Methods for studying spatial behaviour of freshwater fishes in the natural environment

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Abstract

Spatial behaviour of fishes in fresh and brackish water ranges in temporal scales between localized diel movements, often associated with foraging and predator evasion, to seasonal or life-cycle related events involving movements between freshwater habitats or freshwater and marine biotopes. Recent technological advances have resulted in dramatic improvements in the range of techniques available for the study of spatial behaviour of freshwater fishes in the natural environment, and broadly may be divided into two categories: capture dependent and capture independent. The former incorporates those methods that rely on sampling marked fish (mark–recapture) or unmarked fish (density estimates, catch per unit effort) over defined scales of time and space in order to derive information on distribution and movement. Captured fish may also be tagged with transmitters that radiate energy, enabling the fish to be tracked and/or environmental data to be gathered. Biochemical analysis of samples from fish, requiring non-destructive sampling (genetic analysis and scale microchemistry) or destructive sampling (otolith microchemistry) may also provide information on migration and ontogenetic processes. Capture independent techniques include visual observation and video techniques, hydroacoustics and automated fish counting. Catch per unit effort and mark–recapture techniques are most efficient where long-term fishery or monitoring studies are in place and data on crude spatial and temporal scales are acceptable. They also have the advantages of low technical requirements and low equipment costs. Where specific management or ecological questions are pertinent, recapture independent techniques may be more appropriate. Telemetric methods can provide high resolution information at the individual level, while hydroacoustics is increasingly providing information at the population level in large lake and river environments. Biochemical methods are becoming increasingly useful in determining the extent of population segregation, where DNA analysis is used, and in the study of migration and ontogenetic changes in behaviour, where otolith microchemistry and stable isotope analysis is used.

Keywords freshwater fish behaviour, hydroacoustics, migration, otolith microchemistry, tagging, telemetry.

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Received 4 Sep 2000
Accepted 13 Oct 2000

Introduction

Measurement of the use of space through time by fishes is crucial to understanding population and community processes as well as assisting management and conservation of fish stocks. Spatial behaviour of fishes in fresh and brackish water ranges in temporal scales between localized diel movements, often associated with foraging and predator evasion, to seasonal or life-cycle related events involving movements between freshwater habitats or freshwater and marine biotopes. Tagging of fish has been carried out at least as long ago as the 17th century when, in *The Compleat Angler* (first published in 1653), Izaak Walton reported the attachment of ribbon tags to the tails of juvenile Atlantic salmon (*Salmo salar*, Salmonidae) to determine their movements (Walton and Cotton 1921). The technological advances of the past few decades have resulted in dramatic improvements in the range of techniques available for the study of spatial behaviour of fishes. There is a broad range of methods which have been used to examine the distribution and movements of fish in fresh water and in brackish environments (Fig. 1). Some others have been used exclusively in marine environments, but their application to freshwater environments can be foreseen in the very near future in view of recent technical developments (e.g. archival tags; Sturlaugsson 1995; Block *et al*. 1998).

All techniques do not perform equally well for addressing a particular question, nor is any one method applicable to all studies of fish spatial behaviour, as there are species- or environment-specific limitations for all of them. Time scale also is a central problem in studies of fish spatial behaviour, as some methods are particularly suitable for short-term studies, whereas others are more appropriate for long-term studies. In this context, there is always a trade-off between the accuracy of the information gathered, the duration of the study, the numbers of fish from which relevant information can be retrieved, the degree of disturbance of the method, and the availability of resources for the study.

This paper gives an overview of the techniques available for studying spatial behaviour of freshwater fish in the natural environment, focusing on

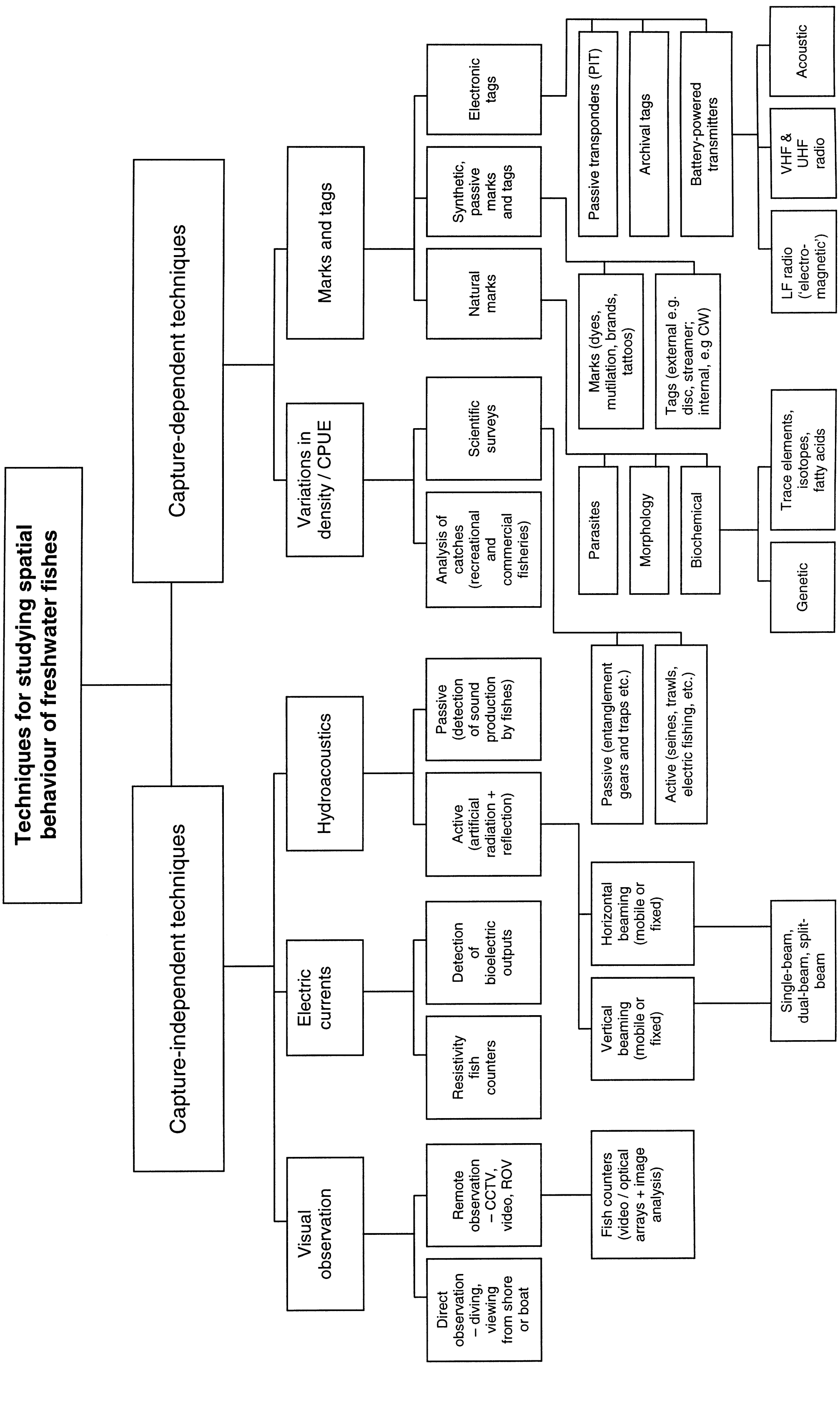

Figure 1 Classification of techniques that may be used for studies of spatial behaviour of fish in fresh and brackish water environments.

state-of-the-art techniques, which offer the most promising perspectives for comprehensive and quantitative approaches (hydroacoustics, telemetry and microchemistry). It was not our intention to exhaustively review and present all literature pertinent to each method, several of which are so widely utilized that individual reviews could be written on them. Instead, we sought to provide a comparative but detailed review of all those methods that may be useful for studying migration and behaviour in fresh water and in brackish environments (many of which are also relevant to marine studies), something that we believe has not been attempted for the full array of options that are currently available to the fish biologist.

Although classification of methods and techniques is always a questionable task, methods useful for study of spatial behaviour of fishes may be broadly divided into two categories: capture dependent and capture independent. The former incorporates those methods that rely on sampling marked fish (mark–recapture) or unmarked fish (variations in density or catch per unit effort) over defined scales of time and space in order to derive information on distribution and movement. Captured fish may also be tagged with electronic tags which usually radiate energy, enabling the fish to be tracked and/or environmental data to be gathered. Biochemical analysis of samples from fish, requiring non-destructive sampling (genetic analysis and stable isotope/trace element analysis of non-vital tissue) or destructive sampling (otolith microchemistry) may also provide information on migration and ontogenetic processes. Techniques that do not rely on fish capture include visual observation and closed circuit television, resistivity fish counters and hydroacoustics.

Capture independent methods

Visual observation

Helfman (1983) argued that direct observation is a valuable and frequently neglected tool in fisheries research. The most obvious form of direct observation is that employing naturally radiated energy within our visual spectrum. Basic methods of visual observation involve snorkelling, SCUBA diving and observations from the shore or boats, as well as the deployment of remote stills- or video-camera systems (Helfman 1983; Wardle and Hall 1994; Dolloff *et al*. 1996). The major advantage of observational methods is that as long as disturbance is minimized, fish behaviour will be as near normal as possible because fish are not manipulated in any way. Direct visual observation (diving, boat- and bank-based viewing) has provided information on fish abundance, distribution, habitat preferences and behaviour in a variety of freshwater habitats (Keenleyside 1962; Helfman 1981, 1983; Heggenes *et al*. 1993; Dolloff *et al*. 1996). However, observations are dependent on proximity to the fish, time of day (or availability of natural light), water depth, clarity and flow conditions, and small or benthic fishes are often difficult to see. Site specific information or evidence can be recorded on hand-held underwater stills- or video-cameras, although most underwater recording is usually carried out on plexiglass plates or on a cylindrical 'diving cuff' fixed around the forearm (Dolloff *et al*. 1996). It is usually not possible to identify individual fish unless they are tagged with numbered or coloured external tags (Heard and Vogele 1968; Helfman 1981) and this requires fish capture, or tagging *in situ*. In shallow water, individual colour codes may be more easily distinguished than alphanumeric coding, but from a practical viewpoint the number of colour codes that can be distinguished is extremely limited. Fluorescent isotope tags have been used to identify and observe night-time behaviour of fish in clear, shallow streams (Clough *et al.* 2000). These factors tend to make direct observations of fish movement limited to localized site monitoring (e.g. migration to shallow spawning grounds, Baras 1994; diel migration studies, Helfman 1981, 1983). These methods are of very limited value in some tropical rivers where turbidity may be high all year round (e.g. Fernandes and de Mérona 1988), although visual observation has been used successfully in the Amazon on several species (Goulding 1980).

Closed circuit television, combined with video recording, provides an effective method of surveying fish and their behaviour under relatively clear-water conditions (Collins *et al*. 1991; Wardle and Hall 1994). Modern charge-coupled device (CCD) monochrome cameras are sensitive at low light levels and have been miniaturized to a high degree. Most applications of this approach have been and continue to be located at specific sites past which fish are migrating, such as at fish passes, where detailed behavioural information can be obtained (Haro and Kynard 1997). These methods have been accompanied by the development of image analysis techniques for automatically sensing, counting and sizing fishes using video or light emitting diode (LED) arrays (Irvine *et al.* 1991; Fewings 1994; Larinier 1998). Recent attempts to develop accurate computer driven real-time image capture and analysis counter systems have been successful for adult migratory salmonids and in some multispecies environments (Larinier 1998), but have been of limited success for smaller fish, where fish are in shoals or where a variety of morphologically similar species occur (Fewings 1994; Larinier 1998). Under very low light conditions, infra-red light sources, to which most freshwater fishes are insensitive, may be used in conjunction with infra-red sensitive cameras (including many monochrome CCD cameras) to monitor fish behaviour. Video cameras attached to remotely operated vehicles (ROVs) have proved useful for examining fish behaviour in deep lakes (Dolloff *et al.* 1996; Davis *et al.* 1997), although their high cost of operation has restricted their use. Three dimensional stereographic and video tracking techniques (Boisclair 1992; Hughes and Kelly 1996) have proved useful in bioenergetic studies to examine local foraging behaviour and activity levels of fishes (e.g. Trudel and Boisclair 1996) and have been used to assess energy expenditure of upstream migrating sockeye salmon (*Oncorhynchus nerka*, Salmonidae) through measurement of tailbeat frequency under varying local water velocity conditions (Hinch and Rand, in press).

