Oxygen consumption of active rainbow trout, *Salmo gairdneri* Richardson, derived from electromyograms obtained by radiotelemetry

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A radiotelemetry apparatus is described for sensing and transmitting electromyograms (EMGs) from free-swimming fish. EMGs are recorded from the epaxial muscles of adult rainbow trout during periods in spontaneous (= routine) activity, and forced-swim, respirometers. When such EMG records are integrated, subjected to spectral analysis, and computer-averaged, the EMG values (in µV) are highly correlated with the fish oxygen consumption during the activity periods. However, there is a marked difference between the regression slopes for oxygen *v.* EMG value for the data from the spontaneous, and forced-swim, respirometers; the former slope is the steeper. The probable explanation of this phenomenon is that whereas in forced swims the epaxial myomeres are responsible for most of the activity of the fish, in spontaneous activity other muscle systems (e.g. of the lateral, dorsal and ventral fins) come to account for a greater relative proportion of body movement. The difference in slope, although great, is evidently a regular phenomenon. The shift from one regression to the other occurs at a fairly precise epaxial EMG value (*c.* 5 µV). This suggests that the laboratory calibration of EMG value in terms of oxygen consumption can be utilized in the wild so that EMG records from free-swimming fish, fitted with telemetry packages can be used to deduce oxygen consumption attributable to activity. It also appears that such records can be used as a guide to the type of activity of the fish, i.e. desultory movements or free cruising.

I. INTRODUCTION

Reliable estimates of the respiratory (oxycaloric) costs of activity of fish in the wild are scanty, which has thwarted a widespread desire of fish biologists for an accurate accounting of the entire fish energy budget. The following rationale underlies our approach to the problem of how to obtain suitable data on the respiratory requirements of fish at liberty. Subsequently, an account is given of the techniques we are developing and a sampling of our experimental results.

It can be basically assumed that oxygen demands of muscular activity in fish at any given temperature are rigorously determined by biochemical processes at the tissue level. At the level of the whole muscle (or muscle system), strength, frequency, duration of contraction, and also the bulk of the active muscle, will combine to determine its oxygen consumption. In most fish, the axial muscles, which are the main swimming muscles, consist of myomeres arranged in a bilaterally symmetrical series. These myomeres characteristically comprise most

of the total bulk of the body muscle and are involved in most body movements. For many species of fish, the demand for oxygen associated with the bodily muscular activity of ' steady state ' swimming can be explored by having a fish swim against a water current at constant (but adjustable) velocity in a ' forced-swim ' chamber (Fry, 1971).

However, in addition to its respiratory requirements (i.e. in terms of oxygen consumption, or energy expenditure), a contracting muscle generates a characteristic bioelectrical signal, the electromyogram (EMG), the configuration of which is related to the strength and duration of the muscle's contraction. In the case of the fish myomere, which, as stated, is one of a linear series, the EMG of any one myomere might be assumed to be representative other myomeres. The configuration of the EMG of a representative myomere (as well as those of other myomeres in the series) might be assumed to be highly correlated with oxygen consumption resulting from the activity of the entire myomere series.

Since 1976 we have been developing and testing techniques that utilize radiotelemetry to detect EMGs from the myomeres of free-swimming fish (Sayre, 1978; Luke *et al.*, 1979; Weatherley *et al.*, 1980; Rogers *et al.*, 1981). Our experiments have been confined to fish swimming in laboratory containers. These fish have radiotelemetry packages attached to their bodies capable of transmitting EMGs to apparatus in the same laboratory that can receive, display, and record the EMG signals. These techniques have not been adapted to use in the wild—which is to be one of the next major steps in the programme. Our studies to this point, which utilise EMG values to estimate oxygen consumption during activity in rainbow trout, do appear to justify this preliminary report.

II. MATERIALS AND METHODS

The rainbow trout, *Salmo gairdneri*, used in the experiments ranged from 30 to 37 cm fork length (F.L.) (400–650 g live weight); they were the smallest fish able to bear radiotelemetry packages of the present size without obvious disturbance of balance or swimming capability.

