SHORT PAPERS AND NOTES

A Method for Measuring Swimming Speed in Oxygen Consumption Studies on the Aholehole *Kuhlia sandvicensis*[1, 2]

INTRODUCTION

It is well established that the oxygen consumption of fish increases with activity, and many studies have been made of fish either stimulated to a state approaching maximum activity or induced by confinement and isolation to a state of relative quiescence. Measurements of maximum activity are generally expressed as some function of swimming speed. Measurements of low levels of activity have thus far been expressed as some function not of swimming but of nonspecific movements. Spoor (1946), for example, suspended a paddle in the fish chamber. Movements of the fish swung the paddle, which closed a switch and activated a counter. Beamish and Mookherjii (1964) replaced this with a thermostatic heater probe set at a temperature slightly higher than that of the chamber water. Movements of the fish generated water currents cooling the probe. The amount of electricity required to reheat the probe was considered a measure of activity.

Because in both of these studies oxygen consumption and activity were found to be linearly related over a fairly wide range, they demonstrate the need to measure accurately low levels of activity in oxygen consumption studies. Their common defect is that the measure used is arbitrary. Thus only one ultimately useful datum is obtainable per fish — the extrapolated oxygen consumption at zero activity. Brett (1964) recently has attacked the problem by inducing fish to swim against a water current of controlled velocity. His methods were efficient in determining the relation between oxygen consumption and medium-to-high swimming speeds in sockeye salmon, but were not well suited to the low-to-medium range. The methods described below were developed specifically to measure low-to-medium levels of activity as a function of swimming speed.

F. E. J. Fry (pers. comm.) has measured swimming speed using photosensitive resistors mounted on the wall of a doughnut-shaped chamber.

As the fish swims around the circular raceway of the chamber, it interrupts beams of light focused on the surface of the photocells and the interruption is recorded on a digital counter. Using the same type of chamber the present writers attempted to find a means to detect the passage of a fish without employing lights which might disturb the fish and which limit the application of the method to certain light conditions. Proximity detectors based on changes in capacitance, successfully employed by terrestrial ecologists (for example Kavanau, 1961), were investigated but found unsuitable because of the apparent dielectric similarity of the fish and water. This approach was soon abandoned when our attention was drawn to a device perfectly suited to this application.

Cummings (1963) tested a Pflueger Fish Finder (Enterprise Manufacturing Co., Akron 9, Ohio) for detecting fish movement. Employing the Doppler effect, the instrument emits a burst of audio-frequency noise coinciding in time with the movement of a fish in the sensing field. As used by Cummings the Fish Finder measures activity in arbitrary units.

The method described in the present report adapts the Fish Finder to Fry's circular chamber so that swimming speed can be measured. This method has the distinct advantage that swimming of spontaneously active fish can be monitored under any conditions of ambient light. To achieve uniform speeds in the work reported here, the fish were induced to swim in a semicircular shadow created by a disc rotating above the chamber. Sample data of the effect of swimming speed on oxygen consumption, with reference to size of fish, are included to illustrate the application.

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[2] Hawaii Marine Laboratory Contribution No. 233.

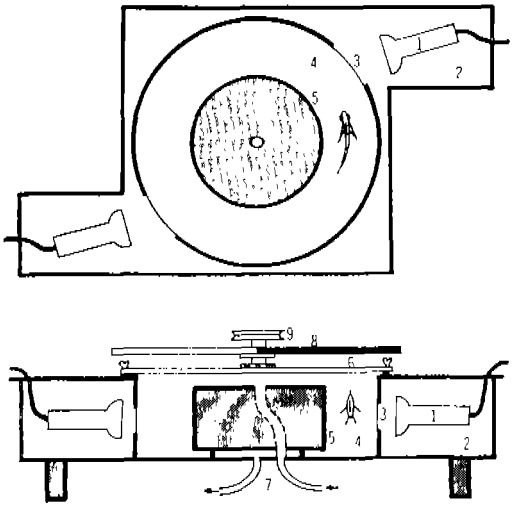

FIGURE 1.—Diagram of the activity chamber. Upper: top view with rotating disc and covers for constant-temperature bath and fish chamber removed. Lower: cut-away side view with disc and covers in place. 1. Fish Finder; 2. well for Fish Finder continuous with water bath; 3. fiberglass window; 4. circular raceway of chamber; 5. solid center; 6. clear plexiglass top for fish chamber; 7. water circulation for chamber; 8. rotating disc; 9. drive pulley for rotating disc.

