# COMPARATIVE STUDY OF ADAPTATIONS FOR CONTINUOUS SWIMMING AND HYDROSTATIC EQUILIBRIUM OF SCOMBROID AND XIPHOID FISHES

JOHN J. MAGNUSON[1, 2]

## ABSTRACT

Scombroid fishes swim continuously with pectoral fins extended as lifting hydrofoils to counter their weight in water. Their gas bladder is often reduced or absent. Typical speeds were observed from seven species and compared with the speeds expected from them to maintain hydrostatic equilibrium. The expected speeds were computed from a model I developed using data on the lifting area of extended pectoral fins and the weight of the fish in water.

Lifting areas of the pectoral fins were determined from photographs of dead fishes. Mass-length relations were determined and converted to weight in water from data on water density and fish density.

Typical observed speeds varied among species from 0.33 to 2.19 lengths/sec. Scombroids of the same fork length differed greatly in mass, density, and pectoral fin areas. Swimming speed required for maintaining hydrostatic equilibrium should be greater for fishes with greater mass, higher density, and smaller pectorals. Expected speeds were computed. They were highly correlated with observed speeds, $r = +0.89$. Thus, the model accurately predicted typical swimming speeds of scombroids, which suggests that variations in mass, density, and the lifting area of the pectoral fins, through the mechanism of maintaining hydrostatic equilibrium, can account for about 80% of the variation in typical swimming speeds. Expected speeds (centimeters per second) generated from the model either increased with fork length or reached a maximum and declined for larger fish. The latter pattern occurred if gas bladders were relatively larger in older fish or even absent in younger fish.

Scombroids with faster typical speeds have larger dark muscles and higher concentrations of blood hemoglobin than those with slower speeds. Differences in body shape were not closely related to differences in typical speeds.

Larger fishes should have more difficulty maintaining a speed which is sufficient for hydrostatic equilibrium without a gas bladder or large pectoral fins. The occurrence of gas bladders and long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes. Both were more common among larger species. Each species with a maximum mass $\geq 70$ kg had a gas bladder while only 26% of those species $\leq 6$ kg had a gas bladder. Further analyses suggested that a gas bladder and large pectorals may be increasingly more important for large species if they are to swim at energetically prudent speeds.

Scombroid fishes are negatively buoyant, pelagic, oceanic fishes. The scombroids include the mackerels, tunas, and bonitos. They swim continuously with pectoral fins extended. This behavior produces lift that balances their weight in water. Some attain large size. Xiphoids are the largest teleosts and powerful swimmers that share the pelagic environment with the scombroids.

General considerations of buoyancy mechanisms of negatively buoyant fishes are discussed by Aleev (1963) and Alexander (1967, 1968).

In regard to scombroids, Magnuson and Prescott (1966) observed that continuous swimming was apparently not entirely determined by a need for gill ventilation, as Pacific bonito,

*Sarda chiliensis*, swam with their mouth closed as much as 40% of the time. Presumably the fish could have conserved energy by swimming more slowly with the mouth open more often. Minimum speed was also not regulated for food search (Magnuson, 1969); kawakawa, *Euthynnus affinis*, swam at the same speed day and night even though they were exclusively diurnal feeders. When deprived of food for several days, they swam slower and slower in absence of food stimuli. If typical speed had been regulated by feeding motivation, the fish would have been expected to swim faster—become more active—as motivation to feed increased.

Typical swimming speeds of *E. affinis* were well explained by the minimum speed required to produce sufficient lift on the pectoral fins to keep from sinking. Magnuson (1970) presented a model to predict minimum speed required of *E. affinis* to maintain hydrostatic equilibrium. Minimum speeds were estimated from the animal's weight in water and the lifting area, primarily of the pectoral fins.

Differences between the morphology and typical speeds of yellowfin tuna, *Thunnus albacares*, and *E. affinis* (Magnuson, 1966a) suggested that the variations in area of pectoral fins and volume of gas bladder might also be explained as various solutions for countering negative buoyancy. Many other specializations of scombroids related to swimming speed and activity may be adaptations to the speeds required for hydrostatic equilibrium rather than maximum, burst speeds (Magnuson, 1970).

In regard to xiphoids, a recent review on their functional morphology by Ovchinnikov (1970) did not consider the gas bladder or buoyancy mechanisms in discussions on the function of pectoral fins.

Purposes of the present paper are to (1) test whether the model mentioned above generally predicts typical swimming speeds of scombroid fishes, (2) consider the adaptive radiation in the morphology especially of the gas bladder and pectoral fins which together with swimming speed contribute to the mechanism by which scombroids maintain hydrostatic equilibrium, and (3) consider problems associated with large body size and maintenance of hydrostatic equilibrium among scombroid and xiphoid fishes.

## SWIMMING SPEEDS

Typical swimming speeds were observed for five scombroid fishes in 7.2-m diameter swimming pools at Kewalo Basin, Honolulu, Hawaii, from underwater photographs of wahoo, *Acanthocybium solandri*, swimming at sea, and from previously published records on *Sa. chiliensis* (Magnuson and Prescott, 1966). Observed swimming speeds were determined or available for seven species of six different genera.

Methods for obtaining swimming speeds were described by Magnuson (1969). Fishes were observed for short periods at 1- to 4-hr intervals (0000-2400) during their first month in captivity. Observations were made for two consecutive 24-hr periods during which the fish were fed and not fed (Figure 1). On fed days they were fed to satiation with thawed smelt or shrimp once or twice usually at 0900 and 1600 hr. Data collected during the "day not fed" and the "night after not fed" were used for the estimates of the minimum typical swimming speed to compare with body morphology. These estimates were based on 19-212 min (median 68 min) of recorded speeds for each species. With the exception of 36-cm long bigeye tuna, *Thunnus obesus*, where only 1 fish was observed, measurements from 6 to 40 fish (median 12 fish) made up each estimate. Water temperatures were 23°-26°C and salinity 33‰.

Typical speeds of *Ac. solandri* were from 17 cinema sequences averaging 2.59 sec each. The films were taken from underwater viewing ports in the RV *Charles H. Gilbert* and an observation raft described in Nakamura (1972).
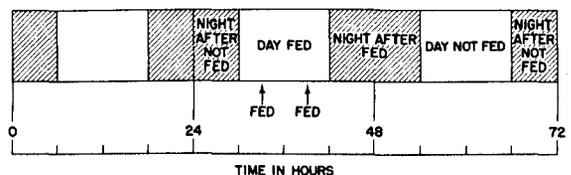


FIGURE 1.—Observation schedule for measurements of typical swimming speeds presented in Figure 2.

The observations that scombroid fishes swim continuously (Figure 2) would appear to be generalizable but the speeds, expressed either as body lengths per second (*l*/sec) or centimeters per second (cm/sec), differ considerably from one species to another or within species depending upon the size. Typical speeds ranged from 0.33 *l*/sec for *Ac. solandri* to 2.19 *l*/sec for the bullet mackerel, *Auxis rochei*. All species other than *Ac. solandri*, namely the skipjack tuna, *Katsuwonus pelamis*, *Sa. chiliensis*, *E. affinis*, *T. obesus*, *T. albacares*, and *Au. rochei*, had typical speeds greater than 1 *l*/se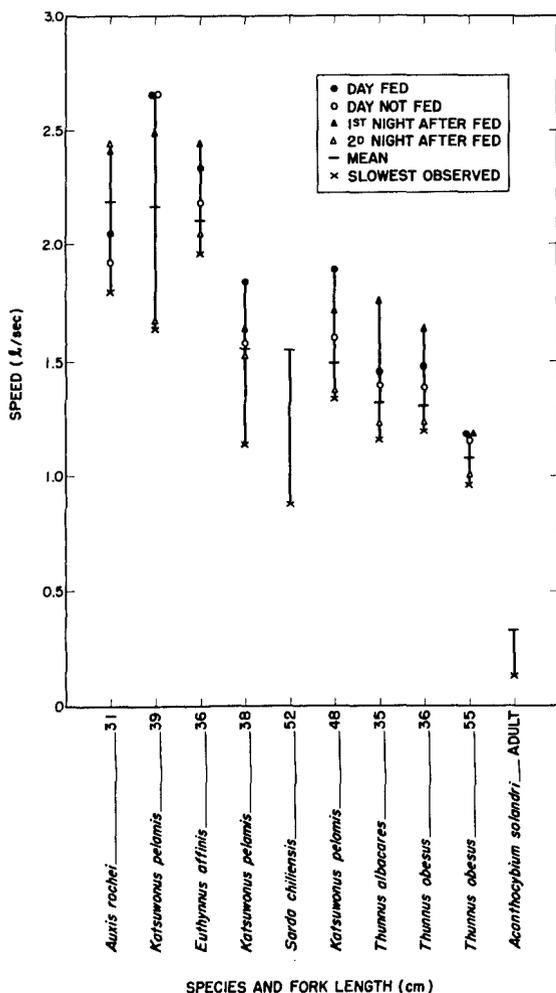c. None of the species ever stopped swimming. The slowest speeds observed ranged from 0.12 *l*/sec for *Ac. solandri* to 1.97 *l*/sec for *E. affinis*. The typical speed of *T. obesus*, 36 cm FL (fork length), was 1.31 *l*/sec but the larger 55-cm *T. obesus* swam only 1.08 *l*/sec. Three length groups of the *K. pelamis* were also observed and their speeds differed among sizes.

