An automated ultrasonic telemetry system for the assessment of locomotor activity in free-ranging rainbow trout, *Salmo gairdneri*, Richardson

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A new automated ultrasonic telemetry system for monitoring the swimming activity of adult rainbow trout, *Salmo gairdneri*, at liberty in the wild is described. The transmitter detects bioelectric potentials (i.e. electromyograms) associated with the contraction of the epaxial myomeres during swimming. Transmitter output is relayed to the signal processing system via submerged hydrophones. The incoming signals represent averaged electromyograms which have been shown in earlier studies to correlate well with swimming activity and concurrent oxygen consumption of rainbow trout in the laboratory.

Electromyogram records obtained from rainbow trout released into a small lake and monitored for up to 4 weeks, indicate a fairly regular pattern of elevated midday activity contrasting with periods of relative quiescence during the evening and morning. This midday peak in locomotory activity is the result of an increased feeding activity which is evidently a response to a concomitant increase in the activity of the fish's prey.

I. INTRODUCTION

Fishery scientists have long sought a means of accurate assessment of the amount and nature of locomotory activity displayed by fish at liberty. Such information would permit precise estimates of the metabolic costs of the daily activity regimen of a fish. This, in turn, would provide biologists with a highly sensitive tool for the evaluation of numerous ecological problems, including feeding biology, pollution impact biology and energy relationships between species.

Field estimates of fish activity based on capture/recapture techniques, direct observation, sonar, etc. have been too inaccurate. The advent of underwater biotelemetry during the past 20 years has made it possible to assess the gross movements of fish by means of simple location transmitters (radio or ultrasonic) attached to the fish. However, to translate such movements, based as they are on interpolations between instantaneous records of fish location, into an evaluation of the metabolic costs of field activity is fraught with difficulty—essentially because the interpolations cannot account for the intricacies of paths swum or

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velocity changes between locations (Priede & Young, 1977; Weatherley, 1976; Weatherley *et al.*, 1982). Progress in other aspects of underwater biotelemetry has led to the monitoring of physical and physiological variables such as tail-beat frequency (Stasko & Horrall, 1976; Ross *et al.*, 1981), swimming speed (Voegeli & Pincock, 1980) and heart rate (Priede & Young, 1977) in free-living fish, though attempts to deduce the metabolic costs of activity from data on these variables have also proved error prone (Rogers *et al.*, 1981; Weatherley *et al.*, 1982).

Rogers *et al.* (1981) and Weatherley *et al.* (1982) described a laboratory-based radiotelemetry system for the detection of electromyograms (EMGs) from the main swimming muscles of adult rainbow trout, *Salmo gairdneri*. Electromyograms emanating from these muscles correlated well with activity and with concurrent oxygen consumption rates of fish under both routine and constant forced-swimming conditions.

The present report describes an automated ultrasonic biotelemetry system for the detection of EMGs from fish at liberty in the wild, the development of which was based on the radiotelemetry laboratory system. The transmitters were attached to adult rainbow trout that were then released in a small lake for continuous monitoring of the locomotory activity of the animals for up to 4 weeks. The data obtained demonstrated the dynamics of the daily activity displayed by these fish.

II. MATERIALS AND METHODS

The study was performed at Lake St George between October and December, 1982. This lake is located 2 km east of Oak Ridges, Ontario in the Lake St George Conservation Area and consists of two basins (Fig. 1) of similar depth (max. 15–16 m) connected by a narrow, shallow channel. The total area of the lake is 10·3 ha (McQueen, 1981).



FIG. 1. Map of Lake St George, Ontario showing the depth contours, the positions of the omnidirectional hydrophones (H) and the receiving hardware (R). (Modified after McQueen, 1981.)



FIG. 2. Ultrasonic receiving system block diagram. See text for detailed description.

The object of this study was continuous monitoring of electromyograms (EMGs) from rainbow trout at liberty in the lake for a period of not less than 1 month. The EMGs obtained were then to be compared quantitatively and qualitatively to the laboratory values already obtained from these fish and from which the metabolic (oxycaloric) costs of activity could be inferred. Ultrasonic transmission was chosen primarily because of the eventual requirement for precise location of individual fish and the availability of suitable receiving equipment.

