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SWIMMING SPEED, TAIL BEAT FREQUENCY, TAIL BEAT AMPLITUDE, AND SIZE IN JACK MACKEREL, *Trachurus symmetricus*, AND OTHER FISHES

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ABSTRACT

The tail beat frequency and tail beat amplitude of jack mackerel, *Trachurus symmetricus*, 4.5 to 27.7 cm were measured at speeds of 15 to 212 cm/sec. Tail beat amplitude was a constant proportion of length at all speeds but tail beat frequency changed with speed; thus speed depended only on frequency of the tail beat and length. A simple mathematical model for estimating swimming speed from tail beat frequency and fish length was derived from the *Trachurus* data and applied to data for three marine fish — *Scomber japonicus*, *Triakis henlei*, and *Sardinops sagax* — and to data for freshwater fish from the literature. The general form of the model was $V - V_0 = L(KF - F_0)$ where V is fish speed, V_0 is length-dependent minimum swimming speed at minimum tail beat frequency F_0, and L is fish total length. The model represented a major improvement over previous equations because it provided an unbiased correction for length, was sensitive to specific differences, and provided a more accurate estimation of speed.

Of the variables that determine the swimming speed of a fish, the size of the fish, the frequency of the tail beat, and the amplitude of the tail beat are among the most important. Knowledge of the relationships between swimming speed and these variables is important not only for an understanding of the mechanism of locomotion in fish but because it may be used to forecast maximum swimming speeds (Bainbridge, 1958), to estimate swimming speeds indirectly by analysis of tail beat frequencies, and possibly to estimate fish size and make specific identifications of fish targets with doppler Continuous Transmission Frequency Modulated sonar (Hester, 1967).

Bainbridge (1958) described the relationship between tail beat frequency, tail beat amplitude, and size for three species of freshwater fish: dace, *Leuciscus leuciscus*; trout, *Salmo gairdneri* (*S. irideus*); and goldfish, *Carassius auratus*. He concluded that the amplitude of the tail beat increased with the tail beat frequency to about 5 tail beats/sec and thereafter became constant. Speeds above 5 beats/sec were dependent only on the frequency of the tail beat and the length of the fish. The relationship between speed, frequency, and length above 5 beats/sec was nearly the same in the three species studied; consequently, he used a single equation to express this relationship for all three species. No similar study exists for marine fish although some measurements of tail beat frequency and amplitude have been made incidental to other studies. Yuen (1966) measured the tail beat frequency of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, from cine photographs taken from the viewing port of a research vessel and Magnuson and Prescott (1966) measured the tail beat frequency of Pacific bonito, *Sarda chiliensis*, from cine photographs taken through a window in an oceanarium. The slopes of the lines relating tail beat frequency to speed in body lengths per second for skipjack and yellowfin tunas and bonito were sufficiently different from those of Bainbridge (1958), for Hester (1967) to speculate that species might be identifiable by this relationship. The measurements were taken from lateral photographs of free-swimming schools; thus the tail beat amplitude and the absolute

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Manuscript received January 1971.
FISHERY BULLETIN: VOL. 69, NO. 2, 1971.

size of the fish were not measured and tail beat frequency was measured over a limited speed range. Fierstine and Walters (1968) measured both tail beat frequency and amplitude of wavyback skipjack, *Euthynnus affinis,* from dorsal cine photographs of free-swimming fish in circular swimming pools but only five, one-beat sequences of swimming were analyzed.

The objective of the present study was to determine the relationships between swimming speed, fish length, tail beat amplitude, and tail beat frequency in a pelagic marine fish, jack mackerel, *Trachurus symmetricus.* To accomplish this objective, dorsal cine photographs were taken of fish swimming in currents of different speeds in a specially designed activity chamber. For comparative purposes tests were also run on three other marine fish: chub mackerel, *Scomber japonicus;* Pacific sardine, *Sardinops sagax*; and a shark, *Triakis henlei.*

