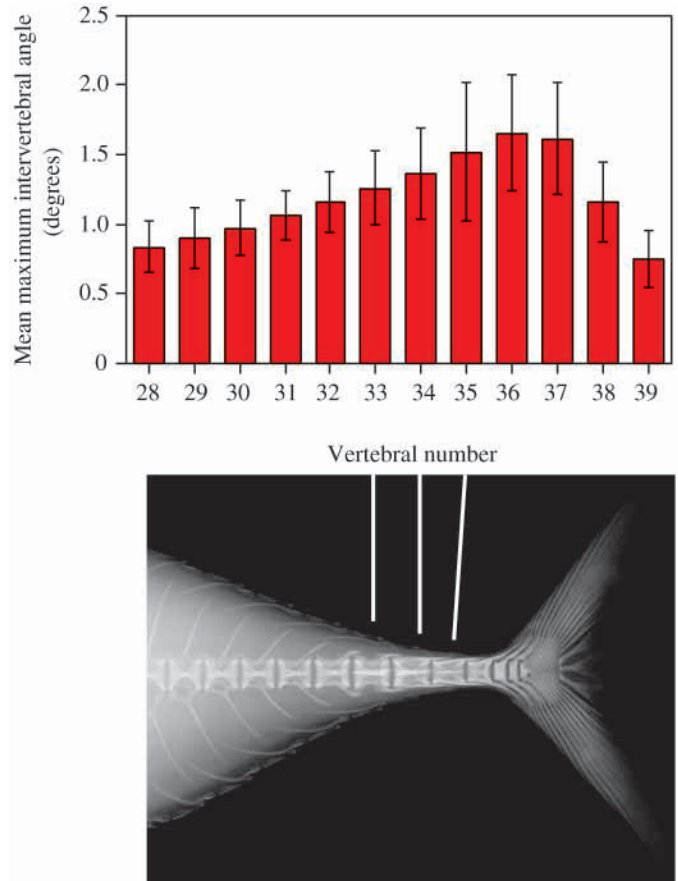


Fig. 7. Mean maximum intervertebral bending angles for the intervertebral joints anterior to vertebrae 28–39, the last vertebra, in the kawakawa and an X-ray of the caudal region (lateral view) of a 260 mm fork length kawakawa. The bony lateral keel is on vertebrae 33, 34 and 35, indicated by the lines. Values are means \pm S.D. ($N=3$).

at the vertebrae containing the caudal keel were not unusually low. The maximum bending angles for the intervertebral joints between vertebrae 33 and 35 (anterior to vertebrae 34 and 35) were higher than for more anterior joints (Fig. 7). The maximum bending angles were even higher for the joints anterior to vertebrae 36 and 37, but declined for the more posterior joints within the caudal fin complex (Fig. 7). Perhaps in steadily swimming tunas, flexion at the intervertebral joints is not influenced so much by the presence of the keel or the degree of articulation of the vertebrae along the axial skeleton as it appeared to be in the isolated vertebral columns studied by Hebrank (1982). In the intact body of a tuna, other features that may affect axial bending, such as the distribution of the locomotor muscle and muscle–tendon connections to the vertebrae, may be more important than the presence of the bony keel in determining the degree of bending that occurs at different positions along the body during sustained swimming (Videler, 1985; Westneat et al., 1993; McHenry et al., 1995; Shadwick et al., 1999; Graham and Dickson, 2000).

The unusual anterior, axial red muscle position in tunas and the anterior displacement of the entire myotomal muscle mass

may act to reduce axial flexibility and may affect the mechanical advantage, force generation and kinematics at the tail (Nursall, 1956; Westneat et al., 1993; Shadwick et al., 1999; Graham and Dickson, 2000). The anterior location of the red muscle and the relatively long posterior oblique tendons connecting to the backbone in tunas allow red muscle contraction at one position to cause bending at a position located more posteriorly; this focuses red muscle contractile force towards the tail and allows the anterior regions to undergo less lateral movement (Shadwick et al., 1999). This morphology also results in a lower mechanical advantage (input motion/output motion) and a higher velocity ratio (the inverse of mechanical advantage) in tunas compared with mackerels (Westneat et al., 1993), which is reflected in the lower tailbeat amplitudes and higher tailbeat frequencies in the kawakawa in the present study. Axial stiffness may also be affected by the nature of red muscle activation patterns in swimming fish (Knower et al., 1999) or may be increased if the axial muscles perform negative work (Long and Nipper, 1996). However, the latter is unlikely in tunas during steady sustained swimming, because recent studies of the skipjack tuna have shown that the red aerobic muscle fibers generate only positive work, with the force of muscle contraction being transferred to the caudal fin *via* stiff posterior tendons (Knower et al., 1999; Shadwick et al., 1999).