A diagram of the EMG telemetry receiving system is presented in Fig. 2. It consisted essentially of an omnidirectional hydrophone located centrally at mid-depth (i.e. 7–8 m) in each of the two basins of the lake (Fig. 1). These hydrophones were cable-linked to a shore-based CR40 receiver ('Communications Associates') that had been modified to permit computer control of the channel selection via a custom built pulse interval processor (PIP) and a microcomputer. The receiver was able to scan six crystal-controlled frequencies (65 to 80 kHz @ 3 kHz increments) and provide a logical output for a detected input signal which in turn was relayed to the PIP. The PIP determined and stored the time intervals between successive pulses in a queue and was designed to serve as an interface for data collection between such ultrasonic receivers and general purpose computers (Pincock *et al.*, 1981). The PIP also contained a real-time clock which could be set and read by the host computer.

The host computer for this application was a Z-80 based Intertec Superbrain desk top computer. In operation, the computer executes a data acquisition program which first selects a channel and instructs the PIP to pass it the current time interval for that transmitter, as well as the time of day. Each active transmitter is recorded in the same manner, and the cycle repeats. The data fills a buffer which is periodically stored on disk for later analysis. In addition, the data are displayed on the computer's monitor and are continually updated with each successive data acquisition. The operator has control over which transmitters are to be logged as well as the sampling interval. Continuous sampling of six transmitters every 26 s will fill one $5\frac{1}{4}$ inch disk in 37 h. Data processing is currently being done off-line. In the present application, a sampling interval was selected so that an EMG average for each fish in the lake was obtained every 23 s. Because the time interval between any two successive pulses is representative of the rectified average of the bioelectrical potentials generated in the epaxial muscles in the region of the electrodes and is directly related to the amount of locomotory activity displayed by the animal (Weatherley *et al.*, 1982), this system provides a continuous record of a fish's activity over time.

The key to the field study is the EMG transmitter which is capable of continuous EMG monitoring for up to 1 month. A schematic diagram is shown in Fig. 3. Overall functioning is as follows. The EMG is amplified and filtered, rectified, averaged and this average is converted to a time interval by a pulse position modulation generator (PPM). The PPM output gates a crystal controlled transmission frequency oscillator through to a Class D power amplifier, which drives the output transducer. To reduce transducer size and cost, all transmitters use a 6.0 mm diameter tube resonant at 135 kHz. Further details on circuit design and transmitter construction are available (see Church, 1983). The voltage regulator, A7, prevents pulse interval changes as the battery voltage decreases. The transmitter is energized by means of a magnetic reed switch in the negative supply line.



FIG. 3. EMG transmitter schematics. See text for detailed description. Notes: A1 - A7 = 3078 powered from V⁺ and V⁻; G1 - G2 = 4007; PPM gen. = 3096.

The construction technique used is referred to as 'chip and wire ' and produces a hybrid circuit. It utilizes miniature passive components and active devices in die form or subminiature packages. Conventional printed circuit materials are employed in conjunction with an ultrasonic wire bonder. This technique allows moderate complexity in the miniature transmitters at very modest cost. In addition, design changes are quickly and easily incorporated. The EMG transmitters were encapsulated in epoxy resin in the desired shape. Figure 4 shows three stages in the construction of the EMG transmitters, (1) etched circuit boards, (2) components mounted, and (3) encapsulated transmitter. Figure 5 is another view of the completed transmitter which illustrates the streamlined shape to reduce drag. The transmitter was sutured to the side of the fish by means of the small 'ears' on the package.

A total of four large male rainbow trout were released into Lake St George during the months of October and November, each fitted with an ultrasonic transmitter (Table 1). These fish had been hatchery-reared and raised in our laboratory for up to 3 years. Over this time they had been fed a dry, pelletized trout food diet (Martin Feed Mills, Elmira, Ontario) biweekly at a level slightly above maintenance. Prior to introduction to the field they were acclimated to the same temperature as the lake surface waters (i.e. 6° C) and their diet was changed to one exclusively of live minnows.