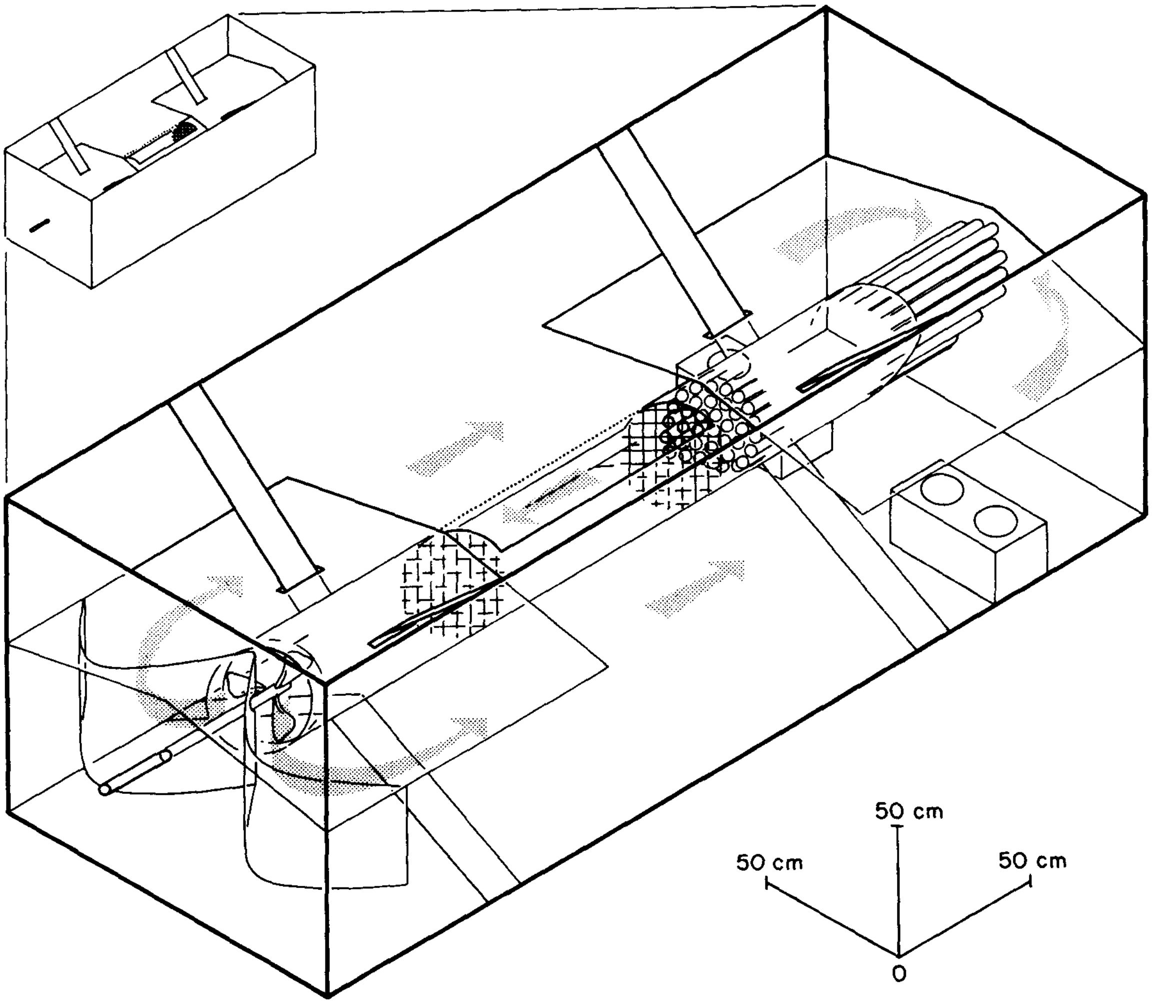

FIGURE 1.—Apparatus used to measure swimming speeds of fishes. Inset upper left apparatus shown with opaque walls; center, isometric, three dimensional scale drawing, walls, deflectors and other structures are shown as transparent for purposes of illustration; arrows indicate direction of current flow; and lower right, scale for vertical and horizontal planes of drawing.

APPARATUS

Swimming speeds were measured in an activity chamber (Figure 1) built after that of Beamish (1966). A fiber glass tube 230 cm long and 41 cm in diameter was immersed in an open bath. An 80-cm section of tube was the swimming compartment. The compartment had metal screens at the ends and a transparent acrylic plastic hatch which conformed to the contours of the tube. The walls of the tube within the swimming compartment were white and had black stripes spaced at 5.0-cm intervals to provide a visual reference for the swimming fish. Water velocity in the chamber was regulated by the speed of a 39-cm propeller driven by a variable speed 50-hp motor and by changing the screens at the two ends of the swimming compartment. Water was drawn into the compartment from the bath over deflectors, and through baffles and screens. The screens, baffles, and deflectors reduced turbulence and provided water of relatively uniform velocity throughout the swimming compartment. Their arrangement and design were determined empirically by measurement of the horizontal and vertical distribution of flow in the chamber.

The speed range of the apparatus was 12 to 212 cm/sec. The full range was obtained by changing the screens at the ends of the swimming compartment. A velocity range of 12 to 69 cm/sec was obtained when screens of 39% open area were used, one of 15 to 139 cm/sec for screens of 56% open area, and one of 19 to 212 cm/sec for screens of 75% open area.

A digital voltmeter measured to the nearest millivolt the voltage produced by a voltage generator attached to the propeller shaft. The voltage produced by the generator was proportional to propeller revolutions and was used to regulate them. An impeller flowmeter (Marine Advisers Inc., Model B-7C)[2] was used to relate propeller revolutions in volts to water flow in the apparatus. The meter sampled an area 7.6 cm in diameter and had an accuracy of ± 2.5 cm/sec when moved through static water at a known speed (for a description of the meter and a calibration curve see Olson, 1967).

Propeller revolution was related to water speed in the chamber by three series of calibrations, one for each of three screen types used. Nine to 19 different speed levels were measured in each series of calibrations. More levels were required for slow speed ranges than for fast ones because the response of the flowmeter was nonlinear at low speeds. At each level water speed was measured at 12 different radial positions midway in the swimming compartment. The speed of the water at a given level was the average of the 12 measurements, adjusted for the extent of the area sampled by the meter (Tranter and Smith, 1968). Variation among the 12 sampling points did not exceed ±10% of the mean speed and was usually much lower. The relationship between mean water speed in the chamber and propeller revolutions was linear, and the error in estimating the mean water speed from revolutions did not exceed ± 0.2 cm/sec. Thus, the principal sources of error in estimating the speed of the water in which a fish swam were the possible 10% variability in flow within the chamber and the ± 2.5 cm/sec accuracy of the flowmeter.

Fish swimming in the compartment were assumed to be swimming at the mean speed of the water in the compartment. They were photographed from above with a 16 mm high-speed motion picture camera at speeds of 64 to 200 fps. Camera speed was adjusted to provide about 10 frames per complete tail beat. A viewing box floated on the water surface above the swimming compartment to eliminate distortion in the photographs caused by ripples.

METHODS

Film was analyzed by use of a coordinate reader and digitizer (Hunter, 1966) and a computer program was used to calculate tail beat frequency and tail beat amplitude from the digitized information. One tail beat was one complete oscillation of the tail, and the tail beat frequency was the number of beats per second. Tail beat amplitude was the distance in centimeters between the lateral most excursion of

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[2] Reference to commercial products does not imply endorsement.

the tip of the tail measured perpendicular to the axis of progression plus the mirror image of that measurement on the other side of the axis of progression.

The film sequences selected for analysis were usually ones in which the fish held a constant position in the current and swam steadily. Occasionally at higher speeds it was not possible to obtain such a sequence because the fish did not maintain a constant position but rather accelerated and decelerated. In this case a sequence was chosen in which no net movement existed between the beginning and end of the sequence although the fish moved slightly forward and backward within the sequence. Usually 5 complete tail beats were analyzed per speed level but occasionally as few as 2.5 and as many as 11 were analyzed.

Sixteen speed levels were used in the experiments; seven of the levels, 15 to 60 cm/sec, were graduated at intervals of 25% of the preceding level and nine of the levels, 69 to 212 cm/sec were graduated at intervals of 15%. A speed level interval greater than 10% was used because of the possible 10% variability in flow within the swimming compartment.

A grand total of 176 speed tests was analyzed for 14 jack mackerel, varying in total length from 4.5 to 27.7 cm. Owing to the differences in length, no fish was able to swim at all levels. All 14 fish swam at five levels, 24, 30, 38, 48, and 60 cm/sec, and all but the two smallest fish swam at the next five higher levels, 79, 91, 105, 121, and 139 cm/sec. Only fish of 16 cm or larger were tested at speeds above 139 cm/sec and only those less than 16 cm were tested at 15 cm/sec.

