Aquaculture International 3, 77–102 (1995)

Fish telemetry in aquaculture: review and perspectives

Etienne Baras[1]* and Jean-Paul Lagardère[2]

[1]*Laboratory of Fish Demography and Aquaculture, University of Liège, 10 Chemin de la Justice, B-4500 Tihange, Belgium*
[2]*CNRS–IFREMER, Centre de Recherche en Ecologie Marine et Aquaculture de l'Houmeau, Place du Séminaire, BP 5, F-17137 l'Houmeau, France*

The assessment of the behaviour or physiology of cultured fish has always been difficult due to the timing of sampling, differences between experimental and aquaculture conditions and to methodological bias arising from repeated fish handling. The development of biotelemetry techniques offers a wide range of possibilities to improve both production and management in aquaculture through monitoring of behaviour or physiology of free-swimming fish inside their culture environment. Thus knowing how key parameters are changing can allow faster adjustment of feeding times to activity rhythms, more objective identification of the preference/tolerance margins towards environmental variables and precise assessment (from 'the fish's point of view') of the impact of environmental or operational stressors on fish. This paper briefly reviews the techniques that might be applied in aquaculture and focuses on relevant systems and estimators of fish activity: movements, vertical distribution, use of demand-feeders, muscular activity and heart rate. Species or size-related limitations and use of automatic monitoring stations are reviewed and evaluated. Perspectives of integrated biomonitoring in aquaculture are discussed, using telemetered fish as reliable probes in the detection of abnormal situations such as changes of water quality or altered environments.

KEYWORDS: Fish behaviour, Physiology and biomonitoring, Telemetry

INTRODUCTION

Aquaculture is nowadays turning to a high rearing density 'aquaindustry' (Hempel, 1993), facing economic and environmental constraints that lead producers to fine-tune their operations, increase feeding efficiency and minimize food waste to cope with the rising costs of feedstuffs and increasing concern over pollution resulting from poorly organized feeding schedules (Poxton, 1991; Seymour and Bergheim, 1991). Predictive feeding charts (based on food ratio, texture and diet formulation) account for factors that control long-term variations of food intake but may prove inefficient at the levels – daily or subdaily – actually controlling fish activity or appetite. Feed conversion rates and fish growth can be improved by adapting meal frequency or timing of food distribution to the species (e.g. Greenland and Gill, 1979, on channel catfish, *Ictalurus punctatus*; Noeske and Spieler, 1984, on common carp, *Cyprinus carpio*, and Carrillo *et al.*, 1986, on sea bass, *Dicentrarchus labrax*; review, Boujard and Leatherland, 1992) but clearly need some sort

*Author to whom correspondence should be addressed.

0967–6120

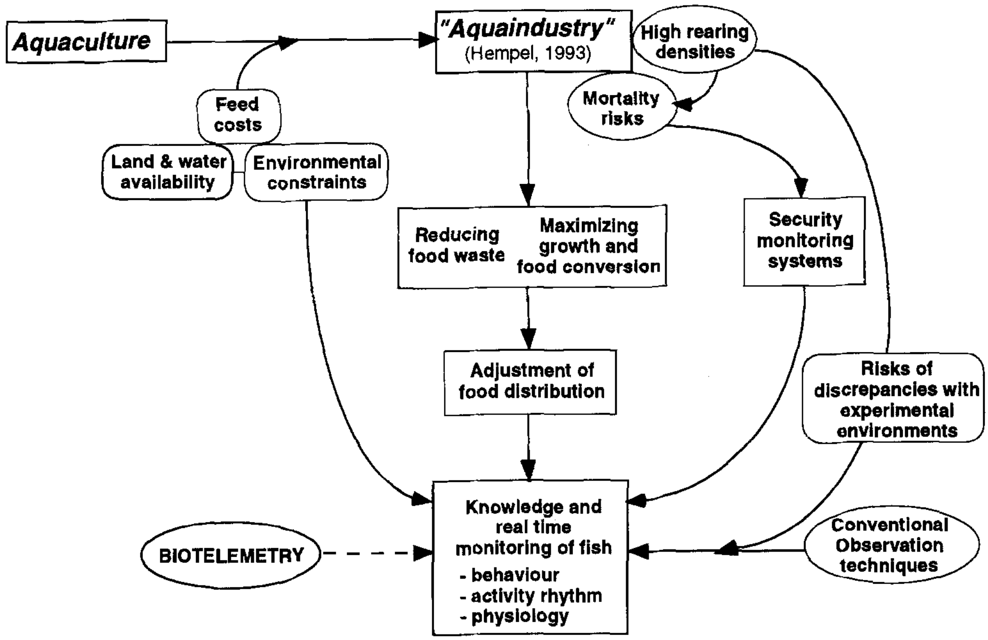

FIG. 1. Relational diagram of the use of biotelemetry in aquaculture.

of feedback or indication. Similarly, high rearing densities in modern aquaculture increase mortality risks and urge the need for efficient alarm-coupled monitoring systems to detect environmental degradation that could interfere with fish survival, stress and growth. In a recent review, Poxton (1991) pointed out that realistic criteria of environmental quality and safety margins under intensive farming conditions were generally unavailable and that methods should be developed to control water quality fluctuations and impact on fish health.

In this context (Fig. 1), selected aspects of fish behaviour and physiology are probably the most objective variables to be assessed in culture conditions. Their real-time monitoring would represent one of the most relevant steps in improving aquaculture management through the answer to fundamental questions such as:

- How are fish distributed in the culture environment?
- How do the activity and physiological rhythms of fish depend on culture conditions (density, light intensity, temperature, ...)?
- To what extent may their appetite be affected by environmental variations (wind, oxygen concentration, turbidity, ...) or operational stressors (delousing, transfer, removal of dead fish)?
- What delay is required for fish conditioning and what is its long-term efficiency?

These questions may be difficult to address in aquaculture environments when using only conventional observation techniques (Scherer, 1992), mainly due to major restrictions imposed by the culture environment itself (light intensity, turbidity, depth, distance, ...) on the continuous assessment of fish behaviour. On the other hand, conclusions from laboratory experiments may be misleading due to discrepancies between experimental and actual aquaculture conditions (fish density, environment).

The study by Tang and Boisclair (1993) on the influence of size of enclosures on the swimming characteristics of fish show that models of spontaneous swimming cost, developed using respirometry experiments in small aquaria, may not represent the complexity of swimming patterns, and consequently the cost of spontaneous swimming in large enclosures or in the field. This statement is also relevant for alarm systems using probe fish (e.g. 'truitomètre' or ichthyotest; Huve, 1982).

Various techniques have been used to assess the behaviour of cultured fish (review, Poncin and Ruwet, 1994). Investigations of diurnal and tidal rhythms of both appetite and swimming activity in Atlantic salmon, *Salmo salar*, in commercial cages were made using a video camera (Kadri *et al.*, 1991). Floen *et al.* (pers. comm.), Huse and Holm (1993), and Juell (1993) applied PC-based echo integration to the study of the vertical distribution of Atlantic salmon in net pens. The leaping behaviour in Atlantic salmon was monitored through the use of infrared cells for the assessment of stress situations (Furevik *et al.*, 1993). The timing and intensity of demand-feeding activities have been assessed through computerized monitoring of self-feeders (Anthouard and Wolf, 1988; Bégout *et al.*, 1994). In addition to these techniques that provide information on the average behaviour of fish, there have been new developments of underwater telemetry techniques with various possibilities for real time monitoring of many aspects of activity and physiology of free-swimming individual fish. Since its beginning in 1957, underwater biotelemetry has been applied to more than 160 aquatic species, including 110 fish species (Baras, 1991). Surprisingly, its use in aquaculture environments is more recent (Mohus and Holand, 1983; Holand, 1987; Bégout and Lagardère, 1993) and the investigated species far less numerous, despite logistic advantages arising from restricted range or ease of tag recovery. This paper briefly reviews the possibilities of improving stock management through the use of underwater biotelemetry.

BASIC CONCEPTS IN BIOTELEMETRY

Potentially, biotelemetry allows the remote sensing of the positions, movements, aspects of physiological or behavioural variables of an animal – or of environmental conditions around it – by means of radio (30–150 MHz) or acoustic signals (20–300 kHz). An individual can be equipped with a transmitter sending a signal which can be carrying information about heart rate or some other measurement of interest. Different transmitters are individualized by different frequencies or coded pulses. The signal is detected by hydrophones for acoustic and antennas for radio signals respectively. The distance at which the signals will be detected will mainly depend on the power radiated by the transmitter, the sensitivity of the receiving station and propagation losses.

The propagation of radio signals in air and water has been extensively investigated (Velle *et al.*, 1979). The received signal strength (RSS, dBm) in an open environment is given by the equation:

$$\mathrm{RSS} = \mathrm{ERP} - \mathrm{Loss}_{\mathrm{water}} - \mathrm{Loss}_{\mathrm{if}} - \mathrm{Loss}_{\mathrm{air}} + \mathrm{Gain}_{\mathrm{ra}} - \mathrm{Loss}_{\mathrm{tr}} \quad (1)$$

where ERP is the external radiated power of the transmitter (dBm); $\mathrm{Loss}_{\mathrm{water}} = d_w \times (\partial L_w/\partial d_w)$, with d_w = depth of transmitter (m) and $\partial L_w/\partial d_w$ = propagation loss depending on conductivity and frequency (-1.75 dB m^{-1} for each increment of 100 μS cm^{-1} at frequencies between 30 and 150 MHz); $\mathrm{Loss}_{\mathrm{if}}$ is the loss at the air–water interface

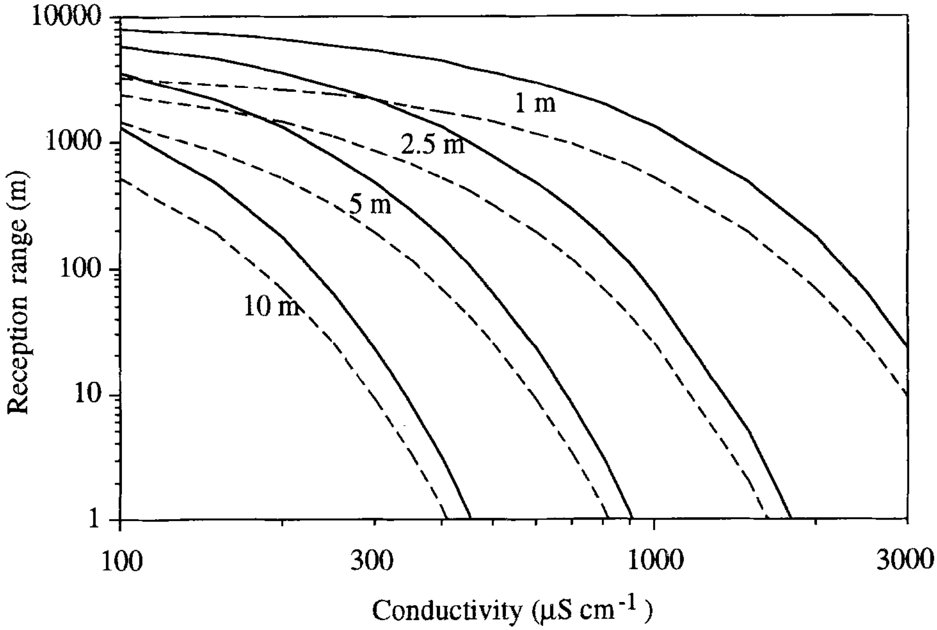

FIG. 2. Conductivity-related variations of the reception range for a fish standard radio transmitter (ERP = −40 dBm) detected in an open environment by a three-element Yagi antenna (+6 dBd) connected through a 30 m RG_{58U} feeder to a receiver with a −145 dBm sensitivity. Immersion depths, 1–10 m. Solid curves, 40 MHz; broken curves, 150 MHz.