Transmitters were attached to each fish at lake-side on the day of introduction to the lake. Each fish was anaesthetized with tricaine methanesulphonate (approximately $60 \,\mu l \, l^{-1}$) and the transmitter was sutured to its right dorso-lateral aspect, just anterior



FIG. 4. A plate showing three stages in the construction of an EMG transmitter. The etched circuit boards (a), with the components mounted (b), are encapsulated in an epoxy resin (c). This prototype transmitter has the EMG-sensing electrodes removed.



FIG. 5. Another view of the transmitter shown in Fig. 4 illustrating its streamlined shape.

	Transmitter life span (days)	15 26 1 + +
	Reason for termination	Battery failure Battery failure Ice on lake Ice on lake
	Last day of record	10 Nov. 29 Nov. 10 Dec. 10 Dec.
	Date of release	27 Oct. 10 Nov. 14 Nov. 19 Nov.
of 1982	Date of attachment	27 Oct. 5 Nov. 14 Nov. 19 Nov.
	Transmitter frequency (kHz)	50 68 74 65
	Transmitter type	Pinger EMG EMG EMG
	Weight (g)	885 690 1075 1350
1	Length (cm)	43-0 39-8 43-6 47-7
	Fish no.	-0.04

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I. Experimental	
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FIG. 6. Plate showing an EMG transmitter attached to the right dorso-lateral aspect of a 43.6 cm (1075 g) rainbow trout, *S. gairdneri*. Note the implantation site of the EMG-sensing electrodes at a point just posterior to the dorsal fin in the region of the 20th epaxial myomere from the tail.

to the dorsal fin (Fig. 6) using 8 lb monofilament fishing line. In the case of the EMG transmitters, the sensing electrodes trailed posteriorly from the body of the transmitter with their tips implanted to a depth of 1.50 to 1.75 cm in the mosaic muscle fibres of the epaxial musculature in the region of the 20th myomere from the tail (see Weatherley *et al.*, 1982). The electrodes were held in place by sutures close to their point of entry into the skin (Fig. 6).

The EMG transmitters had a transmission range in water of approximately 1 km. Hence, signal reception was possible from all locations within the lake system. Transmitter weight in water was 9.8 g.

Transmitters, once attached, were activated by removal of the magnet controlling the reed switch. The fish were placed in a holding cage in the lake until recovery from anaesthesia was complete and a system check of the receiving hardware was completed. Once satisfied that the overall system was functioning correctly, each fish was released in the southern portion of the east basin.

The length, weight, date of transmitter attachment, type of transmitter, date of release and the transmitter frequency of each fish are given in Table I.

The precise location of each fish in the lake was determined intermittently by means of a boat-mounted directional hydrophone (Vemco Inc. Model V-10) and a direct conversion receiver.

The 'averaged' EMGs cited in this text each represent the arithmetic mean of 78 consecutive EMG samples displayed over a 30 min period (i.e. 1 sample 23 s^{-1}). Although such averages could be derived for any time interval, 30 min was chosen so that swimming speed, as well as future metabolic approximations, could be obtained through extrapolation of previous laboratory calibrations which employed a similar time interval (Rogers & Weatherley, 1983; Weatherley *et al.*, 1982).



FIG. 7. Scattergram depicting averaged EMGs received from a 43.6 cm (1075 g) rainbow trout, S. gairdneri, in relation to the time of day. The values shown represent a composite of all those obtained from this fish over the 26 day experimental period.

III. RESULTS

In light of the tremendous volume of data collected from the three EMG-tagged fish over the experimental period, we have chosen to present only those results obtained from a single individual (i.e. the 74 kHz fish). The activity levels displayed by the fish in the results presented here, together with the implied behaviour patterns, are typical of those exhibited by the other two fish. Figure 7 is a scattergram of the averaged EMG values obtained from this fish versus the time of day over the 26 day (14 November to 10 December 1982) experimental period. Complete records for each individual day were not always available due to persistent problems arising in the receiving hardware which brought about cessation in sampling for varying periods of time. Nevertheless, the data obtained signify a marked elevation in activity levels occurring fairly regularly between 11.00 and 15.00 hours on each day of record.

