

## SUSTAINED SPEED OF JACK MACKEREL, *Trachurus symmetricus*

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### ABSTRACT

Jack mackerel, *Trachurus symmetricus*, were forced to swim for up to 6 hr at various speeds in an activity chamber. The probit estimate for the swimming speed at which 50% of *Trachurus* would fatigue during 6 hr was 93.4 cm/sec (8.4 *L*/sec) for fish 10.0 to 11.9 cm and was 22.4 *L*<sup>0.6</sup>/sec for fish 9.0 to 17.6 cm where *L* is the total length of the fish in centimeters. At higher speeds, *Trachurus*, 15 cm, swam for 3 min at 160 cm/sec or 10 *L*/sec. The swimming speed at which 50% fatigued declined exponentially with time for about the first 22 min of swimming and thereafter declined linearly with time. The possible significance of the time-speed relationship for *Trachurus* is discussed.

Although a substantial literature on the swimming speed of fishes exists (see Bainbridge, 1958; Gray, 1968), few reliable estimates of maximum sustained speed exist. Much of the literature on swimming speed of fishes is concerned with estimates of maximum speed or burst speed, that is, speeds that can be maintained for only a few minutes or less. A sustained speed implies, on the other hand, that the animal is capable of swimming at that speed for hours. For example, Brett (1967) recommended a minimum of 200 min for a fixed sustained speed test. Fairly wide agreement exists that 2 to 3 *L*/sec can be maintained for an hour or more and salmonids and herring seem capable of sustaining 3 to 4 *L*/sec for such periods (Blaxter, 1969). These conclusions were drawn primarily from studies of freshwater fish and salmon; no estimates of maximum sustained speeds have been made for fast-swimming pelagic marine forms. The object of this study was to determine the sustained speed threshold of jack mackerel, *Trachurus symmetricus*, a pelagic marine fish of commercial importance. The body form and musculature of *Trachurus* appear to be designed for greater hydrodynamic efficiency at high speeds than other species heretofore studied. In *Trachurus*, lateral musculature is concentrated in the anterior portion of the trunk, and inserts by tendons on a small deeply forked caudal fin.

In addition to the interest in comparing the sustained speed capabilities of *Trachurus* with that of fish with other body forms, sustained speed data have significance in prediction of migratory capabilities and physiological limits.

### APPARATUS AND METHODS

The apparatus used in the experiments was an activity chamber provided with a water current of various calibrated speeds. The apparatus was the same as the one described and figured by Hunter and Zweifel (1971) in this issue except that a port was provided in the transparent hatch of the swimming chamber so that fatigued fish could be removed by hand from the downstream screen without reducing the flow in the chamber. The error in estimating the water speed in the swimming chamber did not exceed 10% and it was assumed that the fish were swimming at the estimated speed.

The experimental design was essentially the same as that used by Brett (1967) for determining the sustained speed threshold for sockeye salmon, *Oncorhynchus nerka*. Fifty-five groups of five *Trachurus* (9.0 to 17.6 cm total length, mean = 12.43 ± 0.11 cm) were subjected to a fixed speed of 38 to 160 cm/sec for 360 min or longer after an introductory period of about 30 min at a low speed. A time-lapse camera photographed the fish at 1-min intervals and the time to fatigue for each fish was determined from the photographs. The temperature of the water in the activity chamber and in the holding

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tank (a plastic swimming pool 15 ft in diameter) was maintained by a temperature regulation system at about 18.5° C. The mean test temperature was  $18.48 \pm 0.03$ ° C. The fish were captured near Santa Catalina Island, Calif., on 12 September 1969. Tests began 2 weeks later and ended on 21 November 1969. Fish were fed an abundant ration of chopped squid, anchovies, and frozen brine shrimp. Probit analysis, a statistical technique first applied to sustained speed data by Brett (1967), was used to estimate sustained speed thresholds.

Variability in length posed a problem in the analysis. Although all fish were from the same school, differences in length existed; also the fish grew in the course of the study. These differences were insufficient, however, to determine the form of the relationship between length and sustained speed. In general, the relationship between length and sustained speed for other species (Bainbridge, 1962; Brett, 1965), theoretical considerations (Gray, 1968; Fry and Cox, 1970), and relationships between length and other swimming capabilities (Magnuson, 1970), indicate that speed is proportional to a fractional power of length equal to about  $L^{0.6 \pm 0.1}$ . In addition, the minimum swimming speed of *Trachurus* was proportional to  $L^{0.6}$  when estimated from Magnuson's equation (Hunter and Zweifel, 1971). In light of the above evidence it seemed preferable to use 0.6 as the coefficient of length, although unity has been commonly employed in cases where length coefficients were unknown. As an alternative to this procedure I also estimated the percent fatigued at different speeds in centimeters per second and in body lengths per second for a narrow length range (10.0 to 11.9 cm total length) where the effect of differences in length would be negligible.