(30 dB); $Loss_{air}$ = 17.7 + 20 log (d_{air}/wavelength) (dB), with d_{air} = linear distance between transmitter and receiving antenna (m); $Gain_{ra}$ is the gain of the receiving antenna (dBd); and $Loss_{tr}$ is the loss in the transmission line (dB m^{-1}; e.g. 0.0317 dB m^{-1} for a standard coaxial RG_{58U} line). As illustrated in Fig. 2, the use of radio signals is restricted to relatively shallow waters (< 10 m) with low or medium conductivity (< 500–1000 μS cm^{-1}).

Acoustic signals propagate omnidirectionally in water, the spheric propagation mode implying that the range dependency of the intensity obeys the inverse square law. This spreading loss is further modified by losses due to signal absorption or scattering when acoustic waves encounter a target (MacLennan and Simmonds, 1992). The overall acoustic propagation losses (compared with a transmitter source at 1 m) are given by the general equation (Anon., 1968):

$$Hr = 10 \log r_1 + 10 \log r + a_o + A \quad (2)$$

where r is the distance to the transmitter source; r_1 is the mean depth of the environment; a_o is the absorption loss and A is the scattering loss. A 100 kHz transmitter radiating at a power of 0.01 W cm^{-2} and giving a level of 151 dB/re 1 μPa at a distance of 1 m will undergo a signal loss of 71 dB through propagation, corresponding to a detection range of approximately 500 m (Mohus and Holand, 1983). Scattering loss and frequency attenuation are 51 dB and 20 dB, respectively. Under bad weather conditions, the range of this transmitter would be cut down to 200 m due to ambient noise (e.g. 25 dB decrease of signal-to-noise ratio during heavy rain). In earthen ponds or salt marshes used in aquaculture, the attenuation of acoustic signals can be as high as 25 dB in less than 10 m (Lagardère *et al.*, 1990). In this type of environment, the useful range of a standard fish transmitter (e.g. V2B-2L model from Vemco, 136 dB/re 1 μPa at 1 m) is cut down to 20–25 m. Acoustic signals are thus preferred in marine or freshwater deep and calm environments and are limited by the presence of vegetation, water turbulence, ambient noise and non-detection through ice or thermocline.

Both systems have intrinsic limitations but their variety allows the experimenter to choose the appropriate technique in almost all aquaculture environments. Combined acoustic/radio tags (e.g. Solomon and Potter, 1988) are less disadvantaged by environmental restrictions but may require larger batteries or have a shorter life span for the same weight of transmitter. In any case, the experimenter will be confronted by traditional trade-off constraints between the operational life of the transmitter and its bulk or weight (see 'transmitter attachment') and to a lesser extent by its radiated power and detection range, because range is restricted in most modern culture modes.

A possible way of partly solving this trade-off constraint is provided by the use of pulsed signals. Pulsed signals not only permit the telemetry of various parameters through variations of the transmitter pulse rate, using various sensors and circuits (see below), but also increase the operational life of the transmitter, in comparison with continuous signals. In addition, the use of different pulse intervals on the same frequency allows discrimination between several individual transmitters using this frequency, resulting in higher scanning performances by heterodyne receivers. The latest developments in transmitter technology involve digitally encoded signals (e.g. Lotek Engineering Inc., 1992) coupled to very low pulse rates (around 12 pulses min^{-1}). Using these transmitters permits up to 170 fish per frequency with operational life or power increased by 400% but requires automatic stations for individual identification. Further information on underwater telemetry techniques is given in Stasko and Pincock (1977), Winter (1983), Baras (1991) and Priede and Swift (1992).

Simple – position only – radio or acoustic transmitters currently cost between US $150 and US $200 (+ US $ 20–30 for temperature or mercury tilt activity circuit; + US $ 200–300 for electromyogram tags). Receivers cost from US $ 700 to over US $ 10 000 for automatic data-logging stations. This investment implies that a fish should keep its transmitter as long as its battery operates or at least for the duration of the study. However, the attachment procedure granting the maximum retention rate may not be the most adapted to secure a minimum interference with fish physiology.

TRANSMITTER ATTACHMENT

In any tagging study, the experimenter is hoping that equipping fish with radio or acoustic transmitters does not interfere with fish survival, growth, performances or behaviour. Three attachment modes are most frequently used in fish: external attachment by a harness (lateral or mid-dorsal), gastric insertion, or surgical implantation inside the body cavity. Both general and procedure-specific biases have been found in numerous studies (Baras, 1991). A ratio of transmitter weight to fish weight exceeding 2.5% often induces unrecoverable negative buoyancy (bluegill, *Lepomis macrochirus*, Gallepp and Magnuson, 1972; Atlantic salmon, Fried *et al.*, 1976). Recent developments in battery technology (use of lithium thionyl chloride cells which have an energy density about 18 times higher than that of Ni-Cad cells) have partly solved the traditional compromise between transmitter weight – or bulk – and range or operational life. The smallest available radio and acoustic transmitters still weigh about 0.8 g and 1.3 g, respectively, restricting the use of telemetry tags to fish above 30–40 g.

Regardless of attachment mode and transmitter-to-fish-weight ratio, fish handling and/or presence of transmitter may result in hyperactivity post-release (e.g. Atlantic cod, *Gadus morhua*, Hawkins *et al.*, 1974; sole, *Solea solea*, Lagardère *et al.*, 1988) and an increase in oxygen consumption (rainbow trout, *Oncorhynchus mykiss*, Lewis and Muntz, 1984) or in hypoactivity (rainbow trout, Zimmermann, 1980). Normal activity rhythms, though, do not systematically imply that fish are not affected by the tagging procedure: Lagardère (unpublished) showed that sea bass weighing around 400 g lost 10 to 15 g during the first post-operative week despite their feeding activity (detected from faecal analysis and use of self-feeder) being similar to those of untagged fish (see also Fig. 4). Weight losses in tagged fish may also originate from lower feeding rates (e.g. largemouth bass, *Micropterus salmoides*, Ross and McCormick, 1981) and are either maintained in the long run (e.g. largemouth bass, Mesing and Wicker, 1986; channel catfish, *Ictalurus punctatus* Carmichael, 1991) or rapidly recovered (barbel, *Barbus barbus*, Baras, 1992).

External transmitters can be rapidly fixed (2–3 min) using a harness with attachment wires passing through the dorsal musculature. The procedure may not require a complete anaesthetization of fish and allows a rapid recovery as well as the direct identification of tagged fish. Wounds are usually treated with antibiotic paste (e.g. polymixin sulphate or bacitracin) and further abrasion may be reduced by the use of neoprene pads between the tag and the epidermis. Depending on their position on the body of the fish, externally attached transmitters may, however, cause balance modifications, increase drag and be responsible for irregular swimming (e.g. Atlantic salmon, Thorpe *et al.*, 1981; largemouth bass, Mellas and Haynes, 1985), especially in fast-flowing environments (e.g. raceways). In the long run, the drag may result in the erosion of dorsal muscles (Baras, 1992). In ponds, transmitters may get entangled in the vegetation (e.g. yellow perch, *Perca flavescens*, Ross and McCormick, 1981; pike, *Esox lucius*, Lucas *et al.*, 1993). However, Lagardère (unpublished) showed that this attachment mode was valid to study the activity of turbot, *Scophthalmus maximus*, at medium to high rearing densities in saltmarshes (up to twelve 300 g fish m^{-2}).

Stomach insertion of a sterilized transmitter with a plunger requires only a sedation of fish and is usually completed within 30–60 s. Originally developed for anadromous salmonids non-feeding during their upstream migration, this attachment procedure may interfere with feeding because it modifies the degree of stomach fullness. Its use is further questioned by possible regurgitation (e.g. yellowtail, *Seriola quinqueradiata*, Ichihara *et al.*, 1972; sea trout, *Salmo trutta trutta*, Solomon and Storeton-West, 1983) or induced gut atrophy (chinook salmon, *Oncorhynchus tshawytscha*, Haynes, 1978). It is thus probably unsuitable in most aquaculture applications.

Intraperitoneal implantation is undoubtedly the most invasive procedure, because it requires complete anaesthetization, ventral incision, transmitter insertion and use of suture material to close the insertion (Hart and Summerfelt, 1975). Surgical staples (Mulford, 1984; Filipek, 1989) or cyanoacrylate adhesives (Nemetz and MacMillan, 1988) enable faster closing of the incision but their efficiency is still to be investigated in most species. More detailed information on anaesthesia and surgery procedures provided by Summerfelt and Smith (1990). Surgery is more likely to cause infection than other methods. Prophylactic treatment with antibacterial and fungicidal agents may thus be worth employing to maximize post-operative survival (Vallière *et al.*, 1986) although their influence may not be significant (Lucas, 1989, for rainbow trout). Intraperitoneally implanted transmitters may cause rectal erosion (e.g. rainbow trout, Bidgood, 1980) or alteration of gonads or viscera (e.g. grass carp, *Ctenopharyngodon idella*, Schramm and Black, 1984). Transmitters may be encapsulated by peritoneum (Lucas, 1989) or even by an adventitious loop of the intestine, resulting in transintestinal expulsion (Marty and Summerfelt, 1986), an alternative pathway to expulsion through the rupture of the incision zone (Prince and Maughan, 1978) or through the body wall (Lucas, 1989). However, many workers have found no apparent effects of this attachment procedure on survival, growth or behaviour of fish (e.g. cod, Pedersen and Andersen, 1985), at least not beyond the post-operative stress period (barbel, Kalpers *et al.*, 1989). It has also been proved reliable for long-term retention of transmitter (e.g. 2 y in barbel, Baras, 1992; 3 y in common carp, Johnsen, 1980, and even 9 y in walleye, *Stizostedion vitreum* (J. D. Winter, pers. comm.). As with gastric insertion, the transmitter is closer to the centre of gravity of the fish and causes less interference with swimming and long-term growth processes than external transmitters with attachment harnesses passing through the dorsal musculature.

It should be pointed out that the success and innocuity of a given attachment procedure is highly variable from one species to another, depending on environment, physiology or behaviour. Solomon and Storeton-West (1983) showed that adult Atlantic salmon retained transmitters inserted into their stomach whereas regurgitation consistently occurred within 15 days in sea trout. In barbel (Kalpers *et al.*, 1989) or chub, *Leuciscus cephalus* (Baras, unpublished.), surgical incisions closed with resorbable suture material (catgut) using atraumatic needles gave significantly better growth and long-term survival than with permanent suture material (silk, nylon) and cutting needles. The opposite trend was observed in tilapia *Oreochromis aureus* (Thoreau and Baras, 1995), due to their very thick and hard skin, resulting in larger tunnelling and holes when using atraumatic needles.