Other species were tested for comparative purposes but fewer observations were made. Seventy-four swimming sequences of five *Scomber*, 26.3 to 32.2 cm total length, were analyzed, nine sequences of five *Sardinops*, average length 13.6 cm, and seven sequences of one *Triakis*, 23.6 cm.

All fish were tested singly except for *Sardinops*, which was tested in a group of five. Fish were held in the swimming compartment at a low speed for about 30 min before an experiment began. Seawater temperature ranged from 17.0° to 19.5° C among experiments but did not vary over a degree within an experiment.

RESULTS

The tail beat amplitude of *Trachurus* did not change with speed but was constant at all speed levels and was directly related to length (Figures 2 and 3). Tail beat frequency, on the other hand, changed with speed and, therefore, was the only speed modulator measured in these experiments. In all species studied the relationship between tail beat frequency and velocity

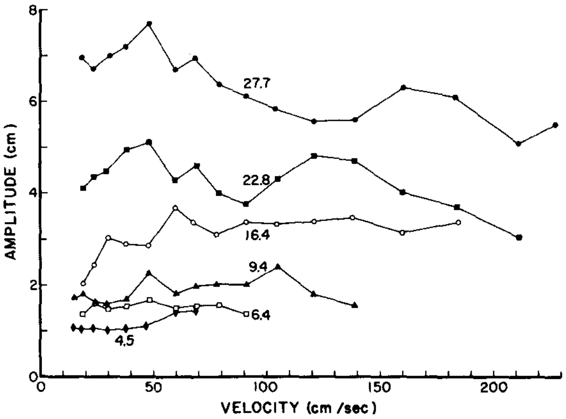

FIGURE 2.—Tail beat amplitude at various speeds for six *Trachurus*, 4.5 to 27.7 cm total length.

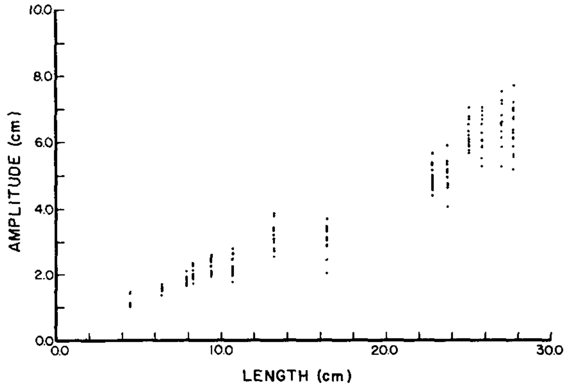

FIGURE 3.—Relationship between tail beat amplitude and total length for 14 *Trachurus*, 4.5 to 27.7 cm total length. ($A = 0.23177L$, $s_{yx} = 5.068$, and $N = 176$.)

was linear throughout the range of test speeds, but the slope and intercept of the regression lines varied with fish length (Figure 4, Table 1).

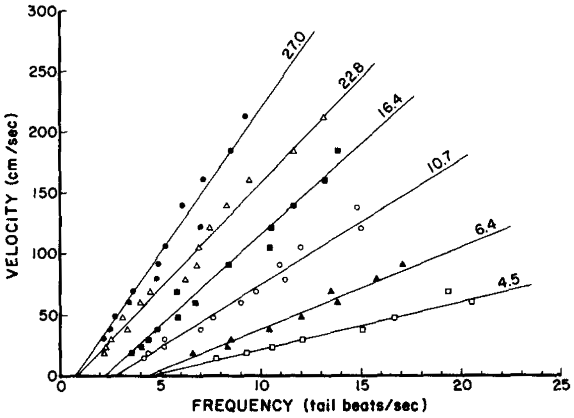

FIGURE 4.—Relationship between speed and tail beat frequency for six *Trachurus*, 4.5 to 27.0 cm total length. Equations for regression lines shown in figure are given in Table 1.

TABLE 1.—Standard deviation (s_{yx}), intercept (a), and slope (b) for regression of speed (cm/sec) on tail beat frequency and slope and intercept for regression of speed/length on frequency for *Trachurus*.

Length (cm)	N	Speed (cm/sec) on frequency			Speed/length on frequency	
		a	b	s_{yx}	a	b
4.5	8	−17.786	3.996	3.889	−3.952	0.888
6.4	9	−29.761	6.838	4.284	−4.650	1.068
7.9	11	−37.527	8.326	4.135	−4.624	1.054
8.3	11	−39.736	9.374	10.096	−4.787	1.129
9.4	13	−35.241	8.953	5.258	−3.749	0.952
10.7	13	−29.012	10.431	5.612	−2.781	0.975
13.2	13	−19.860	11.514	10.762	−1.504	0.873
16.4	14	−32.541	14.780	9.060	−1.984	0.901
22.8	15	−15.407	17.497	6.945	−0.676	0.767
23.7	13	−13.723	19.753	6.457	−0.579	0.833
25.0	15	−33.403	23.394	11.832	−1.336	0.936
25.8	13	−23.220	21.730	8.734	−0.900	0.842
27.0	13	−20.521	23.960	9.157	−0.760	0.887
27.7	15	−11.240	20.509	9.182	−0.406	0.740
Total	176					

The length-dependent differences in intercept were probably a function of differences in minimum speed and minimum tail beat frequency. Fish have a minimum tail beat frequency and a minimum swimming speed below which they cannot swim by movement of the caudal fin and these minima were a function of body length. In the past, speed was scaled directly to length; that is, speed was divided by length and regressed on frequency (Bainbridge, 1958; Magnuson and Prescott, 1966; Yuen, 1966). Our data suggest, however, that division of speed by length would introduce bias because of the existence of a minimum speed and tail beat frequency different from zero, the dependence of minimum speed on length, and possible length-dependent differences in the slope of the regression of speed on frequency. For example, when we divided speed by length, size-dependent differences in intercept and possibly the slope still existed (Table 1, last two columns). In addition a curvilinear trend is introduced at low speeds in the combined data because of the lack of an intercept (minimum speed) correction. Thus an equation that relates speed to tail beat frequency for fish of different length must include an adjustment for size-dependent differences in minimum swimming speed, minimum tail beat frequency, and perhaps also for size-dependent differences in the slope coefficient.

