Journal Fisheries Research Board Ganada

Journal de l'Office des recherches sur les pêcheries du Canada

Volume 34, No. 9, September 1977

Volume 34, n° 9, septembre 1977

Review of Underwater Biotelemetry, with Emphasis on Ultrasonic Techniques

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Contents

ABSTRACT 1262

RÉSUMÉ 1262

Introduction 1262

Historical Development

Signals

Ultrasonic signals

Radio signals

Choice of signal type

EQUIPMENT FOR ULTRASONIC BIOTELEMETRY 1266

Basic Transmitter

Transducer and driving amplifier

Battery

Electronics

Encapsulation and activation

Transponders

Hydrophones

Useful frequency range

Directionality

Noise performance

Basic Receiver

Methods of Localization

Mobile systems

Directional receiving system

Sonar systems

Fixed systems

Vertical position

Transmission of Information

Modulation methods

Single channel

Multiple channels

Printed in Canada (J4615) Imprimé au Canada (J4615) Transmitters with sensors

Temperature

Pressure

Other sensors

Decoding

BIOLOGICAL APPLICATIONS OF UNDERWATER

TELEMETRY 1273

Methodology

Transmitter attachment

External attachment

In stomach

Surgical implantation

Invertebrates, reptiles, and mammals

Effect on behavior

Minimizing the effects

Testing for effects

Biological Studies

Location-only transmitters

Migration orientation
Movements at obstructions

Behavior and ecology

Transmitters with sensors

Temperature measurements

Swimming depth

Heartbeats

Other factors

Conclusion 1279

Acknowledgments 1280

REFERENCES 1280

Abstract

STASKO, A. B., AND D. G. PINCOCK. 1977. Review of underwater biotelemetry, with emphasis on ultrasonic techniques. J. Fish. Res. Board Can. 34: 1261–1285.

Underwater biotelemetry includes studies of movements, behavior, and physiological functions of underwater animals, as well as environmental conditions surrounding them. In such studies data are received via signals from a transmitter on or in an animal. Ultrasonic signals were used in early work. More recently both ultrasonic and radio signals have been used.

In the two decades since the first underwater biotelemetry studies in the mid-1950s there have been considerable technical advances. Transmitters have become smaller, more powerful, and have longer operating life. Coding of individual transmitters has become more reliable and decoding more automated. Transmitters capable of sensing environmental, behavioral, and physiological factors from free-swimming animals have been built. Receiving systems ranging from small ones for tracking from canoes to large ones for oceangoing vessels have been developed.

With this equipment about 60 species of underwater animals have been studied. Various techniques of transmitter attachment have been developed and different methods of tracking explored.

Underwater biotelemetry has been applied to studies of fish migration, orientation mechanisms, movement patterns at obstructions, ecology, behavior, and physiology of animals.

Key words: telemetry, underwater biotelemetry, tracking, sonic tags, transmitters, receivers, hydrophones

Résumé

STASKO, A. B., AND D. G. PINCOCK. 1977. Review of underwater biotelemetry, with emphasis on ultrasonic techniques. J. Fish. Res. Board Can. 34: 1261–1285.

La biotélémétrie sous-marine inclue des études de mouvements, de comportement et de fonctions physiologiques d'animaux sous l'eau, de même que l'étude des conditions ambiantes qui les entourent. Dans de telles études, les données sont obtenues par voie de signaux provenant d'un émetteur placé sur ou dans l'animal. Dans les travaux du début, on a utilisé des signaux ultrasonores; plus récemment on s'est servi de signaux radiophoniques aussi bien qu'ultrasonores.

On a accompli beaucoup de progrès techniques au cours des deux décennies qui ont suivi les premières études de biotélémétrie sous-marine au milieu des années 1950. Les transmetteurs sont devenus plus petits, plus puissants et à période d'opération plus longue. Le codage d'émetteurs individuels est devenu plus fiable, et le décodage plus automatisé. On a construit des émetteurs capables de détecter des facteurs d'environnement, de comportement et de physiologie provenant d'animaux pélagiques. On a mis au point des systèmes de réception allant de petits récepteurs pour le dépistage depuis des petites embarcations à de grands récepteurs pour océaniques.

A l'aide de cet outillage, on a étudié environ 60 espèces d'animaux sous-marins. On a développé diverses techniques de fixation des émetteurs et exploré différentes méthodes de dépistage.

La biotélémétrie sous-marine a été appliquée à des études de migrations des poissons, de mécanismes d'orientation, de types de mouvements face à des obstructions, d'écologie, de comportement et de physiologie des animaux.

Received October 18, 1976 Accepted May 9, 1977 Reçu le 18 octobre 1976 Accepté le 9 mai 1977

Introduction

Underwater biotelemetry encompasses the instrumentation and application of the technique of remote signaling by means of ultrasonic or radio signals from a transmitter on or in an animal. Applications include tracking the movements of underwater animals, as well as measuring environmental conditions surrounding an animal, and physiological and behavioral factors of animals. Echo sounding is not part of underwater

biotelemetry in the present context; neither is underwater telemetry from inanimate objects. The present paper is a review of technical and biological aspects of underwater biotelemetry.

The application of underwater biotelemetry has grown dramatically since the first report in 1956. Studies have ranged from the migratory movements of salmon (Stasko et al. 1976) to the daily behavioral patterns of Norway lobsters (Chapman et al. 1975); from animals as large as a gray whale (Evans 1974) to ones as small as

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Atlantic salmon smolts (McCleave and Stred 1975). In 1972 Malinin and Svirskii reviewed 35 papers on underwater biotelemetry. This is less than one quarter of the publications available at the writing of the present paper.

HISTORICAL DEVELOPMENT

Underwater biotelemetry is a relatively new field. The first work on instrumentation (Trefethen 1956) and application (Johnson 1960) was done at the Seattle laboratory of the National Marine Fisheries Service. Adult chinook salmon, Oncorhynchus tshawytscha, fitted with externally attached ultrasonic transmitters, were followed as they migrated up the Columbia River. In 1964 the same equipment was used to study movements of chinook salmon in the San Joaquin River delta in California (Hallock et al. 1970), followed in 1967 by a study on migrations of American shad, Alosa sapidissima, in the Connecticut River (Leggett and Jones 1973).

Development of an ultrasonic telemetry system for tracking smaller fish was begun at the University of Wisconsin in the early 1960s (Hasler and Henderson 1963; Henderson et al. 1966). Other early developments were those of Baldwin (1965), Bass and Rascovich (1965), Poddubny (1969), Poddubny et al. (1966), and the predominantly radiotelemetry approach of MacKay (1964, 1970).

By January 1975 there were over 147 underwater biotelemetry publications and reports (Stasko 1975a) with 163 authors representing an estimated 56 research teams in seven countries — USA, Canada, Russia, U.K., Japan, Norway, and Germany. The 59 species studied included 40 fishes, 10 mammals, 4 reptiles, and 5 invertebrates.

SIGNALS

Ultrasonic and radio signals have been used with success for underwater biotelemetry.

Ultrasonic signals — Acoustic pressure waves at ultrasonic frequencies can be created through the use of lead–zirconate–titanate (PZT), electric-to-acoustic transducers (Schofield 1963). To achieve reasonable efficiency with such devices, it is necessary to operate at a frequency at or near one of the mechanical resonances (Camp 1970). Cylindrical transducers are almost universally used, since no other shape, except the expensive and difficult-to-mount sphere, gives even approximately omnidirectional radiation at resonance.

The frequency range of interest for ultrasonic

biotelemetry is approximately 20-300 kHz. Absorption losses increase with frequency and, therefore, low frequencies are attractive, but a limit is imposed by the need for transducer operation at or near resonance. For example, a cylindrical transducer resonant at 20 kHz is approximately 4 cm diam, far too large for use with small fish. On the other hand, there is little size advantage in increasing the frequency much beyond 300 kHz because at 300 kHz the transducer is already so small (about 3 mm diam) as to make an insignificant contribution to the overall transmitter size. Thus, the choice of frequency usually involves a compromise between small transducer with large acoustic output at high frequencies and large transducer with smaller acoustic output at low frequencies.

The choice of frequency is greatly simplified if for a specified signal range and set of receiver characteristics, the acoustic output required at different frequencies is known. In the ocean, where noise and attenuation are well characterized (Urick 1975), such a relationship is easily determined and the results of typical calculations are shown in Fig. 1A. These results, which assume noise conditions of sea state 3 with 9 dB added to sea-state noise to account for coastal effects (Albers 1965), show the required transmitter acoustic output as a function of frequency to achieve a signal-to-noise ratio of 0 dB in a bandwidth of 1 kHz at various ranges. With well-designed receiving system of moderate directionality, this represents approximately the threshold of reception and Fig. 1 can be used directly to predict range. In a number of tests using transmitters with frequencies between 20 and 100 kHz and range capabilities from 200 to 5000 m, we have found good agreement with the curves. Correction of the range predictions for a detection threshold of the receiver-hydrophone combination different from 0 dB or receiver bandwidth different from 1 kHz is straightforward (Mitson and Young 1975).

Other sources of noise can on occasion be important. During heavy rain or in waters where snapping shrimp are abundant, noise levels can be as much as 25 dB in excess of sea-state noise (Albers 1965). Under these conditions, at the lower frequencies, transmission levels up to 25 dB higher than those indicated in Fig. 1 are required to assure 0 dB signal-to-noise ratio. In addition, certain marine mammals can create sounds containing energy at frequencies up to and beyond 100 kHz (Tavolga 1967). Most other sources of noise are at sufficiently low frequencies that they can be readily rejected by RF filtering.