The EMG signal that accompanies muscle contraction in axial myomeres was detected by a pair of flexible, kynar-insulated, silver-coated, copper wire electrodes, twisted together with their bared tips 1 mm apart. In applying the electrodes and telemetry packages, rainbow trout were anaesthetized with tricaine methanesulphonate (MS 222, 60 ppm), and the electrodes were implanted dorso-laterally and sutured in the epaxial myomeres, to a depth of 1·5 cm, at a site posterior to the dorsal fin. The electrode leads pass forward to the epoxy-encased radiotransmitter package, which is also sutured in place dorsolaterally (Weatherley *et al.*, 1980). The shape of the present package has been evolved from that of a simple cylinder to a more streamlined form measuring approximately 3·5 cm in length, and 1 cm in largest diameter and weighing 7 g in air (Fig. 1).

Figure 2 shows the system and Fig. 3 the schematics of the radiotransmitter (Sayre, 1978). Figure 4 is a typical EMG from this implantation site.

Fish activity was obtained by use of two types of apparatus: (1) a forced-swim chamber of the Blažka-Fry type, of lucite construction and a volume of 48 l (Fry, 1971); and (2) a spontaneous (or routine) activity chamber of 220 l volume and cuboidal shape, also of lucite construction, able to be hermetically sealed, and with internally rounded corners to discourage fish from settling in one place.

Rainbow trout can be trained to swim constantly for extended periods against water currents of any required speed up to a limit that is a function of size. In the present study, trout were trained to maintain station at speeds up to 2·5 body lengths per second (bl s^{-1}).
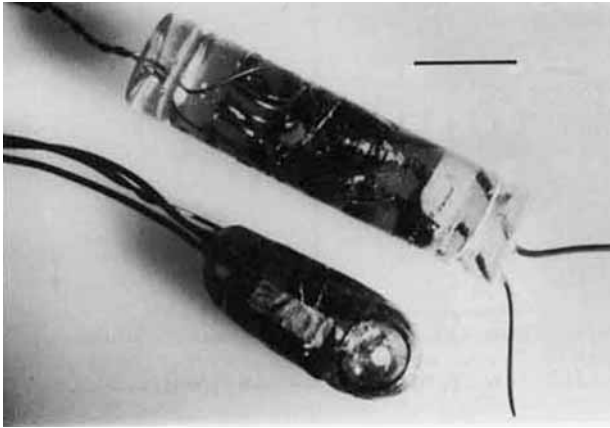
FIG. 1. Radiotelemetry packages for detection and transmission of electromyograms (EMGs) from axial muscles of free-swimming fish. The upper package is an early model; the lower package is a more recent model which has undergone considerable size reduction and streamlining. Both contain the components shown in Fig. 3. Scale bar, 10 mm.
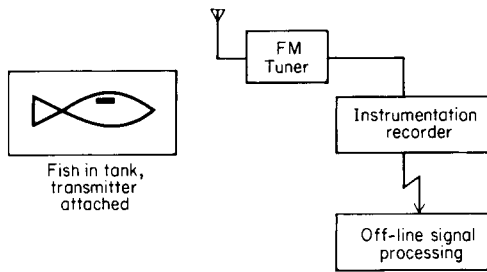

FIG. 2. Diagram of the telemetry system used in laboratory work. Transmitter uses FM to broadcast electrode voltages on standard FM broadcast band (88–108 MHz) detectable by a standard FM tuner. Analysis of recorded EMGs is carried out by a PDP 10/11 computer.
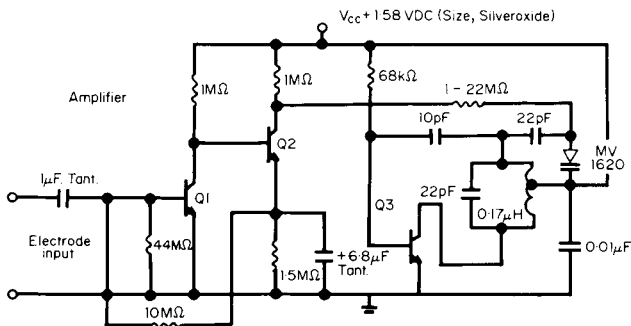