## SPEEDS REQUIRED FOR HYDROSTATIC EQUILIBRIUM

Variations in the typical swimming speeds among scombroids would result from differences in both the weight of the fish in water and the lifting area of the pectoral fins. Weight in water depends on mass and density of the fish. All specimens of chub mackerel, *Scomber japonicus*, and *Sarda chiliensis* used for morphometric and mass measurements were collected near Los Angeles, Calif. Specimens of all other species were collected in the central Pacific almost always near the Hawaiian Islands.

### Variations in Weight

Not all scombroids have the same mass-length relationship (Figure 3). *K. pelamis* was heaviest and *Ac. solandri* lightest at a given length. For example, at a length of 75 cm, *Ac. solandri* has a mass less than 2 kg and *K. pelamis* greater than 9 kg. Other species were intermediate.

When submerged in water the fish displaces water which also has mass. If the gas bladder is large enough, the volume of water that a fish displaces may have the same mass as the fish. The weight of the fish in water, or conversely the lift required to keep the fish from sinking, is equal to the excess mass of the fish times the acceleration of gravity (Alexander, 1967; Magnuson, 1970). The excess mass of the fish is the difference between the mass of the fish and the mass of the water it displaces. It can be computed by multiplying the mass of the fish by $(1 - \frac{D_e}{D_f})$ where $D_e$ is the density of the environment or seawater and $D_f$ is the density of the fish. The



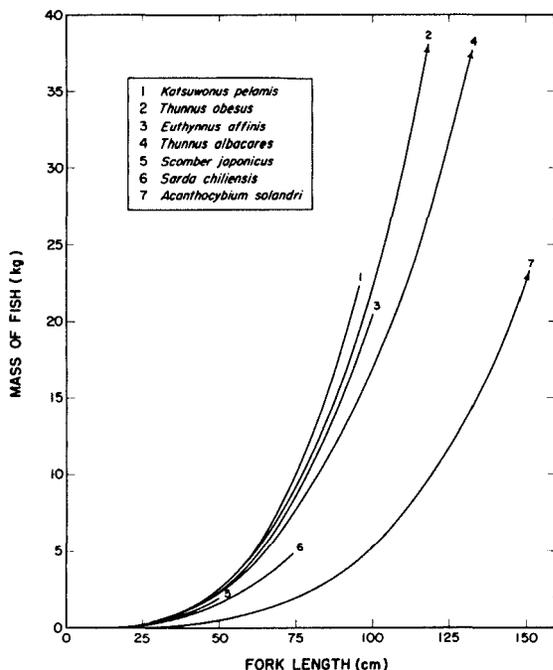FIGURE 2.—Typical swimming speeds of seven scombroids.

FIGURE 3.—Comparison of mass against length relationships among seven scombroid species. Information on regression equations in Table 4.

acceleration of gravity, $g$, is equal to approximately 980 cm/sec².

The influence of a gas bladder can be clearly seen by contrasting data for *K. pelamis* with *T. albacares*. Gas bladder volumes were determined with an x-ray method of Chang and Magnuson (1968) on fish immediately after they were killed. *K. pelamis* has no gas bladder but *T. albacares* has a gas bladder which grows allometrically, becoming progressively larger as the fish increases in mass (Figure 4a). *T. albacares*, 2 kg or less, has no gas in the bladder, but the gas bladder then grows rapidly until the fish is at least 8 kg. These differences in gas bladders of *K. pelamis* and *T. albacares* influence the density of the two species (Figure 4b). The density of *K. pelamis* remains approximately the same over the entire size range. However, once the gas bladder begins to grow in *T. albacares* the density of the fish becomes less, decreasing from approximately 1.09 g/ml for 2-kg fish to 1.05 g/ml for 10-kg fish. These differences in density have a corresponding influence on the lift

required to keep the fish from sinking (Figure 4c). The lift required for *K. pelamis* increases in almost direct proportion to the increase of mass. But the lift required to keep *T. albacares* from sinking increases more slowly as the density of the fish becomes less. In fact, the lift required to keep *T. albacares* from sinking appears to approach asymptotically a maximum near 200 × 10³ dynes.

Variations in the densities of various species and sizes can be examined in Table 1, where the mean densities of various species are given and the multipliers are computed to convert the mass of the fish to the lift required to keep them from sinking. All species with markedly lower densities, such as *Sc. japonicus*, *T. albacares*, *T. obesus*, and *Ac. solandri*, have gas bladders at some point in their life history. The more dense species, *Sa. chiliensis*, *Au. rochei*, *E. affinis*, and *K. pelamis*, have no gas bladder.

Lift to prevent the fish from sinking is 10 to 20 times greater for larger *K. pelamis*
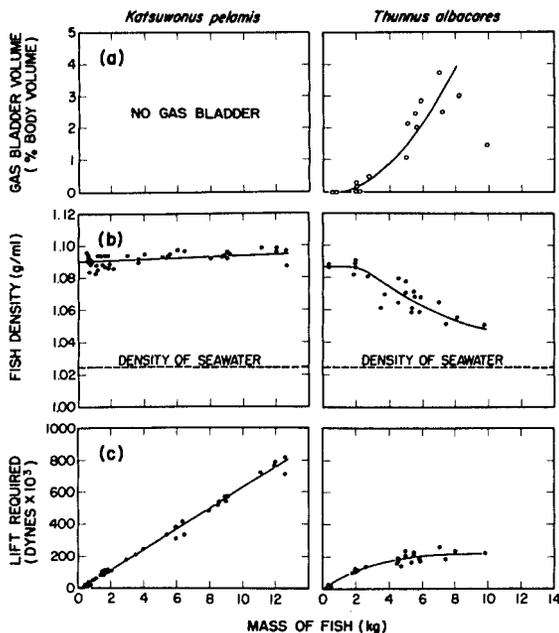


FIGURE 4.—Comparisons between *Katsuwonus pelamis* and *Thunnus albacares* of the relations between fish mass and (a) gas bladder volume, (b) fish density, and (c) lift required for hydrostatic equilibrium.

TABLE 1.—Densities $(D_f)$ of eight scombroid species by size group and the multipliers to convert mass of fish $(M_f$ in grams) to the lift ($L$ in dynes) required for hydrostatic equilibrium. Multipliers[1] computed for seawater with densities of 1) 1.022 g/ml and 2) 1.025 g/ml. Measurements by methods described by Magnuson (1970).

| Mass | Scomber japonicus | Acanthocybium solandri | Sarda chiliensis | Auxis rochei | Euthynnus affinis | Katsuwonus pelamis | Thunnus albacares | Thunnus obesus |
|---|---|---|---|---|---|---|---|---|
| **0.00-1.99 kg:** | | | | | | | | |
| Number of fish | 18 | | 3 | 12 | 36 | 47 | 3 | 1 |
| $D_f$ (g/ml): | | | | | | | | |
| Mean | 1.054 | | 1.075 | 1.086 | 1.087 | 1.090 | 1.086 | 1.066 |
| SD | 0.011 | | 0.004 | 0.002 | 0.004 | 0.003 | 0.003 | |
| Range | 1.024 | | 1.069 | 1.082 | 1.074 | 1.083 | 1.082 | |
| | 1.069 | | 1.080 | 1.089 | 1.093 | 1.096 | 1.088 | |
| Multiplier (1) | 28.0 | | 48.4 | 57.8 | 58.6 | 61.2 | 57.8 | 40.5 |
| (2) | 28.0 | | 45.7 | 55.1 | 56.0 | 58.5 | 55.1 | 37.7 |
| **2.00-3.99 kg:** | | | | | | | | |
| Number of fish | | | 10 | | 23 | 4 | 4 | 17 |
| $D_f$ (g/ml): | | | | | | | | |
| Mean | | | 1.080 | | 1.088 | 1.090 | 1.087 | 1.047 |
| SD | | | 0.006 | | 0.009 | 0.003 | 0.004 | 0.010 |
| Range | | | 1.067 | | 1.082 | 1.086 | 1.081 | 1.026 |
| | | | 1.086 | | 1.094 | 1.094 | 1.090 | 1.064 |
| Multiplier (1) | | | 52.7 | | 59.5 | 61.2 | 58.6 | 23.4 |
| (2) | | | 50.0 | | 56.8 | 58.5 | 56.0 | 20.7 |
| **4.00-5.99 kg:** | | | | | | | | |
| Number of fish | | | | | 3 | 4 | 12 | |
| $D_f$ (g/ml): | | | | | | | | |
| Mean | | | | | 1.091 | 1.094 | 1.068 | |
| SD | | | | | 0.004 | 0.001 | 0.007 | |
| Range | | | | | 1.086 | 1.093 | 1.059 | |
| | | | | | 1.095 | 1.095 | 1.080 | |
| Multiplier (1) | | | | | 62.3 | 64.6 | 42.2 | |
| (2) | | | | | 59.3 | 61.8 | 40.0 | |
| **6.00-7.99 kg:** | | | | | | | | |
| Number of fish | | | | | | 2 | 2 | |
| $D_f$ (g/ml): | | | | | | | | |
| Mean | | | | | | 1.097 | 1.058 | |
| SD | | | | | | 0.000 | 0.006 | |
| Range | | | | | | 1.097 | 1.052 | |
| | | | | | | 1.097 | 1.065 | |
| Multiplier (1) | | | | | | 67.0 | 33.4 | |
| (2) | | | | | | 64.4 | 30.6 | |
| **8.00-9.99 kg:** | | | | | | | | |
| Number of fish | | | | | | 6 | 2 | |
| $D_f$ (g/ml): | | | | | | | | |
| Mean | | | | | | 1.094 | 1.054 | |
| SD | | | | | | 0.001 | 0.002 | |
| Range | | | | | | 1.093 | 1.051 | |
| | | | | | | 1.096 | 1.056 | |
| Multiplier (1) | | | | | | 64.6 | 29.8 | |
| (2) | | | | | | 61.8 | 27.1 | |
| **≥ 10.00 kg:** | | | | | | | | |
| Number of fish | | 7 | | | | | 5 | |
| $D_f$ (g/ml): | | | | | | | | |
| Mean | | 1.028 | | | | | 1.096 | |
| SD | | 0.007 | | | | | 0.004 | |
| Range | | <1.022 | | | | | 1.088 | |
| | | 1.042 | | | | | 1.099 | |
| Multiplier (1) | | 5.78 | | | | | 66.3 | |
| (2) | | 2.94 | | | | | 63.5 | |
| **All sizes (without gas bladders only):** | | | | | | | | |
| Number of fish | | | 13 | 12 | 62 | 68 | | |
| $D_f$ (g/ml): | | | | | | | | |
| Mean | | | 1.078 | 1.086 | 1.087 | 1.091 | | |
| SD | | | 0.006 | 0.002 | 0.004 | 0.004 | | |
| Range | | | 1.067 | 1.082 | 1.074 | 1.083 | | |
| | | | 1.086 | 1.089 | 1.095 | 1.099 | | |
| Multiplier (1) | | | 51.0 | 57.8 | 58.6 | 62.0 | | |
| (2) | | | 48.2 | 55.1 | 56.0 | 59.3 | | |