This brief and non-exhaustive review stresses the need for feasibility studies, using dummy transmitters or sham attachment, to tailor the attachment procedure to the species in question when no information is at hand in the literature. Experimenters should also be aware of national legislation on animal welfare, e.g. requesting a licence to practice surgery on fish. In this context, aquaculture environments offer logistic facilities to assess and measure post-operative stress inside the environment where the telemetry study will be conducted, minimizing methodological biases that may arise from environmental discrepancies. As a corollary, these facilities also represent an ideal test-bed for feasibility studies on wild fish.

FISH POSITIONING SYSTEMS

Fixing the position of fish in the horizontal plane of its culture environment may prove relevant for many purposes in aquaculture: e.g. defining the optimal size of the culture environment, determining wintering places or sites to catch breeders or ranched fish ('Judas' fish concept; Hasler and Henderson, 1963; Johnsen, 1980). Additionally, monitoring the visits of fish to discrete sites such as feeding areas allows the evaluation of feeding schedules with fish activity and/or appetite (e.g. Atlantic salmon, Juell and

Westerberg, 1993; sea bream, *Sparus aurata*, Bégout and Lagardère, 1994), or of the efficiency of fish conditioning towards aggregating devices (cod, Midling and Øeiestad, 1993).

Horizontal positioning can be conventionally achieved by triangulation, using directional antennae or hydrophones (Holliday *et al.*, 1974) or by more sophisticated systems (see respective advantages and limitations in Table 1). Because most culture modes in modern aquaculture (net pens, cages, raceways, tanks, ...) restrict fish movements to a fixed range, a convenient alternative to conventional triangulation is to determine the relative arrival times of acoustic signals to a fixed array of omnidirectional hydrophones (Fig. 3(a)); the position of the transmitter corresponds to the intersection of the hyperbolas traced from signal arrival times and sound velocity (inverse of the principle of hyperbolic navigation; e.g. Hawkins *et al.*, 1974; Holand *et al.*, 1974; Lagardère *et al.*, 1990; Juell and Westerberg, 1993). A similar system has been evaluated for radio signals (Lemnell, 1980) but requires a high accuracy for the measurement of signal time arrival, due to the high propagation velocity of electromagnetic waves (e.g. 33 ns gives a 10 m accuracy). Armstrong *et al.* (1988) proposed an elegant alternative system (RAFIX), using combined acoustic/radio transmitters located in polar coordinates with a single (but mixed) receiving station: the signal source direction is given by a directional hydrophone or antenna and range is measured from the time lag between the arrival of radio and acoustic signals. Sound velocity (C, m s^{-1}) in water varies with environmental conditions, following the equation (Anon., 1968; Medwin, 1975):

$$C = 1410 + (4.21\,T^{\circ} - 0.037\,T^{\circ 2}) + 1.10\,S + 0.018\,D \tag{3}$$

with T° is the water temperature (°C), S is salinity (‰) and D is depth (m). Algorithms for the calculation of two-dimensional Cartesian coordinates from a minimum of two time lags of signal arrival to three hydrophones are given in Tobias (1976), Rindorf (1981), Hardman and Woodward (1984) and Lagardère *et al.* (1990). Hydrophones are often connected via underwater cables to a shore-based receiver and time-interval counter (e.g. Lagardère *et al.*, 1990; Urquhart and Smith, 1992; Juell and Westerberg, 1993). Konagaya (1982) and Konagaya and Cai (1989) used radio (27 or 40 MHz) sonobuoys to relay acoustic pulses to shore-based stations. Despite its elegance, this system is more prone to signal jamming by citizen's band (CB) sets on fishing boats in coastal waters, depending on the official allocation of frequencies by governmental offices. In any case, experimenters should be aware of the frequencies allocated by their national agencies to minimize any major interference by any other kind of radio signals.

Systems based on acoustic time lags have variable accuracy, depending on the output level of the transmitter or on signal attenuation and scattering (e.g. caused by dense fish schools in intensive aquaculture). Juell and Westerberg (1993), however, found that the range and accuracy of this system was adequate while monitoring the movements of Atlantic salmon in a population of 1750 fish within a 12 × 12 × 7 m sea cage. Positional accuracy is also dependent on the number and respective positions of the hydrophones within the array (usually triangular arrays with at least three hydrophones spaced 20, 200 or 300 m apart) and on the position of the transmitter within the array, with maximum disparities when the hyperbolae intersect at small angles. The accuracy of acoustic position fixing is also dependent on signal processing. Heterodyne receivers that allow the monitoring of positions of several transmitters tuned to different frequencies (±0.5 kHz within the range 71–86 kHz) face technical constraints (frequency changes to obtain low-frequency outputs) limiting the accuracy of time arrival to about 1 ms, resulting in errors of real positions of about 1 m (e.g. Hawkins *et al.*, 1974, 1980; Hawkins and Urquhart, 1983; Urquhart and Smith, 1992). Glass *et al.* (1992) monitored with this equipment up to eight individuals of saithe, *Pollachius virens*, equipped with 14.9 g tags (165 dB/re 1 μPa at 1 m) with an array of six hydrophones extending to 17 756 m^2. If the study requires a very precise tracking of a single fish in a restricted space (e.g. use of self-feeders, precise estimate of fish activity budget), a much better accuracy can be obtained by acoustic emission pulse analysers having constant response time after the first acoustic pulse is detected. Lagardère *et al.* (1990) observed disparities between real and mean calculated positions as small as 6–36 cm for 6 g (136 dB/re 1 μPa at 1 m) transmitters in a 30 m^2 pen situated in a saltmarsh surveyed by an array of four hydrophones. Recent developments of this system now allow an accuracy of 10 μs in detecting signal time arrival, resulting in a theoretical position-fixing accuracy of 2 cm in the centre of the array and a practical accuracy of 10 cm (Bégout and Lagardère, 1994).

An alternative to fish location is to monitor discrete key sites, such as visits to feeding areas (e.g. Juell and Westerberg, 1993; Bégout *et al.*, 1994; Fig. 4) or to aggregating devices (tuna sp., Holland *et al.*, 1990; skipjack, *Katsuwonus pelamis*, Caure, 1991; cod, Midling and Øeiestad, 1993). Various systems have been developed to monitor the overall distribution of food in a culture environment, using electromechanical sensors coupled to demand-feeders (e.g. Anthouard and Wolf, 1988). However, when using demand-feeding systems, it is generally assumed that all fish have learned to operate the trigger, though it does not imply that all fish bite with the same frequency, resulting in highly variable individual growth patterns. This hypothesis can only be checked through a system combining the automatic recording of individual fish with the monitoring of the demand-feeding system. Brännäs and Alanärä (1993) used the PIT (passive integrated transponder)-tag entry stations developed by Prentice *et al.* (1990) on Arctic charr, *Salvelinus alpinus*, as small as 48 g (tag inserted into the isthmus of the fish, posterior to the pectoral fin) in 1 m^3 standard rearing tanks. At low densities (15 fish m^{-3}), accuracies of bite detection ranging from 91% to 99.5% were obtained with small detecting loop antennae (inner diameter: 13 cm) placed around the trigger of the demand-feeder. This technique allowed Brännäs and Alanärä to show that there was a strong dominance hierarchy in which one or two individuals monopolized the trigger and had the highest growth rate. This powerful and time-saving tool, however, has basic limitations at high rearing densities, because the detection range of PIT-tags is limited to a few cm whereas food is often distributed over a larger surface in which the presence of other fish may represent an obstacle to tag detection. Additionally, code identification may fail when the antenna is attacked from an oblique angle or, as a corollary, if some tags are injected obliquely into fish (Brännäs and Alanärä, 1993). In such environments, radio or acoustic tags can be used and detected by antennae or hydrophones connected via a switching box to a programmable data-logging receiving station (e.g. Lotek Engineering Inc. SRX-400 receiver with Event Log PGM; Fig. 3(b)). This receiver scans a programmed frequency table at fixed ($\geqslant$ 0.1 s) or variable intervals, depending on a programmed algorithm defining a priority scan of frequencies detected on a master antenna. This concept is similar to that of the sonobuoy automatic listening stations developed by Solomon and Potter (1988) and used by Potter (1988; radio and combined acoustic/radio tags) and Moore *et al.* (1990; micro acoustic tags, 1.3 g) to study salmonid migrations in estuaries. The latest developments in automatic stations now allow the monitoring of the presence/

TABLE 1. Advantages and limitations of telemetry location-finding systems (see text for specific, propagation-related, limitations of acoustic and radio signals)

System	Advantages	Limitations	References (examples)
Direct systems: source positioning from conventional manual triangulation			
Directional antennas (radio) Directional hydrophones (acoustic)	Portable, low-cost equipment	Low positioning frequency Low accuracy when fish move Manpower required	Holliday *et al.* (1974)
Automatic direction finding: source positioning from automated signal direction finding			
Mechanical scanning (using motor-driven antennas)	Long range	Large integration time, negatively influenced by animal movement	Deat *et al.* (1980)
Doppler system (measure of frequency modulation in a rotating dipole or of staircase phase modulation in an array of eight dipoles	High theoretical accuracy (0.1°) High bearing frequency	Restricted to open environments away from multipaths sources) Very large antenna arrays to cope with frequency propagation in water	Burchard (1989)
Range and direction finding: range determined from the delay between arrival of radio and acoustic signals at a receiving station equipped with directional hydrophone and antenna			
RAFIX, using combined acoustic/radio transmitters	Functional in most environments Positioning with one receiving station	Transmitter weight increased, restricted to larger fish	Armstrong *et al.* (1988)

Automatic positioning systems: inverse of the principle of hyperbolic navigation			
Array of radio antennas	Long-range applications	Requires time-measurement accuracy (33 ns for 10 m location accuracy)	Lemnell (1980)
(a) Array of three or more omnidirectional hydrophones (heterodyne receivers) – Fixed hard wired – Buoy mounted with radio relay	Good accuracy (≥ 1 m) Possibilities of frequency scanning (8–10 fish tracked at a time) Easy installation and transportation	Range limited by ambient noise Accuracy limited by signal scattering Jamming by radio parasites	Urquhart and Smith (1992) Juell and Westerberg (1993) Konagaya (1982)
(b) Hydrophone array with constant frequency pulse analyser	Very high positional accuracy (2–10 cm)	One fish tracked at a time Range limited by ambient noise	Lagardère *et al.* (1990) Bégout and Lagardère (1994)
Automatic site monitoring: monitoring fish passage or presence in discrete sites			
Sonobuoy listening stations	Easy installation and transportation	Relatively low accuracy	Solomon and Potter (1988)
PIT-tag entry stations (using coded passive integrated transponders)	Light transponder weight (0.2 g) Billions of individual codes	Range restricted to a few cm	Prentice *et al.* (1990) Brännäs and Alanärä (1993)
Hard-wired multiple antenna event-logging station with coded transmitters	Very high scanning frequency (2000 fish on eight sites in 5 s) Long range	Lower accuracy than acoustic systems Precise calibration required	Lotek Engineering Inc (1992)