Implicit in the range predictions is the assumption that reception is noise limited. Usually this

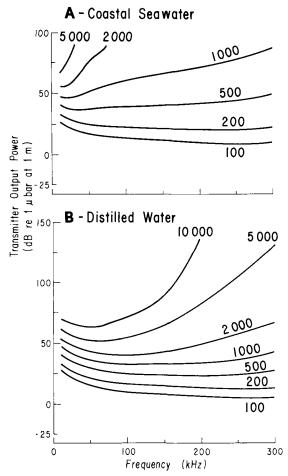


Fig. 1. Transmitter acoustic output needed at sea state 3 for OdB signal-to-noise ratio at various frequencies and distances (metres) using a receiver with 1 kHz bandwidth (A) in coastal seawater and (B) in distilled water.

is true. However, in at least two important cases, i.e. sonar receivers and simple receivers such as ones built into transponders, reception often has a sensitivity limit as well. In such cases, the curves presented by Mitson and Young (1975) should be used to predict range.

In freshwater, predicting range is difficult because of the lack of comprehensive data on either sound absorption or noise levels. Sound absorption varies from one body of water to another because of different amounts of suspended matter, even in very clean water (Braithwaite 1974), and low frequency noise in lakes and rivers may differ from that in the ocean. Nevertheless, useful predictions can often be made by assuming noise conditions similar to those in the sea and absorption similar to that in distilled water. Calculations

based on these assumptions indicate significantly increased range over that in the ocean at a given transmission level (Fig. 1B). In a limited number of tests conducted in relatively clear lakes, we found that range predictions based on Fig. 1B were valid.

In certain cases, losses not included in the calculations shown in Fig. 1 cause very serious range reductions (Pincock 1977). First, absorptions of 1 dB/m or more can occur at the frequencies of interest if significant concentrations of air bubbles (Heuter and Bolt 1955), mud, or algae (Meister and St. Laurent 1960) are in the water. Second, in shallow water there is often no direct path between transmitter and receiver because of bottom contours or vegetation and, therefore, signals reaching the receiver can only do so after several reflections, each of which has an associated loss. When any of these conditions are significant, theoretical predictions of range are difficult to make and the suitability of ultrasonic telemetry for a particular application is best verified by in situ measurements.

Radio signals — Radio signals in water attenuate quickly and cannot be received by an underwater antenna unless it is very close to the transmitter. The high index of refraction between water and air, however, causes rays reaching the water surface at an angle within about 6° of the vertical to emerge as shown in Fig. 2. These can be received by an antenna in the air. Rays more than 6° away from the vertical are reflected back downward by the water-air interface. Thus, the distance traveled by rays in water, where attenuation is high, is approximately equal to the depth of the transmitter; the remainder of the distance to the antenna is in air, where attenuation is low. provided any significant energy Therefore, emerges from the water, reception at long ranges is possible from the air (Winter et al. 1973) and on land (Lonsdale and Baxter 1968).

Using standard results for the propagation of electromagnetic energy in a lossy medium (Adler et al. 1960), one can derive curves giving attenuation per metre as a function of a frequency (Fig. 3). From these, two conclusions regarding the use of radio transmission for underwater telemetry can be drawn: First, except for animals swimming at the surface, radiotelemetry has little application in seawater unless efficient antennae of small size can be developed for frequencies in the range of 100 kHz or less. But even then telemetry would be possible only to a depth of a few metres. Second, radiotelemetry has great value in freshwater to depths of 50 m or more, with the useful depth increasing as the conductivity of the water

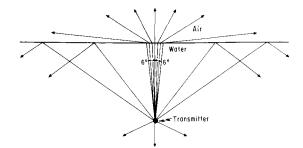


Fig. 2. Emergence of radio signals from water.

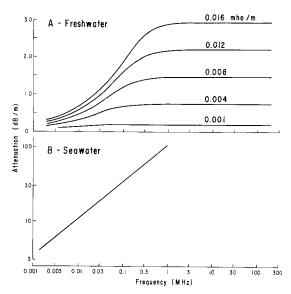


Fig. 3. Attenuation of radio signals as a function of frequency (A) in freshwater of various conductivities and (B) in sea water.

decreases. Accordingly, considerable work has been done with radio transmitters in lakes and rivers (Anon. 1975; Winter et al. 1973), while use in the ocean has so far been limited to transmissions from the surface with information (e.g. depth of dive) coded and stored while the animal was underwater (Evans 1971, 1974).

Calculations analogous to those from which Fig. 1 was drawn should also be done for radio transmission. Sea state would have little effect on the useful range of a radio transmitter, but depth of the transmitter and water conductivity would have to be considered. Such calculations are difficult because the exact nature of the "signal source" at the water surface reradiating energy into the air has not been determined.

To obtain maximum benefits from radiotelemetry, considerable work is needed on characterizing antennae. Useful results have been obtained in the frequency range 25–100 MHz using "whip" (Winter et al. 1973) and loop (AVM. Champaign, Ill.; Knight 1975; Lonsdale and Baxter 1968) antennae, but design aspects of such antennae have not been published. In particular, little is known about what the penalties of shortened antenna length are, what approach should be used to provide a ground plane, and how much energy at what efficiency can be transmitted from the small transmitter packages required for biotelemetry.

Choice of signal type — In the early years of underwater biotelemetry ultrasonic signals were predominant. More recently, use of radio signals has increased.

Radio signals have several advantages over ultrasonic signals. Radio signals can be detected with receiver and antennae located entirely in air. The performance of a radiotelemetry system is not seriously affected by turbulence, weeds, or algae in the water; these conditions can render ultrasonic systems virtually useless (Schiefer and Power 1972; Ziebell 1973). Radio signals can be detected through ice. The high frequencies used for radiotelemetry (two orders of magnitude above ultrasonic telemetry) make possible a wider bandwidth, giving a potentially much higher information rate as well as easy identification of a large number of transmitters by assigning a different frequency to each.

The advantages for radiotelemetry are so compelling that use of ultrasonic signals is rapidly becoming limited to those applications for which radio signals are unacceptable.

Ultrasonic telemetry is superior to radiotelemetry in two major applications. In salt water, or in freshwater where a combination of high conductivity and depth produces unacceptable attenuation of radio signals, ultrasonic telemetry is the only choice. In studies where precise location of the animal (within a few metres) is needed (Young et al. 1972; Hawkins et al. 1974), ultrasonic telemetry provides better accuracy. This is due to the easy realization of highly directional hydrophones because of the shorter acoustic wavelengths (e.g. 2-cm wavelength at 75 kHz), and to the greater precision with which signal arrival time can be measured with the slow velocity of sound (1500 m/s compared to 3 \times 108 m/s for radio signals).

The remainder of this paper will concentrate on ultrasonic biotelemetry. For radio biotelemetry, except for the considerations having to do with antennae mentioned above, the equipment and methodology are identical to that for studying movements of terrestrial animals for which an abundant literature exists (MacKay 1970, 1974).

Equipment for Ultrasonic Biotelemetry

In this section the emphasis is on design concepts from a practical, user viewpoint. This performance of a tracking system, whether simple or complex, depends critically on three basic components: transmitter, hydrophone, and receiver or detector. These are discussed in the three sections below.

BASIC TRANSMITTER

The basic transmitter consists of four major components: transducer and driving amplifier, battery, electronics, and encapsulation.

Transducer and driving amplifier — As mentioned above, cylindrical PZT electric-to-acoustic transducers vibrating in the radial direction are almost universally used. These transducers should be short (no longer than one diameter) to give omnidirectionality and to ensure noninteraction of resonances. In order that significant electric power can be delivered to these highly capacitive devices and, hence, be converted to acoustic energy, it is usual to resonate the transducer with a coil. This coil is often incorporated into a step-up transformer to enable the required power output to be drawn from a low-voltage battery.

Proper design of the driving amplifier permits electric power to be delivered to the transducer at an efficiency of over 90% (Chubbodiak and Page 1969). With proper mounting of the transducer, electric-to-acoustic efficiencies of the order of 85% can be achieved, giving an overall efficiency from battery energy to acoustic energy of over 75%. In small transmitters less efficient amplifiers must be used, since space is not available for the number of components required for an efficient power amplifier. This can result in an overall efficiency of 10% or less.

Battery — The battery is the largest and heaviest component in most ultrasonic transmitters. Therefore, the most crucial factor in the choice of a battery is its efficiency expressed as energy per unit volume or weight. Four battery types have useful characteristics: lithium, mercuric oxide, silver oxide, and alkaline.

The recently introduced lithium cells are potentially the best because their volumetric efficiency is highest. At present the smallest lithium battery available is 14×23 mm (Power Conversion, Inc., Mount Vernon, N.Y.). Therefore, these batteries as yet are suitable only for the larger transmitters.

Mercuric oxide (commonly called mercury) and silver oxide batteries are roughly equal in

terms of their volumetric efficiency, which is higher than that of any other battery except lithium (Lyman 1975). They come as small as 5.6×3.2 mm and are the ones most commonly used in ultrasonic transmitters. Both maintain a nearly constant voltage until almost completely discharged, silver oxide being slightly superior in this respect. In the past, mercury batteries did not operate well at temperatures close to 0°C (Mac-Kay 1970) and had a short shelf life if not refrigerated. This is no longer the case (Mallory Battery Co. personal communication) and the operating characteristics of the two types of batteries are now very similar. However, for silver oxide batteries improvements are expected that will greatly increase their efficiency (Lyman 1975).