The existence of size-dependent variables introduces certain problems in the interpretation of these data because of the possibility that specific differences in size dependency may exist. For example, differences exist among species in the coefficients used to relate size to various swimming characteristics such as burst and sustained speeds (Bainbridge, 1960) but it is uncertain whether or not these differences reflect real specific differences or if they are simply differing estimates of a common coefficient. Owing to the great variability inherent in swimming speed studies and because of the sensitivity of the length coefficients to the size range of animals in the sample, these two alternatives are equally plausible. In addition, specific differences in the relationship between size and swimming functions may also depend on the particular function considered (Bainbridge, 1960). For example, the coefficient relating size to maximum sustained speed may be different from the one that relates size to beat frequency or burst speed. Thus, species may differ from one another in the way each swimming function is related to size. If such specific differences exist then direct comparisons between species are impossible, but if they do not exist then a general model can be derived from our data which can be used to make specific comparisons. In the interpretation of our data on *Trachurus* we will consider the alternatives, Case I where all swimming functions are related to size on a species-specific basis, and Case II where swimming functions are proportional to the same power of length in different species.

To evaluate Case I where length coefficients are considered to be species-specific we regressed speed on frequency by the general relationship.

$$V = \alpha_1 L^{\alpha_2} + \alpha_3 L^{\alpha_4} * F$$

where V is swimming speed in centimeters per second, F is tail beat frequency in beats per second, L is total length in centimeters and $\alpha_1 L^{\alpha_2}$ is the intercept function and $\alpha_3 L^{\alpha_4}$ is the slope function for the tail beat frequency-swimming speed relationship. Estimates were obtained by use of Marquardt's Algorithm for fitting nonlinear models (Conway, Glass, and Wilcox, 1970). For *Trachurus* the 90% support-plane confidence intervals (Conway et al., 1970) for α_3 and α_4 were $0.72 < \alpha_3 < 1.82$ and $0.72 < \alpha_4 < 1.01$ where $\hat{\alpha}_3 = 1.28$ and $\hat{\alpha}_4 = 0.86$.

To evaluate Case II where length coefficients are the same for all fish we assumed the slope coefficient α_4 equaled one. When $\alpha_4 = 1$, $\hat{\alpha}_3 = 0.86$ with 90% confidence limits of $0.79 < \alpha_3 < 0.91$. On the basis of the *Trachurus* data alone there seems to be little or no difference between the use of unity for the slope coefficient or use of the estimated value of 0.86. The similarity in the two estimates is apparent when the actual fish lengths are substituted into the two equations and the two sets of slopes are compared (Table 2, columns 1 and 2).

We fitted the Case I model to four additional species to determine the extent they differed in the length coefficient for the slope in the speed-tail beat frequency relationship. Used in this comparison were data we collected on *Scomber*, and data presented in scatter plots of velocity and frequency for individual *Carassius*, *Salmo*, and *Leuciscus* by Bainbridge (1958). We used the XY digitizer to transcribe Bainbridge's data onto cards. We may have failed to interpret correctly some of the overlapped points in his graphs but the effect of these errors on the statistical parameters we estimated would be negligible. We did not use the data presented by Magnuson and Prescott (1966), Yuen (1966), or Fierstine and Walters (1968) because in these studies the absolute speeds and the lengths of the fish were unknown.

Our estimates of the slope coefficient for the speed-tail beat relationship, $\hat{\alpha}_4$, varied from 0.76 in *Salmo* to 1.22 in *Carassius*, and the 90%

TABLE 2.—Slopes for the speed-frequency relationship for individual *Trachurus* when the general relationship is slope $= 1.28\ L^{0.86}$ (Case I) and when slope $= 0.86L$ (Case II); estimated minimum speed (V_0) for each fish when $V_0 = 0.80L^{2/3}$; lowest observed test speed (V_{obs}); the minimum tail beat frequency (F_0) estimated by substitution of V_0 the Case II equation for each fish; and the lowest observed tail beat frequency (F_{obs}).

Length (cm)	$b = 1.28L^{0.86}$ Case I	$b = 0.86L$ Case II	$V_0 = 0.80L^{2/3}$	V_{obs}	$F_0 = 3.98L^{-1/3}$ Case II	F_{obs}
4.5	4.67	3.87	2.19	14.9	2.41	7.77
6.4	6.32	5.50	2.77	18.9	2.14	6.60
7.9	7.57	6.79	3.19	24.0	2.00	6.75
8.3	7.90	7.14	3.30	24.0	1.97	6.68
9.4	8.79	8.08	3.59	15.1	1.88	5.22
10.7	9.83	9.20	3.92	15.0	1.81	4.18
13.2	10.98	11.35	4.51	15.0	1.68	2.91
16.4	14.19	14.10	5.21	19.0	1.56	3.56
22.8	18.84	19.61	6.50	18.9	1.40	2.18
23.7	19.48	20.38	6.67	24.1	1.38	1.86
25.0	20.39	21.50	6.91	19.8	1.36	2.46
25.8	20.95	22.19	7.06	24.7	1.35	2.11
27.0	21.78	23.22	7.28	31.4	1.33	2.16
27.7	22.27	23.82	7.40	19.0	1.32	1.78

support-plane intervals for $\hat{\alpha}_4$ in all species included unity (Table 3). Clearly if a common slope-length coefficient exists among these species, it must be close to 1. We conclude the assumption of unity for the slope-length coefficient is an acceptable practice and that it appears to introduce no significant bias in the species studied.

We now turn to the problem of estimation of the length-dependent coefficient for the intercept of the speed-tail beat relationship, that is, α_2. We noted previously that the biological significance of the existence of an intercept different from zero in the speed-frequency relationship may be that fish have a minimum speed below which they cannot swim by movements of the caudal fin. If we assume that the intercept is a function of the minimum swimming speed of a fish we can make an independent estimate of the intercept coefficient using an equation derived by Magnuson (1970) for estimation of the minimum swimming speed (V_0) of *E. affinis*. A somewhat simplified form of his equation is:

$$V_0 = \left(1 - \frac{D_e}{D_f} \right)^{1/2} * \left[\frac{g * Ma}{(C_{lf}A_{ft}) * \frac{p}{2}} \right]^{1/2}$$

where D_e is 1.025 (the density of sea water), D_f is the density of the fish, g is 980 cm/sec (the acceleration of gravity), Ma is mass of fish in air, C_{lf} is the coefficient of lift for the pectorals (assumed to equal 1), A_{ft} is the total lifting area of the extended pectoral fins in square centimeters, and p is the density of sea water, 1.025 g/cc. If we let $Ma = 0.004407$ $L^{3.21215}$ (the length-weight relationship for *T. symmetricus*, $N = 264$, unpublished data, Na-

TABLE 3.—Estimates of length coefficients for slope and intercept for five species of fish.