Although the intensity of the activity displayed by this fish over any given time period is highly variable (Fig. 7), examination of the standard errors of the means (S.E.M.) of the EMG values obtained during each 1 h time period (Fig. 8) confirms a substantial rise in locomotory activity during the midday period. Figure 9 shows the records for this fish obtained on the second and fourth days after release. As will be discussed, the midday peaks prior to the fourth day, although present, did not attain intensity levels comparable to those found on this day, and all subsequent days.



FIG. 8. Hourly averages and their associated standard errors of measurement of the EMG records obtained from a 43.6 cm (1075 g) rainbow trout, *S. gairdneri*, over the 26 day experimental period.



FIG. 9. Daily EMG records obtained from a 43.6 cm (1075 g) rainbow trout, S. gairdneri, on the second (▲) and fourth (●) days after release (16 and 18 November 1982).

Tracking studies of this individual, performed by use of the boat-mounted directional hydrophone, indicated that he spent most of his time in the northern half of the east basin but made frequent excursions into the west basin. On a number of occasions, when the fish was tracked during the midday hours, he was noted to move fairly rapidly over a considerable area of the lake, as indicated by the EMG records. On four separate occasions the fish was visually observed when he ventured into shallower waters during this period. At these times he was noted to be actively pursuing and feeding upon schools of emerald shiners, *Notropis atherinoides*. In this preliminary report, no attempt will be made to derive metabolic expenditures associated with the activity displayed by this fish. Although calibration data of averaged EMG values versus oxygen uptake and swimming speed do exist for these fish (Weatherley *et al.*, 1982), temperature differences between the two experimental situations do not permit such an analysis at this time. Nevertheless, some indication of the swimming speeds exhibited, particularly during the more active periods, is given.

IV. DISCUSSION

The occurrence of regular daily cycles in the locomotory activity of fish at liberty in the wild has been a recognized phenomenon and has received considerable attention in recent years (Hoar, 1942; Davis, 1964; Thorpe, 1978; Johnson & Johnson, 1981). The nature of such cycles is extremely diverse, not only between different species but also within the same species, and is usually the result of complex interactions between fish (or their population) and the biotic and abiotic environments. Nevertheless, two environmental factors can be considered paramount in governing the activity cycles in most fish: (1) light, and (2) the availability of a suitable food resource. In predatory fish, it is reasonable to suppose that daily rhythmic activity cycles are strongly influenced by feeding behaviour and that the peaks in these cycles may represent periods when the physical (i.e. light conditions, temperature, etc.) and biological (i.e. prey composition, abundance and activity) factors are optimal for exploitation of a selected food resource. Hence, cycles will vary in accordance with a wide range of environmental factors.

There is abundant literature on the importance of light as a governing factor of the activity cycles of a wide range of fish species (Alabaster & Robertson, 1961; Chaston, 1968; Muntz & Wainwright, 1978; Oswald, 1978; Cerri, 1983). The rainbow trout is an obligate visual predator (Ware, 1972), so that light is an important ecological factor in which both quantity and quality of illumination influence fish activity (Ritter & MacCrimmon, 1973). In the present study, the regular pattern of elevated midday activity, evidenced by the EMG records, in combination with the direct observation, on several occasions, of the fish feeding during this time, indicate that the activity peaks are associated with feeding behaviour.