[1] $[(1 - \dfrac{D_e}{D_f})980]$ where $D_e$ is the density of environment.

(no gas bladder) than for *Ac. solandri*, which has a large gas bladder. These differences would also significantly influence the speed required to maintain hydrostatic equilibrium, and on this basis species without gas bladders are expected typically to swim faster than those with gas bladders.

## Variations in the Lifting Area of Pectoral Fins

The lift produced by a hydrofoil is directly proportional to its lifting area, thus those species with a larger lifting surface should be capable of swimming at a slower speed, all other things being equal. The primary lifting surfaces of *E. affinis* are the pectoral fins (Magnuson, 1970), although other surfaces such as the caudal keel may counter some of the weight. The lifting area of the pectoral fins is the area of the extended pectoral fins as viewed from above plus the area of the body between the fins. It was determined for the various species from photographs of dead fish as described by Magnuson (1970).

Pectoral fins of scombroids are analogous to variable sweepback wings; they can be fully extended, swept back, or laid against the body (Magnuson, 1970). Species such as *E. affinis* and *K. pelamis* swam with the fins swept back about 40°, but the two species with the largest pectoral fins, *T. albacares* and *T. obesus*, swam with the fins swept back about 60° (Table 2). Sweepback angles measured from dead fish used for morphometric measurements were not as great as those from fish swimming in tanks. Measurements from dead fish were 7° and 14° for *E. affinis* and *K. pelamis* and 29° and 36° for *T. albacares* and *T. obesus*. Thus, some bias occurs in the estimation of the lifting area for swimming fish from the dead fish. This bias is probably slight because, although the actual area of the pectoral fin decreases rapidly as the fins are swept back, the total lifting area does not (Magnuson, 1970). Measurements of sweepback from other dead fishes used for morphometric measurements averaged 10° for *Sc. japonicus*, 24° for *Ac. solandri*, 16° for *Sa. chiliensis*, and 10° for *Au. rochei*.

Differences in pectoral fin lifting areas among scombroids are illustrated in diagrammatic dorsal views of seven species at the same length (Figure 5). Lifting areas differ markedly among species and among sizes for the same species (Figure 6). *T. obesus* has, among the species here, the largest lifting

TABLE 2.—Average sweepback of pectoral fins for swimming captive fishes. *n* equaled the number of fish. Λ was averaged for left and right fins.

| Species | Day fed Λ (degrees) Mean | Day fed Λ (degrees) SD | Day fed n | Day not fed[1] Λ (degrees) Mean | Day not fed[1] Λ (degrees) SD | Day not fed[1] n | Fed and not fed combined Λ (degrees) Mean | Fed and not fed combined Λ (degrees) SD | Fed and not fed combined n |
|---|---|---|---|---|---|---|---|---|---|
| *Euthynnus affinis* | 34 | 8.5 | 15 | 32 | 12 | 15 | 43 | 10 | 30 |
| *Katsuwonus pelamis* | 43 | 15 | 101 | 43 | 13 | 53 | 43 | 14 | 154 |
| *Thunnus albacares* | 61 | 3.1 | 11 | 55 | 3.7 | 3 | 60 | 4.0 | 14 |
| *Thunnus obesus* | 61 | 5.0 | 64 | 56 | 7.5 | 45 | 59 | 6.7 | 109 |

[1] Two days after fed for *E. affinis* and *T. albacares*; 1 day after fed for *K. pelamis* and *T. obesus*.
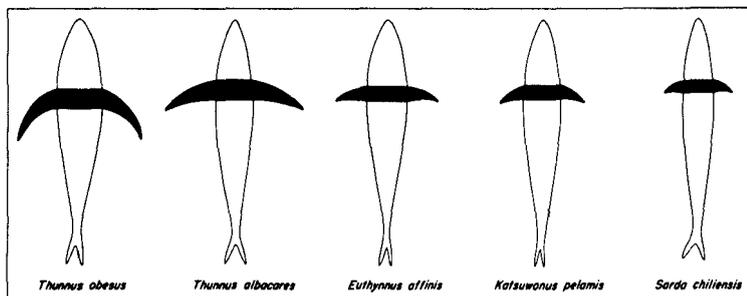


FIGURE 5.—Diagrammatic dorsal views of five scombroid species to dramatize the variation in the lifting areas of the pectoral fins for various species. Drawn from photographs of dead fish ca. 50 cm in fork length.

*Thunnus obesus*  *Thunnus albacares*  *Euthynnus affinis*  *Katsuwonus pelamis*  *Sarda chiliensis*

area at a given length, and *Ac. solandri* has the smallest. For example, at a fork length of 125 cm, *T. obesus* has a lifting area greater than 500 cm², whereas *Ac. solandri* has a lifting area near 150 cm² (Figure 6). These differences should have a marked effect on the minimum speed required to maintain hydrostatic equilibrium. Those with larger pectorals such as *T. albacares* and *T. obesus* should have a slower minimum speed than those with smaller pectorals.

## Predicted Swimming Speed

The model used by Magnuson (1970) to predict the minimum speed required for hydrostatic equilibrium was

$$V_{100} = \left[ \frac{L_t}{\rho/2 \; (C_{L_f} A_{f_t} + C_{L_k} A_k)} \right]^{\frac{1}{2}} . \quad (1)$$

All terms used here and elsewhere in this paper are listed below:

$l$ = fork length (cm)
$L_t$ = total weight of fish in water (dynes)
$L_f$ = all lift produced by the total lifting area of the pectoral fins (dynes)
$L_k$ = lift produced by keel (dynes)
$A_{f_e}$ = area of pectoral fins
$A_{f_t}$ = total lifting area of pectorals (cm²)
$A_k$ = lifting area of keel (cm²)
$C_{L_f}$ = coefficient of lift for the pectoral fins based on all lift produced by pectorals and on total lifting area of pectorals
$C_{L_k}$ = coefficient of lift for the keel
$V_{100}$ = speed of fish with pectorals continuously extended (cm/sec)
$\Lambda$ = sweepback angle of pectoral fins (degrees)
$D_e$ = $\rho$ = density of water = 1.022 g/ml in Kewalo tanks, 1.025 g/ml at sea
$D_f$ = density of fish (g/ml)
$M_f$ = fish mass.

To test predictive value of this model for a number of species, computed speeds were compared with observed speeds. Typical swimming speeds were computed twice: first, assuming the keel provided significant lift, and
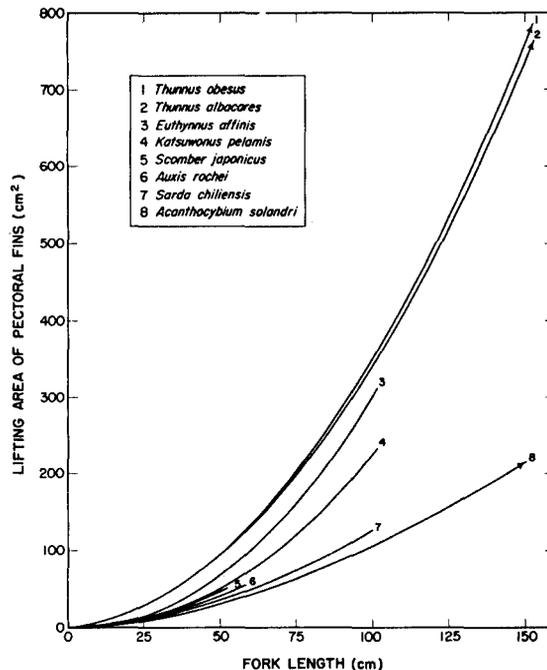


FIGURE 6.—Comparison of lifting area of pectoral fins against length relationships among eight scombroid species. Information on regression equation in Table 4.

second, assuming all the lift was provided by pectoral fins. Results from these computations and the data used to make them are presented in Table 3. Regressions in Table 4 were used to determine the mass of the fish and the area of the lifting surfaces for calculations of minimum hydrostatic speeds. The mass of the fish was converted to required lift by using the conversion factors from Table 1. Lift coefficients were from Table 7 of Magnuson (1970)—those determined for *E. affinis* on the basis of total lifting area of the pectorals.