Species	$V = \alpha_1 L^{\alpha_2} + \alpha_3 L^{\alpha_4} \bullet F$	90% support-plane interval[1]
Trachuhus symmetricus	$V = -44.57L^{-0.24} + 1.28L^{0.86} \bullet F$	$-111.18 < \alpha_1 < 22.65$ $-0.80 < \alpha_2 < 0.31$ $0.73 < \alpha_3 < 1.82$ $0.72 < \alpha_4 < 1.01$ $s_{vf} = 11.41$
Scomber japonicus	$V = -0.56L^{0.55} + 1.20L^{0.83} \bullet F$	$-160.78 < \alpha_1 < 159.66$ $-84.14 < \alpha_2 < 85.25$ $-8.15 < \alpha_3 < 10.57$ $-1.46 < \alpha_4 < 3.13$ $s_{vf} = 21.42$
Leuciscus leuciscus[2]	$V = -3.36L^{0.40} + 0.80L^{0.98} \bullet F$	$-14.95 < \alpha_1 < 8.24$ $-0.84 < \alpha_2 < 1.65$ $0.47 < \alpha_3 < 1.12$ $0.85 < \alpha_4 < 1.12$ $s_{vf} = 7.81$
Salmo gairdneri[2]	$V = -1.77L^{0.64} + 1.40L^{0.76} \bullet F$	$-14.79 < \alpha_1 < 11.26$ $-0.70 < \alpha_2 < 2.97$ $0.33 < \alpha_3 < 2.46$ $0.52 < \alpha_4 < 1.00$ $s_{vf} = 14.16$
Carassius auratus[2]	$V = -0.12L^{1.52} + 0.40L^{1.22} \bullet F$	$-0.89 < \alpha_1 < 0.64$ $-0.50 < \alpha_2 < 3.53$ $0.17 < \alpha_3 < 0.63$ $1.01 < \alpha_4 < 1.44$ $s_{vf} = 5.54$

[1] Simultaneous confidence intervals for all parameters (Conway, Glass, and Wilcox, 1970).
[2] Data from Bainbridge (1958).

tional Marine Fisheries Service, La Jolla, Calif.), Area $= 0.02811L^{1.9124}$ (lifting area of pectorals of *T. symmetricus* was equal to twice the pectoral fin area), and $D_f = 1.03$ (the density of *T. trachurus* from Alexander (1959b), a closely related species to *T. symmetricus*), we obtain an estimate of $V_0 = 0.86L^{0.65}$ for *Trachurus*. This value is considerably below $10L^{0.50}$ obtained for *Euthynnus* by Magnuson (1970). The minimum swimming speed of *Trachurus* would be expected to be lower than that of *Euthynnus* because *Euthynnus* lacks a swim bladder and has a high specific gravity. Indeed, the minimum speed of *Euthynnus* is close to the endurance speed of many fishes with swim bladders (Magnuson, 1970).

In all other species except *Carassius* estimation of minimum speed was not possible because we had few or no estimates of the variables required in Magnuson's equation. In *Carassius* we used the specific gravity for carp, 1.002 g/cc (Alexander, 1959a), the pectoral fin area relationship of Area $= 0.02811L^{1.9124}$ from data we collected on seven *Carassius* 4.6 to 22.5 cm total length (the lifting area of the pectorals equaled twice the pectoral fin area) and the length-weight relationship of $Ma = 0.0065L^{3.20}$ for the seven *Carassius*. The estimate of minimum swimming speed V_0 for *Carassius* from these data was $0.87L^{0.65}$. This estimate was nearly the same as the one estimated above for *Trachurus* and it had the same coefficient of length. Thus, in *Trachurus* and in *Carassius* the minimum speed coefficient of length or, in our equation, the intercept coefficient $\hat{\alpha}_2$, was 0.65.

That the length coefficient for the intercept was the same in *Carassius* and *Trachurus* supports the basic assumption of the Case II model, that is, the existence of common length coefficient among different species. To further test this assumption we estimated the intercept coefficient by fitting the combined data from all five species listed in Table 3 to the reduced Case II model

$$V = \alpha_1 L^{\alpha_2} + \alpha_3 L * F$$

The estimate α_2 for the combined data was 0.68 with 90% confidence limits of $-0.56 < \alpha_2 < 1.92$. Although the limits were wide, the estimate was very close to the other independent estimate for *Carassius* and *Trachurus* and suggests that the true value may be close to 2/3.

The evidence we presented supported the use of the Case II equation and the use of 2/3 for the length-dependent coefficient for the intercept function and of unity for the length-dependent coefficient of the slope function. Thus, we fit the reduced Case II model

$$V = \alpha_1 L^{2/3} + \alpha_2 L * F$$

to the data from each of the five species listed in Table 3 and to that from two additional species *Triakis* and *Sardinops* for which we had a small number of observations. The resultant equations were useful nonbiased predictive models for the estimation of speed (V) from length (L) and tail beat frequency (F) in each species (Table 4). The regression lines for these equations do not pass through the origin, however. They cut the abscissa before zero and consequently the intercept terms are negative. We pointed out previously that we believe the existence of a negative intercept in the raw data implied that the fish had a minimum swimming speed below which they cannot swim by beating only the caudal fin. Thus, to make the model more biologically meaningful we adjusted the elevation of the intercept function to correspond to the theoretical minimum swimming speed, V_0. (It should be remembered that the length-dependent slope of V_0 was about the same as the length coefficient, α_2, and it was this similarity that led us to use 2/3 as the intercept coefficient.)