Close examination of the individual EMG data points, 78 of which were averaged to obtain each of the values in Figs 7 and 9 (i.e. 1/23 s), clearly shows that the activity peaks are the result of tremendous variations in swimming speed displayed by the fish. The records characteristically show high instantaneous EMG outputs, in excess of $120 \,\mu$ V, mainly occurring between 10.00 and 14.00 hours, that can be shown, from laboratory experiments, to correspond to burst swimming speeds in excess of 7 body lengths s⁻¹ intermixed with much reduced swimming activity. Such bursts of activity are not evident anywhere else in the daily records. For a non-migrating salmonid, such as the rainbow trout, to exhibit such bursts of swimming speed, it must incur significant oxygen debts characteristic of the use of the white, glycolytic fibres of the axial muscle series (Driedzic & Hochachka, 1978). These fibres are supposed to become progressively more active at higher swimming speeds (i.e. ≥ 2 body lengths s⁻¹) and can only remain functional for short periods of time before exhaustion of their metabolic substrates occurs (Bone, 1978; Driedzic & Hochachka, 1978), but see Weatherley et al. (1982). The rainbow trout used in this study have been shown to have a maximum sustainable swimming speed (i.e. maximum aerobic capacity) in the range of 2.0 to 2.6 body lengths s^{-1} (Rogers, 1982). The bursts of activity witnessed in these records far exceed these limits and are indicative of the sort of activity associated with prey capture or with predator avoidance. As the only other large predator that is found in this lake is the northern pike, Esox lucius, which, in this instance, seldom grows beyond 90 cm, it is unlikely that predatory attacks on these trout occurred. Thus, these bursts of high velocity swimming occurring regularly during the midday activity peaks are presumably the result of predatory lunges made by the trout at prospective prey items. As mentioned, these fish were laboratory-raised and fed at irregular intervals prior to release in the field. Hence, the regular predatory behaviour alluded to above must be a response learned in situ by the individual fish. If this is so, such a learning process should be implied in the EMG records. This does, in fact, appear to be the case as evidenced by data obtained over the first 4 days following release (Fig. 9). EMG records from 14 to 17 November did show the characteristic midday activity peak, but the intensity of these peaks was markedly lower than those evident on all subsequent days on record. During these first 3 days, the averaged EMG values of the peak never exceeded $8.0 \,\mu$ V, whereas from 18 November to the end of the study, the peaks were always highlighted by averaged EMG values in excess of 13 µV (Fig. 9). Thus, it may be tentatively proposed that within these first 3 days the fish did little or no feeding but that gradually over this period they came to recognize schools of minnows as potential prey items and soon began active predation at regular intervals. This supposition gains considerable support from the work of Ware (1971) who found that rainbow trout required, on average, 4 days of exposure to unfamiliar food before recognizing it as a food item. He found that the reaction distance (i.e. the distance from which the trout attacked food) improved after the initial period of familiarization. Furthermore, as the reaction distance increased, the rate of discovery of prey accelerated (Ware, 1972). In the present case, the brief (1 week) exposure of the trout to minnows as a food item in the laboratory just prior to release may have reduced the time required by the fish to recognize them as prey items in the lake.

It still remains unanswered as to why the trout adopted a monophasic daily activity regime and why such a peak occurred regularly every day. The rainbow trout is a highly positive phototactic animal and, since visual acuity is a very important aspect of its predatory feeding, the fish may be responding to the optimal light intensities during the day. Natural light intensities occurring at the lake during the experimental period were not measured; nevertheless, when averaged EMG levels were examined in relation to minutes of sunshine experienced during each hour of the day, no relationship was apparent. In addition, the fish displayed the same rhythmic activity whether the sky was clear or overcast. Even when the lake experienced intense morning sunshine and overcast afternoon conditions, the time of the peak remained unchanged. There would be no reason to pre-suppose that feeding would not occur at any time during the daylight hours. Hence, all these factors tend to indicate that illumination levels may, in fact, not be the *major* single factor governing the nature of this cycle. There is little doubt, though, that the activity of the trout is dependent on the presence of light and, as evidenced by the data obtained, the onset of locomotory activity occurred at dawn each day and increased throughout the day until its attenuation as evening approached. The midday peak, may, however, be a response mediated by some other factor intrinsic to this lake. Indeed, it is our contention that this peak is probably the result of an increased availability of food occurring each day in accordance with the prey species' own endogenous activity rhythms.