There is a bewildering array of formulations for silver oxide and mercury batteries. Variations in the formulation can significantly affect secondorder properties of the battery which are crucial to its use in biotelemetry transmitters. In particular, since signals are usually pulsed, batteries must deliver a relatively large current at a low duty cycle. This imposes two conflicting requirements on the battery, high current capability and long discharge time. How a particular battery performs in such a situation will depend on the Particularly actual formulation. vexing changes made by the manufacturer to bring about some specific improvement which can have dramatic effect on secondary properties required for biotelemetry. Thus, two batches of seemingly identical batteries may give significantly different performances (R. B. Mitson, Lowestoft, England, personal communication). Battery manufacturers will provide advice on which of the many available batteries might be best for a particular application but because of the limited market, are not usually willing to provide special formulations or test data.

A further problem with mercury and silver oxide batteries is that the soldering of leads to the battery can cause damage that results in a decreased battery life. Attaching solder tabs by spot welding is safer. Battery manufacturers are often willing to do this.

For high-power transmitters (i.e. acoustic output of 1 W or more) alkaline batteries are better able to deliver the high currents required during the transmission. Unfortunately the voltage of alkaline batteries varies significantly during discharge; this can cause problems if the performance of portions of the transmitter circuitry is voltage dependent. Lawson and Carey (1972) solved this problem by incorporating a voltage regulator into their circuitry and using its output

to power voltage-critical circuitry, while Pincock and Luke (1975) used a separate silver oxide battery for this circuitry. In both cases, the amplifier driving the transducer was powered directly by the alkaline battery.

Electronics — Except for some early work (Hasler et al. 1969; McCleave and Horrall 1970; McCleave and LaBar 1972; Stasko et al. 1973), pulsed transmission has been almost universally used to extend the life of transmitters. The electronics necessary to produce these pulsed transmissions are discussed below.

Three basic functions must be performed by the electronics, transmission-frequency generation, pulse-width control, and pulse-repetitionrate control. In small transmitters, economy of space is important and the three functions are usually all accomplished in a one-transistor, squegging oscillator circuit (Henderson et al. 1966; MacKay 1970; Young et al. 1972). Such circuits are difficult to set up and usually the three functions cannot be set independently. In addition, large and unpredictable variations can occur in response to temperature changes unless great care is taken in design and choice of components. For example, when developing an early pressure-sensing transmitter with a squegging oscillator (Luke et al. 1973) we found objectionable variations of the repetition rate caused by variations of the dissipation factor of the capacitor setting the transmission frequency. Therefore, when size is not critical, it is often convenient to use separate circuitry to control frequency repetition rate, and pulse width (Lawson and Carey 1972; Pincock and Luke 1975).

Progress in technology is beginning to provide alternatives to discrete electronic components for the fabrication of ultrasonic transmitters. A particularly attractive approach is the bonding of transistor, integrated circuit, and capacitor chips either onto a thick-film substrate on which the resistances have been deposited (Pincock and Luke 1975), or onto a flexible circuit board. Another possibility is the use of so-called breadboard integrated circuits such as used by Rochelle (1974). These are merely assemblages of uncommitted transistors and resistors in an integrated circuit; the components can be interconnected by the manufacturer (e.g. Interdesign Inc., Sunnyvale, Calif.) according to user instructions. With any of these approaches set-up costs are sufficiently modest that they should be investigated whenever the construction of more than a few dozen transmitters is contemplated. In addition to the economic advantages of these automated approaches, they can provide more circuitry in a small package

and, therefore, better performance or more complex functions than is possible with discrete circuitry.

Integrated circuits are attractive because of the performance that can be achieved, but set-up charges are of the order of several hundred thousand dollars.

Encapsulation and activation — Two methods are commonly used for transmitter encapsulation. In one the assembled components are inserted in a thin tube (usually plastic) which is then filled with oil and sealed (Mitson and Storeton-West 1971). This has the advantages of easy battery replacement and good coupling between the transducer and water, resulting in a high electric-toacoustic efficiency. In the second method the assembled components are molded in a potting compound. Since only a thin layer need cover the components, this results in a slightly smaller package which is very rugged. We have successfully tested immersed transmitters encapsulated in epoxy to pressures corresponding to depths of up to 1500 m. We have obtained high electric-toacoustic efficiency by backing the transducer with some pressure release material such as cork and using only a thin layer of potting compound over the transducer.

Activation of transmitters is usually done by soldering together a pair of wires which are outside the package (e.g. Smith-Root, Seattle). This approach is simple, but care must be taken to prevent water from finding its way into the package along the wires.

A second approach is the use of a magnetic reed switch kept open by a small external magnet which is removed to activate the transmitter. Our experience with reed switches has led us to abandon them. Unless transmitters with attached magnets are kept well separated, magnetic fields can cancel each other, allowing one or both reed switches to close. There have also been a number of failures of the switches themselves.

A third approach is to use an electronic switch that closes (shorts) when the transmitter is immersed in water (Gayduk and Malinin 1971; Lawson and Carey 1972). Water-activated switches are most satisfactory with large transmitters in salt water. With small transmitters the required circuitry and external contacts add to transmitter size. In most freshwaters, conductivity is low and difficulty can be encountered in selecting a resistance threshold that turns the transmitter on without accidental activation due to dirt around the contacts.

Transponders — A transponder is a transmitter that emits a signal only when interrogated by an

acoustic source. With it, the distance between receiver and transmitter can be accurately determined by measuring the delay between interrogation and reply. This ability to measure range between hydrophone and transmitter can be useful in many applications. Mitson and Storeton-West (1971) describe a miniature transponder for fish. The circuit of White et al. (1975), developed for studying movements of pebbles, is also suitable for biotelemetry.

Often it is assumed that battery life can be extended if a transponder is used in lieu of a pinger (e.g. MacKay 1970). Usually, however, the current drain required by the receiving portion of a transponder is sufficiently high that battery life is in fact less for transponders except when large acoustic output is required.

HYDROPHONES

Biotelemetry hydrophones, in general, use the same PZT transducers described above for transmitters. The more important properties of a hydrophone are frequency range, directionality, and noise performance.

Useful frequency range — Hydrophones operated at a frequency below their mechanical resonance respond uniformly to a wide band of frequencies and have a much faster response than at resonant frequencies. These advantages, however, are often outweighed by the low efficiency of nonresonant hydrophones (Woollet 1970) which reduces their ability to detect signals near the thermal noise limit (Mellen 1952). Under conditions in which thermal noise is dominant, a resonant hydrophone with its narrower bandwidth (typically 10–20% of resonant frequency) and slower response time gives greater effective signal range.

In the ocean, however, thermal noise is not the dominant effect at lower frequencies (at least up to 50 kHz) and it is possible to make a hydrophone capable of detecting signals down to or very near the actual noise levels over a wide range of frequencies. Stansfield (1975) describes the construction of such broadband hydrophones with a useful frequency range extending to almost 100 kHz.

Directionality — Design considerations for resonant omnidirectional hydrophones are the same as those for underwater sound projectors and, hence, cylinders mounted in a similar fashion to that already described for transmitters are often used. Spherical transducers are also used, since the considerations that caused them to be unsuitable for disposable transmitters (cost and

difficulty of mounting in a small package) are not as important for hydrophones. For nonresonant omnidirectional hydrophones any transducer shape can be used if the signals to be received are at frequencies well below any of its mechanical resonances. Liddiard (1963) gives details on the construction of such hydrophones and the performance to be expected from various shapes and polarizations.

As the length of a transducer (or any other antenna) increases along a particular axis the directionality along that axis increases. Relatively high directionality can be achieved with hydrophones of reasonable size. For example, a length of 10 cm gives a 3-dB beamwidth of approximately 16° at 50 kHz (Urick 1975). However, it is usually not feasible to achieve such directional behavior with a single transducer element because interaction of resonances degrades performance. Instead, it is customary to sum the outputs of an array of short elements, e.g. a number of cylinders, arranged in a line (Camp 1970).

Use of an array of elements allows electronic steering, i.e. the processing of element outputs to change the axis of maximum sensitivity (Urick 1975). The great speed of electronic steering allows almost simultaneous examination of a whole sector, or even 360° if a circular array is used.

Directionality is sometimes obtained through the use of reflectors to focus incoming sound waves to a hydrophone element; however, the acoustic-to-electric efficiency of such hydrophones is often very low. This arises because the geometry is such that the simple ray theory, which predicts constructive interference at the transducer, is not valid. For example, the hydrophone described by Stasko and Polar (1973) has an efficiency of less than 5%. Despite this, such hydrophones have been the ones most commonly used in ultrasonic biotelemetry.

Noise performance — In most applications, the receiver is noise limited rather than gain limited. Therefore, any degradation of the signal-to-noise ratio caused by the hydrophone results in a decrease of range capability. The principal causes of such degradation are hydrophone inefficiency and electrical interference picked up between the hydrophone and receiver. Procedures to obtain reasonable hydrophone efficiency have been described above. Procedures for minimizing electrical interference are described below.

Amplitude of the electrical interference picked up between hydrophone and receiver depends on the length of connecting cable and the quality of its shielding. For the frequencies used in underwater biotelemetry a shielded cable with twisted pair leads gives less interference than coaxial cable (Morrison 1967).

Since hydrophone output due to a weak acoustic signal can be less than a microvolt, even short cable lengths between hydrophone and receiver can result in considerable reduction in range capability. Therefore, a low-noise preamplifier should be placed as near the hydrophone as possible to reduce the effect of electrical interference. The choice of gain of this preamplifier is a compromise between decreased effect of electrical interference and decreased receiver dynamic range with increasing gain.