## RESULTS

Within a few minutes after *Trachurus* were placed in the swimming compartment they became quiescent, swam steadily, and remained in about the same position in the compartment throughout the test or until they became fatigued and fell against the rear screen. This

was in contrast to some other species which did not swim steadily, but swerved and oscillated from side to side.

The relationship between water speed and percent fatigue had the normal sigmoid form of a dosage response curve (Finney, 1952). Probit estimate of the applied water speed at which 50% fatigue occurred in 360 min of swimming and the 95% confidence limits were  $94.40 \pm 5.15$  cm/sec for *Trachurus* 10.0 to 11.9 cm total length,  $N = 127$  (Figure 1, Table 1). Thus,

TABLE 1.—Swimming endurance of *Trachurus symmetricus* in cm/sec and in  $L^{0.6}$ /sec.

Length 10.0-11.9 cm					Length 9.0-17.6 cm		
Speed cm/sec	N	Percent fatigued	Length		Speed <sup>1</sup> $L^{0.6}$ /sec	N	Percent fatigued
			Mean	SD			
71	8	0	10.69	0.61	15.9	3	0
78	16	13	10.71	0.47	16.9	10	0
85	16	31	10.84	0.67	17.8	14	0
92	14	50	10.97	0.54	18.7	17	6
99	21	62	11.23	0.43	19.7	18	17
106	21	76	10.85	0.56	20.6	23	39
113	15	100	11.41	0.42	21.5	39	31
120	8	100	11.27	0.45	22.5	42	67
138	8	100	11.20	0.51	23.4	19	58
Total	127				24.3	20	60
					25.3	29	72
					26.2	19	100
					27.2	9	100
					28.1	4	100
					29.0	3	100
					30.0	1	100
					30.9	3	100
					31.8	7	100
					32.8	10	100
					33.7	4	100
					Total	294	

<sup>1</sup> Total speed range divided into 20 equal intervals; speeds listed are midpoints of those intervals.

50% of *Trachurus* in this length range could be expected to sustain a speed of about 8.4  $L$ /sec or 22.1  $L^{0.6}$ /sec for 360 min. For all *Trachurus* ( $N = 294$ ) the water speed at which 50% fatigue occurred after 360 min of continuous swimming and the 95% confidence intervals were  $22.4 \pm 1.2$   $L^{0.6}$ /sec. The first estimate, based on a narrow length range, and the second one, based on all data, were reasonably close. On the other hand, when all data were in the form  $V/L^{1.0}$  the 50% threshold was 9.34  $L$ /sec which is higher than the preceding estimates. Inspection of these data, however, showed that the coefficient for length clearly was less than one and that use of unity biased the estimate.