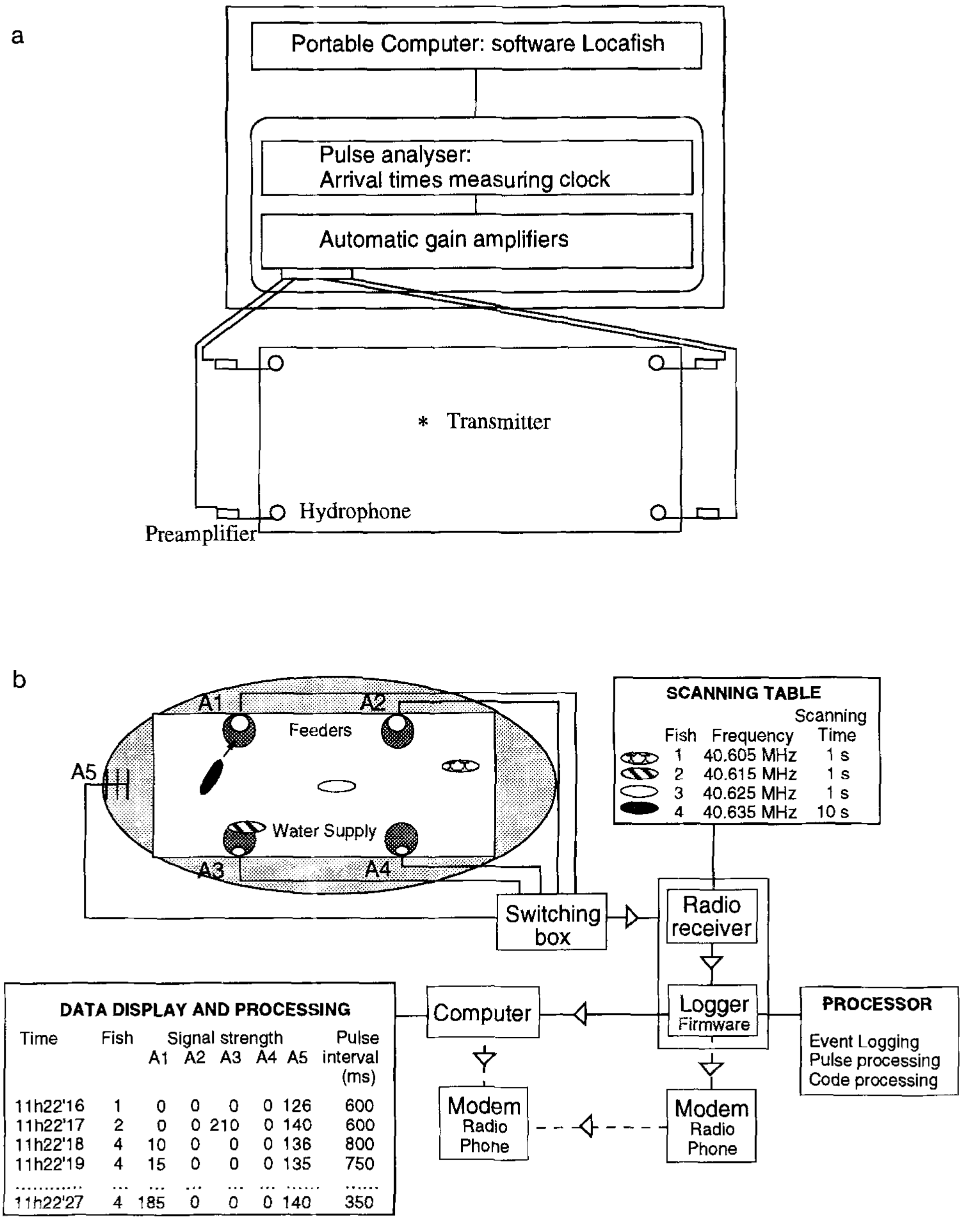

FIG. 3. (a) Functional diagram of an acoustic positioning system using an array of four omnidirectional hydrophones. Fish are located from the relative signal arrival times at the hydrophones. (b) Diagram of a radio telemetry site-monitoring system scanning programmed frequencies on antennas (A1–A4) with restricted range (shaded areas). A full-size antenna (A5) masters the whole area for the permanent monitoring of a tag (fish 4) equipped with a sensor and circuitry modifying the interpulse interval (e.g. depending on movement). Increasing received signal strengths for fish 4 on antenna 1 indicates that the fish comes closer to the site surveyed by the antenna. The data logger is equipped with event log processing for site monitoring, pulse processing for special telemetry applications (temperature, oxygen, heart rate) and code processing for digitally encoded transmitters.

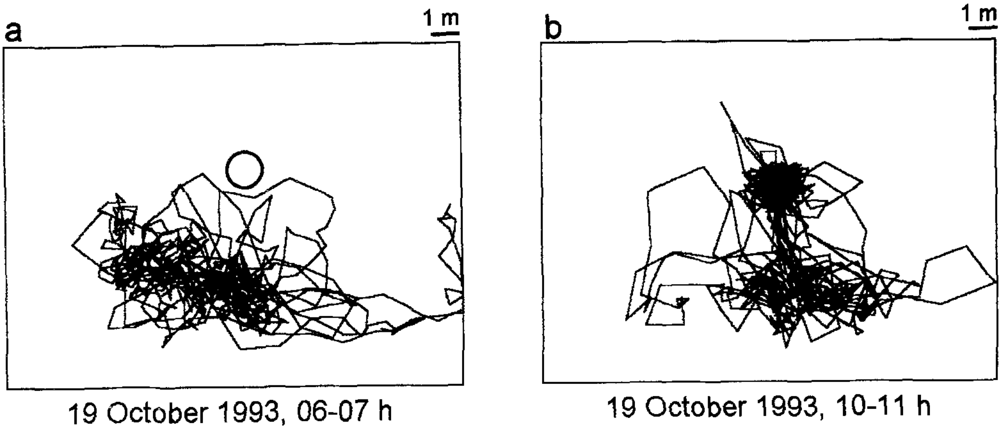

FIG. 4. Track diagrams and use of a self-feeder (open circle) by an acoustically tagged sea bass in a shoal of 60 fish in a saltmarsh. (a) Fish track before feeding; (b) fish track during feeding with indication of residence under the self-feeder.

absence of up to 2000 fish in eight sites within 5 s with a single receiver when using digitally encoded signals (Lotek Engineering Inc., 1992).

In addition to fish location in the horizontal plane, knowledge of the vertical distribution of fish may also be relevant in defining the optimal depth in culture environments, feeding regime or timing of food distribution, especially when fish are confronted with trade-off constraints between light-induced surface avoidance and food attraction (e.g. Atlantic salmon in marine net pens; Juell, 1993; Fernö *et al.*, 1995). Because depth influences sound propagation in water (Anon., 1968), it can be deduced from time arrivals of acoustic signals to hydrophones. Algorithms for the calculation of three-dimensional coordinates from an array of four hydrophones are provided by Hardman and Woodward (1984). Similarly, using signal strengths from radio sources of known location may help in determining fish depth (depending on conductivity and frequency; Velle *et al.*, 1979), although the use of pressure-sensing transmitters (Luke *et al.*, 1973; Williams, 1990) gives more reliable estimates, independent of signal attenuation.

FISH ACTIVITY RHYTHM AND BEHAVIOUR

Knowledge of fish activity rhythms in aquaculture environments represents a key item in tailoring feeding schedules to fish appetite (Kadri *et al.*, 1991). As mentioned above, fish activity rhythms can be obtained by monitoring the frequency and duration of visits of fish to feeding areas or food distribution by coupling a transmitter to demand feeders (Bégout *et al.*, 1994). These systems may nevertheless fail to assess individual feeding activities of pronounced bottom feeders or when the food portion distributed exceeds the appetite of the biting fish. With some exceptions (Boujard and Leatherland, 1992), locomotor and feeding activities are synchronous or consecutive, at least in non-starving fish (e.g. atipa, *Hoplosternum littorale*, Boujard *et al.*, 1990). Estimates of feeding rhythms can thus be deduced from locomotor activity rhythms and obtained from distances travelled between successive tracking locations, with an accuracy depending on positioning frequency and accuracy (e.g. Lagardère *et al.* 1990).

Within the error polygon constructed from accuracy estimates, tracking techniques using heterodyne receivers cannot easily discriminate small-scale changes in position: a clumping of successive locations on a discrete spot may be interpreted as rest or as intense activity. This problem can be simply solved by equipping transmitters with an activity circuit coupled to a mercury tilt and switching the interpulse interval to short or long period depending on the position of the tilt (e.g. Baras, 1995). Using this technique, Baras *et al.*, (1995) studied the adaptation of tilapias, *O. aureus*, to different timings of food distribution and found that fish could match the new timing within 24 h. Similarly, they showed that arrhythmic activities were consistently observed consecutively to a major environmental stress (e.g. 4–7 °C variation in water temperature inside the culture environment), accounting for the higher feed conversion rates achieved at that time with 24 h feeding schedules.

Stress or health status in cultured fish may also be reflected by abnormally high frequency of typical behaviours. Furevik *et al.* (1993), using infrared cells and underwater video cameras, showed that high leaping activity in Atlantic salmon was associated with acute stress or heavy louse infestation, whereas high rolling activity reflected buoyancy compensation subsequent to stress exposure (delousing, anaesthesia). These typical behaviours can also be discriminated from telemetry signals based on specific sequences of signal amplitudes and pulsation rhythms of activity-circuit transmitters (e.g. Nams, 1989; Baras, 1992).

FISH PHYSIOLOGY AND METABOLISM

In addition to activity and behaviour, physiological variables from fish are the most likely candidates to shed some light on how culture conditions affect fish health, especially when measuring stress or components of energy budgets (e.g. muscular activity, ventilation rate, heart rate; see list of telemetered parameters and references in Baras, 1991).

Stasko and Horrall (1976) observed that the undulations of the body and tail of fish generated a Doppler effect, causing rhythmic beats in continuous-wave transmitters which reflected tailbeat frequency. Continuous-wave transmitters have, though, been abandoned in favour of pulsed transmitters with circuits that change the interpulse interval proportionally to the value of the variable sensed by the transmitter. Ross *et al.* (1981) detected variations of tail beat frequency in brown trout from tags sending a pulse for each impulse over a 50 μV threshold sensed by the electrodes anchored into caudal red muscles. When considering energy expenditures, it should be stressed that changes of speed, direction and position are more energy-demanding than swimming at constant speed, as shown by Weatherley *et al.* (1982) in respirometry studies coupled to telemetered electromyograms from epaxial myomeres in rainbow trout. Electromyogram transmitters have also been used to monitor jaw movements with electrodes inserted into the *adductor mandibulae* muscles (e.g. brown trout, Oswald, 1978) and respiratory frequency, with electrodes inserted into *levator arcus palatini* muscles (e.g. rainbow trout, Rogers and Weatherley, 1983). The acoustic system developed for field use (Rogers *et al.*, 1984) has been further improved to allow long-term monitoring (up to 7 months for a 16–20 g package; Kaseloo *et al.*, 1992).

