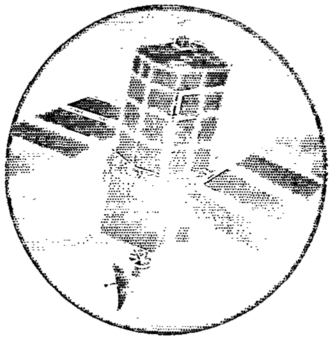
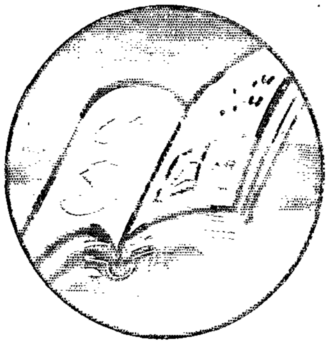
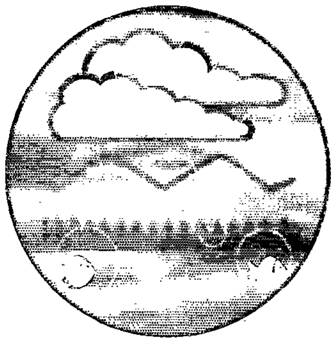
Coarse Fish Migration Occurrence, Causes and Implications

Research and Development

Technical Report

W152

ENVIRONMENT AGENCY

Coarse Fish Migration Occurrence, Causes and Implications

Technical Report W152

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Statement of use
This report summarises the findings of aliterature reveiw of the occurrence, causes and implications of coarse fish migration in UK rivers. The information within this document is for use by EA staff and others involved in the management of fish stocks in rivers and those involved in habitat modification works which may have an impact on the free movement of coarse fish.

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Amendments
Any corrections or proposed amendments to this manual should be made through the regional Agency representative on the Water Resources National Abstraction Licensing Group.

CONTENTS

1. EXECUTIVE SUMMARY

A literature review was undertaken to consider existing knowledge concerning the occurrence, causes and implications of migration by coarse fish (non-salmonid freshwater fish) occurring in England and Wales. The review concentrated on riverine migration, defined in its broadest sense, and considered information from outside the UK where relevant. A critique of methods appropriate to the study of coarse fish migration was also carried out. Literature published up to April 1998 was covered, resulting in the examination of over 2000 articles of which nearly 450 are cited in this review. Additionally, information from continental Europe was obtained through visits to the Water Research Institute, Prague, Czech Republic, and the Laboratory of Fish Demography and Aquaculture, University of Liège, Belgium.

Although the occurrence of migration by coarse fish is now generally accepted, detailed published information is limited. Five main movement patterns were defined: pre- and post-spawning migration, young-of-the-year movement, feeding migration, refuge migration, and post-displacement movements. Spawning migrations are often the most extensive and most widely reported migration type, for many British freshwater species including several cyprinids (mainly rheophiles such as barbel *Barbus barbus*, chub *Leuciscus cephalus* and dace *Leuciscus leuciscus*, but also some limnophiles such as roach *Rutilus rutilus* and bream *Abramis brama*). The effects of stimuli on patterns of movement are discussed, particularly physical environmental factors such as river discharge, water temperature and light levels. Although these factors are shown to be important for stimulating and influencing migration they have not been well studied or their effects quantitatively defined.

Several implications of coarse fish migration are identified. In particular, the effects of barriers to migration are considered. A Model for the Assessment of Barriers to FISH migration (MABFISH) is proposed, which seeks to prioritise the circumstances under which fish passes might be installed to most effectively aid freshwater fish migration.

Radio-tracking, hydroacoustics and automated Passive Induced Transponder (PIT) tag systems are identified as the most effective methodologies available for identifying the nature and extent of coarse fish migration, the influence of environmental factors such as flow on migration, and for measuring the effects of barriers on fish migration. These techniques are complementary for studying the range of river habitats over which fish migration occurs, and for appropriate data acquisition, and would be most beneficially used in an integrated fashion. Further information quantifying coarse fish migration in lowland rivers is needed, and in particular, an understanding of its relationship with environmental factors, and the influence of barriers, in order to improve effective fisheries management.

We have provided individual species summary tables of all information concerning migration within an Appendix to this report.

Keywords: Literature review, coarse fish, migration, spawning, feeding, refuge, flow, temperature, telemetry, tracking, hydroacoustics, barriers, weirs, impoundments, fish pass.

2. INTRODUCTION

Coarse fish, especially cyprinids, are often the major component of fish communities of the middle and lower reaches of temperate, lowland rivers. These river systems are increasingly subject to impoundment and weir construction (Welcomme, 1994). The ecological importance of longitudinal and lateral connectivity of river systems is increasingly being realised and efforts to maintain and reintroduce these characteristics are now regarded as important. Some riverine cyprinids are recognised as being migratory (Smith, 1991) but in the UK the possible importance of migration and other movements in the life-cycle of coarse fish species has received inadequate attention. O'Hara (1986) argued that such information was urgently needed in order to develop sound fisheries management practice. However, the impetus for such work only really increased in the last few years. In recognition of this need the Environment Agency, in April 1997, began a project to review the extent of our knowledge concerning the migration of coarse fish in its broadest sense. This report is the result of that review process.

The overall aim of this review is to determine the extent of knowledge of 'coarse' fish migration, its purposes and triggers and its implications for river management. Within this overall aim three specific objectives were identified:

(i) To determine by literature review and through interviews with key Environment Agency staff and other individuals, the extent of known and suspected migration in 'coarse' fish, taking account of relevant information on differences between species, distances travelled, swimming speeds, timing, purposes and triggers.

(ii) To determine, from the review process, the purposes and triggers of natural migratory patterns in coarse fishes.

(iii) A critique of methods used for studying 'coarse' fish migration (e.g. radio-tagging, PIT tagging, acoustic surveys).

(iv) To predict the influences and implications of human-induced changes to environmental conditions on migratory patterns, including; (a) the effects of barriers to migration such as water retention structures (weirs, locks, dams, sluices etc.); (b) the efficiency of fish passes in enabling fish to pass through these structures; (c) the influence of water quality, including temperature plumes, changes in river sediment loads, oxygen and ammonia levels, etc.; (d) abstraction; (e) water transfer schemes; (f) consequence of wash-out; (e) habitat management; (f) the influence of restocking policy and fish transfers within the same river system and between rivers, and (g) implications for coarse fish in lakes, which may utilise rivers for spawning or other aspects of their behaviour.

(v) To make recommendations for river management schemes and operational activities, as far as is possible, within the constraints of limitations in the available knowledge of coarse fish migration.

(vi) On the basis of the information gathered, to suggest monitoring and assessment criteria by which the success of fish passes may be evaluated with confidence.

(vii) To identify important gaps in our knowledge of the migration and movement of coarse fish in rivers, as well as within/to/from stillwaters, and to make recommendations for further research.

In conducting this review it was agreed between the contractor and the Environment Agency that the focus would be on coarse fish movements in freshwater riverine (including canals) environments only. We have considered studies in lacustrine environments where fish move between lakes and rivers or where information on fish behaviour or techniques used may be relevant to studies of coarse fish migration in riverine environments.

Under the Environment Agency's terms of reference coarse fish were defined as:

(i) All native (and naturalised) British cyprinids (Family *Cyprinidae)*
(ii) All native (and naturalised) British perciforms (Family *Percidae*)
(iii) Pike *Esox lucius*
(iv) Grayling *Thymallus thymallus*
(v) Eel *Anguilla anguilla*
(vi) Wels Catfish *Siluris glanis*
(vii) All native British loaches (Family *Cobitae*)
(viii) Bullhead *Cottus gobio*
(ix) The freshwater sticklebacks (Family *Gasterosteidae*)
(xi) Lampreys (Family *Petromyzontia*)

Under the Agency's terms of reference we have excluded from the review:

(i) All marine fish
(ii) All salmonids.
(iii) Burbot *Lota lota*
(iv) Coregonids
(v) *Alosa* spp. - a separate R&D project is being conducted on shad
(vi) The sturgeons (Order *Chondrostei*).

However, much of the literature on fish migration originates abroad and is based on non-native species. This review takes account of this literature where it is appropriate to the coarse fish listed above and to British conditions. Additionally, where information is known about the migratory behaviour of marine fish which regularly migrate into freshwater (e.g. bass *Dicentrarchus labrax*, flounder *Platichthys flesus* and thin-lipped mullet *Liza ramada*) this was also taken into account.

3. METHODS

This review is the result of five processes;

(i) An extensive literature review using the collections of the authors of this review, on-line bibliographic services such as BIDS and ASFA and the comprehensive library facilities of the University of Durham and RHIER.

(ii) A questionnaire of selected Environment Agency fisheries staff requesting information on published work, internal and external reports and personal observations together with follow-up discussions and visits.

(iii) A review of work in continental Europe through visits to E. Baras and J. C. Philippart at the Laboratory of Fish Demography and Aquaculture, University of Liège, Tihange, Belgium and to the Water Research Institute, Prague, Czech Republic co-ordinated by O. Slavík

(iv) Requests for further unpublished work and personal observations from other experts in this field.

(v) Discussion and evaluation of draft material by other experts in the field.

4. INCIDENCE AND CAUSES OF MIGRATORY BEHAVIOUR IN COARSE FISH

4.1 Introduction

Fish form the most mobile component of the permanent aquatic community. Locomotor muscle normally comprises 70-80% of body volume in freshwater fish and, in combination with rayed fins, provides the necessary power and stability for life in flowing waters. However, conditions in rivers are often highly variable in space and time. Fish behaviour is particularly influenced by factors such as flow, temperature and water quality, and habitat use may alter with changes in environmental conditions (Garner, 1997). Movement is one of the main options available to river fish when responding to changes in their river environment. That migrations of fish should occur, is therefore not surprising. Yet, despite this, the movements of coarse fish species have not been studied in detail. Until recently, most non-salmonid freshwater fish were regarded as non-migratory and considered to be static populations with their longitudinal location in the river defined by habitat preferences, leading to zonation (Huet, 1949). Indeed, in some cases, movements of coarse fish have been considered unimportant by many scientists and fisheries managers in the United Kingdom as the following quote from Beach (1984) confirms:

> "As well as salmon and sea trout, rivers often have stocks of coarse fish and eels. Coarse fish migrations are generally local in character and although some obstructions such as weirs may allow downstream passage only, they do not pose a significant problem. Eels, like salmon and trout, travel both up and down river during the course of their life histories. However, the climbing power of elvers is legendary and it is not normally necessary to offer them help, while adult silver eels migrate at times of high water flow when downstream movement is comparatively easy: for these reasons neither coarse fish nor eels are considered further".

There is considerable variation in the extent of movements between species; ranging from very limited movement of small, cryptic fishes such as bullhead to long migrations covering hundreds of kilometres, as for Atlantic salmon *Salmo salar*. To the fishery manager such variation in the use of time and space by fishes makes effective river management difficult for a number of reasons:

(i) Movements of fishes between parts of a river system, for example from the main river to a tributary and back, can introduce errors in stock assessment.

(ii) There can be difficulties in establishing the importance of fish movement in relation to trophic dynamics and energy flux within rivers, for example predator-prey interactions.

(iii) There is a need to define the impact of numbers and types of river obstruction on individual fish species and whole fish communities of rivers.

(iv) an appropriate degree of free passage for fish must be established to enable access to all habitats required for successful completion of their life history and therefore the natural maintenance of stocks.

(v) Movement can lead to the loss of fish from river systems, to sea for example, through active or passive movement, both for natural populations and stocked fish.

4.2 Defining Migration

Northcote (1984) provides a convenient definition of migration as those movements that result in an alternation between two or more separate habitats, occur with a regular periodicity and involve a large proportion of the population. In the United Kingdom four types of migration can be recognised:

(i) Anadromous - spawning in freshwater, but spending a substantial proportion of time at sea, e.g. sea lamprey *Petromyzon marinus*

(ii) Catadromous - spawning at sea, but spending a substantial proportion of time in freshwater, e. g. European eel.

(iii) Amphidromous - migrating between sea and freshwater, but movements are not directly related to spawning but occurs in a substantial proportion of the population, e.g. thin-lipped mullet.

(iv) Potamodromous - migrating entirely in freshwater, e.g. barbel *Barbus barbus*

The definition of amphidromy derives from Myers (1949). However, all amphidromous fishes spawn in either freshwater or marine environments and can therefore also be classified as either anadromous or catadromous. The term amphidromous has tended to be applied where diadromous migrations (between freshwater and marine habitats) have been limited in extent or duration, often involving periods of residence in brackish water. In this review all diadromous species will be classified as anadromous or catadromous depending on where they spawn. These definitions can be applied to migratory movements ranging from just a few metres to hundreds of kilometres or over time periods ranging between diel cycles to the lifetime of the fish.

Northcote (1978) argued that three types of habitat can be recognised; one for reproduction, one for feeding and one for refuge in periods of unfavourable conditions. Individual fish can maximise their genetic fitness if they move between these habitats at the right times during their lifecycles (Figure 1).

This is a good definition for some species of fish including many salmonids whose spawning and feeding areas are clearly separable geographically. However, many freshwater species remain within a more confined area, such as a single river or lake, throughout their life cycle but select various habitats for particular purposes (Figure 2).

For example, barbel, dace *Leuciscus leuciscus* and chub *Leuciscus cephalus* use the same areas for spring spawning and summer feeding but move to a different refuge habitat in unfavourable conditions, most commonly in winter. Bullhead, stone loach *Barbatula barbatulus* and gudgeon *Gobio gobio* broadly use the same habitats for all three purposes and consequently do not need to migrate long distances.

Spawning and refuge migrations tend to be more directed and greater in extent than feeding movements which are usually more random. These patterns of movement are also often complicated by the ontogenic stage of the individual with many species having nursery areas in which juveniles feed or take refuge but which adults never use (Northcote, 1984).

Migration may also occur if an individual is displaced from its home area. In this case some fish may be able to return to this area after this displacement. This will benefit those fish that have invested in territorial defence, parental care or acquiring local knowledge (Smith, 1991).

Migratory movements can therefore be broadly described by the following five categories:

(i) Pre- and post-spawning migration

(ii) Young-of-the-year (YOY) migration.

(iii) Feeding migration

(iv) Refuge migration

(v) Post-displacement migration.

Although recent information is increasingly demonstrating that coarse fish often display extensive and directed movements, the regular cyclical migration between specific habitats is largely unproven. Therefore, in this review the term 'migration' as applied to coarse fish is used in its very widest sense to consider most movements.

Different species occupying different parts of a river catchment will undertake these migrations at different times of the year with varying levels of duration and extent. Figure 3 shows a "typical" meandering river with each different type of migration superimposed onto the diagram. The nature and extent of migration may be influenced by biotic environmental factors such as predation-risk and abiotic environmental factors such as temperature. Furthermore, anthropogenic influences such as the building of artificial embankments near towns and industrial sites, dams, weirs and outfalls from sewage farms and power stations may restrict or elicit migration.

In this section the incidence and causes of these five types of migration in non-salmonid freshwater fish are reviewed. Table 1 summarises those species of British coarse fish for which published information or anecdotal observations are available which indicate some form of migratory behaviour. Cowx & Welcomme (1998) provide lists of migratory freshwater fish which move between marine and freshwater environments, within rivers or between rivers and lakes. These lists differ from Table 1 in that a considerable number of species identified as being migratory do not appear in Cowx & Welcomme (1998), probably reflecting the paucity of objective, quantitative information for these species and variability between catchments or regions.

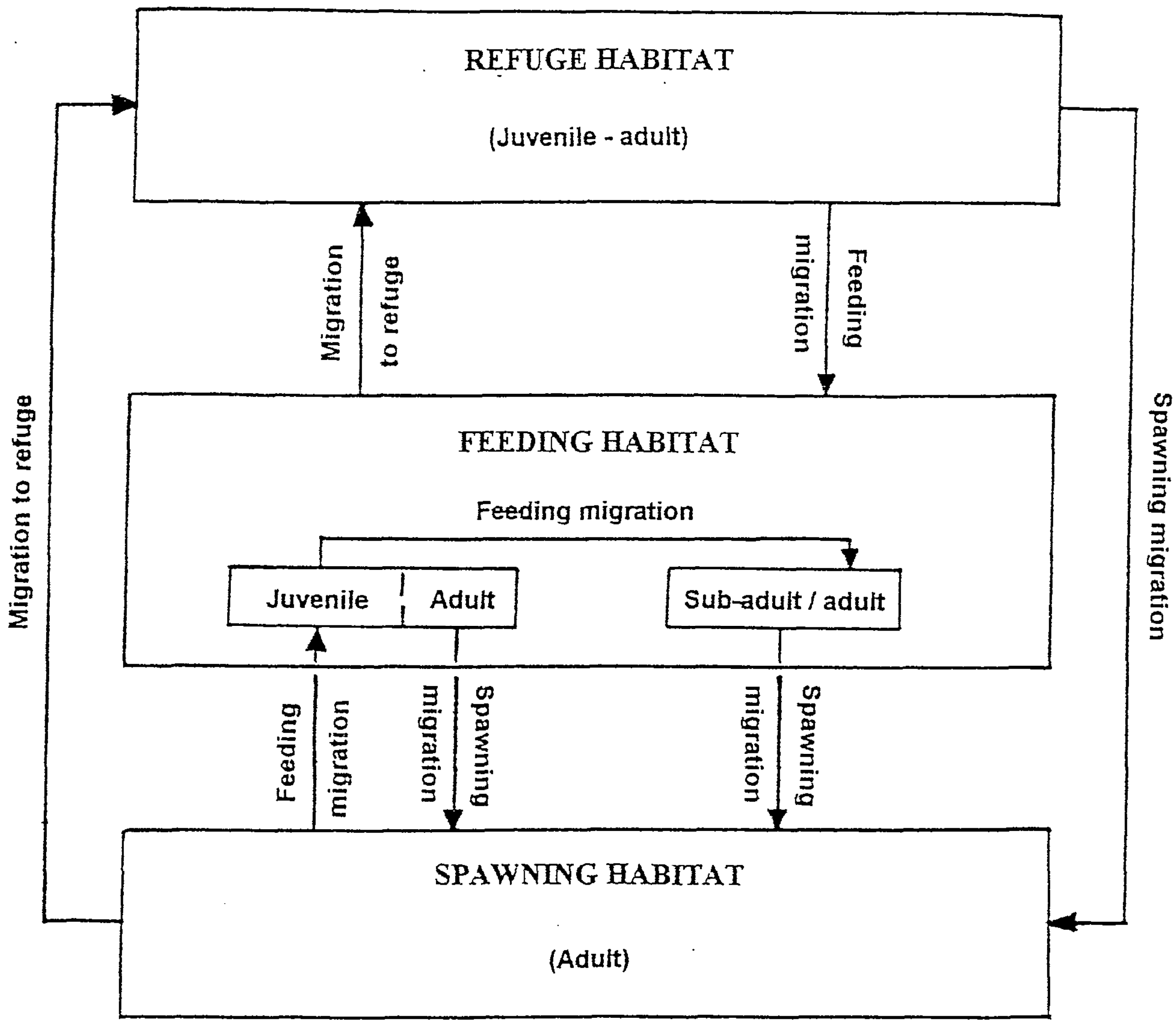


Figure 1 Schematic "Northcote" model of fish migration between three principal habitats (Modified from Northcote, 1978).

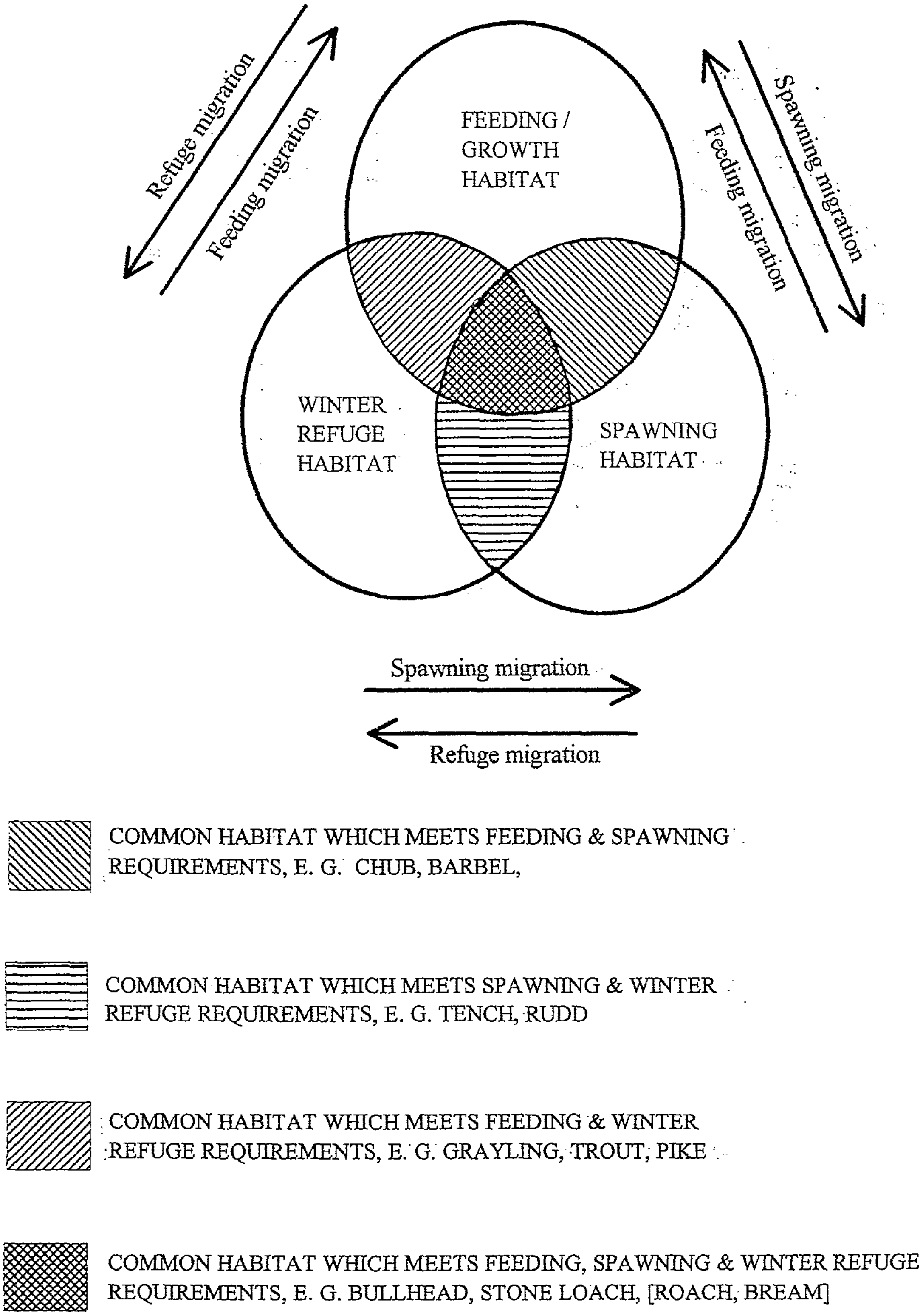


Figure 2 Schematic model for migration of resident, freshwater adult/sub-adult fish between principal habitats in UK rivers.

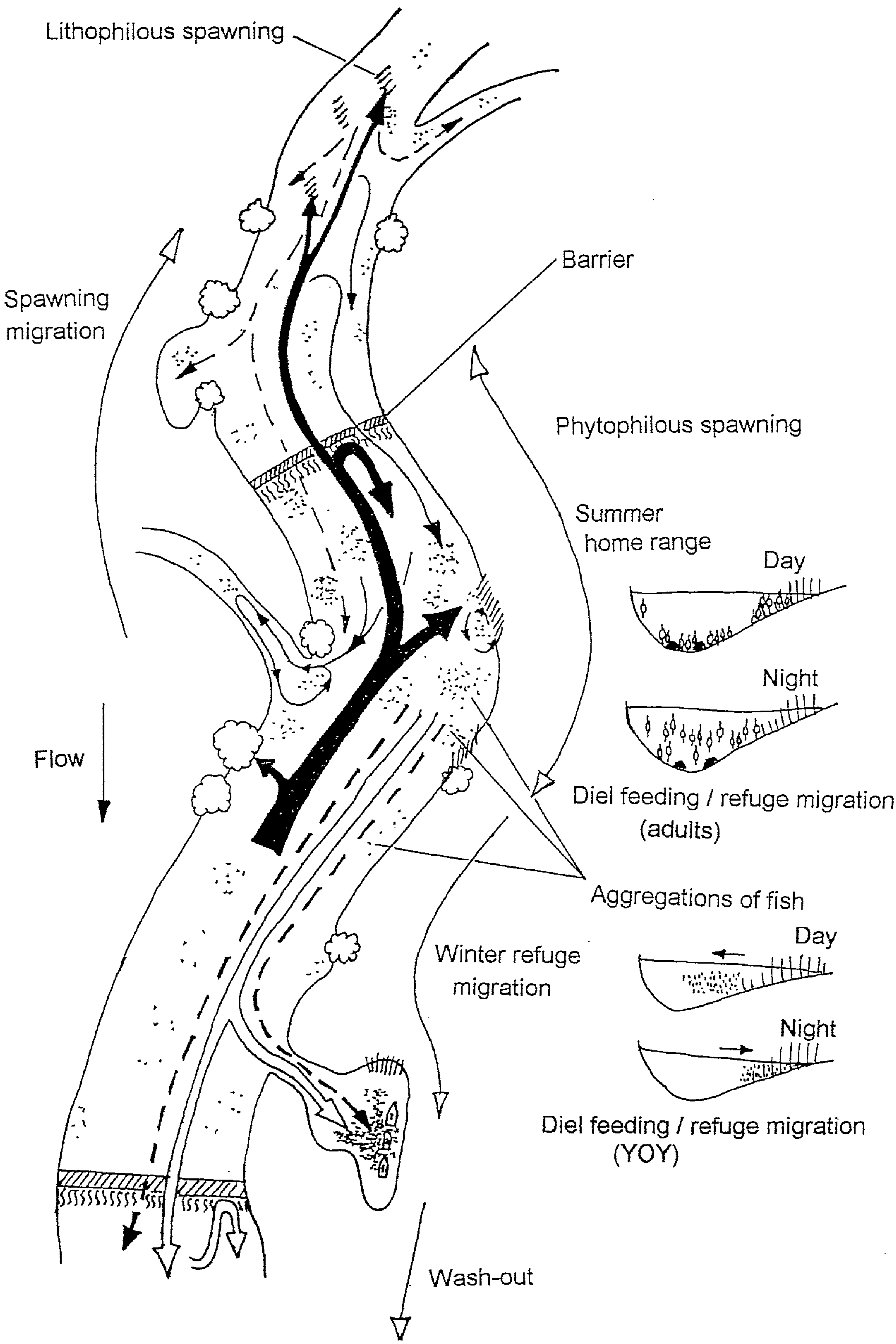


Fig. 3. Schematic representation of coarse fish migration patterns in a lowland river. Continuous lines indicate movements of adult fish; broken lines indicate movement of Young of Year. The bold black line represents the main spring spawning (adults) / redistribution (juveniles) migration, while wide, open line represents the main winter refuge migration (adults, juveniles).

Table 1 List of coarse fish occurring in British waters for which published information or anecdotal observations are available which indicate some form of migratory behaviour together with those for which little or no information is available. For the species in the latter category, migratory behaviour may not exist.

Migratory	No information
Lampreys (Petromyzonidae)	Carps (Cyprinidae)
River lamprey *Lampetra fluviatilis*	Common carp *Cyprinus carpio*
Brook lamprey *Lampetra planeri*	Crucian carp *Carassius carassius*
Sea Lamprey *Petromyzon marinus*	Goldfish *Carassius auratus*
Eels (Anguillidae)	Bitterling *Rhodeus sericeus*
Eel *Anguilla anguilla*	Rudd *Scardinius erythropthalamus*
Pike (Esocidae)	Tench *Tinca tinca*
Pike *Esox lucius*	Grass carp *Ctenopharyngodon idella*
Grayling (Thymallidae)	Perch (Percidae)
Grayling *Thymallus thymallus*	Ruffe *Gymnocephalus cernua*
Carps (Cyprinidae)	
Barbel *Barbus barbus*	
Gudgeon *Gobio gobio*	
Common bream *Abramis brama*	
Bleak *Alburnus alburnus*	
Minnow *Phoxinus phoxinus*	
Roach *Rutilus rutilus*	
Silver (white) bream *Blicca bjoerkna*	
Chub *Leuciscus cephalus*	
Dace *Leuciscus leuciscus*	
Ide (Orfe) *Leuciscus idus*	
Loaches Cobitidae)	
Spined loach *Cobitis taenia*	
Stone loach *Barbatula barbatulus*	
Catfishes (Siluridae)	
Wels *Silurus glanis*	
Sticklebacks (Gasterosteidae)	
3-spined stickleback *Gasterosteus aculeatus*	
9-spined stickleback *Pungitius pungitius*	
Sculpins (Cottidae)	
Bullhead *Cottus gobio*	
Perch (Percidae)	
Perch *Perca fluviatilis*	
Zander *Stizostedion lucioperca*	
Mullets (Mugilidae)	
Thin-lipped mullet *Liza ramada*	
Golden-grey mullet *Liza aurata*	
Thick-lipped mullet *Mugil cephalus*	
Bass (Serridae)	
Sea Bass *Dicentrarchus labrax*	
Flatfish (Pleuronectidae)	
Flounder *Platichthys flesus*	

4.3 Spawning migration

4.3.1 Anadromous species

Lampreys

In the northern hemisphere there are few non-salmonid species which spawn in freshwater and migrate to the sea to feed. The most notable of these are the sea lamprey and river lamprey *Lampetra fluviatilis* (Table 2). After metamorphosis from the larval form, anadromous lampreys move downstream towards the sea or estuary where they feed. After a period of one to three years they return upriver during their spawning migration, spawn and then die (Hardisty, 1979; Maitland, 1980a). Sea lampreys moving upstream have an estimated rate of progress of about 0.18 km h^{-1} although this may vary with the strength of the downstream current opposing this movement (Hardisty, 1979). Migrations of 300 km or more are known although some individuals spawn just above the tidal limit (Bigelow & Schroeder, 1953). Unlike the salmonids there is no evidence to suggest that anadromous lampreys home to their natal streams. In fact, Bergstedt & Seelye (1995) demonstrated that of 555 sea lampreys tagged with coded wire tags just after metamorphosis none returned to their natal streams as spawning adults. Nikolskii (1961) described the occurrence of both winter and spring migrations in this species with spring-run lampreys having more mature gonads than winter. In sea lamprey and river lamprey, males have a tendency to reach the spawning grounds first and begin preliminary nest building (Hardisty, 1979; Maitland, 1980a).

Table 2 British coarse fish species which carry out anadromous spawning migrations. ? indicates that no information is available.

Species	Timing	Age	Distance upstream	References
River lamprey *Lampetra fluviatilis*	autumn	1-4 years	tidal limit to 300 km	Bigelow & Schroeder (1953); Hardisty (1979); Maitland (1980a); Sjöberg (1980); Lucas (1998a); Lucas *et al.* (1998)
Sea lamprey *Petromyzon marinus*	spring & winter	>3 years ?	often over 50 km	Nikolskii (1961); Hardisty (1979); Maitland (1980a); Lucas *et al.*, 1998
Pike *Esox lucius* (Bothnian Sea)	May	adult	6 km	Johnson & Müller (1978) and Müller (1982)
3-spined stickleback *Gasterosteus aculeatus trachurus*	spring	1 year	lower limits only	Wootton (1976), McDowall (1988)
9-spined stickleback *Pungitius pungitius*	?	?	?	McDowall (1988)

Sticklebacks

Two species of stickleback are facultatively anadromous - the three-spined stickleback *Gasterosteus aculeatus* and the nine-spined stickleback *Pungitius pungitius*. The life cycle of *G. aculeatus* is complex and the species occurs in three forms (Wootton, 1976):

(i) '*trachurus*' - often anadromous, sometimes fully marine;
(ii) '*leirus*' - not anadromous;
(iii) '*semi-armatus*' not anadromous.

McDowall (1988) states that migratory three-spined sticklebacks are clearly anadromous although migration to the sea is not essential for sexual development. Adults that over-winter in the sea migrate into freshwaters in the spring as one year old fish. Spawning usually takes place in the lower reaches of freshwater streams. Kedney *et al.* (1987) argued that the energetic requirements of upstream migration to spawn in freshwater were relatively low and, although hatching takes longer in freshwater, there is lower predation in rivers. After hatching the young feed and grow in freshwater before returning, together with adults that have survived spawning, to the sea in the summer and autumn. There is little information on the migratory behaviour of the nine-spined stickleback although McDowall (1988) speculates that this species may be marginally anadromous.

Other species

Other species that are not normally considered to be diadromous may also exhibit anadromy in certain circumstances. Johnson & Müller (1978) and Müller (1982) showed that pike in the coastal area of the Bothnian Sea were, in many cases, anadromous. Pike ascend up to 6 km into the coastal rivers to spawn. After spawning the pike leave the stream and migrate back to the sea. Such migration is unlikely in the United Kingdom although pike are known to winter in some brackish water systems in East Anglia.

4.3.2 Catadromous species

Eel

The most well-known non-salmonid catadromous species in European waters is the eel. The large-scale migration of this species between its spawning grounds in the Sargasso sea and freshwater feeding habitats are well documented (Harden-Jones, 1968; Tesch, 1977). This review is primarily interested in migratory behaviour in the freshwater environment so attention will be focused on this stage of the eel life cycle. The migration of silver eels to their spawning grounds takes place in the late summer or autumn. The exact month, however, may vary as a result of a temporal shift from inland waters to coastal waters with the earliest migrations occurring furthest from the sea (Tesch, 1977). There is also some migratory activity in the spring and it is argued that this is due to eels which are prevented from migrating in the autumn becoming inactive in the winter to resume their migration in the spring (Frost, 1950). The migration of males and females do not coincide which may be due to larger females coming from inland waters whereas the smaller males occur in coastal areas (Tesch, 1977).

Silver eels drift downstream in the middle depths of rivers, often together in groups (Tesch, 1977). The distances covered by migratory silver eels vary depending on the individuals swimming capacity, swimming speed and current (Table 3).

Svedang & Wickstrom (1997) argued that the high proportion of lean silver eels at a number of sites in Sweden refuted the hypothesis that eels must accumulate fat to a critical level before events associated with spawning are possible. They postulated that this suggested that either many eels will not be able to spawn successfully or that the energy needs of migrating eels have been exaggerated. Svedang & Wickstrom (1997) argued that it was more likely that eel maturation is more flexible than previously thought. The transition from the growth phase to the migratory phase may be a step-wise process which can be arrested at various stages as observed for salmon by Mills (1989). Svedang & Wickstrom (1997) showed that landlocked eels could revert from silver to yellow and resume feeding.

Other species

Mullet species often spend considerable periods of time in brackish water and freshwater, but return to sea to spawn. These species may therefore be regarded as catadromous, but in all cases movement into freshwater is a facultative behaviour. Thin-lipped mullet often penetrate well into freshwater and may spend long periods of time in rivers during spring and summer. Thin-lipped mullet and golden-grey mullet *Liza aurata* have a southerly distribution and are most abundant in rivers flowing to the south England coast. Thick-lipped mullet *Mugil cephalus* are found all around the British Isles. Juvenile bass *Dicentrarchus labrax* often accumulate in estuaries, and sometimes freshwater, particularly in summer, but always return to the sea to spawn. Various flatfishes (Family *Pleuronectidae*) and soles (Family *Soleidae*) may also be present in brackish or freshwater (McDowall, 1988). The most common flatfish which spends time in British rivers is the flounder, again principally in the juvenile phase, returning to sea to spawn. It must be stressed that for all of these species the principle reasons for incursions into freshwater are normally for feeding or predator avoidance, and that catadromous spawning migrations are simply the resultant response to these incursions.

Table 3 British coarse fish species which carry out catadromous spawning migrations.

Species	Timing	Age	Size	Distance	References
Silver eel *Anguilla anguilla*	summer & autumn	6-16 years	maturing (35 cm)	variable	Tesch (1977); Mann & Blackburn (1991); Lühmann & Mann (1958)
Thin-lipped mullet *Liza ramada*	autumn	yearly	mature (> 20cm)	up to 200-300 km	Hickling (1970); McDowall (1988); Maitland & Campbell, 1992
Golden-grey mullet *Liza aurata*	autumn	yearly	mature (>20 cm)	few km	Maitland & Campbell (1992); Lucas, unpubl. data
Thick-lipped mullet *Mugil cephalus*	autumn	yearly	mature (>30cm)	few km	Maitland & Campbell (1992); Lucas, unpubl. data
Sea bass *Dicentrarchus labrax*	autumn?	2-3+	immature (<20cm)	few km	Maitland & Campbell (1992); Pickett & Pawson (1994); Lucas, unpubl. data
Flounder *Platichthys flesus*	autumn	2-3+	immature (<20cm)	up to 50 km	Nikolskii (1961); Berg (1962); Summers (1979, 1980); McDowall (1988)

4.3.3 Potamodromous species

Although there are few examples of large-scale spawning migrations in potamodromous species there is evidence to show that small-scale migration plays a significant role in spawning in many freshwater species (Table 4).

Lampreys

The movements of anadromous lampreys have already been discussed in section 4.3.1 but as Malmqvist (1980) pointed out spawning in the brook lamprey *Lampetra planeri* is also preceded by upstream migration, although this generally involves limited distances of up to a few kilometres. Additionally, there is a landlocked population of river lampreys in Loch Lomond, Scotland (Maitland *et al.*, 1994). The River Endrick is the largest feeder stream of Loch Lomond and Maitland *et al.* (1994) found, by trapping at Drymen Bridge, that adult river lampreys started to appear in the river in late September with the main spawning runs in October to December. It was argued that this was the only stream used by spawning river lampreys from Loch Lomond.

Pike

The majority of studies of the spawning migration of pike have been carried out in lakes and reservoirs where movements during the spawning season are significantly higher than at other times (Diana *et al.*, 1977; Diana, 1980; Wright, 1980, Lucas, 1992). Few studies have investigated pike spawning movements in streams although Clark (1950) showed that pike migrated from Lake Erie, Ohio into feeder streams. He suggested that the objective of this migration was to find marsh-like conditions for spawning. Any stream or ditch was utilised provided that some vegetation or debris, with enough water to partially cover the fish, was available. Males predominated in the early upstream movement and females in the later part of the run. Franklin & Smith (1963) also showed that pike moved out of Lake George, Minnesota to spawn in a feeder stream. However, they were unable to find any differences in sex ratios as the spawning run progressed nor did they show any changes in the size of pike over the time of the run. Adult fish began leaving the breeding grounds shortly after spawning. Some individuals remained for considerable periods but 62-64 % of fish had left within 40-60 days of spawning. Miller (1948) observed that individual pike were not faithful to a single spawning ground but would move around visiting several spawning grounds.