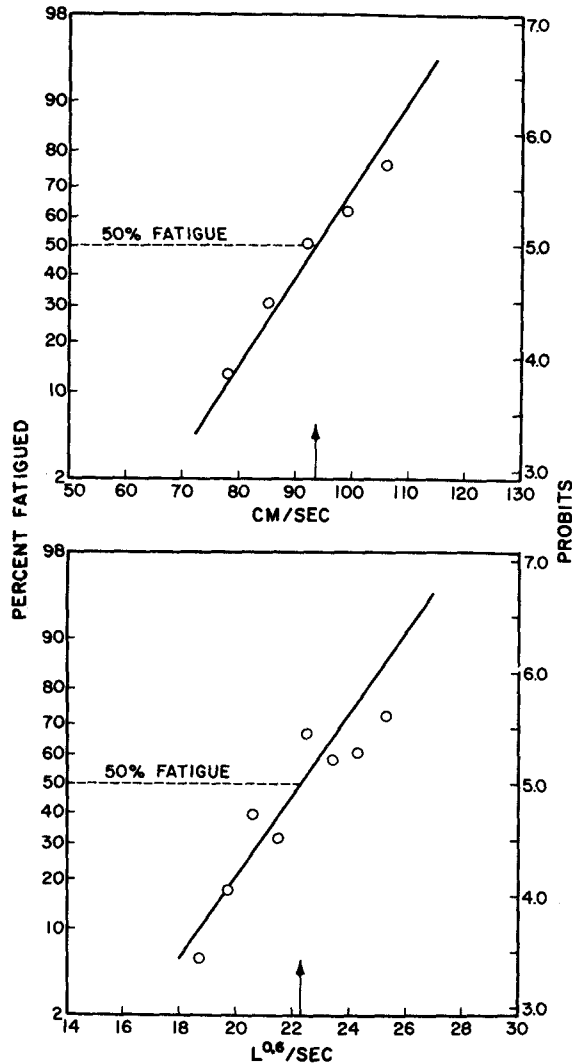


FIGURE 1.—Probit lines for sustained speed threshold for 6 hr of forced swimming at 18.5° C in juvenile *Trachurus symmetricus*. Upper panel, range fish length 10.0 to 11.9 cm  $N = 127$ , probit =  $0.077X - 2.238$ ; lower panel, range fish length 9.0 to 17.6 cm,  $N = 294$ , speed expressed in  $L^{0.6}/\text{sec}$  where  $L$  is the total length of the fish, probit =  $0.355X - 2.958$ .

To determine the form of the relationship between the duration of the swimming period and the ability to maintain a certain speed, probit estimates of speed for five levels of fa-

tigue were made for swimming periods varying from 10 to 360 min. The form of the relationship was about the same for all fatigue levels; speed estimates declined exponentially with time for short swimming periods and linearly with time for longer ones (Figure 2). The point

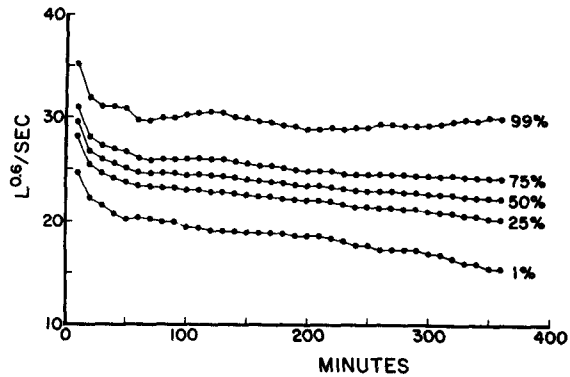


FIGURE 2.—Relation between speed in  $L^{0.6}/\text{sec}$  and the time it can be sustained for 1, 25, 50, 75, and 99 percent fatigue levels in *Trachurus symmetricus*. Estimates of speed for each fatigue level made at 10-min intervals of cumulated time.

of inflection from the exponential to the linear relationship was examined in detail for the 50% fatigue level. Probit estimates of the speed at which 50% of the fish fatigued were made for 2-min intervals of swimming cumulated over the first 100 min of observation. The data were plotted on semilog paper and a line fit by eye to the exponential function. The point of inflection appears to occur at about 22 min (Figure 3). Thus, speed at which 50% fatigued and the duration of the swimming period were exponentially related for durations up to about 22 min and were linearly related for longer periods of swimming.

The performance of juvenile *Trachurus* at high speed was of interest. Fifteen fish 14.6 cm mean total length (range = 13.4 to 16.6 cm) swam at the highest speed used in the study (160 cm/sec) for 2 to 6 min, mean time 3.4 min. Thus, *Trachurus* 15 cm total length were able to swim for about 3 min at about 10  $L/\text{sec}$  or about 32  $L^{0.6}/\text{sec}$ . A slightly higher level of

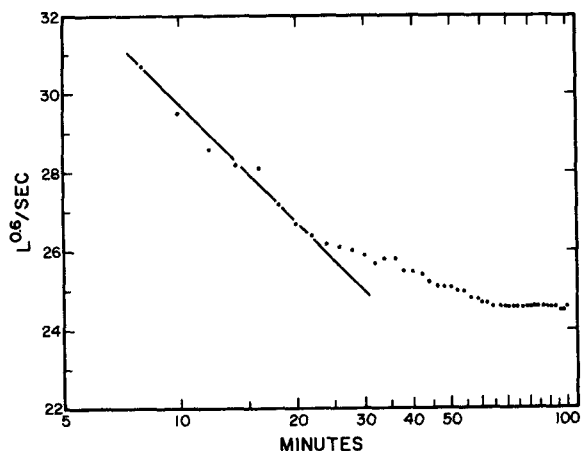


FIGURE 3.—Relation between speed at which 50% *Trachurus* fatigued and the duration of the swimming period. Duration of swimming period in minutes plotted on log scale to show exponential trend; line fit by eye. Speed estimates made at 2-min intervals of cumulated time over the first 100 min of swimming.

performance in length per second is obtained if we consider smaller fish. For example, fish of mean length 11.2 cm (length range 10.4 to 11.9 cm,  $N = 8$ ) swam for 3 to 5 min (mean = 4.5 min) at 139 cm/sec or about 12  $L/\text{sec}$ . This difference between large and small fish becomes negligible if 0.6 is used as a coefficient of length instead of unity because, as was pointed out previously, the length coefficient for *Trachurus* appears to be less than 1.