BASIC RECEIVER

In a biotelemetry receiver the input signals are filtered and amplified, usually through the use of an intermediate frequency, before being passed to a detector.

The ability of a receiving system to extract a signal from background noise is maximized when the receiver bandwidth is equal to the transmitted signal bandwidth (Schwartz 1970). A wider bandwidth passes more noise than is necessary, while a narrower bandwidth results in loss of signal information. Since almost all the energy of a pulsed transmission is contained in a bandwidth given by the reciprocal of pulse width, the best receiver bandwidth in principle is 1 kHz for 1 ms pulses, 0.1 kHz for 10 ms, etc. Two factors often necessitate a wider bandwidth. The first is frequency variations of the transmitted signal either unintended as a result of the simple circuitry used, or intended in the form of frequency modulation. The second is frequency broadening of signals which is a result of the thermal microstructure of most bodies of water and which increases with distance traveled by the signal (Urick 1975).

The response time of a receiver is inversely proportional to band width. Therefore, an application requiring accurate determination of signal arrival time (e.g. for transmitter localization) should have a wide bandwidth. As a consequence, the transmitter pulse width must be correspondingly short to maximize signal range for a given battery power consumption.

The final decision about presence or absence of a signal is made either electronically or through conversion to audio frequencies for listening. Electronic detection, in which a logic signal is produced to indicate reception of transmitted signal, permits automatic signal processing for animal localisation or for demodulation and display of information contained in the signal.

Detection can be based on signal level, or phaselocked loops can be used as tone decoders (Pincock et al. 1974). Aural detection, although simple for those applications in which automation is not required, requires wider transmitter pulses than needed with electronic detection; the human ear requires a much higher signal-to-noise ratio for detecting short pulses than long ones (Green et al. 1957). Thus, while the ideal pulse for aural detection is approximately 20 ms or longer, such a pulse length would dictate an optimum receiver bandwidth that is in most cases an order of magnitude too narrow (i.e. 50 Hz or less) to accommodate the frequency spreading effects described above. Thus, for aural detection, the receiver bandwidth must be considerably wider than the optimum. Proportionally less widening of receiver bandwidth is needed when electronic detection is used with narrow pulses.

In summary, despite the relatively high signalto-noise ratio necessary for electronic detection, it usually permits a given signal range to be achieved with less transmitter power output.

METHODS OF LOCALIZATION

For studies in which the animals are expected to travel long distances in open bodies of water (Yuen 1970; Stasko et al. 1976) or in which the position of a number of widely separated animals must be determined periodically, tracking is usually carried out from a boat. Such tracking is manpower intensive and is, therefore, of limited duration. When movements of an animal are confined to a small area, a system using fixed receiving sites can be used. If the fixed system is automated, it can provide detailed information over long periods of time. Easily programmed and inexpensive logic, particularly in the form of microcomputers, is starting to make such automated systems more practical.

Mobile systems — Two methods are used for mobile tracking systems. Much of the equipment necessary for both is available commercially. The first is tracking with a boat-mounted directional hydrophone and receiver. By navigating the boat in the direction of the signal it is possible to periodically place the boat over the transmitter and, hence, to determine its position. The second is tracking of a transponding transmitter using a directional sonar on the boat. When the transponder is activated by the sonar, a distinct display corresponding to the transmitter location will be seen on the sonar screen.

Directional receiving system — In its simplest form, this technique involves the use of a steer-

able directional hydrophone connected to a receiver that is decoded aurally. As the tracking boat approaches and passes over the signal source, signal levels from ahead increase to a maximum, become omnidirectional, then become directional astern. The precision of locating a sonic-tagged fish relative to the boat with such a system depends on: (1) swimming depth, (2) swimming speed, (3) pulse-repetition rate, (4) dynamic range of receiving system, (5) weather, and (6) experience of tracker.

- 1) When a fish is within a few metres of the surface, the change from maximum signal ahead to omnidirectional to maximum signal astern is pronounced and rapid as the tracking boat passes the fish. Under optimal conditions the location of a fish near the surface can be determined to within a few metres. When the fish is deeper the change in signal directionality is less pronounced due to simple geometrical relationships affecting the rate of change of the angle between fish and hydrophone. Using equipment described by Stasko (1975b) with a transmitter 30 m below the surface suspended from a buoy, we could under ideal conditions (no wind, stationary transmitter, experienced tracker) position the boat within 10-15 m of the transmitter.
- 2) As the fish's swimming speed increases, the accuracy of determining its position decreases. However, the precision needed for rapidly moving fish may be less than for sedentary fish. For sedentary fish a shift of position of only a few metres can signify a change in behavior, while for migrating salmon at sea an error in actual position of several hundred metres may not affect the conclusions derived.
- 3) Precision decreases as the pulse repetition rate drops below a convenient minimum of, say, 100 pulses/min. At slower rates one has to perform the searching operations more slowly, since some minimum number of pulses must be compared to pick out the direction of signal maximum.
- 4) Dynamic range of the receiving system must be sufficient to avoid electronic saturation when the signal is very close. If not, directional information is lost and the distance at which saturation occurs places a limit on precision.
- 5) On windy days the rolling and pitching of the boat superimpose uncontrolled hydrophone movements on the searching mode. Wind drift and extraneous noise further reduce the accuracy of locating the fish.
- 6) An experienced tracker will locate the signal more quickly and with greater precision than an inexperienced one.

Modifications of the basic system described

above can simplify tracking. Instead of a steerable hydrophone, one can use a circular array of hydrophone elements and process the signals so as to give a continuous indication of bearing to the fish (Tesch 1976). Accuracy of localization can be improved by the use of a transponding system that allows more accurate determination of distance to the transmitter. Another method is described by Holand et al. (1974) and depends on synchronism between crystal-controlled transmitter pulses and a reference signal at the receiver. Any subsequent deviation from synchronism of the two signals is then attributed to a change in distance between receiver and transmitter. However, gradual drift of the transmitter and receiver oscillator frequencies renders this method suitable for a short period only, up to a few hours if a precision of a few metres is required.

The above discussion has concentrated on pinpointing the position of the fish. Another attribute of a mobile system is the ease with which contact with the transmitter can be maintained. In addition to the obvious factor of range capability of the transmitter-hydrophone-receiver combination, the ability to maintain signal contact depends critically on the hydrophone mounting. If the hydrophone housing is not streamlined, the fish's bearings can be taken only when the boat is almost motionless. Mounting and streamlining of hydrophones is discussed by Lawson and Carey (1972), Stasko and Polar (1973), and Stasko (1976). Such arrangements can withstand speeds up to 10 knots. In recent tests with a hydrophone similar to that in Fig. 4, mounted directly on the hull of the boat, good signal contact was maintained at speeds up to 20 knots (Pincock and Carey unpublished data). The relatively low directionality of this hydrophone, while decreasing somewhat its range capability, is probably beneficial in that it makes searching easier.

Sonar systems — The use of transponding transmitters with a sonar is particularly useful where detailed information is needed on the movements of a transmitter with respect to other transmitters or to some underwater object. By using a sector scanning sonar Harden Jones et al. (1973) were able to observe the movements of transponder-fitted fish in response to an approaching trawl which formed a distinct sonar target. The main drawback of a sonar-based system is cost of the sonar, particularly when high power, high resolution, and/or sweep rate are required.

Fixed systems — A simple fixed system is one that monitors passage of transmitter-fitted fish in a river or narrow waterway. The basis of such

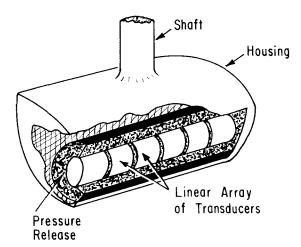


FIG. 4. A directional hydrophone for underwater telemetry.

systems is a narrow beamwidth hydrophone directed across the waterway. Since such studies are often of long duration, it is usual to record the receiver output. Recording is usually done only while a signal is detected. The system described by Thorson et al. (1969) recorded the actual incoming signal which was later decoded aurally. Pincock et al. (1974) used electronic detection and digital recording for subsequent automatic decoding.

Various methods of triangulation can be used to determine transmitter position in areas small enough so that a transmitter is always within range of the fixed hydrophones. Young et al. (1972) used remotely controlled directional hydrophones to take bearings of the transmitter manually. If automation is required, systems with three or more omnidirectional hydrophones designed to determine signal arrival time are probably simpler (Hawkins et al. 1974; Holand et al. 1974).

Triangulation systems based on signal arrival time can be accurate to within 1 or 2 m. Except for very short ranges, systems based on bearings are less accurate. Degradation of accuracy of both types of triangulation systems can result from irregularities in the medium. In particular, temperature gradients can cause bending of sound rays or a difference in the average velocity of sound between a transmitter and two different hydrophones.

Vertical position — The third position coordinate, i.e. swimming depth, can be determined in several ways. The linear-array hydrophone described by Gardella and Stasko (1974) is an inexpensive method that works with slow-moving fish at close range. Directional hydrophones for determining the vertical direction of the incoming signal have been used by Yuen (1970) and Tesch (1972). This approach is inaccurate mostly because of inadequate estimates of distance to the transmitter. The use of a transponding transmitter permits accurate distance determination. Kuroki et al. (1971) used a transponder and calculated vertical bearing from the signal arrival sequence and delays at three spatially separated hydrophones. A very sophisticated method is the use of a transponding transmitter in conjunction with a sector-scanning sonar on a stabilized shipboard platform (Mitson and Storeton-West 1971; Greer-Walker et al. 1971). Depth estimates based on vertical bearing are reliable only when the signals travel in straight lines, an assumption not valid when temperature or steep salinity gradients are crossed.