Heart rates can be telemetered from electrodes inserted into the muscles near the pericardium, using feedback circuits to filter most of the high-frequency noise from muscle activity. The electrodes have to be inserted carefully: a recent study by Keen and Farrell (1994) using an *in situ* working-perfused-heart preparation, emphasizes the necessity to leave intact the pericardium to maintain normal heart rate. The signal transmitted is either the whole electrocardiogram (ECG FM transmitters; Nomura and Ibaraki, 1969; Wardle and Kanwisher, 1974) or the heart rate itself, by coupling a linear potentiometer to trigger a high-power pulse for each R wave of the QRS complex of the ECG (Priede and Young, 1977; Armstrong *et al.*, 1989; Sureau and Lagardère, 1991). Monitoring systems removing false pulses caused by noise have recently been developed for use on personal computers (Floen *et al.*, pers. comm.). In Dover sole, heart rate is closely correlated to locomotor activity (Sureau and Lagardère, 1991; Fig. 5(a)), whereas in cod (Priede and Tytler, 1977) or in sea bass (Sureau and Lagardère, 1991; Fig. 5(b)), the two variables are dissociated, at least for routine movements. Heart rate is more closely related to metabolism (Lucas *et al.*, 1991) and allows estimates of meal energy intake. Lucas and Armstrong (1991) obtained a correlation, with r^2 as high as 0.988, between meal energy and standardized estimated cost for digestion from heart rates in pike.

Additionally, monitoring how fish apportion their time working at different metabolic rates may help in predicting mortality risks or assessing the implications of environmental or operational stressors. Bjordal *et al.* (pers. comm.) studied the impact on Atlantic salmon of different operational procedures in fish farming. They showed that operations as common as removal of dead fish in cages may cause a mild stress in fish and interfere with their appetite. Fish handling or delousing procedures increased heart rates by over 100%, the stress extending until the following morning. Conversely, the frequency of missing heart beats can be used as a general index of sensory responsiveness and well-being of the fish (Priede, 1983).

FISH ENVIRONMENT

The exposure of fish to environmental fluctuations in factors such as temperature, light, dissolved oxygen and organic compounds may variously affect fish health, appetite or growth. Various automated water-quality data acquisition systems have been developed for aquaculture purposes (e.g. Losordo *et al.*, 1988; review, Poxton, 1991) but need some feedback about the correspondence between sampling sites and places actually occupied by fish, especially in heterogeneous environments. Combining real-time monitoring of fish position and of environmental variables in aquaculture will thus be most relevant if what is happening in fish culture systems is to be understood and correctly managed to minimize food waste and pollution.

In natural culture environments (pond, lagoon, saltmarsh), fish have few possibilities to buffer the impact of environmental (meteorological and hydrological) variations through vertical or horizontal migrations. Changes of spontaneous activity or swimming in response to these environmental stressors are often among the first symptoms observed but are difficult to quantify (Scherer, 1992). Lagardère and his co-researchers (Lagardère *et al.*, 1988, 1994; Bégout and Lagardère, 1993) used acoustic tracking systems coupled to environmental monitoring to study the influence of wind and rain on the swimming activity of Dover sole and sea bass. They found a significant increase in swimming activity under gusty winds and a decrease of feeding activity under heavy rain. Similar applications of telemetry techniques (Mosneron Dupin and Lagardère, 1990; Sureau and Lagardère, 1991; Rabben and Furevik, 1993; Baras, 1995) have confirmed in

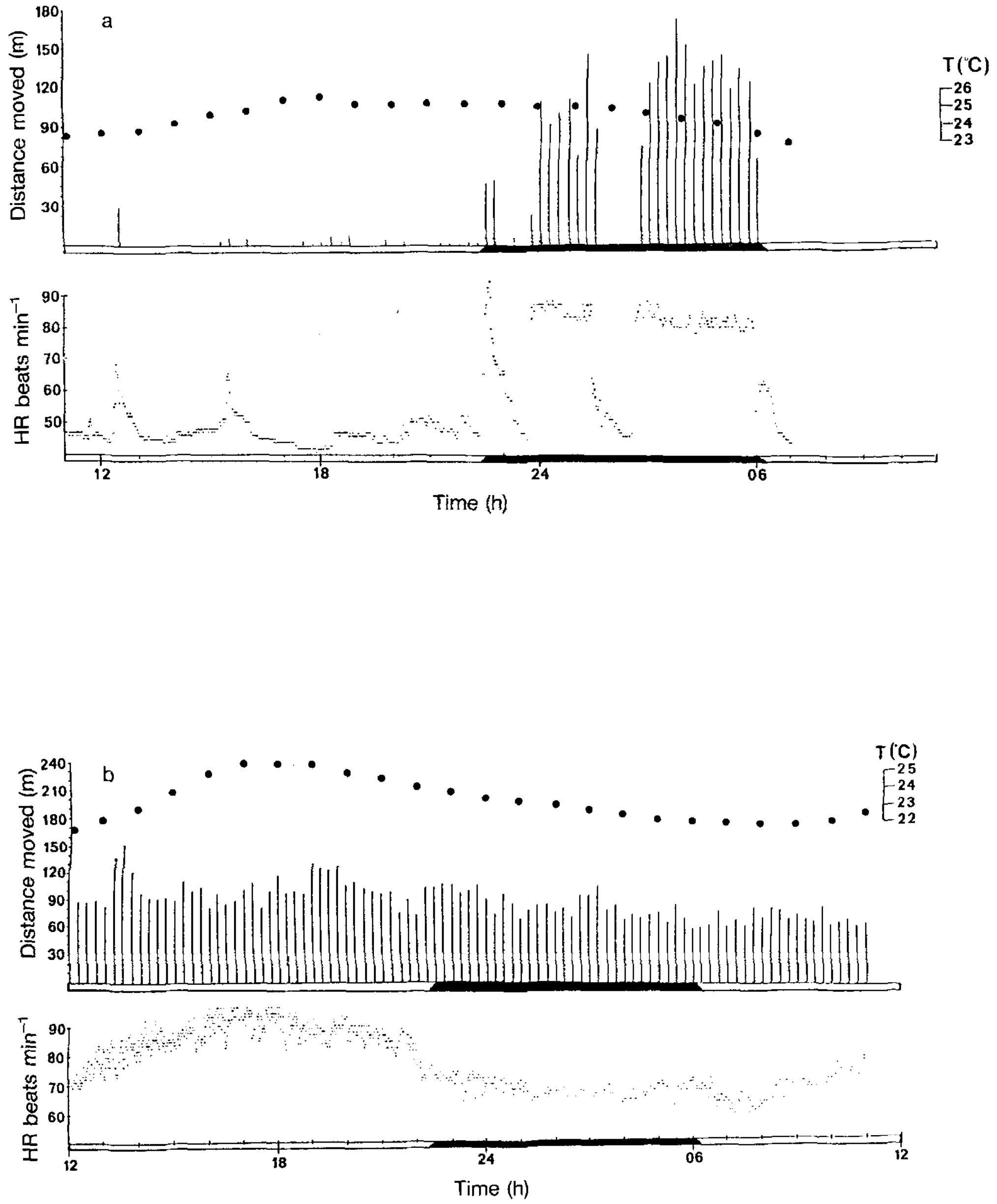

FIG. 5. Synchronous monitoring by acoustic telemetry of swimming activity and heart rate in marine fish. Variables are closely associated in Dover sole (a) and dissociated in sea bass (b), at least under a minimum effort threshold. Vertical bars show distance moved in 15 min; note differing vertical scales.

natural environments the influence of temperature evidenced in experimental aquaria or tanks. Juell and Westerberg (1993) showed how the social environment (fish density) interferes with the activity of Atlantic salmon.

A further improvement is to monitor environmental variables in the places actually occupied by fish, using transmitters equipped with various sensors detecting the variations of temperature (e.g. Berman and Quinn, 1991), salinity (Priede, 1982) or dissolved oxygen (Priede *et al.*, 1988). Using 'probe fish' equipped with environmental sensing transmitters represents an efficient alternative to combined environmental remote sensing and fish positioning systems, especially for a precise and fast assessment of the actual environmental preferences of new cultured species (Sutterlin and Stevens, 1992). This probe fish concept can also be transposed outside of the culture environment itself, i.e. to monitor physiological variables from fish during their transportation or to test for the adaptation of cultured fish to their restocking environment (e.g. Baras and Philippart, 1989).

NEW DEVELOPMENTS AND PERSPECTIVES

By comparison with other applications of telemetry techniques (animal migration and distribution, interspecific relationships, reaction to gears), aquaculture environments represent ideal test-beds for the development and use of state-of-the-art technologies. Fish of different species, size, age and more or less used to handling are available and can be tagged with sophisticated, expensive tags thanks to the ease of tag recovery and the possibility to reduce functioning costs to battery replacement. Considering the short range required, the trade-off constraint between battery size and performance can be orientated towards the latter parameter. Recent developments in 'intelligent' programmable tags further allows one to increase the operational life of the transmitter, e.g. through a day/night option circuit, activating the transmitter during the most critical period of the 24 h cycle (i.e. night-time and early morning when the concentration of dissolved oxygen reaches its daily minimum). Similarly, these tags may be programmed not to pulse during a time corresponding to the post-operative stress (e.g. MMT transmitters from ATS Inc. for radio tags, delayed-start pingers from VEMCO for acoustic tags).

Future developments and applications of telemetry systems in aquaculture will mainly depend on the following.

1. Advances in battery miniaturization and reduction of tag weight and bulk, e.g. through the replacement of piezoelectric ceramics by PVDF films (polyvidilene or polyvinylidene fluoride; G. G. Urquhart, pers. comm.).
2. Improvement of the sensitivity of receivers (−150 to −160 dBm) and signal processing, using more sophisticated methods of analysing the signals from simple and inexpensive transmitters (Shields, 1980; Nams, 1989).
3. Developments in sensor technology, because any variable that can be sensed electronically can be carried by a radio or acoustic signal, with a precision mainly depending on the accuracy of interpulse measurement (1 ms with digital receivers). The 'probe fish' mentioned earlier can be further improved to reach an integrated biomonitoring stage, using the telemetry of electrophysiological activities from fish olfactory – or gustatory (see amendment in Hara, 1993) – epithelium to detect with

higher precision and reliability minute concentrations of pollutants that cannot be detected with available chemical probes (Kudo and Ueda, 1976; A. Moore, pers. comm.). Similarly, sensors for stress hormones such as cortisol could be expected, although their emergence is not in sight.

