

MINIMUM SWIMMING SPEED OF ALBACORE, *THUNNUS ALALUNGA*

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ABSTRACT

Measurements of density and pectoral lifting area of albacore, *Thunnus alalunga*, were made and compared with those previously described for yellowfin tuna, *Thunnus albacares*; bigeye tuna, *Thunnus obesus*; and skipjack tuna, *Katsuwonus pelamis*. Albacore have densities within the range of yellowfin tuna of similar size. The pectoral lifting area of albacore was always greater than skipjack tuna but similar to yellowfin tuna and bigeye tuna for fish less than 70 cm long. Larger albacore had increasingly larger fins than did the other species.

Minimum speed necessary for hydrostatic equilibrium of albacore was calculated and compared at 50 and 80 cm fork lengths to values calculated for the species above. Albacore minimum speeds were slower than those for skipjack tuna, similar to those of yellowfin tuna, and greater than those of bigeye tuna. Density variations of albacore, attributed to fat content and gas bladder volume, significantly affected estimates of minimum speed. Calculated speeds were slower than those estimated for albacore tracked at sea or estimated from tag returns.

Albacore tuna, *Thunnus alalunga* (Bonnaterre), being negatively buoyant in seawater, must swim continuously to maintain their position in the water column. The albacore's long pectoral fins help to compensate for their negative buoyancy by providing lift, thus lowering the swimming speed necessary to maintain hydrostatic equilibrium.

A model developed by Magnuson (1970) proposes that the minimum swimming speed of a scombrid fish is set by the necessity to maintain hydrostatic equilibrium rather than to provide adequate gill ventilation. When the lift provided by the pectoral fins necessary to compensate for the weight of the fish in water is estimated, the corresponding swimming speed can be considered the minimum necessary for the maintenance of hydrostatic equilibrium. This model was used by Magnuson (1973) to compare minimum speeds of several species of scombrid fishes that differed in pectoral lifting area, body shape, body density, and the presence or absence of a gas bladder.

The purpose of this paper is to 1) estimate the minimum swimming speed of albacore; 2) compare the minimum swimming speed of albacore with those for other scombrids; and 3) compare calculated minimum swimming speeds of albacore with swimming speeds estimated from sonic tracking of albacore at sea and from long distance tag returns.

MATERIALS AND METHODS

To compute the minimum swimming speed with Magnuson's (1970) model, it is necessary to determine the mass of the fish, the lifting area, the density of the seawater, and the density of the fish. As the peduncle keels probably provide negligible lift (Magnuson 1973), they are excluded in the computation of minimum speeds.

To determine the mass of albacore, 477 specimens caught between long. 130° and 140°W and lat. 30° and 40°N during June 1974 were weighed to the nearest gram on a magnetically dampened pan balance and their fork lengths recorded to the nearest millimeter. Specimens were weighed and measured within 15 min after capture.

A regression $\ln M = \ln a + b(\ln L)$, where M is mass in grams and L is fork length in millimeters, was fitted to the length-mass data. The resultant equation was

$$M = 4.514 \times 10^{-5} L^{2.8746} \quad (1)$$

with 95% confidence limits on the exponent from 2.8245 to 2.9246.

The total pectoral lifting area (A) is equal to the projected surface area of the pectoral fins plus the projected body area between them, due to their analogy to wings in which the pressure distribution set up by the wings extends across the fuselage (Magnuson 1970). The pectoral lifting area was determined by tracing the outline of the

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detached left pectoral fin on a piece of paper having a thickness of 0.25 mm. The outlined form was cut out and weighed to the nearest 0.01 g on a balance. Projected area was calculated from a ratio of the paper weights to a standard, and doubled to account for the other pectoral fin.

Thirty-three 100 cm² pieces of the paper were measured with a micrometer and weighed to determine the affect of variations in paper thickness and cutting accuracy on the calculations. The thickness of the paper varied less than 1% around the mean, and cutting accuracy varied by $\pm 2\%$. The affect on calculations of pectoral lifting area was, therefore, assumed to be negligible.