Using models based on the morphology of the tendons that attach the red muscle to the axial skeleton, and assuming muscle shortening of 10%, Westneat et al. (1993) estimated intervertebral bending angles of 3.6° for the little tunny (*Euthynnus alletteratus*) and of 3.3° for the king mackerel (*Scomberomorus cavalla*). The maximum intervertebral angles for both species in the present study did not exceed 2° except for the value of 3.5° at 85% *TL* in *S. japonicus* (Fig. 6B), which implies that red muscle shortening is less than 10% at the sustained speeds studied or that the models are oversimplified. Muscle shortening was not measured in the present study, but Shadwick et al. (1998, 1999) measured red muscle strain of $\pm 8\%$ of resting length in a 23 cm *FL* chub mackerel swimming at $1.75 FL s^{-1}$ ($40 cm s^{-1}$) and of $\pm 5\text{--}8\%$ of resting length in 40–49 cm *FL* skipjack tuna swimming $1.1\text{--}2.3 FL s^{-1}$.

Implications for the evolution of thunniform locomotion and endothermy in tunas

The interspecific differences in body bending patterns documented in the present study show that the kawakawa swims with less lateral movement than does the chub mackerel and support the hypothesis that the kawakawa and chub mackerel use different modes of locomotion. An increase in swimming efficiency has been postulated as the selective advantage of the thunniform locomotor pattern unique to tunas (Lighthill, 1970, 1975; Lindsey, 1978; Magnuson, 1978; Blake, 1983; Webb, 1975, 1998; Graham and Dickson, 2000). Thus, the kawakawa would be predicted to be a more efficient swimmer than the chub mackerel. However, the maximum sustainable swimming speeds and net cost of transport are the

same for these two species, and the total cost of transport is greater in the kawakawa, when the effects of fish size are accounted for (Sepulveda and Dickson, 2000). Thus, improved swimming performance seems not to be a consequence of reduced lateral flexion during sustained swimming, at least in the juvenile scombrids in the present study. It is possible that increases in efficiency may be manifested in the tunas when they reach larger sizes or during voluntary swimming *in vivo*. However, there may be trade-offs to the thunniform mode of locomotion that have not previously been considered. For example, we found that the reduced lateral displacement in the kawakawa results in a lower tailbeat amplitude than in the chub mackerel at the same speed. The kawakawa thus requires a greater tailbeat frequency to swim a given speed, and this should increase locomotor costs because each beat of the tail requires energy for muscle contraction. We also found that the amount of yaw, which is assumed to lead to the production of drag, did not differ significantly between the kawakawa and chub mackerel. There would, however, be some reduction in drag in the posterior regions of the body because of the reduced lateral displacement. The combination of this with the added cost of higher tailbeat frequencies may result in a net cost of transport that is similar in the kawakawa and the chub mackerel.

Rather than swimming efficiency acting as a selective force in the evolution of thunniform locomotion, the locomotor style of tunas may simply be a consequence of their ability to conserve metabolic heat to maintain elevated muscle temperatures (i.e. they are endothermic). The anterior and axial red myotomal muscle placement has been hypothesized to have contributed to the evolution of endothermy in tunas because it results in reduced conductive heat loss across the body surface (Carey, 1973; Block et al., 1993). The higher tailbeat frequencies at a given speed observed for the kawakawa may result in higher heat production rates within the red muscle and thereby contribute to endothermy.

Future studies of similar-sized bonitos, members of the sister taxon to tunas, and of the slender tuna *Allothunnus fallai*, the most basal member of the tuna clade (Graham and Dickson, 2000), may resolve these questions and help to ascertain whether thunniform locomotion evolved before or after the evolution of endothermy. The bonitos have many characters related to swimming performance that are intermediate between those of mackerels and tunas, but they are not endothermic (Kishinouye, 1923; Godsil, 1954; Collette, 1978). Using the only known kinematic data on bonitos swimming at controlled speeds (Pyatetskiy, 1970), we made a preliminary comparison between one (16.0 cm *TL*) Atlantic bonito (*Sarda sarda*) and individuals of approximately the same size from the present study. Since chub mackerel and kawakawa were distinguished on the basis of their tailbeat frequency *versus* speed relationships, these data were extracted for the Atlantic bonito from Pyatetskiy (1970). Because temperature may affect the swimming kinematics of these fishes, chub mackerel kinematic data at $18^\circ C$ (J. M. Donley, unpublished results), the temperature at which the Pyatetskiy (1970) study was

conducted, were also examined. The relationship between tailbeat frequency and swimming speed has a similar slope but lower y-intercept in the bonito than in the chub mackerel at the same temperature, which is opposite to the relationship found between the kawakawa and chub mackerel. This suggests that the bonito may be more similar to the chub mackerel and thus might utilize the carangiform swimming mode. However, because this comparison is based on very limited data, it does not shed much light on the question of when thunniform locomotion first appeared within the family Scombridae. A more comprehensive study of bonito swimming kinematics, including a quantitative body-bending analysis, is needed to characterize the swimming mode of the bonitos and to assess locomotor adaptations among the scombrids.

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