Several comments should be made about the use of the lift coefficients from *E. affinis* for all species considered in the present text. The lift coefficient calculated on the basis of the total lifting area of pectorals represents lift on the pectorals, interference lift on the body owing to the pectorals, and the interference lift on the pectorals owing to the presence of the body. At best the coefficient is only a convenient but arbitrary standard frequently used in aerodynamic literature.

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TABLE 3.—Computed speeds required for hydrostatic equilibrium and the morphometric data used to make the computations along with the typical swimming speeds observed for scombroids. Lift coefficients from Magnuson (1970). Masses, areas, and required lift from equations in Table 4 and fork length of captive fishes.

| Species | $l$ (cm) | (a) $M_f$ (g) | (b) Multiplier to convert $M_f$ to $L_t$ | (a × b) $L_t$ (dynes × 10³) | $A_k$ (cm²) | (c) $A_{f_t}$ (cm²) | Surface loading of pectorals ($L_t \div A_{f_t}$) (dynes/cm²) | Computed hydrostatic speeds ($V_{100}$)[1] Without keel[2] (cm/sec) | (l/sec) | With keel[3] (cm/sec) | (l/sec) | Observed speed of fishes (cm/sec) | (l/sec) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Auxis rochei* | 31 | 498 | 57.8 | 28.8 | [4]3.3 | 17.7 | 1,630 | 56 | 1.8 | 57 | 1.8 | 68 | 2.2 |
| *Katsuwonus pelamis* | 39 | 1,090 | 61.2 | 66.7 | 5.51 | 27.4 | 2,430 | 69 | 1.8 | 70 | 1.8 | 84 | 2.2 |
| *Euthynnus affinis* | 36 | 832 | 58.6 | 48.8 | 5.41 | 31.6 | 1,540 | 55 | 1.5 | 56 | 1.6 | 76 | 2.1 |
| *Katsuwonus pelamis* | 38 | 996 | 61.2 | 61.0 | 5.20 | 25.9 | 2,360 | 68 | 1.8 | 69 | 1.8 | 59 | 1.6 |
| *Sarda chiliensis* | 57 | 2,320 | 52.7 | 122. | 11.8 | 45.9 | 2,660 | 72 | 1.3 | 71 | 1.2 | 88 | 1.5 |
| *Katsuwonus pelamis* | 48 | 2,180 | 61.2 | 133. | 8.79 | 43.7 | 3,040 | 77 | 1.6 | 78 | 1.6 | 72 | 1.5 |
| *Thunnus albacares* | 35 | 858 | 57.8 | 49.6 | 6.11 | 47.0 | 1,060 | 45 | 1.3 | 47 | 1.4 | 46 | 1.3 |
| *Thunnus obesus* | 36 | 854 | 40.5 | 34.6 | 5.87 | 52.1 | 664 | 36 | 1.0 | 38 | 1.0 | 47 | 1.3 |
| *Thunnus obesus* | 55 | 3,290 | 23.4 | 77.0 | 15.8 | 116. | 664 | 36 | 0.66 | 38 | 0.68 | 60 | 1.1 |
| *Acanthocybium solandri* | 125 | 512,400 | 65.78 | 71.7 | 51.6 | 163. | 440 | 29 | 0.23 | 28 | 0.22 | 741 | 0.33 |

[1] With equation 1.    [2] $C_{L_k} = 0$, $C_{L_f} = 1$.    [3] $C_{L_k} = 0.9$, $C_{L_f} = 0.8$.
[4] Estimated by comparing data with *K. pelamis* and then taking from *K. pelamis* regression.
[5] Estimated from length-weight relation given by Iversen and Yoshida (1957).
[6] From Table 1, $D_e = 1.022$ g/ml.
[7] Speed (cm/sec) = speed (l/sec) × length (cm) = 0.33 × 125 = 41.

Lift coefficients vary with sweepback, angle of attack, aspect ratio, the ratio of fin span to body width, and taper ratio (Lawrence and Flax, 1954). The differences in these parameters among species or within species were not evaluated, but comparisons made below between observed and calculated speeds suggest that the assumption about a constant lift coefficient based on total lifting area was not too bad. The coefficients used here should be more accurate for scombroids with short pectorals because *E. affinis* has short pectorals. The span of the pectorals, tip to tip, for *E. affinis* is about 2.4 times the body width.

Correlation coefficients (Table 5) were computed to discover how closely the observed swimming speeds were associated with fork lengths of the fish, the mass of the fish, the required lift to keep the fish from sinking, the lifting area of pectoral fins, the surface loading of pectoral fins, and the predicted swimming speed. Relations between observed speed and fork length, mass of fish, required lift, and lifting area of the pectoral fins were all nonsignificant statistically. But when required lift and the lifting area were considered jointly as surface loading of the pectorals, the correlation was significant ($P < 0.005$). Surface loading is the weight carried per unit area of lifting surface. Predicted speeds were also highly correlated with observed speeds (Table 5, Figure 7). The highest correlation, +0.89, between observed and predicted speeds in body lengths per second suggested that the hydrostatic equilibrium requirement of continuous swimming accounts for approximately 80% of the variation in observed swimming speeds. The model predicts typical swimming speeds of scombroids well and suggests that the variations in mass, density, and the lifting area of the pectoral fins can account for almost all variations in observed swimming speeds among scombroids.

Observed speeds averaged 9.8 cm/sec or 0.2 l/sec faster than computed speeds. The computation of $V_{100}$ assumed that the pectorals were continuously extended but this was not always the case. Thus, the fact that observed speeds were greater than $V_{100}$ is not surprising. *E. affinis*, for example, had the pec-

TABLE 4.—Regression equations (log $y$ = log $a$ + $b$ log $l$) with relevant data and 95% confidence intervals used to compute fish mass $(M_f)$, area of pectoral fins $(A_{f_e})$, lifting area of pectoral fins $(A_{f_t})$, and keel area $(A_k)$ for nine species of scombroid fishes. Measurements made by methods described in Magnuson (1970).

| $y$ | Species | $n$ | Range in $l$ (cm) | log $l$ | log $y$ | log $a$ | $a$ | $b$ | $S_b$ | SE est. | Confidence limit on $b$ | Confid. limit on $\overline{\log y}_{\overline{\log l}}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $M_f$ | Sc. japonicus | 20 | 26.9- 41.4 | 1.5434 | 2.7630 | −2.4353 | 0.00367 | 3.37 | 0.1458 | 0.0345 | ± 0.31 | ± 0.0725 |
| | Ac. solandri | — | — | — | — | — | — | — | — | — | — | — |
| | Sa. chiliensis | 13 | 45.3- 65.1 | 1.7524 | 3.3647 | -1.4100 | 0.0389 | 2.72 | 0.1770 | 0.0284 | ± 0.39 | ± 0.0625 |
| | Au. rochei | 11 | 33.9- 40.4 | 1.5546 | 2.9038 | -2.3143 | 0.00485 | 3.36 | 0.4557 | 0.0290 | | |
| | E. affinis | 63 | 31.6- 67.8 | 1.6251 | 3.1383 | -1.9666 | 0.0108 | 3.14 | 0.0388 | 0.0632 | ± 0.08 | ± 0.1265 |
| | K. pelamis | 68 | 24.1- 82.9 | 1.6395 | 3.1977 | -2.3098 | 0.00490 | 3.36 | 0.0180 | 0.0212 | ± 0.04 | ± 0.0424 |
| | T. albacares | 52 | 28.4-106.9 | 1.7859 | 3.6236 | -1.4828 | 0.0329 | 2.86 | 0.0420 | 0.0325 | ± 0.08 | ± 0.0653 |
| | T. obesus | 26 | 36.3-150.5 | 1.8421 | 3.8440 | -2.0173 | 0.00961 | 3.18 | 0.0868 | 0.1606 | ± 0.18 | ± 0.3315 |
| $A_{f_e}$ | Sc. japonicus | 25 | 26.9- 40.1 | 1.5407 | 1.0005 | -2.1543 | 0.00701 | 2.05 | 0.1864 | 0.0426 | ± 0.39 | ± 0.0881 |
| | Ac. solandri | 7 | 122.8-148.8 | 2.1112 | 1.9565 | -2.1931 | 0.00641 | 1.97 | 0.7864 | 0.0551 | ± 2.02 | ± 0.1417 |
| | Sa. chiliensis | 13 | 45.3- 65.1 | 1.7524 | 1.3020 | -2.2358 | 0.00581 | 2.02 | 0.4993 | 0.0800 | ± 1.10 | ± 0.1761 |
| | Au. rochei | 11 | 31.9- 40.4 | 1.5499 | 1.0380 | -2.0348 | 0.00923 | 1.98 | 0.7455 | 0.0586 | ± 1.69 | ± 0.1326 |
| | E. affinis | 37 | 33.7- 64.3 | 1.6440 | 1.3759 | -2.3010 | 0.00500 | 2.24 | 0.0940 | 0.0475 | ± 0.19 | ± 0.0964 |
| | K. pelamis | 33 | 24.3- 82.9 | 1.7271 | 1.3722 | -2.3840 | 0.00413 | 2.17 | 0.0562 | 0.0477 | ± 0.11 | ± 0.0974 |
| | T. albacares | 32 | 28.4-148.8 | 1.7920 | 1.9453 | -1.2351 | 0.0582 | 1.78 | 0.0631 | 0.0602 | ± 0.13 | ± 0.1229 |
| | T. obesus | 25 | 46.1-150.5 | 1.8496 | 2.0613 | -1.0477 | 0.0896 | 1.68 | 0.0445 | 0.0828 | ± 0.09 | ± 0.1713 |
| $A_{f_t}$ | Sc. japonicus | 25 | 26.9- 40.1 | 1.5407 | 1.3394 | -1.7012 | 0.0199 | 1.97 | 0.2520 | 0.0576 | ± 0.65 | ± 0.1481 |
| | Ac. solandri | 7 | 122.8-148.8 | 2.1112 | 2.2192 | -1.5031 | 0.0314 | 1.76 | 0.5700 | 0.0399 | ± 1.25 | ± 0.0878 |
| | Sa. chiliensis | 13 | 45.3- 65.1 | 1.7524 | 1.6472 | -1.4634 | 0.0344 | 1.78 | 0.3892 | 0.0613 | ± 0.86 | ± 0.1350 |
| | Au. rochei | 10 | 31.9- 40.4 | 1.5505 | 1.3546 | -1.2418 | 0.0573 | 1.67 | 0.7115 | 0.0557 | ± 1.64 | ± 0.1284 |
| | E. affinis | 37 | 33.7- 64.3 | 1.6440 | 1.6920 | -2.0182 | 0.00959 | 2.26 | 0.0855 | 0.0432 | ± 0.17 | ± 0.0877 |
| | K. pelamis | 33 | 24.3- 82.9 | 1.7271 | 1.7402 | -2.1255 | 0.00749 | 2.24 | 0.0545 | 0.0462 | ± 0.11 | ± 0.0943 |
| | T. albacares | 32 | 28.4-136.0 | 1.7920 | 2.1402 | -1.2154 | 0.0609 | 1.87 | 0.0478 | 0.0456 | ± 0.10 | ± 0.0931 |
| | T. obesus | 25 | 46.1-150.5 | 1.8496 | 2.2599 | -1.2090 | 0.0618 | 1.88 | 0.0391 | 0.0366 | ± 0.08 | ± 0.0757 |
| $A_k$ | Sc. japonicus | — | — | — | — | — | — | — | — | — | — | — |
| | Ac. solandri | — | — | — | — | — | — | — | — | — | — | — |
| | Sa. chiliensis | 13 | 45.3- 65.1 | 1.7524 | 1.0761 | -1.2104 | 0.0616 | 1.30 | 0.4784 | 0.0766 | ± 1.05 | ± 0.1687 |
| | Au. rochei | — | — | — | — | — | — | — | — | — | — | — |
| | E. affinis | 41 | 33.7- 67.8 | 1.6479 | 0.9548 | - 3.0017 | 0.000996 | 2.40 | 0.1501 | 0.2477 | ± 0.30 | ± 0.5011 |
| | K. pelamis | 34 | 24.3- 82.9 | 1.7128 | 1.0154 | - 2.8386 | 0.00145 | 2.25 | 0.0761 | 0.1308 | ± 0.16 | ± 0.2667 |
| | T. albacares | 36 | 34.0-136.0 | 1.8005 | 1.3687 | - 2.7033 | 0.00198 | 2.26 | 0.0986 | 0.1786 | ± 0.20 | ± 0.3624 |
| | T. obesus | 25 | 46.1-150.5 | 1.8496 | 1.4489 | - 2.8729 | 0.00134 | 2.34 | 0.1284 | 0.2387 | ± 0.27 | ± 0.4940 |