Salmoniforms - grayling

Most information available concerning grayling migration comes from lake populations which migrate to afferent streams to spawn. The grayling population in Gouthwaite Reservoir migrates into the River Nidd in April and spawns in the stem of the river above Gouthwaite Reservoir (Lucas, unpubl. data). Gustafson, in Jankovic (1964) followed spawning migrations, after ice thaw, from Storsjö Lake to the small brook, Svärtbacken, Sweden. He found that 50 % of females migrated between April 23 and 27. Spawning took place 3 km from the lake. Woolland (1972) also showed that grayling moved out of lakes to afferent streams in a study in Llyn Tegid, North Wales.

A large amount of data concerning the numbers and timing of spawning migrations is available in a number of unpublished reports of counts of fish occurring in fish passes in continental

Europe. These data are summarised in Figure 4 which provides composite histograms derived from the numbers of fish caught in fish passes on the Garonne and Dordogne, south-west France (Travade *et al.* 1996), the Meuse, Belgium (Philippart *et al.*, 1988, 1992, 1993, 1994, 1996; Prignon *et al.*, 1996) and Netherlands (Lanters, 1993,1995), the Mehainge, Belgium (Philippart, 1997) and the Mosel, Germany (Pelz, 1985). There is a peak in the occurrence of grayling in theses fish passes in the early spring which precedes the normal spawning period of this species and may indicate that, in some rivers, grayling migrates to spawn.

Cyprinids

Barbel are highly mobile in the spawning season (Baras & Cherry, 1990; Baras, 1992; 1993a; Baras *et al.*, 1994a; Lucas & Batley, 1996). Barbel spawning migrations show strong seasonal periodicity with peaks in May in the Rivers Meuse and Ourthe, Belgium (Baras, 1992; 1993a; Baras *et al.*, 1994a). In the River Nidd, northern England, both males and females migrate in spring to spawning grounds (Lucas & Batley, 1996, Figure 5). During the summer, barbel movements become much more stable reflecting fidelity to a defined activity area with very high local activity (Baras, 1993b; Philippart & Baras, 1996). Baras *et al.* (1994a) showed that the first fish in the migration are males and immature individuals on their way to spawning grounds in the River Méhaigne. Males usually gather at the spawning grounds at least one week before the beginning of spawning (Baras, 1992). The migration peak is characterised by the synchrony of mature individuals and by a short time-lag between the migration of males and females. This difference between sexes is due to males which already occupy the spawning grounds prior to the arrival of the females (Hancock *et al.*, 1976; Baras, 1994). The sex ratio of the spawning migratory population was significantly different from that of populations at other times of the year which Baras *et al.* (1994a) attributed to the higher mobility of females during the spawning period (10-15 km for females, up to 600 m for males). Females move downstream from summer onwards. Males remain on the spawning grounds for longer, apparently searching for receptive females (Lucas & Batley, 1996). Further evidence of spawning migrations in barbel is provided by their seasonal occurrence in fish passes which peaks in the spring just prior to the main spawning period (Figure 4).

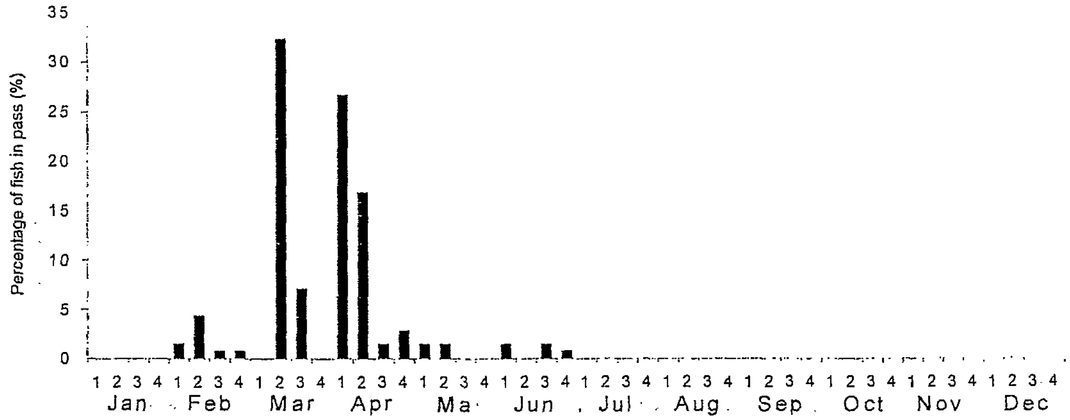
Table 4 Coarse fish species in Britain which carry out potamodromous spawning migrations. ? indicates that no information is available.

Species	Timing	Distance	References
Brook lamprey *Lampetra planeri*	Apr-May	few km	Malmqvist (1980)
River lamprey *Lampetra fluviatilis* (landlocked)	Sep-Nov	few km	Maitland *et al.* (1994)
Pike *Esox lucius*	Mar-Apr	few km	Miller (1948); Clark (1950); Franklin & Smith (1963); Lucas (1992); Armstrong (1996)
Grayling *Thymallus thymallus*	Mar-Apr	1-5 km	Gustafson, in Jankovic (1964); Woolland (1972); Whitton & Lucas (1997); Lucas (unpubl. data)
Barbel *Barbus barbus*	Mar-Jun	2-20 km	Baras & Cherry (1990); Baras (1992; 1993a); Baras *et al.* (1994a); Philippart & Baras (1996); Lucas & Batley (1996); Prignon *et al.* (1996); Travade *et al.* (1996); Waidbacher & Haidvogl (1996); Lucas & Frear (1997)
Gudgeon *Gobio gobio*	Apr-May	?	Jurajda *et al.* (1996)
Common bream *Abramis brama*	May-Jun	5-60 km	Whelan (1983); Caffrey *et al.* (1996); Prignon *et al.* (1996); Travade *et al.* (1996)
Silver (white) bream *Blicca bjoerkna*	Mar-May	?	Lelek & Libosvárský (1960); Prignon *et al.* (1996)
Bleak *Alburnus alburnus*	Apr-Jul	?	Jurajda *et al.* (1996); Prignon *et al.* (1996); Travade *et al.* (1996)
Minnow *Phoxinus phoxinus*	May	250 m -1 km	Pitcher (1971); Kennedy (1977)
Roach *Rutilus rutilus*	Mar-Jun	100 m -5 km	Lelek & Libosvárský (1960); Champion & Swain (1974); Diamond (1985); L'Abee-Lund & Vøllestad (1985, 1987); Maitland & Campbell (1992); Armstrong (1996); Jurajda *et al.* (1996); Prignon *et al.* (1996); Travade *et al.* (1996); Lucas *et al.* (in press)
Chub *Leuciscus cephalus*	Mar-Jun	1-20 km	Lucas *et al.* (1998); Frederich (1996); Frederich & Ohman (1996); Frederich *et al.* (1997); Jurajda *et al.* (1996); Prignon *et al.* (1996)
Dace *Leuciscus leuciscus*	Mar-May	3-15 km	Starkie (1975); Champion & Swain (1974); Lucas & Mercer (1996); Lucas (1998b); Prignon *et al.* (1996); Lucas *et al.* (in press); Clough & Beaumont. (in press)
Ide *Leuciscus idus*	Feb-Apr	1-22 km	Winter (1996); Winter & van Densen (in press)

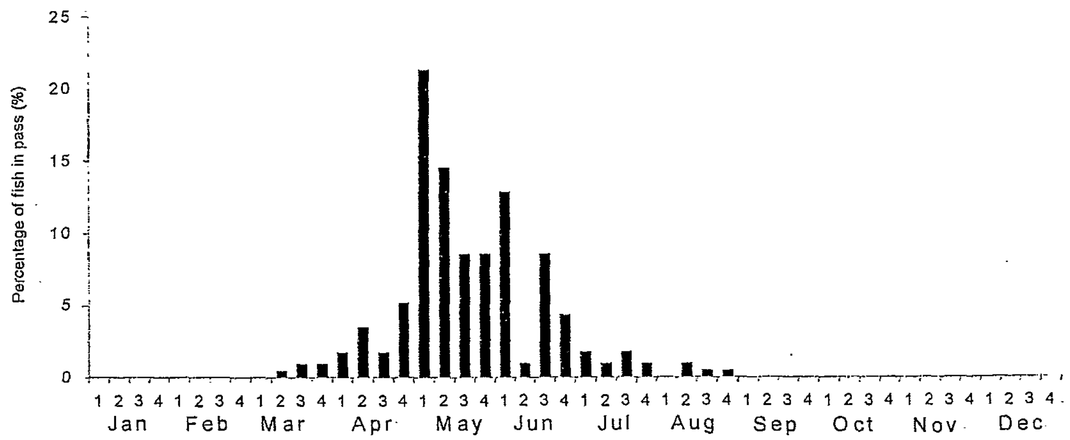
Table 4: continued

Species	Timing	Distance	References
Perch *Perca fluviatilis*	Mar-Apr	?	Armstrong (1996)
Zander *Stizostedion lucioperca*	spring	up to 38 km	Berg, in Deelder & Willemsen (1964); Fickling & Lee (1985); Schmutz & Giefang (1997)
3-spined stickleback *Gasterosteus aculeatus*	spring	15 km	Harvey *et al.* (1997)
9-spined stickleback *Pungitius pungitius*	spring	15 km	Harvey *et al.* (1997)
Stone loach *Barbatula barbatulus*	spring	?	Axford (pers. comm.)
Spined loach *Cobitis taenia*	Mar-Apr	200-800 m	Slavík & Rab (1995, 1996)
Bullhead *Cottus gobio*	May-Jun	few km	Crisp *et al.* (1984); Bless (1990); Crisp & Mann (1991)
Wels catfish *Siluris glanis*	spring	short distances	Lelek (1987); Cowx & Welcomme (1998)

Grayling ($n = 10^1$)



Barbel ($n = 10^1$-10^2)



Bleak ($n = 10^3$-10^4)

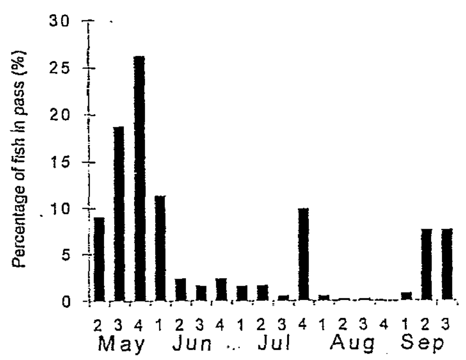
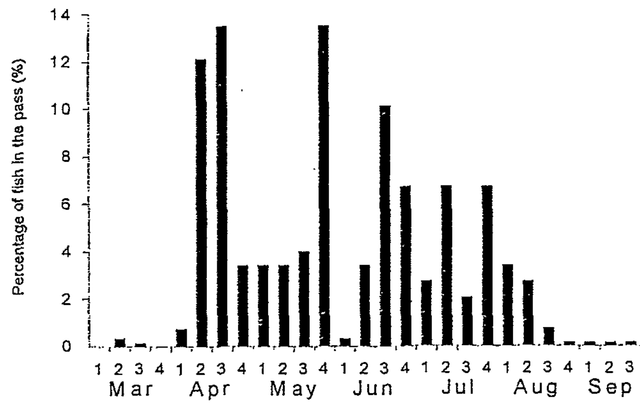
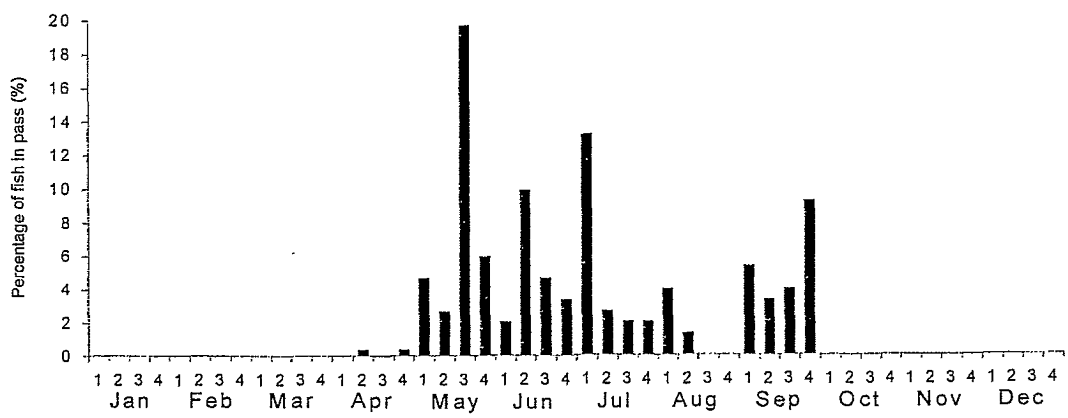


Figure 4 Composite histograms of the occurrence of fish in fish passes. Derived from unpublished reports on the numbers of fish caught in fish passes on the rivers Garonne and Dordogne, south-west France (Travade *et al.* 1996), the Meuse, Belgium (Philippart *et al.*, 1988, 1992, 1993, 1994, 1996; Prignon *et al.*, 1996) and Netherlands (Lanters, 1993,1995), the Mehainge, Belgium (Philippart, 1997) and the Mosel, Germany (Pelz, 1985).

Bream (n = 10^1-10^2)



Chub (n = 10^1-10^2)



Dace (n = 10^1-10^2)

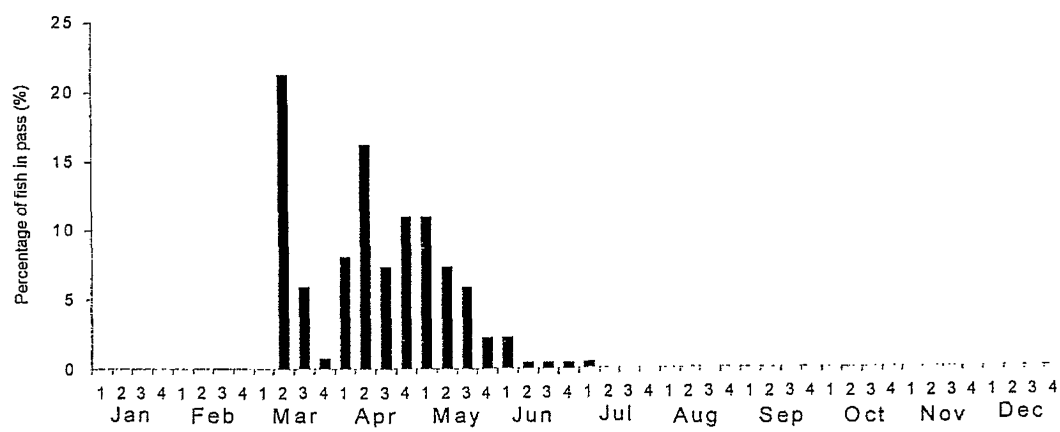
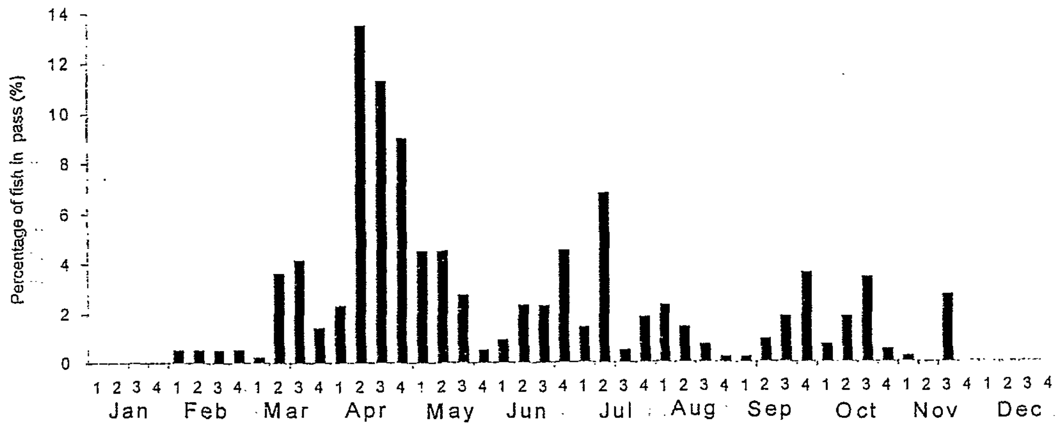


Figure 4 Continued.

Roach (n = 10^2 - 10^4)



Silver bream (n = 10^1-10^3)

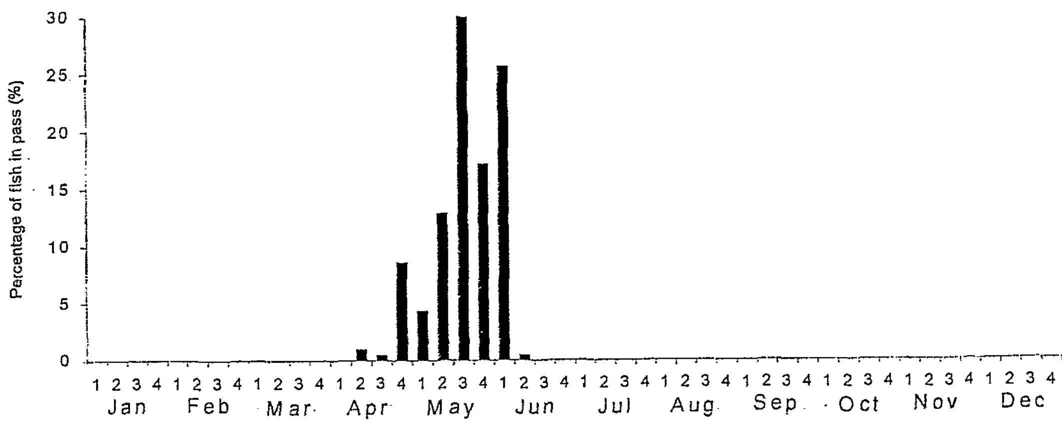
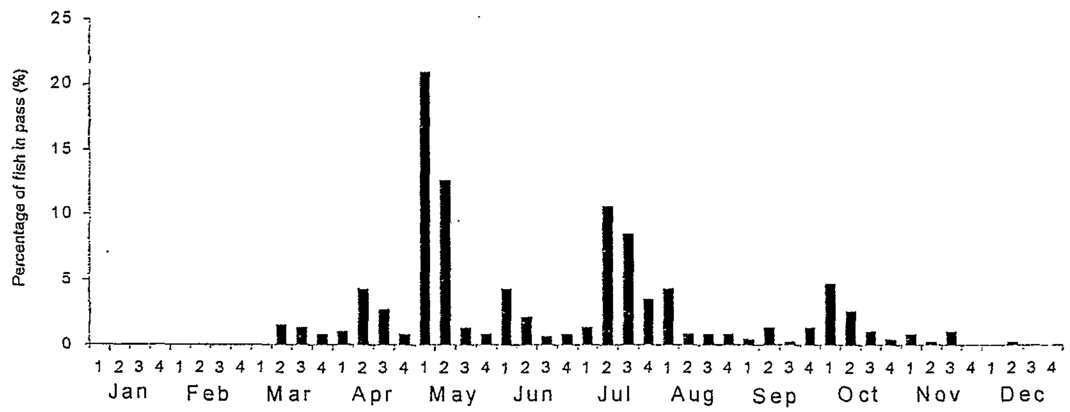


Figure 4 Continued.

Perch (n = 10^1-10^2)



Zander (n = 10^1-10^2)

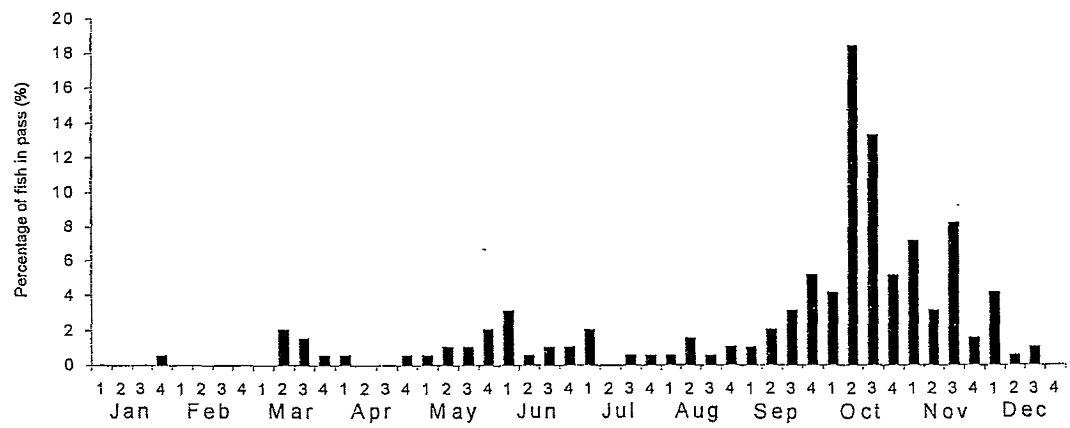


Figure 4 Continued

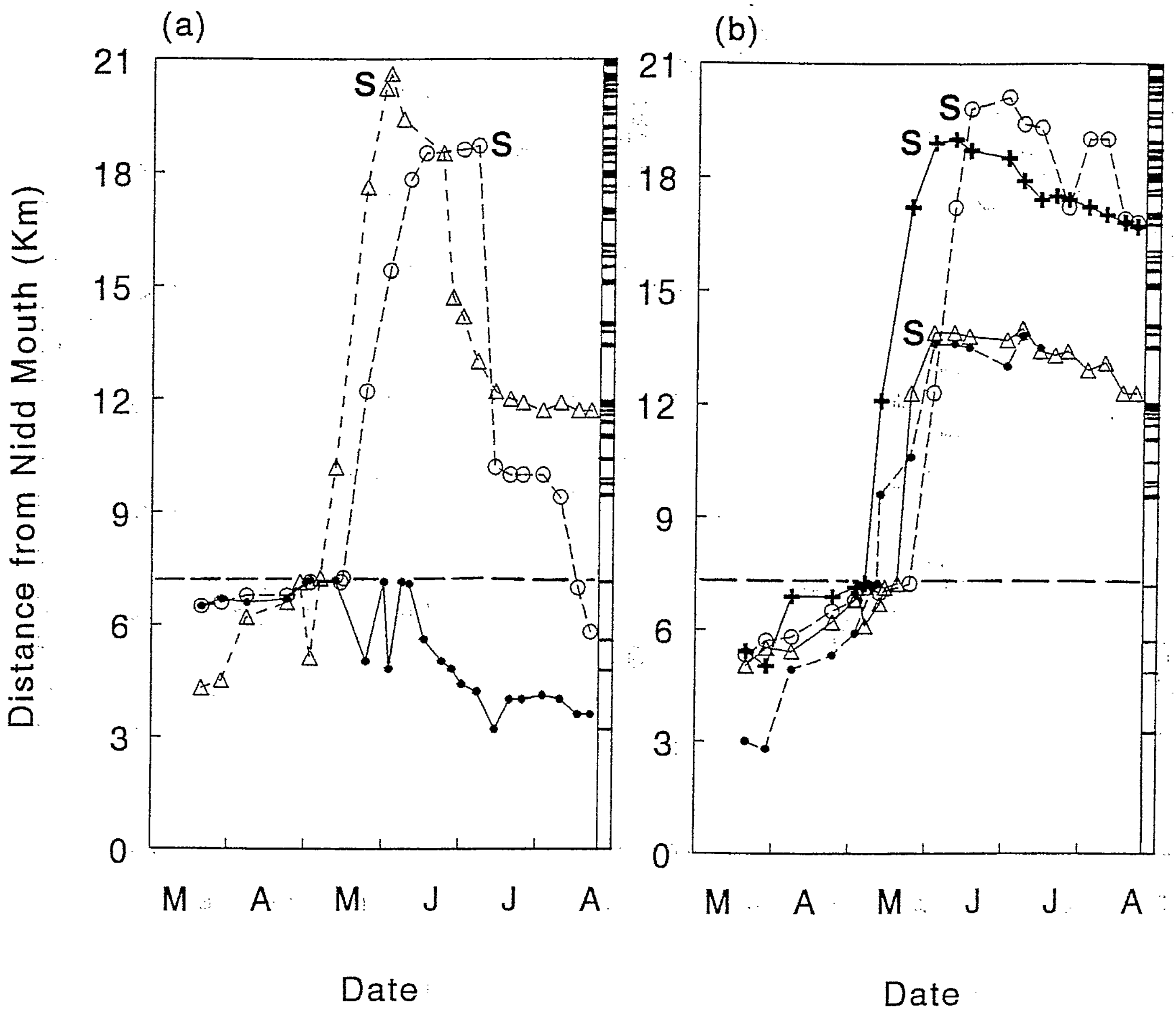


Figure 5 Example tracks for barbel released below Skip Bridge which were ultimately successful (Δ, O) and unsuccessful (●) in passing upstream over Skip Bridge weir. (b) Tracks of other barbel which negotiated the gauging weir. The horizontal dashed line indicates the position of the gauging weir. The bars in the right-hand column of each graph display the distribution of spawning habitat along the stretch of river, while S denotes location of the tagged fish in the presence of spawning/courting conspecifics. (Reproduced from Lucas & Frear, 1997).

Whelan (1983) showed that some individual bream were capable of exceptional movements of up to 59 km. Most fish however, remained in shoals which displayed regular spawning migrations of up to 10 km. Observations of bream at the Derrycahill spawning site on the River Suck, Eire over several years showed that there was a resident Derrycahill shoal, a shoal which was upstream to the site and two shoals which moved downstream producing a spawning shoal of over 4000 fish. After spawning the aggregation broke down into separate shoals which returned to their respective feeding grounds. Caffrey *et al.* (1996) found that the movements of radio-tracked bream in the Barrow, Grand and Royal Canals in Ireland became erratic during the spawning season and shoals moved considerable distances from their home ranges. However, other fish did not move from their home range and the extent of movements during the spawning season was similar to movements at other times of the year. This led Caffrey *et al.* (1996) to conclude that these movements could not necessarily be attributed to spawning migration. Data from fish passes shows that there is a peak in the occurrence of bream in the spring which would appear to precede the main spawning period although there is also a second peak which may coincide with feeding movements (Figure 4). The spring peak in occurrence is less clearly defined than for barbel and movements of bream through fish passes are more variable and occur over a more extended period.

Radio-tracked chub in the River Spree, Germany exhibited an upstream spawning migration in May of up to 13 km. After spawning they homed back to their original location (Frederich, 1996; Frederich & Ohmann, 1996; Frederich *et al.*, 1997). They also undertook a second spawning migration in June (and a third in 1996) in which they moved to the same spawning grounds as before. This extended and repeated pattern of spawning movements may account for the appearance of chub in fish pass catches over an extended period from May to September (Figure 4).

Pitcher (1971) observed that minnows *Phoxinus phoxinus* undertake a spawning migration in May in which they move 250 m to 1 km upstream to gravel beds in open shallow water. Kennedy (1977) showed that tagged minnows homed back to their non-spawning area after about a month on the spawning grounds.

Diamond (1985) showed that spawning shoals of roach migrate each year to utilise the same spawning grounds in a variety of different environments. Lucas *et al.* (in press) also demonstrated that radio-tracked roach were very mobile during the spawning season with fish ascending Skip Bridge weir on the Nidd and moving upstream individually or in groups of 2-4 to spawning areas 0.1-4.5 km upstream of the weir. Other fish remained close to weir to spawn and five migrated downstream approximately 1 km after 4 weeks, again probably to spawn. Radio-tracking of adult dace in the Nidd demonstrated that even small fish species are capable of substantial migration (Figure 6). Dace are rheophilic and spawn on sand/gravel riffles in early May in north-east England. The dace moved from the Ouse into the lower reaches of the Nidd, where they were tagged, and subsequently moved further upstream to areas with suitable spawning habitat 3.5-14 km upstream of Skip Bridge weir (Lucas & Mercer, 1996; Lucas *et al,* in press). Starkie (1975) showed that marked dace in the River Tweed moved average distances of 6.3 km. He also found that the majority of dace 1+ and older moved distances in excess of 1 km arguing that this demonstrated greater mobility than in previous studies. He did not, however, provide any explanations for this mobility. Data from fish pass catches (Figure 4) show that there is a clear peak in roach occurrence in the spring corresponding with the main spawning migration in this species although two smaller peaks occur in the summer and autumn possibly related to feeding or refuge migrations.

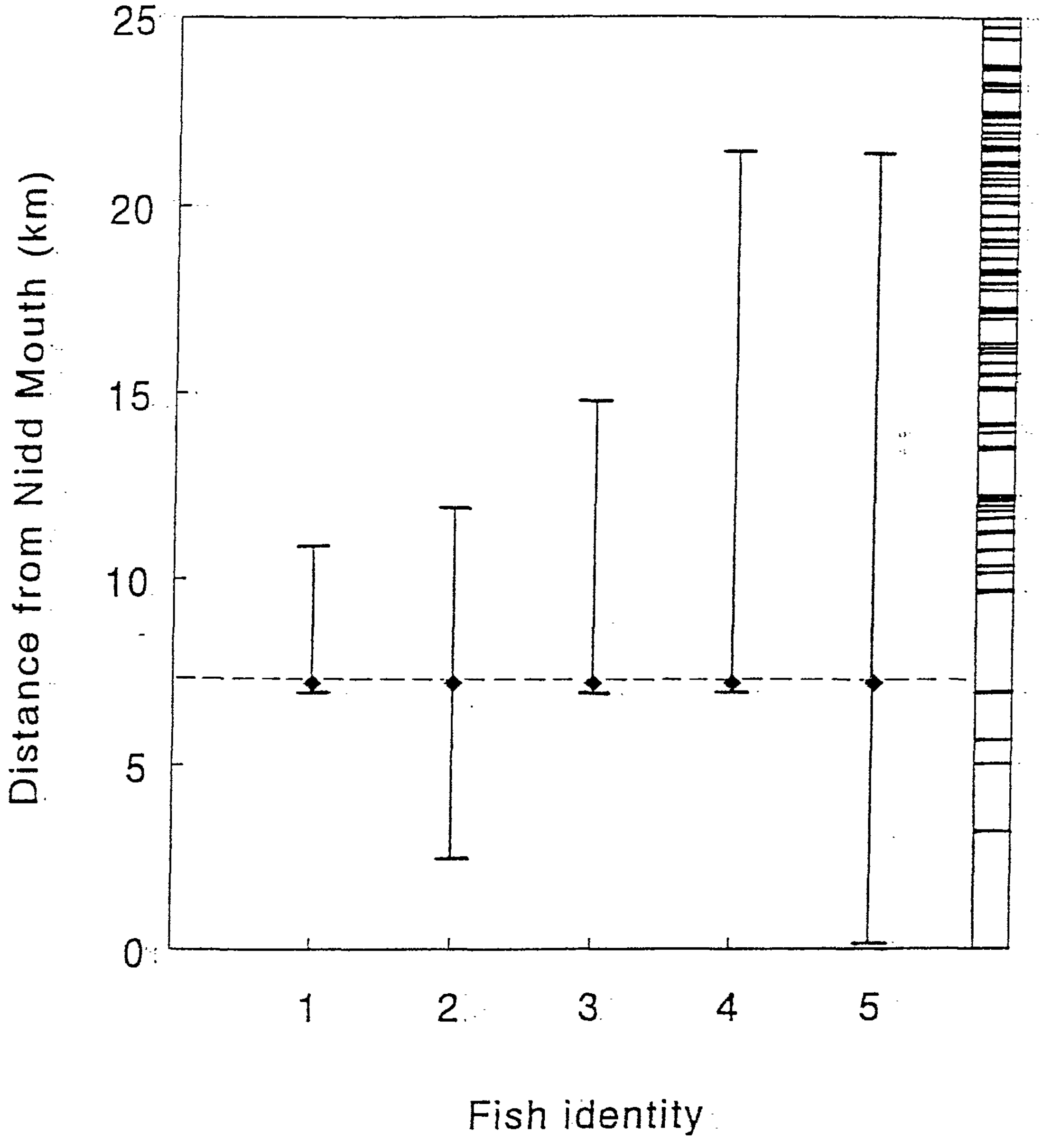


Figure 6 Ranges of movement of five radio-tracked dace during their spawning migration. Upstream limits of movement were associated with spawning. Areas of suitable spawning habitat are shown as shaded bars on the right hand column.

Champion & Swain (1974) recorded counts of coarse fish passing through the Ministry of Agriculture, Fisheries & Food (MAFF) fish trap on the River Axe, Devon at monthly intervals from 1960-69 inclusive. They showed that the main downstream movements of both roach and dace occurred regularly during March, April and May and were probably associated with spawning movements. This is notable in that most recorded potamodromous spawning migrations are in an upstream direction (Figure 4).

Lelek & Libosvárský (1960) used electric fishing in a fish pass to determine the migration of fish in the Dyje River, Breclav, Czechoslovakia. The whole pass was fished with the pass blocked off with a steel screen to prevent downstream migration. The pass was reopened at successive intervals to determine the number of fish per 6 hour period. Roach *Rutilus rutilus* and silver bream *Blicca bjoerkna* were the main species in the pass. Of the 31 species in the river, only 19 entered the ladder - roach, silver bream, bleak *Alburnus alburnus*, nase *Chondrostoma nasus*, chub, ide *Leuciscus idus*, bream *Abramis brama*, schneider *Alburnoides bipunctatus,* rudd *Scardinius erythropthalamus*, perch *Perca fluviatilis*, barbel, zährte *Vimba vimba*, Danube bream *Abramis sapa*, whitefin gudgeon *Gobio albipinnatus*, blue bream *Abramis ballerus*, dace, asp *Aspius aspius*, eel, tench *Tinca tinca* and wels. Fish appeared in the ladder after April 20 when temperatures rose above 8 ^{0}C. The maximum occurrence was from the end of April to the end of May. Water temperatures varied from 12-20 ^{0}C. There was a mass occurrence of fish between May 2-13, 1958 when the average daily temperature during this period increased by 10 ^{0}C in ten days. The occurrence of fish in the pass after this was negligible with only nine individuals between July and October. It was argued that the presence in the pass of silver bream and roach during this period of peak abundance was due to a spawning migration. Other species were not so numerous and were not considered to be migrating.

Loaches

Stone loach are not normally considered migratory, however, Axford (pers comm.) has caught stone loach with enlarged gonads crossing weirs in the River Sheaf, South Yorkshire, in spring, suggesting that they may in fact migrate to spawn.

Slavík & Rab (1995, 1996) studied an isolated population of spined loach *Cobitis taenia* in the Pšovka Creek, Bohemia, Czech Republic.. Downstream movements started in March (mainly males) and April (rest of males followed by females). Spawning occurred in June followed by an upstream migration in July. The youngest and oldest reproductively inactive females remained in over wintering sites and did not migrate to spawn. Juveniles steadily migrated upstream from the spawning area over the summer period, reaching wintering areas by October. Distances of 200-800 m were moved.

Sticklebacks

Harvey *et al.* (1997) showed that three- and nine-spined stickleback underwent simultaneous spring migrations in the Chignik catchment, Alaska. In the summer and autumn one year old and young-of-the-year fish emigrated upstream from Black Lake towards Chignik Lake, an estimated distance of 15 km. All migrating fish had enlarged mature gonads and had developed spawning colouration. Upstream migration ceased at the end of June and returning two-year-old fish were found in poor condition suggesting that spawning mortality was high. The extent of stickleback migrations in British waters is unknown.

Bullhead

Mills & Mann (1983) described the bullhead as a solitary animal driving off other individuals from its territory to which it showed a strong homing instinct. However, they also suggested that bullhead migrate to deeper water to spawn although presented little evidence to support this. Crisp *et al.* (1984) and Crisp & Mann (1991) showed that the numbers of bullheads in many streams above Cow Green Reservoir on the River Tees in north-east England, varied from year to year and also showed some seasonality after impoundment. Peak numbers occurred in mid-summer and numbers diminished rapidly during autumn and winter and increased again in spring or early summer. They argued that the best explanation for this was that fish formed part of the reservoir breeding population, over-wintering in the reservoir and returning to the streams after spawning. Bless (1990) recorded upstream movement in German rivers, which was pronounced in May and June.

Percids

There is little information available on the migration of perch in rivers. However, Figure 4 shows that perch do occur in fish pass catches with a peak in the spring which may coincide with the spawning period. The fact that they occur in fish passes indicates migratory behaviour.

Fickling & Lee (1985) showed that introduced zander (pikeperch) *Stizostedion lucioperca* in the Great Ouse Relief Channel exhibited movements of up to 38 km which could possibly be have been spawning migrations although it was also possible that these movements were due to dispersal of the introduced population or to prey searching behaviour. Schmutz & Giefang (1997) radio-tracked 15 adult zander below the weir and bypass channel of the Marchfeldkanalsystem, Germany and found little movement occurred an concluded that zander was not migratory. However, the occurrence of zander in fish pass catches (Figure 4) suggests that they do in fact carry out migratory movements although it is not clear whether these are related to spawning.

4.4 Young of the year movements

4.4.1 Anadromous species

Lampreys

Hardisty (1979) argued that within a river system the distribution of larval lamprey populations results from the interaction of the passive downstream drift of the larva and the rheotactic upstream migration of the spawning adult. Thus, throughout the larval period the larval population will tend to move downstream towards the middle and lower reaches of the river but this is counteracted each year by the ascent of spawning adults to higher reaches (Hardisty & Potter, 1971a).

Sticklebacks

After hatching young three-spined sticklebacks feed and grow in freshwater before returning together with adults that have survived spawning to the sea in the summer and autumn. Wootton (1976) showed that in the late summer individual sticklebacks undergo physiological changes which make them intolerant of long periods in freshwater. Conversely in the spring they are less tolerant of saline conditions.

4.4.2 Catadromous species

Flatfish

Young flounder stay in brackish to freshwater and then migrate with adults to the sea to spawn (Nikolskii, 1961; Berg, 1962). Post-larval flounders acquire increased tolerance to fresh water as they develop and after metamorphosis they actively swim towards fresh rather than sea water (McDowall, 1988). Dando (1984) found that young flounder from the River Tamar spent less than two weeks in the sea and Summers (1979, 1980) and Kerstan (1991) emphasised the importance of tidal rivers as nursery and feeding grounds.