FIG. 3. Schematic of EMG transmitter. The oscillator, Q3, is of the Hartley type, with modulation achieved by means of a varactor diode. The coil is made up by winding 5·3 turns of No. 22 AWG tinned copper tapped 3·5 turns from collector end; space wound on $\frac{1}{4}''$ mandrel; length 0·6 cm. The component values shown determine oscillation at about 90 MHz and the modulation sensitivity is typically 500 Hz mV^{-1}. Q1 and Q2 amplify the electrode signal with a gain of about 300 in the bandwidth 0·2–300 Hz. Thus the standard 75 kHz deviation, compatible with a commercial FM receiver, is achieved with a 500 µV peak signal at the electrodes.
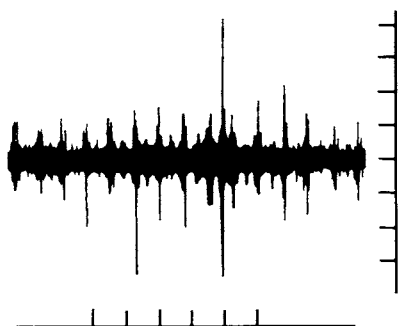
FIG. 4. Representative axial muscle EMG from 30 cm rainbow trout swimming at 1 bl s⁻¹. Vertical
scale, 1 division = 25 µV; horizontal scale, 1 division = 0·5 s. The signal transmitted is taped,
demodulated, and filtered (high pass = 20 Hz; low pass = 150 Hz).

In the spontaneous activity chamber, individual fish usually swam more or less
continually without need for artificial stimulation. However, we occasionally resorted to
prodding fish gently during measured activity periods with a round-ended metal rod which
entered the chamber through a flexible, watertight diaphragm. This caused fish to be more
active, thus permitting the range of EMG values to be increased.

All rainbow trout were acclimatized and tested at 12° C, and periods of oxygen measure-
ment and simultaneous EMG recording were of 30 min duration, except for a few of
60 min. However, the fish used would remain in the activity chamber (telemetry packages
attached) for periods exceeding 300 h (spontaneous) and 120 h (forced-swim). Fish were
not fed for 48 h prior to the onset of a trial.

In forced swims, the procedure was to hold fish fitted with functioning transmitter
packages overnight in the chamber, swimming gently at 20 cm s⁻¹. During this period, the
system would be on recirculation, i.e. receiving fully aerated water at 12° C pumped
continuously through the chamber from a 100 gal reservoir. To begin each forced-swim
series, the swim chamber was disconnected from recirculation and sealed for a 30-min
swim at 20 cm s⁻¹, during which oxygen consumption was measured and EMGs were
continuously recorded. Following this procedure, the chamber was returned to
recirculation, and current speed was raised 10 cm s⁻¹. After 30 min, the system was sealed
again for a further 30-min swim. This procedure was repeated up to a final speed not
exceeding 2·5 bl s⁻¹. This speed was determined by fatigue as characterized by a visible
failure of the fish to maintain constant station against the water current. The oxygen
content in the forced-swim chamber always returned to air saturation values soon after the
system was restored to recirculation following each 30-min swim.

In the spontaneous activity chamber, fish fitted with telemetry packages were allowed
overnight exposure to the chamber while on recirculation. Each 30-min experiment was
begun by disconnecting from the recirculation tank and sealing the spontaneous chamber.
Between periods of EMG recording and oxygen consumption determination, the chamber
was returned to recirculation, which rapidly restored oxygen values to saturation levels.