Resistivity fish counters and detection of bioelectric outputs

If an electric potential is set up between two electrodes in freshwater, a small current is passed, but this will be influenced by the presence of a fish (or other large, dense organism) which has a lower electrical resistance than the water it displaces, in the close vicinity of the electrodes. Resistivity fish counters, which detect characteristic changes in resistance in the overlying water column as a fish crosses one or more pairs of electrodes, can measure fish passage past specific points and have been used extensively in the monitoring of adult salmonid migrations through rivers and fish passes (Lethlean 1953; Bussell 1978; Dunkley and Shearer 1982; Reddin *et al.* 1992; Fewings 1994; Aprahamian *et al.* 1996; Smith *et al.* 1996). In open river channel environments, conventional resistivity fish counters are flatbed structures, usually placed on sloping structures such as weirs, the velocity profile of which encourages fish swimming upstream to pass close to the weir face on which the counter's electrodes are positioned. Some success has been obtained with portable resistivity counters deployed on the stream bed (Smith *et al.* 1996) but sites have to be chosen carefully to maximize uninterrupted passage close to the electrodes. Resistivity fish counters are frequently coupled to continuous time-lapse or automatically triggered video camera systems (switching from time-lapse to real-time mode) for fish record validation, sizing and identification purposes (Fewings 1994; Aprahamian *et al.* 1996). Resistivity counters tend to be much less efficient at recording downstream movement of fishes due to their wide variation in swimming depths and inconsistent path of travel over the counter electrodes (Dunkley and Shearer 1982; Smith *et al.* 1996).

Resistivity counter sites are normally inaccessible to most non-salmonid fish due to their lower swimming performance. This problem can be partly overcome by using resistivity counters of tubular construction, through which the fish swims (Lethlean 1953), but this limits their use to sites where a culvert or fish pass is present (Bussell 1978). Moreover, reducing the speed of upstream travel of fish past the electrodes encourages lingering or non-steady traversal of the electrodes, complicating reliable counting. Most resistivity counters exhibit poor efficiency in detecting small fish (less than about 25 cm, but the critical size depends on fish morphology) and poor resolution of fish migrating together in shoals (Aprahamian *et al.* 1996). Variations in water depth and conductivity also complicate signal interpretation, although automatic calibration in response to environmental variables is now common. Resistivity counters become unusable in brackish or tidal conditions where the resistance signature of a passing fish becomes difficult to detect against the lower electrical resistance of saline water. The suitability of using resistivity counters for studying fish movement is thus clearly dependent on fish size, behaviour and environmental conditions.

Several large taxa of freshwater fishes, principally the mormyroid (suborder Mormyroidea) and gymnotiform (order Gymnotiformes) electric fishes, produce distinct electric organ discharges (EODs) that can easily be recorded. These are often species and sex specific (Heiligenberg 1991), and in some cases, following detailed signal analysis, are individually recognizable (Friedman and Hopkins 1996). In a novel study, the latter authors showed that small EOD differences between individuals of two species of *Brienomyrus* (Mormyridae) could be used to track their day-to-day movements in their natural stream habitat in West Africa, with fish normally returning to the same daytime hiding place on successive days. Due to the limited range of signal detection (*c.* 1 m), it is unlikely that such a technique would enable tracking of electric fishes over long distances and time periods, although Friedman and Hopkins (1996) did manage to track movements of *Brienomyrus* in excess of 100 m over several days using this technique.

Hydroacoustics

Sonar (the acronym of SOund NAvigation and Ranging) is a general term for any device, including echosounders and acoustic telemetry systems, that uses propagated acoustic energy to enable the remote detection and positioning of objects underwater. Active sonar produces sound while passive sonar systems detect naturally occurring sound. A variety of teleost fishes produce sounds that are often distinct between species and sexes, and which can be located with a sensitive directional hydrophone (Hawkins 1993). Most of the better-known examples of sound production by fishes have been reported from marine environments and although there is evidence that, in a few cases, individual fishes can recognize conspecifics of the same sex from their vocalizations (Hawkins 1993), this method does not yet appear to have been used to identify and locate individual fishes in the natural environment. The sonar methods that are most useful for examining distribution and behaviour of fishes therefore use active sonar.

Since their advent, echosounders have traditionally been used to direct acoustic beams vertically downwards but may also be used to transmit sound beams near horizontally across shallow waters, such as found in many freshwater environments. Acoustic energy is transmitted in pulses at a particular frequency (usually between 100 and 400 kHz) by means of a transducer producing a directional sound beam. Almost all echosounding transducers are composed of a series of elements which, through interference between the signals of the elements, usually result in the overall beam pattern incorporating a narrow, sensitive cone on the acoustic axis (the main lobe), surrounded by several smaller side lobes, separated by signal null points. On encountering a fish target, in particular the gas bladder, the sound pulse is reflected in all directions and some is 'back-scattered' towards the transducer. The transducer detects the back-scattered sound (namely, the echo) and converts it to a quantified electrical signal. Where fishes are relatively well-spaced in the water column, echoes may be grouped as individual fish by software algorithms and the number of individual fish counted. An alternative approach, particularly suitable where fish occur as shoals or cannot easily be identified as single targets, is the use of echo integration, whereby the total reflected energy received by the transducer is measured and reallocated into individual fish targets (MacLennan and Simmonds 1992). The echosounding approach for measuring fish distribution and abundance is commonly referred to as 'hydroacoustics' and is dealt with in detail in several texts (MacLennan and Simmonds 1992; Brandt 1996). Hydroacoustic techniques do not strictly exclude other telemetric techniques which employ detection of acoustic transmitters attached to fish. Nevertheless, due to widespread use in the literature, 'hydroacoustics' is used here to refer to the reception of reflected artificial acoustic radiation and 'acoustic tracking/telemetry' is reserved for the detection of artificially generated sound from a tag or transponder.

Hydroacoustics is a well-established tool for fish studies in the marine environment, where it has been widely used to assess fish stocks and examine fish spatial heterogeneity (MacLennan and Simmonds 1992). Increasingly, it has been utilized for similar purposes in freshwater (Brandt 1996). It has the advantage over many other techniques in not being intrusive, except for possible interference between the observing boat, where used, and the fish. Noisy environments and entrained air prohibit clear signal analysis and so, in freshwater, hydroacoustic techniques are generally restricted to lakes and non-turbulent areas of rivers. A key feature of echosounding is measurement of target strength, so that information on fish size and number can be obtained. Echosounders, particularly more advanced designs, permit the direct measurement of individual target strengths over considerable distances (tens to hundreds of metres) and in fine detail.

Single-beam echosounders indicate the distance of a target from the transducer, but provide no information on the direction of movement or orientation of a fish. When using single-beam vertical transmission of sound, targets are in the same approximate orientation (dorsal view) and sizing may be quite accurate, with correction applied for distance from the transducer. However, when single-beams are used in horizontal orientation, reliable sizing is much more problematic due to the range of orientations (side-on, head-on and tail-on, and variations in between), which dramatically influences the strength of the returned echo, with no immediate way of determining that orientation. Dual-beam echosounders, which utilize concentric rings of transducers that are alternately activated and interrogated separately, can determine the distance of a target from the transducer and the distance off the axis of the sound beam, enabling correction for both distance and orientation, resulting in improved sizing and fish discrimination characteristics. Split-beam echosounders divide signal analysis of reflected sound to four quadrants of the transducer that are then compared through algorithms which examine the relative magnitude and timing of signals. Briefly, single targets can be discriminated from multiple targets by analysing the signal phase coherence, with each phase change corresponding to an additional target. Individual targets can be identified in true 3-D space within the sound beam, enabling accurate measurement of echo target strength and 3-D tracking through a limited volume of the water column insonified by the sound beam.

All types of echosounders rely on technical calibration of the relationship between echo strength for an object with known reflectance characteristics, usually a tungsten carbide calibration sphere, in accordance with international practice (Foote *et al.* 1987; MacLennan and Simmonds 1992). Beyond this, in order to determine the sizes of those fish being ‘observed’ acoustically, there is also a need to calibrate relationships between measured target strength for fishes (ideally live fish) of known size, species and orientation. Echosounding does, however, have to be combined with live capture techniques to obtain information on species composition over the survey range. Where the fish community is dominated by one or two species this is less problematic, as for hydroacoustic studies in Loch Ness, Scotland, where over 95% of pelagic fish are Arctic charr (*Salvelinus alpinus*, Salmonidae) (George and Winfield 2000) or in many rivers dominated by anadromous salmonids where most fish larger than about 30 cm are returning adults of one or a few species (e.g. Ransom *et al.* 1998).

Vertical beaming hydroacoustics

Until the early 1990s, freshwater hydroacoustics mostly employed vertical beaming in relatively deep (> 5 m), open water to determine abundance and distribution of pelagic fishes (Thorne 1979; Brandt 1996). Increasingly, in deep freshwater, hydroacoustics is being employed to answer questions concerning the factors influencing fish distribution and behaviour. A variety of studies have used hydroacoustics to examine vertical migrations of pelagic fishes in deep lake environments, often in response to light variations and zooplankton distribution (Bohl 1980; Janssen and Brandt 1980; Luecke and Wurtsbaugh 1993; Brandt 1996). George and Winfield (2000) used vertical beam echosounding to examine horizontal and vertical distribution of fish, mostly Arctic charr, in relation to zooplankton and phytoplankton abundance in Loch Ness, Scotland, and demonstrated aggregation of fish in the southern part of the loch in the top 30 m of water, associated with high overall levels of zooplankton. At a finer spatial scale within this large zooplankton patch, hydroacoustics, combined with zooplankton sampling, showed a clear negative correlation between abundance of small fish (1–5 cm) and of *Eudiaptomus* (Copepoda), interpreted as the result of local depletion of these zooplankters by Arctic charr. With the advent of more sophisticated echosounders, capable of resolving near-bottom echoes, it is also possible to survey profundal fish species, using beams that are vertical or offset from vertical, although the ease of use of such techniques is complicated by uneven lake bed characteristics or vegetation.

Hydroacoustics using downward-orientated sound beams is inappropriate for many relatively shallow freshwater environments due to the small sampling volume and boat-avoidance behaviour by the fish. Use of horizontal beaming in freshwater with conventional transducers of older design is difficult due to the confounding effects of reverberations from surface and bottom boundaries, particularly from acoustic side lobes, resulting in low usable range (Kubecka 1996). Following the commercial production of narrow-beamed transducers with negligible beam side-lobes, it has become possible to use echosounders horizontally in shallow waters with depths between 1.5 m and 5 m (Mesiar *et al.* 1990; Kubecka *et al.* 1992; Thorne and Johnson 1993; Kubecka 1996). The development of echosounder transducers producing elliptical beams in cross section has also been an im-portant development for the use of hydroacoustics in horizontal-beaming mode in shallow water, with the narrow axis of the ellipse orientated in the vertical plane, helping to maximize usable range, and the broad axis of the ellipse orientated horizontally, giving a wider range over which to detect and, for split-beam systems, to track the fish's progress (Ransom *et al*. 1998). Horizontally deployed echosounders can be used in two sampling modes:

(i) by fixed location where the transducer is fixed at one location from which the sound beam is directed across a river or lake, and

(ii) by mobile surveying where the transducer is attached to a rigid frame in front of a boat and the sound beam is directed across the river or lake whilst the boat is underway, usually close to the shore.

The majority of fish behaviour studies using echo monitoring devices in shallow freshwater have been confined to the former sampling mode, but recent studies have shown the potential of the latter mode.

Fixed location horizontal beaming hydroacoustics

Since the 1960s, fixed location hydroacoustic techniques have been used to count non-intrusively upstream migrations of anadromous salmonids (mostly *Oncorhynchus* spp., Salmonidae) returning up the very large clear-water rivers on the west coast of North America and facing obstacles such as hydroelectric dams (Ransom *et al*. 1998; Thorne 1998). These systems are used to count and size fish passing a particular point and increasingly are routinely used to assist stock management of anadromous salmonids (Ransom *et al*. 1998). Fixed location hydroacoustic techniques have also been widely used at North American hydroelectric facilities to understand the behaviour of downstream-migrating juvenile salmonids in relation to turbine entrainment and bypassing facilities (Thorne and Johnson 1993).