Since these trout were known to be feeding on schools of minnows and it was determined through our tracking studies that they mostly remained in shallower surface waters (i.e. in the upper few metres, probably above the thermocline as they had been acclimated to these temperatures), it may be reasonable to assume that the prey's abundance only became optimal for foraging by the trout at this time every day. This period may, in fact, represent the time at which the minnows were most active as they themselves moved into shallower waters to feed, probably in response to light levels reaching their specific optimum for visual acuity and detection of their own items of prey. Species of minnows such as the emerald shiner are known to move inshore with the decreasing autumn temperatures and when the water is rough (Campbell & MacCrimmon, 1970)—as would be the case as the day progressed and wind velocities increased. Hence, as the activity of the minnows increased in response to their own feeding rhythms, their presence would become more apparent to the trout which, in turn, would bring about the onset of their feeding behaviour. Such an interpretation is obviously tentative and considerably more study of endogenous activity patterns of the species involved in this lake is warranted before a conclusive statement is possible.

As mentioned, this study was undertaken to test the field operation and capabilities of a new telemetry system. Transmitter performance and attachment durability proved extremely reliable. Only one transmitter failed during the study and this occurred after some 25 days, which was close to the predicted life expectancy of the transmitter. The other two transmitters remained active long after the freezing of the lake's surface waters necessitated removal of the main receiving hardware.

Procedures for attaching the transmitter to the trout proved highly satisfactory. Close visual observations of two of the fish more than 15 days after release showed that no loosening of the sutures had occurred. These fish were seen to be feeding normally without apparent difficulty caused by the transmitter's presence. Also, the problem of transmitter dislodgement by the fish on the heavy submerged vegetation around the fringes of the lake, a persistent occurrence in earlier studies involving externally attached transmitters on northern pike, *E. lucius*, in this lake (L. Onisco, pers. comm.), was not evident in this study.

Further developments in the system will involve the deployment of a triangular array of hydrophones in each of the basins so that positional fixes for each fish can be obtained automatically and recorded in the computer's data file simultaneously with EMG data. In addition to the release of rainbow trout, walleye, *Stizostedion vitreum vitreum*, will also be released to investigate their extremely interesting photo-reactive activity patterns (Ryder, 1977). It is also hoped to attach transmitters to yellow perch, *Perca flavescens*, and to pike, *E. lucius*, so that the activity and other aspects of the metabolic budget of several species of predatory fishes in close association with each other can be studied within a single lake ecosystem. More complete biological studies involving the active measurement of the growth and bioenergetics of released individuals will also be attempted.

The initial field performance of this telemetry system has proved highly encouraging and with the further developments planned for the future, it may become possible to provide users with an extremely versatile tool for application to a wide variety of problems in fishery sciences.

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References

- Alabaster, J. S. & Robertson, K. G. (1961). The effect of diurnal changes in temperature, dissolved oxygen and illumination on the behaviour of loach (*Rutilius rutilus L.*), bream (*Abramis brama L.*) and perch (*Perca fluviatilis L.*). Anim. Behav. 9, 187-192.
- Bone, Q. (1978). Locomotor muscle. In Fish Physiology (W. S. Hoar & D. J. Randall, eds), Vol. VII, pp. 361–424. New York: Academic Press.
- Campbell, J. S. & MacCrimmon, H. R. (1970). Biology of the emerald shiner, Notropis atherinoides Rafinesque, in Lake Simcoe, Canada. J. Fish Biol. 2, 259-273.
- Cerri, R. O. (1983). The effect of light intensity on predator and prey behaviour in cyprinid fish: factors that influence prey risk. *Anim. Behav.* **31**, 736-742.
- Chaston, I. (1968). Influence of light on activity of brown trout (Salmo trutta). J. Fish. Res. Bd Can. 25, 1285-1289.
- Church, D. W. (1983). Transmitter design for miniature ultrasonic telemeters. Ph.D. Thesis, Technical University of Nova Scotia.
- Davis, R. E. (1964). Daily 'predawn' peak of locomotion in fish. Anim. Behav. 12, 272-283.
- Driedzic, W. R. & Hochachka, P. W. (1978). Metabolism in fish during exercise. In Fish Physiology (W. S. Hoar & D. J. Randall, eds), Vol. VII, pp. 503-543. New York: Academic Press.
- Hoar, W. S. (1942). Diurnal variations in feeding activity of young salmon and trout. J. Fish. Res. Bd Can. 6, 90-101.
- Johnson, J. H. & Johnson, E. Z. (1981). Feeding periodicity and diel variation in diet composition of subyearling coho salmon, Oncorhynchus kisutch, and steelhead, Salmo gairdneri, in a small stream during summer. Fish. Bull. Nat. Ocean Atmos. Adm 79, 370-375.
- McQueen, D. J. (1981). Second Annual Report, Lake St George Hypolimnetic Aeration Project, pp. 205.
- Muntz, W. R. A. & Wainwright, A. W. (1978). Annual cycles in the light environments and visual mechanisms of fishes. In *Rhythmic Activity of Fishes* (J. E. Thorpe, ed.). New York: Academic Press.
- Oswald, R. L. (1978). The use of telemetry to study light synchronization with feeding and gill ventilation rates in Salmo trutta. J. Fish Biol. 13, 729-739.