Oxygen consumptions were determined by analysis for oxygen concentration of a sample
of the water from each chamber at the beginning and completion of each 30-min experi-
mental period. Mixing of water was automatic in the forced swims. Good mixing in the
spontaneous chamber resulted from fish activity, plus movements of the metal prodder, in
most instances.

Oxygen was determined by the azide modification of the Winkler method (APHA, 1975).
Samples of 60 ml were collected, of which 15 ml aliquots were used for micro-
determination by titrating with 0·020N sodium thiosulphate to a standard endpoint using a
Gilmont® 2 ml microburette. This technique permits an accuracy, in ppm of oxygen, of
two decimal places in small samples.

The EMG signals were received by means of a commercial FM tuner (Sony ST 295
OSD), filtered, amplified, and tape-recorded on a Sony TC-765 reel-to-reel tape deck.
Signals were integrated, analysed in terms of their frequency spectra, and averaged (in µV)

by the use of a PDP 10/11 computer. The EMG mean signal values in μV as reported represent the actual mean voltages, as measured with the intramuscular electrode pair with 1 mm tip separation *in situ* as implanted in the contracting myomeres.

III. RESULTS

Figure 5(a) depicts EMG signal averages and Fig. 5(b) gives corresponding fish oxygen consumptions for a single rainbow trout, for swim speeds ranging 20–80 cm s^{-1} in the forced-swim chamber.

A linear regression accounts for the oxygen consumption rate *v.* corresponding EMG values, with high correlation [Fig. 5(c)]. In principle, therefore, oxygen consumption could be accurately estimated in trout swimming steadily in the wild, e.g. as in migrating movements, if fitted with suitable telemetry apparatus with the capability of transmitting EMGs between fish and a shore-based observer.

Figure 6 plots data obtained from one fish for swims in both the forced-swim and the spontaneous activity chamber. The data are in two distinct sets. Those for the steeper curve [Fig. 6(b)] represent the spontaneous activity, and for the other curve [Fig. 6(a)] the forced swims. Correlation coefficients are high for both data sets. While each relationship indicates that estimates of oxygen consumption could be based on EMG values for either activity mode, the marked slope differences are real and require comment and explanation.
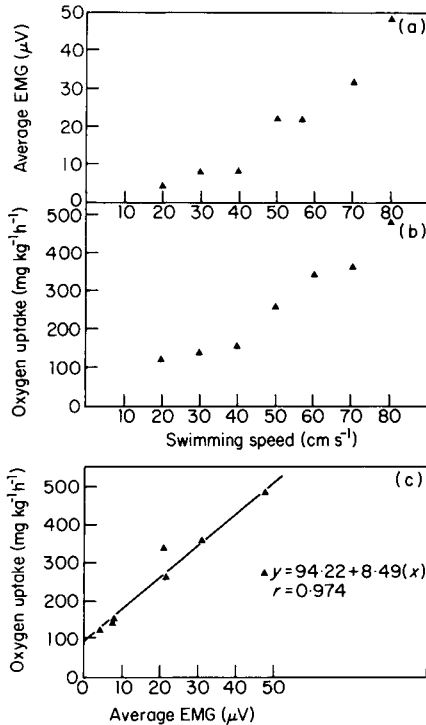

FIG. 5. (a) Average EMG values (μV); (b) corresponding oxygen consumption values *v.* swimming speed for a 32·4 cm (471 g) rainbow trout in the forced-swim chamber; (c) the oxygen consumptions of (b) *v.* corresponding EMG values of (a).
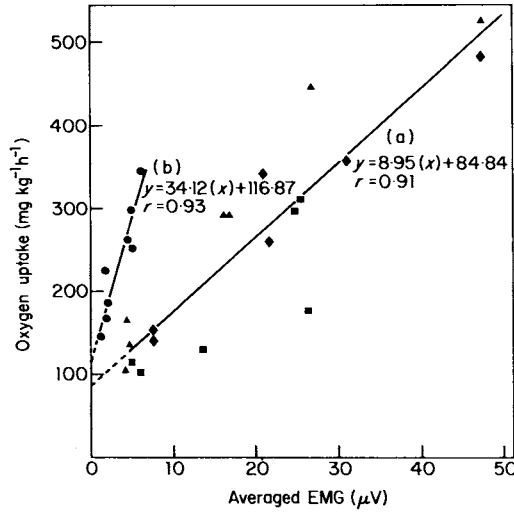
FIG. 6. Oxygen consumptions *v.* corresponding EMG values in μV for a 32·4 cm (471 g) rainbow trout: (a) swimming in the forced-swim chamber over a range of speeds from 20–80 cm s^{-1}; (b) in the spontaneous activity respirometer. Note the two distinct regressions. Symbols ▲, ◆, ■, represent forced-swim experiments on three separate, successive days; ●, represents spontaneous activity. See text for further explanation.