TABLE 5.—Correlations between observed speeds of scombroids and the fork length, mass, required lift for hydrostatic equilibrium, surface loading, and computed speeds with and without the keel included in the calculation.

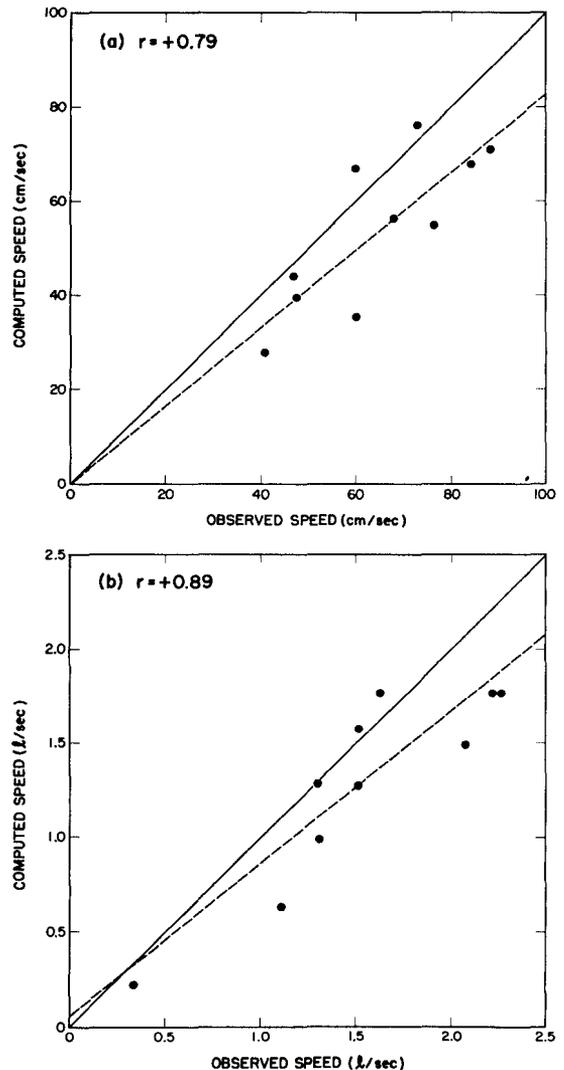| | Correlates | $r_{xy}$ | $P(n = 10)$ |
|---|---|---|---|
| $y$ | $x$ | | |
| $V_{obs}$ (cm/sec) | Fork length ($l$) (cm) | - 0.37 | N.S. |
| $V_{obs}$ (cm/sec) | Mass of fish ($M_f$) (g) | +0.44 | N.S. |
| $V_{obs}$ (cm/sec) | Required lift ($L_t$) (dynes) | +0.44 | N.S. |
| $V_{obs}$ (cm/sec) | Lifting area of pectorals ($A_{f_t}$) (cm²) | - 0.54 | N.S. |
| $V_{obs}$ (cm/sec) | Surface loading of pectorals (dynes/cm²) | + 0.77 | <0.005 |
| $V_{obs}$ (cm/sec) | $V_{100}$ without keel (cm/sec) | + 0.79 | <0.005 |
| $V_{obs}$ (cm/sec) | $V_{100}$ with keel (cm/sec) | + 0.78 | <0.005 |
| $V_{obs}$ ($l$/sec) | $V_{100}$ without keel ($l$/sec) | + 0.89 | <0.0005 |



FIGURE 7.—Correlation between observed swimming speeds of scombroids and the computed minimum speed for hydrostatic equilibrium (a) in cm/sec, and (b) in body lengths/sec. Data from Table 3. Solid line shows expectation for perfect agreement and dashed line is the linear regression of expected speed on observed speed. Correlation coefficients, $r$, are given on graph.

torals extended only about 75% of the time at typical speeds. The percent of extension of the pectorals varied greatly from species to species. The species with the longest pectorals, *T. obesus* and *T. albacares*, almost never appressed their pectoral fins while swimming at typical speeds.

Typical speeds of each species over its length range (Figure 8) were computed from equation 1 using values for $M_f$, $A_{f_l}$ from Table 4, and values of $D_e$ from Table 1, $\rho$ was set at 1.025 g/ml. Since the inclusion of lift from the keel had little effect on computed speeds (Table 3), the computations were made on the basis that all lift came from the pectorals.

The three species with the fastest predicted swimming speeds—*K. pelamis, Sa. chiliensis,* and *E. affinis*—have no gas bladder (Figure 8), while species with the lowest predicted speeds—*T. albacares, T. obesus, Sa. japonicus,* and *Ac. solandri*—have gas bladders. *Ac. solandri,* the species with the lowest predicted speed, has the largest gas bladder and the lowest density.

Among the three species without gas bladders, *K. pelamis* is the heaviest for its length and has the fastest minimum speed. The predicted speeds of *Sa. chiliensis* and *E. affinis* are quite similar, even though *E. affinis* is considerably heavier at a given length than

*Sa. chiliensis* (Figure 3). This difference results from the difference in the lifting area of pectoral fins (Figure 6). *E. affinis* has lifting areas twice the size of *Sa. chiliensis* at a given length. Interestingly, the minimum speeds predicted for *K. pelamis* were almost identical to the speeds predicted by Shuleikin

(1966) as most efficient for migration by aquatic organisms.

Among the species with gas bladders, *T. albacares* and *T. obesus* have the largest pectorals, but *Ac. solandri* with small pectorals swims the slowest. The difference appears to be primarily from differences in gas bladder volume and resulting density. The large gas bladder and low density of *Ac. solandri* more than compensate for small pectoral fins.

At larger sizes all species swim slower in body lengths per second (Figure 8b), but owing to the allometric growth of the gas bladder, both large *T. albacares* and *T. obesus* can swim at slower speeds even in absolute units (centimeters per second). Their weights in water increase more slowly than their lifting areas after the fish attain approximately 50 cm FL.

A word of warning about Figure 8 is that the predicted speeds are extrapolated outside of the range for which morphometric and body density data were available. In addition, the density data for *Ac. solandri* was based only on animals 125 cm long. Likewise, the density data on *T. obesus* was limited.