- Pincock, D. G., Church, D. W. & Voegeli, F. A. (1981). A conductivity-temperature-depth telemeter. Proc. IERE Conf. Electronics for Ocean Technology, Birmingham, England, pp. 149–158.
- Priede, I. G. & Young, A. H. (1977). The ultrasonic telemetry of cardiac rhythms of wild brown trout (*Salmo trutta* L.) as an indicator of bioenergetics and behaviour. J. Fish Biol. 10, 299–318.
- Ritter, J. A. & MacCrimmon, H. R. (1973). Effects of illumination on behaviour of wild brown trout (Salmo trutta) and rainbow trout (Salmo gairdneri) exposed to black and white backgrounds. J. Fish. Res. Bd Can. 30, 1875-1880.
- Rogers, S. C. (1982). The development and laboratory calibration of a radiotelemetry system for the assessment of the metabolic costs of activity in free-swimming adult rainbow trout (*Salmo gairdneri*, Richardson). M.Sc. Thesis, University of Toronto.
- Rogers, S. C., Weatherley, A. H., Pincock, D. G. & Patch, J. R. (1981). Telemetry, electromyograms, and oxygen demands of fish activity. In Proc. 3rd Internat. Confer. Wildl. Biotelemetry. University of Wyoming, Laramie, July, 1981, 141-150.
- Rogers, S. C. & Weatherley, A. H. (1983). The use of opercular muscle electromyograms as an indicator of the metabolic costs of fish activity in rainbow trout, *Salmo gairdneri* Richardson, as determined by radiotelemetry. J. Fish Biol. 23, 535-547.
- Ross, L. G., Watts, W. & Young, A. H. (1981). An ultrasonic biotelemetry system for the continuous monitoring of tail-beat rate from free-swimming fish. J. Fish Biol. 18, 479–490.
- Ryder, R. A. (1977). Effects of ambient light variations on behaviour of yearling, subadult and adult walleyes. J. Fish. Res. Bd Can. 34, 1481–1491.
- Stasko, A. B. & Horrall, R. M. (1976). Method of counting tail-beats of free-swimming fish by ultrasonic telemetry techniques. J. Fish. Res. Bd Can. 33, 2596–2598.
- Thorpe, J. E. (ed.) (1978). Rhythmic Activity of Fishes, pp. 291. London: Academic Press.
- Voegeli, F. A. & Pincock, D. G. (1980). Determination of fish swimming speed by ultrasonic telemetry. *Biotelemetry Patient Monit.* 7, 215-220.
- Ware, D. M. (1971). Predation by rainbow trout (Salmo gairdneri). The effect of experience. J. Fish. Res. Bd Can. 28, 1847–1852.
- Ware, D. M. (1972). Predation by rainbow trout (Salmo gairdneri): the influence of hunger, prey density, and prey size. J. Fish. Res. Bd Can. 29, 1193-1201.
- Weatherley, A. H. (1976). Factors affecting maximization of fish growth. J. Fish. Res. Bd Can. 33, 1046–1058.
- Weatherley, A. H., Rogers, S. C., Pincock, D. G. & Patch, J. R. (1982). Oxygen consumption of active rainbow trout, *Salmo gairdneri* Richardson, derived from electromyograms obtained by radiotelemetry. J. Fish Biol. 20, 479-489.