4.4.3 Potamodromous species

Pike

Franklin & Smith (1963) showed that pike alevins began to emigrate from their nursery stream into Lake George, Minnesota at 16-24 days after hatching. Juvenile fish left the nursery stream in mid-May to early June and in two out of three years 98 % of juvenile fish left the stream within 20 days of the start of emigration. Studies of feeder streams like this show that the availability of spawning and nursery areas in small tributaries can be important for the maintenance of pike populations in some lake systems.

Grayling

Bardonnet *et al.* (1991) found that, in June and July the young of grayling in the River Suran, France moved away from microhabitats and low velocities associated with banks into the channel and areas with higher velocities. This was then followed by a downstream migration out of this spawning and nursery area. This downstream migration ended in the complete desertion of the Suran by young-of-the-year fish. Scott (1985) demonstrated a similar pattern of movement of larval grayling in the River Frome, Dorset. It could be argued that passive downstream drift of young-of-the-year fish is not a migratory movement because it does not involve an active movement by the fish. However, Valentin *et al.* (1994) showed that young-of-the-year grayling (2 months old) were highly resistant to flow changes by seeking refuge sites during periods of high velocity. This suggests that young grayling probably make an active decision to allow themselves to drift downstream at a certain point in their life-cycle.

Cyprinids

Until recently there has been little direct evidence on the downstream dispersal of 0+ coarse fish from spawning sites in British rivers or on how extensive these movements might be. Some indirect evidence indicating the occurrence of young fish in the open waters of rivers was gathered by Solomon (1992) in his report on the entrapment of fish at water intakes and outfalls. This showed that the most vulnerable fish to be entrained in the water abstracted from rivers were salmon smolts, juvenile coarse fish, predominantly cyprinids, and the smaller newly hatched stages. Large numbers of 0+ roach, dace and chub were caught by a louver screen trap installed in the Walton Waterworks intake from the River Thames. Between April 25-September 9 1989 87408 YOY fish 25-35 mm in length were caught, an additional 1093 1+ fish and an unknown quantity of fish larvae <18 mm in length were also captured. From records of daily catches, the peak period of capture was between June 15 to July 6. The 25-35 mm long fish were probably 1-2 months old, since roach and dace were observed to spawn in the Shepperton Reach, upstream of the Walton Intake, between May 15-19 1992 (Duncan & Kubecka, 1993a) and this observation suggests an active or passive juvenile downstream dispersion.

Similar evidence of the vulnerability of 0+ coarse fish to entrainment at water intakes is available for the Hampshire Avon (Solomon, 1992) and for the much larger Meuse, in the Netherlands (Ketelaars *et al.*, in press). 0+ roach, dace, chub and bream were caught in a fish farm intake on the Avon over a period from mid-July to early September 1986 at sizes between 20-40 mm (Solomon, 1992). An ichthyoplankton net suspended in the water intake of the De Gijster Reservoir on the Meuse captured large numbers of 0+ pikeperch, bream, roach and perch together with a number of other species between mid-May to early July 1996 (Ketelaars *et al.*, in press). The occurrence of the predominant species followed their hatching times, with the percids appearing first and the cyprinids dominating later. At the maximal rate of capture on June 13 when roach fry were the predominant fish, the mean nightly rate was as much as 1200 fish h^{-1} compared with a day rate of approximately 90 fish h^{-1}. In general, night catches were higher than in the day for all species except pikeperch and constituted approximately 80 % of the mean 24 hour total number of fish. The drift of young-of-the-year fish in open river waters has also been shown acoustically for large European rivers like the Elbe and Vltava, Czech Republic (Kubecka & Duncan, pers. comm.).

Penaz *et al.* (1992) used a 0.5 mm mesh size ichthyoplankton net to determine the downstream drift of larval and juvenile fish at two sites 5 km apart on the French upper River Rhone in the old by-passed river bed between a dam and its powerhouse. Sampling was conducted in August and the main drift occurred at twilight and during the night hours. Only 84 fish 24 h^{-1} were caught at the upper site where few backwaters existed compared with 271 fish 24 h^{-1} at the lower site adjacent to a natural floodplain showing the importance of the latter for providing spawning sites and nursery areas as well as a source of recruitment for riverine fish. 0+ roach formed 67 % of the 'drift' at the upper site together with chub (13 %) and nase (6 %) whereas the composition was more rheophilic at the lower site (chub, 40 %), roach (36 %) and barbel (10 %).

Baras & Nindaba (in press) used pre-positioned electric fishing frames to examine seasonal variations in the diel dynamics of young-of-the year dace occupying inshore bays in the River Ourthe, Belgium (Figure 7). Juvenile dace moved into the bay in the morning with a peak in numbers around midday and then a progressive movement out of the bay into neighbouring riffles during the late afternoon or evening. Small fish moved into the bay earlier and moved out of the bay later than larger fish. By the end of September most fish had left the bays but returned when temperatures were less than 7-12 ^{0}C. During the autumn and winter juvenile dace of all sizes were exclusively found in inshore shelters with submerged macrophytes or leaf out of inshore bays in the River Ourthe. As with dace they found seasonal variations in the diel movements of chub in these bays. In early summer chub moved between the middle of the bay and riparian areas. Then, later in the season they exhibited similar movements to dace.

Drift nets set at 40 cm depths in the River Danube and a tributary, the Fischa, were used to study the diurnal and seasonal intensity of passive drift of larval stages of nase and barbel between May 12 and June 12 1997 (Purtscher *et al.*, 1998). The drift was low during daytime but started to increase at dawn and attained maximal level between 20:00-24:00. The highest drifts in the Fischa began in May but one month later in June in the Danube. This was attributed to earlier spawning in the Fischa, which was warmer compared to the cooler water temperatures of the larger Danube.

Displacement of 0+ fish communities after major flood events in the River Rhone has been studied by Pont *et al.* (1998). The impact of a major flood in October 1993 at one site with natural and 'old-engineered' sites was minimal because most of the 0+ fish migrated to the natural backwaters as refuges. 0+ roach and chub adopted this strategy and their numbers did not decline whereas 0+ nase and gudgeon did not and their numbers were reduced due to increased transport of bed-material. At another site where by-pass sections of the old river bed had been isolated by a series of dams, low flows generated lentic conditions which were good for spawning and development. In this situation, however, 0+ fish were found only in the side-arms of the by-pass sections after a flood in October 1993 and another in January 1994, thus revealing the refuge role of side-arms during major flooding.

Lightfoot & Jones (1979) observed the longitudinal dispersion of young roach in the River Hull, north-east England, during June and July 1973 whilst they grew from 7.5 mm to 29 mm in length in a nursery area close to the spawning sites. The smallest fish were confined to the shallow margins and amongst *Sparganium* sp. weed beds where the current velocities were lowest. As the fish grew larger, they extended their range into deeper water with fewer plants and greater flows where they could maintain station. At about 29 mm in length, the fry became scarce locally, left the nursery area and dispersed downstream.

In the Great Ouse, shallow water, coarse substratum, zero velocity and floating and submerged plant cover was the preferred habitat of 0+ roach during August and September (Garner, 1995). The scarcity of such conditions might be the cause of downstream dispersion by older fry. Garner *et al.* (1995) showed that weed beds provided young fish with both high food densities of 'larger' cladocerans and refuge during periods of elevated flows. Cutting vegetation (largely *Nuphar lutea*) significantly reduced the availability of the preferred and more nutritious 'larger' cladocerans which supported optimal growth and the fry turn to less nutritious 'aufwuchs' with a subsequent reduction in growth (Garner *et al.*, 1995). Roach and chub 0+ fry in the Great Ouse fed continuously during the day and night but fewer prey were caught at night because a proportion of the fry migrated offshore beyond the weed beds where food was less abundant but predators were also fewer (Garner, 1996). Conversely, Copp (1990) interpreted a shift of juvenile roach in the upper Rhone floodplain from deeper water with macrophytes into shallower open waters as a need for a refuge from fish predation.

Table 18 Types of chemical tags for use in capture-mark-recapture studies.

	Dye & paint marks	Latex marks	Radio-isotopes
Description	Most UK freshwater fish studies use Panjet inoculators to batch mark fish, or utilise binary codes of marks to identify smaller numbers of individual fishes. Alcian Blue most appropriate dye in terms of recognition and longevity. Sub-epidermal injections of acrylic paint are used for eels because they cause minimal disturbance and produce long-lasting marks. Different colour combinations can be used to identify batches or individuals. Mercuric chloride introduced by hypodermic injection most effective for larval ammocoetes of lampreys.	Coloured liquid latex introduced by hypodermic injection most effective for larval ammocoetes of lampreys.	Method using radioisotopes of the rare earth Euridium (^{152}Eu and ^{155}Eu) to mark elvers.
Advantages	Easy to apply, require a low handling time and can be used for small fish or early life stages. Do not affect fish behaviour.	Cheap, non-toxic, last for several months and can be used in several colour combinations enabling individual identification. Do not affect fish behaviour	Easy to apply, require a low handling time and can be used for small fish or early life stages. Able to identify four of their animals three years after they were first captured. Do not affect fish behaviour
Disadvantages	The main disadvantages are that individuals cannot be identified and, in the majority of cases, retention times are low. Small fish could be damaged by force of Panjets. Mercuric chloride was considered to be too expensive and toxic for widespread use.	Not permanent	Cannot identify individuals
References	Hart & Pitcher (1969); Axford (1978); Schoonoord & Maitland (1983); Baras *et al.* (1996); Gollmann *et al.* (1986); Knights *et al.* (1996); Smith (1997)	Schoonoord & Maitland (1983)	Hansen & Fattah (1986)

Cerri (1983) argued that the potential success of predatory fish decreased with increasing light intensity. During periods of increased predator activity young of the year fish may move to the shallow littoral zone (Schlosser, 1991; Slavík & Bartos, in press) where they occupy highly structured habitats which they use as refugia from predators (Hyanch *et al.*, 1983; Fraser & Emmons, 1984).

4.5 Feeding migration

4.5.1 Introduction

A comparison of the global distribution of diadromous species provides circumstantial evidence that migration is from areas of low production (poor feeding) to areas of high production (rich feeding) (Gross, 1987; Gross, *et al.*, 1988). Catadromous species are more common at low latitudes where primary production in fresh waters tends to be higher than in the seas. Anadromous species are more common at high latitudes where it is the marine environment that has the higher rate of primary production.

Feeding migrations are not restricted to large-scale movements between marine and freshwater environments. In some fish inhabiting lakes a diurnal vertical migration occurs. Brett (1971) suggested three functions for this vertical migration. The first was that fish were following the vertical migration of their prey, the zooplankton. The second was that during daylight fish move into darker water to avoid predation. The third was that fish are maintaining a homeostatic control over their rate of energy expenditure by moving after feeding into cooler waters where their rate of energy expenditure is reduced. Diel movements in riverine environments have been less well studied and it is clear the Brett's work may only apply to large rivers. However, acoustic surveys of coarse fish populations in the Rivers Ouse and Thames in England show that fish are more active in the water column during the night than in the day. This can lead to sevenfold differences in densities of fish over long stretches of river (Duncan & Kubecka, 1996; Lucas *et al.*, 1998). These findings may be associated with diel feeding migrations in shallow rivers evidence for which is reviewed in this section.

4.5.2 Large-scale feeding migrations

Table 5 summarises data on those species which undertake large-scale feeding migrations.

On hatching, larval ammocoetes of sea and river lampreys burrow into mud and silt along sluggish stream margins and live for several years as filter-feeders. Mark-recapture studies in the River Aln during the summer showed considerable site fidelity by ammocoetes to one feeding locality, even following floods (Smith, 1997). A metamorphosis takes place during the summer and autumn (Hardisty & Potter, 1971b) and the small sub-adults migrate downstream during the autumn. In general they do not feed until they reach the sea although adult lampreys do sometimes feed in freshwater (Davis, 1967; Maitland, 1980a, 1980b). In the sea they live as parasites for about 28 months.

On completion of their oceanic migration leptocephali of the European eel metamorphose into transparent glass eels which migrate into estuaries. They then undergo a transition phase as they adjust to freshwater. They then metamorphose into the pigmented elver stage and commence feeding. Some of these may stay in the estuary or join coastal stocks, others migrate upstream during their first year in fresh water or as juveniles in subsequent years (White & Knights, 1997). As the eels move up-river they become more pigmented (Tesch, 1977). Young eels can become fully pigmented at 7-8 cm in length and only small numbers of eels migrating upriver are greater than 20-30 cm in length (Tesch, 1966; Penaz & Tesch, 1970; Larsen, 1972). However, migrations deeper into catchments can continue in successive years until eels reach sizes as large as 40-45 cm and 10+ years of age (Moriarty, 1990). The elver is capable of migrating 150 km upstream before it is fully pigmented (Tesch, 1965). Once it is fully pigmented it can travel considerably further in its first year although this may be less if hindered by obstructions. Upstream migration of young eels is slow with some individuals still found in the lower reaches of rivers after two or more years (Tesch, 1977). Moriarty (1986) showed that the size of eels in the River Shannon decreased throughout the season due to a later and shorter migration period of small eels. Baras *et al.* (1996a) also showed a marked variation in yellow eel size throughout the migratory season in the River Meuse but that this was structured differently. This led them to conclude that yellow eels migrate in waves and that these waves were independent of environmental parameters. Pigmented eels do not make use of the main current for migration. They continue to swim even if the current is reduced or ceases completely. As a result they often end up in backwaters and only relocate the current after some delay (Tesch, 1977). At about 30 cm in length young eels complete the migratory stage and become relatively sedentary and migrate only as a result of meteorological, hydrological or seasonal factors. During this period home ranges are very small. Mann (1965) showed that on the River Elbe, 16 out 47 eels were recaptured where they were originally caught and 21 had moved only 10-60m. Baras *et al.* (in press) radio-tracked seven yellow eels in the Awirs stream, a small tributary of the Meuse, demonstrating a low level of movement. Net journeys were higher in May and June which corresponded to the immigration of migratory yellow eels from the Meuse. Baras *et al.* (in press) argued as a result of this that eels adopt a sedentary lifestyle in fast flowing streams when eels in the main river were usually migratory. However, this may not be the case since the fish Baras *et al.* (in press) was tracking were larger than yellow eels that are normally considered migratory (max. 45 cm).

If eels do change habitats during this stage movement takes place during the transition phases between summer and winter. McGovern & McCarthy (1992) used acoustic tracking to show that yellow eels in the Clare River were relatively sedentary. Movements did however, increase in the autumn and were attributed to eels moving to over-wintering habitats.

Baras *et al.* (1996a) argue that, although it represents most of the freshwater life of *A. anguilla*, migration at the yellow eel stage is the least extensively studied part of its lifecycle. They argue that this is due to the difficulties in discriminating between migratory and resident fractions of the eel population. They studied eels at a fish pass on the Ampsin navigation weir on the Meuse to overcome this problem. They showed that the period of yellow eel migration was relatively stable from year to year (around 2 June). This differed from Moriarty (1986) who found a higher variation in the dates of migration of small eels in the River Shannon. Baras *et al.* (1996a) estimated a migration rate of 45 km $yr.^{-1}$. This is much higher than the 8 km $yr.^{-1}$ in the Tadnoll Brook (Mann & Blackburn, 1991), 15 km $yr.^{-1}$ in the Shannon (Moriarty, 1986), the 10-15 km $yr.^{-1}$ in the River Dee and the 20-30 km $yr.^{-1}$ in the River Severn (Aprahamian, 1988). Baras *et al.* (1996a) argued that migration rates in small eels could be even higher (75 km $yr.^{-1}$) if they had moved through the Albert Canal, which provides a shorter route to the Ampsin-Neuville weir than using the Meuse. They argued that these higher migration rates may have been due to smaller eels being less inhibited by light (Sörensen, 1951) and therefore more inclined to migrate in daylight. Aprahamian (1988) argued that the slower migration of eels in the Dee was due to the steeper gradient of this river making migration difficult.

Baras *et al.* (1996a) showed that the length frequency (average of 29-30 cm) of migrant yellow eels at Ampsin was similar to those observed elsewhere for whole and non-migratory populations (Philippart & Vranken, 1983; Aprahamian, 1988; Vøllestad & Jonsson, 1988). Baras *et al.* (1996a) also demonstrated using mark-recapture studies that the majority of eels migrated through the sluices of the Ampsin navigation weir and not through the fish pass.

Large-scale feeding migrations in other non-salmonid fishes are less well understood. The majority of studies focus on diel feeding migrations and there have been few studies clearly demonstrating long distance feeding migrations in non-salmonid freshwater fish (Table 5). For most adult/sub-adult coarse fish the summer feeding period is associated with relative stability of fish populations.

Table 5 Long distance feeding migrations of coarse fish found in Britain. ? indicates that no information is available.

Species	Timing	Age	Size	Distance	References
Eel *Anguilla anguilla* unpigmented elver pigmented yellow eel	 Jun-Sep Jun-Sep	 -	 <8 cm 20-30 cm	 150 km to headwaters	 Tesch (1965); Tesch (1977); White & Knights (1997); Moriarty (1986); Vøllestad & Jonsson (1986) Aprahamian, (1988); Moriarty (1990); Baras *et al.* (1996a)
River lamprey *Lampetra fluviatilis*	autumn	sub-adult	15 cm	to sea	Hardisty & Potter, 1971b
Sea lamprey *Petromyzon marinus*	autumn	sub-adult	15 cm	to sea	Hardisty & Potter, 1971b
Pike *Esox lucius* (mainly in lakes)	variable	adult	NA	?	Malinin (1972); Vostradovsky (1975, 1983 (in Raat, 1988); Bregazzi & Kennedy (1980); Chapman & Mackay (1984); Cook & Bergersen (1988)
Bream *Abramis brama*	variable	adult	NA	up to 3 km	Whelan (1983); Caffrey *et al.* (1996)
Roach *Rutilus rutilus*	summer	juvenile	?	into afferent streams	L'Abée-Lund & Vollestad (1987)
Ide *Leuciscus idus*	Apr-May	1+ and 2+	?	lakes to rivers & within rivers	Winter & van Densen (1998)

Many coarse fish species exhibit restricted movements during the summer feeding period, associated with occupation of home range. This behaviour, interspersed with sporadic longer distance movements to new locations, is shown by a broad range of species.

The majority of studies of movements of pike outside the spawning season have been conducted in lakes and reservoirs and their are few studies of feeding migration in riverine environments. Most of these previous studies have shown pike to be relatively sedentary outside the spawning season except for sporadic long distance movements (Malinin, 1972; Vostradovsky, 1975, 1983 (in Raat, 1988) Chapman & Mackay, 1984, Cook & Bergersen, 1988) (Table 5). Vostradovsky (1975, 1983, in Raat, 1988) found that pike which exhibited these longer movements showed higher daily gains in weight than resident pike which they argued was due to a greater chance of encountering prey. Bregazzi & Kennedy (1980) also attributed the migration of pike to the movements of prey species in Slapton Ley. Pervozvanskiy *et al.* (1989) argued that because of high flow conditions on riffles in the Keret River, pike foraging on migratory salmon were unable to migrate long distances. However, Armstrong (unpubl. data) has found pike which may have been migrating with salmon smolts (Figure 8).

Tracking and mark-recapture studies on species such as bream, barbel and dace have generally shown limited movements within summer home ranges of less than 3 km and occasional longer distance movements (Whelan, 1983; Caffrey *et al.*, 1996; Lucas & Batley, 1996; Lucas & Frear, 1997; Clough & Beaumont, in press). Shoaling species such as bream tend to be more nomadic than more solitary fish such as barbel.

Fickling & Lee (1985) showed that individual zander also exhibited sporadic long distance movements (up to 36 km) which could be attributed to foraging movements although no direct evidence for this was available.

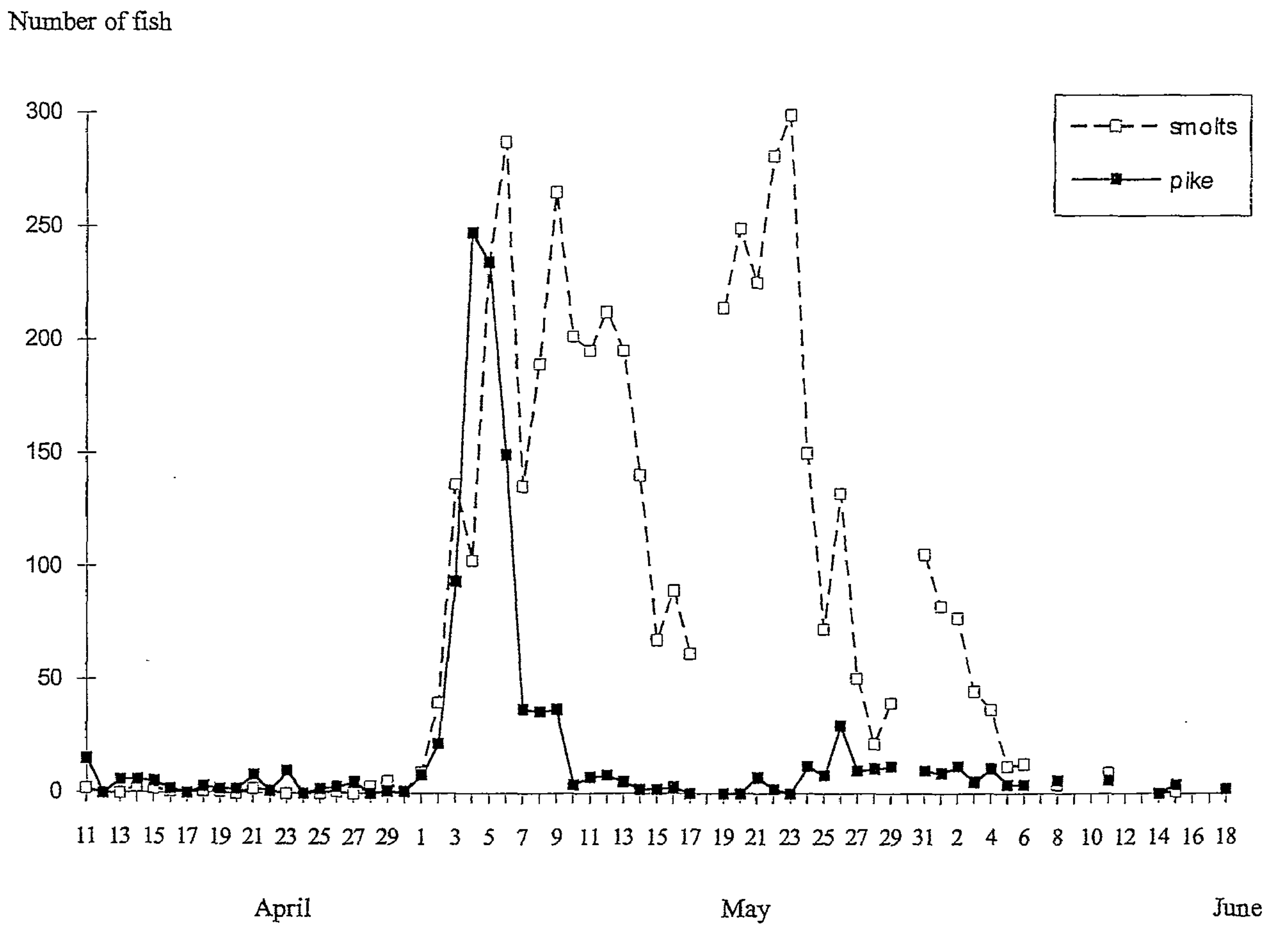


Figure 8 Daily numbers of salmon smolts and juvenile pike caught in a trap on the River Conan, Scotland (Armstrong, unpubl. data).

4.5.3 Diel feeding movements

A number of freshwater species demonstrate diel changes in position related to foraging movements (Table 6).

Sanders (1992) showed that night electro-fishing catches contained significantly higher numbers of species, individuals, weight and biological index scores than day catches. Catch differences were attributed to diel movements from offshore to nearshore waters during the evening-twilight period. These movements were again attributed to movements from refuge to foraging habitats. Other authors report similar findings. Kubecka (1993) provides some evidence that some fish species of deep or large lakes spend the day offshore and migrate inshore during the non-spawning summer period. There were fivefold differences between day and night catches in inshore seining in Loch Ness, Scotland and Lake Baikal, Siberia. Densities of fish were seventeen times greater in night catches in the Czech Rimov Reservoir while, in the London reservoirs, fish were only caught at night. Daily horizontal fish migrations between inshore and offshore zones were demonstrated in two Canadian lakes using acoustic techniques by Gaudreau & Boisclair (1998) and Comeau & Boisclair (1998). They showed, however, that movement occurred in the reverse direction, from the littoral to the pelagic at night. Piscivorous fish were present in these lakes and the authors postulated that the reverse migration was associated with their presence. In two other lakes without piscivorous fish, the highest relative densities in the pelagic zone occurred during the day. Although these studies were carried out in lake environments it is possible that similar diel movements occur in larger rivers. This is shown by Kubecka & Duncan (1998a) using acoustic monitoring of fish behaviour over a 24 hour period in the littoral and open water (3 m deep) zones of the Thames. At night larger fish moved to the surface and towards the littoral zone, returning to deeper layers during the day. The vertical movements of fish were more marked in the open water of the river where fish were oriented to the current. In the littoral zone movements were more random.

Table 6 British coarse fish exhibiting diel feeding migrations.

Species	Time of day	Age	Distance	References
Bream *Abramis brama* (in lakes)	day/night	adult	between littoral and pelagic zones	Schulz & Berg (1987)
Dace *Leuciscus leuciscus*	dawn/dusk	YOY	in and out of inshore bays	Baras & Nindaba (in press)
	dawn/dusk	adult	350 m	Clough & Ladle (1997). NOTE: Interpretation was of movement between feeding and refuge areas, but proof of feeding was not obtained.
Chub *Leuciscus cephalus*	dawn/dusk	YOY	in and out of inshore bays	Baras & Nindaba (in press)

Baras & Nindaba (in press) argued that the marked diel movements of young-of-the-year dace and chub in inshore bays in the Ourthe reflected a trade-off between the utilisation of food resources and avoidance of predators (Figure 7). Small fish are able to obtain all of their food requirements in these bay areas. Larger fish, however, could no longer fulfil their requirements within the bays. Their larger size enabled them to exploit faster flowing sites which cover a larger area of the stream and where other prey types were available. The low numbers of fish in the bay at dawn and dusk could, therefore be related to the search for prey in neighbouring riffles. These are the periods when 0+ dace are known to feed in the summer (Weatherley, 1987). The diel dynamics of the use of these bays by dace and chub was completely opposite to those in lakes and large rivers where fish were more abundant in the littoral zone in darkness rather than daylight as in the Ourthe. However, Baras & Nindaba (in press) were unable to sample at night and suggested that large juveniles may also occupy the bays at night as was shown by autumn sampling.

4.6 Post-displacement movements

A number of fish species make directed movements back to their original areas after displacement due to floods or experimental removal (Table 7).

Yellow eels displaced from their home waters are capable of finding their way back (Mann, 1965; Tesch, 1966, 1970; Deelder & Tesch, 1970). Most eels were capable of finding their way home at distances of 100 km. Beyond this distance, the percentage of successful returns becomes much smaller. However, isolated individuals were capable of homing from distances of up to 200 km (Tesch, 1977).

Champion & Swain (1974) showed that the numbers of roach moving upstream through the MAFF fish trap on the Axe increased after floods in November 1965 and February 1969 which they argued was the result of their downstream displacement by the flood. However, no fish moved upstream after floods in April 1961 or December 1965.

Goldspink (1978) showed that marked bream captured in the Zwartemeer and released in the Tjeukemeer, Netherlands left the lake into the surrounding canals and then showed some homing behaviour once into the Ijsselmeer. The maximum distance travelled was 60 km. Langford (1981) showed that in the River Witham several bream were flushed downstream when flows increased suddenly as hydraulic weirs were lifted after heavy rainfall. Some bream moved several kilometres. He also showed that pike in the Thames of were washed up to 1.5 km downstream of weirs during major spates. Following these floods almost all fish returned upstream to their original location demonstrating a strong homing tendency after displacement.

Lucas *et al.* (in press) observed that, in mid-June 1997, six radio-tracked chub were congregated at spawning sites in the Nidd. A flash flood then occurred over a period of two days and these fish moved into the Ouse, over distances of 3-13 km. After a week when flows had subsided they then returned to the same spawning sites in the Nidd. Fredrich (1996) also showed that chub, displaced up to 2 km upstream or downstream, homed back to their capture site.

Table 7 Post-displacement movements by British coarse fish. ? indicates no information available.

Species	Age	Distance	References
Eels *Anguilla anguilla*	yellow	up to 200 km	Mann (1965); Tesch (1966, 1970, 1977); Deelder & Tesch (1970)
Pike *Esox lucius*	adult	1-5 km	Langford (1981)
Barbel *Barbus barbus*	adult	2 km	Baras & Cherry (1990); Baras *et al.* (1994a); Baras (1996); Lucas *et al.* (1998)
Bream *Abramis brama*	adult	1.5-60 km	Goldspink (1978); Langford (1981)
Chub *Leuciscus cephalus*	adult	3-13 km	Lucas *et al.* (in review)
Roach *Rutilus rutilus*	adult	?	Champion & Swain (1974)
Minnow *Phoxinus phoxinus*	adult	200 m	Kennedy & Pitcher (1975); Kennedy (1977); Slavik (unpubl. data)
Gudgeon *Gobio gobio*	adult	?	Stott *et al.* (1963)
Chub *Leuciscus cephalus*	adult	2 km	Frederich (1996)

Baras *et al.* (1994a) argued that the presence of barbel in the fish pass of the Ampsin-Neuville weir on the Meuse in mid-April was not related to spawning since most individuals were immature. Since these captures followed high flow conditions, they were regarded as compensatory upstream movements of individuals flushed downstream during flow increases as found in the Ourthe (Baras & Cherry, 1990) and Nidd (Lucas *et al.*, 1998). In the Nidd in summer these were usually brief and followed by a subsequent upstream homing migration to the location occupied prior to the high flow (Figure 9). In autumn and winter, however, successive downstream movements associated with high flow resulted in a step-wise pattern of downstream migration (Lucas *et al.*, 1998). Baras (1996) examined the homing behaviour of six barbel outside the spawning season. He found that, after experimental displacement close to the site of capture, individual barbel homed to their previous residence area. When displaced further, however, fish downstream of their capture site homed more accurately than those upstream of the capture site. It was argued that this difference may have been due to a lack of orientation cues for fish upstream of the capture site.

Slavik (unpubl. data) found that 10% of fin-clipped minnows washed downstream during high flow events caused by discharges from a small hydroelectric plant were displaced greater than 200 m downstream but returned to their original position once flows had subsided.

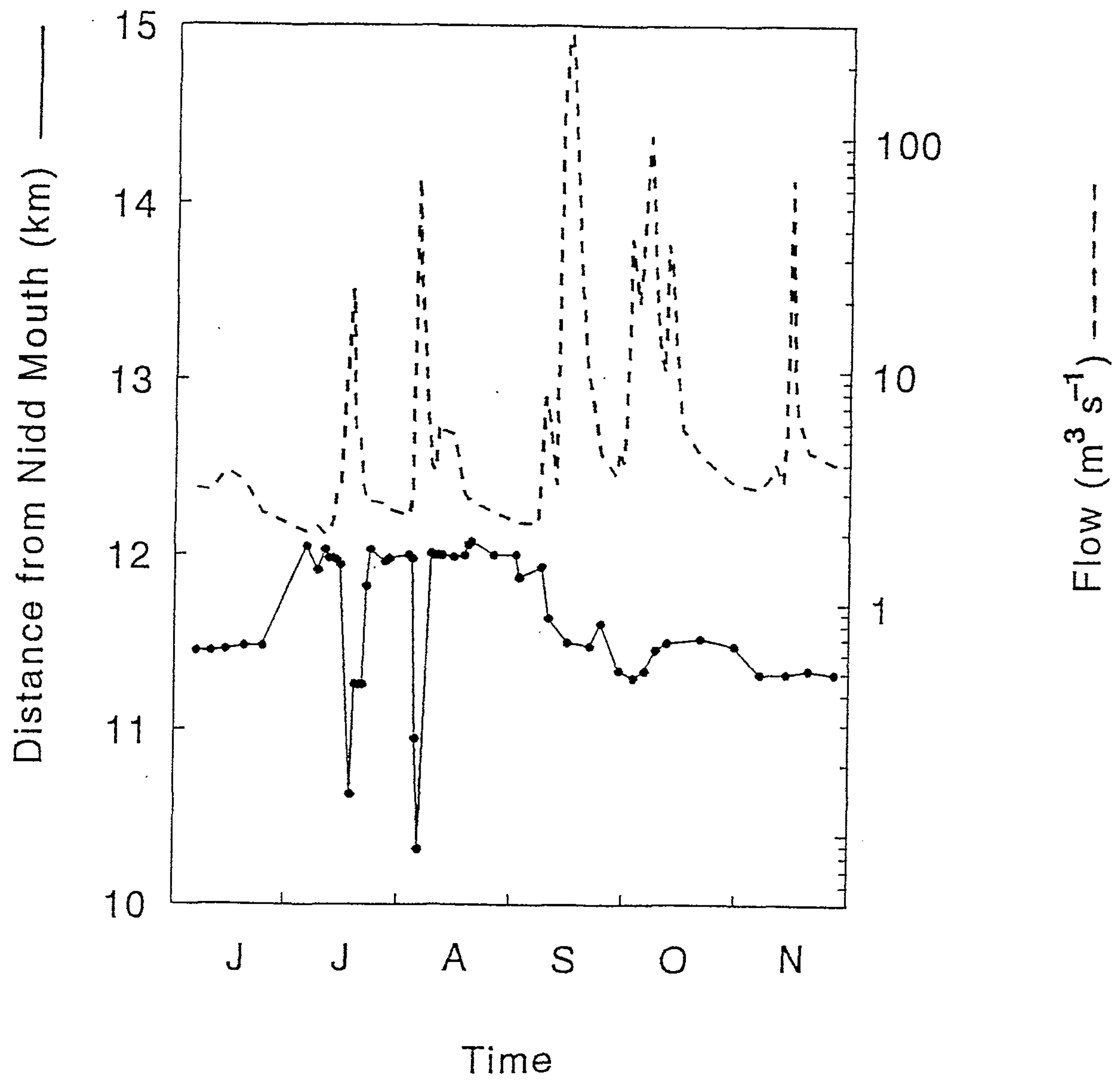


Figure 9 An example of a barbel track displaying several downstream movements associated with summer high flow events, each rapidly followed by a homing response. From September onwards, high flow events were associated with downstream displacement, but without subsequent homing, resulting in net downstream movement. (Reproduced from Lucas *et al.*, 1998).

4.7 Refuge seeking

There is some evidence to suggest that many coarse fish species will migrate to seek refuges avoiding unfavourable conditions. These migrations can be divided into two types; large-scale migrations in response to seasonal changes in environmental conditions and small-scale diel movements to different habitats, usually to avoid predators (Table 8).

4.7.1 Seasonal refuge seeking migration

Seasonal changes in the habitats of otherwise sedentary yellow eels are probably to avoid unfavourable conditions in winter. Surface ice, cold water and ground ice formation are all conditions which eels avoid (Tesch, 1977). In rivers, brackish areas and tidal waters eels move to quiet backwaters and channels where the water is deep enough to buffer the effects of winter. In the River Hunte, Lübben & Tesch (1966) found eels at depths of 2-2.5 m five kilometres from where they were first captured the previous summer and where they were again captured the following summer. Aker & Koops (1973) found that in the River Eider, a North Sea coastal river, the autumnal migration of eels was directed downstream in the middle reaches of the river and upstream in the coastal regions. They argued that both populations were migrating to a common area in which to spend the winter. Similar movements to over-wintering habitats were observed by McGovern & McCarthy (1992). Such movements may, however, be dependent on the suitability of habitats. If suitable refuges are available within an individual's home range then there will be no need to migrate. For example, Baras (pers. comm.) tracked eels which utilised gaps in stone walls along riverbanks which provide refuges of up to 1 m into the riverbank. Yellow eels occupying these habitats did not, therefore, need to move to seek refuge.

Lucas & Batley (1996) showed that barbel in the Nidd moved downstream in autumn and winter. They argued that barbel may be displaced or seek refuge downstream during high flow conditions which occurred frequently in the Nidd in the autumn and winter (Figure 10).

Jordan & Wortley (1985) suggest that large scale seasonal movements of adult coarse fish in the Norfolk Broads must explain the variable results from Wortley's extensive series of fish surveys carried out between 1978-84 (Anglian Water Authority, Norfolk & Suffolk Division Internal Reports) using quantitative techniques described in Coles *et al.* (1985). During winter months, the mean fish biomass from the open waters of the rivers and broads were < 1 g m^{-2} compared with 9.4 g m^{-2} during the summer. At certain sites adjacent to rivers connected to broads, very large winter aggregations of fish were found, with densities up to 36.7 fish m^{-2} and biomass up to 1787 g m^{-2}. These aggregations were found in off-river and off-broad dykes often associated with winter moorings and in particular river catchments, e.g. River Thurne and River Bure. The fish were largely adult roach, small common bream and some roach-bream hybrids. At two sites, the roach were 3+ or older, which were scarcely caught in summer surveys (Wortley, 1981). Wortley suggests that these exceptionally high winter densities explain the relative lack of fish in open waters in winter and that they must result from adult migration to the winter refuges offered by particular boatyards. The importance of such off-channel waters and marinas has also been demonstrated for YOY fishes (Copp, 1997).

Harvey *et al.* (1997) argued that adult stickleback moved up the Black River in May to avoid high discharges and low water temperatures caused by the June snowmelt. In the winter available habitat in the Black Lake declined by up to 85% due to ice cover resulting in low dissolved oxygen levels. The migration of sticklebacks into the deeper Chignik Lake may therefore be to find a more stable environment in which to over-winter.