The most direct method of measuring swimming depth is by means of pressure sensors built into the transmitter (see section "Transmitters with sensors").

TRANSMISSION OF INFORMATION

In addition to locating an animal, transmitters can be designed to identify individual animals and to telemeter information on behavioral and physiological factors of the animal and environmental conditions to which it is exposed.

Modulation methods — The choice of methods for modifying pulsed transmissions is limited by the transmission medium and by the simple circuitry used in miniature transmitters. Variation in width of the transmitted pulse is a possibility but errors can result from pulse-length distortion in locations where echoes are significant. Variations in carrier signal frequency or spacing between pulses are the most common methods of modulation.

Single channel — The transmission of a single piece of information is most commonly accomplished by variations in pulse repetition rate. Pulse repetition coding is easy to design and permits decoding by counting the number of received pulses in a fixed time interval without need for special decoding apparatus. Except for identification of groups of transmitters, use of frequency coding is less common because of the need for complex receiving equipment to demodulate the code.

Variation of pulse spacing according to some digital coding scheme is recommended for two applications. One is with transponding transmitters whose code can be recognized on the sonar display (R. B. Mitson personal communica-

tion). The second is with a large number of transmitters where many unique codes are needed for transmitter identification.

Multiple channels — At least two schemes that do not depend on special receiving systems have been used with success. The first transmits a coded pulse repetition rate for each sensor output in turn (Standora et al. 1972). The second codes two sensor outputs by varying pulse repetition rate with one sensor and slightly varies the transmission frequency with a second sensor so as to give a shift in the tone heard at the receiver (Kanwisher et al. 1974a).

Another possibility is the use of a separate transmission frequency for each channel. This is a useful technique when transmitter size is not critical since separate oscillators (and possibly separate transducers) are required for each transmission frequency. Its main advantage is the ability to quickly check any one of the several channels by tuning to the appropriate frequency.

The scheme based on the pattern of a train of pulses described by Clark (1974) allows the coding of several sensors by means of simple circuitry but requires electronic decoding.

Transmitters with sensors — Temperature — Many transmitter circuits have their repetition rate controlled by a resistor that can be replaced by a suitable thermistor for monitoring temperature (MacKay 1970). The thermistor can be either integral with the transmitter (Chipman Instruments, Madison, Wis.) or brought out on a probe (Lawson and Carey 1972; Rochelle 1974). This latter approach has much faster thermal response and allows temperature to be monitored at a position different from that of the transmitter, e.g. internal body temperature with an externally attached transmitter and vice versa.

The glass bead thermistors normally used have nonlinear temperature-resistance characteristics (Oliver 1971) resulting in a nonlinear relationship between temperature and pulse repetition rate. In addition, the large resistance variation of these thermistors usually gives rise to an undesirably large spread of repetition rates, e.g. 60 pulses/min at 0°C to 300 at 30°C. Rates slower than 60 pulses/min make tracking difficult, and such high rates of 300 or more are difficult to count by ear and lead to excessive battery drain in the transmitter.

Some of the above problems can be overcome through the use of a diode as the temperature sensor, since the voltage drop across a conducting diode increases linearly with temperature at a rate of about 2 mV/°C. However, with such an approach the circuitry required to achieve ade-

quate performance with the expected voltage variations of even silver or mercury batteries is complex and demanding on battery power. Thermolinear elements (Yellow Springs Inc., Yellow Springs, Ohio), which are temperature probes made up of two thermistors resulting in a linear temperature-resistance characteristic, are a good solution.

Pressure — The ability to monitor the pressure, and hence swimming depth, of a transmitter-fitted fish provides the third coordinate of the fish's location.

A component whose resistance is proportional to pressure can be used with the same simple circuitry described above for temperature-sensing transmitters. One such component is closed aircell conductive rubber; such sensors suffer from large inaccuracies due to hysteresis (Ichihara et al. 1972). Pressure sensors based on a bellows arrangement, which moves the wiper of a linear potentiometer or an opaque vane between a lightsource-and-photoresistor combination (Ferrel et al. 1973), are more accurate but are too large and use too much battery current for small transmitters. Various pressure-sensitive inductors and capacitors can be used to modulate the transmission frequency (MacKay 1970; Holand and Mohus 1973), but more complex receiving equipment is necessary because of the requirement for frequency demodulation.

The increasing availability and decreasing costs of pressure transducers made up of strain-gauge bridges make these devices attractive pressure sensors for underwater biotelemetry. Of the large number of devices available only a few come in suitable packages (i.e. small, saltwater resistant). We have found the BT-300 series (Bio Tech Corp., Pasadena, Calif.) suitable.

Strain-gauge bridges require significantly more circuitry than do other sensors described above. The bridge gives a differential voltage output (rather than a variable circuit resistance, inductance or capacitance) and, hence, the bridge cannot simply replace a component in an existing circuit. A transmitter with a strain-gauge bridge has been realized in a package 47×13 mm using thick film circuitry (Pincock and Luke 1975). It would be difficult to make it much smaller because of the circuit complexity, and also because the current taken by the sensor requires a relatively large battery. This current requirement could be reduced somewhat by sampling the bridge output only periodically, but such an approach can lead to large temperature effects unless great care is taken in the design. In summary, strain-gauge bridge sensors offer the advantages of ready availability, accuracy, and reproducibility.

Other sensors — Factors other than pressure and temperature can be monitored in a similar way. Development of suitable sensors is the major limitation. Various types of measurements done in underwater biotelemetry applications are discussed in the section "Biological studies."

Commercial availability of temperature-sensing, pressure-sensing, and other types of telemetering transmitters is very limited. There is not enough demand for any particular type of transmitter to make its manufacture commercially attractive.

Decoding — As has been indicated above, decoding of telemetered information by ear is possible from one or even several sensors. In most cases, however, even with a single-channel transmitter the task of manual decoding and recording of data at frequent intervals is onerous. Receivers with automatic detection followed by circuitry that decodes and displays the information are increasingly used. With pulse spacing codes, the required logic circuitry is straightforward. A further refinement is the recording of information in computer-readable form, such as on magnetic casette tape, for sebsequent automatic data reduction.

The advent of easy-to-use microprocessors permits much of the decoding, display, and recording with a minimum of circuitry. In addition, because of the more powerful logic available, an increasing amount of data reduction will be possible in real time as the signal is received.

Biological Applications of Underwater Telemetry

METHODOLOGY

To here the emphasis has been on technical aspects of underwater biotelemetry. The remainder of this paper will deal with biological applications.

Transmitter attachment — In general, the transmitter should be attached to fish so as to reduce the possibility of trauma and to minimize adverse effects on posture, buoyancy, and locomotion (e.g. increased drag and snagging). To meet these requirements one must consider the size, weight, and shape of transmitters relative to the size of the animal, as well as location and method of attachment.

External attachment — The first sonic tracking of fish was done with a transmitter held in place by two metal claws clamped into the musculature behind the dorsal fin of chinook salmon (Tre-

fethen 1956; Johnson 1960). For improved retention a saddle secured to pins or wires through the dorsal muscles has been used (Greer Walker et al. 1971; Young et al. 1972; Tesch 1972). Attachment through the dorsal musculature is possibly more acceptable for slow-moving fish such as brown trout, *Salmo trutta* (Holliday et al. 1972/73), and for sturgeon, *Acipenser* sp., which have external bony plates (Poddubny et al. 1966).

On small fish for short-term studies, transmitters can be attached to the dorsal fin by an alligator clip (McCleave and Horrall 1970; McCleave et al. 1967). Attachment with a leader threaded through the dorsal musculature (Shepherd 1973a) creates a wound at the point of attachment and appears to alter behavior in cutthroat trout, *S. clarki*.

On large tough-skinned fishes transmitters can be attached externally by a small harpoon head with the external transmitter attached at the end of a leader (Bass and Rascovich 1965; Lawson and Carey 1972). Standora et al. (1972) used a flat bracket to keep the transmitter from wobbling on the back of slow-moving sharks. For more active fishes a radially symmetrical design may be better. Thorson et al. (1969) attached transmitters to sharks by wires through the dorsal fin.

In stomach — Pushing a transmitter down the esophagus into the stomach of fish is a quick and easy procedure. In most cases transmitters were not disgorged (Table 1A); one Atlantic salmon S. salar, retained a transmitter for at least 10 mo (Stasko 1975b). Some species could disgorge a transmitter but mostly did not (e.g. Morone chrysops: Hasler et al. 1969; Anguilla rostrata: Stasko and Rommel 1974). Some species retained transmitters in one study but not in another, possibly due to the irritation of electric leads in the throat connecting internal transmitter with external sensors (Coutant 1969; Kanwisher et al. 1974a). Still other species consistently disgorged transmitters (Table 1B).

Some fishes have a muscular food-crushing pharyngeal apparatus which prevents passage of transmitters, e.g. tautog, *Tautoga onitis* (Olla et al. 1974), while in the shortnose sturgeon, *Acipenser brevirostrum*, transmitters were successfully inserted past the pharyngeal apparatus (J. D. McCleave, University of Maine, Orono, Maine, personal communication). Another difficulty was encountered with the American eel, *Anguilla rostrata*. Eels shut their jaws so tightly that they cannot be forced open without breaking the jaws unless anesthetics are used (A. B. Stasko unpublished data).

TABLE 1. Underwater biotelemetry studies in which transmitters were placed in the fish's stomach.