IV. DISCUSSION

There have been attempts to determine the oxygen requirements of fish active in the wild. These include the use of telemetry, radio or ultrasonic signals being transmitted from moving fish by means of which their positions may be determined by use of a suitable array of directional hydrophones (Henderson *et al.*, 1966; Lonsdale, 1967; Lonsdale & Baxter, 1968; Young *et al.*, 1972; Hawkins *et al.*, 1974; Young *et al.*, 1976; Stasko & Pincock, 1977). The path swum by a fish thus equipped can be depicted by joining the sequentially recorded positions. Since this procedure must necessarily ignore the inevitable path curvatures that occur, the estimated distance swum over time must always be a *minimal* estimate. If estimates of swimming speed (estimated distance divided by total elapsed time) are based on such faulty estimates of distance, then the speeds will also be minimal estimates. This latter point is especially true, since, in normal swimming, velocity will be far from uniform. Approximations of oxygen consumption or energy requirements of such estimated swimming speeds will therefore be minimal as they are derived from the oxycaloric demands of fish forced to swim in chambers at speeds based on the above estimates of speeds obtained from observations in the wild (Weatherley, 1976). Holliday *et al.* (1974) monitored the movement of brown trout in a Scottish loch by means of tags emitting ultrasonic signals and calculated that the metabolic costs of such movements were likely to amount to approximately 10% of the standard metabolic rate. As already stated, such an estimate will tend to be minimal (Weatherley, 1976).

There have been attempts to use heart rates of fish as indices of swimming activity, using ultrasonic methods (Kanwisher *et al.*, 1974; Wardle & Kanwisher, 1974; Priede & Young, 1977) and radiotelemetry (Frank, 1968; Nomura &

Ibaraki, 1969; Nomura *et al.*, 1972; Weintraub & Mackay, 1975). Priede & Young (1977) have correlated trout heart rates with oxygen consumption in laboratory forced swims; therefore, heart rate might be usable in an index of activity energetics. But heart rate in fish responds readily to environmental factors (Randall, 1970), and because of this fact, and also because heart output is related to stroke volume, heart rate may not be a reliable index of physical activity or oxygen consumption (Weatherley *et al.*, 1980).

These are some of the reasons we have considered the EMG as a possibly superior alternative physiological correlate of the oxycaloric cost of physical activity in fish.