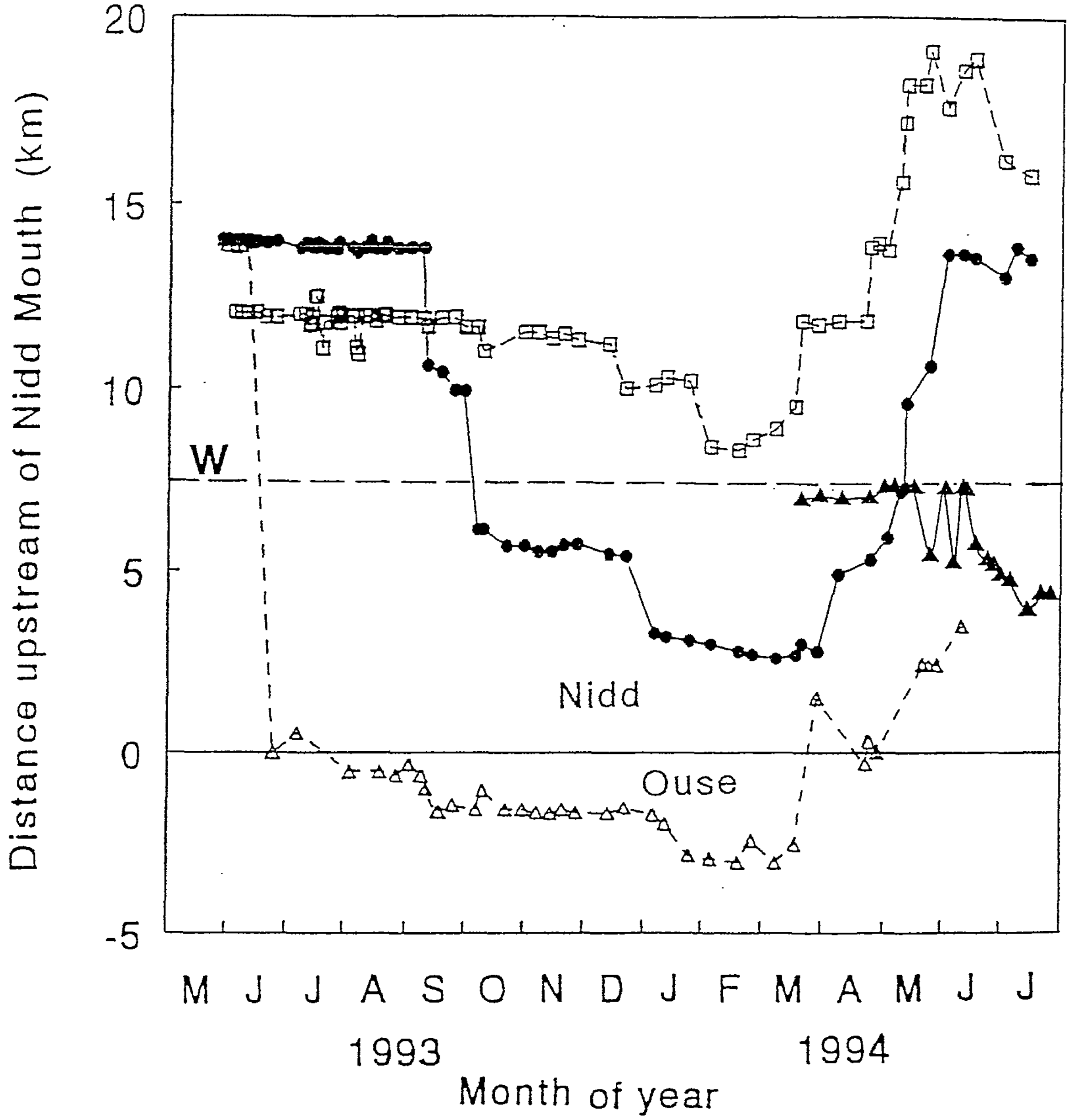


Figure 10 Long-term movements of three radio-tagged barbel in the River Nidd. Autumn and winter movements were characterised by a step-like pattern of downstream movements without subsequent upstream homing suggesting a refuge migration form high winter flows. (Reproduced from Lucas & Batley, 1996)

4.7.2 Diel refuge seeking migration

The diurnal rhythmic movements of many potamodromous species has already been described (section 4.5.3) in relation to foraging activity. However, when these species are not foraging they move to an alternative habitat during daylight where they show little activity (Schulz & Berg, 1987; Carl, 1995; Clough & Ladle, 1997). It has already been discussed that the potential success of predators decreases with increasing light intensity (Cerri, 1983). The movements of young of the year fish into more structured habitats provides a mechanism for avoiding predators (Hanych *et al.*, 1983; Fraser & Emmons, 1984). Copp & Jurajda (1993) sampling two adjacent stretches of bank (one shallow sand, one steep boulder) showed that as light levels decreased numbers of whitefin gudgeon and roach decreased along the boulder bank as numbers increased along sand bank suggesting a dusk migration to sandbank - probably to avoid predation. This finding was corroborated by a significantly higher number of potentially piscivorous fish (perch and chub ≥80 mm) along the boulder bank at night. Clough & Ladle (1997) described this behaviour as movement between feeding and safe resting sites (the 'roost').

Baras & Nindaba (in press) argued that as light intensity increased prey become less available to juvenile dace and chub and the fish themselves become more susceptible to predation. They then move to inshore bays at a time when the risk of being eaten outweighed the benefits of foraging. They also showed that the smallest fish, which are at greater risk of predation, enter the bay first. The shift from day to night use of inshore bays in the autumn may be the result of seasonal changes in habitat use. Juvenile dace and chub move to calmer deeper habitats in autumn (Baras *et al.*, 1995) where they may encounter nocturnal predators. The use of inshore bays at night may be a mechanism to avoid these predators.

Avoidance of predators is not, however, the only stimulus for diel migration in some species. Slavik (unpubl. data) found that twice daily pulses of water form small hydro-electric power plants in small Czech streams caused 90 % of fin-clipped minnows to move into side-streams during these peaks in flow (Figure 11).

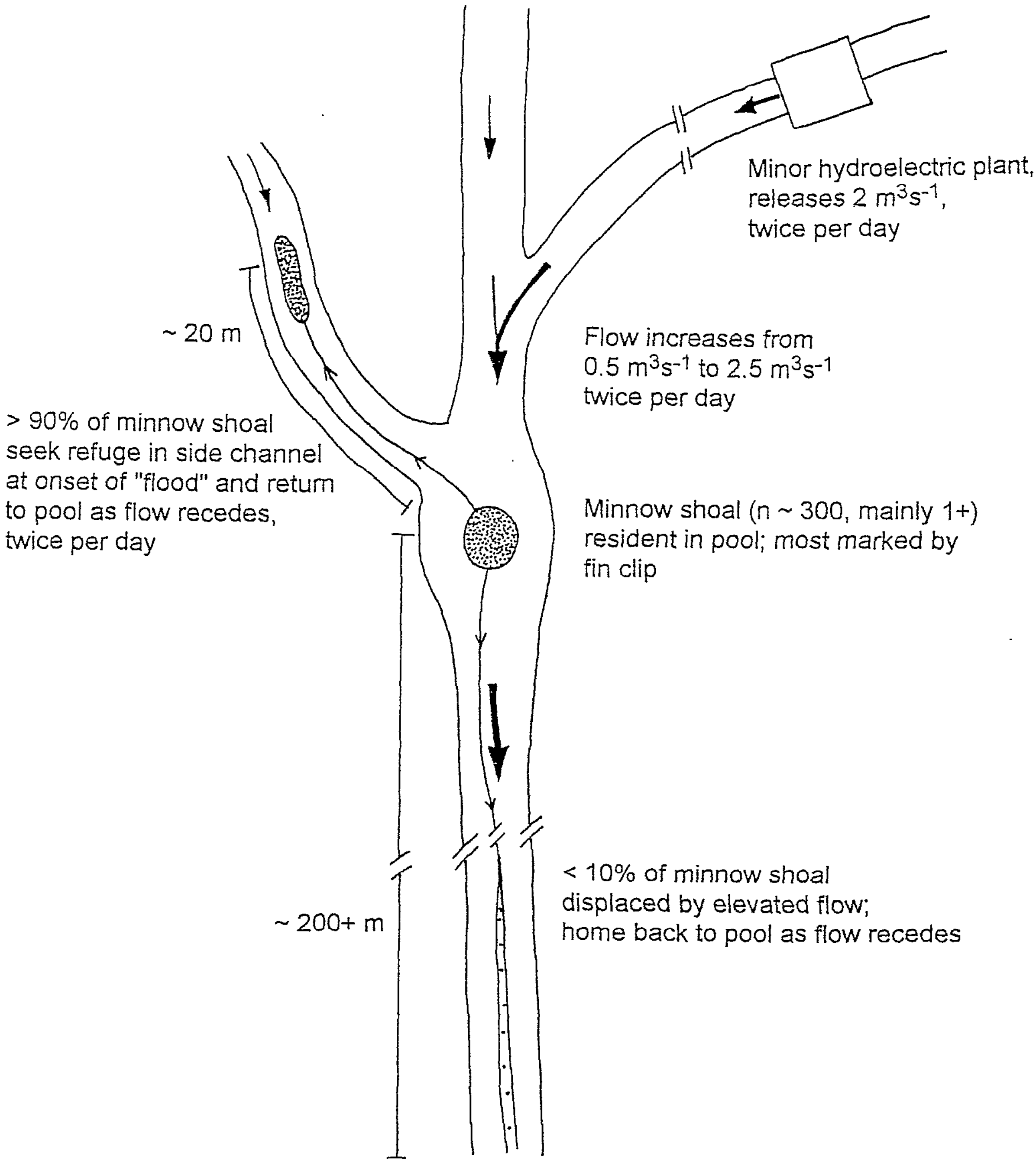


Figure 11 Schematic illustration of the twice-daily migration of minnows from their home area in a stream pool to a slack water refuge in a side-channel in response to elevated flows resulting from hydro-electric discharges (Slavík, unpubl. data).

Table 8 British coarse fish species which migrate to seek refuge from unfavourable conditions or to avoid predators.

Species	Age	Distance	Refuge type	References
Eels *Anguilla anguilla*	yellow	up to 5 km	over-wintering	Lübben & Tesch (1966); Aker & Koops (1973); Tesch (1977); McGovern & McCarthy (1992)
Sticklebacks *Gasterosteus aculeatus* *Pungitius pungitius*	adult	several km	overwintering	Harvey *et al.* (1997)
Barbel *Barbus barbus*	adult	up to 10 km	overwintering	Lucas & Batley (1996)
Roach *Rutilus rutilus*	juvenile adult	short open water to backwaters	diel anti-predator overwintering	Copp & Jurajda (1993) Wortley (1981)
Bream *Abramis brama*	juvenile	open water to backwaters	overwintering	Wortley (1981)
Dace *Leuciscus leuciscus*	adult juvenile	345 m into and out of backwaters	diel anti-predator diel anti-predator/foraging	Clough & Ladle (1997); Baras & Nindaba (in press)
Chub *Leuciscus cephalus*	juvenile	into and out of backwaters	diel anti-predator diel anti-predator/foraging	Baras & Nindaba (in press)
Minnow *Phoxinus phoxinus*	1 year	10-50 m	flood evasion	Slavik (unpubl. data)
Sea bass *Dicentrarchus labrax*	juvenile	several km (~ length of estuary)	predator evasion [+ feeding]	Pickett & Pawson (1994); Lucas, unpubl. data.
Flounder *Platichthys flesus*	juvenile	up to 50 km	predator evasion [+ feeding]	Maitland & Campbell (1992); Lucas, unpubl. data

5. THE CAPACITY AND STIMULUS TO MIGRATE

5.1 The capacity to migrate

Although downstream migration may be achieved with little expenditure of energy, by passive drift on currents, the capacity to migrate in an upstream direction requires the fish to swim faster than the water velocity; necessitating substantial energy expenditure from locomotor activity. The extent and duration of movement by fishes are, to some degree, related to body size through the influence of swimming performance. Absolute swimming performance has two components: the speed ($m\ s^{-1}$) at which a fish can swim, and swimming capacity, the time for which a fish can swim at a set speed, both of which increase with fish length (Wardle, 1977; Beamish, 1978). Swimming capacity decreases as a power function of swimming speed. This size-performance relationship clearly explains why small fish are often unable to maintain position in fast-flowing water through which larger fish of the same species can swim with ease. In general, larger rather than smaller species, and adults rather than juveniles are more capable of upstream migration. Other primary factors influencing swimming performance are temperature (Beamish, 1978) and ontogeny of locomotor and cardio-respiratory tissues (Webb, 1994).

However, coarse fish have a wide range of body forms, energy metabolism strategies and oxygen uptake/transport strategies. This results in diversity in swimming modes and performance, from the sluggish, serpentine locomotion of eels and lampreys, to the phenomenal acceleration during prey capture but poor sustained swimming performance of pike, and the high, sustained swimming performance of rheophilous species such as grayling (Webb, 1994).

Comment regarding physiological aspects of coarse fish migration is not considered further in this section of the report; such factors are being addressed in the Agency National R & D project "Fish swimming speeds".

5.2 The stimulus to migrate

5.2.1 Introduction

Behaviour is the outcome of internal and external cues which interact to stimulate a response (Figure 12). Individual fish may respond differently to the same stimulus on different occasions because of motivational (non-structural) or structural changes which directly affect its capacity to act (Colgan, 1993). Figure 12 summarises those internal and external cues which may stimulate a fish to migrate.

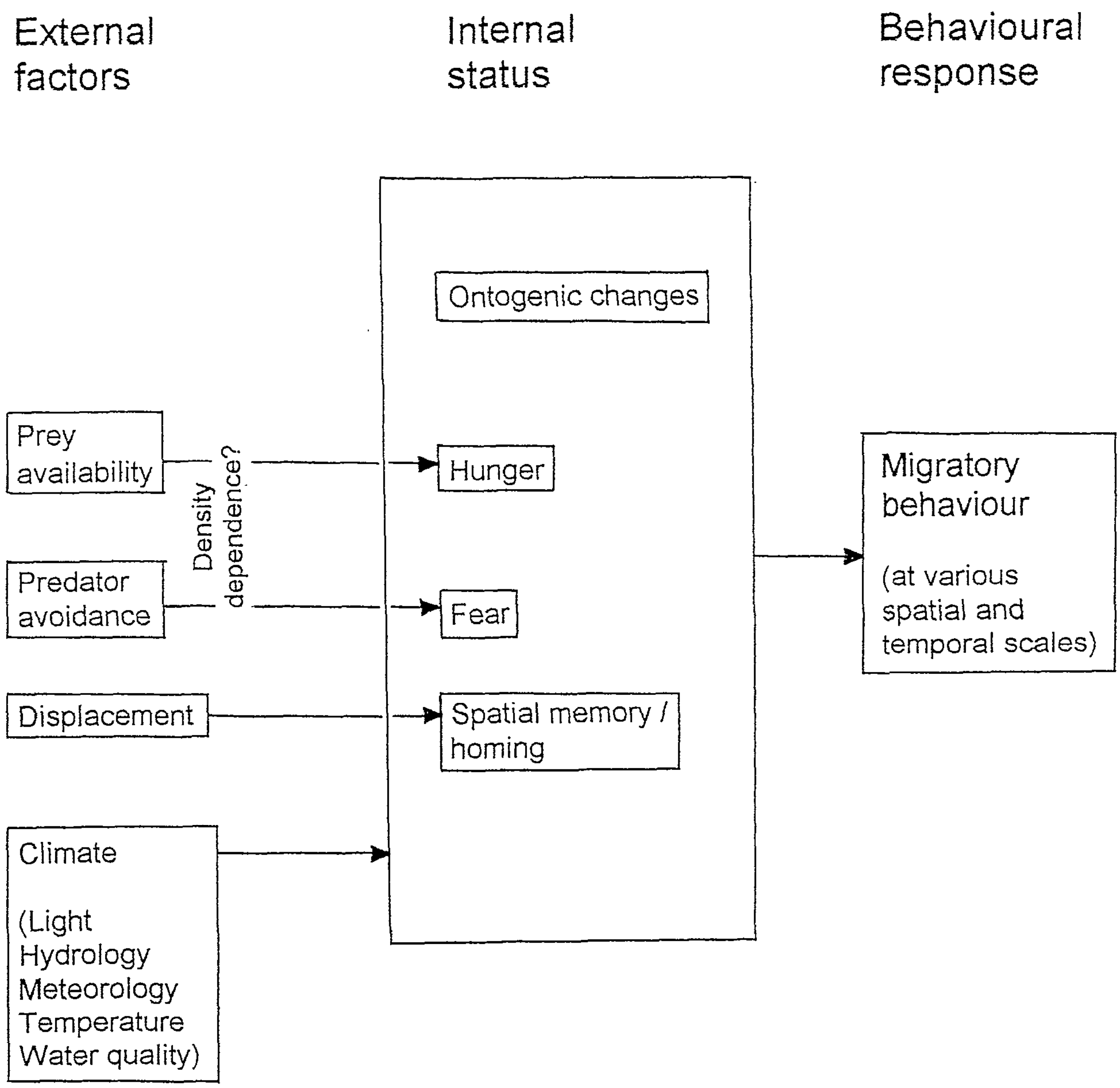


Figure 12 Flow diagram of the nature and influence of internal and external stimuli on the behaviour of fishes.

5.3 Internal

5.3.1 Ontogenic changes

Ontogenic changes in motivational and structural responses to stimuli result from both maturation, which involves intrinsic processes, and environmental experience (Colgan, 1993). For example, seasonal changes in the motivation to feed in Atlantic salmon are associated with different patterns of growth and maturation (Metcalfe *et al.*, 1986).

The most obvious ontogenic change in behaviour is that related to spawning activity which, as already discussed (section 4.3), has a marked impact on the migratory behaviour of many fish species. Additionally, the movement of young-of-the year fish from spawning grounds is also an important ontogenic change (section 4.4).

Linfield (1985) showed that larger fish were found in the upper reaches of rivers and smaller younger fishes in the lower reaches and argued that this was largely a result of predominantly downstream movement of YOY fish, followed by progressive net upstream movement of older fish. However, Lucas *et al* (1998) found a more complicated pattern in the Nidd with the broadest range of size classes being found 7-24 km from the confluence with the Yorkshire Ouse, but more restricted size ranges upstream and downstream of this section. They argued that these differences may have been partly related to the existence of weirs which restricted upstream movement of adult fish.

5.3.2 Hunger/prey availability

It was shown in section 4.5 that many fish species migrate in search of food, sometimes over considerable distances and at increased risk of predation. The stimulus to migrate in search of food involves both a gastric factor based on gut fullness and a systemic factor reflecting metabolic balance. There are, however, few studies of the impact of hunger on the migratory behaviour of non-salmonid species.

Thomas (1977) showed that the acceptance and rejection of food items during a meal have marked and opposite influences on behaviour in sticklebacks. After an acceptance fish search more intensively in the immediate vicinity. In contrast, after a rejection a stickleback is more likely to leave the area. Thomas (1977) argued that, in addition to the effects of satiation extending over an entire meal, acceptances and rejections result in respective short-term positive and negative changes in feeding motivation. These changes are adaptive if prey are patchily distributed. This kind of behaviour may account for the periodic long distance movements of some species between locations where movements are normally short (Langford, 1981; Chapman & Mackay, 1984; Schulz & Berg, 1987, Hockin *et al.*, 1989).

5.3.3 Homing and displacement

Homing in spawning migrations brings an individual fish back to an environment which is known to be suitable for reproduction at a time when other sexually mature fish will also be present (Wootton, 1992). It is evident, therefore, that the ability to home is an important strategy in maintaining an individuals genetic fitness.

The ability to home to a particular spawning location after migrations of hundreds of kilometres has been well-documented for salmonid species (Hasler, 1983). Increased sex hormone levels in migratory salmon are correlated with high sensitivity to the odour of their home stream and post-spawning salmon with low levels of sex hormone no longer respond to their home-stream odour (Hasler & Schulz, 1983). Evidence of homing during spawning migrations in non-salmonid species is, however, sparse (Table 9).

Bergstedt & Seelye (1995) showed that adult sea lampreys are partially attracted to spawning streams by a pheromone produced by larvae. In some ways this mimics homing in that adult lampreys will be attracted to streams that have been successfully used for spawning in the past. However, the stream may not necessarily be the natal stream of the returning adults.

Richard, in Raat (1988) suggested that adult northern pike were capable of homing to their spawning grounds by the smell of decaying organic material. Evidence for homing is supported by Bregazzi & Kennedy (1980) who found that pike in Slapton Ley returned to the same area each year to spawn. Franklin & Smith (1963) did not however find any homing tendency in pike in Lake George.

Whelan (1983) showed that aggregations of bream at the Derrycahill spawning site on the Suck broke down into three separate shoals after spawning which returned to their respective feeding grounds suggesting that this species was capable of homing to both spawning and feeding locations. Marked bream captured in the Zwartemeer and released in the Tjeukemeer, Netherlands left the lake into the surrounding canals and then showed some homing behaviour (Goldspink, 1978). The maximum distance travelled was 60 km. Caffrey *et al.* (1996) showed that bream in the Irish canals showed a strong homing ability at distances of up to 13 km. Roach in Lake Årungen (Norway) demonstrate two kinds of homing behaviour. First they spawn both within the lake and in five inflowing streams. A tagging study revealed that fish migrating into tributaries to spawn exhibited considerable repeat homing (L'Abée-Lund & Vøllestad, 1985). Additionally, the newly emerged young drift downstream to the lake and then carry out a second migration into the stream (L'Abée-Lund & Vøllestad, 1987).

There is some evidence that species which exhibit diel foraging migrations are capable of homing back to their refuge habitats (Carl, 1995; Clough & Ladle, 1997). The homing behaviour of dace is so strong that they can return to the same small refuge area and occupy the same position in the shoal relative to other recognisable fish (Clough & Ladle, 1997). Barbel in the Ourthe, Belgium also showed some ability to home to well-defined resting sites after periods of foraging. Baras & Cherry (1990) suggested that this non-spawning related homing may result in a reduction in bio-energetic requirements by resting in non-riffle habitats after foraging. They also suggested that fish species which generally exhibit aggregative behaviour, e.g. cyprinids, may be attracted to the odour of conspecifics present in their residence area thus maintaining group fidelity. Baras (1996) also examined the homing behaviour of six barbel outside the spawning season. Fish displaced at some distance from their capture site exhibited varying degrees of homing. Fish downstream of their capture site homed more accurately than those upstream of the capture site, possibly due to a lack of orientation cues for fish upstream of the capture site.

Minnows will return to their home ranges after spawning, displacement or eviction by pollution (Kennedy, 1977). Kennedy & Pitcher (1975) demonstrated homing of minnows in a two-compartment tank after reciprocal transfer of two shoals. They found that individuals would still home even if half of each shoal was transferred. They showed that the strength of homing depended on the length of time the fish spent in the tank arguing that fish needed to learn something about their environment. Kennedy (1977) observed that both olfaction and vision were involved in homing behaviour. Gudgeon, are also able to return to their home range after displacement (Stott *et al.*, 1963).

Table 9 British coarse fish species which exhibit homing migrations. ? indicates no information.

Species	Type of homing	Distance	References
Pike *Esox lucius*	spawning	?	Richard (1979 in Raat, 1988); Bregazzi & Kennedy (1980)
Bream *Abramis brama*	feeding-spawning-feeding post-displacement	10-59 km up to 60 km	Whelan (1983) Caffrey *et al.* (1996)
Roach *Rutilis rutilis*	feeding-spawning (in lakes) post-displacement	into afferent streams 2-3 km	Goldspink (1977); L'Abée-Lund & Vøllestad (1985, 1987) Lucas & Mercer (1996)
Dace *Leuciscus leuciscus*	feeding-refuge-feeding	345m	Clough & Ladle (1997)
Minnow *Phoxinus phoxinus*	experimental system	experimental system	Kennedy & Pitcher (1975); Kennedy (1977);
Gudgeon *Gobio gobio*	post-displacement	experimental system	Stott *et al.* (1963)
Barbel *Barbus barbus*	feeding-refuge post-displacement	?	Baras & Cherry (1990) Baras (1996)

5.3.4 Individual differences

Individuals within a population may behave differently in their ability or motivation to migrate. Stott (1967) showed that populations of both gudgeon and roach consisted of a static component and a more mobile component. It was argued that this mobile component failed to accept a home range and could be considered to be the exploratory element of the population. Such a population structure has been suggested in pike from mark-recapture studies (Mann, 1980); chub (Libosvárský, 1961; Nicolas *et al.*, 1994); barbel (Hunt & Jones, 1974); minnow (Kennedy & Pitcher, 1975) and zander (pikeperch) (Fickling & Lee, 1985) and is important when considering the affect that barriers to movement may have on the dispersal capabilities of these species. However, radio-tracking studies on barbel and chub have demonstrated a continuum of ranges of movement between individuals ranging from low to high.

Bruylants *et al* (1986) studied two habitats in the Kleine Nete, a eutrophic canalised lowland river in northern Belgium. One habitat was homogenous with respect to depth, substrate and current and the other was a pool and riffle system They also showed that there were two components to the population and found perch in the homogenous section were more mobile than in the heterogeneous section suggesting that lack of suitable habitat may be responsible for the failure of some fish within the population to adopt a home-range. Broadly similar results were obtained from radio-tracking studies of chub in habitat rich and habitat poor stretches of river (Challis & North, unpubl. data).

5.3.5 Fear/predator avoidance

There is clear evidence that many fish species and life stages use movement as a method of avoiding predators (section 4.7). There are, however, few studies which have studied the effect of fear on the movements of coarse fish. Laboratory studies have demonstrated that shoaling cyprinids alter their foraging behaviour following experience of predators such as pike (Pitcher *et al.*, 1986). These processes may influence local movements in natural systems. Evidence to support the role of fear of predators in habitat selection, mediated through movement, is provided through studies of habitat segregation between young pike and their adult conspecific predators (Grimm, 1981; Grimm, 1994).

5.4 External

5.4.1 Light

The movements and activity of many species are affected by the circadian rhythms of night and day (Table 10). These movements are usually anti-predator responses during the day but in many cases the exact reason for such patterns are unknown and often change over the course of the year. As discussed in section 4.4, light intensity plays an important role in the movements of young-of-the-year fish in determining their movements in response to predators (Cerri, 1983; Hanych *et al.*, 1983; Fraser & Emmons, 1984; Copp & Jurajda, 1993; Baras & Nindaba, in press).

Throughout the early stages of the spawning migration, anadromous lampreys avoid light, hiding under rocks or river banks in the daytime, only resuming their upstream movement during the night (Hardisty, 1979). Commercial fisheries in eastern Europe used this behaviour by illuminating rivers with lamps leaving only a narrow corridor through which the lampreys swim and are trapped (Abakumov, 1956). Claridge *et al.* (1973) showed, using laboratory studies, that this diurnal pattern varied with the season. Greatest night-time activity was in November and December which coincided with lampreys entering freshwater. In March peaks in activity shifted by 2-3 hours and in April activity in the daytime was the same as in the dark. This activity coincided with the main period of nest building and pre-spawning activity.

Just prior to ascending into freshwater, glass eel activity is also highest at night (Deelder, 1952, 1984). However, young eels do not show any differences in migratory activity between day and night (Tesch, 1977). Conversely, silver eels are most often caught at night and Tesch (1977) suggested that light may therefore also have a significant effect on seaward migratory activity. McGovern & McCarthy (1992) showed that the movements of yellow eels were predominantly nocturnal and that swimming speeds tended to be higher in eels that moved during the day. LaBar *et al.* (1987) showed that radio-tagged eels covered a larger area of a small lake in south-western Spain at night than during the day. Average distances moved between observations were also significantly higher at night.

The greatest movements of breeding pike in the feeder streams of Lake Erie and Lake George occurred at night (Clark, 1950; Franklin & Smith, 1963 respectively). Light intensity also played an important role in controlling the emigration of alevins form these nursery streams once they had reached the appropriate size (20 mm) (Franklin & Smith, 1963). On cloudy days heavy emigration only occurred if the sun appeared while on clear days emigration occurred at sunrise. Only a few fish emigrated at night and these only because of displacement.

Clough & Ladle (1997) showed that dace migrated between discrete day and night habitats and that they demonstrated regular daily homing. Radio-tagged dace occupied a short section of the East Stoke Millstream, a tributary of the Frome. There was no active foraging during day but at or shortly before dusk fish moved to one of two new positions in the main river - a pool of 1.3 m depth 345 m upstream of the daytime site with 20 % macrophyte cover and a second area used by one fish only. Both sites were immediately downstream of extensive areas of riffle. At dawn fish rapidly returned to the same daytime site. The tagged dace homed to the same small area within the daytime site and occupied the same position in the shoal relative to other recognisable fish.

Schulz & Berg (1987) demonstrated that bream show rhythmical diurnal migrations between littoral and pelagic zones of Lake Constance. Sanders (1992) attributed the higher numbers of species, individuals and biomass of fish in night electric-fishing catches to diel movements from offshore to nearshore waters during the evening twilight period. These kinds of diel migrations between littoral and pelagic zones may occur in larger rivers as shown by Kubecka & Duncan (1998a) in the Thames. Here, the greatest activity of the larger fish (mainly roach, dace, gudgeon and perch) followed immediately after the onset of dusk and continued in the surface of the open river and littoral zone until dawn as light intensities increased. During daylight hours fish activity was not detectable acoustically as the larger fish were near the bottom.

Table 10 The effect of light on movements and activity of British coarse fish.

Species	Effect	References
Anadromous lampreys	Avoid light in early days of spawning migration. Diurnal pattern varies with season	Hardisty (1979) Claridge *et al.* (1973)
Eel *Anguilla anguilla*	Yellow eels predominantly nocturnal swim faster during day. Silver eels most active at night.	Tesch (1977); McGovern & McCarthy (1992)
Pike *Esox lucius*	Movements of spawning adults greatest at night.	Clark (1950); Franklin & Smith (1963).
	Emigration of juveniles (20 mm) only on sunny days	Franklin & Smith (1963).
Grayling *Thymallus thymallus*	Peak movements of grayling fry out of nursery stream occur at start and end of night	Bardonnet *et al.* (1991)
Dace *Leuciscus leuciscus*	Adults show little activity in daytime moving between discrete day and night habitats.	Clough & Ladle (1997)
	Juveniles move into and out of bays in response to predation risk at different light intensities	Baras & Nindaba (in press)
Chub *Leuciscus cephalus*	Juveniles move into and out of bays and from littoral to pelagic zones in response to predation risk at different light intensities	Schulz & Berg (1987); Baras & Nindaba (in press)
Roach *Rutilis rutilis*	Adults attempt to cross Skip Bridge weir at dawn.	Lucas & Frear, 1997; Lucas & Mercer, 1996; Lucas *et al.*, in review
Gudgeon *Gobio gobio*	Vertical migration in large rivers - more abundant near bottom during day and in surface at night	Copp & Cellot (1988)
Barbel *Barbus barbus*	Diel movements between refuge and forage areas.	Baras (1995)
	only attempt to cross Skip Bridge weir at night.	Lucas & Frear (1997)
	Seasonal variation peaks of activity in early morning and late evening in summer. Dormant in winter.	Lucas & Batley (1996)

Roach and barbel would only attempt to ascend Skip Bridge weir on the Nidd during the early morning or at night (Lucas & Frear, 1997; Lucas & Mercer, 1996; Lucas *et al.*, in press). Lucas & Batley (1996) showed that barbel activity varied greatly on both seasonal and diel temporal scales and was mostly associated with foraging. During summer there was typically a bimodal pattern of diel activity with peaks in the early morning and evening. In winter fish were relatively dormant. Baras (1995) also showed diel patterns in foraging behaviour in barbel with movements between refuge habitats and foraging areas. The level of this activity also varied with temperature.

5.4.2 Hydrology & Meteorology

Malmqvist (1980) showed that the upstream migration of brook lampreys was inhibited by high flows during periods of heavy rain probably because of the energetic cost of swimming against strong flows.

Sörensen (1951) showed that the upstream migration of elvers is inhibited by high flow conditions. During their non-migratory stage, yellow-eels will still make sporadic movements during periods of unstable weather conditions. Tesch (1977) argued that during flood conditions the area of river-bed available to eels for foraging will be increased with eels moving to take advantage of this. As water levels recede eels must leave these new areas or risk being stranded in unsuitable conditions. LaBar, *et al.* (1987) provided some evidence for this increased use of space during flood conditions. They radio-tracked eels in a small lake in south-western Spain and showed that eels used a larger area in rainy weather than did those tracked during drier more stable conditions. In the Elbe the greatest number of eels are caught occurred during periods of high flow (Lühmann & Mann, 1961). However, Tesch (1977) argued that it was not water level but increased flow rate which influenced eel migration. Vøllestad *et al.* (1986) supported this view, finding that the migration of silver eels in the River Imsa, Norway started earlier in autumns with high water discharge. Deelder (1954) found that the direction of migration of silver eels was also influenced by the direction of water flow. White & Knights (1997), however, found no relationship between eel migration and flow velocity or tidal cycles. Cullen & McCarthy (1996) found that variations in the daily catches of downstream migrating silver eels were influenced by wind speed and direction and river discharge and that these factors largely obscured an underlying lunar periodicity in silver eel activity. Peak catches were often associated with stormy conditions.

Clark (1950) observed that the main factor controlling the movement of pike into feeder streams of Lake Erie was the level of ice cover on the stream riffles. When no ice was present spawning fish were seen in early February. Franklin & Smith (1963) also showed that pike did not enter feeder streams until there was sufficient clearance between the inshore ice and the bottom to allow access to the stream.

Montgomery *et al.* (1983) showed that six fish species, including salmonids, cyprinids and the sea lamprey, simultaneously emigrated from the Riviére à la Truite, Quebec as water levels and discharge declined indicating the importance of migration as a strategy for avoiding drought conditions.

Baras & Cherry (1990) found no relationship between discharge conditions and movement of barbel in the Ourthe except for a few downstream movements caused by displacement due to high flow conditions. Lucas & Frear (1997) also found no significant effect of flow in allowing the passage of barbel across Skip Bridge weir on the Nidd. Baras *et al.* (1994a) however, did show that flow through the Ampsin fish pass on the River Meuse was important in attracting barbel to the pass. Slavík (1996), on the other hand, observed the passage of many barbel through a fish ladder in the Elbe, after rain and associated with considerably increased conductivity and decreased water transparency. Champion & Swain (1974) argued that a major flood on the Axe lead to displacement of fish downstream followed by an upstream compensatory migration.

5.4.3 Temperature

As poikilotherms, fish are generally more active at higher temperatures and migration tends not to occur in most coarse fish at temperatures below 5 ^{0}C. Consequently, temperature is known to act as a trigger for fish movements in a number of fish species (Table 11).

Long-term temperature trends influence the onset and duration of the spawning season in lampreys and, once spawning has started, the behaviour of spawning lampreys is markedly affected by relatively small changes in stream temperature (Sjöberg, 1977). In the two *Lampetra* species, spawning usually begins when spring water temperature rises rapidly to about 11 ^{0}C but the sea lamprey spawns later at 15 ^{0}C (Sjöberg, 1980). Malmqvist (1980) showed that, in one year of their study upstream migration in brook lamprey was primarily triggered by a threshold temperature of 7.5 ^{0}C. Additionally, increased temperature was indirectly responsible for decreased dissolved oxygen concentrations in summer which stimulated larvae to drift or actively swim from streams into lakes.

Various studies have shown that the ascent of glass eels into freshwater may be initiated by temperatures of around 6-8 ^{0}C (Deelder, 1952; Creutzberg, 1961; Tesch, 1971). At the pigmented young eel stage migratory activity depends on temperature (Mann, 1963; Larsen, 1972; White & Knights, 1997). Tesch (1977) showed that migratory activity of eels in the Elbe declined at temperatures below 10 ^{0}C. Moriarty (1986) observed that the onset of migration of small yellow eels in the River Shannon was correlated with water temperatures of 13-14 ^{0}C. White & Knights (1997) found a similar relationship between temperature and migration of elvers and yellow eels at the tidal and lower non-tidal limits of the Severn. At the Ampsin navigation weir on the Meuse, Baras *et al.* (1996) found that the effect of temperature on migration was highly variable. This was probably related to the unusual temperatures resulting from the warm effluent from the Tihange power plant. They argued, that because of this, the role of temperature would be secondary to the time of year. However, the relationship between temperature and migrating eels decreased with increasing distance upstream. This correlated with the increasing proportion of older and larger eels upstream which were less temperature sensitive and with the number of physical barriers. White & Knights (1997) argued that, because of this relationship between temperature and the migration of elvers and juvenile eels, global warming may be partially responsible for the current downward trend in eel recruitment (Moriarty, 1990; White & Knights, 1994). Temperature also plays a significant role in the onset of the seaward migration of adult silver eels. In the Elbe estuary Tesch (1977) showed that in years with extended summers, migration was delayed arguing that minimum temperatures were needed to initiate migration and Vøllestad *et al.* (1986) showed a similar pattern in the Imsa River, Norway. Migration in the Imsa occurred between 9 and 12 ^{0}C although no threshold temperature was observed. It is also possible that extremely low temperatures cause a cessation in migratory behaviour in silver eels. In the River Bann, Northern Ireland, Frost (1950) showed that eel migration ceased with the onset of frost and Tesch (1972) showed that eels released into brackish water at temperatures of 6 ^{0}C did not actively migrate.

Clark (1950) found that spawning pike began their movements into the feeder streams of lake Erie, Ohio when water temperatures were 32 ^{0}F (0 ^{0}C) and ice covered the pools. No spawning activity took place, however, until temperatures were 48 ^{0}F (8 ^{0}C). Franklin & Smith (1963) found that slightly higher temperatures of 36-37 ^{0}F (2-3 ^{0}C) for the onset of the spawning migration were required in the feeder streams of Lake George, Minnesota.

Baras & Cherry (1990) showed that temperature (and discharge) variations influenced the movements of radio-tracked barbel in the Ourthe immediately before and after spawning but had little effect in early spring and summer. Maximum movements occurred in temperatures ranging from 10-22 ^{0}C while cold (pre-spawning) and hot (summer) periods were characterised by barbel home range stability. The onset of spawning typically occurs at temperatures of 14-18 ^{0}C although there is considerable variation depending on local conditions (Varley, 1967; Hancock *et al.*, 1976; Baras, 1994). Lucas & Batley (1996) demonstrated that mean daily localised activity of barbel in the Nidd was linearly correlated with monthly water temperatures even during the months when movement to and on the spawning sites occurred.