## OTHER FEATURES ASSOCIATED WITH BASAL SPEED

Scombroid fishes have many adaptations for efficient continued movement through the water. They have a high hemoglobin level (Klawe, Barrett, and Klawe, 1963), a large dark muscle (Kishinouye, 1923) for continuous locomotion (Rayner and Keenan, 1967), and a streamlined shape (Walters, 1962; Aleev, 1963; Alexander, 1967). The following analyses were to determine whether these adaptations were strongly associated with the basal or typical swimming speed. If differences in these characteristics varied closely with differences in typical speed, then I would argue that these adaptations were primarily selected for continuous slow swimming rather than maximum, burst speeds. Data on the burst or maximum speeds of these species are limited but do not indicate a strong association with typical speed. The burst speeds of 6-21 *l*/sec for *T. albacares* and 12-19 *l*/sec for *Ac. solandri* measured by Walters and Fierstine (1964) with a piscatometer at sea were approximately the same even though typical speed observed for *Ac. solandri* was less than one-fourth those of *T. albacares* (Table 3). Maximum speeds of four species measured photographically at sea or in shoreside tanks differ from species to species but not in relation to the typical speeds (Table 6).
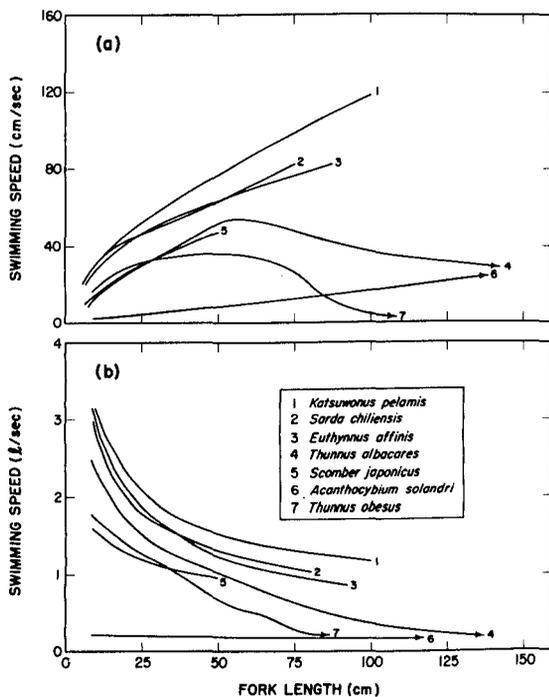


FIGURE 8.—Estimated minimum swimming speeds of seven scombroid fishes for maintaining hydrostatic equilibrium in (a) cm/sec and (b) body lengths/sec. Estimates from equation 1 and data in Table 4. See text for explanation.

TABLE 6.—Comparison of typical and maximum speeds observed from four scombroids.

| Species | Speed (*l*/sec) | | Source for maximum speeds |
| | Typical (Table 3) | Maximum | |
|---|---|---|---|
| *Thunnus albacares* | 1.3 | 10 | Yuen (1966) |
| *Sarda chiliensis* | 1.5 | 6.5 | Magnuson and Prescott (1966) |
| *Katsuwonus pelamis* | 1.5 1.6 2.2 | 14.4 | Yuen (1966) |
| *Euthynnus affinis* | 2.1 | 12.5 | Walters (1966) |

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Dark muscle size was determined from dissections of fresh material—the difference in the coloration of the dark muscle and the rest of the muscle block was sufficiently visible that the entire dark muscle could be removed and weighed. Its size was expressed as a percentage of fish mass. Body shape was determined from dorsal and lateral photographs of fresh dead fish. The maximum body height ($H$) and maximum body width ($W$) as a percent of fork length were averaged to represent the maximum thickness ($\frac{H + W}{2}$) of the body. The position of maximum thickness along the length of the fish was expressed as percent of fork length. It was determined by averaging the measurements from both dorsal and lateral views. Usually the position of maximum height for a species was 1 to 3% (of fork length) more posterior than the position of maximum width.

Data on dark muscle, blood hemoglobin, maximum body thickness, and the longitudinal position of maximum body thickness are presented for seven scombroid species in order of decreasing typical swimming speeds in Table 7. The size of the dark muscle (Table 7) ranged from 1.8% of the body mass for *Ac. solandri*, 125 cm long, to 10.3% of body mass for *Au. rochei*, 31 cm long. Within single species, the relative size of the dark muscle is smaller for larger animals. For example, *T. obesus* approximately 55 cm long have a dark muscle 7.7% of the body mass, whereas those 125 cm long have a red muscle of 4% of the body mass. I observed the same trend but with different magnitudes for other species for which a wide range of lengths were examined. Blood hemoglobin ranged from 10.4 g/100 ml of blood for *Ac. solandri* to 19.2 g/100 ml for *Au. rochei* (Table 7). This range includes values comparable to mammals—man for example has ca. 15 g/100 ml.

Typical speeds were positively correlated (Figure 9) with dark muscle size ($r = +0.86$, $n = 9$, $P < 0.005$) and with blood hemoglobin ($r = +0.83$, $n = 9$, $P < 0.005$). Approximately 70% of the variation in both dark muscle size and hemoglobin concentration are associated with variation in typical speeds. The size of the dark muscle and the concentration of hemo-

TABLE 7.—Relative size of dark muscle, blood hemoglobin concentration, and body morphology of various scombroids for comparison with the typical swimming speeds. Dark muscle and body morphology from present study. Fish ordered by decreasing typical swimming speeds (l/sec).

| Species | Fork[1] length (cm) | Observed speed (l/sec) | Dark muscle (%$M_f$) | Dark muscle 95% confidence interval on mean | Dark muscle n | Hemoglobin (g/100 ml) | Hemoglobin n | Hemoglobin Source | Fork[2] length (cm) | n | H Maximum body height (% l) | W Maximum body width (% l) | ($H + W$) ÷ 2 Maximum thickness (% l) | Distance from snout to position of maximum thickness (% l) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Au. rochei* | 31 | 2.19 | 10.3 | ±0.4 | 7 | 19.2 | — | Barrett and Williams (1965) | 32- 37 | 10 | 24.3 | 17.4 | 20.8 | 40.2 |
| *K. pelamis* | 39 | 2.17 | 8.4 | ±0.2 | 15 | 16.7 | — | Barrett and Connor (1962) | 37- 43 | 9 | 25.4 | 17.8 | 21.6 | 43.0 |
| *E. affinis* | 36 | 2.11 | 8.1 | ±0.5 | 22 | — | — | — | 37- 43 | 7 | 27.2 | 18.0 | 22.6 | 40.4 |
| *K. pelamis* | 38 | 1.55 | 8.4 | ±0.2 | 15 | 16.7 | — | Barrett and Connor (1962) | 37- 43 | 9 | 25.4 | 17.8 | 21.6 | 43.0 |
| *Sa. chiliensis* | 57 | 1.54 | 6.2 | ±0.4 | 4 | 12.9 | — | Barrett and Williams (1965) | 45- 65 | 12 | 21.8 | 15.1 | 18.4 | 39.5 |
| *K. pelamis* | 48 | 1.49 | 7.5 | ±0.3 | 18 | 16.7 | — | Barrett and Connor (1962) | 44- 57 | 12 | 26.3 | 18.6 | 22.4 | 42.0 |
| *T. albacares* | 35 | 1.31 | 7.4 | — | 2 | 14.3 | — | Barrett and Connor (1962) | 28- 45 | 6 | 27.8 | 16.8 | 22.3 | 41.2 |
| *T. obesus* | 36 | 1.31 | — | — | — | 15.6 | — | Barrett and Williams (1965) | 46- 48 | 3 | 28.6 | 17.9 | 23.2 | 35.5 |
| *T. obesus* | 55 | 1.08 | 7.7 | ±0.6 | 13 | 15.6 | — | Barrett and Williams (1965) | 50- 60 | 13 | 28.7 | 18.5 | 23.6 | 37.5 |
| *Ac. solandri* | 125 | 0.33 | 1.8 | ±0.5 | 6 | 10.4 | — | Barrett and Williams (1965) | 123-130 | 6 | 14.6 | 10.4 | 12.5 | 37.3 |

[1] Lengths of fish observed for swimming speed. Dark muscle data for fish of approximately same lengths.
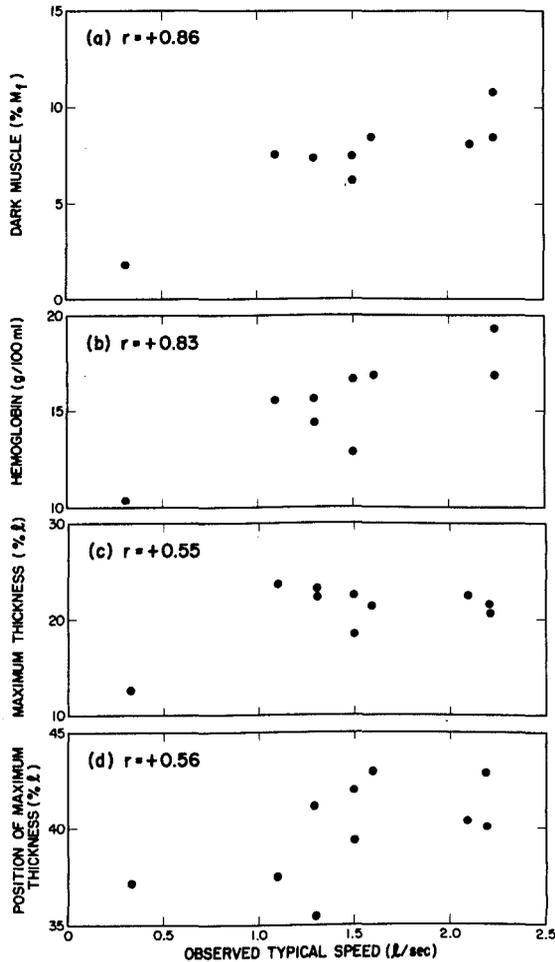[2] Lengths for body morphology.