Species	References
A. Transmitters retained in stomach	
American shad (Alosa sapidissima)	Leggett and Jones (1971); Dodson et al. (1972); Katz (1972); Dodson and Leggett (1973, 1974)
Pink salmon (Oncorhynchus gorbuscha)	Stasko et al. (1973)
Chum salmon (O. keta)	Stasko (unpublished data)
Coho salmon (O. kisutch)	Madison et al. (1972)
Sockeye salmon (O. nerka)	Groot et al. (1972, 1975); Madison et al. (1972); Liscom (1973); Stasko et al. (1976)
Chinook salmon (O. tshawytscha)	Coutant (1969); Becker (1973); Monan et al. (1975)
Rainbow trout (Salmo gairdneri)	Coutant (1969); Becker (1973); Falter and Ringe (1974); Monan et al. (1975)
Atlantic salmon (S. salar)	Elson et al. (1972); Stasko (1975b)
Lake trout (Salvelinus namaycush)	Stasko (unpublished data)
Brown bullhead (Ictalurus nebulosus)	Kelso (1974)
American eel (Anguilla rostrata)	Stasko and Rommel (1974)
Atlantic cod (Gadus morhua)	Hawkins et al. (1974); Wardle and Kanwisher (1974)
White bass (Morone chrysops)	Hasler et al. (1969)
Striped bass (M. saxatilis)	Koo and Wilson (1972)
Skipjack tuna (Euthynnus pelamis)	Yuen (1970)
Bluefin tuna (Thunnus thynnus)	Carey and Lawson (1973)
B. Transmitters consistently disgorged	
Rainbow trout (Salmo gairdneri)	Coutant (1969)
Atlantic salmon (S. salar)	Kanwisher et al. (1974a)
Northern pike (Esox lucius)	Kendle and Morris (1965)
White sucker (Catostomus commersoni)	Kelso (1976)
Atlantic cod (Gadus morhua)	Kanwisher et al. (1974a)
Yellow perch (Perca flavescens)	Kelso (1976)
Skipjack tuna (Euthynnus pelamis)	Kanwisher et al. (1974a)

TABLE 2. Underwater biotelemetry studies in which transmitters were surgically implanted into the body cavity of fish.

Species	References
Muskellunge (Esox masquinongy)	E. J. Crossman, Toronto, personal communication
Channel catfish (Ictalurus punctatus)	Ziebell (1973)
Flathead catfish (Pylodictis olivaris)	Hart and Summerfelt (1973)
White bass (Morone chrysops)	Henderson et al. (1966)
Smallmouth bass (Micropterus dolomieui)	Peterson (1975)
Spotted bass (M. punctatus)	Peterson (1975)
Largemouth bass (M. salmoides)	Clugston (1973); Smith (1974); Coutant (1975);
- ,	Peterson (1975); Warden and Lorio (1975)

For those species that retain a transmitter in the stomach, especially salmon during their non-feeding period, stomach placement is a good method. It is quick and involves minimal trauma to the fish. The transmitter lies near the fish's center of gravity, is often small compared to the size of prey normally swallowed by the fish, and does not snag or contribute to drag resistance. Feeding and behavior of white bass (Henderson et al. 1966) and Atlantic salmon (Stasko 1975b) with transmitters in their stomachs appeared to be normal.

For those species that do not retain a trans-

mitter in the stomach, forced retention by means of a stiff rod from transmitter to the ithmus on the lower jaw has been tried (Kendle and Morris 1965; Peterson 1975). However, surgical implantation in the body cavity is a better alternative.

Surgical implantation — Surgical implantation of transmitters into the body cavity of fish through an incision in the ventral body wall (Table 2) is a technique well suited for long-term experiments. It has all the advantages of internal placement but there is the initial disadvantage of postoperative trauma. Such temporary effects are presum-

ably of little consequence in studies lasting many months.

The surgical technique is relatively simple (Ziebell 1973; Hart and Summerfelt 1975; Peterson 1975; Warden and Lorio 1975). Hart and Summerfelt (1975) concluded that, for at least two species, surgery performed in the field with immediate release of the fish into its natural habitat is preferable to postoperative care in holding tanks prior to release. The relative merits of postoperative care in tanks versus immediate release may vary with species, habitat, and type of experiment.

Surgical implantation of a transmitter with an external sensor protruding ventrally through the body wall of the fish has also been used successfully (Coutant 1975).

Invertebrates, reptiles, and mammals — On hardshelled, slow-moving invertebrates external attachment is relatively easy. Transmitters were tied to the shell of the queen conch, Strombus gigas (Clifton et al. 1970) and king crab, Paralithodes camtschatica (Monan and Thorne 1973). A cylindrical transmitter on the underside of the Norway lobster, Nephrops norvegicus, was held in place with elastic bands around the body (Chapman et al. 1975). Transmitters were glued to the dorsal surface of the spiny lobster, Panulirus argus (Clifton et al. 1970; Herrnkind and McLean 1971). A saddle-shaped transmitter was attached dorsally to American lobster, Homarus americanus, with a stiff wire around the rostrum anteriorly and hooked under the rear edge of the carapace posteriorly (Lund and Lockwood 1970).

On hard-shelled, slow-moving reptiles such as turtles (Baldwin 1972; Moll and Legler 1971) and alligators (Smith 1974) transmitters can be attached by wires passed through holes drilled through the hard integument.

Attachment of transmitters to marine mammals is difficult even with a simple harpoon head (Schevill and Watkins 1966). Streamlined transmitter packages have been developed to fit around the dorsal fin of captive dolphins and small whales (Martin et al. 1971; Evans 1971, 1974); these were held in place by a bolt through the dorsal fin. Other approaches, tested on a grey whale, *Eschrichtius robustus*, include tying the transmitter package with strong cords surgically imbedded in the back (Sweeney and Mattsson 1974), or securing the transmitter to a stretchable harness around the body (Norris and Gentry 1974).

Attachment of transmitters to Weddell seals, Leptonychotes wedelli, has been done by various surgical procedures (Siniff 1970). Ingested tem-

perature-sensing transmitters have been used for short-term studies on captive dolphins (Mackay 1964; Reid and Mackay 1968) and captive seals (Mattsson and Seeley 1974).

Effect on behavior — Implicit in all biotelemetry studies is the assumption that presence of the transmitter, its radiated signal and receiving system (e.g. boat) does not seriously affect the animal. Since behavioral side effects can occur (Shepherd 1973a), care must be taken to minimize them.

Minimizing the effects — For minimum disturbances fish should be removed from the catching gear, tagged, and released as quickly as possible. Dodson et al. (1972) were able to insert a transmitter and release American shad within 1 min from the time the fish hit a gill net. Where transportation from capture site to release site is involved, various anesthetics can be used to calm the fish (Bell 1964). If MS-222® is used, care should be taken to buffer the solution to prevent physiological side effects due to acidity (Allen and Harman 1970; Wedemeyer 1970).

Weight and volume of a transmitter should be as small as possible. A neutrally buoyant transmitter is preferable but can be achieved only at the expense of increased size. The usual practice is to minimize transmitter size. Some transmitter-to-fish weight ratios have been 0.002 for 350-kg giant bluefin tuna, *Thunnus thynnus* (Lawson and Carey 1972), 0.006 and 0.025 for 3-kg Pacific salmon, *Oncorhynchus* sp. (Stasko et al. 1973, 1976), 0.017 for 300-g white bass, *M. chrysops* (Hasler et al. 1969), and 0.06 for 85-g Atlantic salmon smolts (McCleave and Stred 1975). For pelagic fishes the weight ratio is probably more critical than for bottom-dwelling fish and invertebrates.

Drag resistance of externally attached transmitters can affect swimming performance (Shepherd 1973a; McCleave and Stred 1975) and is particularly important when dealing with migratory species such as salmonids and active pelagic species such as scombroids. A streamlined transmitter is important for preventing accumulation of weeds (Evans 1974), as well as for improving the stability of the transmitter package during locomotion.

Frequency of transmitted signals should be outside the audio range of the animals tracked. For fish, the upper audio frequency limit is around 1 kHz for most species, but up to 7 kHz for some (Hawkins 1973). Thus, the 20–300-kHz frequency range used in ultrasonic telemetry is outside the audio range of fish.

For marine mammals the upper audio frequency limit can be in excess of 100 kHz (Terhune 1976). With radio signals the frequencies used are much higher (usually 50 MHz and up) and, therefore, less likely to be detected by animals (Presman 1970).

Presence of a tracking boat is often part of the experimental procedure, and motor boats make considerable underwater noise. Stasko and Buerkle (1975) tested several small boats and found that the noise was above the audio threshold of Atlantic cod, Gadus morhua, 500 m away. Although the noise is audible to fish, it may not necessarily affect the fish's behavior. When attempts were made to influence the course of a moving fish by making repeated rapid approaches with the tracking boat, in most cases no changes in the fish's locomotory pattern could be detected within the limits of tracking precision with a location-only transmitter: e.g. pink salmon, O. gorbuscha, sockeye salmon, O. nerka (A. B. Stasko unpublished data); chinook salmon (J. H. Johnson, Seattle, Washington, personal communication); Atlantic salmon, American eels, white bass (A. B. Stasko unpublished data); and largemouth bass, Micropterus salmoides (Warden and Lorio 1975). Skeena River sockeye salmon, on their migration in Babine Lake, British Columbia, reacted to the tracking boat only at night (C. Groot, Pacific Biological Station, Nanaimo, British Columbia, personal communication). A response to an approaching boat is reported for dusky shark, Carcharhinus obscurus (Carey and Lawson 1973) and for Atlantic salmon (Poddubny 1971). With the use of a depth-sensing transmitter an Atlantic salmon (Rommel and Stasko 1973) and a white marlin, Tetrapturus albidus (F. C. Carey and D. G. Pincock unpublished data) were observed to dive when a boat passed directly over them.