During a study of fish migration over Skip Bridge weir, on the Nidd Lucas & Mercer (1996) observed a rapid downstream movement of tagged dace together with the disappearance of a large dace shoal from the weir pool. The exact reason for this movement was unknown but appeared to be related to a marked drop in temperature experienced at the time of tagging. Within a four day period in April temperatures fell from 9.1 ^{0}C to 6.4 ^{0}C which they argue was a strong stimulus for dace to return to deeper water. They also showed that temperature played a significant role in the ability of cyprinid species to ascend the weir. They found that the activity of fish observed attempting to pass the weir increased with temperature and was maximal above 12 ^{0}C.

Temperature was also a significant factor in the occurrence of fish in a fish ladder on the Elbe (Slavik, 1996a). The overall composition of the fish assemblage in the ladder was barbel (49 %), eel (41 %), chub (6.8 %), roach (2.4 %), bream (0.5 %), bream/roach hybrid (0.2 %), trout (0.1 %) although this varied from season to season. The start of migration of whole assemblages occurred at temperatures of 10.4-13 ^{0}C during April-May. However, after this temperature threshold the correlation between temperature and intensity of migration was low. Barbel had a maximum migration at 11 ^{0}C then numbers declined in the pass as temperatures increased. Chub however had two maxima (at 11 ^{0}C and 18 ^{0}C) and a minima at 27 ^{0}C. Yellow eel migration was strongly influenced by temperature. They occurred in the ladder after a 21 ^{0}C threshold with maximum abundance at 22 ^{0}C but at 20.5 ^{0}C migration rapidly decreased.

Brown (1979) found that during winter YOY cyprinids in the Rivers Nene and Great Ouse were attracted to and aggregated in those parts of the river affected by heated effluent outflows of 4-10 ^{0}C above ambient temperature.

Table 11 The effect of temperature on movements and activity of British coarse fish.

Species	Effect	References
Lampetra spp.	Spawning usually commences at 11 °C. Upstream migration in adult brook lamprey triggered by threshold of 7.5 °C.	Sjöberg (1980), Malmqvist (1980)
Sea lamprey *Petromyzon marinus*	Spawning usually commences at 15 °C	Sjöberg (1980)
Eel *Anguilla anguilla*	Ascent of glass eel into freshwater initiated by temperatures of 6-8 °C	Deelder (1952); Creutzberg (1961); Tesch (1971).
	Yellow eel migration only occurs above 10 °C.	Tesch (1977); Moriarty (1986);
	Effect of temperature decreases upstream due to increasing number of older eels.	White & Knights (1997)
	Silver eel migration delayed by summers that extend into autumn and also inhibited by extremely low temperatures.	Frost (1950); Tesch (1977)
Pike *Esox lucius*	Adults begin movements into feeder streams in US at 0-3 °C	Clark (1950); Franklin & Smith (1963)
Barbel *Barbus barbus*	Adult maximum movements in temperatures ranging from 10-22 °C while cold (pre-spawning) and hot (summer) characterised by stability.	Baras & Cherry (1990)
	Mean daily local activity of barbel was linearly correlated with monthly water temperatures.	Lucas & Batley (1996)
	Onset of spawning typically 14-18 °C but varies Migration through fish ladders in Meuse occurs at 13-15 °C and in the Dordogne and Garonne rivers at greater than 11 °C	Varley (1967); Hancock *et al.* (1976), Baras (1994); Prignon *et al.* (1996); Travade *et al.* (1996)
Dace *Leuciscus leuciscus*	Rapid downstream movement in Nidd possibly related sudden drop in temperature over 4 day period in April (9.1-6.4 °C). Activity of fish attempting to pass weir increased with temperature and was maximal above 12 °C. Migration of dace through fish pass in Meuse occurs at 10-15 °C.	Lucas & Mercer (1996), Prignon *et al.* (1996)
Roach *Rutilus rutilus*	Upstream migration in tributary of Lake Årungen started at 6-10 °C Activity of fish attempting to pass weir increased with temperature and was maximal above 12 °C. Migration through fish pass in Meuse occurs at 10-15 °C. and in the Dordogne and Garonne rivers at greater than 11 °C	Vøllestad & L'Abée-Lund (1987); Lucas & Mercer (1996); Prignon *et al.* (1996); Travade *et al.* (1996)
Silver (white) bream *Blicca bjoerkna*	Migration through fish pass in Meuse occurs at 10-15 °C.	Prignon *et al.* (1996)
Common bream *Abramis brama*	Migration through fish pass in Meuse occurs at 10-15 °C.	Prignon *et al.* (1996)
Chub *Leuciscus cephalus*	Migration through fish pass in Meuse occurs at 10-15 °C.	Prignon *et al.* (1996)
Sticklebacks	Migrated up Black River, Alaska to avoid June snowmelt	Harvey *et al.* (1997)

5.4.4 Water quality

Some studies using angler catch data have demonstrated very low catch rates immediately below sewage outfalls and have interpreted this as a movement response away form areas of poor water quality (Cowx, 1991). However, Duncan & Kubecka (1993a) reported aggregations of large fish attracted to the actively discharging Abingdon sewage outfall on the upper Thames. Organic pollution has been demonstrated to be responsible for movement of grayling out of large stretches of the River Rhone (Roux, 1984). Nocturnal migrations of cyprinids out of the Vltava backwaters near Prague have been attributed to night-time oxygen depletion of these polluted waters (Slavik, pers. comm.). Hendry *et al.* (1994) demonstrated that roach colonising the Salford Docks were only able to do so during a period in winter when oxygen concentrations were adequate in the Manchester ship canal due to high flows resulting in dilution of pollutants, improved mixing and cool temperatures. Hendry's team are to begin tracking studies in 1998 in the Ship Canal to examine fish responses to changes in temperature and oxygen levels. Libosvárský *et al.* (1967) found that low dissolved oxygen in two Czech brooks polluted with sewage effluent resulted in low abundance of fish in stretches some considerable distance downstream of the pollution source. They showed that the occurrence of fish in affected areas adjacent to a repopulation source changed according to variations in toxicity. This would suggest that fish move into the polluted areas when conditions are favourable and out again when conditions were poor.

Slavík (in press) compared the abundance and sizes of cyprinid fish in the main river and in backwater sites in the Vltava below Prague. The river site was colder in spring and summer and warmer in autumn and winter than the backwater site due to the influence of cold hypolimnetic water coming from the five-reservoir cascade in the upper Vltava. The oxygen concentrations in the river were also lower due to organically polluted water coming from the Prague sewage outfall; also high BOD, more mineral salts and ammonia. Consequently, abiotic conditions (temperature, dissolved oxygen) were less variable for fish than in the backwater. Roach were abundant in both sites and were able to reproduce but other species were less abundant in the river, largely due to their higher temperature requirement for reproduction (bream, bleak, chub, tench, rudd, silver bream and zährte). The response was either to reproduce later in the season at the river site or to migrate into the backwater where the water was warmer. Movement to deeper waters took place earlier (July-August) in the river compared with September in the backwater. By October, all the fish were gone. Diel fluctuations were also important with fish tending to aggregate in the backwater during the day when photosynthetic action oxygenated the water but moving to the main channel at night when oxygen levels declined (Figure 13)

Carline *et al.* (1992) showed that brook trout *Salvelinus fontinalis* migrated to avoid low pH events in streams and it is possible that British fish species may show similar responses although most waters suffering pH fluctuations are dominated by salmonids.

Unhindered migration is also necessary if fish are to recolonise areas affected by pollution incidents. Lelek & Köhler (1989) showed that the reduced abundance of eels in the southern part of the upper Rhine, after a fish-kill caused by a pollution incident from a large chemical factory (Sandoz AG Basel), was quickly compensated by immigration from the tributaries and side-streams.

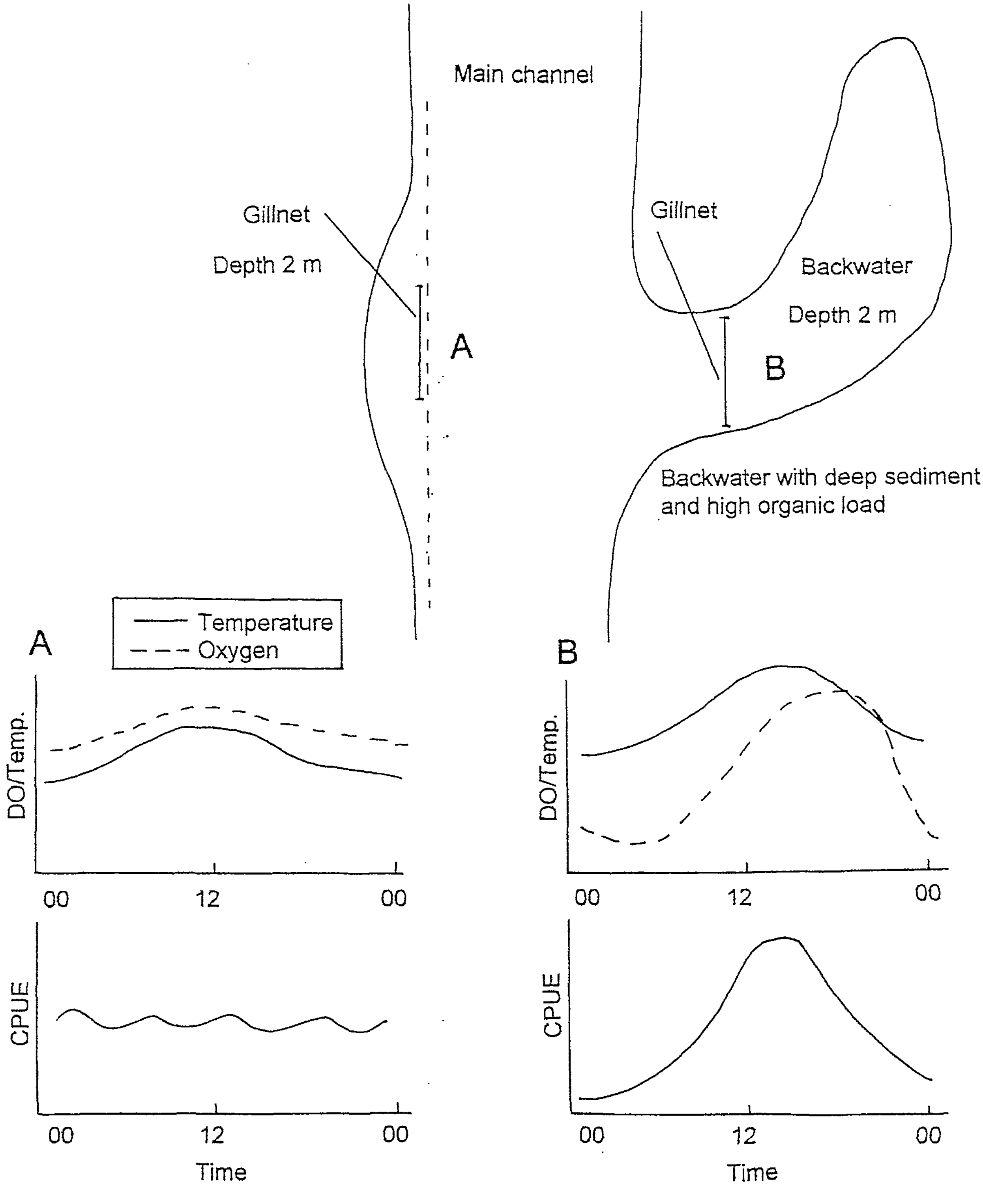


Figure 13 Schematic diagram illustrating the influence of diel fluctuations in water quality on fish movements between the main channel and an organically enriched backwater of the River Vltava, Prague. Fish showed a tendency to aggregate in the backwater during the day, when photosynthetic activity oxygenated the water, leaving at night when oxygen levels declined due to high BOD and lack of photosynthesis.

5.4.5 Prey availability

Fishes may shift their distribution from day to day when the availability of food changes. The food resources in most natural waters vary continuously and the majority of fish have to respond by shifting from pelagic to benthic feeding, from particulate to filter feeding, or by migrating to other habitats.

Global differences in diadromy have already been discussed in terms of differences in production between marine and freshwater environments. Additionally, it was argued that diel migration in many species is the result of a compromise between the need to avoid predation by occupying refuge habitats in the daytime and the need to find food. It is likely, therefore, that prey availability will have a significant impact on the movements of coarse fish at a variety of spatial and temporal scales. Chapman & Mackay (1984) showed that pike generally made short movements within one habitat for a period of days followed by rapid long distance movements between habitats. This, they argued, may be in response to fluctuations in prey availability, short movements being undertaken when prey is abundant followed by long-distance movements to find a new patch of prey. Similar observations have been made by Lucas *et al.* (1991). Bream demonstrate similar movement patterns with sporadic spontaneous movements of several kilometres (Caffrey *et al.*, 1996). Pervozvanskiy *et al.* (1989) showed that pike fed on migratory salmon in the Keret River but were restricted to particular reaches. Armstrong (unpubl. data.), however, found that pike will migrate with salmon, apparently making use of the availability of this abundant resource.

Schulz & Berg (1987) argued that diurnal migrations of bream enabled the favourable use of different resources; dominant benthic organisms in the littoral zone and increased zooplankton abundance in the pelagic zone. Sporadic movements were primarily related to spawning behaviour. However, at other times tagged fish would join aggregations of hundreds of bream responding to high abundance of plankton or emerging insects. Using echosounder surveys, Duncan & Kubecka (1996) detected a large aggregation of coarse fish in a reach of the River Thames as they rose to feed on a mass emergence of mayflies in July. Over a distance of approximately 2 km, fish densities were 21.6 ± 3.2 100 m^{-3} compared to 1-3 100 m^{-3} earlier in the night. It appeared that fish had moved from elsewhere in the river, attracted by the emergence of the mayflies. Hockin *et al.*(1989) also demonstrated that grass carp *Ctenopharygodon idella* movements consisted of short distance movements (<10 m) within restricted feeding habitats together with long-distance movements (>20 m) between such areas.

From these studies it is clear that short diel foraging movements, together with longer distance movements between prey patches and diadromous migrations between spawning and feeding habitats all play an important role in maintaining coarse fish population structure.

5.4.6 Displacement

There is some evidence to show that a number of coarse fish species are capable of homing back to a site after displacement (see section 5.3.3). It is not, however, clear how widespread this behaviour is among coarse fish, particularly those which do not undertake large-scale diadromous migrations.

5.4.7 Density dependent factors

Most studies which have shown that density dependent factors influence fish movements in rivers have been carried out on juvenile salmonids (e. g. Egglishaw & Shackley, 1985). However, Knights (1987) and White (1994) suggested that increasing density and competition may increase migration with low densities suppressing the need to migrate. Aprahamian (1988) and Naismith & Knights (1993) showed that a lack of juvenile recruitment results in low population densities in the upper reaches of rivers and an increase in the proportion of older female eels. These females then form an important component of the breeding stock when they eventually return to the Sargasso (Knights *et al.*, 1996).

Baras *et al.* (1996) argued that eels in the River Meuse migrated in waves which were independent of environmental conditions. It is possible that these waves may have been the result of density-dependent factors which cause yellow eels to migrate after aggregating in large groups similar to the aggregations of elvers which congregate before starting their movement into inland waters (Deelder, 1958).

In a mark-recapture study, Downhower *et al.* (1990) showed that movements of bullhead in a small French stream were density dependent with increased dispersal occurring at high densities. In some cases the earlier migration and occupation of spawning grounds by male coarse fish is probably due to demographic constraints imposed by the sex ratio of the population (Baras, 1994).

6. METHODS FOR STUDYING COARSE FISH MIGRATION

6.1 General Introduction

There is a broad range of methods which have been used to determine the extent of coarse fish movements in freshwater environments (Tables 12 and 13). These can be divided into two types; telemetric and non-telemetric.

Priede & Swift (1992) argue that wildlife telemetry has increasingly (and inaccurately) come to be associated with the use of radio-transmitters for obtaining data on the status of the animal under study (e.g. heart rate telemetry). Priede & Swift (1992), however provide a more useful definition of wildlife telemetry as "all methods of obtaining information on living free-ranging animals by remote means". They go on to argue that obtaining measurements by remote means requires the interception of energy radiated by the animal or reflected by the animal and list five different forms in which this can occur:

i) Direct natural radiation, e. g. acoustic energy of vocalisations..

ii) Reflected natural radiation e.g. light energy reflected from the animal.

iii) Reflected artificial radiation e.g. acoustic echoes from fishes detected by an echo sounder.

iv) Active artificial radiation from a transmitter, e.g. radio frequency energy emitted from a radio transmitter or acoustic pulse from an acoustic pinger.

(v) Active artificial radiation from a transponder, e. g. an acoustic transponder attached to a fish interrogated by sonar.

Interference of an electric field can also be added to this list as this is the method used in resistivity fish counters.

Direct radiation methods are not generally applicable to studies of fish migration because freshwater fish do not generally produce loud noises or other forms of radiation except in electric fishes (Bullock & Heiligenberg, 1986). Therefore, the application of direct radiation telemetry will not be considered here. The most obvious method for detecting reflected natural radiation would be visual observations under natural or enhanced light intensities. For the purposes of this review we consider visual observation separately from mainstream telemetric methods. The remaining definitions are, however, valid and Table 12 summarises the main methods available, describing their advantages and disadvantages and providing an assessment of their use for studies in coarse fish migration.

In addition to visual observations (see above), non-telemetric methods can be considered as those that require regular and repeated direct intervention to obtain information from the fish under study. In migration studies these can be broadly divided into two types.

(i) Capture-mark-recapture - where fish are caught, tagged with one of a variety of marking techniques, released and then recaptured at various time periods and/or at different locations after the initial release.

(ii) Catch-per-unit-effort methods - where the number of fish caught per unit time or area as the result of angling, commercial fisheries, scientific netting or trapping and electro-fishing are used to compare the relative abundances of fish in different places and/or at different times.

Table 13 summarises the main methods available, describing their advantages and disadvantages and providing an assessment of their use for studies in coarse fish migration. The following sections explore in more detail and critically evaluate the use of telemetric and non-telemetric methods for studies of coarse fish migration.

6.2 Telemetric methods

6.2.1 Active radiation from radio and acoustic transmitters.

Winter (1983) argues that "telemetry provides a means to monitor the biology of animals which are not readily visible, to collect data with a minimal influence on the animal's behaviour and health, to collect more data than are gathered by techniques such as mark-recapture and to compare physiological and behavioural data collected in the laboratory and in natural systems." In fact electronic tracking is probably the most important method available for studying fish migration. It provides objective location data with high spatial and temporal resolution (Lucas, 1998b). While the purpose of most location tracking of fishes is to elucidate their movements, home range or habitat use, it has also received increased applied use in the assessment of a wide variety of specific problems such as evaluation of fish responses to obstructions (e.g. Webb, 1990, Lucas & Frear, 1997), establishing the efficacy of fish pass programmes (e.g. Travade *et al.*, 1989), identifying the responses of river fish to acid episodes (e.g. Gagen *et al.*, 1994) and specific conservation programmes (e.g. Moser & Ross, 1995). Telemetry of physiological parameters enables estimation of energy costs for migration and passage of obstructions (Lucas *et al.*, 1993; Hinch, *et al.*, 1996). Telemetry of environmental parameters reveals behavioural responses to variables such as temperature (Berman & Quinn, 1991) and dissolved oxygen (Priede *et al.*, 1988).

Tracking and telemetry of freshwater fish has developed greatly over the last forty years. The earliest tracks of just a few hours duration could give little detail regarding long-term movements, but never-the-less, were informative (Trefethen, 1956). Use of tracking to monitor movements and evaluate home range (e.g. Ridgway & Shuter, 1996) remains important, and is routinely carried out, but has now reached the stage of automated data collection in remote areas with transfer by satellite to distant control stations (Eiler, 1995).

Table 12 Summary of telemetric methods for use in coarse fish migration studies. *Estimates for a 'typical' field study.

	Reflected natural radiation	Reflected artificial radiation	Active radiation from a transmitter		Active radiation from a transponder		Interference with electric field
Limitations	Visual	Echosounding	Radio tagging	Acoustic tagging	Acoustic transponders	PIT tagging	Resistivity fish-counters
Situation	Clear water, restricted site. Small streams and ponds	Low noise, little entrained air, limited plant growth, lowland rivers	Low conductivity (< 500 µS cm^{-1}), shallow, Usually oligotrophic- mesotrophic streams and lakes	Low noise, low turbidity, little entrained air. Usually lakes and slow-moving rivers	Low noise, low turbidity, little entrained air. Usually lakes and slow-moving rivers	Any environment, so long as fish swims within range of antenna	Freshwater, smust be set on Crump-type structure so fish swims within range
Location of sensor	Within sight	Fixed station or mobile on a boat	On land or boat	In water	In water	Within range	Within range
Range (m)	1-10	22	20-2000	20-1000	20-1000	0.05-0.20	
Lifespan (days)	-	No limits	10-600	5-300	5-300	>3000 (or life of fish) if retained	No limits
Water depth (m)	30m for divers, 1-2m for surface and snorkelling	>1.5m	Dependent on conductivity (normally < 3 m)	Dependent on noise (usually 0.5 - 100m)	Dependent on noise (usually 0.5-100m)	Within range (generally < 1m)	Within range (<~ 0.5m)
Minimum fish size	Visible	7-10cm	15cm	15cm	15cm	8cm	20cm
*Technical demand	LOW	HIGH	MODERATE	MODERATE	HIGH	HIGH	MODERATE
*Sample size	10^2	No limits	10^2	10	10^2	10^3	No limits
Disadvantages	Poor range, relies on water clarity, poor for cryptic species	No species identification High data processing requirements	Lower directionality than acoustic systems. Poor range in many lowland waters	Shorter life than radio tags of similar power. Usually requires boat. Sound reflections. Normally fewer tags can be operated than with radio systems	As for acoustic tags. Low availability	Very low range, data collection limited to antenna sites	Very low range, must be sited at strcuture. No individual Identification
Value for fish migration studies	LOW	MEDIUM	HIGH	MEDIUM (in freshwater)	LOW	HIGH (for barrier studies)	LOW
*Equipment costs (£)	Minimal	30000	100 per tag 500-5000 for system	100 per tag 800-5000 for system	300 per tag 10000+ for system	4 per tag 2000-5000 for system	15000 (+ structure)

Table 13 Summary of non-telemetric methods for use in coarse fish migration studies. *Estimates for a 'typical' field study. For capture-mark-recapture methods fish must first be captured using the CPUE methods therefore the advantages and disadvantages of these methods must also be taken into account when planning a capture-mark-recapture study.

	Capture-mark-recapture			Catch-per-unit-effort (CPUE)			
Limitations	Visual tagging	Coded tagging	PIT tagging	Angler statistics	Netting	Trapping	Electric fishing
Situation	Any	Any	in structures	Any	deep waters	deep waters and fish passes	shallow waters
Minimum fish size	5cm	5cm	5cm	5cm	all sizes dependent on mesh size	all sizes dependent on mesh size	5cm (but size selective)
Technical demand	LOW	MODERATE	MODERATE	LOW	MODERATE	MODERATE	MODERATE
*Equipment costs (£)	$10\text{-}10^2$	$10^3\text{-}10^4$	$10^3\text{-}10^4$	$10\text{-}10^2$	10^4	$10^3\text{-}10^4$	$10^3\text{-}10^4$
Advantages	Cheap, large numbers	Large numbers	Large samples, long-term identification	Low labour, widespread sampling	Capture of all sizes, density estimates	Capture of all sizes, density estimates	Low labour, widespread sampling, mobile systems
Disadvantages	Tag loss	Tag recovery requires dissection	Expensive	Requires good angler records	High labour, only suitable for low flow velocities.	Fish behaviour dependent only suitable for low flow velocities.	Shallow water only
Value for fish migration studies	LOW	LOW	LOW	LOW	LOW	LOW	LOW

Radio versus active acoustic systems

Many early tracking studies in freshwater used acoustic methods (e.g. Johnson, 1960), including some on coarse fishes such as bream (Langford, 1974), which while giving greater precision than radio systems, require the use of underwater hydrophones, and transmitters with high power demands (Stasko & Pincock, 1977). 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, and in some cases has been used with other methods such as echo-sounding and physico-chemical measurements to determine the detailed behaviour of fish in relation to thermal stratification and oxygen depletion (Malinin *et al.*, 1992).

Radio-tracking, originally employed in noisy environments such as turbulent rivers (McCleave *et al.*, 1978), has become the preferred method for use in shallow, low conductivity freshwater due to the lower transmitter power consumption, and ease of signal logging by autonomous land-based receiving stations (Winter, 1983), often known in the UK as Automatic Listening Stations (ALSs). In shallow, upland rivers, VHF radio frequencies of 150-200 MHz perform well, and the smaller receiving antennae associated with these shorter wavelengths are easily handled. Lower frequency (40-50 MHz) VHF radio systems are often preferred for tracking fish in deeper and/or higher conductivity water (e.g. Winter, 1983), since signal attenuation is reduced (Velle *et al.*, 1979). As a general guide, the maximum conductivity and depth for which radio-tracking can be expected to be practicable are 500 $\mu S\ cm^{-1}$ and 10 m respectively.

Most development of radio tracking methods has concentrated on migratory salmonids (e.g. Amalaner & MacDonald, 1980; Hawkins & Smith, 1986; Priede & Swift, 1992). More recently work has expanded on other fishes, notably cyprinids in Europe and perciforms in North America, characteristic of lowland rivers and lakes exhibiting greater depths and conductivity (Lucas, 1998b). In the UK most recent tracking studies on coarse fish species have used VHF radio tags: grass carp (Hockin *et al.*, 1980); dace (Beaumont *et al.*, 1996; Lucas & Mercer, 1996; Clough & Ladle, 1997; Lucas, 1998a, 1998b; Lucas *et al.*, 1998); tench (Perrow *et al.*, 1996); barbel (Lucas & Batley, 1996; Lucas & Frear, 1997); chub (Lucas *et al.*, 1998; H. Stone, unpubl. data; R. Challis, unpubl. data); roach (Lucas & Mercer, 1996; Lucas *et al.*, in review) and pike (Perrow *et al.*, pers. comm.). Most groups have used external tag attachment. However, the consensus is that for long-term studies the use of surgically implanted tags is better (Winter, 1983; Lucas, 1998b) (see below).

Further developments

Currently, the minimum size of VHF radio and acoustic tags limits the lower size of fish that can be tagged to about 15 cm (Table 12). The recent development of miniature 300 kHz acoustic transmitters, measuring 17 mm long x 8 mm in diameter, and subsequent validation of tagging methods, has enabled detailed studies of the migratory behaviour of wild Atlantic salmon and sea trout smolts (e.g. Moore *et al.*, 1995) through several UK estuaries. These tags may be applicable to studies of migratory movements of small coarse fish.

One recent problem in freshwater tracking studies has been the limited number of transmitters that can be used at one time. Other than the cost and labour implications, this is influenced by the maximum number of frequency and pulse rate combinations which can be managed simultaneously. 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 & Pincock, 1977). Radio frequencies, utilising greater bandwidth, enable larger numbers of frequencies, usually with a 5 kHz or greater spacing, to be used, although regulatory controls on approval of tag design for all frequencies used may restrict the range of frequencies available. Usually up to three or four pulse rates can be used at each frequency provided that individual fish tend to remain solitary. In this way up to perhaps 100 radio tags might feasibly be operated simultaneously in most countries. The use of coded radio transmitters each emitting an identifiable code of brief radio pulses interrupting the normal longer pauses allows identification of 10-20 transmitters at each frequency, increasing the numbers of tags which can be tracked by nearly an order of magnitude (Eiler, 1995).

Care must also be taken in the planning of any tracking study. For example Baras (in press) argued that the timing of relocating fish in telemetry studies at intervals longer than a day generates a bias in results, particularly in mobility studies. He argued that this may account for discrepancies between the interpretations of the same phenomenon proposed by different authors relying on different sampling strategies. Baras (in press) showed, however, that the loss of accuracy can be predicted and corrected but only in each river under study. He recommended that preliminary work should be carried out in each study to determine the effects of different time intervals between position fixes on the interpretability of results. This would then provide a way of conducting long-term studies relying on the use of transmitters working on duty cycles.

Combined systems

In marine and estuarine environments acoustic tags must be used, but in freshwater radio transmission gives extended tag life. Use of Combined Acoustic and Radio Transmitter (CART) tags has been of great use in studying movements of fishes, principally migratory salmonids between marine and freshwater environments; (Solomon & Potter, 1988; Smith & Smith, 1997); but may be useful for studying the movements of coarse fish in the lower reaches of rivers in tidal regions.

A tracking system described by Armstrong *et al.* (1988) for use from a single station in large freshwater environments has both acoustic and radio phases operating simultaneously with the difference between acoustic and radio pulse propagation times being used to determine fish range (RAFIX), removing the need for triangulation procedures.

Archival tags

Recently, archival or data storage tags have utilised low cost, high memory capacity RAM chips, combined with the low power required to accumulate and store data, in order to obtain and archive large temporal series of one or more environmental parameters. Increasingly used to gather data on the behaviour and movements of tuna, marlin and smaller marine fishes (see Metcalfe *et al.*, 1996), data storage tags have undergone reduction in size combined with maintenance or increase in data storage density, and this has played a key role in establishing their suitability for use with resident freshwater and diadromous fish. Sturlaugsson (1995) first demonstrated the use 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. Such tags might provide useful information concerning responses of coarse fish to environmental parameters during their migrations.

Telemetry of intrinsic and extrinsic parameters

Transmission of information from freshwater fish has dramatically enhanced our understanding of their responses to environmental factors in the natural environment. Telemetry of environmental variables from fish can provide much information regarding responses to physical factors such as temperature (Coutant, 1969; Snucins & Gunn, 1995) and oxygen concentration (Priede *et al.*, 1988) and is of great applied significance in understanding the impact of anthropogenic influences on fish behaviour. Simple tilt-switch transmitters which vary pulse range with changes in the fish's body attitude, widely used for terrestrial applications, but little used for studies of fish, have been used highly effectively in recent studies concerning feeding behaviour of tench *Tinca tinca* in lakes (Perrow *et al.*, 1996), and time-activity budgeting of barbel in relation to temperature (Baras, 1995).

Recent advances in physiological telemetry 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 localised activity (Demers *et al.*, 1996) and evaluated the costs of migration through areas of river with different velocity regimes (Hinch *et al.*, 1996), including those for which passage is difficult.

Physiological telemetry techniques are likely to be useful in examining the energetic consequences of attempted migration past obstructions, through fish passes, and in polluted regions of rivers.

6.2.2 Active radiation transponders - PIT tags

Recently passive integrated transponder (PIT) tags (Prentice *et al.*, 1990a, b, c) have been developed for a wider variety of uses. PIT tags allow the collection of detailed information on large numbers of fish. They are relatively inexpensive, small, can be programmed with an infinite number of individual codes, and have no battery and therefore an infinite life. The PIT tag contains no power source and comprises a coil antenna and integrated circuit (IC) chip encapsulated in glass, which currently may be as small as 12 mm long and 2.1 mm in diameter. Each IC is programmed at manufacture with one of 34×10^9 possible codes, and is interrogated by being energised with a 400 kHz field from an induction coil, after which it retransmits its code at 40 kHz. Hand-held readers can be used to identify tagged fishes or the tag can be recorded automatically as the fish swims through a pipe surrounded by a coil antenna. Several flat-bed systems are currently being developed, to enable more complex behaviour of large numbers of fish to be studied under laboratory conditions and in the natural environment.

Achord *et al.* (1996) used PIT tags to monitor migration timing of chinook salmon smolts in Snake river, Idaho and Oregon. They used an automated tagging system which consisted of an electronic balance, digitizer, tag detector and automatic tag injector. The automatic tag injector used a pushrod system activated by high pressure carbon dioxide. Each injector was fed by clips containing approximately 150 PIT tags each. Fish were tagged, passed through the detector loop which entered the tag code into the computer along with other information. The fish was placed on the balance and the weight automatically entered in the computer. The fish was then placed on the digitizer and an electronic stylus was activated at the tail fork and recorded the length in millimetres in the computer. Detection was carried out at a dam bypass.

Castro-Santos *et al.* (1996) argued that one limitation of PIT tags is that tagged animals must pass through a confined area (less than 1000 cm^2) to be detected by the readers. Getting fish to pass through such small openings is not always feasible and laboratory and field studies using larger fish or fish that must pass impeded through large orifices have been unable to take advantage of PIT technology. They developed an application of PIT technology as part of an ongoing evaluation of simple Denil and Alaska Steeppass fishway designs. Movements were monitored without the constraints of passing fish through small orifices. Antennas were constructed on site and consisted of wire coils mechanically protected by PVC pipe bent to the shape of fishways baffle openings. Pairs of antenna were connected in series with one antenna of each pair installed in a fishway. This arrangement allowed both fishways to be monitored by four antennas each connected to a separate reader. Each PIT tag (32.5 x 3.8 mm) was programmed with unique codes identifying fishway group and individual. Each tag was externally labelled for identification, attached to a fish hook and inserted through the cartilage at the base of the dorsal fin of American shad (*Alosa sapidissima*) blueback herring (*A. aestivalis*) and gizzard shad (*Dorosoma cepedianum*). Fish were allowed to ascend for three hours. They were then removed and their tag numbers, passage status (above or below fishways) and length were recorded. Tags were removed and reused with other fish. Time of passage was verified with video. Only one fish passed through Denil without being detected by readers. Four fish passed through Steeppass but three of these had faulty PIT tags. Reader efficiencies were 96 % and 88 % respectively. The major limitation of this system is still the size of detection field (0.5-1 m) and the read rate. Gap in detection at ground speeds of 2.5-3.5 m s^{-1} in Steeppass and 5.0-7.0 m s^{-1} in Denil and fish migrating in groups affect efficiency. A limitation of this system was that in order to use openings of > 1000 cm2 large PIT tags (approximately 30 mm in length) had to be used which prohibits the assessment of movements of small fish.

Armstrong *et al.* (1996, 1997) used PIT tags coupled with automated monitoring systems to make detailed spatio-temporal observations of known individuals. In an artificial riffle and pool stream alongside the Girnock Burn, Aberdeenshire flat bed antennae separated by about 1.75 m were embedded in the floor of the stream. The antennae were connected to decoder units via paired coaxial cables and then to a computer which stored the details of the fish detected. The areas to the side of the antennae were built up with cobble and boulders held together by netting to funnel fish over the antennae. Sheets of white plastic were placed under the antennae to discourage fish from hiding adjacent to or under the antennae causing multiple recordings of the same static individual. Each time a fish swam over, or came close to, an antenna, the code of the PIT tag was decoded and stored. In this way it was possible to monitor movements of fish in the stream without interference.

In a collaborative pilot project, which began in February 1998, the University of Durham (Lucas), the Freshwater Fisheries Laboratory, Pitlochry (Armstrong) and the Environment Agency NE Region (Agency co-ordinator, D. Hopkins) are developing the use of an automated PIT system for investigating the upstream migration of coarse fish, especially small cyprinids. Armstrong is the UK's leading researcher in the development of automated PIT systems and is currently using such systems to monitor salmonid movements in fish passes.

PIT systems have a low range and must, therefore, be used where fish migration routes are restricted such as in fish passes. PIT systems might be employed in many passes of the Denil and superactive baffle designs, although at some sites steel reinforcing within the concrete can reduce range below tolerable limits. With experience and development it is anticipated that PIT systems can be applied to more demanding conditions.

The specific aim of the current collaborative project is to investigate coarse fish passage through the Denil pass at Stamford Bridge weir on the Yorkshire Derwent in relation to fish size and identifying the effects of environmental parameters such as flow and temperature on the extent and success of upstream migration through the pass.

The ability to log passage of many, individually identifiable fish of a wide range of sizes and species raises the possibility of making detailed assessments of the influence of environmental parameters such as flow and temperature as migratory stimuli; and in determining success of movement through fish passes in relation to size and species. It also links migration studies closely to existing and possible future Agency research and development projects in areas such as fish swimming performance, and fish pass efficiency. Major advantages of this system are that:

(i) Much smaller fish can be logged than by other systems such as radio-tracking or by resistivity counters.

(ii) The system provides the identity of the fish, giving information on species, size etc. which can be related to the success of passage under different conditions.

(iii) The tags, having no battery, survive as long as the fish; so any future study could make use of these tagged fish also.

The detection method is based on that of Castro-Santos *et al.* (1996) and Armstrong *et al.* (1997), involving installation of PIT detectors at the top and bottom of the fish pass. These units emit low frequency electromagnetic interrogation signals and if a tagged fish is within range, the tag is energised and replies with a unique code, which is logged. The detectors are flat, rectangular epoxy-covered antenna arrays, bolted to the concrete base or walls, which will not influence water speed or movement appreciably. The units are powered by mains or battery and employ a datalogger which is downloaded periodically. Numbers and identities of fish attempting to move up through the fish pass are measured from the tags logged at the lower detector. Numbers and identities of fish successfully exiting from the pass are given from the tags logged at the upper detector (at the top exit). Pass efficiency can be calculated from these data. A trap will be placed at the top of the fish pass to enable independent calibration of PIT records.

Measuring efficiency of fish passes is an increasingly necessary aspect of ensuring that the costs of expensive fish pass installation are met in terms of ensuring an acceptable level of fish passage (see section 7). However, to date the Environment Agency has had difficulty in doing so objectively, especially for smaller fish. The advent of automated Passive Integrated Transponder (PIT) tag systems changes this.

6.2.3 Attachment methods

Any method for studying fish should not itself lead to changes in the behaviour or physiology of the individual being studied. Therefore, the attachment of telemetry devices should be carried out in such a way as to minimise their effect on the fish.

In early studies, published between 1956 and 1965, most transmitters were attached externally, at least partly because the transmitter output did not last long enough to make long-term attachment a requirement. However, external transmitters can lead to a loss of buoyancy and postural equilibrium and may be physically snagged resulting in damage to the fish or premature loss of the transmitter (Ross & McCormick, 1981, Perrow *et al.*, 1996). Advances in attachment methodology occurred over the next decade, with intragastric implantation becoming the preferred technique for adult migratory salmonids. However, intragastric transmitters may interfere with the feeding of fish and in, some species, are regurgitated or excreted leading to premature loss of the transmitter (Lucas & Johnstone, 1990; Armstrong *et al.*, 1992; Armstrong & Rawlings, 1995). Increasingly, therefore, intraperitoneal implantation has become the most widely applied method for most other taxa (Table 14). The current situation is the reverse of the 1950s and 1960s, with external attachment the least popular tag attachment method, mainly being used for applications such as telemetry of oxygen levels (Priede *et al.*, 1988) where the sensor must remain in contact with the water, or where re-use of the transmitter is a high priority.