To express the Case II model in terms of minimum speed we used V_0 estimated from Magnuson's equation to solve for a minimum tail beat frequency, F_0, and expressed the final relationship in the form

$$\frac{V - V_0}{L} = KF - F_0 .$$

In species other than *Trachurus* and *Carassius*, a theoretical estimate of V_0 was not possible and consequently we assumed V_0 was propor-

TABLE 4.—Swimming speed-tail beat frequency equations for seven species of fish.

Species	$V = \alpha_1 L^{2/3} + \alpha_3 L \bullet F$	90% support-plane interval[1]
Triakis henlei	$V = -1.39L^{2/3} + 0.93L * F$	$-2.71 < \alpha_1 < -0.01$ $0.77 < \alpha_2 < 1.09$ $s_{vf} = 2.49$
Trachurus symmetricus	$V = -2.50L^{2/3} + 0.83L * F$	$-3.28 < \alpha_1 < -1.59$ $0.78 < \alpha_2 < 0.88$ $s_{vf} = 12.39$
Scomber japonicus[2]	$V = -2.20L^{2/3} + 0.82L * F$	$-3.18 < \alpha_1 < -1.13$ $0.76 < \alpha_2 < 0.88$ $s_{vf} = 12.31$
Leuciscus leuciscus	$V = -1.58L^{2/3} + 0.74L * F$	$-2.21 < \alpha_1 < -0.86$ $0.71 < \alpha_2 < 0.78$ $s_{vf} = 7.78$
Carassius auratus	$V = -0.66L^{2/3} + 0.66L * F$	$-1.47 < \alpha_1 < 0.17$ $0.61 < \alpha_2 < 0.74$ $s_{vf} = 6.09$
Salmo gairdneri	$V = -1.28L^{2/3} + 0.64L * F$	$-2.63 < \alpha_1 < 0.13$ $0.59 < \alpha_2 < 0.69$ $s_{vf} = 17.72$
Sardinops sagax	$V = 0.49L^{2/3} + 0.50L * F$	$-1.61 < \alpha_1 < 2.58$ $0.39 < \alpha_2 < 0.62$ $s_{vf} = 5.77$

[1] Simultaneous confidence intervals for all parameters (Conway, Glass, and Wilcox, 1970).

[2] One deviant fish omitted; if fish included $V = -0.53L^{2/3} + 0.66L \bullet F$, and $s_{vf} = 21.31$.

tional to $L^{2/3}$. The elevation of the line relating V_0 to length for a species was estimated by assuming that the lowest observed speed fell on that line. For *Trachurus* and *Carassius* we recalculated the elevation for a slope of 2/3.

Our estimates of V_0 and F_0 were not definitive. For *Trachurus* no fish were tested at speeds close to the theoretical minimum. Our estimates based on the theoretical minimum speed were closest to the observed minimum speeds in fish 9.4 cm total length and larger (Table 2) because in these larger fish the test speeds were sufficiently low for fish to swim with pectoral fins fully extended, an event that occurs near the minimum swimming speed (Magnuson, 1970). For *Carassius* the agreement between the theoretical estimate of minimum speed and observed minimum speeds was better (Table 5). The explanation for this is that the techniques used by Bainbridge (1958) permitted estimates at much lower speeds than the one we used. These data clearly show that in neither *Trachurus* (Table 2) nor *Carassius* (Table 5) was either V_0 or F_0 seriously overestimated. We feel that our estimates for these two species were reliable.

The fit to the general equation was good in all species (Figure 5, Table 6). The intercept for the regression line did not differ from zero and the scatter at low velocities was less than it was when no intercept correction was used (see figures in Bainbridge (1958) for comparison). The regression coefficient, K, in our equation differed among species. For the five species for which significant data were available, it was the highest in *Trachurus* and lowest in *Salmo*. Since amplitude was a constant, these results implied that the speed output per beat of the caudal fin was greater in *Trachurus* and *Scomber* than it was in *Salmo* and *Carassius*. In *Scomber*, the coefficient, K, may be uncertain because the values of one of the five fish tested deviated considerably from the rest. In Figure 5, all of the values to the right of the regression line above