Our original intention was to measure oxygen consumption and corresponding EMG values over a wide range of fish activity levels, on the tentative supposition that the various higher levels of activity in the spontaneous chamber, and the lower levels in the forced swim chamber, would afford a continuous series of activity levels between least (unstimulated in the spontaneous chamber) and highest (maximum sustainable forced-swim speed) activities. While we believe that—at least for rainbow trout—the high correlation between EMG and oxygen consumption partly fulfills our requirements, the two regression slopes indicated in Fig. 6 demand a reasonable interpretation before they can be used. Initially, it appeared possible that shifts in the deployment of physiologically distinct types of muscle, appropriate to the several stages of the total activity range, might account for this difference (Bone, 1978). However, the muscle in which the electrodes were implanted is the white or glycolytic type—now more usually known as mosaic. This muscle, which constitutes about 95% of the axial muscle mass in rainbow trout (Nag, 1972) contains a mixture of smaller diameter reddish fibres and larger diameter white fibres; the latter predominate. There has been considerable debate concerning the functional significance of this arrangement, leading Webb (1975) to postulate a complex involvement of different elements of the mosaic muscle at different levels of activity. In the past, the muscle has been characterized, because of its supposedly dominant role in fast swimming, as biochemically inoperative and bioelectrically silent at slow swimming speeds (Bone, 1978; Johnston *et al.*, 1975; Hudson, 1973). However, Walker & Emerson (1978) reported increases in fibre diameter in the mosaic muscle of rainbow trout resulting from prolonged swimming at low speeds. In addition, we can obtain EMGs from mosaic muscle at all levels of activity. We therefore propose a functional involvement of mosaic muscle in rainbow trout over a wider range of activity than has generally been supposed. In addition, we tend to the view (e.g. Johnston *et al.*, 1975; Walker & Emerson, 1978), that the smaller fibres of the mosaic, which include most of the reddish fibres, represent earlier growth stages of the larger white fibres (Weatherley *et al.*, 1979).

We were able to record an unbroken series of EMG signals that correlate with activity in rainbow trout, and since we recorded only from one muscle mass (the mosaic), it appears that this is involved in all activity of the axial musculature.

The difference between oxygen consumption *v.* EMG value obtained for the fish in spontaneous activity and in forced swims is to be explained essentially as follows. In forced swims, fish are obliged to concentrate their muscular efforts, i.e. the performance of their axial myomeres, in swimming at constant speed. By contrast, in the spontaneous chamber most fish activity consists of turns, fin

movements, sudden velocity changes, etc. Thus, the EMG values obtained from the epaxial electrode implantation, though still remaining correlated with oxygen consumption in the spontaneous chamber, now reflect much less of the total muscular activity of the fish. Griffiths (1977) confirms these observations and interpretations, though based on a quite different set of observations and data. Smit's (1965) experimental results on the oxygen consumption of goldfish in relation to swimming speed, though rather difficult to compare directly with our own on trout, appear to lend themselves to a somewhat similar interpretation.

However, it might initially appear almost impossible to reconcile the use of these two disparate data sets in estimating and interpreting the oxygen consumption of rainbow trout in the wild. There is fortunately a break between the data sets (Fig. 6). The spontaneous EMG values tend not to exceed 5 µV, whereas this value is the approximate lower limiting EMG value for the forced-swim data.

This interpretation is confirmed by Fig. 7. The forced-swim data are the same as for Fig. 6(a); data from six fish in the spontaneous chamber are given in Fig. 7(b), for which the regression is similar to that for the single trout in Fig. 6(b). The broken line indicates the approximate position of the postulated shift from one activity mode to the other. In addition, actual data values from one fish in the spontaneous chamber are included in Fig. 7. This fish was the single instance of unusual behaviour in this chamber. Its oxygen consumption *v*. EMG values lie not only in the expected position close to regression line (b) in Fig. 7, but some of them lie close to regression line (a). These latter values were recorded when this fish departed from the usual activity mode for the spontaneous chamber and began to swim freely around the chamber. Its speed while thus cruising for several hours was estimated as reaching 40–50 cm s^{-1}, a considerable speed for a 32·4 cm trout swimming freely in a confined space. We note that additional data for trout in forced swims, similar to those in Figs 6(a) & 7(a), are available and will be published later.

It therefore appears that a reasonably clear distinction can be made between fish active in either the spontaneous or the forced-swim chamber. This indicates that, in inferring oxygen consumption from trout active in the wild from their transmitted EMGs, mean values of < 5 µv should be assigned to the spontaneous activity regression, and those values > 5 µv to the forced-swim regression [Figs 6, 7].

This interpretation would permit the observer to infer, merely by inspection of the EMG values recorded, whether rainbow trout in the field were manifesting desultory searching behaviour, dominated by somewhat erratic activity, or were cruising more steadily.