The projected body area between the pectoral fins was determined by multiplying the body width at the pectorals by the width of the pectoral fin at its point of attachment to the body as measured on the fresh fish. Pectoral fin lifting areas were determined for 42 fish caught in the area described above and for 8 larger fish caught off Oregon in October 1974. The following relationship was established between the lifting area (A in square centimeters) and the fork length (L in millimeters):

$$A = 4.7351 \times 10^{-6} L^{2.6727}. \quad (2)$$

Albacore observed cruising under the baitboat kept their pectoral fins extended continuously at a sweepback angle of approximately 45°. The tips of an albacore's fins are also not rigid, and the effect of this on the lifting capacity of the fin has been ignored.

A water density (D_e) of 1.025 g/ml was determined from temperature and salinity data from the offshore region described above. This also equalled the mean water density within the near-shore albacore fishery.

Fish densities were determined for three groups of fish: group 1—seven fish caught during June 1974 in the offshore region; group 2—14 fish caught 60 miles south of San Diego on 23 July 1975, presumably 2 wk after they appeared off the coast; and group 3—37 fish caught on 13 September 1975 in the same region as group 2 but assumed to have been near the coast for 2 mo.

The group 1 fish were frozen immediately after capture and, when returned to the laboratory, thawed and weighed on a spring balance while suspended in seawater to determine the density of the fish in seawater (D_f).

Fish from groups 2 and 3 were weighed in seawater on a pan balance immediately after capture and their densities in seawater determined.

VARIATIONS IN DENSITY

The density of group 1 fish (Figure 1) is well within the range of those determined for fresh fish of similar size indicating that freezing and thawing probably had negligible affect on density determinations. All specimens were caught on or near the surface by jigline or rod and reel, and there was no difference in density attributable to one method of capture over the other.

Rough estimates of the development of the gas bladders of 21 fish in group 3 were made immediately after other measurements were completed. In specimens less than 56 cm FL (fork length), the bladder was small (approximately 1 cm wide and 8 or 9 cm long) and contained little or no gas. In specimens 60 to 70 cm FL, the bladder was approximately 5 cm wide and 16 cm long and filled with gas to a depth of 4 or 5 cm. Fish over 80 cm FL had bladders approximately 30 cm long and 10 cm in diameter which occupied a large volume of

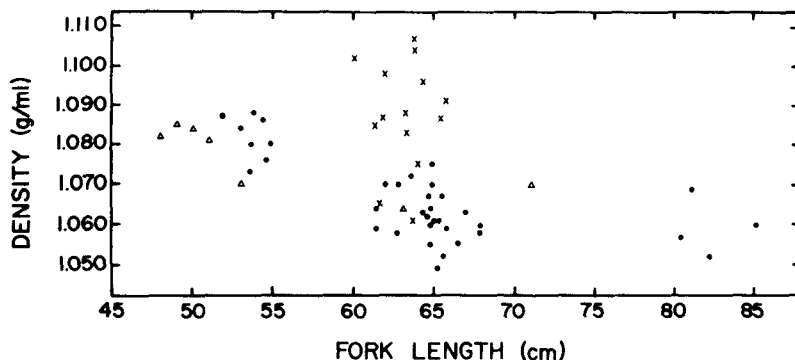


FIGURE 1.—Computed densities for three groups of albacore: group 1 (triangles); group 2 (crosses); and group 3 (dots). See text for explanation of groups.

the gut cavity. All developed gas bladders appeared full with two exceptions, and these may have been damaged during capture or dissection.

Seven albacore caught in September with fork lengths of 63 to 68 cm were examined to determine the effect of the gas bladder on density. Gas was removed from the bladder by a cannula (inside diameter = 1 mm) which was inserted through the ventral surface of the body while the fish was submerged in seawater, and the fish was then weighed while still submerged. The mean density increase with gas extraction was 0.007 g/ml (Table 1). Although this is probably a conservative estimate, the difference in density calculated before and after gas removal is used as the effect of the gas bladder on fish density. In an albacore less than 56 cm FL, the small gas bladder is not expected to affect density whereas the large and fully developed gas bladder of albacore greater than 80 cm FL should reduce density to a greater extent than was measured on the smaller fish above.