Testing for effects — In the field, it is usually impossible to assess directly the effect of transmitter and handling on the behavior of fish.

Confidence in the results from biotelemetry observations can be increased when, for example, in homing studies the tracked fish return to the home area as rapidly and in equal numbers to displaced and marked control fish (Dodson and Leggett 1973; McCleave and Horrall 1970); or when migrating fish travel in the same direction and at rates comparable to marker-tagged fish (Stasko et al. 1973, 1976); or when transmitter-fitted fish feed normally and strike at anglers' bait (Young et al. 1972; Stasko 1975b); or when transmitter-fitted fish travel in a school of untagged fish (Yuen 1970).

Some effect of handling and fitting transmitters on fish has been observed in field studies. Activity of cod was greatest immediately after release from a tank on a boat. Such initial increased activity was eliminated when the fish were held in an underwater quick-release cage for 24 h prior to release (A. D. Hawkins, Aberdeen, Scotland, personal communication). Initial increased activity may be a general phenomenon with other species as well (e.g. European edible crab, Cancer pagurus: Kinnear and Chapman 1976; largemouth bass: Warden and Lorio 1975).

Some tests on effect of transmitters on fish behavior have been done under controlled conditions. Results have ranged from strong effects to no effect. A strong effect was noted when transmitters were attached externally at the end of a short line. Cutthroat trout with towed transmitters showed greater oxygen consumption in the laboratory, and abnormal posture and activity in a lake (Shepherd 1973a, 1973b). Such transmitters reduced swimming stamina in Atlantic salmon (McCleave and Stred 1975).

Temporary effects on buoyancy have been observed in several species. Gallepp and Magnuson (1972) showed that a dummy transmitter in the stomach of a bluegill, Lepomis macrochirus, a physoclystous fish, required compensatory fin movements until neutral buoyancy was gradually reestablished in several hours by inflation of the swimbladder. Atlantic salmon smolts, physostomous fishes, regained buoyancy about 6 h after transmitter insertion, but only when allowed access to the water surface (Fried et al. 1976). When adult pink salmon, sockeye salmon, and lake trout, Salvelinus namaycush, were held in a submerged net after transmitter insertion, they indicated negative buoyancy by continuous swimming with body tilted upwards (A. B. Stasko unpublished data). Such fish came to the surface and gulped air when first given access to the surface, and soon thereafter appeared to be neutrally buoyant.

In two studies presence of a transmitter some time after the fish was handled appeared to have no effect. Young et al. (1972) found that swimming activity, feeding, agonistic behavior, and hierarchical status of brown trout in tanks were not affected by an external tag wired to the dorsal musculature. McCleave and Stred (1975) demonstrated that transmitters in the gut of large Atlantic salmon smolts did not reduce their swimming stamina.

More such controlled experiments are needed on other species under various conditions to evaluate different transmitter-attachment techniques.

BIOLOGICAL STUDIES

A common pattern in most underwater biotelemetry studies is one where fish are fitted with transmitters and released, after which the experimenter becomes a passive observer and recorder of events over which he has no further control. In addition to plotting the locations of the fish, the observer also records various environmental factors.

Location-only transmitters — For the present discussion, studies with location-only transmitters (pingers) are grouped into three somewhat arbitrary categories: migration orientation, movements at obstructions, and ecology and behavior.

Migration orientation — In such studies, usually with diadromous fishes, there has been an initial attempt to describe the basic movement patterns of the fish in a particular area, after which tracking of sensory-impaired fish was envisaged but seldom done to further investigate the role of various senses used in orientation. The orientation studies are discussed separately for coastal waters, estuaries, and freshwater.

In coastal waters, pink and sockeye salmon (O. gorbuscha: Stasko et al. 1973; O. nerka: Groot et al. 1975; Madison et al. 1972; Stasko et al. 1976) showed little consistency in movement patterns that would provide a baseline of comparison for subsequent tracking of sensoryimpaired fish. In fact, on several occasions when two fish were captured simultaneously, handled similarly, and released together, they moved along entirely different paths. Despite such inconsistency in paths of individual fish, general progress toward the home river was observed. Responses to the direction of tidal currents appear to be a major factor in their orientation (Stasko et al. 1973, 1976). In Long Island Sound, near the Connecticut River, American shad also oriented to tidal currents, but consistently against the current (Dodson and Leggett 1973). Tracking of European eels, A. anguilla, in coastal waters of the North Sea showed that silver eels chose a direction of travel opposite to that of yellow eels (Tesch 1972, 1974, 1975).

In estuaries anadromous fish appear to slow down their migration and drift back and forth with the tides (Dodson et al. 1972; Groot et al. 1975; Stasko 1975b). American shad in the Connecticut River remained near the upriver edge of the saltwater wedge prior to entering fresh water (Dodson et al. 1972). Atlantic salmon achieved progress through the estuary by intermittent swimming against the ebb current along with much drifting on both flood and ebb tides (Stasko 1975b).

Once the fish enter freshwater their progress appears to be more rapid and consistent (Groot et al. 1972; Johnson 1960; Katz 1972), except when passing through impoundments with little

current (Malinin et al. 1974; Trefethen and Sutherland 1968).

Experiments with sensory impaired fish (blind, anosmic) show some differences in movement patterns compared to control fish (Dodson and Leggett 1974), but lack of vision or olfaction did not prevent displaced cutthroat trout from homing from open lake to home stream (McCleave and Horrall 1970; McCleave and LaBar 1972). In general, some compass sense unrelated to vision appears necessary for orientation of fishes in open water (McCleave and Horrall 1970; Hasler et al. 1969; Stasko et al. 1973, 1976).

The initial expectations that orientation-navigation mechanisms of fishes would be quickly elucidated by underwater telemetry techniques have not been realized. To date correlation of movements with changes in environmental conditions have been too imprecise. Underwater environmental conditions are complex, changing, and difficult to monitor at the swimming depth of a fish as it moves along. Measurement of subsurface currents along the path of a moving fish is particularly difficult. Yet, unless the swimming speed of the fish relative to the water is measured directly, knowledge of the instantaneous speed and direction of water currents is essential before one can even say whether a fish is swimming or just drifting passively (Stasko et al. 1973). Then there is the problem of determining whether a fish changes its movements because of changes in orientation cues or because of changes in motivation (e.g. resting, feeding, avoiding predators, etc.). And finally, individual fish do have individual behavioral patterns. Since biotelemetry orientation studies are time consuming, sample size is usually small.

Movements at obstructions — Obstructions can be physical barriers such as dams, nitrogen supersaturation below dams, differences in water temperature at the confluence of rivers or at power plants, or chemical pollution in the water. Although gross movements of fish past obstructions can be determined by mark-recapture studies, it is often important to know detailed responses to various aspects of the obstruction so that remedial action can be taken.

Much of the early work with chinook salmon and rainbow trout, Salmo gairdneri, on the Columbia River, for which the first underwater telemetry systems were developed, was related to physical obstructions (Trefethen et al. 1957; Johnson 1960; Monan et al. 1975). It dealt with the behavior of fish below dams, passage through fishways, fallback over spillways, and disorientation in the slow currents of impoundments. In the Soviet Union there has been considerable work on behavior of sturgeon and Atlantic salmon at

dams and in reservoirs (Malinin et al. 1971, 1974; Poddubny 1969, 1971; Poddubny et al. 1966, 1971). The Russian studies show that, in general, migrating fish below dams make repeated attempts to fight their way up where the water flow is greatest. In impounded sections of rivers the fish appear to frequently follow the original river bed.

At less solid obstructions chinook salmon in the Sacramento-San Joaquin River delta avoided waters with less than 5 mg/ ℓ dissolved oxygen (Hallock et al. 1970). Avoidance of river tributaries with high water temperatures has been demonstrated for chinook salmon and steelhead trout, S. gairdneri (Hallock et al. 1970; Monan et al. 1975). On the Columbia River chinook salmon and steelhead traveling past a nuclear generating station avoided the reactor side of the river for several miles downstream. Altered movement patterns in the area of effluent discharge from a nuclear generating station has been shown for brown bullhead, Ictalurus nebulosus, yellow perch, Perca flavescens, and white sucker, Catostomus commersoni (Kelso 1974, 1976). Much work on responses of fish to effluents from generating stations is in progress (Anon. 1975).

Another form of obstruction is fishing nets. American shad (Leggett and Jones 1971) and bream, *Abramis brama* (Malinin 1970) were able to avoid nets while traveling as close as 1 m to them.

An unsuspected form of obstruction was demonstrated by Poddubny (1969), who showed that sturgeon traveling upriver were temporarily disoriented when passing underneath electrical transmission lines.

Behavior and ecology — In this section we consider studies of daily movement patterns of underwater animals. In the open ocean Yuen (1970) found that skipjack tuna, Euthynnus pelamis, near Hawaii have a distinct cycle of feeding on a particular bank during the daytime, traveling irregular paths of 25–40 km per night, and returning to feed on the same bank day after day. Evans (1971) found that Pacific dolphins, Delphinus sp., in California coastal waters tended to travel along deep-water escarpments and sea mounts.