In recent years a wide variety of studies have sought to identify the best transmitter attachment methods, and quantify their effects on fish behaviour and survival (Lewis & Muntz, 1984; Summerfelt & Mosier, 1984; Mellas & Haynes, 1985; Lucas, 1989; Helm & Tyus, 1992; Beaumont *et al.*, 1996). It is clear that wherever surgery is involved fish will be subjected to longer disturbance and it is important to critically evaluate methods prior to their application in fish studies (Baras *et al.*, in press). There are many factors that need to be considered when carrying out implant surgery on fish and Baras *et al.* (in press) provide a review of the most appropriate techniques and considerations to be met. These are summarised in Table 14.

Table 14 Best practice for surgical implantation of active telemetry transmitters in fish. Summarised from Baras *et al.* (in press)

	BEST PRACTICE	REFERENCES
Anaesthesia	Soaked in bath anaesthetics until tolerance stage then placed ventral side up on a support with head and gills immersed in anaesthetic solution. Quinaldine (10-40 mg l^{-1}), tricaine (25-100 mg l^{-1}) and 2-phenoxyethanol (0.25-0.40 ml l^{-1}) most popular.	MacFarland & Klontz (1969), Summerfelt & Smith (1990).
	May be toxic to some species.	Schramm & Black, (1984)
Incision site and length	Should be selected based on different criteria: innocuity, healing dynamics, minimum expulsion risk. Midventral incisions more common because viscera are unlikely to be damaged when fish is upside down.	Hart & Summerfelt (1975), Bidgood (1980), Baras *et al.* (*in press*).
	Lateral incisions may puncture gonads, difficult to close, longer healing, lower survival rates due to infection, cause damage to striated muscle.	Roberts *et al.* (1973), Schramm & Black (1984), Clapp *et al.* (1990), Knights & Lasee (1996)
	Lateral incisions may be advantageous in reducing risk of transmitter exiting through the incision. To minimise trauma take account of transmitter length and flexibility of fish body wall. incision to transmitter diameters 1.4-1.5 (catfish), 1.6-1.8 (cyprinids, salmonids)	Baras (1992), Baras & Westerloppe (1995), Birtles *et al.* (1995), Thoreau & Baras (1996, 1997).
Implant size and weight	Weight of transmitter in water should be less than 1.75% of body weight. Few problems found at this weight. Above this value may get problems with survival, behaviour, swimming capacity, posture, growth, or risk of implant exit.	Hart & Summerfelt (1975) Stasko & Pincock (1977), Winter (1983), Moore *et al.* (1990), Baras (1992). McCleave & Stred (1975); Marty & Summerfelt (1986), Meyers *et al.* (1992), Thoreau & Baras (1996, 1997)
Internal positioning of implant	May move within body cavity and cause damage. Should be placed with least likelihood of movement, e.g. over pelvic girdle. Use of sutures to anchor to body wall worked with cod but led to expulsion by channel catfish.	Chamberlain (1979), Bidgood (1980), Schramm & Black (1984), Pedersen & Andersen (1985), Marty & Summerfelt (1986)

Table 14 Continued

Closing the incision	Suturing with separate stitches most popular technique. Choice of absorbable (catgut) and non-absorbable (nylon or silk) trade off between risk of expulsion risk of infection due to presence of foreign body.	Hart & Summerfelt (1975).
	Surgical staples quicker but are still foreign bodies and require removal of more scales with greater risk of infection.	Mulford (1984), Filipek (1989), Mortensen (1990), Mellas & Haynes (1985).
	Adhesives give fast closure and almost suppress inflammatory response. Only remain for few days leading to more incision exits. Eels remove it by biting. Applying piece of fin over the adhesive gave faster healing rates.	Nemetz & MacMillan (1988), Petering & Johnson (1991).
Healing rate	Temperate species 4 to 6 weeks, longer at low temperature. Juveniles heal faster.	Pedersen & Andersen (1985), Baras (1992), Ross & Kleiner (1982), Moore *et al.* (1990), Knights & Lasee (1996)
Implant exit	Implants become encapsulated by tissues leading to changes in gravity pressure resulting in expulsion through route of least resistance - usually incision site. Also expelled through intestine after capsulation. Encapsulation may occur regardless of coating depending on species. Can reduce risk by positioning implant as far from incision as possible, Reducing transmitter to body weight ratio may help although longer transmitters less likely to enter intestine. Generally recommended not to implant females during spawning season due to pressure by egg mass. However, enlarged gonads reduced transintestinal expulsion risk in African catfish. Prophylactic care to reduce infection may also help.	Marty & Summerfelt (1986), Lucas (1989); Ross & Kleiner (1982), Marty & Summerfelt (1986), Lucas (1989), Winter (1983),
Post-operative recovery	Reduce periods of post-operative care by releasing as soon as fish show spontaneous swimming when recovering form anaesthesia as extended periods of capture have adverse effects on behaviour	Kuechle *et al.* (1981), Otis & Weber (1982)
Post-operative perturbation	After release fish behaviour may still be abnormal. However, deviation form normal behaviour is dependent on species and in many cases individual differences. Therefore, single behavioural traits are poor general indicators of fish well being. Therefore, best to determine when fish start to behave normally *a posteriori*.	Manns & Whiteside (1979), Diana (1980), Mesing & Wicker(1986), Thoreau & Baras (1996, 1997),

6.2.4 Echo-sounding - reflected artificial radiation.

Introduction

Sonar is a general term for any device, for example echosounders or acoustic tags that uses sound to enable the remote detection of objects in water. The echosounder is a particular kind of sonar, one whose acoustic beam can be directed vertically downwards in deep waters or horizontally across shallow waters. It transmits acoustic energy in pulses at a particular frequency by means of a transducer in a directional sound beam. On encountering a fish target, the sound pulse is scattered (reflected) in all directions and some is 'back-scattered' towards the transducer. The transducer detects the backscattered sound (the echo) and converts it to a quantified electrical signal.

Echo-sounding is a well-established tool for fish studies in large waters (MacLennan & Simmonds, 1992). It has the advantage over most other techniques in not being intrusive. It is a tool that can quantify fish densities and the dual-beam and split-beam echosounders are capable of measuring directly the acoustic size or target strength of fish so that the size structure of the fish community can be determined. This can be done extensively over large distances and intensively in fine detail. Echosounding does however, have to be combined with live capture techniques to obtain information on species composition. Until recently, most fisheries sonar applications used vertically-oriented sound beams from surface to bottom which is inappropriate for European rivers. Following the commercial production of narrow-beamed transducers with negligible side-lobes, it has become possible to use sonar horizontally in shallow waters with depths between 1.5 m and 5 m (Butterworth *et al.*, 1993; Kubecka, 1996a). These are the depths in which most coarse fish migrations take place.

Horizontal sonar can be deployed in two sampling modes:

(i) by fixed location where the transducer is fixed at one location from which the sound beam is directed across the river, 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 whilst the boat is underway close to one bank.

The majority of fish migration studies using echosounders in rivers have been confined to the former sampling mode but recent studies have shown the potential of the latter mode.

Fixed location studies for monitoring upstream migrations

Since the 1960s, fixed location acoustic techniques have been used to count non-intrusively upstream migrations of anadromous salmonids (mostly *Oncorhynchus* spp) returning up the very large clearwater rivers on the west coast of North America and in Alaska and facing obstacles such as hydroelectric dams (BioSonics Inc., 1989; Johnston & Steig, 1995; Thorne, 1998). Although not dealing with coarse fish, many lessons can be learnt from these studies in detecting migratory movements of fish under riverine conditions. Application of sonar to the smaller, more turbid, organically-loaded European lowland rivers has revealed limitations in both hardware and software leading to new developments which may be helpful for coarse fish migration studies.

Dual-beam acoustic systems

Most early studies on riverine dual-beam acoustic techniques were applied to salmon migrations (Braithwaite, 1971; Gaudet, 1990; Johnston and Steig, 1995; Gregory *et al.*, 1996; Laughton *et al.*, 1996). However, many of the techniques and recent developments may be applicable to studies of coarse fish migration.

Early (1970s) single-beam echosounders worked well for rivers with large migrations of big fish which tended to move close to the river bank where the sound beam could be located but gave no information on fish size, direction of movement, fish speed or vertical distribution. The need to size the fish led to the use of dual-beam systems with narrow and wide beams in the same transducer and with signal processors which could detect peak echoes and discriminate single targets. Subsequently, the dual-beam data could be processed to track individual fish and provide a mean target strength for each fish (although not yet convertible to its real size. The direction of travel of each fish was determined by employing dual-beam elliptical transducers set at an oblique angle to the river flow. Assuming the fish to travel in parallel to the river bank, a difference in change of range could be detected between upstream and downstream moving 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 the fish entered first.

Subsequent improvements to the earlier techniques increased the output of information. Adding a chart recorder provided more information on each fish as well as fish numbers in the different horizontal strata across the river. Adding a remotely-controlled pan-and-tilt rotator with attached transducer greatly improved the aim of the sound beam and lengthened the maximal usable range (Kubecka, 1996a). Direction of fish movement was determined by aiming transducers upstream or downstream at an angle to river flow. The advent of elliptical transducers meant that fish stayed longer in the beam than with circular ones and the angle of the longer fish trace could indicate direction of travel.

A very important step forward for measuring fish sizes and echosounding of single targets was the development of the dual-beam digital signal processing system which detected, measured and saved for future analysis the echo signal peaks of single targets from both narrow and wide beams. A high proportion of fish targets in lowland rivers at night were found to be single targets (Kubecka *et al.* 1992). The acoustic size or target strength of these single targets could be determined by a method described by Ehrenberg (1972, 1984). Thus it became possible to distinguish whether the fish were moving as a dense shoal or loosely spaced individuals which could be sized. A further post-processing target tracking software was developed which grouped all the echoes from one individual target moving across the beam and gave a better feel for direction of movement (Johnston, 1985). The appropriateness of the grouping of echoes by the tracking system could be checked on the echogram.

Split-beam acoustic systems

In the early 1990s, split-beam acoustic systems became commercially available for studies on salmonid migrations. These had the advantage of lower side-lobes and faster signal processors. They were 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 three dimensional position within the sound beam, velocity of the fish target and less variable fish target strengths.

The development of echosounders based on the entirely different split-beam acoustic system was driven by the need for better and less variable estimation of fish target strengths than in the dual-beam system, although at the expense of more user-unfriendly hardware and software.

The use of split-beam echosounders in riverine migration studies in America in the early 1990s led to additional advantages over the dual-beam system. These included improved ability to track fish passing through the beam in three dimensions and thus not only determine the absolute direction of the fish movement but also the vertical distribution of fish targets in the water column. Downstream movement of riverine debris on the surface of the water could be easily identified and their echo traces eliminated. Aiming split-beam transducers was easier than a dual-beam one with the use of reference targets whose location could be seen in the beam in three dimensions in real time (Johnston and Steig, 1995). Split-beam systems have only recently been applied to fish migration studies in European lowland rivers (Table 15). There has been some development of fully-automated fixed location techniques for monitoring fish migrations at the cooling water intakes of American power plants which also incorporated high frequency sound fish-deterrents (Ross *et al.*, 1993).

Table 15 Fixed location studies in European Rivers

Acoustic system	Rivers	Mode	Taxa	References
Split-beam, 200 kHz elliptical transducer	Spey, Scotland	Horizontal	Salmonid	Laughton *et al* (1996) Johnston & Ransom (1994)
Split-beam, 200 kHz, circular transducer	Wye, Wales	Horizontal	Salmonid	Gregory *et al.* (1996)
Dual-beam, 200 kHz, elliptical transducer	Tavy, England,	Horizontal	Salmonid	Kubecka & Duncan (1994)
Split-beam, 120 kHz, elliptical transducer	Elbe Czech Republic	Horizontal	Coarse fish	Kubecka *et al.* (1996)
Dual-beam, 420 khz, elliptical transducer	Ouse, York,	Horizontal	Coarse fish	Duncan & Kubecka (1993c), Lucas *et al.* (1998)
Dual-beam, 420 kHz, elliptical transducer	Thames, England	Horizontal	Coarse fish	Duncan & Kubecka (1993b); Kubecka & Duncan (1998a)

The mobile acoustic survey technique in shallow waters

The technique using horizontal sonar to survey and assess fish stocks of shallow waters during a mobile survey was developed during the NRA R&D Project 196 (Butterworth *et al.*, 1996; Duncan and Kubecka, 1993b; Kubecka, 1996a) and is now used routinely by the Agency to monitor fish populations over long stretches of various English lowland rivers, such as the Thames (Hughes, 1998), Trent (Lyons, 1998), Ure/Ouse and the tidal Hull (Frear, 1996, 1997).

Although mobile surveys have not as yet been used for coarse fish migration studies, the techniques' potential for surveys of whole stretches of rivers deeper than 1.5 m make it an appropriate tool, in combination with techniques such as radio-tracking and direct sampling techniques, for studies of fish migration at the catchment scale. Thus, extensive surveys of rivers carried out at frequent intervals, in combination with radio-tracking, will enable the interpretation of the movements of individual fish in relation to major changes in fish densities and community size structure. This integrated approach would enable the detection of the extent and timing of spawning migrations (Duncan & Kubecka, 1993b), migration to and aggregation in overwintering refuges (Wortley, 1981), and patchiness in summer distribution (Duncan and Kubecka, 1996).

Moreover, fixed location studies can be combined with mobile acoustic surveys of rivers in order to assess size frequency distributions of fish targets. This combination of sampling modes will be useful to detect the presence of unusual aggregations of fish such as during spawning time or in winter. Regular mobile surveys will indicate the time and place in the river and the fish size structure can be reliably determined by fixed location observations.

Although acoustic ranges in medium-sized rivers are often short (10-20 m in British rivers), the total sampled volume is very large, providing data sets for statistical analysis and a continuous spatial record of absolute fish densities in the water column. It is important that surveys include night work, since this is when many coarse fish species are active in the water column. Fish densities can be determined at short sampling intervals enabling the characteristic patchiness of coarse fish density distributions along a river to be measured (Duncan and Kubecka, 1996). No other technique, whether netting or electro-fishing, has this potential for describing the spatial dimensions of fish abundance as well as the impact of in-river events (a mayfly emergence stimulating feeding migrations) or of external anthropomorphic inputs of various kinds (active discharge of sewage effluents or hot water outflows) upon the distribution of fish stocks.

Table 16 Mobile acoustic fish surveys in European Rivers

System	Rivers	Mode	References
Dual-beam, 420 kHz, elliptical transducer	Thames, England	Horizontal	Duncan & Kubecka (1993a)
Dual-beam, 420 kHz, elliptical transducer	Ouse, England	Horizontal	Duncan & Kubecka (1993c)
Dual-beam, 420 kHz, elliptical transducer	Vltava, Czech Republic	Horizontal	Kubecka (unpubl. data.)
Dual-beam, 420 kHz, elliptical transducer	Thames, England	Horizontal	Hughes (1998)
Split-beam, 120 kHz elliptical transducer	Trent, England	Horizontal	Lyons (1998)
Split-beam, 120 kHz	River Ure/Ouse, tidal River Hull	Horizontal	Frear (1996, 1997)
Split-beam, 129 kHz Dual-beam, 420 kHz	Yorkshire Ouse system;	Horizontal	Lucas *et al* (1998)
Split-beam, 120 kHz, elliptical transducer	Elbe, Czech Republic	Horizontal	Kubecka *et al.* (in press)

Fish sizes

To produce a frequency distribution of the sizes of individual fish targets, fixed location must be used since the orientation of the fish body or aspect being insonified cannot be tracked whilst the boat is moving. 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. Regular fixed location studies with the boat anchored for a short period along the mobile route enables the slope of the fish track across the horizontally-oriented beam to be estimated. In rivers, but not in lakes, fish tend to orient to river flow, and cross the horizontal acoustic beam perpendicularly to the acoustic axis (Kubecka 1996a). This is important, as the echo reflected from a side-aspect fish is much higher than the same fish in head or tail aspect.

Until recently, side-aspect or known aspect target strengths of riverine fish species could not be converted to real sizes of length or weight in the absence of predictive regression between target strength and length/weight for freshwater fish. Existing relationships (Love, 1969, 1971, 1977) refer to marine species in dorsal aspect. The NRA Note 374 (Duncan and Kübecka, 1995; Kubecka and Duncan, 1998b) provides such regressions for a series of riverine fish species in several body aspects (side, head/tail and mean all-aspect) measured by dual-beam echosounders for 200 kHz and 420 kHz. There is a pressing need for a similar set of regressions for 120 kHz and 200 kHz split-beam echosounders which are in routine use by the Agency.

Application of echosounding sonar to the study of coarse fish migration.

Fixed location studies

Initially fixed location studies were mainly used to monitor upstream migrations of adult salmon and sea trout started in Europe (Table 16). A study on a fish ladder at the Strekov Dam on the Elbe, Czech Republic seems to be the first application of a split-beam echosounder for counting coarse fish migrating through a fish ladder (Kubecka *et al.*, 1996). In addition to fish counting and sizing, the split-beam echosounder provided direct information on the direction of fish movement, thus permitting migrants to be distinguished from resident fish in the area above the fish ladder which was not possible with the dual-beam system in the Tavy. Fixed location acoustic studies have not been undertaken to monitor the large-scale longitudinal and upstream migrations of coarse fish, although the "transverse" migrations of fish in and out of backwaters of the alluvial flood plain of the Danube are being studied (G. Rakowitz, pers. comm.).

Fixed location studies can be used for following diurnal behaviour and movements of coarse fish within their home area and, combined with biological work, could provide information on feeding movements. The potential for this is shown by Kubecka and Duncan (in press (a)) in a 24 hour study during June 1992 in the Chertsey Reach of the Thames. Here, the fish community was known: roach, dace, gudgeon, perch, ruffe and other species in lesser abundance. By siting two dual-beam horizontally-directed transducers in the littoral (0.5 m deep beaming to the river) and in mid-river (~3 m deep, beaming across the river), the movements of fish were followed over 24 hours at hourly interval and at three 1 m-depth intervals in mid-river. The larger fish were in the littoral and in top depth stratum of the river during the night and early morning but moved to deeper layers during the day where they were not detectable by the horizontal beam as they were too close to the bottom. In the open river, all the fish oriented themselves to the river flow and swam upstream or down stream, 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. As has been mentioned earlier, similar night inshore migrations of fish have been recorded in large rivers by electric fishing (Sanders, 1992; Copp and Jurajda, 1993) and in several lakes and reservoirs by shore seining (Kubecka, 1993).

Mobile surveys

Only one paper (Lucas *et al.*, 1998) is notable in having information on seasonal changes in fish density distributions using echosounding over the same 27 km stretch in the Yorkshire Ouse. This was achieved by conducting a series of monthly mobile surveys. This study also demonstrated the potential impact of spate river flows on fish densities in the river. During the night of September 9/10 1993, river flow was five times greater (63.5 $m^3 s^{-1}$) than during the previous night (12.7 $m^3 s^{-1}$) and mobile surveys on both nights showed that 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.

A series of mobile surveys were undertaken in the Shepperton Reach of the Thames during April to June 1992 in order to follow fish behaviour during the spawning period. On the nights of May 14/15 and May 19/20 1992, three distinct aggregations of fish were observed acoustically with high fish densities of between 3000-4000 fish ha^{-1} separated by areas of low densities (Duncan and Kubecka, 1993a). That these were the result of a spawning migration was confirmed by shore seining during the day on May 14 and May 19 1992. Ripe roach and dace were caught, with a higher proportion of spent fish on May 19^t and a mass occurrence of pelagic cyprinid larvae in the open river, thus confirming the occurrence of a spawning migration.

Echosounder surveys showed high fish densities recorded in the Culham and Clifton Reaches of the Thames during one night in July 1993 (Duncan and Kubecka, 1996). One particular patch of >100 fish 100 m^{-3} at river mile 103 was located at an active sewage outfall which attracted more large fish than usual in what might be called a diurnal feeding 'migration' timed with sewage effluent output. In September when the survey was repeated, there was no such patch of higher fish density, probably because the sewage outfall was not active during sampling. Similarly, intense fish activity was recorded in response to a mass mayfly emergence in the Clifton Reach of the Thames in July 1993 which took place between 03:00 and 04:15. Earlier in the same night the same reach was surveyed with much lower fish densities.

It is evident that echo-sounding methods can provide an extremely useful tool for studying coarse fish migrations in deep. In particular, they are probably the only methods available for studying the movements of fish communities in deep lowland rivers.

6.2.5 Fish counters

Resistivity fish counters can measure fish passage past specific points and have been used extensively in the assessment of salmonid migrations (Dunkley & Shearer, 1982; Welton *et al.*, 1987; Dunkley, 1991; Fewings, 1994; Aprahamian, *et al.*, 1996a). However, the use of resistivity fish counters in studies of coarse fish migration has been limited. This is for a number of reasons. Firstly, resistivity counters are usually placed on Crump weirs which are normally inaccessible to coarse fish due to their reduced swimming performance. Second, most resistivity counters are not capable of resolving small fish or fish migrating together in shoals (Aprahamian *et al.*, 1996a).

Lethlean (1953) developed a resistivity fish counter which was tubular in construction. This type of counter overcomes the problem of having to install it into a Crump weir but it requires fish to swim through it which limits its use to sites where a fish pass is present (Bussell, 1978; Beach, 1984; Holden, 1988).

Recent attempts to develop computer driven real-time image capture and analysis counter systems have been successful for adult migratory salmonids (Fewings, 1994), but have been of limited use for successful identification of smaller fishes, principally salmon smolts (Fewings, pers comm.). They are therefore unlikely to be of significant use for studying coarse fish migration in the near future.

6.2.6 Direct observation

Helfman (1983) argued that direct underwater observation was a valuable and frequently neglected tool in fisheries research. Basic methods involve snorkelling and SCUBA diving. These methods have provided information on abundance, distribution, habitat preferences and behaviour in some studies (Wankowski & Thorpe, 1979; Heggenes *et al.*, 1993). However, the use of these methods in studies of migration are limited in that only small areas can be observed at any one time, observations are dependent on water depth, clarity and moderate flow conditions and bottom-dwellers or small fish are often difficult to see. It is usually not possible to identify individuals unless specialised tagging methods are used (Heard & Vogele, 1968). These limitations also apply to direct observations from the bank although these have been used to study spawning behaviour in some species (Baras, 1994). Such methods may however, be useful in situations where repeat fine-scale estimates of movements are required such as diel migration studies (Hickley, 1996). The major advantage of observational methods is that as long as disturbance is minimised fish behaviour will be as near normal as possible since fish are not manipulated in any way.

6.3 Non-telemetric methods

6.3.1 Capture-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. This method has provided much important information on the migration, movements and homing of diadromous and resident freshwater fishes. Gerking (1953) used mark-recapture methods to conclude that non-diadromous salmonids were generally restricted in their movements. However, more recent studies show that this is clearly not the case for coarse fish species. Hunt & Jones (1974) used mark-recapture to study the movements of barbel in the Severn and observed that the population was comprised of two components. A static component which remained within 5 km of where they were tagged and a mobile component which roamed up to 34 km. Starkie (1975) used mark-recapture methods to study the movements of dace in the River Tweed and found that these were more extensive than previously thought. Whelan (1983) showed similar movement patterns using Floy tags in capture-mark-recapture studies of bream in the River Suck, Eire. Recaptures were from angling returns, gill netting and fish trapping studies. Mark-recapture has also been used in eel migration studies but their use is limited due to poor recapture rate (Knights *et al.*, 1996). Baras, *et al.* (1996) achieved a recovery rate of migratory yellow eels of only 2.1 % in the Ampsin fish pass on the Meuse but was able to determine migration rates from tag recoveries.

The major drawbacks of mark-recapture methods are poor temporal resolution of fish location, severe bias in spatio-temporal sampling effort with individuals recovered only if trapping is carried out in the right place. Mark-recapture studies also have severe logistic constraints because of the time taken to sample an area making frequent sampling of large areas impractical which is a considerable drawback in their use for migration studies. The repeated capture of fish may also affect their behaviour and survival.

Types of marks

Tagging as a method for studying fish populations has been a recognised technique for hundreds of years (Wydoski & Emery, 1983) and there have been considerable developments in tag design and analysis methods over this time. Wydoski & Emery (1983) describe three broad categories of tagging methods;

(i) Biological or natural tagging (Table 17).

(ii) Chemical tagging (Table 18)

(iii) Physical tagging (Table 19)

The principal requirements of any tag should be that they; (i) remain with the animal for the duration of the study, (ii) should be recoverable and, (iii) should not affect behaviour, physiology and survival. Of these factors (i) and (ii) are the most easily measured in controlled studies such as dual-marking. The effects of tags on behaviour, physiology and survival are more difficult to ascertain. Most active marking procedures will exert some influence, if only in the short-term, as a result of fish collection and handling. Some marking procedures have been shown to affect growth and survival and in general the principle of marking is to use a technique which involves minimal disturbance to the fish.

Table 17 Types of biological or natural tags for use in capture-mark-recapture studies.

	Parasitic markers	Morphological markers	Genetic markers
Description	Parasites are specific to particular habitats and leave marks on host that can later be used for identifying groups or stocks of fish and for determining migration patterns. Mostly used in marine environments.	Meristic counts, pigmentation marks, differences in the shape and size of body parts or scales etc. used to identify individuals or groups of individuals. Little used for studying migration in freshwater fish species. Species for which morphological markers enable the identification of individual fish include pike and grayling	In this method different populations can be distinguished by examining the loci of individual genes
Minimum fish size	None	None	
Advantages	Natural, low-cost, can be used on large water bodies. Do not alter fish behaviour	Natural, low-cost, do not alter fish behaviour.	Natural, do not alter behaviour of individual
Disadvantages	Time needed to research whether parasite can be used, cannot recognise individuals, require well-trained personnel to recognise marks. Limited use in UK freshwater due to almost complete lack of natural populations. Only suitable for the separation of relatively self-contained fish stocks.	Subject to environmental influences and may change over time. Less applicable to studies involving large sample sizes; best for a small number of large individuals.	Expensive for studies involving large numbers of individuals, generally only suitable for determining population mixing or large-scale movements involving substantial components of the population.
References	Sindermann (1961); Kabata, (1963); MacKenzie (1983); Buckley & Blankenship (1990); Yeomans *et al.* (1997)	Buckley & Blankenship (1990); Fickling (1978); Persat (1982), Wydoski & Emery (1983)	Allendorf, *et al.*, 1975; Avise, *et al.*, 1986

Table 18 Types of chemical tags for use in capture-mark-recapture studies.

	Dye & paint marks	Latex marks	Radio-isotopes
Description	Most UK freshwater fish studies use Panjet inoculators to batch mark fish, or utilise binary codes of marks to identify smaller numbers of individual fishes. Alcian Blue most appropriate dye in terms of recognition and longevity. Sub-epidermal injections of acrylic paint are used for eels because they cause minimal disturbance and produce long-lasting marks. Different colour combinations can be used to identify batches or individuals. Mercuric chloride introduced by hypodermic injection most effective for larval ammocoetes of lampreys.	Coloured liquid latex introduced by hypodermic injection most effective for larval ammocoetes of lampreys.	Method using radioisotopes of the rare earth Euridium (^{152}Eu and ^{155}Eu) to mark elvers.
Advantages	Easy to apply, require a low handling time and can be used for small fish or early life stages. Do not affect fish behaviour.	Cheap, non-toxic, last for several months and can be used in several colour combinations enabling individual identification. Do not affect fish behaviour	Easy to apply, require a low handling time and can be used for small fish or early life stages. Able to identify four of their animals three years after they were first captured. Do not affect fish behaviour
Disadvantages	The main disadvantages are that individuals cannot be identified and, in the majority of cases, retention times are low. Small fish could be damaged by force of Panjets. Mercuric chloride was considered to be too expensive and toxic for widespread use.	Not permanent	Cannot identify individuals
References	Hart & Pitcher (1969); Axford (1978); Schoonoord & Maitland (1983); Baras *et al.* (1996); Gollmann *et al.* (1986); Knights *et al.* (1996); Smith (1997)	Schoonoord & Maitland (1983)	Hansen & Fattah (1986)

Table 19 Types of physical tags for use in capture-mark-recapture studies.

	External tags	Coded tags	PIT tags
Description	Most widely used. Consist of fin clipping, branding and physical tags. Physical tags come in a plethora of shapes and sizes. Implanted tags (jaw tags) Have been used in mark-recapture studies with eels.	Coded wire tags most common. Consist of pieces of wire embedded subcutaneously. Allow individual recognition by colour or by reading notches following dissection. Notches can be read by X-ray but complicated by shadowing effects in head. This method is not in widespread use. Magnetic tags can be implanted subdermally, and subsequently detected using a flux-gate magnetometer. Retained for life, as the fish grows. Visual implant (VI) tags, implanted underneath the epidermis of transparent tissues popular for batch or individual identification of fish.	Passive Integrated Transponder (PIT) tags. Contains no power source and comprises a coil antenna and integrated circuit chip encapsulated in glass, which currently may be as small as 10mm long and 1 mm in diameter. Programmed with one of 34 x 10^9 possible codes. Interrogated by energising with a 400 kHz field from an induction coil, retransmits its code at 40kHz. Hand-held readers used to identify tagged fish or can be recorded automatically at instream structure.
Advantages	Can be used to individually mark large numbers of fish which can be identified and returned to the river for long-term studies	Large numbers of fish can be quickly and easily tagged and tags have no effect on fish behaviour. VI tags overcome problem of need for dissection	Collection of detailed information on large numbers of fish. Relatively inexpensive, small, programmed with almost infinite number of individual codes, no battery infinite life. Do not affect fish behaviour.
Disadvantages	Fin clipping - number of individual marking combinations is low. Branding - only used for scaled fish and deteriorates with time. Externally attached tags may cause disease and infection, attracts predators or alter fishes swimming ability and buoyancy control. Growth rates 50% lower in eels with jaw tags.	Cost of tagging and need to dissect fish to recover tag. Low tag recovery rates.	Expensive
References	Hunt & Jones (1974); Starkie (1975); Axford (1978); Whelan (1983); Berg (1986)	Bergman *et al.* (1968, 1992); Jefferts *et al.* (1963), Buckley & Blankenship (1990); Haw *et al.* (1990), Crook & White (1995);	Prentice *et al.* (1990 a, b, c)

6.3.2 CPUE methods

Introduction

Netting, trapping, angling census, match catch data and electric-fishing can all be used to provide Catch Per Unit Effort (CPUE) measures of abundance of different life-cycle stages and species at different times and places (Kell, 1991; Cowx & Broughton, 1986; Cowx, 1990). Fish migration is then implied from variations in the CPUE. These methods are quite cheap and can generate large sample sizes but generally:

(i) they lack the high spatio-temporal resolution of tracking;

(ii) they are often ineffective in fast or deep rivers

(iii) capture efficiency, essential for incorporation into the CPUE analysis of spatio-temporal changes of fish, varies with many factors, but is not easily measured and in most cases no attempt is made.

Census and catch data

Hickley (1996) argues that angler's catch statistics give access to a vast amount of data and provide information over longer time periods than are available with scientific programmes. Angling catch data has been used to follow population trends (Cowx & Broughton, 1986; Cowx, 1990; Axford, 1991). However, only a few studies have used such methods in studies of fish migration. Axford (1991) argued that evidence from angling catch data showed that there were significant seasonal population movements of coarse fish in some rivers. Erection of the Skip Bridge gauging weir on the Nidd was associated with marked reductions in the catch rates of small fish upstream in subsequent years, which Axford (1991) interpreted as being due to the downstream movement of small fish in winter, followed by an inability to ascend the weir during the following spring. More recently, the addition of baffles to the weir appears to have led to a small improvement in the upstream fishery (Figure 14). Similarly angler catches were used to demonstrate that the percentages of flounders in angling catches from the Derbyshire Derwent decreased after the construction of a tidal barrage (Cowx, *et al.*, 1986).

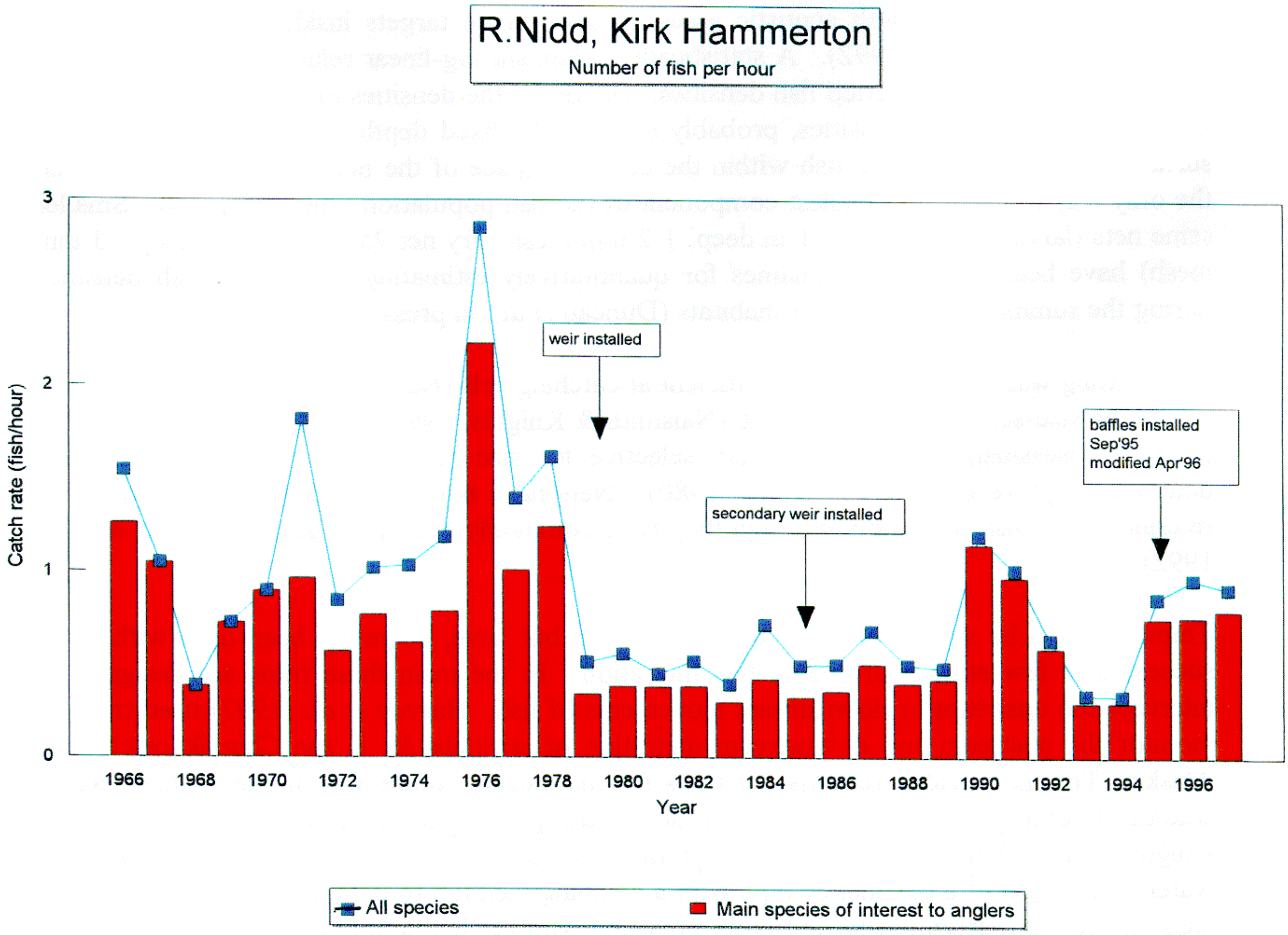


Figure 14 Variations in mean annual CPUE by anglers on the River Nidd at Kirk Hammerton, before and after a flow-gauging weir was constructed immediately downstream. In recent years, since the addition of baffles to the downstream face of the weir there appears to have been some improvement in the fishery upstream. (Axford, unpubl. data).

Netting and trapping

Seine nets and gill nets are the principal types of nets used in riverine environments. Seine nets are limited to horizontal or gently sloping bed profiles in shallow and slow-moving freshwater environments. Ketelaars *et al.* (in press) monitored the intake of 0+ fish from the Meuse into the De Gijster reservoir by suspending a 50 cm hoop-type ichthyoplankton net into the intake pipe. Sampling for 24 hours at four hour intervals on eight occasions between May and July provided information on the months of 0+ immigration (June-July), on the seasonal sequence of immigrating species (pikeperch, perch, roach, bream) which probably followed that of spawning in the river. They also found that most fish entered the net at night. Seine nets for adult fish (75 m long, 4 m deep with 10.20 mm mesh size) have been used quantitatively in the Thames simultaneously with acoustic assessment of single targets inside the set net before hauling (Kubecka *et al.*, 1992). A statistically significant log-linear relationship was obtained between fish targets and netted fish densities. However, the densities of fish targets was about 62 % of the netted fish densities, probably because the fixed depth of the transducer missed surface and bottom-dwelling fish within the confined space of the net. Seine netting is often the only way to catch the smallest component of the fish population (Hickley, 1996). Smaller seine nets (larval net 10m long, 1 m deep, 1-2 mm mesh; fry net 25m long, 3 m deep , 3 mm mesh) have been used in the Thames for quantitatively estimating 0+ and 1+ fish densities during the summer in various microhabitats (Duncan *et al.*, in press).

Fyke netting was found to be very inefficient at catching eels (Naismith & Knights (1990a) and tend to be size-selective for larger eels (Naismith & Knights, 1990 a, b). Gill nets are also used in stock assessment but they are very selective for size of fish and the type of net will determine capture efficiency (Hamley, 1980). Nets have not been widely used in studies of riverine coarse fish migration although they have commonly been used in lakes (Keast & Fox, 1992).