Densities of group 2 fish were considerably higher than those of similar size fish in groups 1 and 3 (Figure 1). Seasonal variations in density due to changes in fat content have been described for other pelagic species by Aleev (1963). Mass estimates were calculated from the length for each fish in all three groups using Equation (1), and compared with the observed values. The mean of the observed values for group 2 fell 403 g below the estimate from the regression line, ranging from 172 g greater to 999 g less. Because fish in group 2 had apparently just migrated into the area of capture, presumably from the central or western Pacific, the loss in mass was assumed to have been caused by the utilization of fat during migration. Group 1 would not yet have utilized this fat, and group 3 is assumed to have added fat by feeding in the rich coastal waters.

The densities in group 2 were recomputed on the assumption that the mass difference between the individuals and the regression curve is attributed to fat loss. An equation was developed by Magnuson (1970) relating the density (D_f) of a scombrid without a gas bladder to the percentage (P) of the total body weight that is fat. The equation

$$D_f = 1.100 - 0.0017 P \quad (3)$$

was used to recompute densities for the fish in group 2. The effect of the gas bladder on density was assumed to be 0.007 g/ml because fish in group

2 were in the same size range as the above fish for which gas bladder measurements were taken. This value was added to the observed density and the percentage body weight in fat calculated. The difference in mass (assumed to be fat loss) of each individual was then added and new densities determined with the increased percentage of body fat. The density effect of the bladder was subtracted from this value to yield a density adjusted for fat loss. When determining fat content in the fish, the density effect of the bladder was taken into account, except for those fish with measured densities greater than 1.100 g/ml, which is the level Magnuson (1970) chose as the density for a scombrid without a gas bladder. Fish with densities greater than 1.100 were assumed to have empty or damaged gas bladders, and the density difference due to the gas bladder was subtracted from the recomputed density.

Recomputed densities of group 2 are plotted in Figure 2 with the measured densities of groups 1 and 3. The close fit of the recomputed densities appears to support the assumption that fat content and gas bladder volume can account for the disparity in densities observed for group 2 in the original data. Density values are, therefore, expected to vary considerably depending on the development and condition of the gas bladder and the fat content of the fish when it is caught.

DETERMINATION OF MINIMUM SPEED

To estimate the minimum speed for hydrostatic equilibrium, it is necessary to calculate the amount of lift a fish must produce. The lift (L_f) required by a scombrid to attain hydrostatic equilibrium, expressed in dynes, is determined from the relation (Magnuson 1970)

$$L_f = M \left[\left(1 - \frac{D_e}{D_f} \right) 980 \text{ cm/s}^2 \right] \quad (4)$$

When the lift is assumed to be provided solely by the pectoral fins, and the coefficient of lift for the pectorals is assumed to be 1.0, then the equation for minimum swimming speed becomes (Magnuson 1970)

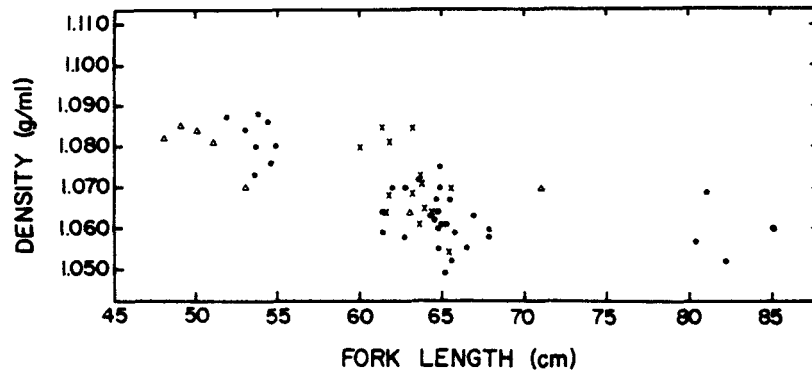
$$V = \left[\frac{L_f}{D_e / 2(A)} \right] \quad (5)$$

Calculations of minimum swimming speed from

TABLE 1.—Density changes in albacore following gas bladder deflation and resultant effect on estimation of minimum speed.