4. Developments in data storage and retrieval: in feasibility studies aiming at studying fish physiology inside the culture environment, the traditional trade-off between power and performance may almost be wiped out through the use of data-storage tags (archival tags) announced by Robinson (1986) and recently used by Metcalfe *et al.* (1992) to monitor the migrations of plaice, *Pleuronectes platessa*, in the open sea. Archival tags do not send any signal but allocate the energy from the battery for sensing variables at a programmed sampling rate ($\geqslant$ 1 s) and storing information on EPROM (permanent memory) with a logging capacity of up to 1 MByte (CSIRO, Tasmania). The data are retrieved when the fish is recaptured, although a monitoring stage could be reached by coupling data logging and transponding technologies, with information transmitted when the tag is energized by an external power source, e.g. in feeding sites or around aggregating devices ('data-storage transponder' concept). The comparison between logged environmental variables and daily growth increments retrieved from otoliths (natural data loggers of growth) would allow a more precise assessment of how fish growth is influenced by environmental variations.

CONCLUSIONS

1. Fish telemetry emerges as a powerful, multipurpose and promising tool in aquaculture research and development: because it is based on individual behaviour, it represents an ideal complement to techniques such as underwater video (e.g. Bjordal *et al.*, 1988), demand-feeder monitoring (Bégout *et al.*, 1994) or PC-based echo integration (e.g. Juell, 1993) that provide information on average behaviour of fish in aquaculture environments.
2. Special attention should be dedicated to the relative innocuity of tagging procedure and duration of post-operative stress, especially if the animal is to be used as a 'probe fish' sensing the quality of its environment.
3. Telemetric systems have intrinsic limitations but their variety nearly always allows the experimenting aquaculturist to choose the appropriate technique meeting both specific and environmental requirements, the major limitation referring to maximum transmitter-weight-to-fish-weight ratio excluding fingerlings from present telemetric investigations.
4. In spatially limited aquaculture environments (short-range detection), interference with farming routines and labour costs can be minimized by using automated systems, either for data logging or for real-time monitoring of fish activity, metabolism, stress and environment (Fig. 6). Automated systems should, however, be precisely calibrated before blind use and application.

In our opinion, experimenters interested in starting telemetry projects or surveys in aquaculture should first answer positively a list of five crucial questions, inspired by Kenward (1987). (a) Is telemetry the best or only way to provide adequate answers to the questions asked? (b) Can I tag the animal? (c) Can I detect it and retrieve information in a

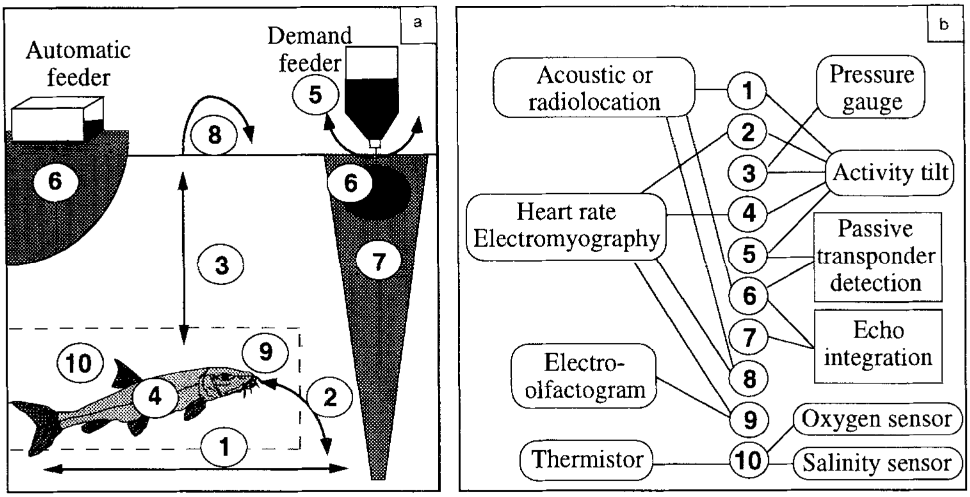

FIG. 6. Illustrated synthesis of most possible applications of telemetry in aquaculture. (a) Investigated aspects. 1, Fish position in horizontal plane; 2, activity; 3, position in water column; 4, metabolism; 5, food distribution; 6, access to feeding zones and site monitoring (shaded areas); 7, food wastage; 8, surfacing activity (leaping); 9, pollutant detection; 10, environmental variables (dashed rectangle). (b) Investigation methods and techniques (details in text). PIT-tag entry stations and PC-based echo integration (open rectangles) as alternative and complementary techniques. From Baras and Philippart (1994).

practical way? (d) Are the precision and sampling frequency compatible with the objectives of the study or survey? (e) Can I afford it? In most cases, technical developments now allow positive answers to be given to questions b, c and d. The major bottleneck remains the overall cost of the telemetry equipment. Although it is not a rule of thumb, according to the opinion of most manufacturers, the cost of equipment is globally in inverse ratio to the numbers manufactured. Such an example was provided in the 1980s by the development of affordable telemetry equipment for numerous hunters interested in tracking their dogs and may be worth considering for the future of telemetry projects in aquaculture.

ACKNOWLEDGEMENTS

The authors wish to thank numerous colleagues in the field of telemetry for fruitful discussions and information on recent technological developments and applications in fish telemetry. E. Baras received a postdoctoral FIRST grant from the Government of the Walloon Region.

REFERENCES

Anonymous (1968) Aide mémoire d'acoustique sous-marine. Détection sous-marine. Marine Nationale Française. Laboratoire de Détection sous-marine du Brusc, 183 pp.

Anthouard, M. and Wolf, V. (1988) A computerized surveillance method based on self-feeding measures in fish populations. *Aquaculture* **71**, 151–158.

Armstrong, J.D., Lucas, M.C., French, J., De Vera, L. and Priede, I.G. (1988) A combined radio and acoustic transmitter for fixing direction and range of freshwater fish (RAFIX). *Journal of Fish Biology* **33,** 879–884.

Armstrong, J.D., Lucas, M.C., Priede, I.G. and De Vera, L. (1989) An acoustic telemetry system for monitoring the heart rate of pike, *Esox lucius* L., and other fish in their natural environment. *Journal of Experimental Biology* **143,** 549–552.

Baras, E. (1991) A bibliography on underwater telemetry. *Canadian Report of Fisheries and Aquatic Sciences* No. 1819, 1–55.

Baras, E. (1992) Etude des stratégies d'occupation du temps et de l'espace chez le barbeau fluviatile, *Barbus barbus* (L.). *Cahiers d'Ethologie* **12,** 125–442.

Baras E. (1995) Seasonal activities of *Barbus barbus* (L.) – Effect of temperature on time-budgeting. *Journal of Fish Biology* **46,**13 pp (In press).

Baras, E., Thoreaux, X., Mélard, C., Grignard, J.C. and Philippart, J.C. (1995) Etude par biotélémétrie de paramètres écologiques, comportementaux et physiologiques chez les poissons d'eau douce en Conditions d'élevage. *Rapports de la station Aquacole de Tihange* (1995) **1,** 115 pp.

Baras, E. and Philippart, J.C. (1989) Application du radio-pistage à l'étude éco-éthologique du barbeau fluviatile (*Barbus barbus* L.). Problèmes, stratégies et premiers résultats. *Cahiers d'Ethologie appliquée* **9,** 467–494.

Baras, E. and Philippart, J.C. (1994) Possible improvement of aquaculture through the use of telemetry: review and perspectives. In: *Measures for Success, Proceedings of the International Conference Bordeaux Aquaculture '94* (eds P. Kestemont, J. Muir, F. Sévilla and P. Williot) Cemagref Editions: Bordeaux, France, pp. 43–48.

Bégout, M.L. and Lagardère, J.P. (1993) Acoustic telemetry: a new technology to control fish behaviour in culture conditions. In: *Production, Environment and Quality* (eds G. Barnabé and P. Kestemont), Special Publication 18, European Aquaculture Society: Ghent, Belgium. pp. 167–175.

Bégout, M.L. and Lagardère, J.P. (1994) An acoustic telemetry study of sea bream (*Sparus aurata* L.): first results on activity rhythm, effect of environmental variables and space utilization. *Hydrobiologia*, (in press).

Bégout, M.L., Vertueux, C. and Lagardère, J.P. (1994) Effets des fluctuations naturelles de l'environnement sur l'alimentation auto-régulée d'un groupe de poissons (*Dicentrarchus labrax* L.) élevé en marais maritime. In: *Measures for Success, Proceedings of the International Conference Bordeaux Aquaculture* '94 (eds P. Kestemont, J. Muir, F. Sévilla and P. Williot) Cemagref Editions: Bordeaux, France, pp. 303–307.

Berman, C.H. and Quinn, T.P. (1991) Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology* **39**, 301–312.

Bidgood, B.F. (1980) Field surgical procedure for implantation of radio tags in fish. Fisheries Research Report of the Fish and Wildlife Division of Alberta 20, 10 pp.

Boujard, T. and Leatherland, J.F. (1992) Circadian rhythms and feeding times in fishes. *Environmental Biology of Fishes* **35,** 109–131.

Boujard, T., Keith, P. and Luquet, P. (1990) Diel cycle in *Hoplosternum littorale* (Teleostei): evidence for synchronization of locomotor, air breathing and feeding activity by circadian alternation of light and dark. *Journal of Fish Biology* **36,** 133–140.

Brännäs, E. and Alanärä, A. (1993) Monitoring the feeding activity of individual fish with a demand feeding system. *Journal of Fish Biology* **42,** 209–215.

Burchard, D. (1989) Direction finding in wildlife research by Doppler effect. In: *Biotelemetry X, Proceedings of the Tenth International Symposium on Biotelemetry* (ed. C.J. Amlaner, Jr) The University of Fayetteville Press: Fayetteville, Arkansas, pp. 169–177.

Carmichael, G.J. (1991) Recovery of channel catfish from abdominal surgery. *The Progressive Fish-Culturist* **53**, 193–195.

Carrillo, M.A., Perez, J. and Zanuy, S. (1986) Efecto de la hora de injesta de la naturaleza de la dieta sobre el crecimiento de la lubina (*Dicentrarchus labrax* L.). *Investigacion Pesquera* **50**, 83–95.

Caure, P. (1991) Behaviour of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish aggregating devices (FADS) in the Comoros Islands as determined by ultrasonic tracking. *Aquatic Living Resources* **4**, 1–12.

Deat, A., Mauget, R., Maurel, D. and Sempéré, A. (1980) The automatic, continuous and fixed radio tracking system of the Chizé Forest. In: *A Handbook of Biotelemetry and Radio Tracking* (eds C. J. Amlaner, Jr and D. W. MacDonald) Pergamon Press: Oxford, pp. 439–452.

Fernö, A., Huse, I., Juell J.E. and Bjordäl, A. (1995) Vertical distribution of Atlantic salmon in net pens: trade-off between surface light avoidance and food attraction. *Aquacultural Engineering* (in press).

Filipek, S. (1989) A rapid field technique for transmitter implantation in paddlefish. In: *Biotelemetry X, Proceedings of the Tenth International Symposium on Biotelemetry* (ed. C.J. Amlaner, Jr) The University of Fayetteville Press: Fayetteville, Arkansas, pp. 388–391.

Fried, S.M., McCleave, J.D. and Stred, K.A. (1976) Buoyancy compensation by Atlantic salmon (*Salmo salar*) smolts tagged internally with dummy telemetry transmitters. *Journal of the Fisheries Research Board of Canada* **33**, 1377–1380.