Traps can also be selective (e.g. Kubecka, 1996b) but have, however, been used with some success in a few studies of coarse fish migration. In the main these traps are designed to intercept the upstream or downstream movements of fish. Harvey *et al.* (1997) used traps to monitor the upstream and downstream migration of sticklebacks in the Chignik catchment, Alaska. The most widespread use of traps for monitoring coarse fish migration has been in studies of eel migrations. Immigrant eels show strong rheotactic behaviour during migration. Knights *et al.* (1996) argue that because of this they can easily be attracted by suitable flows of water to the base of a channel or pipe with a climbing medium to help them ascend. A simple pass can be made from plastic guttering provided with garden netting of 20 mm square mesh (Knights, *et al.*, 1996). White & Knights (1994) found that this material was less size-selective than geotextile matting. White (1994) and White & Knights (1994) marked and released 6418 out of 346000 eels in the Severn and Avon. Only 2 % were recaptured but of these only five had by-passed traps on barriers between capture and recapture. Knights, *et al.* (1996) concluded therefore that these traps were effective in sampling migrants. Vøllestad & Jonsson (1988) used traps to good effect in enumerating migrations into the Imsa in Norway. They also used traps to sample silver eel migrations with relatively high efficiency. Moriarty (1990) also used large conical traps to monitor silver eel migrations in the River Bann, Northern Ireland, again with reasonable efficiency. Baras *et al.*, (1994, 1996) used fish pass traps on the Ampsin navigation weir in the River Meuse to discriminate between resident and migrating eels. They used a cylindrical trap (100 x 40 cm) which consisted of coated 5 mm wire mesh attached to a welded steel brace positioned in a Denil fish pass in the Ampsin-Neuville navigation weir on the River Meuse, Belgium. The size of the sample in the trap was highly correlated with the number of eels migrating through the pass. The trap was also non-selective for fish size within the range of yellow eels (114-614 mm). They argued that this 'point migration sampling' approach would allow a reliable estimate of the dynamics of yellow eel migrations in regulated rivers White & Knights (1997) found that netting and electro-fishing were not very efficient at sampling small eels on the Rivers Severn and Avon. Pass traps on weirs and other obstructions did however yield good indications of relative numbers of migrants with time. Malmquvist (1980) also used a trap in a V-weir to study spawning migrations in brook lamprey in Sweden.

Traps are routinely operated at the upstream outlet of fish passes, particularly of slotted and Denil designs. In most cases this is to examine stock structure of anadromous salmonids migrating upstream, but this also enables quantification of coarse fish species which have successfully ascended. Such trap systems have provided a substantial amount of information concerning the extent of and stimuli for upstream passage by several species, in particular lamprey, eel and rheophilous cyprinids such as barbel and chub (Larinier, 1983; Larinier, 1992; Baras, *et al.*, 1994; G. Armstrong, pers comm.). While these traps are helpful in providing information, on their own they lack the ability to relate supply of fish escaping from the top of the pass to demand for passage in the region of the river below. Neither can they provide information on efficacy of passage or on natural unimpeded migratory behaviour.

Electric fishing

Electric fishing is widely used in fisheries stock assessment. Fishing efficiencies are very variable depending on environmental conditions, operator experience and fish behaviour. Consequently it is widely recognised that electric-fishing does not provide truly quantitative estimates of fish populations (Harvey & Cowx, 1996). Electric-fishing is used in migration studies in a number of ways. It is used to capture fish for use in mark-recapture studies and radio-telemetry studies but it is also used semi-quantitatively in CPUE studies. There has been considerable research into electric-fishing methods and Harvey & Cowx (1996) argue that there is currently little need for further development of these methods. They review recent advances in electric fishing gear design which have improved the efficiency and safety of electric fishing equipment. These include boat based multi-electrode arrays for sampling large rivers, use of ring electrodes and control boxes capable of sequentially energising each ring in the array. These improvements have reduced fish mortalities, increased capture efficiencies and enabled the capture of small fish (<20 mm) thus reducing the selectivity of electric fishing methods. An additional advantage of electric fishing over netting methods is the reduction in manpower and survey times.

These developments have enabled a more representative sample of the fish population to be made but have not necessarily led to improved quantification of fish stocks. This will depend on the type of electric fishing gear used, the depth and velocity of the river and the aims of the study. In small streams and rivers a moderately high sampling efficiency can be achieved by depletion methods (Cowx, 1983) using standard electric fishing gear powered by backpack or small generator. In larger rivers boat-mounted multi-anode arrays are required. Here depletion methods are impractical because specific areas cannot easily be closed off with stop nets. Consequently population estimates in larger rivers are subject to considerable errors. To overcome some of these problems the efficiency of electric fishing needs to be assessed. Gear calibration is one method which may provide a cost-effective method of stock assessment

(Harvey & Cowx, 1996). Two systems are available. The whole system approach estimates efficiency of gear in an isolated population and the probability of capture used to calibrate the main survey. In the point estimate approach gear efficiency is estimated in a small area of the target habitat by assessing the vulnerable population with a high efficiency gear (Harvey & Cowx, 1996).

An alternative to these semi-quantitative methods is to use a measure of relative abundance. Harvey & Cowx (1996) argue that this strategy is particularly useful in assessing whether a fishery is changing in species composition or population structure. Such methods may therefore be appropriate in studies of fish migration. Point abundance sampling provides a useful measure of relative abundance which can be quickly applied and enables changes in populations over short periods of time to be measured, particularly of larvae and 0+ fish (Copp, 1989; Copp & Garner, 1995; Garner, 1995). Copp & Jurajda (1993) used this method to determine numbers of small fish in inshore areas and to demonstrate diel changes in species abundance and composition.

Bain *et al.* (1985) developed an electric fishing device consisting of ac power supply and a rectangular electrode frame. They used a 230 volt, 2.2 KVA generator stepped up with a transformer to 460 volts to overcome low conductance (<100 $\mu S\ cm^{-1}$). The frame consisted of two electrodes kept apart by nylon rope attached at either end. The frame dimensions could be varied. This design produced accurate population estimates within the area encompassed by the frame particularly when the frame was left undisturbed for 10 minutes prior to fishing. Using this method it is possible to quantify fish populations at regular intervals within discrete microhabitats, apply *a priori* sampling design and evaluate multispecies patterns. The main disadvantage is the time required to obtain sufficient sample sizes and the usual limitations of electro-fishing to shallow waters.

7. IMPLICATIONS OF COARSE FISH MIGRATION

7.1 Introduction

Although detailed information is limited, migration of a substantial number of coarse fishes clearly occurs in UK rivers. What, therefore, are the implications of these migrations to the successful management of fish stocks? Such a question requires a more fundamental understanding of the behaviour and ecology of common riverine coarse fish species and consideration of a number of factors;

(i) The influence of fish migration on ecosystem function.

(ii) The effect of fish movements on accurate stock assessment.

(iii)The socio-economic effects of fish migration.

(iv) The implications of fish migration on genetic stock structure.

(v) Water quality and its impact on fish movements.

(vi) The impact of water management structures on coarse fish migration.

(vii) Ameliorating the effects of barriers to fish migration, e. g. through the installation of fish passes.

This section considers each of these in turn.

7.2 Ecosystem function

The fish communities within river ecosystems perform important functions in terms of key food web links and energy/nutrient dynamics (Lucas *et al.*, 1998). These functions are not well understood or quantified. Long-term changes in fish distribution caused by the elimination of migratory processes may lead to alterations in riverine biodiversity at all trophic levels. Although this might not be of primary importance to the fishery manager, improved integration of conservation and river rehabilitation interests within the Environment Agency make an understanding of such wider implications of coarse fish migration an important component of any effective management strategy.

7.3 Stock assessment

Coarse fish migration will lead to variation in the spatio-temporal availability of fish for capture, and hence the success of coarse fisheries. Linked to this are the associated problems of reliable stock assessment carried out by the Environment Agency and other scientific organisations.

If fish are distributed contagiously, then appropriate sampling strategies using netting or electric fishing can be used to measure fish density. However, where fish are known to migrate, it becomes important to sample at the same stage of the migratory period, or ideally outwith this period, in order to make between year comparisons of stock size and structure. Generally, coarse fish are less mobile in summer, than in spring or autumn so this is probably an appropriate sampling time. The winter months should not be neglected even though sampling is often much more difficult due to the inactivity of fish at low temperatures. Nevertheless, it must be appreciated that such stock surveys are probably of limited value in presenting angling interests with data concerning the abundance of fish other than at the time, or at best, season of the survey. It is this dynamic behaviour of coarse fish that results in popular and well-known coarse fisheries in the same river catchment several kilometres apart at different times of the year.

Echosounding methods provide an alternative stock assessment technique which, because long stretches of river can be surveyed in a relatively short time is less affected by fish migration. However, it can only be used in the slower, deeper sections of river catchments.

7.4 Socio-economic effects

It is widely appreciated that migratory patterns, leading to changes in distribution and abundance of migratory salmonids influence fishing success on UK rivers. Furthermore, it is recognised that such variations, in conjunction with natural differences in river habitat, influence the abundance of migratory salmonids within a system, resulting in some stretches having a high angling value and therefore high cash value at sale. Such situations are normally accepted as the *status quo*, but when potential obstructions are built or removed, migratory habits and fish distribution may be influenced. There have been several recent cases where owners of migratory salmonid fishery owners have sought compensation for these effects.

It is not hard to envisage such a similar situation for coarse fishery owners who are able to reasonably demonstrate impact of an obstruction on their fishery by limiting migration to that area. In most cases adequate data may not be available to prove such a circumstance, but long time-series CPUE data can be a strong tool in such cases, as exemplified on the Nidd at Skip Bridge (Axford, 1991). The Environment Agency should be aware of the possibility of future claims for damage to fisheries as a result of limiting or preventing fish migration, in particular by the erection of weirs for flow-gauging purposes, and sluices for flood control.

7.5 Genetic factors

Spawning migrations in fish species which show a high degree of site fidelity as the result of a homing instinct serve to bring a fish (or its offspring) back to an environment which is suitable for reproduction at a time when other sexually mature individuals are also present. A consequence of such strong site fidelity is that gene flow is largely restricted to within the population of fish that home to that location. Genotypes within the population may become highly adapted to the specific environmental conditions experienced there (Wootton, 1992). The species then becomes divided into a series of reproductively isolated populations and only individuals which accidentally find their way to a different spawning site will maintain any gene flow between populations (Wootton, 1992).

Fish migration may serve to maintain heterozygosity within a population, and serve to maintain a large gene pool. This has been considered to be beneficial in terms of improved fitness for survival in the event of small or larger scale environmental changes (Carvalho & Pitcher, 1994). At the same time, genetic differentiation in closed populations is thought to reflect local adaptations (Wootton, 1992). In the medium term prevention of migration would most likely have detrimental effects through a reduction genetic diversity. Bouvet *et al.* (1996) considered the impact that obstructions had on genetic population structure in tributaries of the River Tejo (Portugal), the Rhone (France), the Danube (Austria) and the Rivers Aliakmonas, Aggitis and Ardas (Greece). They found no differences in genotypes on either side of dams in Portuguese chub *Leuciscus pyreaicus*, chub from the lower Rhone and in Greece and roach and nase from the Danube. They argued that this could be explained by the permeability of dams to fish migration, by too recent dates of isolation or by the fact that the populations were large enough fro genetic drift not to take place. They did however, show that there were different genotypes on either side of dams in grayling in the upper Rhone, roach in the lower Rhone and in chub in some Greek rivers. For the Rhone grayling and for roach they found that populations above the dam were distinct from those below the dam which were mixtures of the upstream genotype and local downstream strains. This they argued, provided evidence that no upstream passage through the dams were possible but that young fish drifted downstream or were displaced due to floods. Where fish migration is prevented by barriers, partial mitigation through the use of fish passes may provide adequate migration to maintain mixing of stocks, for retention of genetic diversity. However, in many UK rivers where there has been a great deal of stocking of coarse fish from many sources; the issue of genetic mixing through migration is hardly relevant, given the likely dilution of original gene pools. This factor is further influenced by the Environment Agency's policy of using stock reared at just a few fish farms to restock catchments all over the country.

7.6 Water quality

Migration of coarse fish may be influenced by water quality. Studies on the effects of acid episodes in rivers on fish migration have been confined to salmonids (e.g. Gagen *et al.*, 1994), although in the future effects may be exerted on coarse fish in rivers running through the Nottingham, Yorkshire and Durham coalfields if mine pumping is stopped. More common influences are from oxygen depletion, which may present a pollution barrier to fish movement. In some cases in the lower reaches of rivers, it may be possible for fish to be trapped below a dissolved oxygen sag on an ebbing tide, resulting in large mortalities. On the other hand coarse fish are able to tolerate lower oxygen levels than salmon, as low as just 1-2 mg $O_2\ l^{-1}$ for some limnophilous cyprinids, and are often attracted to organically polluted water by the abundant production of chironomid larvae and tubificid worms.

A better understanding of the influences of water quality and pollution on coarse fish movement would aid management of these stocks. Such work is due to be undertaken by K. Hendry (pers. comm.), beginning in 1998, in a project part-funded by the Environment Agency National Research & Development programme. It will examine how roach move in relation to changes in dissolved oxygen in the Manchester Ship Canal during the spring when dissolved oxygen levels are variable and in the summer when anoxia occurs. This work is being carried out to provide a baseline for future attempts to reoxygenate the canal.

7.7 The impact of water management structures

7.7.1 Physical barriers

Much attention has been paid to the potential and actual impact of obstructions on the passage of migratory salmonids and there is a substantial body of literature describing in detail the behaviour of salmon in relation to obstructions (e. g., Podubnyi, 1971; Power & McCleave, 1980; Nettles & Gloss, 1987; Travade, *et al.*, 1989; Webb, 1990; Larinier & Boyerbernard, 1991; Gosset, *et al.*, 1992) and the design and provision of fish passage facilities to mitigate their effects (Jackson & Howie, 1967; Beach, 1984; Mills 1989; Larinier, 1992). There have, however, been few studies of the possible impact of obstructions on populations of coarse fish despite the ecological and economic importance of this group (Axford, 1991; Smith, 1991). As we have shown so far in this review inland species can move substantial distances within rivers for reproduction and feeding. For these reasons artificial river obstructions may have significant impacts on inland fish communities (Philippart, *et al.* 1988; Harris & Mallen-Cooper, 1994). However, river management practices which minimise the effects of these obstructions on those communities have not been widely implemented (Larinier, 1992). Little information regarding the behaviour of migratory non-salmonid fishes in response to weirs and fish passes is available although improvements in fishpass design and monitoring are now being made in France (Larinier, 1983; Travade & Larinier, 1992). More recently, in continental Europe, there has been an increasing appreciation that coarse fish undertake migrations which are important for life-cycle completion and that river management strategies should take account of this. (Cowx & Welcomme, 1998).

The significance of river obstructions, even on a minor scale, in affecting natural movement patterns of some riverine fishes has probably been underestimated (Lucas & Batley, 1996). Such factors have been identified as causal in population declines of lithophilous and rheophilic cyprinids in the Danube, Rhine and Meuse (Bacalbasa-Dobrovici, 1985; Philipart *et al.*, 1988; Admiraal *et al.*, 1993; Baras *et al.*, 1994) and are important in producing observed changes in fish communities in terms of ecological structure, availability to commercial and recreational fisheries and conservation status (Bacalbasa-Dobrovici, 1985; Welcomme, 1994).

These effects are clearly demonstrated in the Belgian stretch of the Meuse (182 km long). Dredging and canalisation for improved navigation and the construction of fourteen large dams (ranging in height from 4-6 m) have led to the extinction of Atlantic salmon and other anadromous species (Baras *et al.*, 1994). Significant declines in several populations of lithophilous and rheophilous coarse fish have also occurred. As part of a major research programme aimed at the restoration of fish populations the barbel was chosen as an indicator species for research assessing the relationship between natural migratory tendencies and conditions allowing passage through fish pass facilities (Baras *et al.* 1994). Their study was conducted between 1989-1993 on the Ampsin-Neuville weir which is equipped with Denil fish passes on either side of the dam and a hydroelectric plant. Focusing on the pass on the left bank, near the hydroelectric plant, fish were trapped in the pass on 251 occasions from mid-January 1989 to mid-July 1993. A total of 13693 fish were captured belonging to 21 species. The dominant species were chub, bream, bleak and eel. All species were captured in larger numbers in the lower pool of the fish pass than in the upper chambers suggesting that many fish did not fully enter the pass. Barbel were completely absent from the fish pass in all years except 1989. The maximum current speeds through the fish pass on the Ampsin-Neuville (1.2-1.5 m s^{-1}) were far below the swimming capacity of large barbel suggesting that this was not a factor in limiting the movements of barbel through this pass. They argued that a temperature threshold was required to trigger migratory movements in barbel and by the attractiveness of the fish pass. Barbel are rheophilous and would be attracted by the strongest flows which, in this case, were from the outflow of the hydroelectric plant. Therefore, in order to find the entrance of the fish pass they would need to be attracted to it by the presence of another major flow such as the spillway. However, no significant association was found between the flow on the spillway and the number of barbel caught in the fish pass. Baras *et al.* (1994) argued that this was due to barbel failing to find the entrance of the fish pass relative to the flow on the spillway. In 1990-1993 river flows were high and consequently barbel were not attracted away from the hydroelectric outflow resulting in the lack of fish in the pass. Baras *et al.* (1994) argue, therefore, that the failure of barbel to find the fish pass, coupled with pollution and the scarcity of spawning habitats in the Meuse have resulted in the decline of barbel populations in the Meuse. Birtles *et al.* (1997) tracked five barbel below the Grosses Battes dam; the first obstacle to fish migration from the Meuse into its main spawning tributary, the Ourthe. None of the tracked fish successfully negotiated the obstacle despite several attempts to do so through the existing Denil fishpass.

In the Czech Republic smaller dams installed in rivers for bypass hydropower stations were shown to have a significant impact on fish communities (Kubecka *et al.*, 1997). They found that the diverting weir in combination with water abstraction was an important migration barrier for resident fish in 30% of the hydropower dams studied. Water abstraction caused succession from large fish species such as brown trout and dace to small species such as minnow and bullhead.

Axford (1991) collected data obtained from anglers for 30 years on the Nidd and attributed the decline in CPUE occurring after 1978 to the installation of the flow-gauging-weir at Skip Bridge. The main fish involved were small species such as dace and gudgeon, as well as juveniles of a variety of species. Axford (1991) attributed this decline to the downstream movement of fish which were then unable to move upstream past the weir in the spring. Penáz & Stouracova (1991) showed similar reductions in the abundance, biomass and angling catches of barbel after construction of the Dalesice Hydro Power and Dukovany Nuclear Power Stations on the River Jihlava in what was the former Czechslovakia.

Lucas & Frear (1997) tracked 23 adult barbel (10 males, 13 females) in the Nidd, fitted with radio transmitter implants to determine their movements across this weir. The range of upstream movement in the Nidd is restricted by the presence of several weirs, including Skip Bridge gauging weir. There are low levels of barbel spawning activity downstream of Skip Bridge weir due to a lack of spawning habitat (Lucas & Batley, 1996). Therefore, in order to find adequate spawning sites barbel must negotiate the weir. Fifteen of the 23 barbel tracked attempted to cross the weir and of these six were successful. The weir was approached at dusk and dawn but only crossed at night. Successful fish moved up to 20 km upstream passing rapidly through known spawning areas before stopping at one or more sites further upstream. Here they were observed on spawning grounds, some in courtship. Unsuccessful fish moved back downstream in some cases returning to the weir - these were not observed in courtship. Success was not dependent on sex or size. All fish (including successful ones) were delayed by the weir but it was not known if this delay had any effect on reproductive physiology and behaviour. Further studies (Lucas & Mercer, 1996) were carried out on the Nidd with dace and roach revealing that a proportion of dace (28%) and roach (38%) passed the weir. The fact that a high proportion of barbel, dace and roach could not cross Skip Bridge weir may have a detrimental effect on the populations of these species in the river. The decline in the population of dace upstream of Skip Bridge weir since its construction has already been discussed. Lucas & Frear (1997) argued that weirs may have a number of limiting effects on populations. Where spawning areas are limited downstream of the obstruction reproduction and subsequent recruitment may be greatly affected. Distribution will be altered and gene flow restricted. Following catastrophic events such as pollution incidents upstream of the obstruction recolonisation may be restricted to immigration from upstream of the affected area. Upstream movement of tagged roach did not seem to be closely linked to rises in flow, but occurred at a time when water temperature was rising and flow was decreasing. Counts of fish attempting to pass the weir demonstrated that most activity occurred at temperatures above 12 ^{O}C, reflecting the relatively higher optimum temperature for metabolic activity of cyprinid fishes, by comparison to salmonids. Lucas (1998a) argued that, unlike upstream-migrating salmonids, cyprinids face the problems of ascending obstructions at higher early spring flows when their swimming performance and natural activity is low, or ascending obstructions when flows have declined greatly but their swimming performance is nearer its optimum level (Figure 15). These differences in fish physiology and behaviour in relation to environmental conditions, suggest that a fundamental dichotomy in approach may be needed for maximising passage of cyprinids or salmonids past obstacles.

The construction of dams has long been held responsible for the decline of sea lampreys in the USA (Mormon, *et al.*, 1980) and more recently in the commercial river lamprey fisheries in Finland (Tuunainen, *et al.*, 1980). Lampreys do not swim rapidly and therefore will be unable to utilise fish passes designed for teleost fisheries. Prior to the construction of a barrage on the River Leven, Scotland, adult lampreys were occasionally reported in Loch Lomond (Lamond, 1931). Maitland, *et al.*, (1994) reported the occurrence of a single sea lamprey which was attached to a salmon caught by an angler but they were unable to find any evidence of sea lamprey spawning in the loch. Lampreys and eels pass the Denil fishway at the Tees Barrage only during spring high tides when the estuarine water floods the pass (Lucas, unpubl. data).

Crisp, *et al.* (1984) showed that after the closure of the dam on Cow Green Reservoir, Upper Teesdale, Co. Durham brown trout showed no detectable change in distribution. Bullhead, however, prior to impoundment were restricted to the main river and lower reaches of the afferent streams and few were found above the proposed level of the reservoir. After impoundment bullhead were found in varying numbers in most of the afferent streams above the level of the reservoir implying that bullhead populations had moved to occupy these new areas. Minnows occurred in the main river and lowest stretches of the afferent streams before impoundment but afterwards were confined to the reservoir except for occasional movements into the lowest reaches of some afferent streams. Obstructions with vertical drops of approximately 20 cm are regarded as the critical limit of passability for small fish such as bullhead (Bless, 1981; Jungwirth, 1996). Böhmer *et al.* (1996) found that a drop of > 15 cm impeded migration of a number of species including bullhead and stoneloach.

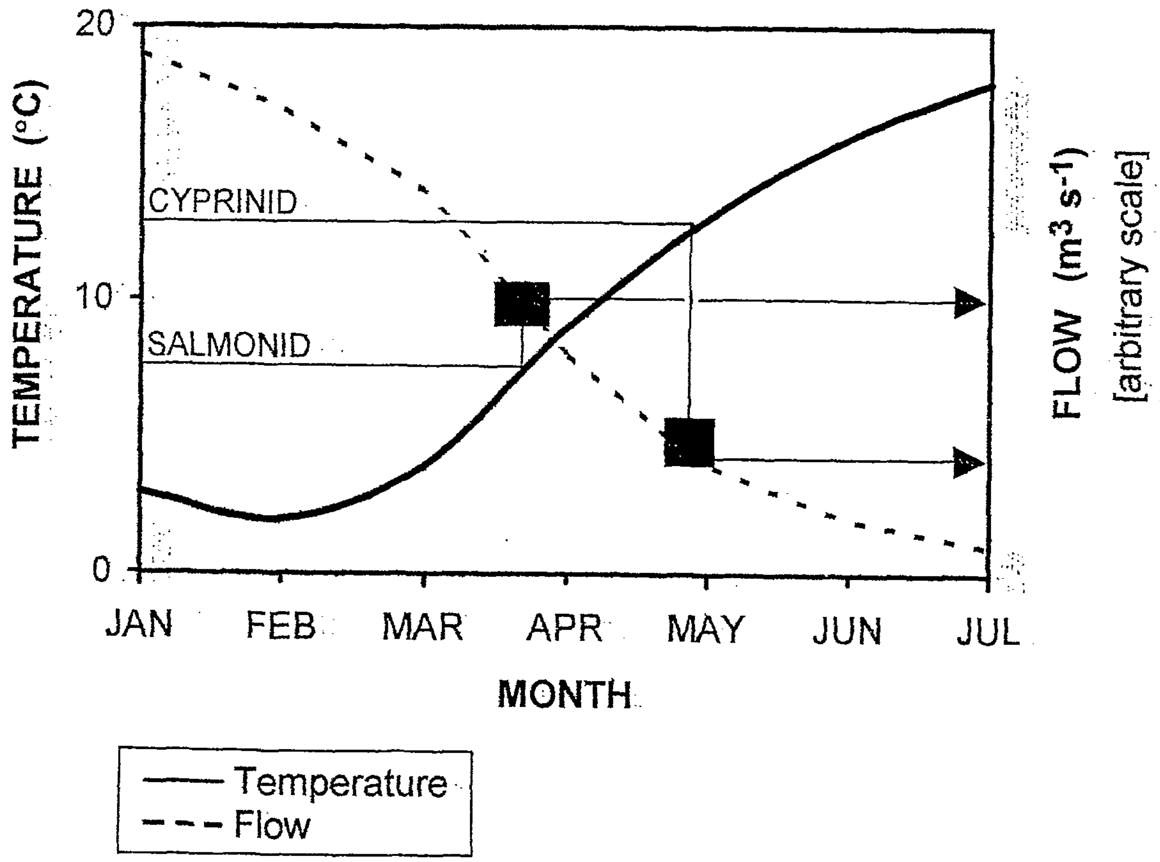


Figure 15 Schematic model illustrating the different flow conditions occurring for spring-migrating salmonids and cyprinids at temperatures for which moderate swimming performance (based on Beamish, 1978) may be expected (reproduced from Lucas 1998a)

Barus, *et al.* (1984, 1985, 1986) investigated fish drift through hydroelectric turbines from Czechoslovakian reservoirs. Fish which passed through turbines were exposed to considerable physical trauma and mortalities of some species, particularly eels, was high. Their studies showed that migration from reservoirs consisted of both passive drift of juvenile stages and active migration of adults. Fish which survived passage through the turbines were shown to make a substantial contribution to the biomass in the river downstream of the dam and many were shown to be engaged in spawning activity. Berg (1986) found similar effects on fish passage through Kaplan turbines at a power plant on the River Neckar, Germany. The most affected species there was the eel with the rate of lethal injuries reaching 50 % even at relatively low flows (40 $m^3 s^{-1}$). Rates of injuries were in fact higher at low flows during the day when an adjacent sluice was opened. During the night when the sluice was closed water flow through the turbine was higher leading to a higher relative opening of the runner blades and a reduced number of injuries. Berg (1986) argued that the use of a suitable bypass to enable downstream passage away from the turbine may reduce injuries to fish.

Krivanec & Kubecka (1990) showed that reservoirs change the temperature regime of rivers. Increasing water temperature and trophic potential downstream of reservoirs leads to decreases in the occurrence of species that prefer lower temperatures. This decrease in water temperature and trophic potential results in substitution of the original fauna with cold water preferring fish. (Penáz *et al.* 1968). Kubecka & Vostradovsky (1995) showed that the cascade of five reservoirs on the Vltava, Czech Republic produced an increased abundance of large fish with downstream distance away from the reservoir due to increased temperatures.

Slavik and Bartos (1997) showed that the situation may have an impact on young-of-the-year fish. Their study examined the same sites as Kubecka & Vostradovsky (1995) and also showed that fish populations were more abundant further from the cold water. Cyprinids generally prefer warmer spawning temperatures and migrate to suitable spawning sites. The temperature effects caused by the dams may result in the loss of otherwise suitable spawning sites even though fish still have access to them. Therefore, the effects of dams may not necessarily be simply the result of direct physical obstruction of fish movement.

Slavik (1996b) studied two sites separated by lock gates on the upper (A) and lower (B) parts of the Podbaba navigation channel on the Vltava, Prague. Water velocity reached 0.55-0.7 m s^{-1} during the filling of the locks. The lock limits or prevents migration from B to A and a high weir (3.3 m) on the main river channel also limits upstream migration of fish. The two sites were fished with gillnets over a 24 hour period every month for a year. An increased abundance of fish occurred at A in the spring while no fish were found in the autumn and winter. A significant relationship was found between species diversity and temperature. At B there was a significant relationship between both fish abundance and species diversity and temperature. Site B was less variable than A in the levels of dissolved O_2 and in temperature and fish abundance and diversity was higher at B. Fish assemblages were heavily affected by the lock which restricted upstream migration. The higher numbers of fish at B were the result of immigration of fish from the main river which could not get to site A because of the lock although, some small fish do get through when the locks are opened. Klinge (1994) also demonstrated that roach and bream were capable of passing through a shipping lock on the Rhine in the Netherlands but that migration was considerably impeded with only seven out of one hundred marked fish passing through.

There are also no studies which have directly investigated differences in motivation between individuals within the same species. The ability to cross a barrier to migration may depend on factors such as the size, sex and health of individual fish. However, Lucas & Frear (1997) showed that the success of barbel in negotiating Skip Bridge weir on the Nidd, was independent of sex or fish size. It is possible that the success of an individual fish in crossing a barrier may depend additionally, on the motivation of the individual. A more motivated individual may make more attempts to cross a barrier than larger conspecifics (the 'try, try and try again' hypothesis). There is clearly more research needed on the effects of motivation on fish migratory behaviour.

In some areas water-courses are often directed through culverts under roads or navigation channels and these may act as a barrier to fish migration. In the Netherlands, de la Haye & Kemper (1998) caught and marked 2571 fish either side of three culverts. They found that the culverts were successfully negotiated during 30-35 % of the year (although no sampling was conducted during the spawning season) by eight species: pike, perch, roach, bream, silver bream, rudd, tench and gudgeon. However, during periods of high flow (> 15 cm s^{-1}) all species were unable to pass through the culverts.

7.7.2 Influence of water intakes on fish passage

Within the UK substantial amounts of water are removed for domestic and industrial supply. In most cases screens are used to retain debris, and fish may also be captured and killed by these screens. Recent studies (Solomon, 1992) have demonstrated that large numbers of coarse fish may drift or move into water intakes. Of particular surprise and concern has been the large numbers of YOY and juvenile cyprinids entrained in such systems, often occurring over very narrow periods of time, when river flows have not been unusually high (Solomon, 1992). This is indicative of large scale movements of YOY coarse fishes at particular ontogenetic stages within large rivers such as the Thames. In recent summers these fish have been observed in large numbers and collected in midstream. There is increasing evidence that young coarse fish may not be restricted in distribution to sheltered marginal habitats, but that they may be quite mobile, with large scale synchronised redistributions occurring over short time scales, which are not wholly suggestive of passive drift.

7.7.3 Impact of river habitat management works

Cowx *et al.* (1986b) showed that the removal of the pool and riffle character and instream vegetation from the River Soar, Leicestershire for land drainage lead to a long-term reduction in fish stocks. Initially the fish stocks in the areas around the drainage works increased possibly due to migration away from the disturbed area. After this, however, the fish populations declined.. It is also important to note that the recovery of fish populations from disturbance will depend on the species but also on the presence of refugia and on barriers to migration, especially when the source populations for recolonisation are relatively distant (Detenbeck *et al.*, 1992).

It is also clear that an understanding of coarse fish movements is required if habitat modification works to improve fish stocks are to be successful. There is little point carrying out improvements to habitats if fish cannot move from other areas to recolonise the newly improved river, although restocking provide a temporary solution.

7.8 Ameliorating the effects of physical barriers to fish migration

7.8.1 Water intakes and screening

With increasing evidence of substantial mortality of young coarse fish entrained at water intakes, there have been increased efforts to devise ways by which fish can be encouraged to avoid water intakes, especially for small fish which lack the swimming performance to escape from such flows once they enter. Such methods include a wide range of visual, electrical and acoustic barriers. Among the most effective, though still requiring further refinement are those which incorporate several barrier stimuli, such as the acoustic and visual barrier properties of bubble screens (Solomon, 1992).

7.8.2 Fish passes

The most appropriate conditions for diverse and balanced coarse fish communities include good longitudinal and lateral connectivity of river systems. In ameliorating the effects of physical barriers to freshwater fish (including salmonids) migration, Cowx & Welcomme (1998) consider that;

"generally the soundest solution ecologically is to remove structures as this not only restores longitudinal connectivity but can also lead to the more general restoration of the habitat".

Where this is not feasible, fish passes may be used to mitigate difficulties of passage past physical barriers.

Fish passes have long been used in attempts to aid the movement of fish across obstructions in riverine systems (Jackson & Howie, 1967; Beach, 1984; Mills 1989; Larinier, 1992). Until recently the majority of these have been developed to assist the migration of anadromous salmonids with little consideration of the needs of coarse fish. This has also been the case in the UK (Beach, 1984; Cowx, 1996). Indeed one of the main UK reference texts for those needing information on fish pass technology (Beach, 1984) specifically discounts coarse fish as being worthy of consideration in relation to fish passes on the basis that obstructions "do not cause a significant problem" for them.

More recently, however, as this review has shown, coarse fish movements have been studied in more detail and it is clear that obstructions to migration can have serious implications for some coarse fish communities. There is a need therefore to determine the most appropriate fish pass designs which will allow the passage of the full range of species occupying river systems. Lucas & Frear (1997) argue that fish passes designed for salmonids are probably unsuitable for most coarse fish and more effort is required in the quantitative monitoring of coarse fish use of fish passes currently in use, and the re-evaluation of designs intended principally to pass coarse fish. In many cases, the most problematic obstructions for providing fish passage solutions are flow-gauging weirs, because concern has been expressed as to the impact of introducing fish passage structures on calibrated weir structures of standard engineering design.

The type of pass used most frequently is the 'pool fish pass'. This consists of a series of pools in steps leading from the foot of the obstruction to the top. Walls separating the pools have weirs, notches, vertical slots or submerged orifices which control water level in each pool and the flow discharge in the pass. Pools serve to provide resting areas for fish and ensure proper dissipation of energy of water flowing through the pass. The slope of the fishway usually varies between 1-15 %.

Continental European workers have demonstrated success in passing coarse fish of a variety of species using baffle fish passes, principally of Denil and Larinier designs (Larinier, 1983, 1992, 1996) and these experiences have been increasingly transferred to the UK (Figure 16). In most cases, although work is ongoing (Travade & Larinier, 1992; Larinier, 1996), adequate efficacy of these or other fish pass designs has still not been demonstrated and published for coarse fish, especially for small species and juveniles. However, some studies provide evidence that the design of the pass itself may lead to significant differences in the numbers of fish able to successfully negotiate an obstacle (Figure 16). Until we have such data, the new installation of such designs may not be the most cost-effective or ecologically appropriate strategy. M. Lucas and J. Armstrong are currently developing pilot work using automated PIT systems which will enable the efficacy of various types of fish pass to be tested for a range of species and size groups.

The biggest problems with fish passes are often associated with flow regimes through the pass and the relation between these flows and the flow through the structures with which they are associated (Baras *et al.* 1994; Böhmer *et al.*, 1996; Larinier, 1996). For a fish pass to be considered effective fish should be able to find the entrance and negotiate it without delay, stress or injury and water velocities in the fishway must be compatible with the swimming capacity of the fish species (Larinier, 1996). Flow pattern is the only active stimulus. If the entrance is a long way from the obstruction the flow must be increased so that it represents a significant fraction of the flow in the river during migration. Baras, *et al.* (1994) argued that reducing the flow of the Ampsin-Neuville hydroelectric plant on the Meuse during the migration period of barbel would lead to higher flows across the spillway resulting in a higher attractivity of the fish pass enabling barbel to negotiate dam. They also argued that interference with the activities of the hydroelectric plant would be extremely limited over the daily cycle due to the crepuscular activity rhythms of barbel at temperatures greater than 10 °C (Baras, 1992).

Although, not strictly a fish pass, Larinier-type superactive baffles were used on Skip Bridge weir, a flat V design, in the Nidd to attempt to reduce flows to aid coarse fish in ascending the structure (Lucas & Mercer, 1996). However, the baffles actually increased flow and water velocity in the central 'V' of the weir and no fish were observed to succeed passing through this section. Where fish were successful they were seen to leap over the weir sill before landing in the baffle zone and attempting to swim upstream at very high tailbeat frequencies. Large fish were actually impeded by the shallow water above the baffles (video footage of this behaviour is available at the Environment Agency in York). Better results seem to have been achieved on another flat V gauging weir on the Exe by the use of partially slotted, wooden baffles placed at an angle to the flow (A. Strevens, pers. comm.). It should also be noted that baffled fishways are generally inappropriate for fish less than 30 cm in length (Larinier, 1996) which would tend to exclude large components of many cyprinid populations.

Böhmer *et al.* (1996) showed that minnow, chub, gudgeon, 3-spined stickleback and bullhead could not negotiate an experimental fishway at gradients of greater than 10 % if distances between current breaking structures were greater than 0.6 m. They also found that bullhead and stoneloach in an artificial channel without a gravel substrate were unable to migrate

Other continental workers (Jungwirth & Schmutz, 1988; Jungwirth & Pelikan, 1989; Schmutz *et al.*, 1995; Eberstaller *et al.*, 1996; Jungwirth, 1996; Mader & Unfer, 1996; Nielsen, 1996) have recently demonstrated the effectiveness of naturalistic bypass channels in enabling efficient passage by a wide range of species, including juvenile and adult coarse fishes. They also provide a route for fish displaced over the obstruction by high flows to return to their home range (Jungwirth, 1996). Additionally because of the naturalistic design of the channel these bypasses actually provide habitat for resident fish (Jungwirth, 1996). Jansen *et al.* (1996) captured fish above, below and within three fish passes on the River Enz, a second order tributary of the Rhine, southern Germany. They compared a wide concrete channel filled with gravel pass (site I) with an artificial stream pass (site II) and a step and pool fishway (site III). The total number of species recorded decreased from 21 at site I to 18 at site II to 17 at site III. There was a significant difference in fish abundance above and below site III which was less pronounced at Sites I and II. Sites I and II provided habitat within the pass and also allowed the passage of earl life stages. The step and pool fishway only enabled the passage of larger fish. Many UK fisheries scientists believe that these structures might be highly appropriate for enabling effective fish migration at obstructions on lowland UK rivers. However, these passes do not appear to satisfy some requirements of other water resource managers, and so have, as yet, received little overall support. Such issues need to be resolved through objective study to provide the integrated, optimal solution.