Early (1970s) single-beam echosounders worked well for rivers with large migrations of big fish moving close to the river bank where the sound beam could be directed, but gave no information on direction of movement, fish speed or vertical distribution. Information on fish size was limited by the inability of single-beam systems to determine the orientation of a fish, which is required to enable conversion of target strength to fish size. The need to size the fish led to the use of dual-beam systems with narrow and wide beams from the same transducer and with signal processors which could detect peak echoes and discriminate single targets. Subsequently, the data could be processed to track individual fish and provide a mean target strength for each fish. With two dual-beam systems located side by side with slightly offset elliptical transducers and transmitting alternately, the direction of travel could be determined by observing which transducer beam the fish entered first. Most early dual-beam acoustic studies in rivers were applied to adult salmonid migrations (Braithwaite 1971; Mesiar *et al*. 1990; Johnston and Hopelain 1990).

In the early 1990s, split-beam acoustic systems, with the advantages of lower side-lobes and faster signal processors, became commercially available for monitoring salmonid migrations. These are also capable of tracking fish targets in three dimensions in real-time. In addition to the absolute direction of a fish's movement, the split-beam system gives its 3-D position within the sound beam, the velocity of the fish target and less variable fish target strengths (Ehrenberg and Torkelson 1996; Ransom *et al*. 1998). Downstream movement of riverine debris on the surface of the water can be easily identified and their echo traces eliminated. There has been increased development of fully automated fixed location techniques for monitoring fish migrations, especially of salmonids, at dams (Steig and Iverson 1998) and at the cooling water intakes of some American power plants which incorporate high frequency sound fish-deterrents (Ross *et al*. 1993). Advanced systems may also incorporate modem options for controlling and transferring data from fixed hydroacoustic systems, particularly those acting as fish counters on rivers (Ransom *et al*. 1998). Advances in microcomputers, electronics and signal processing have made it possible to remotely operate and monitor hydroacoustic systems incorporating up to 16 transducers surveying discrete sites continuously or on programmable duty cycles, with substantial savings on human resources. Current developments further include a system known as BATS (Behavioral Tracking System) in which robotically controlled split-beam transducers are mounted on high-speed dual axis rotators and coupled to a computer (Hedgepeth *et al*. 1999). When a deviation of the target from the transducer's beam is detected, the computer uses a predictive tracking algorithm to realign the transducer. In the meantime, fish position, movement and target strength are recorded to hard disk. The main limitation of the system, which can also be used for tracking acoustic tags, is that narrow-beam transducers require a relatively long time for scanning a radius of a certain length, making their use most suited to relatively shallow water.

Fixed location hydroacoustic methods can be used to study diel behaviour and movements of lake and lowland river fish and, combined with other methods, can provide information on feeding movements (Comeau and Boisclair 1998). Kubecka and Duncan (1998a) used this approach in a 24-h study during June 1992 on the River Thames, England, where the fish community was dominated by roach (*Rutilus rutilus*, Cyprinidae), gudgeon (*Gobio gobio*, Cyprinidae) and dace (*Leuciscus leuciscus*, Cyprinidae), together with ruffe (*Gymnocephalus cernuus*, Percidae) and Eurasian perch (*Perca fluviatilis*, Percidae). By siting one dual-beam horizontally directed transducer in the littoral zone (0.5 m deep, beaming to the river) and one in mid-river (*c.* 3 m deep, beaming across the river), the movements of fish were followed over 24 h at hourly intervals and at three 1-m depth intervals in mid-river. The larger fish occurred in the littoral and the top depth stratum of the river during the night and early morning but moved to deeper layers during the day. In the open river, fish orientated themselves to the river flow and swam upstream or downstream, as detected by the tracked angle of movement across the sound beam. In the littoral area, fish movement was more random in relation to river flow. Similar or diametrically opposed daily patterns of inshore–offshore migrations of fish have been recorded in several lakes and reservoirs by shore seining (Kubecka 1993) and in large rivers by electric fishing (Copp and Jurajda 1993; Baras and Nindaba 1999).

Mobile horizontal beaming hydroacoustic techniques

Use of mobile hydroacoustics employing horizontal beaming to survey the distribution and abundance of fishes in shallow freshwater habitats has rapidly developed over the last decade (Kubecka 1996; Lyons 1998). At temperate latitudes, the approach is normally carried out in summer when the fish are active, and at night when fish move up in the water column (Kubecka *et al.* 1992; Kubecka and Duncan 1998a). Fish densities can be determined at short sampling intervals, enabling the characteristic patchiness of fish density distributions to be measured (Duncan and Kubecka 1996). The method has been used to examine abundance and distribution of fish communities over long stretches of various European lowland rivers, such as (in England) the Thames (Duncan and Kubecka 1996; Hughes 1998), Trent (Lyons 1998), Yorkshire Ouse (Lucas *et al.* 1998) and (in Germany and the Czech Republic) the Elbe (Kubecka *et al.* 2000). Both dual-beam and split-beam echosounders have been employed, with the current trend towards the latter due to their higher performance. Mobile split-beam hydroacoustic techniques have been used highly effectively to quantify daily inshore–offshore migrations of fishes in Canadian lakes (Gaudreau and Boisclair 1998). A common feature of all of these studies is that within apparently homogeneous lowland rivers or along the pelagic–littoral interface of lakes, fish are extremely clumped in distribution, with coefficients of variation for density estimates along a transect being high, often in excess of 100%. From mobile hydroacoustic surveys, Duncan and Kubecka (1996) provided evidence for fish aggregation at sewage outfalls in the River Thames, and indicated their influence on fish daily movement patterns.

Substantial seasonal changes in fish density distributions were demonstrated using a series of monthly mobile horizontal echosounding surveys over the same 27-km stretch in the Yorkshire Ouse (Lucas *et al.* 1998). This study also demonstrated the potential impact of high flow events on recorded fish densities in the river. During one night in September 1993, when river flow was five times greater (63.5 m^3 s^{-1}) than during the previous night (12.7 m^3 s^{-1}), mobile surveys showed that acoustically visible fish densities were three times lower. This was attributed to either downstream displacement of fish by high flows or avoidance by seeking refuge on the bottom or in the margins where flows were reduced.

Size discrimination of fish is relatively simple using vertically orientated echosounders because the fish are all in the same approximate aspect (viewed from above) and appropriate calibrations are generally available (Love 1977; Foote *et al.* 1987; MacLennan and Simmonds 1992), although these can be influenced by tilt angle, body form and swimming behaviour of fish (Brandt 1996). In order to produce a frequency distribution of the sizes of fish targets by horizontal beaming, fixed location is often necessary, because the orientation of the fish body or aspect being insonified cannot be tracked in a moving boat. Without tracking the fish across the sound beam, the acoustic sizes or target strengths cannot be converted to real sizes because the fish aspect (side, head or tail) is unknown. The echo reflected from a side-aspect fish is much greater than the same fish in head or tail aspect. During mobile horizontal hydroacoustic surveys, regular fixed location monitoring with the boat anchored for a short period along the survey route enables the slope of the fish track across the horizontally orientated beam to be estimated. In rivers, fish tend to orientate to river flow (though not in lakes where there is little rheotropic stimulus), and mostly cross the horizontal acoustic beam perpendicularly to the acoustic axis as the boat moves upstream or downstream (Kubecka 1996). Under these circumstances, relatively accurate sizing can be achieved from a moving boat, particularly when the surveying modifications described by Kubecka *et al.* (2000) are used. Most existing target strength–fish size relationships are for marine fishes, usually in dorsal aspect (Love 1977; MacLennan and Simmonds 1992). Increasingly, conversions are available for freshwater fish species in side and other aspects (Kubecka and Duncan 1998b), although due to the range of echosounder types and frequencies used in freshwater research there is still a need for further calibration, especially on live fish. However, it should also be appreciated that where mixed fish communities predominate, detailed species-specific size calibration may be of limited value and that fish aspect to the acoustic beam axis affects echo strength much more than differences between species for fish of similar size.

Further development of hydroacoustics

Hydroacoustic techniques provide an extremely useful approach for quantifying fish distribution, behaviour and migration in freshwater lakes and rivers, as well as in estuaries and brackish water environments (Guillard 1998). Use of fixed-location, split-beam hydroacoustics has become widely used for determining the timing and size of upstream salmonid migrations (Ransom *et al.* 1998) and advanced semi-autonomous systems are now increasingly widely available. Although mobile hydroacoustic surveys have not yet been widely used for studies of large-scale movements by lowland river fishes, the method's potential for surveys of whole stretches of rivers deeper than 1.5 m makes it an appropriate tool for studying spatial behaviour at the population level, particularly in combination with techniques such as radio tracking and direct sampling.

Although maximum usable acoustic range may be short in many freshwater environments (usually 10–30 m for horizontal beaming), the total sampled volume during mobile sampling is very large, providing large data sets for statistical analysis and a continuous spatial record of absolute fish densities in the water column. It is important in shallow, freshwater environments that surveys include night work, since in these habitats this is when many fish species are active in the water column (Kubecka *et al.* 1992; Kubecka and Duncan 1998a) and so more easily insonified and recorded. However, the influence of environmental factors on observed fish abundance is not yet fully understood. This is important because those fish which choose to remain close to the lake or river bed cannot easily be discriminated from the bottom echo. There is now good evidence that lunar phase can have a major modulating influence on the depth distribution of fish at night in freshwater and hence the numbers of echoes counted (Luecke and Wurtsbaugh 1993; Gaudreau and Boisclair 2000). As stated earlier, river flow and water temperature are also likely to be key features. Gas bubble production, especially by photosynthesizing algae and submerged macrophytes, also causes difficulties in the use of the hydroacoustic technique in shallow waters, as do the plants themselves. Indeed hydroacoustics can be used to map the distribution of macrophytes using the software SAVAA[1] (Submersed Aquatic Vegetation Analysis Algorithm). Such mapping can be carried out using data from standard surveys, enabling interpretation of fish behaviour in relation to submerged macrophyte distribution.

There is substantial variation in the cost of hydroacoustic systems. It is possible to obtain a high quality scientific single-beam echosounder with signal processing software for as little as about US$ 10 000, while single frequency dual-beam and split-beam systems cost rather more, at about US$ 30 000 and US$ 40 000, respectively, for systems incorporating a single transducer, laptop computer and software. Increasingly, because of the refinement of narrow, low side-lobe, elliptical beams and advanced signal processing associated with split-beam hydroacoustic systems, these are the preferred choice for use in freshwater, especially when used in horizontal mode in shallow habitats. Most 'split-beam' systems can, in any case, normally be used in single-beam mode. Multi-transducer systems, multiplexed to a single computer station cost in the order of US$ 80 000, depending on the number of transducers (about US$ 10 000 per split-beam transducer), while similar systems incorporating robotically driven transducers (BATS-type system) are likely to cost more.

[1]Obtainable free of charge from B. Sabel at SABOLB@wes.army.mil

Capture dependent methods

Variations in density and catch per unit effort

Variations of fish numbers in the same place over time result from birth, mortality, emigration and immigration. When mortality and birth rates can be estimated, or when the time interval is short enough to neglect these parameters, movements of fish can be implied from measures of abundance of different life-cycle stages and species. These measures may be absolute estimates of density or may be related to fishing effort as catch per unit effort (CPUE) (Casselman *et al.* 1990; Hilborn and Walters 1992). These methods usually have low temporal resolution and they require large sample sizes and/or numerous sampling points. Additionally, capture efficiency may vary substantially between times of the day, seasons, sampling sites and environmental conditions, and to variable extents depending on the capture methods. There is rarely a linear relationship between CPUE and absolute fish density. However, such methods may be useful where sampling is already being carried out for other purposes such as stock assessment, particularly where the sampling regime can be optimized to provide information at the appropriate spatial scale. Moreover, they may currently provide the only realistic option in many large tropical freshwater environments or for fish that are too small to tag, or where hydroacoustic equipment cannot be employed.