Furevik, D.M., Bjordal, Å., Huse, I. and Fernö, A. (1993) Surface activity of Atlantic salmon (*Salmo salar* L.) in net pens. *Aquaculture* **110**, 119–128.

Gallepp, G.W. and Magnuson, J.J. (1972) Effects of negative buoyancy on the behavior of the bluegill, *Lepomis macrochirus* Rafinesque. *Transactions of the American Fisheries Society* **101**, 507–512.

Glass, C.W., Johnstone, A.D.F., Smith, G.W. and Mojsiewicz, W.R. (1992) the movements of saithe (*Pollachius virens* L.) in the vicinity of an underwater reef. In: *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* (eds I.G. Priede and S.M. Swift) Ellis Horwood Ltd: New York, pp. 328–341.

Greenland, D. C. and Gill, R.L. (1979) Multiple daily feedings with automatic feeders improve growth and feed conversion rates of channel catfish. *The Progressive Fish-Culturist* **41**, 151–153.

Hara, T.J. (1993) Role of olfaction in fish behaviour. In: *The Behaviour of Teleost Fishes* (2nd Edition) (ed. T.J. Pitcher) Chapman and Hall: London, etc., pp. 171–199.

Hardman, P.A. and Woodward, B. (1984) Underwater location fixing by diver-operated acoustic telemetry system. *Acustica* **55**, 34–42.

Hart, L.G. and Summerfelt, R.C. (1975) Surgical procedures for implanting ultrasonic transmitters into flathead catfish (*Pylodictis olivaris*). *Transactions of the American Fisheries Society* **104**, 56–59.

Hasler, A.D. and Henderson, H.F. (1963) Instrumentation problems in the study of homing in fish. In: *Biotelemetry* (ed. L. Slater), Pergamon Press: New York, pp. 195–202.

Hawkins, A.D. and Urquhart, G.G. (1983) Tracking fish at sea. In: *Experimental Biology at Sea* (eds A.G. McDonald and I.G. Priede) Academic Press, Inc.: London, pp. 103–166.

Hawkins, A.D., McLennan, D.N., Urquhart, G.G. and Robb, C. (1974) Tracking cod *Gadus morhua* L. in a Scottish sea loch. *Journal of Fish Biology* **6**, 225–236.

Hawkins, A.D., Urquhart, G.G. and Smith, G.W. (1980) Ultrasonic tracking of juvenile cod by means of a large spaced hydrophone array. In: *A Handbook of Biotelemetry and Radio Tracking* (eds C.J. Amlaner, Jr and D.W. MacDonald) Pergamon Press: Oxford, pp. 461–470.

Haynes, J.M. (1978) Movements and habitat studies of chinook salmon and white sturgeon. PhD thesis, University of Minnesota, Minneapolis, 166 pp.

Hempel, E. (1993) Constraints and possibilities for developing aquaculture. *Aquaculture International* **1**, 2–19.

Holand, B.A. (1987) Underwater telemetry as a tool in aquaculture: research and development. *Modeling, Identification and Control* **8**, 11–18.

Holand, B., Mohus, I. and Berntsen, R. (1974) Fish Telemetry. Foundation for Scientific Research at the Norwegian Institute of Technology, Trondheim, *SINTEF Report* STF 48, 89 pp.

Holland, K.N., Brill, R.W. and Chang, K.C. (1990) Horizontal and vertical movements of tunas (*Thunnus* spp.) associated with fish aggregating devices. *Fisheries Bulletin* (U.S.) **88**, 493–507.

Holliday, F.G.T., Tytler, P. and Young, A.H. (1974) Activity levels of trout (*Salmo trutta*) in Airthrey Loch, Stirling, and Loch Leven, Kinross. *Proceedings of the Royal Society of Edinburgh* **75B**, 315–331.

Huse, I. and Holm, J.C. (1993) Vertical distribution of Atlantic salmon (*Salmo salar*) as a function of illumination. *Journal of Fish Biology* **43** (Suppl. A), 147–156.

Huve, J.L. (1982) Un détecteur original de pollution: la truite. *La Recherche* **129**(13), 108–110.

Ichihara, T., Soma, M., Yoshida, K. and Suzuki, K. (1972) An ultrasonic device in biotelemetry and its application to tracking of a yellowtail. *Far Seas Fisheries Research Laboratory Bulletin* **7**, 27–48.

Johnsen, P.B. (1980) The use of longterm ultrasonic implants for the location and harvest for schooling fish. In: *A Handbook of Biotelemetry and Radio Tracking* (eds C. J. Amlaner, Jr and D.W. MacDonald) Pergamon Press: Oxford, pp. 777–780.

Juell, J.-E. (1993) Managing the behaviour and growth of Atlantic salmon (*Salmo salar* L.) in sea cages. PhD thesis, University of Bergen, Norway, 108 pp.

Juell, J.-E. and Westerberg, H. (1993) An ultrasonic telemetric system for automatic positioning of individual fish used to track Atlantic salmon (*Salmo salar* L.) in a sea cage. *Aquacultural Engineering* **12**, 1–18.

Kadri, S., Metcalfe, N.B., Huntingford, F.A. and Thorpe, J.E. (1991) Daily feeding rhythms in Atlantic salmon in sea cages. *Aquaculture* **92**, 219–224.

Kalpers, J., Palata, K., Clotuche, E., Baras, E., Libois, R.M., Philippart, J.C. and Ruwet, J.C. (1989) Application of radio tracking to the survey of wild populations of vertebrate species (mammals, birds, fishes) in Belgium. In: *Biotelemetry X, Proceedings of the Tenth International Symposium on Biotelemetry* (ed. C.J. Amlaner, Jr) The University of Fayetteville Press: Fayetteville, Ankansas, pp. 23–35.

Kaseloo, P.A., Weatherley, A.H., Lotimer, J. and Farina, M.D. (1992) A biotelemetry system recording fish activity. *Journal of Fish Biology* **40**, 165–179.

Keen, J.E. and Farrell, A.P. (1994) Maximum prolonged swimming speed and maximum cardiac performance of rainbow trout, *Oncorhynchus mykiss*, acclimated to two different water temperatures. *Comparative Biochemistry and Physiology* **108A**, 287–295.

Kenward, R. (1987) *Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis.* Academic Press: London. 222 pp.

Konagaya, T. (1982) A new telemetric method of determining the position of swimming fish. *Bulletin of the Japanese Society of Scientific Fisheries* **48**, 1545–1550.

Konagaya, T. and Cai, Q. (1989) Telemetric determination of the swimming activities of silver and bighead carp. In: *East Lake: a Phytoplanktivorous Fishes Dominated Lake Ecosystem* (ed. T. Miura) Otsu Biological Station Press: Kyoto, Japan, pp. 1–61.

Kudo, Y. and Ueda, K. (1976) Underwater radiotelemetry of electrical activities of olfactory bulb in free swimming carp (*Cyprinus carpio* L.). *Annual Meeting of the Japanese Society of Scientific Fisheries Research* 1976, 101. (in Japanese).

Lagardère, J.P., Ducamp, J.J., Frikha, L. and Spérandio, M. (1988) Ultrasonic tracking of common sole (*Solea vulgaris* Quensel, 1806) in a saltmarsh: methods and fish response to some environmental factors. *Journal of Applied Ichthyology* **4**, 87–96.

Lagardère, J.P., Ducamp, J.J., Favre, L., Mosneron Dupin, J. and Spérandio, M. (1990) A method for the quantitative evaluation of fish movements in salt ponds by acoustic telemetry. *Journal of Experimental Marine Biology and Ecology* **141**, 221–236.

Lagardère, J.P., Bégout, M.L., Lafaye, J.Y. and Villotte, J.P. (1994) Influence of wind-produced noise on orientation in the flatfish *Solea solea* L. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 1258–1264.

Lemnell, P.A. (1980) An automatic telemetry system for tracking and physiology. In: *A Handbook of Biotelemetry and Radio Tracking* (eds C.J. Amlaner, Jr. and D.W. MacDonald) Pergamon Press: Oxford, pp. 453–456.

Lewis, A.E. and Muntz, W.R.A. (1984) The effects of external ultrasonic tagging on the swimming performance of rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology* **25**, 577–585.

Losordo, T.M., Piedrahita, R.H. and Ebeling, J.M. (1988) An automated water quality data acquisition system for use in aquaculture ponds. *Aquacultural Engineering* **7**, 265–278.

Lotek Engineering Inc. (1992) Event Log Version 3.1x W18 user's manual. Lotek Engineer Report, 12 pp. (Address: 115 Pony Drive, Newmarket, Ontario, Canada L3Y 7B5.)

Lucas, M.C. (1989) Effects of implanted dummy transmitters on mortality, growth and tissue reaction in rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology* **35**, 577–587.

Lucas, M.C. and Armstrong, J.D. (1991) Estimation of meal energy intake from heart rate records of pike, *Esox lucius* L. *Journal of Fish Biology* **38**, 317–319.

Lucas, M.C., Priede, I.G., Armstrong, J.D., Gindy, A.N.Z. and De Vera, L. (1991) Direct measurements of metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of heart rate telemetry. *Journal of Fish Biology* **39**, 325–345.

Lucas, M.C., Johnstone, A.D.F. and Priede, I.G. (1993) Use of physiological telemetry as a method for estimating metabolism of fish in the natural environment. *Transactions of the American Fisheries Society* **122**, 822–833.

Luke, D.McG., Pincock, D.G. and Stasko, A.B. (1973) Pressure-sensing ultrasonic transmitter for tracking aquatic animals. *Journal of the Fisheries Research Board of Canada* **30**, 1402–1404.

MacLennan, D.N. and Simmonds, E.J. (1992) *Fisheries Acoustics*. Chapman and Hall: London. 325 pp.

Marty, G.D. and Summerfelt, R.C. (1986) Pathways and mechanisms for expulsion of surgically implanted dummy transmitters from channel catfish. *Transactions of the American Fisheries Society* **115**, 577–589.

Medwin, H. (1975) Speed of sound in water: a simple equation for realistic parameters. *Journal of the Acoustic Society of America* **32**, 556–559.

Mesing, C.L. and Wicker, A.M. (1986) Home range, spawning migration and homing of radio-tagged Florida largemouth bass in two central Florida lakes. *Transactions of the American Fisheries Society* **115**, 286–295.

Metcalfe, J.D., Fulcher, M.F. and Storeton-West, T.J. (1992) Progress and developments in telemetry for monitoring the migratory behaviour of plaice in the North Sea. In: *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* (eds I.G. Priede and S.M. Swift) Ellis Horwood Ltd: New York, pp. 359–366.

Midling, K. and Øeiestad, V. (1993) Fjordranching with conditioned cod. In: *Abstracts of the International Symposium on Sea Ranching of Cod and Other Marine Species* (eds D.S. Danielssen and E. Moskness): Arendal, Norway. 47 pp.

Mohus, I. and Holand, B. (1983) Fish telemetry manual. Foundation for Scientific Research at the Norwegian Institute of Technology, Trondheim, *SINTEFF Report* STF 48, 97 pp.