It is hoped that the techniques we have been developing and testing will lead to the use of this type of apparatus for estimations of the oxycaloric costs of activity in natural conditions. This would help in answering a number of questions concerning fish activity energetics that are important for several reasons. Efficient fishery management and aquacultural practice could benefit from reasonably accurate analyses of the total energy budgets of various size (and age) classes in fish populations. Hitherto, the energetics of fish activity on a daily, seasonal, or annual basis has been the persistent unknown in such budgets (Weatherley, 1972, 1976). All other major compartments of the budget—the
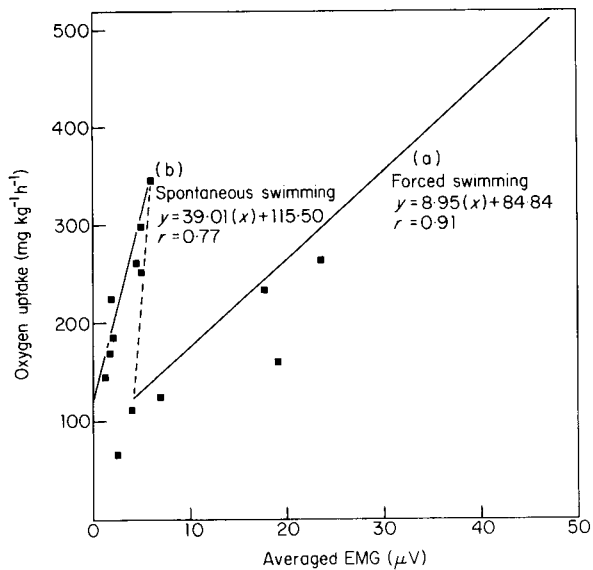
Fig. 7. Regression slopes of oxygen consumption values v. average EMG values for forced swims (a) and spontaneous activity (b). Both the forced swims and periods of spontaneous activity were of 30 min duration at 12°C. Individual points show values obtained from one fish in the spontaneous chamber, which on several occasions (6) swam continuously throughout the experimental trial. These six points can be seen to approximate closely the forced-swim regression. See text for further explanation.

specific dynamic action (SDA), standard metabolic rate (SMR), nitrogen metabolism, and the caloric value of gonad products and other new tissue (growth)—are already determinable with some degree of accuracy.

In addition to the lack of knowledge of activity energetics relative to the energy budget, there is little precise knowledge of the activity patterns and corresponding energy costs of fish in the wild exposed to sublethal but damaging concentrations of toxicants (Weatherley et al., 1980).

Developments in the telemetry apparatus described by Patch et al. (1981), should enable us to utilize ultrasonic telemetry packages of a much reduced size, and with a transmission range of approximately 1 km. While the present system employs radiotelemetry, it is expected that, in its eventual field application, ultrasonics will be employed as a more versatile, reliable and electronically simpler method. It should be possible to attach such packages to much smaller fish, and by pulsing the signal, or using an ' interrogation ' method, active package life should be prolonged over the present two weeks under laboratory use. Use of an Intertech Superbrain minicomputer will permit on-line processing of EMG data. Inclusion of temperature-sensing components in the packages and directional hydrophones in the system will significantly expand the overall capability of the equipment.

Several points may be mentioned in conclusion:

(1) Records of fish EMGs could be employed as direct ' indices of activity ' without the need to translate them into energy units. This could be useful in attempts to identify the onset and intensity of aspects of the annual activity regime such as spawning behaviour, or changes in irritability associated with the presence of environmental toxicants.

(2) The excellent correlations between oxygen consumption and EMG values, down to low magnitudes of the latter (Figs 5–7), give promise of more accurate determinations of fish SMRs than have formerly been possible (Brett, 1964).

(3) Though not described here, EMGs have also been obtained from the levator hyomandibulae et arcus palatini—a small muscle that helps elevate the trout operculum. These data will also be published later.

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