A variety of techniques may be employed for determining spatial and temporal changes in CPUE or absolute density. Especially recreational but also commercial catch statistics are influenced by environmental conditions (Hilborn and Walters 1992), as they depend on the appetite and behaviour of fish, which are known to be extremely dependent on environmental conditions (Hickley 1996; Malvestuto 1996). Recreational and commercial catch records can be useful indicators of local fish abundance and species composition (Hickley 1996), especially in situations where no other capture methods can be implemented efficiently, or for long-term ecological studies, indicating, for example, changes in timing of migration.

Passive capture techniques (entanglement and entrapment gears, see Hubert 1996 for review) can provide substantial information on patterns of movement by fishes, in that they rely on active movement by fishes for their capture. Nets or traps fished at particular sites can therefore be used to quantify migration or movement in a particular locality (Bénech and Peñaz 1995; Quiros and Vidal 2000). Another example of this approach is the use of fish-counting fences in shallow rivers, where migrating fish, usually salmonids, are channelled upstream or downstream into traps (Chadwick 1995). Catches made in this way enable assessment of migratory activity in relation to environmental factors and also provide fish for marking or tagging. Traps and fixed nets are also commonly used to assess patterns of activity on diel scales, often in relation to foraging behaviour (Keast and Fox 1992; Rahel and Nutzman 1994; Hubert 1996). Rahel and Nutzman (1994) used bottle traps to demonstrate that central mudminnows (*Umbra limi*, Umbridae) regularly entered severely hypoxic bottom waters of a lake in northern Wisconsin, USA, to forage on *Chaoborus* (Diptera) larvae during the day.

While increased CPUE in traps and static nets can be indicative of increased locomotor activity or movement into a particular area, susceptibility to capture is also strongly influenced by other features such as net avoidance (usually much higher at elevated light levels) and by the presence of conspecifics (Hubert 1996). Both static nets and traps often show marked selectivity towards fish species or size (Casselman *et al.* 1990; Hubert 1996). Passive netting (e.g. with gill nets) is more efficient in lacustrine habitats (Casselman *et al.* 1990; Keast and Fox 1992) than in riverine environments, where drifting vegetation or debris can damage the gear or interfere with sampling. Traps have been used with success in many migration studies of non-salmonid fishes, such as brook lamprey (*Lampetra planeri*, Petromyzontidae; Malmqvist 1980), three-spined stickleback (*Gasterosteus aculeatus*; Gasterosteidae; Harvey *et al.* 1997) and especially in freshwater eel (Anguillidae) migration studies (e.g. Jellyman 1977; Baras *et al.* 1994; White and Knights 1997). Traps are often operated at the upstream outlet of fish passes, where they can provide quantification of fish species that have successfully ascended, and information concerning the extent of and stimuli for upstream passage by several species (Larinier 1983, 1998; Baras *et al.* 1994). However, such traps fail to quantify the proportion of fish unable to ascend the bypass or the behaviour of fish which may accumulate below the barrier but not ascend the pass.

Active capture netting and trapping methods (seine nets, trawls, dredges and fish wheel) can give valuable information on local abundance of fishes, including sedentary species, but their efficiency is species- and size-dependent, and they perform best in shallow, smooth-bottomed, slow-flowing habitats such as lake shores or backwaters (Casselman *et al*. 1990; Kubecka 1993; Hayes *et al*. 1996). Electric fishing has become one of the most popular methods of catching fish in shallow fresh waters (streams, rivers and lake shores) due to lower manpower requirement than most other active capture techniques. However, its efficiency is highly variable depending on water depth, conductivity, clarity, type of power generator, electrode size, operator experience, fish size and behaviour (Casselman *et al*. 1990; Cowx 1990; Harvey and Cowx 1996), and so correction factors based on gear calibration (e.g. Bütticker 1992) are required before any inference can be made on the actual or relative population size. Recent developments in electric fishing have reduced fish mortalities, increased capture efficiencies in a range of habitats and enabled the capture of small fish ($<$ 20 mm) thus reducing the selectivity of electric fishing methods (Cowx 1990; Harvey and Cowx 1996). Alternatively, point abundance sampling by electric fishing may provide a useful measure of relative abundance which can be quickly applied and enables changes in population distribution over short periods of time to be measured. This applies particularly to larvae and 0+ fish (Copp 1989) and this technique has been used to demonstrate seasonal and diel shifts in distribution of lowland river fish species in natural and regulated systems (e.g. Copp and Jurajda 1993; Copp and Garner 1995).

Most active capture methods, including electric fishing, may cause a fright bias (Cowx 1990; Hayes *et al*. 1996), which is a particular problem with point abundance sampling. Fixed electrodes or frames, energized by AC (Bain *et al*. 1985) or DC (Baras 1995), have been used to reduce this bias, provided that a sufficient delay is allowed between the installation of the frame and its energization. Additionally, the high gradient voltage during operation of these frames results in minimal selectivity towards fish species or size. Using these methods, it is possible to obtain quantitative estimates at regular intervals within discrete microhabitats, based on an *a priori* sampling design. For example, Baras and Nindaba (1999) demonstrated that the diel migrations of 0+ rheophilous cyprinids were size-structured. The main limitations of this approach are the time required to obtain sufficient sample sizes (frame installation plus recolonization delay), the small area sampled at each point, and the general difficulty of electric fishing in deep waters.

Marks and tags

Mark–recapture

Mark–recapture is an important method in fisheries stock assessment because it allows the estimation of population size, mortality and independent assessments of growth rate, but it also provides information on patterns of movement between the sites at which the fish were marked and subsequently recaptured. Complementary to CPUE, this method has provided much important information on home range, migration and homing of diadromous and freshwater-resident fishes. Implicit in these studies are the assumptions that the marking procedure or mark/tag presence do not interfere with fish physiology or behaviour beyond a period of post-tagging stress, which should be as short as possible, and in every case determined as accurately as possible to validate such studies.

On some occasions, the outcomes of mark–recapture studies have been validated by other techniques, e.g. parasite studies and radio-tracking of barbel (*Barbus barbus*, Cyprinidae); Philippart and Baras 1996. However, mark–recapture approaches often underestimate considerably the movements of fish because of spatially limited recapture effort. Indeed, migratory patterns are inferred from recaptured fish only, and fail to take account of missing fish, which may have died, but alternatively may have emigrated beyond the limits of sampling areas. Mark–recapture also suffers from a rather poor temporal resolution of fish location (Gowan *et al*. 1994; Baras 1998), which generates further imprecision and underestimation of the propensity for movement, especially for short-term movements followed by homing behaviour. Additionally, the efficiency of recapture of tagged fish is likely to vary dramatically in time and space. In tropical floodplain systems, fish may have a very high likelihood of recapture when crowded into small pools during the dry season(s), but are much less likely to be captured when they disperse during the rainy season(s). Other techniques, employing naturally occurring marks may be used to reconstruct a fish's geographical origin or habitat use and may not necessitate recapture; these are considered later in this section.

Types of marks and tags

Since the first tagging attempts, at least as early as the 17th century, there have been considerable developments in tag/mark design and analysis methods (Wydoski and Emery 1983; Parker *et al.* 1990; Nielsen 1992); these developments have been on three fronts:

1 increasingly sophisticated, longer-lasting and better-performing tags that enable the measurement of biological or environmental variables in relation to space use (e.g. telemetry tags);

2 reduction in the size and weight of tags, enabling tagging of smaller fish and large numbers of fish in a short period; and

3 an increasing use of intrinsic or extrinsic marks naturally born by the animal, and sophistication of identification and analysis techniques.

These improvements have helped to dramatically increase our knowledge of fish movements and behaviour, and to reduce substantially the biases inherent to fish capture and/or recapture. A series of attributes for a perfect tag/mark are listed in Table 1. Unfortunately, to date, no tag or mark has met or is likely to meet all of these characteristics. Some tagging techniques are adapted to large samples but give low spatial and temporal resolution, others provide high resolution but for limited samples of large individuals only, whereas some others are free from environment or size-restriction but overlook individual identification and resolution. Hence, studies of fish spatial behaviour should focus their objectives and select the most appropriate techniques, alone or in combination. This section briefly reviews the major types of marks and tags, their advantages, limitations and context of application for the study of fish movements, focusing on state-of-the-art techniques.

Synthetic extrinsic marks and tags

This grouping comprises those marks and tags which are applied to the fish, but which can only be identified by close inspection of the fish. External marks consist essentially of dyes or pigments (applied by balneation, aspersion, injection or tattooing), brands (generally freeze branding) or mutilation (McFarlane *et al.* 1990). Although they offer some possibilities for individual coding (e.g. freeze branding and combinations of fin clips), they are better adapted to batch marking, essentially because of their low cost and fast application. However, external marks suffer from numerous specific drawbacks, including confusion with naturally acquired fish injury (fin clipping and freeze branding or dyeing) or melanophore development (black ink pigment), as well as risk for the operator (freeze branding) or the fish during the application (tattooing). Other chemical compounds (rare earth elements, radionuclides, calcein and tetracyclin) can be used as internal markers of fish tissues, mainly in skeletal structures (Hansen and Fattah 1986; Muncy *et al.* 1990), but their application may necessitate long-term stocking and their identification frequently requires tissue biopsy or fish sacrifice. Additionally, both internal and external extrinsic marks have a most limited individual resolution by comparison to most physical tags.

There are numerous types of external 'conventional' tags (reviews in Wydoski and Emery 1983; McFarlane *et al.* 1990; Nielsen 1992), conspicuous

Table 1 Characteristics of the ideal tag or mark (modified from Nielsen 1992)

(1)	No risk of alteration during storage
(2)	Easy and fast application, requiring no anaesthesia or specialized equipment
(3)	High tagging/marking rate
(4)	Minimum bulk and size, applicable to fish of all sizes
(5)	Enables individual identification
(6)	Low cost
(7)	100% retention
(8)	No alteration or fouling of tag material
(9)	No effect on health, physiology, behaviour, performance and fitness of tagged fish
(10)	No influence on the probability of the fish being predated or captured by fishing or sampling gears
(11)	No effect on fish appearance and saleability (e.g. for commercial fisheries)
(12)	No need for specialized equipment or training for detection and identification
(13)	No risk of confusion while identifying tag presence or code
(14)	No handling required for post-tagging identification
(15)	Can be detected and identified at any distance and at any time
(16)	Tag/mark should be relayed to progeny

in shape, size and colour, which can be fixed firmly to the fish body (e.g. Petersen disk, Bachelor button, oval bars or straps) or dangle rather freely at the end of a nylon loop or anchor attachment (e.g. anchor tags and Carlin tags). These are relatively cheap tags, that can be individually coded, and have the major advantage of being detected easily by anyone. High tagging rates can be achieved for some of them, such as the Floy anchor tags (about 500–1000 fish per hour). Each tag type has specific limitations and drawbacks: essentially of a reduction of growth for fish tagged with button or disk tags; and risks of entanglement, drag and erosion of muscles for fish with dangling tags. The retention rate and duration of external tag attachment varies greatly depending on tag type, operator experience, species and environment (structure and current). In general, the longer the migration or the faster the current, the higher the probability that external tags will be shed or affect fish performance, and this may cause substantial biases for studies of fish movements.

These limitations promoted the development of internal tags, some being still externally legible and requiring no specialized equipment for detection, and others being truly internal and necessitating remote sensing (coded wire tags and electronic tags). Among the former category are visible implanted (VI) tags, which consist of small ($2.5 \times 0.9 \times 0.13$ mm thick) rectangular fluorescent polyester sheets coded with three alphanumeric digits and colour, and are usually inserted into the adipose eyelid of the fish (Haw *et al.* 1990). Not all fish species have adipose eyelids as well developed as those of salmonids for which VI tags were originally designed, but other clear tissues overlying the operculum, jaws or dorsal neurocranium, or within fin membranes of large fish, can be used successfully. However, the body reactions to the implant, chiefly encapsulation or overlying by melanophores, may obscure the tag and render its detection or legibility more difficult, especially by anglers or fishermen. Similar problems apply to elastomer visible implant (EVI) tags (droplets of a polymer compound, injected as a liquid into a transparent tissue, then polymerizing as a solid compound within hours; Anonymous 1994), and although viewing with ultraviolet light aids detectability, EVI tags appear to be of limited value for mark recognition in excess of 1–2 years (Close 2000).