Moore, A., Russel, I. C. and Potter, E.C.E. (1990) Preliminary results from the use of a new technique for tracking the estuarine movements of Atlantic salmon, *Salmo salar* L., smolts. *Aquaculture and Fisheries Management* **21**, 369–371.

Mosneron Dupin, J. and Lagardère, J.P. (1990) Réactions comportementales du bar *Dicentrarchus labrax* (Linné, 1758) aux basses températures. Premières données recueillies en marais maritime par télémétrie acoustique. *Comptes-Rendus de l'Académie des Sciences de Paris – Biologie Marine –* **310** (série III), 279–284.

Mulford, C.J. (1984) Use of a surgical skin stappler to quickly close incisions in striped bass. *North American Journal of Fisheries Management* **4**, 571–573.

Nams, V.O. (1989) A technique to determine the behavior of a radio-tagged animal. *Canadian Journal of Zoology* **67**, 254–258.

Nemetz, T.G. and MacMillan, J.R. (1988) Wound healing of incisions closed with a cyanoacrylate adhesive. *Transactions of the American Fisheries Society* **117**, 190–195.

Noeske, T.A. and Spieler, R.E. (1984) Circadian feeding times affect growth of fish. *Transactions of the American Fisheries Society* **113**, 540–544.

Nomura, S. and Ibaraki, T. (1969) Electrocardiogram of the rainbow trout and its radiotransmission. *Japanese Journal of Veterinary Sciences* **31**, 135–147.

Oswald, R.L. (1978) The use of telemetry to study light synchronisation with feeding and gill ventilation rates in *Salmo trutta. Journal of Fish Biology* **13**, 729–739.

Pedersen, B.H. and Andersen, N.G. (1985) A surgical method for implanting transmitters with sensors into the body cavity of the cod (*Gadus morhua* L.). *Dana* **5**, 55–62.

Poncin, P. and Ruwet, J.C. (1994) Applications to freshwater aquaculture of the methods used to measure the behaviour of fish: a brief review. In: *Measures for Success, Proceedings of the International Conference Bordeaux Aquaculture '94* (eds P. Kestemont, J. Muir, F. Sévilla and P. Williot) Cemagref Editions: Bordeaux, France, pp. 271–275.

Potter, E.C.E. (1988) Movements of salmon in an estuary in South-West England. *Journal of Fish Biology* **33** (supplement. A), 153–159.

Poxton, M.G. (1991) Water quality fluctuations and monitoring in intensive fish culture. In: *Aquaculture and the Environment* (eds N. De Pauw and J. Joyce), Special Publication 16, European Aquaculture Society: Gent, Belgium, pp. 121–143.

Prentice, E.F., Flagg, T.A., McCutcheon, C.S., Brastow, D.F. and Cross, D.C. (1990) Equipment, methods and an automated data-entry station for PIT-tagging. In: *Fish Marking Techniques (American Fisheries Society Symposium 7)* (eds N.C. Parker, A.E. Giorgi, R.C. Heidinger, D.B. Jester, Jr, E.D. Prince and G.A. Winans), American Fisheries Society: Bethesda, MD, pp. 335–340.

Priede, I.G. (1982) An ultrasonic salinity telemetry transmitter for use on fish in estuaries. *Biotelemetry Patient Monitoring* **9**, 1–9.

Priede, I.G. (1983) Heart rate telemetry from fish in the natural environment. *Comparative Biochemistry and Physiology* **76A**, 515–524.

Priede, I.G. and Swift, S.M. (eds) (1992) *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*. Ellis Horwood Ltd: New York. 708 pp.

Priede, I.G. and Tytler, P. (1977) Heart rate as a measure of metabolic rate in teleost fishes; *Salmo gairdneri, Salmo trutta* and *Gadus morhua*. *Journal of Fish Biology* **10**, 231–242.

Priede, I.G. and Young, A.H. (1977) The ultrasonic telemetry of cardiac rhythms of wild brown trout (*Salmo trutta* L.) as an indicator of bioenergetics and behaviour. *Journal of Fish Biology* **10**, 299–318.

Priede, I.G., Solbe, J.F. de L.G. and Nott, J.E. (1988) An acoustic oxygen telemetry transmitter for the study of exposure of fish to variations in environmental dissolved oxygen. *Journal of Experimental Biology* **140**, 563–567.

Prince, E.D. and Maughan, O.E. (1978) Ultrasonic telemetry technique for monitoring bluegill movement. *The Progressive Fish-Culturist* **40**, 90–93.

Rabben, H. and Furevik, D.M. (1993) Application of heart rate transmitters in behaviour studies on Atlantic halibut (*Hippoglossus hippoglossus*). *Aquacultural Engineering* **12**, 129–140.

Rindorf, H.J. (1981) Acoustic emission source location in theory and in practice. *Brüel/kjaer Technical Review* **2**, 1–38.

Robinson, B.J. (1986) Data storage tags. In: *Animal Telemetry in the Next Decade*. Proceedings of a meeting held in Lowestoft, UK, pp. 57–59.

Rogers, S.C. and 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. *Journal of Fish Biology* **23**, 535–547.

Rogers, S.C., Church, D.W., Weatherley, A.H. and Pincock, D.G. (1984) An automated ultrasonic telemetry system for the assessment of locomotor activity in free-ranging rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology* **25**, 697-710.

Ross, L.G., Watts, W. and Young, A.H. (1981) An ultrasonic biotelemetry system for the continuous monitoring of tail-beat rate from free-swimming fish. *Journal of Fish Biology* **18**, 479–490.

Ross, M.J. and McCormick, J.H. (1981) Effects of external radio transmitters on fish. *The Progressive Fish-Culturist* **43**, 67–72.

Scherer, E. (1992) Behavioural responses as indicators of environmental alterations: approach, results, developments. *Journal of Applied Ichthyology* **8**, 122–131.

Schramm, H.L., Jr and Black, D.J. (1984) Anaesthesia and surgical procedures for implanting radio transmitters into grass carp. *The Progressive Fish-Culturist* **46**, 185–190.

Seymour, E.A. and Bergheim, A. (1991) Towards a reduction of pollution from intensive aquaculture with reference to the farming of salmonids in Norway. *Aquacultural Engineering* **10**, 73–88.

Shields, L.J. (1980) The determination of free ranging rodent activity by telemetry. In: *A Handbook of Biotelemetry and Radio Tracking* (eds C.J. Amlaner, Jr and D.W. MacDonald) Pergamon Press: Oxford, pp. 667–672.

Solomon, D.J. and Potter, E.C.E. (1988) First results with a new estuary fish-tracking system. *Journal of Fish Biology* **33** (Suppl. A), 127–132.

Solomon, D.J. and Storeton-West, T.J. (1983) Radio tracking of migratory salmonids in rivers: development of an effective system. MAFF (Ministry of Agriculture, Fisheries and Food) *Fisheries Technical Report* (Lowestoft) 75, 11 pp.

Stasko, A.B. and Horrall, R.M. (1976) Method of counting tailbeats of free swimming fish by ultrasonic telemetry techniques. *Journal of the Fisheries Research Board of Canada* **33**, 2596–2598.

Stasko, A.B. and Pincock, D.G. (1977) Review of underwater biotelemetry, with emphasis on ultrasonic techniques. *Journal of the Fisheries Research Board of Canada* **34**, 1261–1285.

Summerfelt, R.C. and Smith, L.S. (1990) Anaesthesia, surgery, and related techniques. In: *Methods for Fish Biology* (eds C.B. Schreck and P.B. Moyle) American Fisheries Society: Bethesda, MD, pp. 213–272.

Sureau, D. and Lagardère, J.P. (1991) Coupling of heart rate and locomotor activity in sole, *Solea solea* (L.) and bass, *Dicentrarchus labrax* (L.), in their natural environment by using ultrasonic telemetry. *Journal of Fish Biology* **38**, 399–405.

Sutterlin, A.M. and Stevens, E.D. (1992) Thermal behavior of rainbow trout and Artic Char in cages moored in stratified water. *Aquaculture* **102**, 65–75

Tang, M. and Boisclair, D. (1993) Influence of the size of enclosures on the swimming characteristics of juvenile brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1786–1793.

Thoreau, X. and Baras, E. (1995) Anaesthesia and Surgery procedures for implanting telemetry transmitters into the body cavity of tilapia *Oreochromis aureus*. In: *Abstracts of the first Conference and Workshop on Fish Telemetry in Europe* (eds E. Baras and J.C. Philippart), University of Liège, Belgium, 32 pp.

Thorpe, J.E., Ross, L.G., Struthers, G. and Watts, W. (1981) Tracking Atlantic salmon (*Salmo salar* L.) smolts through Loch Voil, Scotland. *Journal of Fish Biology* **19**, 519–537.

Tobias, A. (1976) Acoustic-emission source location in two dimensions by an array of three sensors. *Non-Destroying Testing* (Guildford, England) **9**, 9–12.

Urquhart, G.G. and Smith, G.W. (1992) Recent developments of a fixed hydrophone array system for monitoring movements of an aquatic animal. In: *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* (eds I.G. Priede and S.M. Swift) Ellis Horwood Ltd: New York, pp. 342–353.

Vallière, A., Pelletier, S., Patenaude, R. and Dulude, P. (1986) Protocole d'implantation de radio-émetteurs dans la cavité abdominale de saumons atlantiques. MLCP, SAEF, Région de Québec, November 1986. 18 pp.

Velle, J.I., Lindsay, J.E., Weeks, R.W. and Long, F.M. (1979) An investigation of the loss mechanisms encountered in propagation from a submerged fish transmitter. In: *Proceedings of the Second International Conference on Wildlife Biotelemetry* (ed. F.M. Long) University of Laramie Press: Laramie, Wyoming, pp. 228–237.

Wardle, C.S. and Kanwisher, J.W. (1974) The significance of heart rate in free swimming cod, *Gadus morhua*, some observations with ultrasonic tags. *Marine Behaviour and Physiology* **2**, 311–324.

Weatherley, A.H., Rogers, S.C., Pincock, D.G. and Patch, J.R. (1982) Oxygen consumption of active rainbow trout, *Salmo gairdneri* Richardson, derived from electromyograms obtained by radiotelemetry. *Journal of Fish Biology* **20**, 479–489.

Williams, T.H. (1990) Evaluation of pressure-sensitive radio transmitters used for monitoring depth selection by trout in lotic systems. In: *Fish-Marking Techniques (American Fisheries Society Symposium 7)* (eds N.C. Parker, A.E. Giorgi, R.C. Heidinger, D.B. Jester, Jr, E.D. Prince and G.A. Winans) American Fisheries Society: Bethesda, MD, pp. 390–394.

Winter, J.D. (1983) Underwater biotelemetry. In: *Fisheries Techniques* (eds L.A. Nielsen and D.L. Johnsen) American Fisheries Society: Bethesda, MD, pp. 371–395.

Zimmermann, F. (1980) Effet de la fixation d'émetteurs chez le poisson. Utilisation de la méthode de tracking en éco-éthologie. *Cybium* (Ser. 3) **10**, 21–23.