## DISCUSSION

The exponential decline in swimming speed with time in fish is well documented; see for example Bainbridge (1960), Brett (1967), and Blaxter (1969). The general form of the relation between time and swimming speed in other fish resembles that for *Trachurus* although the speeds and endurance times are different in *Trachurus*. The physiological mechanisms responsible for the exponential relationship between swimming speed and endurance are generally believed to be the limited energy stores in the muscle, the rate these stores can be replaced and the rate catabolites are removed from the muscle (Bainbridge, 1960). A study

by Pritchard, Hunter, and Lasker (1971) in this issue has provided an explanation for the form of the speed-time relationship in *Trachurus*. Pritchard et al. found that at speeds where an exponential relationship exists between time and speed the principal cause of failure of *Trachurus* was most likely the depletion of glycogen in the white muscle. On the other hand, fish that failed at speeds near the 6-hr 50% threshold, where a linear relationship exists between speed and time, had depleted not only the glycogen in the white muscle but that in the red muscle and liver as well. Thus, in *Trachurus* the form of the time-speed relationship could be explained on the basis of the extent of glycogen reserves available for locomotion and the time required to mobilize them from sites other than the white muscle. An exponential relationship between speed and time could be produced when the speeds are so high that the glycogen supply would be limited almost entirely to the white muscle because the supply in the white muscle would be used up and the fish would fail before significant amounts of glycogen could be mobilized from other sources. A linear relationship could exist where swimming speeds are sufficiently low that reserves in the white muscle could not be depleted before other sources in the red muscle and the liver are mobilized. We have, on one hand, a high rate of consumption using a more limited supply of fuel which could lead to an exponential relationship between speed and time and, on the other hand, a much lower rate of consumption using a relatively much larger fuel supply which could produce a linear relationship with time. An exponential relationship between energy consumption and swimming speed would enhance these effects.

Let us now consider the significance of the 6-hr sustained speed threshold determined for *Trachurus*. When compared with other determinations, this threshold appears to be unique because of different physiological mechanisms and because it is higher than those estimated for other fish. *Trachurus* at threshold speed appeared to use glycogen as fuel, white muscle for locomotion and maintained a high lactic acid

level in the muscle (Pritchard et al., 1971). These results are inconsistent with the conclusion that at sustained cruising speeds, fish use lipid metabolism to drive red muscle (Bone, 1966; Gordon, 1968; Blaxter, 1969) and that no oxygen debt is incurred (Brett, 1963). Reliance on glycogen as the principal fuel probably severely limits the time a speed can be maintained as compared with one where lipid metabolism is used exclusively. Thus the biochemical evidence indicates that the 6-hr speed threshold for *Trachurus* probably could be maintained only for a period of hours or perhaps days but certainly not weeks as one would expect if fat were used as fuel. The 6-hr threshold was also considerably above sustained speed thresholds for other fish where presumably fat may be employed as fuel. Brett (1967), in a study directly comparable with the current one, found the 50% fatigue time for sockeye salmon was 4 L/sec (about  $11.3 L^{0.6}$ ) whereas for comparable size jack mackerel it would be about 7.6 L/sec or  $22.0 L^{0.6}$ . Other less comparable data give sustained or cruising speeds in the range of 3 to 4 L/sec (Blaxter, 1969). Thus, *Trachurus* has special physiological and structural adaptations that permit swimming for periods of hours at elevated speeds and it was the threshold for this swimming behavior that was measured. Other fishes, especially the scombroid fishes, may have similar abilities. For example, skipjack tuna can swim at 8 knots, or about  $43 L^{0.6}$ , for over an hour (Commercial Fisheries Review, 1969) and yellowfin tuna and skipjack tuna have higher levels of white muscle glycogen than many other species of fish (Barrett and Connor, 1964).

It seems possible another speed threshold may exist for *Trachurus* below the present one where fat is the principal fuel, only red muscle is used for locomotion, and swimming can be maintained almost indefinitely. It would not be surprising if this lower threshold were closer to those determined for other fishes.

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