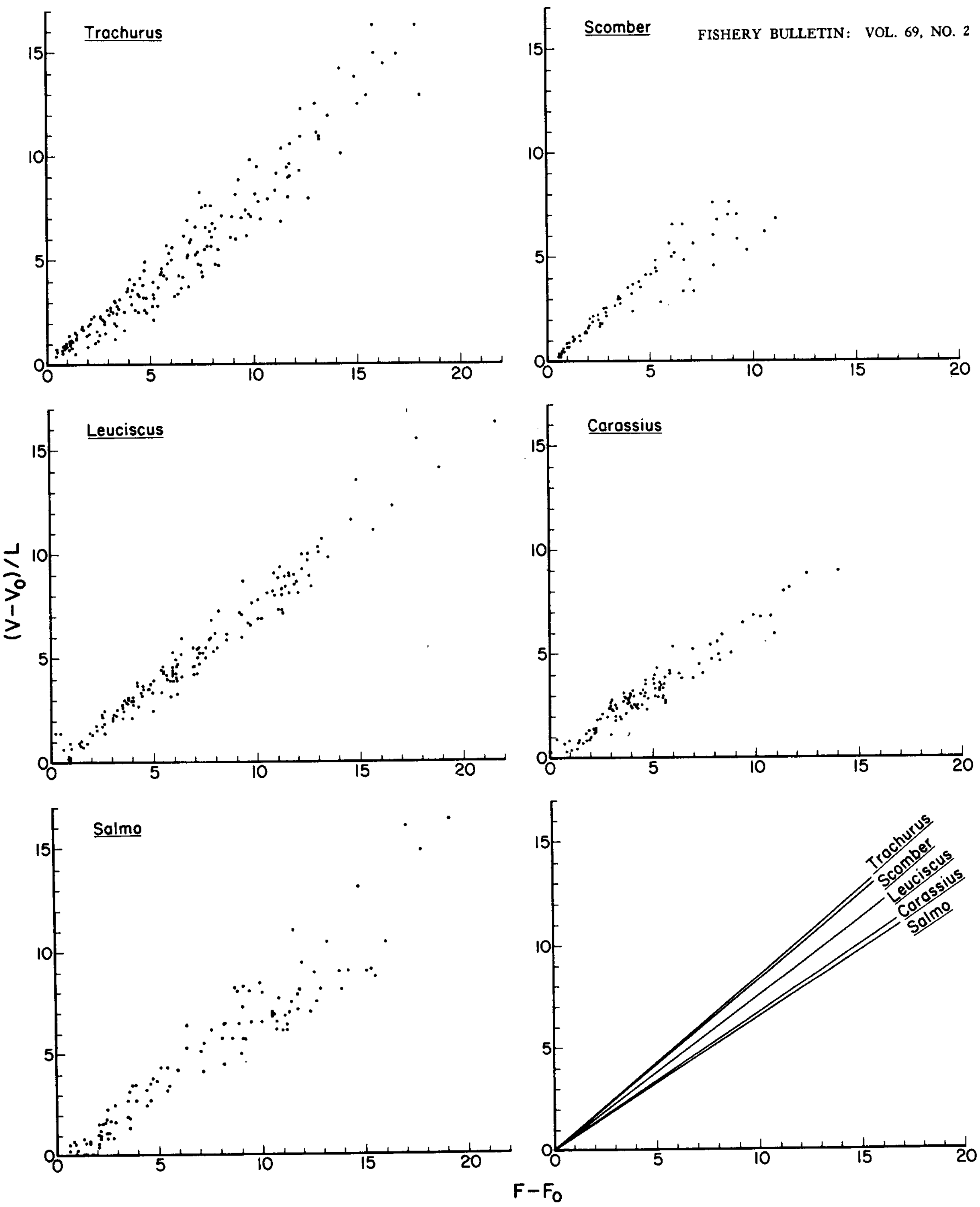

FIGURE 5.—Relationship between swimming speed corrected for minimum speed over length and tail beat frequency corrected for minimum frequency for *Trachurus* and *Scomber* from the present data, and for *Leuciscus*, *Salmo*, and *Carassius* from Bainbridge (1958). Graph at lower right shows individual regression lines for all above species, equations for lines are given in Table 6.

Table 5.—Slopes for the velocity-frequency relationship for individual *Carassius* studied by Bainbridge (1958) when the general relationship is slope $= 0.68L$; estimated minimum speed when $V_0 = 0.81L^{2/3}$; observed minimum swimming speed (V_{obs}); the tail beat frequency F_0 estimated by substitution of V_0 into the corrected slope equation; and the lowest observed tail beat frequency (F_{obs}).

Length (cm)	$b = 0.66L$	$V_0 = 0.81L^{2/3}$	[1]V_{obs}	$F_0 = 2.22L^{-1/3}$	F_{obs}
4.6	3.04	2.25	3.50	1.34	1.30
7.0	4.62	2.98	9.30	1.17	1.52
9.5	6.27	3.66	11.60	1.04	2.03
15.2	10.03	5.01	33.70	0.90	3.38
22.5	14.85	6.52	13.70	0.78	1.63

[1] Data from Bainbridge (1958).

TABLE 6.—Minimum speed (V_0), minimum tail beat frequency (F_0), the coefficient K in equation $V - V_0 = L(KF - F_0)$ arranged in order of K.

Species	N	V_0	F_0	K
Triakis henlei	6	$0.15L^{2/3}$	$1.66L^{-1/3}$	0.93
Trachurus symmetricus	176	[1]$0.80L^{2/3}$	$3.98L^{-1/3}$	0.83
Scomber japonicus	[2]61	$1.31L^{2/3}$	$3.51L^{-1/3}$	0.82
Leuciscus leuciscus[3]	149	$0.67L^{2/3}$	$3.04L^{-1/3}$	0.74
Carassius auratus[3]	111	[1]$0.81L^{2/3}$	$2.22L^{-1/3}$	0.66
Salmo gairdneri[3]	109	$0.52L^{2/3}$	$2.81L^{-1/3}$	0.64
Sardinops sagax	9	$2.23L^{2/3}$	$3.48L^{-1/3}$	0.50

[1] V_0 theoretical estimate based on equation of Magnuson (1970).
[2] One deviant fish omitted; if fish included, $N = 74$, $K = 0.66$.
[3] Original data from Bainbridge (1958).

4 beats/sec on the abscissa were from this single deviant fish. If the deviant fish is included $K = 0.66$, but if not, $K = 0.82$. We are inclined to use $K = 0.82$ because the values for the four fish were very similar and the protocol indicated that the deviant fish may have been overly fatigued when tested. *Triakis* appears to have a relatively high coefficient but not too much significance can be attached to the exact value for *Triakis* or for *Sardinops* because these were based on so few measurements.

In sum, the speed-tail beat equation (Case II) —Table 6—was biologically as well as statistically relevant, was sensitive to specific differences in swimming behavior, provided an unbiased correction for length, and made possible a more accurate estimation of swimming speed from tail beat frequency than heretofore has been possible.

TAIL BEAT AMPLITUDE

We pointed out previously that tail beat amplitude was a constant and was directly proportional to length and consequently the size coefficients for amplitude are probably the same as those for length. Thus amplitude (A) in centimeters can be substituted for length in the original Case II equation $V = \alpha_1 A^{2/3} + \alpha_3 L * F$. When this was done for *Trachurus* using all individual amplitude values ($N = 176$), we obtained the equation; $V = -6.5767A^{2/3} + 3.5637A * F$. The amplitude coefficient may be also estimated by substitution of the amplitude-length relationship for *Trachurus* ($A = 0.23177L$), into the Case II equation.

The tail beat amplitude data collected by Bainbridge (1958) were insufficient for specific estimates of an amplitude coefficient. The mean amplitudes for each of the fish we studied and for each of those studied by Bainbridge were nearly the same, when adjusted for body length. Variation within a species was as great as that between species (Figure 6). The relationship between mean tail beat amplitude and length for all species combined was $A = 0.21L$.

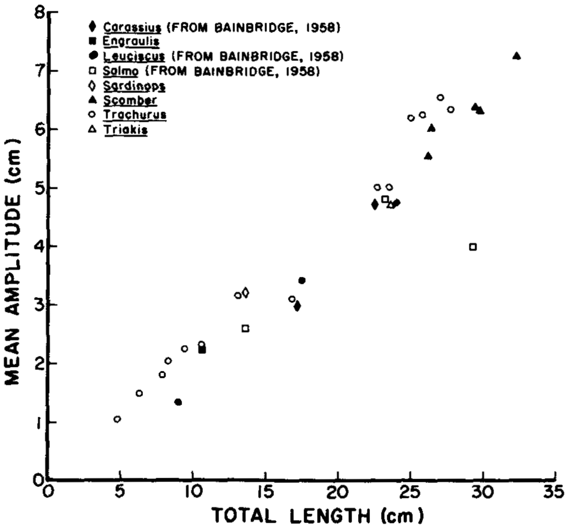

FIGURE 6.—Relationship between mean tail beat amplitude and length for every fish we studied and all those studied by Bainbridge (1958), $A = 0.21L$.