Characteristic	Albacore no.							Mean
	1	2	3	4	5	6	7	
Fork length (mm)	627	643	646	648	653	679	679	654
Density with gas bladder (g/ml)	1.058	1.063	1.062	1.055	1.061	1.060	1.058	1.059
Density without gas bladder (g/ml)	1.063	1.069	1.068	1.058	1.067	1.067	1.071	1.066
Change in density due to gas bladder (g/ml)	0.005	0.006	0.006	0.003	0.006	0.007	0.013	0.007
Minimum speed with gas bladder (cm/s)	45.0	48.6	48.7	44.5	49.8	47.3	47.9	47.4
Minimum speed without gas bladder (cm/s)	47.9	52.2	52.4	46.5	53.9	51.7	56.3	51.6
Change in minimum speed due to gas bladder (cm/s)	2.9	3.6	3.7	2.0	4.1	4.4	8.4	4.2

FIGURE 2.—Computed densities for three groups of albacore with group 2 densities (crosses) recomputed after correction for fat loss. Recomputation of group 2 densities is explained in the text.



this equation assume 100% extension of the pectoral fins.

The mass of the fish (M) and the lifting area (A) can be calculated using Equations (1) and (2), respectively. The density of the environment (D_e) is 1.025 g/ml. If we use $M = 2,540$ g, $D_e = 1.082$ g/ml, $A = 77.4$ cm² for a 50-cm fish, the calculated minimum speed V is 54 cm/s.

Density variations due to fat content and gas bladder volume can affect the minimum swimming speed necessary to maintain hydrostatic equilibrium. For a 65-cm albacore, a loss of 10% of its body weight in fat would result in a 10% increase in minimum speed. Loss or emptying of the gas bladder results in an 8% increase in minimum speed. Minimum speeds calculated from data on fish with full gas bladders and in good condition are therefore considered to be the minimum obtainable while retaining hydrostatic equilibrium.

COMPARISON OF MINIMUM SPEEDS OF FOUR SCOMBRIDS

Minimum speeds were calculated for albacore; yellowfin tuna, *Thunnus albacares*; bigeye tuna, *T. obesus*; and skipjack tuna, *Katsuwonus pelamis*, at fork lengths of 50 and 80 cm. The speeds are given in Table 2 with the density, mass, and pectoral lifting area used in the computations.

The minimum swimming speed of albacore

TABLE 2.—Estimated minimum speeds of four species of scombrids at fork lengths of 50 and 80 cm. The mass of the fish (M), pectoral lifting area (A), and density of the fish (D_f) used in the computations are also given.

Species	Fork length (cm)	M (g)	A (cm ²)	D_f (g/ml)	V (cm/s)
<i>Thunnus alalunga</i> ¹	50	2,588	77.40	1.082	57
	80	9,992	271.04	1.056	45
<i>Thunnus obesus</i> ²	50	2,429	96.63	1.047	32
	80	10,825	233.80	1.030	21
<i>Thunnus albacares</i> ³	50	2,501	91.56	1.087	55
	80	10,338	220.50	1.050	47
<i>Katsuwonus pelamis</i> ⁴	50	2,539	47.88	1.090	78
	80	12,567	137.20	1.096	107

¹Data from present paper.

² M , A , and D_f from Magnuson (1973).

³Extrapolated value.

⁴ M calculated from Chatwin (1959), A and D_f from Magnuson (1973).

decreases from 57 cm/s when they are 50 cm FL to 45 cm/s at 80 cm FL. The decrease is a direct result of the allometric growth of the pectoral fins (Yoshida 1968) and the gas bladder (Gibbs and Collette 1966). The gas bladder of albacore does not have significant development when the fish is less than 55 cm long, but has considerable volume at a fish length of 65 cm, and apparent complete development when the fish has reached 80 cm FL (data, this paper). Combined with the increasing length of the pectoral fins, the result is a relatively

abrupt drop in minimum speed between 60 and 70 cm FL (Figure 3).

Albacore and yellowfin tuna have very similar densities (Table 2), but the pectoral fins of albacore are smaller in young fish (Gibbs and Collette 1966), increasing very rapidly in size as the fish mature (Figure 4). Thus, small albacore have a faster minimum swimming speed than small yellowfin