Coded wire tags (CWTs; Jefferts *et al.* 1963) are the smallest tags available, among the cheapest ones (US$ 0.1) and the most widely used, with more than 50 million fish tagged in this way each year. The tags are sections of stainless steel wire (0.25 mm in diameter), cut at a standard length (1.1 mm or 0.5 mm for half-length tags), magnetized, and marked with notches by a hand-held or automatic injector, enabling tagging rates of about 200 and 600 fish per hour, respectively. They can be injected into any part of the body, although the most frequent location is the ethmoid region of the cranium, with species-specific head moulds being used to standardize the tag positioning. Fully automatic injectors, requiring no fish handling at all, have recently been developed for salmonids and these enable tagging rates as high as 1500–3000 fish per hour for fish of similar body size. Tagged fish can be detected remotely as they pass through or near magnetic coils, but the identification of the tag code requires that, unless X-radiographed, the tag be extracted from the fish tissues and examined under a microscope (20–30 × magnification). This implies that the fish be sacrificed except for tags sited in translucid tissue (e.g. adipose eyelid) or non-vital parts of the body (e.g. adipose fin). Most of their applications refer to group tagging, although individual tagging can be achieved by using sequential coding. Traditionally, CWTs were notched to give binary coding, but are now available with etched alphanumeric codes which can be read in the field with a hand-held microscope.

Coded wire tags have no major drawback, except for the low temporal resolution that is characteristic of mark–recapture techniques, the need for specialized equipment for tagging and detecting tagged fish, and the frequent need to sacrifice the fish for batch or individual identification. Because of the tiny dimensions of CWTs, their impact on fish health and performance is almost restricted to capture and handling. However, there has been recent evidence that CWTs injected into the skulls of small juvenile pink salmon (*Oncorhynchus gorbuscha*, Salmonidae) may damage the nervous system, especially the olfactory rosettes, and later modify the orientation capacities of these fish during their homing migration (Habicht *et al.* 1998).

Natural intrinsic and extrinsic marks

Instead of tagging a fish to determine where it goes, one can take advantage of natural marks carried by the fish to identify its origin and to reconstruct its migration path or spatial segregation. These include truly intrinsic characteristics (genome and morphology), as well as extrinsic marks becoming incorporated in (in the case of chemical elements and isotopes) or fixed to the animal during its migration or residency time (in the case of parasites). Key features of all these marks are the absence of marking/tagging bias, the need for specialized equipment for detection or identification, and their indirect nature. Indeed, movements can only be implied from a data base on the spatial distribution of the measured features, the size and completeness of which frequently conditions their accuracy.

Morphological characteristics (meristic variables and pigmentation patterns) are usually of extremely limited value to studies of spatial behaviour because they are frequently subject to ontogenetic changes and the influence of environmental conditions. Persat (1982) demonstrated the identification of individual European grayling (*Thymallus thymallus*, Salmonidae) from dots and scale patterns. Symbionts or parasites that induce no major pathogenic sublethal effects can also be used, alone or in combination with other techniques to map the habitats used by fish during their migration (e.g. Margolis 1982). Analyses of genetic markers (Carvalho and Hauser 1994; Park and Moran 1994) offer a much broader range of perspectives, either at the population level (enzymatic polymorphism and mitochondrial DNA) or at the individual level (variable number of tandem repetitions, VNTRs; i.e. hypervariable mini- or microsatellites). For example, VNTRs now make it possible to map the dispersal of the progeny of an individual fish. Coupling this analysis with tracking of the parent fish migration pattern would enable determination of the extent to which gene flow is dependent on migratory behaviour of the parents and/or progeny. A major advantage is that genetic material can be obtained from blood or fin tissue without killing the fish. Mitochondrial DNA analyses are in routine use for the determination of stock structure, and can provide valuable information on the level of dispersal and the integrity of migratory populations (Avise *et al.* 1986; Carvalho and Hauser 1994). Microsatellite genetic analysis in combination with mark–recapture has been used to independently demonstrate limited dispersal of two species of barbel (*Barbus barbus* and *B. meridionalis*, Cyprinidae) and its influence on the maintenance of a hybrid zone (Chenuil *et al.* 2000). Microsatellite analysis has also been used to investigate the role of dispersal in rapid speciation of haplochromine cichlids (Van Oppem *et al.* 1997) and, together with mitochondrial DNA analysis, to reconstruct recolonization routes of Eurasian perch into Norway following the last glaciation (Refseth *et al.* 1998).

Screening fish hard parts (cartilage, bone, scales, otoliths) for trace elements or isotopic ratios gives the opportunity to reconstruct habitat conditions during the fish's life (Coutant 1990). The chemical composition of water, sediments and food items varies in space and time, and as a fish grows some of these elements are incorporated into hard structures and may provide distinct chemical signatures associated with the fish's habitat (Coutant 1990). The degree to which composition of hard structures reflects past exposure to particular elements or isotopes depends on the initial incorporation of these, and on the stability of the matrix into which the elements are incorporated. Scales can provide a valuable source of material for analysis without the need for killing fish and have been successfully used in a number of microchemistry studies (Pender and Griffin 1996). However, scales can be replaced and material can be reabsorbed from original scales, as well as from bone and cartilage.

The crystalline structure of otoliths, largely formed from aragonitic calcium carbonate on an organic matrix, appears to be relatively inert and retains a fine structure and chemistry that reflects deposition of material over the fish's lifetime (Campana and Neilson 1985). The majority of inorganic material laid down in otoliths and other hard parts of bony fishes is calcium, but other minor or trace elements are incorporated at levels which tend to reflect their availability and ultimately depend on the relationship between ambient water and otolith chemistries (Secor *et al.* 1995). Among the most significant of these minor constituents, from the viewpoint of markers of spatial behaviour, is strontium, which is much more abundant in saline water than freshwater and substitutes for calcium. Although diet and temperature may influence Sr/Ca ratios, it is thought that around 85% of variability in the Sr/Ca ratio is due to changes in salinity (Secor *et al.* 1995). Ratios between strontium and calcium have therefore become important indicators of diadromous life histories at the individual fish level and are providing exciting opportunities for studying lifetime spatial behaviour of a wide range of species. For European eel (*Anguilla anguilla*, Anguillidae) and Japanese eel (*Anguilla japonica*, Anguillidae), historically regarded as obligately catadromous, otolith Sr/Ca analysis has demonstrated that substantial components of these populations may never enter fresh or brackish water (Tsukamoto *et al*. 1998). For primary freshwater fishes, such as common bream (*Abramis brama*, Cyprinidae) and pikeperch (*Stizostedion lucioperca*, Percidae), fine-scale information is now emerging on the migratory behaviour of some population components between freshwater and brackish environments (Kafemann *et al*. 2000).

Barium, another divalent metal ion, with an ionic radius similar to that of calcium, also effectively replaces calcium. Barium tends to occur at higher relative concentrations in freshwater than seawater and can therefore often be used as an indicator of freshwater residence, although there may be substantial variations in barium levels between catchments associated with differences in catchment geology. From analyses of barium and strontium levels in scales, Pender and Griffin (1996) demonstrated that barramundi (*Lates calcarifer*, Centropomidae) from around the Mary River, northern Australia, display facultative catadromy and suggested that marine stocks remote from freshwater inflows probably have no freshwater phase. As well as being significant to our understanding of migratory behaviour, such findings have major implications for issues of resource allocation between freshwater sport fisheries and marine commercial exploitation. A variety of other trace elements, including heavy metals such as copper, cadmium and lead, often associated with industrial pollution, have also been suggested as markers in hard parts, although biologically unregulated elements such as lead and cadmium are likely to be most useful (Coutant 1990; Campana 1999). Although whole scale/otolith wet analysis by a variety of spectroscopic techniques can be used (Coutant 1990; Pender and Griffin 1996), fine-scale sampling by one of several methods, combined with incremental age analysis, is increasingly preferred to enable detailed habitat reconstruction to be achieved (Coutant 1990; Tsukamoto *et al*. 1998; Campana 1999; Kafemann *et al*. 2000). Microdrilling methods may be used to obtain small samples of material from discrete locations on otoliths and scales, but *in situ* use of a laser ablation microprobe and inductively coupled plasma mass spectrometry (LA-ICPMS) is increasingly the preferred (albeit expensive) method, enabling fine-scale, precise measurement of most elements and even isotopes with minimal risk of sample contamination (Campana 1999).

Determination of variations in stable isotope ratios of key elements such as ^{13}carbon, ^{15}nitrogen and ^{34}sulphur in body tissues is increasingly well known in ecology as a technique for examining trophic structure of communities, but is now also proving to be a valuable method for assessing the history of space use by individual fishes (Hobson 1999). Dietary shifts and/or changes in trophic status are often intimately associated with habitat shifts and ontogeny, and may result in distinct changes in ratios of stable isotopes. This approach has been used to examine migratory fish in the Mackenzie River, Canada (Hesslein *et al*. 1991), and appears suitable for larval settlement studies (Herzka and Holt 2000). Similarly, the oxygen isotope fractionation ($^{18}O/^{16}O$) in tissues can be used as indicator of growth in low and high salinities and at different temperatures (Coutant 1990), while isotope ratios of elements such as strontium ($^{87}Sr/^{85}Sr$) in hard parts may also be useful habitat indicators (Campana 1999).

Electronic tags – telemetry

The development of electronic tags has proved to be one of the most important advances for studying fish behaviour and migration (Stasko and Pincock 1977; Baras 1991; Priede and Swift 1992; Winter 1996). They enable rapid, long-term and often long-range identification and positioning of fishes, with high temporal and spatial resolution, including in environments hardly accessible to human observers. While the purpose of most telemetry studies of fishes is to elucidate their movements, home range or habitat use, it has also received increased use in the assessment of a wide variety of specific problems associated with fish behaviour and space use, including: evaluation of fish responses to obstructions (e.g. Lucas and Frear 1997); establishing the efficacy of fish pass programmes (e.g. Travade *et al*. 1989; Bunt *et al*. 1999); quantifying survival during migration (e.g. Jepsen *et al*. 1998); measuring energy expenditure during foraging and migration (e.g. Lucas *et al*. 1993; Hinch *et al*. 1996); identifying the responses of river fish to artificial freshets (e.g. Thorstad and Heggberget 1998) and acid episodes in rivers (e.g. Gagen *et al*. 1994); and obtaining information for specific conservation programmes (e.g. Moser and Ross 1995).

Passive integrated transponders

Passive integrated transponder (PIT) tags are small (the smallest currently commercially available are 10.3 mm long × 2.1 mm in diameter) glass cylinders comprising a coil and an integrated circuit, programmed to transmit one of some billions of codes (Prentice *et al.* 1990a, b, c). PITs are interrogated with the field of an induction coil, commercially available at 125, 134 or 400 kHz, which energizes and causes a tag to retransmit its code to the reader. As PITs contain no power source, their life is theoretically infinite, and because their identity is electronically coded, they enable a fast and reliable identification of individual fish with minimum handling. PITs are normally used as internal tags that can be implanted into the peritoneal cavity of fish as small as 1–2 g, using syringe injectors (Prentice *et al.* 1990a) or surgical techniques (Baras *et al.* 2000), or into the musculature of larger fish (Bergensen *et al.* 1994). Automated tagging systems, consisting of an electronic balance, digitizer, tag detector and automatic tag injector activated by high pressure carbon dioxide have been developed for salmonids, and these enable tagging rates as high as 150 fish per hour (Prentice *et al.* 1990c; Achord *et al.* 1996). Implanted PITs are unlikely to be shed once the incision has healed (3–15 day depending on fish species, age, size and temperature; Baras *et al.* 2000), except for some rare cases of transintestinal expulsion, but these seem to be restricted to Siluroidei (Baras and Westerloppe 1999).