DISCUSSION

In all previous studies speed was divided by length then related to tail beat frequency. In our data when speed was converted to body lengths per second the relationship between speed and frequency was nearly identical to that given by Bainbridge (1958) for *Carassius*, *Leuciscus*, and *Salmo* The confidence intervals for the slopes in the speed-frequency relationship in *Euthynnus* and *Thunnus* (Yuen, 1966) and in *Sarda* (Magnuson and Prescott, 1966) overlap the slope in the Bainbridge equation and the ones for *Trachurus* and *Scomber* when the body length conversion is used. Thus, when speed is in body lengths per second, the relationship between it and frequency is about the same in all fish studied to date from goldfish to mackerel and is adequately described by the Bainbridge equation $V/L = bf$. Thus the Bainbridge equation provides a description of the average relationship for fish in general but little significance can be attached to specific differences in slope. If more than a rough estimate of speed is required or if specific differences are important, or if estimates are needed near the minimum swimming speed it would be necessary to use the equation developed in this study.

Bainbridge (1958) concluded from his data that the frequency-speed relationship was curvilinear below a frequency of about 5 beats/sec because fish modulated their tail beat amplitude. His evidence for this conclusion was that in some fish amplitude appeared to decrease at lower frequencies, and that the distance per beat, calculated by dividing speed by frequency, declined at frequencies below 5 beats/sec but was constant above that frequency. His evidence for amplitude modulation at low speeds was weak. In the three *Salmo* studied no trend existed; in *Carassius* he suggested there might be a decrease in amplitude in one of the two fish studied, and in one of the two *Leuciscus* studied a trend existed slightly stronger than the one in *Carassius*. In sum, the evidence for a decline in amplitude measurements was based on possible trends in two of the seven fish studied. Two fish could easily give a misleading picture of the general trend in the data, especially when the variability in amplitude measurements are considered. In our studies we measured the tail beat amplitude in every fish at all possible speed levels and no evidence existed for a consistent change in amplitude with speed.

In Bainbridge's data the departure of distance traveled per beat from a constant at low frequencies was caused by the division of speed by frequency. Had the line relating frequency to speed passed through the origin, no bias would have existed but because the line intersected the abscissa at about 1 beat/sec division by frequency produced an artificial curvilinear trend at lower frequencies. We produced the same trend in distance per beat in our data by dividing speed by frequency but the trend was eliminated when a correction for the intercept was used. Thus the curvilinear trend in distance per beat in Bainbridge's data was an artifact caused by the method of calculation and consequently distance per beat was a constant at all frequencies. In addition, the apparent nonlinearity below 5 beats/sec in his graphs relating speed divided by length to frequency was also the result of the same intercept problem. Therefore, no evidence exists for consistent amplitude modulation at any speed range and speed appears to be related only to tail beat frequency and length in the species studied by Bainbridge (1958) as well as in the ones we studied. We concluded that during steady swimming at any speed, tail beat amplitude is a constant proportion of body length of the order of 0.21 *L*.

That the mean amplitude during steady swimming was constant does not mean that amplitude is not modulated under certain conditions. It is widely known that fish modulate tail beat amplitude when they accelerate (Gray, 1968). Further, we had the impression that some of the variability in the speed-frequency relationship was caused by differences in amplitude. These differences were infrequent and irregular in occurrence and consequently we were not able to evaluate them statistically. We are inclined to believe, however, that fish occasionally made minor adjustments in amplitude and frequency over the entire range of speeds, but these adjustments were merely individual deviations from the general relationship we have described.

We do not wish to detract from the original and important contribution of Bainbridge (1958), by emphasis on the differences between his and our conclusions. His basic conclusions and equations were not greatly different from our own. We were able to examine more closely the form of the relationships he described because of a larger sample size made possible by the availability of automatic film analysis equipment and because of the existence of his data in the literature.

The question of species-specific size effects remains unresolved. In our general model a good fit was obtained in seven species when the minimum stalling speed was proportional to $L^{2/3}$, the frequency at this minimum speed was proportional to $L^{-1/3}$, and the slope coefficient was proportional to $L^{1.0}$. A comparative study on speed-related size effects in fishes would certainly be of value.

It also remains to be resolved whether or not it was appropriate to apply the minimum swimming speed equation developed by Magnuson (1970) for *Euthynnus affinis*, a fish that lacks a swim bladder, to such a broad assortment of species. The equation implies a functional relationship between minimum speed and hydrostatic equilibrium and implies existence of negative buoyancy at minimum speeds. We do not know if these relationships exist in all species; nevertheless his equation did provide a reasonable estimate for minimum speed and it functioned well in our equation.

The relationship between swimming speed and tail beat frequency we have described could be used in any application where it is necessary to measure swimming speeds of fish. For example, a sonic internal tag could be developed that telemetered tail beat frequency and thus the speed of free-swimming fish could be monitored continuously over extended periods.

The tail beat frequency-speed relationship could be used for size or species identification using Continuous Transmission Frequency Modulated sonar as suggested by Hester (1967). The increase of speed with frequency (our K value) varied from species to species and thus might be used for identification. If size were known, the minimum observed velocity would provide additional information for identification. Alternatively, if the species were known, minimum (or maximum) speed would provide an indication of size. The equation could also be used to estimate size from tail beat amplitude, but caution should be exercised because in our study amplitude was not modulated and consequently, we do not know whether or not speed and tail beat amplitude are linearly related within an individual.

ACKNOWLEDGMENTS

We wish to thank David Holts and George W. Rommel of the NMFS Fishery-Oceanography Center, La Jolla, Calif., who assisted in conducting the experiments and in calibration of the apparatus. Albert Good wrote the program for digitizing the photographic data, and John J. Magnuson, Department of Zoology, University of Wisconsin, Madison, Wis., reviewed the manuscript.

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