Although we are not concerned here with other possible applications, the principle can be used in a wide variety of situations where the investigator wishes to follow the responses or spontaneous movements of experimental aquatic animals. Because no uncorrectable interference was encountered between the two Fish Finders used, it would appear that a series could be employed to study movement through a variety of one- or two-dimensional gradients.

APPARATUS

The Fish Finder consists of a high frequency CW transmitter and receiver in a small submersible case. Energy radiated by the transmitter is focused in a narrow, presumably conical, 4-degree field. Movement of a fish in this field shifts the frequency of any reflected signal (Doppler effect). The transmitted and reflected signals are compared (heterodyned) in the receiver and simply cancel out if there is no moving object to shift the frequency. The instrument is sensitive enough to detect the movement even of a single fin. The frequency used, about 800 kc, is far above the hearing range of teleosts (Tavolga, 1964) and appears to have no effect on the fish.

The fish chamber (Figure 1) is doughnut-shaped, the circular swimming channel being 7.6 cm wide and 9.5 cm deep. The mean swimming circumference is 87.6 cm and the volume 6.6 liters. The center portion is raised from the bottom; outflowing water is collected from all directions under it and inflowing water radiated over the top. Two wells attached at tangents to the circular channel house the Fish Finders. The inner and outer walls of the chamber are of sheet aluminum overlaid with fiberglass cloth and resin. Oval windows in the aluminum adjacent to the wells allow passage of the signals. The windows are covered with fiberglass to separate the water in the wells from that in the fish chamber and to hide the transducers from the fish. The chamber is opaque except for a clear plexiglass top. A more recent version of the chamber is made entirely of plexiglass (opaque bottom and walls) which has been found to offer no resistance to the transducer signals. The Fish Finders are mounted in a constant-temperature water bath in which the fish chamber is immersed.

The Doppler effect requires that movement be towards or away from the face of the transducers. Tangential positioning of the Fish Finders ensures that the sensing field is maximum for this type of movement. In actual practice, however, the positioning is adjusted until adequate sensitivity is obtained and the sensing fields do not overlap. Thus a fish swimming around the chamber passes through the individual fields of the two Fish Finders in an alternate manner.

When the Fish Finders are powered from a d-c source the passage of the fish can be heard through the earphones provided. The passage results in continuous noise which varies in amplitude and frequency depending on the speed and swimming characteristics of the fish. If the fish should stop swimming and rest in the field of the transducer it can usually still be detected by noise resulting from fin movements.

The rest of the apparatus is electronic circuitry which takes any signal indicating that the fish is present in one field and stores this

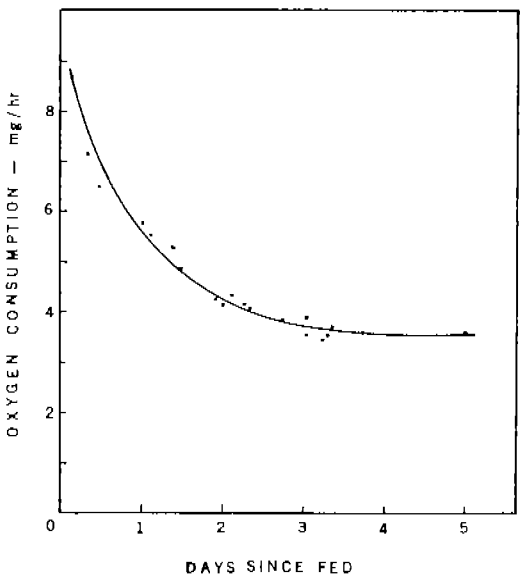

FIGURE 2.—Oxygen consumption for aholehole 5, maintained at a swimming speed of 0.23 body lengths per second for 5 days following a period of normal feeding.

information on one-half of a latching relay. A signal from the other Fish Finder completes the circuit and registers one revolution on the counter.

The output of each Fish Finder passes through a separate amplifier multivibrator unit. The output of the 4-stage amplifier triggers a one-shot multivibrator operating a plate relay. Movements of the fish within the field of the Fish Finder cause the multivibrator to pass through one or more cycles of operation during each of which the plate relay is operated. The successive operation of the plate relays from both units opens and closes a latching relay. One opening and closing cycle of the latching relay, indicating a complete revolution of the fish, results in one count on a counter and on a recorder. The strip-chart recorder provides the number of revolutions for any time interval.