With respect to fish migration studies, PITs have often been used in mark–recapture programmes (Douglas and Marsh 1996; Ombredane *et al.* 1998). However, because transponder interrogation and detection relies on inductive coupling, they can also be detected at some distance (*c.* 20 cm for the smallest PITs; *c.* 50 cm or more for larger (32.5×3.8 mm) transponders; Castro-Santos *et al.* 1996), and their code can be automatically stored, together with passage time, by a PIT-tag data entry station (Prentice *et al.* 1990b; Adam and Schwevers 1997). Most remote detection antennae are of tubular or square construction, and impose that fish swim through them, restricting their use to the monitoring of fish passage in special facilities like fish passes. More recently, flat-bed antennae (1.0×0.3 m) have been developed (Armstrong *et al.* 1996) and these can be applied to the study of fish movements in more open environments as well as at fish passes (Armstrong *et al.* 1997; Lucas *et al.* 1999). A recent study using 23.1×3.9 mm PIT tags, together with loop antennae in the form of two adjacent 4×1.2 m rectangular frames at an 8-m wide stream site has demonstrated the ability to monitor fish movements across the width of whole streams with high efficiency (G. Zydlewski, K. Whalen, A. Haro and S. McCormick, personal communication, 2000). Roussel *et al.* (2000) have described a new portable reading unit, incorporating a chest-mounted palmtop computer, a reader and a 12-V battery enclosed in a backpack, connected to a 60-cm diameter coil mounted on a 4-m pole. The antenna is moved above the stream surface to search for tags and when used with 23.1×3.9 mm PIT tags the equipment has a range of 1 m.

It is worth noting that for several reasons the reading efficiency of automatic stations may be less than 100%. Because inductive coupling depends on the respective orientations of the detection antenna and tag coil, PITs which are misaligned at the time of tagging or become misorientated during fish growth may compromise reading efficiency (e.g. Pirhonen *et al.* 1998; Baras *et al.* 2000), especially when the tag is close to the maximum detection range of the antenna. Irrespective of distance or tag orientation, the passage of several fish at a time may exceed the detection capacity of the data entry station (about 8 and 20 fish s^{-1} for 125 and 400 kHz, respectively), and not all individuals may be detected. Similarly, detection can be impaired when the residence time at the detector is less than the minimum time for interrogation and detection, and this may happen at fast swimming speeds (e.g. 5–7 m s^{-1} through a 1-m long antenna tunnel; Castro-Santos *et al.* 1996). Conversely, a fish sitting above or inside an antenna coil may block the detection system and prevent other passing fishes from being detected. This implies that antennae should ideally be installed so as to discourage fish from hiding or sitting close to them, and that the length of antenna tunnels should be adapted to the maximum expected swimming speed of fish, as well as to the numbers of tagged fish.

Signal propagation and detection of battery-powered transmitters

The detection of acoustic signals (usually at 30–300 kHz) from battery-powered transmitters or transponders requires a hydrophone to be immersed in the water, whereas VHF radio signals (usually at 30–170 MHz) can be detected by underwater or aerial antennae, making it possible to radiotrack from a boat, while on land or from an aircraft. Ultra high frequency (UHF) radio signals are rapidly attenuated in water but allow high rates of data transfer to orbiting satellites, including the ARGOS (Advanced Research and Global Observation by

Satellite) system which allows wildlife satellite telemetry applications. If a high-power UHF transmitter can gain at least three uplinks to an overpassing ARGOS satellite, its position can be located by Doppler shift, and stored data can be transferred (Priede 1992; Winter 1996). Individual acoustic or radio transmitters can be identified from their specific frequency, pulse rate or pulse coding sequence (Winter 1996). The smallest acoustic transmitters (also named pingers) usually are slightly larger than the smallest radio transmitters (*c.* 0.5 g in air, *c.* 12 × 5 × 5 mm). They have higher power requirements and shorter life than equivalent-sized radio transmitters, but they can give greater accuracy while positioning the fish (in theory *c.* 0.1–0.2 m with advanced 3-D positioning systems, vs. *c.* 1.0–5.0 m for radio tags).

Acoustic and radio signals are variously affected by environmental features, which restrict their optimum application to particular sets of environmental conditions. Acoustic signals propagate omni-directionally in water at constant velocity for any given temperature and salinity (Voegeli and Pincock 1996). Absorption losses of sound energy are proportional to frequency. This makes lower frequencies of greater potential use for acoustic tracking. However, because the resonant frequency of the ceramic transducer used in acoustic tags is inversely proportional to its diameter, frequencies lower than 30 kHz are impractical for tracking all but the largest fishes. Frequencies used for tracking in freshwater normally lie between 60 and 300 kHz. Reception range of acoustic transmitters is strongly dependent on ambient noise levels, as well as the influence of signal scattering from entrained air or at physical boundaries such as thermoclines.

Radio signals propagate omni-directionally in the water but only those wave vectors almost perpendicular (± 6°) to the air–water interface emerge into the air and can be detected by an aerial antenna. Hence a key variable influencing range of radio transmitters is water depth, together with conductivity (Velle *et al.* 1979). Because signal attenuation with increasing depth and conductivity is proportional to the carrying frequency of the radio signal, relatively low frequencies (30–50 MHz) may be preferred in deep and/or highly conductive environments. However, reduced range at high frequencies may be compensated for by the smaller size of directional antennae and resultant ease of use in the field (e.g. 1 m for a Yagi antenna at 150 MHz vs. 3 m at 50 MHz). The use of an internal coiled antenna within the transmitter can reduce the reception range by *c.* 30%, in comparison to that of a whip antenna, but it may be less detrimental to fish in some circumstances where the transmitter is surgically implanted (see below). Radio tracking has become the preferred method for use in shallow (usually < 5 m), low conductivity (usually < 500 $\mu S\ cm^{-1}$) lakes, ponds, rivers and streams. In slow, deep rivers, lakes and reservoirs, and many lowland or brackish waters with high conductivity, acoustic tracking has continued to provide the most appropriate tracking technology. Combined acoustic and radio transmitters (CARTs), switching automatically between these modes using internal clock circuitry or a salinity sensor, have been developed for diadromous species (Solomon and Potter 1988; Smith and Smith 1997).

In some deep, highly conductive and noisy environments (e.g. deep and fast-flowing estuaries) or where complex physical structures occur in highly conductive water (e.g. harbours) neither acoustic nor VHF radio signals can be detected confidently. In these circumstances, electromagnetic tags employing low frequency radio waves (LF radio = 30–300 kHz) may be appropriate. Most passive integrated transponders work in this frequency range, but battery-powered transponders or battery-powered transmitters can also be useful. While PIT tags have very low ranges, active transponders, interrogated by inductive coupling in the same way as PIT tags but powered by a battery transmitting the signal to the receiving antenna, can achieve a range of a few tens of metres. Breukelaar *et al.* (1998) used this technology to identify the migration routes of anadromous salmonids in the rivers Rhine and Meuse delta in the Netherlands. Because of their extremely large size and weight (85 mm long × 15 mm in diameter, 25 g in water), these tags are restricted to large fish (> 1.4 kg) only. However, battery-powered coded LF radio transmitters, such as those developed for tracking decapod crustaceans on artificial reefs, have been made with dimensions of 40 mm diameter and 10 mm depth (Collins 1996; Smith *et al.* 1998) and, with modification, may be appropriate for localized tracking of moderated-sized fish under the adverse conditions described above.

Transmitter positioning

Following the line of the strongest signal is the most frequent way of tracking fish, information from which can be plotted on maps using landscape marks or GPS technology. With both acoustic and radio signals, horizontal positioning can be obtained by triangulation, using directional hydrophones or antennae (e.g. loop, Yagi and Hadcock), with a minimum of two bearings, preferably at 50–120° from one another (Winter 1996).

While using acoustic signals, one may also achieve automatic positioning of a fish, and thus track its movements more accurately by measuring the relative arrival times of acoustic signals to a fixed array of omni-directional hydrophones (Hawkins *et al.* 1974; Lagardère *et al.* 1990). Three hydrophones give a 2-D position, and four hydrophones enable to 3-D positioning (inverse principle of hyperbolic navigation). The positioning of fish with omni-directional radio antennae is quite impractical, as radio signals travel much more rapidly (3×10^8 ms^{-1} vs. 340 m s^{-1} for acoustic signals), and so the measurements of signal time arrivals lack accuracy. For example, a difference in signal arrival time of 1 ms (the current resolution of most systems) corresponds to 34 cm for acoustic signals, and to 300 km for radio signals. Although multiple automated, rotating directional-antenna radio stations may be used to fix radio transmitter positions by triangulation, precision is much poorer than that with automated acoustic systems. While using combined transmitters producing both radio and acoustic signals, fish can be located from a single bearing in polar coordinates using a directional hydrophone or antenna to determine the bearing, and measuring the distance from the difference between the arrival times of the radio and acoustic signals (RAFIX system, Armstrong *et al.* 1988). As an alternative to active tracking and position-fixing, the monitoring of the passage of fish at discrete sites with automatic listening stations (ALSs) coupled to fixed antennae or sonarbuoys (Solomon and Potter 1988) may be of great value in fish migration studies, especially at obstructions (Lucas and Frear 1997) or in remote environments (Eiler 1995). These ALSs may be remotely interrogated by modem, radio or satellite (Eiler 1995), saving time and effort for locating fish between sites covered by ALSs.

Telemetry of intrinsic and extrinsic parameters

Electronic transmitters can also be equipped with physiological or environmental sensors that change the pulse rate or pulse width of the transmitter proportionally to the measured values. A similar approach can be used with archival tags that store information until the tag is recovered or the data is transmitted to a satellite (see later). Telemetry of environmental variables from fish can provide much information regarding responses to physical factors such as temperature (Coutant 1969; Snuccins and Gunn 1995), salinity (Priede 1982), depth (Williams and White 1990; Gowans *et al.* 1999) and oxygen concentration (Priede *et al.* 1988) and is of great significance in understanding the behaviour of fish in relation to natural variations in environmental factors, as well as the influence of anthropogenic disturbances to the freshwater environment. Comparing internal and external temperatures obtained from a two-channel transmitter equipped with two temperature probes (one external and one internal) can also provide useful information on digestive processes, chiefly through the measurement of the heat increment resulting from the specific dynamic action (SDA). Tunas are known to warm their viscera by several degrees after feeding (Gunn *et al.* 1994), but recent findings suggest that differences of 0.5–0.7 °C can be measured in typical poikilotherm fish (E. Baras, unpublished data).

Pressure sensors coupled to electronic tags provide information on ambient pressure, and thus on the swimming depth of the fish (up to 3000 m), but they require proper calibration. Light sensors sufficiently sensitive to detect light down to several hundred metres in clear water can also be incorporated into electronic tags. While using archival tags for fish making long-range migrations, these sensors can provide key information on the longitude (time of sunrise and sunset) and latitude (day length), provided that water turbidity is homogenous and swimming depth is measured simultaneously. For these reasons, their use is best for pelagic fishes in oceans or large lakes rather than in rivers where turbidity changes and vegetation or physical structures may influence ambient light intensity.

Simple tilt-switch transmitters that vary pulse rate with changes in the fish's body attitude provide an excellent means by which to quantify the activity of fish (e.g. Baras *et al.* 1998). Such transmitters have also proved effective for recording feeding behaviour of fishes such as tench (*Tinca tinca*, Cyprinidae), which tip-up to feed on benthos (Perrow *et al.* 1996). Accelerometer transmitters, the output of which is directly proportional to fish movement, permit a finer discrimination between different behaviours, such as redd cutting and quivering in spawning Atlantic salmon (Johnstone *et al.* 1992; Økland *et al.* 1996). However, such tags require a detailed series of calibrations of the correspondence between behaviours and transmitter output. Swimming direction can now be measured by sensors measuring compass heading with a 1° accuracy, provided that the sensor is kept at a few degrees off horizontal, which is a major limitation for studying the vertical migrations of fish.

Further advances in telemetry of heart rate and electromyograms have enabled a much better appreciation of the internal status and physiology of free swimming fishes. Physiological telemetry is increasingly being used as a method of estimating energy costs of fishes in the natural environment (Lucas *et al.* 1993). Recent studies using EMG telemetry have identified the existence of costly localized activity (Demers *et al.* 1996) and evaluated the energy costs and success of migration through areas of river with different velocity regimes, including those for which passage is difficult (Hinch *et al.* 1996; Hinch and Bratty 2000).

Telemetry tag attachment methods

Any method for studying fish behaviour in the natural environment should not itself lead to changes in the behaviour or physiology of the individual being studied, and this applies particularly to telemetry tags, which exceed all other types of marks and tags in size and weight. With few exceptions, fish maintain near neutral buoyancy by adjusting the volume of their gas bladder which, in freshwater, represents about 7% of the fish volume and has an adjustment capacity of about 25% (Alexander 1966). Consequently, it is usually recommended that the weight of the transmitter in water should be less than 1.75% of the fish body weight (Gallepp and Magnuson 1972; Stasko and Pincock 1977; Winter 1996; Baras *et al*., in press).