FIGURE 9.—Relation between observed swimming speeds and (a) the relative size of the dark muscle and (b) the concentration of blood hemoglobin, (c) maximum thickness of body, and (d) the position of maximum thickness along the length of the fish. Data from Table 7. Correlation coefficients, $r$, are given on graph.

globin are also highly correlated ($r = +0.82$, $n = 8$, $P < 0.005$). As expected, the dark muscle used for continuous slow speed is larger for species with faster typical swimming speeds. However, concentrations of blood hemoglobin also appear to be keyed to typical speeds and routine metabolism. Differences in need to transport oxygen sufficient for burst speeds apparently influenced hemoglobin levels little. Perhaps this is so because an oxygen debt can be temporarily incurred for burst activity.

Typical speeds in body lengths per second (Figure 9c, d) were also correlated with maximum thickness of the body ($r = +0.55$, $n = 10$, $P < 0.05$) and with the position of maximum thickness ($r = +0.56$, $n = 10$, $P < 0.05$). If speed is given in centimeters per second, the correlation $+0.21$ and $+0.49$ with maximum thickness and the position of maximum thickness are not statistically significant at $P < 0.05$.

Maximum thickness of the body ranged from 12.5 to 23.6% of fork length but only *Ac. solandri* had a value less than 18% (Table 7). Only 30% of the variability in thickness is associated with typical speeds. Thus, these variations do not appear to be closely related to differences in typical speeds (Figure 9c) with the exception that the species with the lowest typical speed, *Ac. solandri*, also had a low thickness ratio that would not be expected to minimize drag. Minimum drag should result from thickness ratios near 22% (Alexander, 1967). Differences among *Auxis*, *Katsuwonus*, *Sarda*, and *Thunnus* vary over a narrow range near 22% in a manner not related to typical swimming speeds.

Scombroids with faster typical speeds tend to have the thickest part of their body more posteriad (Figure 9d). Only 30% of this variation is associated with basal speed, but the trend is sensible in that the more laminar flow profiles should occur in the faster fishes.

In conclusion, all four characteristics, size of dark muscle, hemoglobin concentration, body thickness, and the position of the thickest part of the body are statistically related in a sensible manner to the variations in slow typical speeds of scombroids. The relations are poorer for the two characteristics involved in reducing drag, apparently because these features are more important at burst speeds than at typical speeds.

## PROBLEMS ASSOCIATED WITH LARGE SIZE

Among the scombroid and xiphoid fishes, there is a great diversity in maximum body size, areas of pectoral fins, and the presence or size of the gas bladder. Data on these

TABLE 8.—Published data for scombroid and xiphoid fishes on maximum mass, the presence or absence of a gas bladder, and the relative length of pectoral fins. Species are ordered from smallest to largest known mass. Where only the length was known, mass was estimated from Figure 3 from a similarly shaped species.

| Species | Maximum size | | | Gas bladder | | Pectoral fins | |
| | Mass | Fork length | Source[1] | Present | Source[1] | Short (<20% FL) Long (≥20% FL) | Source[1] |
|---|---|---|---|---|---|---|---|
| | kg | cm | | | | | |
| Rastrelliger faughni | — | (20) | 24 | Yes | 24 | Short | 24 |
| Rastrelliger brachyosoma | — | (22) | 19 | Yes | 24 | Short | 19 |
| Rastrelliger kanagurta | — | (28) | 19 | Yes | 24 | Short | 19 |
| Cybiosarda elegans | 1 | — | 6 | No | 10 | Short | 9 |
| Scomberomorus multiradiatus | — | — | — | — | — | Short | 10 |
| Scomber japonicus | — | (35) | 3 | Yes | 24 | Short | 9 |
| Scomber australasicus | — | (45) | 1 | Yes | 24 | Short | 24 |
| Scomberomorus queenslandicus | 2 | (75) | 6 | — | — | Short | 10 |
| Scomberomorus sierra | 2 | (59) | 7 | — | — | Short | 10 |
| Scomberomorus koreanus | — | (60) | 10 | — | — | Short | 10 |
| Scomberomorus sinensis | — | (65) | 10 | — | — | Short | 10 |
| Scomberomorus guttatus | — | (82) | 6 | No | 9 | Short | 9 |
| Auxis rochei | — | (60) | 6 | No | 9 | Short | 8 |
| Scomberomorus concolor | — | (68) | 10 | No | 9 | Short | 9 |
| Sarda orientalis | 3 | — | 20 | No | 13 | Short | 13 |
| Scomber scombrus | 3 | — | 3 | No | 24 | Short | 9 |
| Auxis thazard | 4 | — | 15 | No | 9 | Short | 41 |
| Scomberomorus tritor | 4 | (98) | 31 | No | 9 | Short | 9 |
| Scomberomorus maculatus | 5 | — | 2 | No | 9 | Short | 9 |
| Euthynnus lineatus | 5 | — | 5 | No | 12 | Short | 12 |
| Sarda sarda | 5 | — | 4 | No | 21 | Short | 9 |
| Scomberomorus semifasciatus | — | (100) | 25 | No | 9 | Short | 25 |
| Scomberomorus niphonius | — | (101) | 25 | No | 9 | Short | 25 |
| Sarda chiliensis | — | (72) | 16 | No | 12 | Short | 9 |
| Scomberomorus lineolatus | 6 | — | 18 | No | 40 | Short | 40 |
| Grammatorcynus bicarinatus | 11 | — | 36 | Yes | 36 | Short | 36 |
| Orcynopsis unicolor | 13 | — | 32 | No | 32 | Short | 9 |
| Allothunnus fallai | 14 | — | 6 | No | 35 | Short | 6 |
| Thunnus atlanticus | 16 | — | 17 | Yes | 11 | Long | 11 |
| Scomberomorus regalis | 16 | — | 3 | No | 9 | Short | 9 |
| Euthynnus affinis | — | (100) | 6 | No | 21 | Both | 41 |
| Katsuwonus pelamis | 22 | — | 6 | No | 39 | Short | 14 |
| Euthynnus alleteratus | — | (122) | 23 | No | 12 | Short | 12 |
| Thunnus tonggol | 27 | — | 6 | No (rudimentary) | 11 | Both | 11 |
| Scomberomorus cavalla | 37 | — | 4 | No | 10 | Short | 25 |
| Thunnus maccoyii | — | (145) | 11 | Yes | 11 | Long | 11 |
| Thunnus alalunga | 44 | — | 6 | Yes | 11 | Long | 11 |
| Gasterochisma melampus | — | (165) | 6 | Yes | 9 | Short | 22 |
| Scomberomorus commerson | 59 | — | 29 | No | 10 | Short | 25 |
| Acanthocybium solandri | 63 | — | 6 | Yes | 9 | Short | 9 |
| Gymnosarda unicolor | 80 | — | 21 | Yes | 21 | Both | 37 |
| Tetrapterus pfluegeri | 90 | — | 33 | Yes | 28 | Both | 33 |
| Tetrapterus angustirostris | 90 | — | 33 | Yes | 28 | Short | 34 |
| Tetrapterus belone | 90 | — | 33 | Yes | 33 | Short | 33 |
| Istiophorus albicans | 90 | — | 33 | Yes | 28 | Short | 33 |
| Tetrapterus albidus | 90 | — | 33 | Yes | 28 | Both | 33 |
| Thunnus albacares | 135 | — | 6 | Yes | 11 | Long | 11 |
| Istiophorus platypterus | 150 | — | 30 | Yes | 28 | Short | 27 |
| Tetrapterus audax | 180 | — | 33 | Yes | 28 | Both | 34 |
| Thunnus obesus | 198 | — | 6 | Yes | 11 | Long | 11 |
| Xiphias gladius | 536 | — | 27 | Yes | 26 | Short | 27 |
| Makaira mazara (Jordan and Snyder) | — | (430) | 27 | — | — | Both | 27 |
| Makaira indica | 700 | — | 30 | Yes | 28 | Long | 27 |
| Thunnus thynnus | 730 | — | 38 | Yes | 11 | Both | 11 |
| Makaira nigricans | 900 | — | 33 | Yes | 28 | Both | 34 |

[1] Abe and Takashima (1959).
[2] Beardsley and Richards (1970).
[3] Bigelow and Schroeder (1953).
[4] Breder (1948).
[5] Calkins and Klawe (1963).
[6] Collette and Gibbs (1963).
[7] Collette, Talbot, and Rosenblatt (1963).
[8] Fitch and Roedel (1963).
[9] Fraser-Brunner (1950).
[10] Gibbs and Collette (pers. comm.).
[11] Gibbs and Collette (1966).
[12] Godsil (1954).
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[14] Godsil and Byers (1944).
[15] Gosline and Brock (1960).
[16] Hildebrand (1946).
[17] Idyll and de Sylva (1963).
[18] Jones and Silas (1962a).
[19] Jones and Silas (1962b).
[20] Kikawa (1963).
[21] Kishinouye (1923).
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[39] Waldron (1963).
[40] Williams (1960).
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characters were surveyed from the literature and are presented in Table 8. To determine whether the hydrostatic requirements of swimming have had some influence on or interact with the maximum size, the occurrence of gas bladders and the occurrence of long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes (Table 9). The distinction between short and long fins was arbitrarily set at a pectoral length of 20% or more of body length at any point in the life history.

Larger species apparently require a gas bladder but smaller species do not. All of the 14 species $\geq$ 70 kg had gas bladders but only 26% of 19 species $\leq$ 6 kg had gas bladders (Table 9). Medium size fish, 7-69 kg, were intermediate. The largest species without a gas bladder was *Scomberomorus commerson* at 59 kg (Table 8). Apparently the presence of a gas bladder is obligatory for those species greater than 60 kg. The gas bladder overcomes some weight in water, reduces minimum required speeds, and results in a design that could reduce energy expenditures for the larger species.