The fish is induced to swim at given constant speeds by rotating a disc above the clear plexiglass top of the chamber. One-half of the disc is black and the other clear. The majority of the fish remain in the semicircular shadow created by the disc and swim around the chamber at any reasonable speed the investigator chooses. The fish is normally held at one speed for about 4 hours to insure that the flowing water reaches equilibrium and that the fish has settled down. In most cases the fish faithfully follow the disc but the activity monitor is essential to verify this, particularly because the fish chamber is isolated and usually unattended. Periodic water samples are taken from the outflow tube and from a sampling line from the inflow water, and oxygen determinations made with a Beckman model 777 analyser using a magnetic stirrer.

RESULTS

A series of the euryhaline aholehole *Kuhlia sandvicensis* ranging from 9 to 60 gms was acclimated to freshwater at 23 C. When introduced into the chamber larger specimens generally sought the shadow of the disc and followed it when it was rotated. In most cases the fish would respond even to the shadow resulting from moonlight entering a nearby window. Smaller fish showed more variation in response; some could be induced to follow the disc by the use of an overhead bright light but most would not follow it for a sufficient length of time.

Determination of the effect of swimming speed on oxygen consumption generally requires that the fish be held in the chamber for about 3 days. It is therefore necessary to consider the effect of progressive starvation. As shown in Figure 2 the oxygen consumption of a 44.4-gm aholehole maintained at a constant level of activity (0.23 body lengths per second) decreases from a peak after feeding and reaches a minimum in about 3 days. The curve is similar in shape to those given by Beamish (1964) for standard metabolism. In the remaining experiments reported here, the fish were deprived of food for approximately 3 days before being placed in the chamber. Thus the effect of feeding should be eliminated from the oxygen consumption data.

For those fish which would follow the disc for sufficient periods of time and at a number of speeds, the effect of swimming speed on oxygen consumption appeared to be linear. That is, straight lines could be fitted to the data on arithmetic plots. Some of the lines for fish of different weights showed a consider-

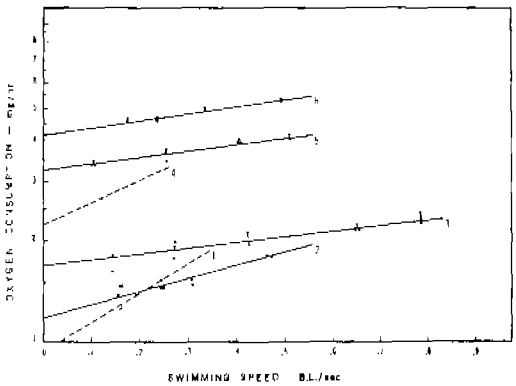

FIGURE 3.—The effect of swimming speed on oxygen consumption for six aholehole ranging from 9 to 60 gms. All fish were deprived of food for 3 days before experiment began. Swimming speeds for fish 1 and 4 are not comparable to those for other fish (see text) and their data points are not shown.

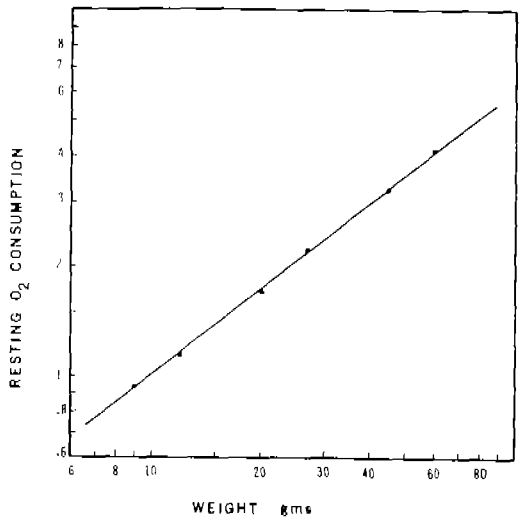

FIGURE 4.—The effect of body weight on resting oxygen consumption. The oxygen consumption values shown were obtained by extrapolation to zero swimming in Figure 4. Data from Table 1.

able divergence, larger fish having a greater slope, suggesting that a semilogarithmic transformation might result in parallel lines. For six fish the plots of the logarithm of oxygen consumption against swimming speed in fork lengths (herein termed body lengths) per second are shown in Figure 3. Straight lines are again obtained and three are nearly parallel. Because swimming speeds great enough to detect nonlinearity in an arithmetic plot apparently cannot be obtained with this apparatus, the selection of either base remains tentative until higher rates of swimming are examined. From his studies on the medium-to-high range in salmon, Brett (1964) postulated the logarithmic relationship

$$Y = ae^{bX}$$

where Y is oxygen consumption in mgm per hour, a is the resting oxygen consumption, X is swimming speed in body lengths per second and b is the regression coefficient. Empirical consideration of our data, based on maximum sustained swimming rates and oxygen consumptions found in the literature (e.g., those of Brett) give us no cause to reject his postulation.