In early studies, most transmitters were attached externally, as streamer tags, or using a pannier-type mount, usually adjacent to the dorsal fin. However, external transmitters can lead to a loss of postural equilibrium, increase drag and may be physically snagged resulting in damage to the fish or premature loss of the transmitter (Ross and McCormick 1981; Mellas and Haynes 1985; Perrow *et al.* 1996). Because telemetry tags have become increasingly long-lived, surgical attachment has become the most popular tag attachment method. External attachment is now mostly restricted to applications where the sensor must remain in contact with the water (e.g. for measuring dissolved oxygen, light intensity and salinity), or where tag recovery is a high priority (e.g. archival tags).

Intragastric implantation of transmitters has been widely used for attachment to adult anadromous salmonids, which do not eat during their return freshwater migration. In other species, intragastrically inserted transmitters are likely to interfere with feeding, and in some species are quickly regurgitated leading to premature loss of the transmitter (Armstrong *et al.* 1992; Armstrong and Rawlings 1993). However, intragastric transmitters may still prove valuable when they can be voluntarily ingested by fish which are difficult to access or capture (e.g. deep lake fishes).

The implantation of telemetry tags into the peritoneal cavity, close to the centre of gravity of the fish, has the greatest potential for long-term studies (Lucas, in press). In fishes where the urogenital ducts lead to the body cavity (e.g. female salmonids, sturgeons, dipnoans, bowfins, male hagfish and agnathans), tags can be inserted into the body cavity through the gonoduct (Peake *et al.* 1997). In all other fish species, intraperitoneal implantation requires surgery (Box 1). It is clear that whenever surgery is involved, fish will be subjected to disturbance, the duration and extent of which varies substantially depending on fish species, age and tag to body weight ratio (Box 1). Surgically implanted tags can be shed through the incision (Marty and Summerfelt 1986), through an intact part of the body wall (Summerfelt and Mosier 1984; Lucas 1989) or through the intestine (Marty and Summerfelt 1986; Baras and Westerloppe 1999), although the latter process seems almost restricted to siluroid fishes. Hence it is important to critically evaluate implantation and other attachment methods prior to their application in fish studies. Baras *et al.* (in press) provide a review of the most appropriate techniques and considerations to be met. It is also important to bear in mind that in many countries surgical implantation of transmitters is a regulated procedure, often requiring a licence. Guidance on national regulations for surgical procedures is provided at http://www.hafro.is/catag, the site of the recent project on tagging of fishes for scientific research, funded by the European Union. Additionally, trans-national problems may occur in terms of inadequate consolidation of use of frequencies for animal tracking, which has resulted in research groups tracking other groups' fish when they have migrated across borders, or of interference problems for other users of radio frequencies.

Box 1. Recommended practice for surgical implantation of electronic tags in fish

The following information is summarized from Baras *et al.* (in press).

Anaesthesia. Except in extremely cold water, surgery requires that fish are chemically anaesthetized. Quinaldine (10–40 mg L^{-1}), tricaïne (25–100 mg L^{-1}) and 2-phenoxy-ethanol (0.25–0.40 mL L^{-1}) are among the most popular anaesthetics (Bonath 1977; Summerfelt and Smith 1990). Fish are immersed in an anaesthetic bath until the tolerance stage, then placed in dorsal recumbency in a support adapted to their morphology, with head and gills immersed in the anaesthetic.

Incision site and length. The site and length of the incision should be selected according to several criteria, including innocuity, healing dynamics and minimum expulsion risks. Midventral incisions reduce the risks of damaging the viscera when the fish is upside down, and striated muscles, which heal slowly (Roberts *et al.* 1973; Knights and Lasee 1996). Lateral incisions are suitable in fish with a midventral ridge, which prevents midventral tag insertion (e.g. serrasalmids), but are prone to puncture the gonads (Schramm and Black 1984), to damage striated muscles, and to cause bleeding, the latter being involved in adhesions and tag expulsion processes (Rosin 1985). Incision length should be as short as possible to minimize trauma and to limit the risks of tag exit via the incision. Recommended incision length to tag diameter ratios depend on the flexibility of the body wall, and thus on species and incision site: e.g. 1.4–1.5 in catfishes, 1.6–1.8 in salmonids, cyprinids and cichlids, and up to 2.5 for ventrolateral incisions in serrasalmids.

Internal positioning of the implant. Internal positioning should be done so as to minimize risks of damage to internal organs arising from tag movement inside the body cavity (Chamberlain 1979; Bidgood 1980; Schramm and Black 1984) and minimize pressure over abdominal tissue to reduce expulsion risks. Tag placement over the pelvic girdle is the most frequent position. Suturing the transmitter to the body wall was effective in Atlantic cod (*Gadus morhua*, Gadidae; Pedersen and Andersen 1985), but led to expulsion in channel catfish (*Ictalurus punctatus*, Ictaluridae; Marty and Summerfelt 1986).

Incision closure. Incision closure is traditionally achieved with separate stitches (Hart and Summerfelt 1975; Summerfelt and Smith 1990). Choice of absorable (e.g. catgut and Dexon) or non-absorbable (e.g. nylon and braided silk) suture material is often a trade-off between risk of expulsion through an unhealed incision when the filament dissolves, and the risks of infection due to the presence of transcutaneous foreign bodies (e.g. Thoreau and Baras 1997).

Surgical staples permit quicker incision closure (Mulford 1984), but they require removal of scales with greater risks of infection. Tissue adhesives give fast closure and so help to suppress the inflammatory response (Nemetz and MacMillan 1988; Petering and Johnson 1991), but the adhesive can be shed within a few days and is difficult to apply innocuously in small fish.

Healing rate. The rate of healing is proportional to the growth potential of the fish, and is thus faster in fast growing species, proportionally faster in juveniles than in adults (Thoreau and Baras 1997; Baras and Westerloppe 1999), and faster at warm than at cold temperatures (Knights and Lasee 1996). Juvenile tropical catfishes such as *Heterobranchus longifilis* (Clariidae) can heal abdominal incisions within 4 days (Baras and Westerloppe 1999), whereas adults of temperate or cold water species (e.g. Atlantic cod, Pedersen and Andersen 1985) require 4–6 weeks for complete healing. Permanent transcutaneous bodies, such as non-absorbable suture filaments or externally trailing antennae frequently promote a chronic inflammatory response (Roberts *et al.* 1973).

Implant encapsulation and exit. Irrespective of their coating (Helm and Tyus 1992), implanted tags often become encapsulated into host tissues in a classical foreign body reaction. Tags free in the

Box 1. *continued*

body cavity or encapsulated in connective tissue may be shed via an unhealed incision, or through the intact body wall, due to proliferating granulation tissue and contraction of myofibroblasts in the capsule (Marty and Summerfelt 1986, 1990; Lucas 1989) that force the tag through the route of least resistance. When the capsule adheres to the intestine, the intestinal wall may become disrupted, the tag enters the intestine, and is expelled by peristalsis. This process mostly seems restricted to siluroids (Marty and Summerfelt 1986; Baras and Westerloppe 1999). Implant exit is favoured by all factors inducing an internal pressure, such as heavy tags, enlarged gonads and infection, making prophylactic measures highly recommended and methods of positioning the tag far from the incision worthwhile (Ross and Kleiner 1982).

Post-operative recovery. Recovery should be as short as possible to prevent any detrimental effect of confinement on fish health and behaviour (Otis and Weber 1982).

Post-operative perturbation. Perturbation after the operation may extend over variable periods of time, and may affect fish to different respects including posture (Chamberlain 1979; Thoreau and Baras 1997), activity (Diana 1980), predator avoidance (Adams *et al.* 1998), swimming capacity and migration (Haynes and Gray 1979; Mellas and Haynes 1985; Moore *et al.* 1990; Adams *et al.* 1998).

Limitations of telemetry systems

Major drawbacks of telemetry systems relate to the costs of individual tags and detection equipment, numbers of fish tracked at a time, tag endurance and minimum fish size. A simple radio or acoustic tag costs US$ 200 or US$ 300, respectively. The cost of simple receivers for manual tracking ranges from US$ 500 to US$ 2 000, and ALSs including data logging computers range from US$ 5000 to more than US$ 10 000, depending on the software included. Automatic positioning systems with sonarbuoys and remote links may exceed US$ 50 000. Currently, the minimum size of VHF radio and acoustic tags limits the lower size of fish that can be tagged to about 12 cm.

The battery typically constitutes more than 80% of the transmitter weight and more than 50% of transmitter volume (Winter 1996). For a given power output, adapted to the study environment, transmitter endurance is proportional to battery size of a given type (e.g. 3-V $LiMnO_2$), restricting long-term studies to large fish only. However, longer life can be obtained without compromising range by programming a delayed start or longer interpulse interval (Voegeli and McKinnon 1996) or to operate on long-period duty cycles. For example, female barbel have been tagged with transmitters operating 70 days per year only, in order to investigate their spawning migrations and fidelity towards spawning grounds year after year (E. Baras, unpublished data). These tags have been operating over 3–4 years, whereas the normal endurance of a standard transmitter with identical power and size characteristics would not exceed 12 months.

An additional problem is the rather limited number of transmitters that can be tracked at one time. For acoustic transmitters, receiver bandwidth limits the number of frequencies to about 6–10, which can adequately be spaced over a range of about 15–20 kHz around the receiver's nominal frequency, and multipath effects limit the number of pulse rates of simultaneously operating tags to no more than 2–3 (Stasko and Pincock 1977). Radio frequencies enable larger numbers of frequencies to be used, usually with a 5-kHz or greater spacing, although national legislation on radio frequencies may restrict the range of frequencies available. Provided that tagged fish tend to remain solitary, standard radio transmitters can also be differentiated by pulse rates, with no more than three or four different pulse rates per frequency for easy identification by an operator. However, if automatic acoustic or radio receivers with the ability of identifying the interpulse period to the nearest millisecond are used, then tens of tags at each frequency can be employed, increasing the numbers of tags that can be tracked by over an order of magnitude. The use of coded radio or acoustic transmitters, each emitting an identifiable code of brief pulse(s) interrupting the normal longer pauses, provides another method of identification of 10–20 transmitters at each frequency (Eiler 1995; Voegeli and McKinnon 1996). Because these tags have longer interpulse intervals, tag life is also greater, but their identification requires a sophisticated receiver. These transmitters are of particular value for studies of fish migration at obstructions, where tagged fish may accumulate in high concentrations.

Care must also be taken in the sampling strategy of any tracking study. For example, Baras (1998) argued that the timing of relocating fish in telemetry studies at intervals longer than a day generates a bias in results, particularly in studies of home range movements or in detection of infrequent excursions outside the normal home range. In some species, the loss of accuracy can be predicted and corrected, but only in the river or lake under study. Hence, preliminary studies should be carried out to determine the effects of different time intervals between position fixes on the interpretability of results, and the optimum positioning intervals to be used later in long-term studies relying on the use of transmitters working on pre-programmed daily, weekly or monthly duty cycles. Similar issues must be considered in relation to the effect of time of day when fish are located; tracking at the same time of day may give a very biased impression of the fish's activity. Clough and Ladle (1997) showed that during summer dace in a small stream exhibited localized use of different areas during day and night, with rapid movements between these at dawn and dusk. Daytime or night-time tracking of these fish would have given the false impression that they were very sedentary.

Archival tags

Archival (data-storage) tags were recently developed to record large temporal series of environmental characteristics along the migration routes of fish travelling through contrasting and poorly accessible environments, such as the open sea (Metcalfe *et al.* 1992; Gunn *et al.* 1994; Sturlaugsson 1995; Sturlaugsson and Johansson 1996; Metcalfe and Arnold 1997; Sturlaugsson *et al.* 1998). Pre-programmed duty cycles of operation result in the periodic measurement of environmental and internal variables that are stored into a high memory capacity RAM chip instead of being immediately transmitted.