In the Soviet Union, Malinin (1971a), working on impounded rivers, showed that in the summer northern pike, *Esox lucius* and *A. brama* had distinct activity peaks at dusk and at dawn, while some individuals showed a third activity peak at mid-day. In winter *A. brama* for the most part remained motionless, while *E. lucius*, although moving less than in summer, still had the dusk and dawn activity periods (Poddubny et al.

1970). Malinin (1971a, b) showed that during the day burbot, *Lota lota*, remained inactive in the deeper waters along the edge of a channel, hunting at night when they sometimes moved into shallow water as well. In contrast, *E. lucius* and *A. brama* often ventured into shallow water but always returned to the deeper channel during stormy weather. In the Soviet studies, attempts to describe the individual territories of the various fishes were much hampered by the short operating life (2 days) of the external transmitters.

Other biotelemetry studies on home ranges, daily movement patterns, homing, etc. have been done with the slider turtle, *Pseudemys scripta* (Moll and Legler 1971); brown trout (Holliday et al. 1972/73); flathead catfish, *Pylodictis olivaris* (Hart and Summerfelt 1973); tautog (Olla et al. 1974); the Norway lobster, (Chapman et al. 1975); and largemouth bass, smallmouth bass, *M. dolomieui*, and spotted bass, *M. punctulatus* (Peterson 1975; Warden and Lorio 1975).

With the increasing availability of transmitters having a predicted life in excess of 1 yr (D. G. Pincock unpublished data; D. Brumbaugh, Tucson, Arizona, personal communication) the number of long-term ecological studies is expected to increase.

Transmitters with sensors — Temperature measurements — Temperature sensors are relatively easy to incorporate into biotelemetry transmitters, hence the large number of trials reported with temperature-sensing transmitters. They range from transmitters for medium-size fish (Ichihara et al. 1972; Kuroki et al. 1971) to transmitters for alligators (Smith 1974), sharks (Standora et al. 1972), cetaceans (Evans 1974; MacKay 1964; Reid and MacKay 1968), and seals (Mattson and Seeley 1974).

Published results with emphasis on biological results are few but increasing rapidly (Underwater Telemetry Newsletters). Carey and Lawson (1973) demonstrated that giant bluefin tuna control their body temperature at 18–20°C over a range of ambient temperatures from < 10°C to 17°C; bigeye tuna, *Thunnus obesus*, and dusky shark did not regulate their body temperatures. Movements of several species of fish have been studied in relation to changes in water temperature: blue shark, *Prionace glauca* (Sciarrotta 1974), white sucker (Kelso 1976), largemouth bass (Coutant 1975), and yellow perch (Kelso 1976).

Swimming depth — Swimming depth of animals is one of the more important factors to measure in field studies. From a knowledge of swimming depth one can determine the environmental con-

ditions to which the animal is exposed, using profiles of environmental factors measured by standard shipboard methods.

Indirect measurements of swimming depth of transmitter-fitted fish have been attempted with temperature-sensing transmitters and concomitant measurements of temperature profiles during tracking (Ichihara et al. 1972; Kuroki et al. 1971). Such a method is useful only in waters with pronounced temperature gradients. A similar approach with light-sensing transmitters and concomitant measurements of illumination profiles is limited by inadequate illumination at night or in deep or turbid waters (Gayduk and Malinin 1971; Gayduk et al. 1971). More direct methods for determining swimming depth have been discussed in the section on "Pressure".

Extensive data on depth of dives of dolphins, *Delphinus* sp., off California have been obtained by Evans (1971) using a device that recorded the maximum depth achieved during each dive and transmitted the stored information when the animal broke surface. Pressure-sensing transmitters were used for determining swimming depth of Pacific angel sharks, *Squatina californica*, and blue sharks (Standora et al. 1972), of Atlantic salmon (A. B. Stasko unpublished data), and American eels (Stasko and Rommel 1974). Some experiments with pressure-sensing transmitters appear to have been largely field trials of the equipment (Baldwin 1965; Evans 1974; Kanwisher et al. 1974a, b).

Heartbeats — The electrical voltages associated with heartbeats can be detected by wire electrodes and converted into suitable electrical inputs for biotelemetry transmitters. Heartbeat telemetering systems have been designed for marine mammals (Baldwin 1965), alligators (Smith 1974), and fish (Kanwisher et al. 1974a; Lonsdale 1969).

Data on heartbeats from fish under laboratory conditions have been published for sockeye salmon (Nomura and Ibaraki 1969; Nomura et al. 1972), rainbow trout (Nomura and Ibaraki 1969; Nomura et al. 1972; Weintraub and Mac-Kay 1975), and Atlantic cod (Wardle and Kanwisher 1974). Kanwisher et al. (1974a) and Wardle and Kanwisher (1974) used ultrasonic signals; in the other heartbeat studies radio-telemetry was used.

Other factors — Illumination has been measured with a photo-resistive cell incorporated in a transmitter such that the pulse repetition rate is a function of illumination level at the fish (Gayduk and Malinin 1971). In this case, however, illumination measurements were used mainly to determine the swimming depth of the fish (Gayduk et al. 1971). Standora et al. (1972) measured

illumination levels at sharks as an environmental variable to correlate with cycles of activity.

Activity of brown trout has been measured using a transmitter equipped with an external bimorph element that is deflected as the fish moves its tail (Holliday et al. 1972/73; Young et al. 1972). A tailbeat transmitter with a steel ball rolling into the air gap of a pot core has been designed by Holand (1975). Another measure of activity, obtained only with a continuous wave ultrasonic transmitter, is the Doppler shift resulting from undulations of the body and tail of a swimming fish (Stasko and Horrall 1976).

Swimming speed of sharks has been measured directly using a transmitter fitted with a deflector arm or a miniature drogue which creates electrical signals proportional to the arm deflection or to the pull of the drogue, both calibrated to give swimming speed (Standora et al. 1972; Sciarrotta 1974). Apparatus for measuring the swimming speed of sea turtles has been devised by Baldwin (1972) using a deflecting wand and, later, a miniature two-axis fluxgate magnetometer.

Compass orientation of the body axis of sharks has been measured with a rotating magnetized drum that alters the amount of light reaching a photocell from a miniature light source (Standora et al. 1972). A spinning magnetometer was used by Baldwin (1972) to measure the compass direction of a float towed by sea turtles.

Opercular rates of fish have been measured as a by-product of heartbeat measurements, since heartbeat transmitters pick up the electric potentials associated with opercular movements of fishes as well as heartbeat potentials. In fact, synchronism of the two was the principal question addressed by Weintraub and MacKay (1975) and touched on by Nomura et al. (1972). Respiration of cetaceans has been studied in terms of frequency of surfacing, since the transmitter was activated only while the air-breathing animal was breaking surface (Evans 1971, 1974).

Preliminary work on telemetering electrical activity from the brain of a free-swimming captive smooth dogfish, *Mustelus canis*, has been done by Kotchabhakdi et al. (1973) using metal electrodes in the cerebellum and optic tectum.

Finally, biotelemetry techniques in reverse can be used to provide controlled stimuli to free-swimming animals. A remote-controlled system for delivering odor stimuli selectively to each nostril of a shark has been designed by Baldwin and Ingle (1964).

Conclusion

In the two decades since the first underwater biotelemetry studies in the mid-1950s there have been considerable technical advances. Transmitters have become smaller, more powerful, and have longer operating life. Coding of individual transmitters has become more reliable and decoding more automated. Transmitters capable of sensing environmental, behavioral, and physiological factors from free-swimming animals have been built. Receiving systems ranging from small ones for tracking from canoes to large ones for oceangoing vessels have been developed.

With this equipment about 60 species of underwater animals have been studied. Various techniques of transmitter attachment have been developed and different methods of tracking explored.

Underwater biotelemetry has been applied to studies of fish migration, orientation mechanisms, movement patterns at obstructions, ecology, behavior, and physiology of animals.

In the past, development of biotelemetry equipment was seldom in phase with the needs of the user; the time lag between initiation of equipment development and reliable prototypes available for biological studies was too great. By now there have been enough engineering studies to create a body of specific knowledge and expertise so that equipment should be more easily available with less lead time. The increasing body of biological experience should also help in choosing the right approaches for solving specific biological problems.

In the future, underwater biotelemetry will likely become more readily available for the casual user as a standard method for locating individual animals in long-term ecological studies as well as for making detailed behavioral observations in short-term studies. Use of multisensor transmitters can be expected to increase. The study of physiological functions of free-swimming animals is a relatively little explored application and should receive more attention. In a strict sense, laboratory studies on the physiology of animals are not complete until the findings have been verified under natural conditions with unrestained animals.

Acknowledgments

We thank the following colleagues for their helpful comments during the preparation of the manuscript: F. G. Carey (Woods Hole, Massachusetts), J. D. McCleave (Orono, Maine), A. D. Hawkins (Aberdeen, Scotland), D. McG. Luke (Fredericton, New Brunswick), R. B. Mitson (Lowestoft, England), and J. W. Saunders (St. Andrews, New Brunswick). The figures were prepared by P. W. G. McMullon (St. Andrews).

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¹The Underwater Telemetry Newsletter is available from many biology libraries in eastern Canada and libraries of establishments where underwater biotelemetry work has been done. Copies for interlibrary loan are available at the Library of the Biological Station, Fisheries and Marine Service, St. Andrews, N.B. E0G 2X0. Most of the Fish. Res. Board Can. Transl. Ser., later called Fish. Mar. Serv. Res. Dev. Transl. Ser., are available from the National Research Council, Canada Institute for Scientific and Technical Information, Montreal Road, Ottawa, Ontario K1A 0S2.

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