The larger fishes also tend to have relatively longer pectoral fins. Of the 15 species $\geq$ 70 kg, 67% have long pectorals at some stage in their life history but none of the 25 species $\leq$ 6 kg ever have long pectorals (Table 9). Medium size fish, 7-69 kg, were intermediate.

The two adaptations that make slower speeds possible, large pectorals and a gas bladder, have some tendency to occur together. Of 24 species without a gas bladder, 92% (22 species) have short pectoral fins and of 25 species with a gas bladder only 48% (12 species) have short pectoral fins (Table 8). Apparently small species require neither large pectorals nor a gas bladder to have a required swimming speed slow enough to maintain. For these species, in most cases, the advantages of not having a gas bladder or the drag associated with large pectoral fins have overweighed the advantage of a slow required speed in the course of evolutionary history. Apparently large species have achieved speeds slow enough for a consistent overall design by the joint effects of pectorals and the presence of a gas bladder. For these species if the gas bladder were large enough, large pectorals were not necessary; but if the gas bladder were not large enough, selection occurred for large pectorals.

Thus large species have a gas bladder and may or may not have long pectoral fins, while small species may or may not have a gas bladder and in neither case have long pectorals. In addition, large xiphoids with the large gas bladder may be able to use the pectoral for functions other than lift production. For example, the reduction of pelvic fins among xiphoids means that the pectorals must also produce any downward forces often ascribed to the pelvics.

The joint influences of maximum mass, body density, and lifting areas on minimum possible speeds give some perspective to the problem of large size (Figure 10). Surfaces of minimum swimming speeds were calculated for hypothetical 1-, 10-, and 100-kg scombroids with a lift coefficient of 1.0 for the pectoral fins. The keel was assumed to produce no lift. As expected, the smaller the gas bladder, that is, the greater $(D_f - D_e)$, the faster the fish must swim to maintain hydrostatic equilibrium. Also, the smaller the pectoral fins $(A_{f_l})$, the faster the fish must swim.

For small scombroids of 1 kg, changes in the density have little influence on required speed. And once the pectoral fins reach at least 50 cm² , further increases in area have little influence on required speed. A 1-kg scombroid would be about 40 cm long. Fish this long
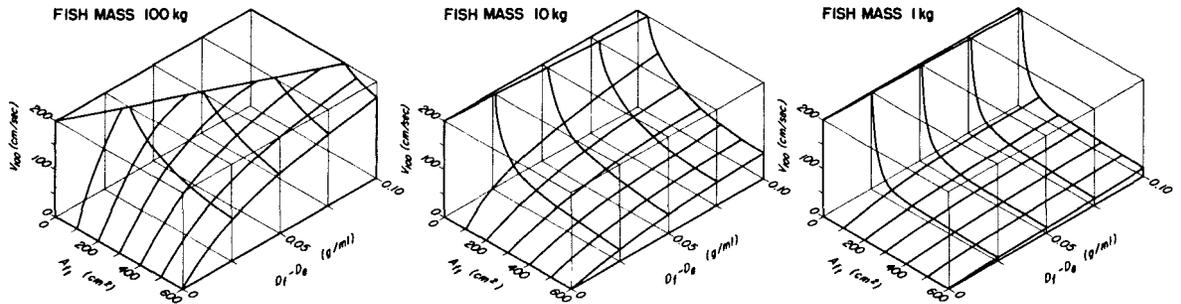
TABLE 9.—Occurrence of a gas bladder and the occurrence of long pectoral fins among scombroid and xiphoid fishes with different maximum masses. (A summary of Table 8.)

| Item | Maximum mass (kg) | | | | | | |
|---|---|---|---|---|---|---|---|
| | $\leq$ 6 | | 7-69 | | 70-900 | | Total |
| | No. | % | No. | % | No. | % | No. |
| Gas bladder: | | | | | | | |
| Present | 5 | 26 | 6 | 40 | 14 | 100 | 25 |
| Absent | 14 | 74 | 9 | 60 | 0 | 0 | 23 |
| Total | 19 | 100 | 15 | 100 | 14 | 100 | 48 |
| Pectoral fins: | | | | | | | |
| Long | 0 | 0 | 5 | 33 | 10 | 67 | 15 |
| Short | 25 | 100 | 10 | 67 | 5 | 33 | 40 |
| Total | 25 | 100 | 15 | 100 | 15 | 100 | 55 |

FIGURE 10.—Surfaces of minimum speeds required for hydrostatic equilibrium computed with different values of $A_{f_t}$ and $(D_f - D_e)$ for hypothetical scombroids with a mass of 1, 10, or 100 kg. Speeds were computed from equation 1 with $C_{L_f}$ set at 1.0 and $D_e$ or $\rho$ set at 1.025 g/ml.

should be able to maintain speeds near 100 cm/sec according to data from nonscombroids summarized in Figure 18 of Magnuson (1970). If there were some disadvantage to having a gas bladder, the loss of the bladder would not impose impossible levels of activity. Thus, the absence of a gas bladder and the occurrence of small pectorals among some small scombroids are consistent with the expectations of Figure 10 for 1-kg fish.

If hypothetical 10-kg and then 100-kg scombroids are considered (Figure 10), the presence of a gas bladder can be seen to be increasingly important to retain low levels of swimming activity. Required speed decreases rapidly with increasing pectoral size up to about 100 cm² for 10-kg fish and up to 200 cm² for 100-kg fish compared to 50 cm² for 1-kg fish. For a 100-kg fish and $(D_f - D_e)$ = 0.025, as lifting areas increase from 200 to 700 cm², required speed declines to about 100 cm/sec. This constitutes a significant reduction in speed and helps explain why 100-kg *Thunnus* have pectoral lifting areas as great as 700 cm². Large scombroids could reduce energy expenditures with larger than expected pectoral fins.

Computed minimum speeds were slower than 40 cm/sec for a 100-kg *Thunnus* (Figure 8). If its pectoral fins were as small as those of *K. pelamis*, it would have to swim at least 90 cm/sec; and if it also had no gas bladder, its minimum speed would have to be 160 cm/sec.

Adaptations that serve to make low activity possible for large scombroids and xiphoids may reduce required speed well below the endurance speed or even below the most physiologically efficient speed for a species to migrate. No data on maximum endurance speeds are available for fish this large, but endurance speeds of sockeye salmon, *Oncorhynchus nerka*, in centimeters per second, increases as length increases (Brett, 1965). The relationship, speed = 19 $l^{0.5}$, was determined from *O. nerka*, 8 to 54 cm FL, over periods only as long as 1 hr. Another data set (Hunter, 1971) for the jack mackerel, *Trachurus symmetricus*, is similar but based on shorter fish, 9-18 cm long, for longer periods, 6 hr. The relation was speed = 22 $l^{0.6}$. Extrapolation of these relationships from a salmonid, 50 cm long, or a carangid, 18 cm long, to scombroids, about 80 and 180 cm long, seems a bit unrealistic, but if done indicates that the required speeds, even for a large hypothetical fish with short pectoral and no gas bladder, are considerably below the extrapolated endurance speeds. And a 100-cm *T. albacares* with its gas bladder and large pectorals swims at speeds less than one-sixth the extrapolated endurance speeds of a salmonid and less than one-fourth the speeds predicted by Shuleikin (1966) as most efficient for migration. Shuleikin's theoretical model was based on the speed at which the fish expended the least energy to overcome internal friction of muscles and external friction from movement through water.

Perhaps for the large fish the capability for low speed, makes possible speeds which are energetically prudent in an ecological sense.

Unfortunately the energy balances for these species are not known, especially in regard to energy expended for energy encountered as prey and in regard to energy conserved by low activity during times of day that feeding does not occur. However, in my view the most consistent explanation for the adaptations that reduce required speeds among larger scombroids and the xiphoids is that the speeds must be energetically prudent; and the larger the fish, the less likely this would be possible without a gas bladder and large lifting hydrofoils. Alternatively, but less likely in my opinion, perhaps Brett's and Hunter's estimates of endurance speeds and Shuleikin's estimate of the most efficient speed for migration are overestimates of the physiological capabilities of large scombroids and xiphoids for sustained swimming.

Larger scombroids are then not able to avail themselves of whatever advantages have been achieved by some smaller species and individuals of scombroids by the loss of a gas bladder. Problems of large size among scombroids become either the possibility of an energetically imprudent basal speed requirement to maintain hydrostatic equilibrium or a loss (Magnuson, 1966b; Aleev, 1969), owing to a large gas bladder, in vertical mobility especially near the sea surface. I have observed *K. pelamis*, a species without a gas bladder, swim vertically upward at burst speeds in the top 10 m of the sea. Large scombroids and xiphoids would be expected to live either (1) deep in the water column where rapid vertical excursions have little effect on gas expansion or (2) immediately below the surface and making no rapid upward excursions. The pressure change experienced in an ascent from 10 m to the surface results in a 100% increase in the volume of an unrestricted gas bladder but an ascent from 100 to 90 m results in an increase in volume of only 10%. Alternatively, (3) to retain rapid vertical mobility, those with gas bladders and living near the surface would require remarkably strong-walled gas bladders that could maintain the gas at greater than ambient pressures. A casual review of the natural history of large scombroids and xiphoids suggests that all three alternatives are evidenced in one form or the other. The most unlikely species would be one with a large, thin-walled gas bladder that also cruised at 10 m below the surface and chased its prey or escaped predation vertically toward the sea surface.

## ACKNOWLEDGMENTS

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