The regression values for the intercepts (oxygen consumption at zero swimming) and the slopes are given in Table 1 with other pertinent data. The slopes for fish 3, 5, and 6 are quite similar although a slight divergence is still apparent. The divergence may be due to a number of factors. It is possible that larger fish encounter more difficulty in swimming the circular channel. The data for fish 4 were obtained using an early and very crude version of the rotating disc, which proved unsatisfactory. The fish tended to swim in bursts rather than in a smooth continuous fashion characteristic of the other fish. Fish 1, the smallest of all, would not follow the disc for sufficient lengths of time even when a bright light was placed overhead (the same response was observed with three other fish of similar size). The data shown for fish 1 were obtained during periods of spontaneous swimming without the rotating disc. The swimming speeds are averages for 2-hour intervals. Thus the steep slopes obtained for fish 1 and 4 may not be very meaningful; in any case they are not comparable to those for the other four fish.

The steep slope observed for fish 2 cannot be explained away because data for three trials for this fish all fall on the same line under conditions the same as those for fish 3, 5, and 6. Thus it cannot be determined from the present data whether the relation between swimming speed and oxygen consumption is the same for all sizes of aholehole. Differences

TABLE 1.—*Weight and length data for six aholehole and regression coefficients for the effect of swimming speed on oxygen consumption as shown in Figure 4*

Fish	Weight (gms)	Fork length (cm)	Fork lengths per revolution	Intercept mgm O_2/hour	Slope
1	9.0	8.2	10.68	0.94	2.12
2	11.9	9.1	9.63	1.16	0.93
3	20.3	10.3	8.50	1.69	0.39
4	27.0	11.7	7.49	2.24	1.59
5	44.4	13.7	6.39	3.27	0.44
6	60.1	14.8	5.92	4.17	0.49

observed might be due to variation in response to the chamber, to variation in individual fish, or to a real change in swimming characteristics with size.

Despite the variation in slope, the extrapolated oxygen consumption at zero swimming appears to be a good statistic. The logarithms of these values are plotted against the logarithms of body weights in Figure 4. The points give a good fit to the line

$$\log Y = \log 0.1664 + 0.7845 \log X$$

Thus it would appear that the extrapolated point serves as an anchor and that variations in swimming characteristics affect the slope of the line originating from this point.

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LITERATURE CITED

BEAMISH, F. W. H. 1964. Influence of starvation on standard and routine oxygen consumption. Trans. Amer. Fish. Soc. 93: 103–107.

BEAMISH, F. W. H., AND P. S. MOOKHERJII. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. Part 1. Influence of weight and temperature on respiration of goldfish, *Carassius auratus* L. Canadian J. Zool. 42: 161–175.

BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Canada 21: 1183–1226.

CUMMINGS, W. C. 1963. Using the Doppler effect to detect movements of captive fish in behavior studies. Trans. Amer. Fish. Soc. 92: 178–180.

KAVANAU, J. L. 1961. Identification of small animals by proximity sensing. Science 134: 1694–1696.

SPOOR, W. A. 1946. A quantitative study of the relationships between the activity and oxygen consumption of the goldfish and its application to the measurement of respiratory metabolism in fishes. Biol. Bull. 91: 312–325.

TAVOLGA, W. N. 1964. Psychophysics and hearing in fish. Natural History 73: 34–41.

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Observations on the Swimming Ability of Adult American Shad (*Alosa sapidissima*)

INTRODUCTION

For several years the Bureau of Commercial Fisheries, under contract with the U. S. Army Corps of Engineers, has been investigating various factors influencing the behavior of adult salmonids in relation to fish passage problems on the Columbia River and its tributaries (Collins and Elling, 1960). In the course of these investigations, incidental observations were made on the American shad (*Alosa sapidissima*) which utilized the same waterways as the salmonids. Observations presented in this report were made during the period of 18 to 28 July 1961.

The objective of the primary study on salmonids was to gain further knowledge of the maximum water velocities that could be negotiated. The presence of shad during the experiments, however, also made it possible to obtain information on the swimming ability of this species. Specifically, this report covers the channel distances negotiated by the American shad in water velocities ranging from 11.4 to 13.6 feet per second.

Although velocities of this magnitude may not often be encountered by American shad ascending the rivers and fishways at existing dams, a knowledge of their swimming ability in these higher velocities is meaningful. The continuing effort to develop more efficient and economical fish passage facilities in the Columbia River drainage requires a thorough knowledge of the physical requirements and swimming abilities of the various species of fish involved.

Even though American shad in the Columbia River are not at present regarded with the