In principle, any kind of sensor can be coupled to an archival tag, and combinations of sensors enable reconstruction of fish tracks with acceptable accuracy, provided there is sufficient knowledge of environmental variables within the fish's presumed home range or migration path. For example, coupling of pressure and temperature sensors to archival tags attached to plaice (*Pleuronectes platessa*, Pleuronectidae) enabled demonstration of selective tidal stream transport over an unprecedented time-scale, together with accurate track reconstruction of this species in the North Sea (Metcalfe and Arnold 1997). Similarly, the coupling of light, pressure and temperature sensors permitted CSIRO scientists to highlight the long-range migrations of bluefin tuna (*Thunnus thynnus*, Scombridae) between Australia and South Africa (Gunn *et al.* 1994). Sturlaugsson (1995) first demonstrated the potential of data storage tags on adult Atlantic salmon during coastal migration, and the technique has now been used to examine river to sea, and return, movements of adult sea trout (*Salmo trutta*, Salmonidae; Sturlaugsson and Johansson 1996) and Arctic charr (Sturlaugsson *et al.* 1998). To date, archival tags are still large units, and their use is restricted to fish exceeding 500 g, but improvements in size reduction and increased storage capacity can reasonably be foreseen.

Archival tags are relatively expensive units (at least US$ 500 each) and the number recovered may be low. However, this is compensated for by the enormous amount of information that can be retrieved from a single tag. Recovery of tagged fish or tag information is thus a key factor in research programmes relying on archival tags. This may be achieved through an extensive recapture effort, including the assistance of fishermen for commercially important species. The probability of efficient tag recovery by fishermen requires easy identification of fish tagged with archival tags, and thus that these tags be attached externally (Metcalfe and Arnold 1997), or that the fish be double-tagged with an external passive tag or mark when internal archival tags are used. Additionally, tag recovery is assisted by adequate publicity and by incentives to declare tag recovery. When the probability of recapture is exceedingly low, detachable tags are worth considering. Pop-up tags, which release themselves from the fish after a pre-set time interval (Baba and Ukai 1996), have been used successfully on bluefin tuna in the Atlantic Ocean (Block *et al.* 1998). These are low-drag, positively buoyant units with a float and 16-cm aerial antenna. When the tag pops up to the surface, the float maintains the antenna in an upright position, and a limited amount of data can be transmitted to an ARGOS satellite. Similar applications can be reasonably foreseen in large lakes, with the absence of waves easing the recovery of archived data, but bulk and weight (*c.* 60 g) of pop-up tags restrict their application to very large fish only (> 5 kg, e.g. Nile perch, *Lates niloticus*, Centropomidae and lake sturgeon, *Acipenser fulvescens*, Acipenseridae). Prospects for development of much smaller 'pop-up' radio tags or Communicating History Acoustic Transponder (CHAT) tags that could be interrogated by automated underwater or land-based receivers are considered in a useful review by Moore *et al.* (2000). Nevertheless, the major problem with the use of archival tags is that migration paths can only be reconstructed from environmental data (light, pressure, temperature and salinity). Implicit in their application is that the environment is variable and documented sufficiently to permit this reconstruction. There also are additional limitations specific to each sensor type, including the risks of fouling of external sensors. Foreseeable applications of these techniques to freshwater fish are thus restricted to large lakes and to diadromous species.

Conclusions

As explained within this review, all techniques and methods for investigating the spatio-temporal behaviour of freshwater fish suffer from intrinsic, environmental and specific limitations. This is exemplified in Table 2, which presents a comparison of some key characteristics of several methods that may be used to study spatial behaviour of fishes in freshwater environments. Therefore, before starting any study on aspects of spatial behaviour of fishes in freshwater, one should define its objectives most clearly, and adapt existing techniques, alone or in combination, to the environment and target species of the study.

Generally, telemetry techniques can almost always prove valuable for species large enough to be tagged with transmitters. Beyond bringing direct knowledge on fish migration, activity patterns or energy expenditure, they can also help to delimit more efficiently the areas, seasons and times of the day to sample with capture or hydroacoustic techniques, or to look for tagged fish in the course of mark–recapture studies, including those involving archival tags. They can also pinpoint which sites may represent actual obstacles to fish migration from the fish's point of view (Hinch *et al.* 1996; Lucas and Frear 1997; Hinch and Bratty 2000), and help further study to focus on these. However, telemetry may not always be the best way of investigating fish spatial behaviour, especially when large samples are needed or when access to the environment is so difficult that tracking would not bring more information than recreational or commercial fish catches, such as in many tropical floodplain environments.

Catch per unit effort and mark–recapture techniques are most efficient where long-term fishery or monitoring studies are in place and data on crude spatial and temporal scales are acceptable. They also have the advantage of low technical requirements and low equipment costs. Where targeted studies with specific management or ecological questions are pertinent, recapture independent techniques may be more appropriate. Telemetric methods can provide high resolution information at the individual level, while hydroacoustics is increasingly providing information at the population level in large lake and river environments. Biochemical methods are becoming increasingly useful in determining the extent of population segregation through DNA analysis and for study of migratory and ontogenetic changes in behaviour through microchemistry of hard parts and stable isotope analysis. Studies which integrate several of the approaches mentioned above are likely to prove extremely informative for answering particular questions. For example, combinations of genetic marks and telemetric methods to investigate the functional basis of gene flow; combinations of otolith microchemistry and archival tags for better (and independent) mapping of history of habitat use; and telemetric methods together with hydroacoustics to determine whether the spatial behaviour of fishes in 'deep' habitats is influenced by social interactions.

Advances over the past 30 years have resulted in techniques for studying fish spatial behaviour in natural freshwater environments that are so diverse and of such high performance that most problems of a fundamental or applied nature can now be tackled with adequate accuracy at the appropriate spatial scale, provided suitable methods are selected and applied, alone or in combination. Advances in information technology, particularly through the world wide web, also make it possible to relay, almost immediately, methodological information on a global scale from specialists in particular techniques or to share data bases of information from mark–recapture experiments. The addresses of a

Table 2 Comparison of characteristics of selected methods for use in studies of freshwater fish behaviour.

Characteristics	Reflected natural radiation	Reflected artificial radiation	Active radiation from a transmitter	Active radiation from a transmitter	Active radiation from a transponder	Active radiation from a transponder	Interference with electric field
	Visual	Hydroacoustics	VHF radio tagging	Acoustic tagging	Powered LF transponders	PIT tagging	Resistivity fish-counters
Situation	Clear water, restricted site. Shallow streams, rivers and lakes	Little noise or entrained air, few plants. Lowland rivers and lakes	Low conductivity ($< 500\ \mu S\ cm^{-1}$), shallow. Usually oligotrophic-mesotrophic streams and lakes	Low noise, low turbidity, little entrained air. Usually lakes and slow-moving rivers	Any aquatic environment Usually deep, noisy and highly conductive, e.g. harbour, barrage	Any environment, so long as fish swims within range of antenna	Freshwater, must be set in such a way that fish swims within range
Location of sensor	Within sight	Fixed station or mobile on a boat	On land or boat or air	In water	Within range, usually on river bed	Within range	On river bed, on weir or in fish pass
Range (m)	1–10	20–200	20–5000	20–1000	2–30	0.1–2.0	<0.5
Typical lifespan (days)	For tags, limited by tag's algal growth	No limits	20–600	10–300	30–300	$>$ 3000 (or life of fish) if retained	No limits
Water depth (m)	$<$ 30 for SCUBA, $<$ 2 for snorkelling	$>$ 1.5	Dependent on conductivity (normally $<$ 5)	Dependent on noise (usually 0.5–100)	Within range (usually 2–10)	Within range (generally $<$ 1)	Within range (*c.* $<$ 0.5)
Minimum fish size (cm)	Visible (*c.* 5)	1	12	12	30	5	20
*Technical demand	Low–Moderate	High	Moderate	Moderate	High	Moderate–high	Moderate
*Sample size	10–10^2 †	No limits	10^2–10^3	10–10^2	10–10^2	10^2–10^5	No limits
Disadvantages	Poor range, relies on water clarity, poor for cryptic species, difficult to obtain long-term tracks	Poor species and individual identification. High data processing requirements	Lower directionality than acoustic systems. Poor range in deep, lowland waters. May influence behaviour (next three columns also) and lacks population scale measurement (next two columns also)	Shorter life than equivalent radio tags Usually requires boat. Poor range in noisy environs. Sound reflections. Fewer tags can be operated cf. radio	Low range, narrow range of utility. Data collection limited to vicinity of antenna (non-mobile)	Very low range, data collection limited to antenna sites or with recaptured fish	Very low range, usually must be sited at structure. No individual identification, limited size sorting
Value for fish behaviour studies	Low	High	High	Medium (in freshwater)	Low	High (at bypasses/ streams and for small fish)	Low
*Approx. equipment costs (US$)	5×10^2–$> 10^3$	10^4–10^5 (boat, etc., extra)	$\geqslant 2 \times 10^2$ per tag 5×10^2–10^4 for system	$\geqslant 3 \times 10^2$ per tag 10^3–4×10^4 for system	$\geqslant 4 \times 10^2$ per tag $\geqslant 10^4$ for system	4 per tag $\geqslant 2 \times 10^3$ for system	$\geqslant 10^4$ (+ structure)

*Estimates for a field study typical of those reported in this review.

†Estimate for identification of individuals.

Table 3 A selection of some useful web sites providing technical information on various methods of use for studying spatial behaviour of freshwater fishes. These are a small selection of web sites and a range of other companies also provide similar products and advice. Reference to manufacturer's internet sites does not infer our endorsement of their products

Web site	Nature and originator of site	Information
http://www.hafro.is/catag	European Union concerted action project on tagging methods (CATAG)	Detailed advice on all aspects of conventional, archival and telemetry tags, including suppliers, methods, health and welfare
http://www.atstrack.com	Advanced Telemetry Systems, Inc. Manufacturer of teleomertry equipment	Technical information on telemetry equipment and tags
http://www.biomark.com	Biomark. Manufacturers of PIT equipment	Technical information on PIT tags and equipment
http://www.biotrack.co.uk	Biotrack Ltd. Manufacturer of telemetry equipment	Technical data, programme for predicting transmitter life/range
http://www.lotek.com/lotek/index.htm	Manufacturer of telemetry equipment, archival tags	Technical information on telemetry equipment and tags, research developments
http://sonotronics.com	Sonotronics. Manufacturer of acoustic telemetry equipment	Technical information on acoustic tags and equipment
http://www.star-oddi.com	Star-Oddi. Manufacturer of archival tags	Technical information on archival tags
http://www.ukid.co.uk	UKID systems. Manufacturer of PIT tags and equipment	Technical information on PIT tags and equipment
http://www.vemco.com	Vemco. Manufacturer of acoustic telemetry equipment	Technical information on acoustic tags and equipment
http://www.wildlifecomputers.com	Wildlife Computers. Manufacturer of satellite tags and archival tags	Technical information on satellite tags and archival tags
http://www.nmt-inc.com	North-west Marine Technology, Inc. Manufacturer of conventional and archival tags	Technical information, research developments, case studies
http://www.biosonicsinc.com	Biosonics, Inc. Manufacturer of fisheries hydroacoustic equipment	Technical information, research developments, case studies
http://www.htisonar.com	Hydroacoustic Technology, Inc. Manufacturer of fisheries hydroacoustic equipment	Technical information, research developments
http://www.ife.ac.uk/echosums	Hydroacoustics users' group site, run by NERC Centre for Ecology and Hydrology	Discussion group, advice, research developments
http://www.fisheries.org/links/fisheries_vendors_links.com	American Fisheries Society	Lists many suppliers of equipment for fish behaviour studies
http://dfomr.dfo.ca/science/mfd/otolith	Otolith Research Laboratory, Bedford Institute of Oceanography	Research developments in otolith microchemistry
http://pectinid.efan.no/efan	European Fish Ageing Network (EFAN) site. EU concerted action project	Site mainly deals with ageing but has bulletin boards on otolith research meetings, developments and reports synthesizing information on otolith microchemistry relevant to spatial behaviour of fishes

variety of useful web sites that provide information on many of the methods described in this paper—or manufacture equipment—are given in Table 3. Therefore, limitations on gathering pertinent biological information on time and space use by fish are increasingly becoming determined only by our imagination and available resources.

Acknowledgements

We thank Annie Duncan, who recently passed away and to whom this article is dedicated, for her contagious enthusiasm and for useful discussion on advances in shallow-water hydroacoustics. E. Baras is a scientific research worker of the Belgian FNRS. Reference to manufacturers or trade names does not infer our endorsement of those products.

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