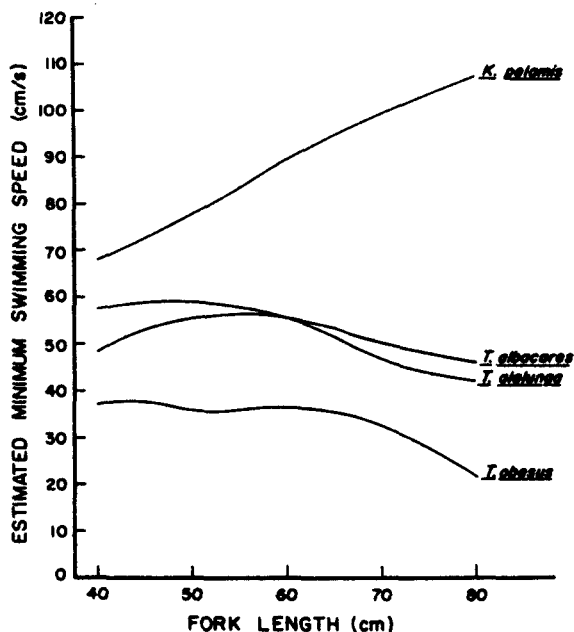


FIGURE 3.—The estimated minimum swimming speed of four scombrids using Magnuson's (1970) model for hydrostatic equilibrium.

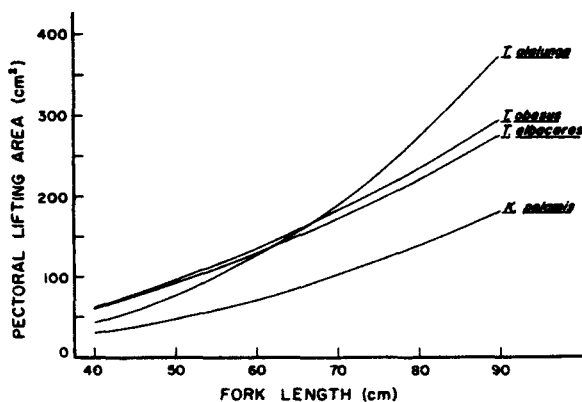


FIGURE 4.—Regression curves for pectoral lifting area (A) versus fork length. Curves for *Thunnus obesus*, *T. albacares*, and *Katsuwonus pelamis* are from Magnuson (1973). The curve for *T. alalunga* is from Equation (2) in the text.

tuna, and albacore over 65 cm have a slower minimum swimming speed than the same size yellowfin (Table 2, Figure 3) assuming similar fat content and gas bladder development.

Because bigeye tuna have a larger gas bladder than albacore and also have large pectoral fins, both of which grow allometrically (Gibbs and Collette 1966), their estimated minimum swimming speed is only half that of albacore at both 50 and 80 cm in length (Table 2).

The minimum swimming speed necessary for hydrostatic equilibrium of 50-cm albacore is 70% that of 50-cm skipjack and only 40% when each is 80 cm long (Table 2). Unlike albacore, skipjack have no gas bladder and always have small, short pectoral fins; therefore, skipjack tuna must swim faster as their mass increases in order to maintain hydrostatic equilibrium (Figure 3).

In Table 2 and Figure 3, density values for bigeye tuna were extrapolated beyond observed values and those of albacore were chosen from "fat" fish; therefore, actual values shown may not be exact, but the gross relationships among species are expected to hold true.

FIELD ESTIMATES OF ALBACORE SWIMMING SPEEDS

During August 1972, the National Marine Fisheries Service in cooperation with the American Fishermen's Research Foundation tagged six albacore with sonic tags and tracked their movements off the coast of Monterey Bay, Calif. (Laurs et al. 1972).²

Mean speeds observed during sonic tracking of three fish near 85 cm fork length were 95 cm/s during daylight hours and 62 cm/s during the night. These speeds are higher than the calculated minimum of 42 cm/s for a fish this size.

Each of two tagged albacore approximately 80 cm long, which were caught after a trans-Pacific migration, had a computed minimum or straight line speed (based on great circle route and time free) of 26 nautical miles/day or 55 cm/s (Japanese Fisheries Agency 1975). The calculated minimum speed of 45 cm/s is remarkably close to the estimated minimum migration speed of these two

²Laurs, R. M., H. S. H. Yuen, and J. H. Johnson. 1972. Study of the small-scale movements of albacore using ultrasonic tracking techniques. In Report of Joint National Marine Fisheries Service-American Fishermen's Research Foundation Albacore Studies Conducted during 1971 and 1972, p. 54-72. Unpubl. Rep. SWFC, NOAA, La Jolla.

fish but could be an artifact of many interacting processes and events.

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