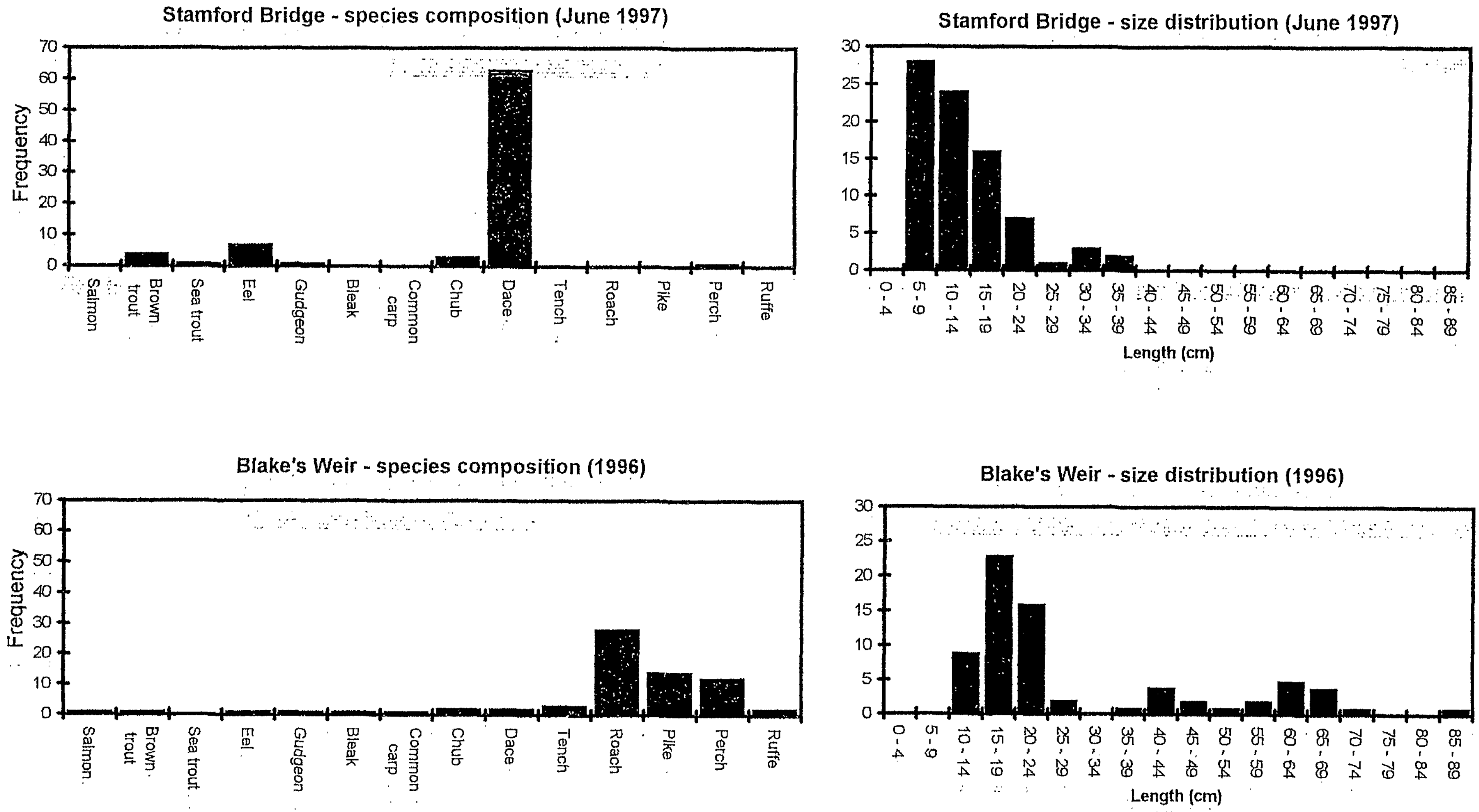


Figure 16 Species and size composition of fish trapped above a Denil fish pass at Stamford Bridge on the Yorkshire Derwent (June 1997) and above a Larinier (Super-Active Baffle) fish pass at Blake's Weir at the confluence of the Kennet with the Thames (1996). A high proportion of fish trapped at Stamford Bridge were immature dace.

The case for installation of fish passage facilities

Installation of fish passes provides a method for enabling coarse fish migration past physical obstructions. This sections considers the case for installation of fish passes in relation to coarse fish, although more detailed, but taxonomically more general reviews with examples of fish passes are given in Mann & Aprahamian (1996), the proceedings of an Environment Agency training workshop on fish passes, in Clay (1995) and in Cowx & Welcomme (1998).

From an ecological viewpoint it is preferable that limitation of natural fish movement is minimised. However, the installation of a fish pass is an expensive process. More importantly, in relation to most coarse fish, especially cyprinids, it is a poorly-substantiated method of allowing effective migration. Although there are examples of large numbers of coarse fish being passed through some fishways (see above) there are extremely few measurements of efficiency other than those of Linlokken (1993) for grayling using pool and weir passes and Denil passes, and of Lucas & Mercer (1996) for roach and dace using a flow-gauging weir with super-active baffles attached. Until such information is available, traditional fish passes installed for coarse fish may be a poor decision in cost-benefit terms.

The construction of a fish pass is expensive, as is monitoring of the effectiveness and efficiency (*sensu* Aprahamian *et al.*, 1996b) of the pass. From a fisheries perspective, there may be little noticeable gain from the provision of a fish pass under some circumstances, at least in terms of angler catches and fish densities. However, where distinctly migratory fish such as dace and barbel are present; an ability to move downstream of a barrier during refuge migrations, but a difficulty in moving back upstream past it may well lead to local differences in species composition or recruitment and biomass of these species, particularly if there is a lack of refuge or feeding habitat upstream of the barrier, or spawning habitat downstream of the barrier (Lucas & Frear, 1997). Even if total fish biomass remains constant, the loss of popular angling species from a fish community, and perhaps replacement by other species, may be undesirable.

Clearly, the decision to construct a fish pass for which the main purpose is to pass coarse fish depends on a series of decisions relating to the site, such as the ecological value of the river, fishery value, fish community composition, availability of feeding, refuge and spawning habitats upstream and downstream of the proposed site, and of course, an assessment of the likely changes which would result from the incorporation of a fish pass of a particular design.

A Model for the Assessment of Barriers to FISH migration (MABFISH), is presented in Table 20 as a proposal for an objective method of prioritising the need for fish passage installation for a given range of barriers to freshwater fish migration. The method is principally intended for use by fishery staff as a decision-making tool. While not presuming acceptance of the principle by other parties, the model could still form the basis of logical argument by fishery managers for the inclusion of fish passage facilities at hypothetical proposed structures which would impede fish migration. The model requires scores to be entered for a range of factors shown below, with information sources given in parentheses. The information will largely be available in-house.

(i) Conservation value of the site of an existing or proposed barrier (conservation section)

(ii) Fish community in the vicinity of the site (fish survey data)

(iii) Ratio of habitat availability upstream and downstream of the site, each for spawning habitat, feeding habitat and refuge habitat (river habitat surveys, river corridor surveys).

(iv) Passability of the barrier (experience for other similar barriers, catch data, research, visual inspection in some cases)

(v) Angling value in the vicinity of the site (angler catch data, angling clubs).

(vi) Proximity of confluence with main river/tributary (maps)

(vii) Need for the barrier (flood defence/hydrometrics/navigation section)

(viii) Benefits of the barrier to the fish community (water chemistry, fish survey).

Following summation of the component scores, the model identifies three possible outcomes: no change, provision of an appropriate fish pass, and removal of the barrier. The last outcome is included given that increasingly river rehabilitation schemes are considering removal of barriers where the structure does not serve an over-riding purpose, and where removal is highly desirable and achievable. The model discriminates between existing barriers and proposed barriers, on the basis that the Agency expects to be more sensitive to current proposals for barriers than was possible in the past. Thus the thresholds for action being required are lower for proposed barriers than existing ones.

Figure 17 presents a flow chart of the suggested process for using the model and evaluating the outcomes. It is anticipated that any such scheme would involve the instigation of a national data base in which area/regional experience for individual cases would be entered. This would be necessary for the wider dissemination of experience, and would progressively improve the data input to MABFISH, or enable its improvement.

Given the current wide realisation across Europe that a wide variety of freshwater fish migrate significant distances to find resources necessary for the completion of their life cycles, it seems sensible to base decisions on improving fish passage on a wide range of relevant questions concerning the fish community and their aquatic environment, rather than just to ask whether migratory salmonids are present.

Table 20 Proposed Model for the Assessment of Barriers to FISH migration (MABFISH). The model is designed to prioritise fisheries-based arguments for installation of fish passes, removal of barriers to fish migration and prevention of construction of new barriers. It is not intended to presume acceptance of the model by other interests but could form the basis for logical defence of requests for fish passes to be included as an integral part of a new obstruction, where appropriate.

Parameter			Calculation example		
			Nidd Sk B*	Ouse L L#	Derw. St B+
Conservation value of area (For SSSi, SAC or AONB score 5)	[low (1)	high (5)]	2	2	3
Fish community	salmonids	4	-	-++	4
	rheophiles	3	3	3	3
	eels / lampreys	2	2	2	2
	predators	1	1	1	1
	limnophiles	1	1	1	1
Habitat Availability ratio	spawning [low (1)	high (3)]	3/1	1/2	2/2
$HA_{upstream} / HA_{downstream}$	feeding [low (1)	high (3)]	3/2	2/2	2/2
	winter refuge [low (1)	high (3)]	2/2	2/2	2/2
Angling value	[low (1)	high (5)]	4	4	3
Existing or likely passability All fish, most occasions = 1 Few fish / few occasions = 5	[low (1)	high (5)]	3 (3?)**	4 (3)**	5 (3)**
Proximity of major tributaries If tributary, proximity to main stem river (up to ~ 20 km) If main stem river, proximity to next major tributary upstream "	[far (1)	near (5)]	3	1	2
Necessity for obstruction Flood Defence, Flow-Gauging, Navigation, Recreation etc.)	[high (1)	low (5)]	3 (F-G)	2 (N, R, F-G)	2 (F-G, F-D, R)
Positive benefits of barrier to fish community e.g. oxygenation, spawning habitat for rheophiles	[many (1)	few (3)]	2	1	1
	Maximum score:	46	29.5	23.5	30

Score-based decisions

	If new obstruction	If existing obstruction	(Existing onstructions)		
Take no action	If score <15	If score < 20	-	-	-
Install fish pass of **suitable** design	If 15 < score < 25	If 20 < score < 35	***** *****	***** *****	***** *****
Remove barrier / do not construct barrier	If 25 < score	If 35 < score	-	-	-

* Skip Bridge flat-V flow-gauging weir, Nidd. Has experimental baffles on downstream weir face.
\# Linton Lock, Yorkshire Ouse. Steep weir + navigation lock. Pool and orifice fish pass.
\+ Stamford Bridge, Yorkshire Derwent. Steep crested weir. Denil fish pass (installed 1996).
++ A few salmon do spawn in the Ure upstream of Linton Lock, but for the purpose of calculation for a limnophile-dominated lowland river they have been ignored
** Values are situation without fish pass and are used here in final scores; (x) is situation with fish pass.

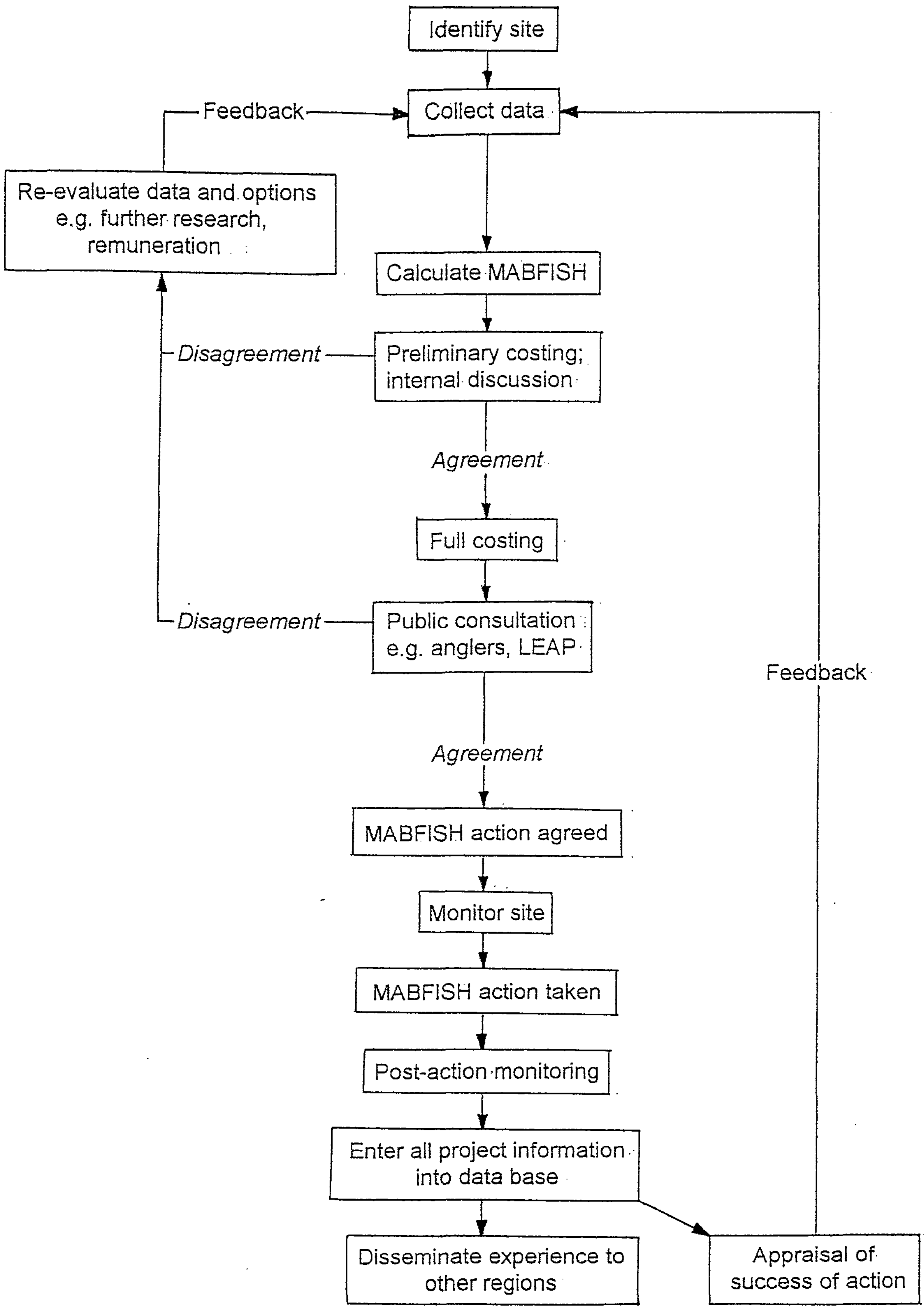


Figure 17 Suggested decision-making flow chart for use with the proposed Model for the Assessment of Barriers to Fish migration (MABFISH) [see Table 20].

8. CONCLUSIONS

The results of this review process have clearly shown that the extent of small and medium scale migratory movements of many coarse fish species is much wider than previously appreciated; particularly for rheophilous cyprinids such as chub, barbel and dace; but in deeper, lowland systems also for strongly aggregating species such as roach and bream. Of all species included within the remit of "coarse fish migration", not surprisingly the greatest amount of information presented concerns eels, reflecting the relatively greater depth of knowledge concerning this species.

A great deal of the information detailing the occurrence, extent and stimuli for migration and movements of coarse fish has recently been obtained. This area of research is currently active, highly productive and has substantial applied value to the sensitive management of UK freshwater systems, especially rivers and canals.

For those coarse fish species found in the UK, the extent and scope of knowledge regarding migration patterns and causes is generally greater within continental Europe than within the UK. However, in a variety of cases, such experiences may not necessarily extrapolate to the UK due to differences in factors such as climate, hydrology, ecology, size of rivers, past history of regulation, modification of river environments and fishery management practices.

While progress has been made in describing the nature and magnitude of migrations for a variety of species, our understanding of the influences of environmental factors on migratory behaviour are poor. Even within the UK there are major variations in the nature and extent of key environmental fluctuations such as flow and temperature between river systems e.g. southern aquifer-fed rivers and unregulated Pennine rivers. An understanding of the relationships between these factors and coarse fish movements, in the manner instituted for salmonid species, remains a key goal, and would enable more effective management of freshwater fisheries and conservation of lowland coarse-fish dominated ecosystems.

There is a need to identify and quantify the factors, such as physical obstructions, habitat degradation and pollution, which restrict or strongly influence natural migratory movements of coarse fishes. Linked to this is the need to identify and evaluate the most effective ways of mitigating obstructions. In particular, there is a need to quantify "supply and demand" of coarse fish at obstructions and fish passes, and to measure the efficacy of fish pass designs under various circumstances for different fish communities. Currently, in most cases, successful ascent only is monitored which provides little information on the fish population attempting to cross barriers. Behaviour of coarse fish at obstructions may be as important as swimming performance in determining their ability to traverse them.

An adequate understanding of the aforementioned factors cannot be obtained from the current experiences of experts in the field. Further directed research will be required to achieve these aims. The range of habitats, fish species and factors under consideration requires a multidisciplinary approach for the successful achievement of these goals. Such research will require the use of the most informative technologies of which telemetry (including automated Passive Integrated Transponder monitoring) is the most important. Successful use of these methods requires substantial expertise by experienced workers.

We should consider the physiological implications of migratory movements in relation to environmental factors such as pollution or physical obstruction. Physiological telemetry and modelling approaches may be helpful here.

9. FUTURE RESEARCH AND DEVELOPMENT NEEDS

9.1 Basic research

At the Warrington Coarse Fish Migration workshop held in February 1998 a conundrum became evident. It was agreed that far too little was known about basic coarse fish ecology, and of the spatio-temporal dynamics of coarse fish. It was suggested by some Agency personnel that such work was appropriate to the Natural Environment Research Council's (NERC) funding remit. However, it was pointed out by all non-Agency scientists present that funding for such work was not forthcoming from NERC and related bodies, despite repeated attempts to gain funding for coarse fish projects of high scientific merit. It is therefore likely to be necessary for the Agency to fund such "basic" research and development. In the longer term the Agency may seek to target joint initiatives with NERC to fund non-salmonid fish ecology.

The Agency's Fisheries Research & Development Programme does not currently appear to have sufficient finance to fund large field-based projects such as would be preferable for the study of coarse fish spatio-temporal dynamics. Therefore such research needs to be phased.

9.2 Influences of environmental factors on coarse fish migration

In our opinion, the priority area for future research is to further quantify the nature and extent of annual migrations for riverine coarse fish, and to identify the relationships between movement patterns and environmental factors. Only by understanding and quantifying these relationships will we be able to apply management practices designed to sustain and improve coarse fisheries where fish migration is a factor in stock distribution, survival and availability to anglers.

9.2.1 Study sites

Research on coarse fish migration should concentrate on larger river systems for several reasons. Firstly, it is the larger river systems which provide the main resource for coarse fisheries. Secondly, at the catchment scale, large rivers usually contain all of the main habitats for spawning, summer feeding and winter refuge phases. Thus while working on a large system it will be possible to quantify and integrate these migratory patterns within the life histories of coarse fish species.

It is crucially important to understand what stimulates and influences coarse fish migration. Because hydrography, water chemistry and climate vary between different regions it is unsuitable to carry out field research in one catchment. We would therefore recommend that research be carried out over several years in a number of catchments. The catchments chosen should necessarily differ in hydrographical regime and climate in order to present opportunities in defining the influences of these two most important physical environmental factors on migration. Ideally background information on fish migration should already have been carried out in order to minimise time wastage. Where possible, there should be differences in the number and types of barriers on these rivers, to provide opportunity for comparison.

9.2.2 Methods

Work on a whole catchment scale will require the use of an integrated approach, combining several methodologies to maximise information obtained, and to circumvent the disadvantages of individual techniques. Radio-telemetry, by active and passive means, of statistically relevant numbers (> 30) of adults of key fish species such as chub, bream, dace and roach should be carried out in conjunction with measurement of environmental variables such as water temperature, flow and daylength to provide data for multivariate analysis of the influence of environmental factors in determining their significance. The use of Geographical Information Systems (GIS) and spatially explicit statistics, which are increasingly being used to analyse complex relationships between animal movements and environmental parameters in terrestrial environments, may also be illuminating methods for determining the factors influencing fish migration from and to specific zones. Radio-tracking of smaller species will be very difficult in the deeper, wider sections of many lowland rivers such as the Nene, Thames, Trent and Great Ouse where conductivities are usually over 1000 $\mu S\ cm^{-1}$. Acoustic tracking with pinger tags provides insufficient advantage in relation to the logistic difficulties to make a large scale programme feasible. However, radio tags can be tracked more easily in the lower conductivity rivers (~ 500 $\mu S\ cm^{-1}$) such as the Yorkshire Ouse and perhaps also the Severn. Radio-tracking will enable objective monitoring of the responses of radio-tagged fish to barriers.

In the deeper water sections of the catchment(s), mobile echosounder surveys should be carried out at night, combined with fixed location work at appropriate intervals (days/weeks/months according to expected migration) to enable examination of fish behaviour at a scale closer to the population, than may be achieved by radio-tracking of individual fish. Tracking should be carried out at the same time as echosounder surveying to enable data to be combined. Simultaneous netting should be carried out to enable fish species composition of aggregations to be identified. Static echosounder surveys should be employed to enable sizing of fish. Data analysis will enable changes in the longitudinal density of coarse fish in the main river, as well as their patchiness, to be related to environmental conditions, such as flows, temperature, dissolved oxygen etc., set in the context of information on movements of fish from tracking analyses.

Where fish passage is restricted, such as at fish passes, automated fish identification and passage techniques should be used, simultaneously with measurements of environmental parameters to identify the factors influencing movement of different sizes and species of fish past these points. Techniques involving remote PIT monitoring currently have unrivalled potential for examining the behaviour of a wide range of sizes and species at one time at such locations and can provide fish passage efficiency data and enable modifications to structures to improve success of migration.

We strongly urge the development of effective collaborative links in any Research and Development proposal on coarse fish migration. For example, there are existing programmes of monthly echosounder survey on some deep stretches of rivers, and these can define seasonal migrations of fish in these areas. It would be cost-effective and scientifically sound to integrate these measurements into a programme of coarse fish migration research.

9.2.3 Project phases

In order to facilitate the ability to carry out strategic research on coarse fish migration, while respecting the low budget available, we recommend that funding be considered for several phases of work. These are, to a degree, independent of one another, but will be less productive than one large project because of (i) the reduced opportunities for multi-disciplinary cross-linking of research, (ii) reduced opportunity for identifying the effects of rarer environmental fluctuations in flow, temperature etc. and (iii) relatively higher management costs for small field-based projects than for large ones. The proposed phases of work are:

(i) Factors influencing the nature and timing of spring spawning migrations of adult coarse fish

(ii) Factors influencing the nature and timing of autumn/winter refuge movements of adult and juvenile coarse fish.

(iii) The nature of, and factors affecting YOY movements.

If project phases are regarded as discrete it would be sensible to carry out successive phases on the same catchment to aid interpretation of results in the light of other phases. Each project phase, examining in some detail one of the key migration stages would be expected to last one year.

9.2.4 Timescale and cost

Each project phase would be expected to last one year. Carrying out such a project in an effective manner requires skilled support staff for fieldwork and data analysis. Furthermore equipment and consumables will be required, even by those researchers who are active in the field and have some of their own equipment. We estimate the cost of each unit of a work programme on coarse fish migration, involving 3-6 months of fieldwork, and requiring the remainder of a year for planning, data analysis and report writing, would cost £60-65 K.

9.3 Fish migration past barriers

9.3.1 Future studies

Further effort needs to be made in measuring the effects of barriers, especially physical barriers, to coarse fish migration. Three main areas require attention. Firstly, what are the effects of installing a physical barrier? Currently, large numbers of weirs are still being planned and installed for hydrometric purposes. On the basis of data from the Environment Agency's regional and area hydrometric catalogues we estimate that the number of weirs and similar structures for flow measurement that have been constructed in England and Wales, in streams and rivers with a mean discharge of $> 1\ m^3\ s^{-1}$ is:

1974 - 1983	212
1984 - 1993	196

We would recommend that a national Research & Development programme is established to identify several of the current proposed flow-gauging weir sites, on rivers in which coarse fish, particularly cyprinids, occur, and would seek to measure the nature and extent of natural migration in the area of the proposed site for as long as possible (minimum of a year) prior to construction and subsequently after construction. The most appropriate method for use would be radio-tracking, perhaps combined with a mark-recapture programme. The work should identify the extent, timing and rate of any migration, together with environmental data prior to construction. Following construction, monitoring should repeat these measurements, and quantify efficiency, rate and delay of passage. Appropriate methodologies are given in Lucas & Frear (1997). Measurement of fish stocks above and below the weir site, before and after construction would also be desirable; together with assessments of available spawning, feeding and refuge habitats, in order to try and determine the effects on recruitment.

Their should also be an investigation of the degree of "wasted" energy in repeated attempts to pass physical obstructions or from suffering the effects of water quality barriers such as areas of low dissolved oxygen from pollution plumes. One of the most appropriate techniques for quantification of these stress effects is through the use of physiological telemetry techniques (Lucas *et al.*, 1993).

Further study on the use of alternative styles of fish pass around physical barriers should be considered. The use of natural bypass channels should be encouraged where possible. The main objection to this normally comes in terms of problems of flow measurement at hydrometric structures. We would recommend that the levels of migration in relation to environmental factors be studied at natural bypass channels sited around less contentious structures. In particular we would recommend, that bypass channels would be in-keeping with river rehabilitation schemes, for which bypass channels could have other conservation benefits. Some bypass channel schemes are underway in some regions (e.g. Thames). It is important that quantitative monitoring of passage, and of influence on the fish population is carried out before and after such schemes.

9.3.2 Existing data and studies

Existing Environment Agency data concerning coarse fish passage should be analysed and presented in an accessible form to other workers within the Agency and outside. Much of this data comes from fish traps at the tops of fish passes; or from video records at counters. Some of this information is currently being analysed, with the intention of publication (G. Armstrong, pers. comm.).

In 1997, as part of a project examining the migration of salmon smolts in the Frome, Dorset, the Institute of Freshwater Ecology also obtained video footage of coarse fish migrating past the Frome fish counter together with environmental data (Beaumont, unpubl. data). These data comprise thousands of observations of a wide variety of species including dace, roach, pike, mullet and eel. These data are of high quality and should be analysed to provide information on the nature and timing of coarse fish movements.

A further source of data, apparently of high quality, and with detailed environmental information concerns downstream movement of fish, principally eels, recorded on video triggered by fish counters on the Test and Itchen. However, given the large amount of information concerning migration of eels, this must be regarded as rather low priority, unless there is a specific management requirement for such information.

There is currently a proliferation of Agency led regional projects using telemetry to study coarse fish movements and behaviour (Table 21). Most of these studies are being carried out using small sample sizes for a variety of management purposes. Although useful, it is unlikely that these data will be sufficiently robust to enable statistically rigorous interpretation. However, if set in the context of a National R & D programme examining fish movements these regional studies, if conducted under strict scientific protocols, might provide additional complementary information.

Table 21 Fish tracking studies carried out by Environment Agency regional staff. P = Proposed; O = Ongoing, F = Finished.

Status	Lead staff	Year	Species	River	Method	Sample size
P	J. Lyons	1998	Bream	Trent	Acoustic	~ 6
P	N. Bromage	1998	Bream	Witham	Radio	~ 5
O	R. Challis	1995-1997	Chub	Severn tribs	Radio	~ 12
F	H. Stone	1995	Chub, barbel	Thames	Radio	~ 5
P	H. Stone	1998	Chub	Thames trib.	Radio	~ 12
P	R. Challis	1998	Chub	Severn	Radio	~ 5

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Appendix I Summary tables of the extent of knowledge of coarse fish migration for species occurring in Britain

1 Lampreys

SUBJECT	NOTES	REFERENCES
Spawning migration	Sea and River lampreys Move from sea into rivers to spawn. Minimum distance of just above the tidal limit to a maximum of 300km. Two migrations in spring and winter - spring run lampreys have more mature gonads. Males reach spawning grounds first to start nest building. Sea lampreys in Loch Lomond also show a potamodromous spawning migration into the River Endrick - the largest feeder stream. Brook lamprey Spawning preceded by short (few km) upstream migration.	Bigelow & Schroeder (1953); Nikolskii (1961); Hardisty (1979); Maitland (1980a); Malmquvist (1980); Sjoberg (1980); Maitland *et al.* (1994); Lucas (1998a); Lucas *et al.* (1998)
Feeding migration	On hatching larval ammocoetes burrow into mud and silt along stream margins and filter feed showing strong site fidelity. Metamorphose in summer and autumn and begin migration - no feeding.	Hardisty & Potter (1971b); Smith (1997)
Post-displacement movements & homing	Adult sea lampreys are partially attracted to spawning streams by larval pheromone. Not to their own natal stream, however.	Bergstedt & Seeleye (1995)
Effects of light	Diel In early stages of spawning migration sea and river lampreys avoid light - hiding during daytime. This varies with season. Peak night-time activity in November and December when lampreys enter freshwater. In March peaks shift by 2-3 hours and in April activity is the same both day and night coinciding with the period of nest-building.	Hardisty (1979)
Effects of temperature	Long-term temperature trends influence the onset and duration of the spawning season in lampreys and once spawning has started activity is markedly affected by small changes in daily temperature. In *Lampetra* spp. spawning begins when spring temperature rises rapidly to 11°C, 15°C for sea lampreys. Upstream migration of brook lamprey triggered by temperature threshold of 7.5°C	Malmquvist (1980); Sjoberg (1980)
Meteorological and Hydrological effects	Upstream movement in brook lampreys inhibited by high flows	Malmquvist (1980)

2 Eels

SUBJECT	NOTES	REFERENCES
Spawning migration	Silver eel migration late/summer autumn. Some migration in spring possibly due to interrupted migration in winter. Male and female migration does not coincide due to more females from upper reaches of rivers, smaller males in coastal areas. Drift in middle of river. Distance depends on swimming capacity, speed and flow rate. Tadnoll Brook 8km per year, Severn 20-30 km per year; Dee 10-20 km per year, Shannon 15 km per year; Tweed 46 km per year. Differences depend on population density and availability of refuges. Migration is flexible eels capable of returning from silver eel to yellow eel stage if conditions for migration unsuitable	Frost (1950); Tesch (1977); Hussein (1981); Moriarty (1986); Aprahamian (1988); Mann & Blackburn (1991); Svedang & Wickstrom (1997).
Feeding migration	Glass eels adjust to freshwater, metamorphose to elver stage and begin feeding. Some stay at coast or estuary. Some migrate upriver in first year others as juveniles later. Most upstream migrating eels 20-30 cm in length but some as large as 40-45 cm. Elver capable of migrating 150 km before fully pigmented. Further after this. Upstream migration is slow and variable. Smaller eels migrate later and less far. Migrate in waves possibly related to population density Stop migration at 30 cm in length and become sedentary.	Mann (1965); Tesch (1965, 1966, 1977); Penaz & Tesch (1970); Larsen (1972); Moriarty (1986, 1990); Aprahamian (1988); Mann & Blackburn (1991); Baras *et al.* (1996a); White & Knights (1997)
Post-displacement movements & homing	Yellow eels capable of homing after displacement up to distances of 200km	Deelder & Tesch (1970); Tesch (1970, 1977).
Refuge seeking & predator avoidance	Seasonal changes in habitats of otherwise sedentary yellow eels probably to avoid unfavourable conditions in winter	Lubben & Tesch (1966); Aker & Koops (1973); McGovern & McCarthy (1992).
Effects of light	<u>Diel effects</u> Glass eel activity highest at night just prior to entry into freshwater Tesch (1977) suggests young eels not influenced but McGovern & McCarthy (1992) found yellow eels move at night. Silver eels mainly active at night.	Tesch (1977); Deelder (1984); McGovern & McCarthy (1992).
Effects of temperature	Ascent of glass eels initiated by temperatures of 6-8^{o}C. Migration of pigmented eels temperature-dependent - declines below 10^{o}C. Onset of migration correlated with water temperatures of 13-14^{o}C. Temperature effects in Meuse secondary to time of year at the Ampsin-Neuville weir due to the warm effluent form the Tihange power plant. Extremely low temperatures may cause cessation of migration in silver eels. Migration ceases with onset of frost	Frost (1950); Tesch (1971, 1977); Moriarty (1986); White & Knights (1997); Baras *et al.* (1996a)
Density-dependent effects	Eels in Meuse may migrate in waves possibly due to density dependent effects. Higher densities of eels may lead to increased migratory behaviour	Knights (1987); White (1994); Baras *et al.* (1996a).

3 Pike

SUBJECT	NOTES	REFERENCES
Spawning migration	Anadromous pike in coastal areas of Bothnian Sea - unlikely in UK. Majority of studies in lakes and reservoirs. Migrate from lakes to streams to spawn. Not faithful to same spawning sites.	Miller (1948); Clark (1950); Franklin & Smith (1963); Johnson & Müller (1978); Müller (1982)
YOY migration	Emigrate from streams to lakes 16-24 days after hatching. All left streams by mid-May / early June.	Clarke (1950); Franklin & Smith (1963).
Feeding migration	Few studies in rivers. In lakes relatively sedentary outside spawning season except for sporadic long-distance movements which are probably associated with prey seeking. Possibly follow salmon migration	Malinin (1972); Vostradovsky (1975, 1983) Bregazzi & Kennedy (1980); Kennedy (1980); Chapman & Mackay (1984); Cook & Bergersen (1988); Pervozanskiy *et al.* (1989); Armstrong (unpubl. data)
Post-displacement movements & homing	Capable of homing from distances of up to 1.5km after displacement due to floods. May home to spawning grounds by smell of decaying material although Franklin & Smith (1963) found no evidence of homing.	Richard (1979); Bregazzi & Kennedy (1980); Langford (1981).
Effects of light	<u>Diel</u> Greatest movements of breeding pike in feeder streams occurs at night in Lake Erie and Lake George. Light may also affect movement of fry from nursery streams - only emigrate on sunny days.	Clark (1950); Franklin & Smith (1963)
Effects of temperature	Pike begin movements to feeder streams in Lake Erie at $0\ ^{o}C$ (did not spawn until $8\ ^{o}C$) Onset of movement slightly higher temperature in Lake George ($2\text{-}3^{o}\ C$)	Clark (1950); Franklin & Smith (1963)
Meteorological and hydrological effects	Movement of adult pike into spawning streams dependent on lack of ice cover.	Clark (1950); Franklin & Smith (1963)
Individual behaviour	Population consists of static component and more mobile component of fish which fails to accept a home range	Mann (1980)

4 Grayling

SUBJECT	NOTES	REFERENCES
Spawning migration	Lake populations known to move to afferent streams to spawn. Peaks in occurrence in fish passes in spring preceding main spawning season.	Gustafson, in Jankovic (1964); Woolland(1972); Pelz (1985); Philippart *et al.* (1988, 1992, 1993, 1994, 1996); Lanters (1995, 1996); Philippart (1997); Prignon *et al.* (1996); Travade *et al.* (1996); Lucas (unpubl. data)
YOY migration	In June and July YOY moved from bank habitats with low velocity to mid-channel with high velocity followed by downstream migration out of nursery area resulting in complete desertion by fish	Scott (1985); Bardonnet *et al.* (1991)
Effects of light	<u>Diel</u> Downstream migration of fry out of Suran had bimodal diel rhythm with peaks at start and end of night.	Bardonnet *et al.* (1991)

5 Barbel

SUBJECT	NOTES	REFERENCES
Spawning migration	Highly mobile in spawning season. Strong seasonal migration periodicity with peaks in spring in the Meuse and Nidd. Males and immature females are first to migrate in the River Méhaigne, Belgium about 1 week before females. Females quickly move downstream after spawning, males stay longer. Both sexes move downstream in autumn and winter. Sizes of fish migrating through fish pass on Meuse were 443 mm (males) 544 mm (females) 481 mm (immature individuals). Sex ratio in fish pass was 1.08 male to female compared to 15 male to 1 female in resident populations. Spring peak in occurrence of barbel in fish passes preceding main spawning period.	Pelz (1985); Philipart (1987, 1997); Philippart *et al.* (1988, 1992, 1993, 1994, 1996); Baras & Cherry (1990); Baras (1992, 1993a) Baras *et al.* (1994), Lanters (1995, 1996); Lucas & Batley (1996); Prignon *et al.* (1996); Travade *et al.* (1996).
YOY migration	Downstream drift in May and June.	Purtscher *et al.* (1988)
Feeding migration	Characterised by relatively little movement in home area interspersed with sporadic long-distance movements.	Lucas & Batley (1996); Lucas & Frear (1997)
Post-displacement movements & homing	Immature barbel present in the Ampsin-Neuville fish pass, River Meuse outside the spawning season probably compensatory migration for downstream displacement. Similar movements found in Ourthe and Nidd. In Meuse barbel are capable of homing to defined resting sites after foraging. Outside spawning season experimentally displaced barbel will home to their activity areas.	Baras & Cherry (1990); Baras *et al* (1994); Baras (1997); Lucas *et al.* (in press).
Refuge seeking & predator avoidance	Barbel move downstream in autumn and winter possibly seeking refuge during high flow conditions - although may also be the result of displacement	Lucas & Batley (1996)
Effects of light	<u>Diel</u> Barbel only attempted to ascend Skip Bridge weir during night or at dawn. Diel movement between refuge and foraging habitat	Baras (1995); Lucas & Mercer (1996); Lucas & Frear (1997); Lucas *et al.* (in press).
Effects of temperature	Migration affected by temperature but only just before and after spawning. Maximum movements occurred at 10-22 ^{o}C. Spawning at 14-18 ^{o}C although there is considerable variation depending on local conditions. Complicated at Ampsin-Neuville fishpass on the Meuse by flow conditions. Mean daily activity correlated with temperature. Fish in fish passes occur at > 11 ^{o}C.	Baras & Cherry (1990); Baras *et al.* (1994); Lucas & Batley (1996); Slavík (1996a)
Hydrological effects	At the Ampsin-Neuville weir on the River Meuse, the attractiveness of the fish pass depends on relative flows between the hydroelectric plant, the spillway and the fish pass. High flows at the hydroelectric plant lead to failure of barbel migrations through the fish pass.	Baras *et al.* (1994)
Individual behaviour	Populations consist of a static component and a more mobile component which fails to accept a home range.	Hunt & Jones (1974)

6 Chub

SUBJECT	NOTES	REFERENCES
Spawning migration	Repeated migrations of up to 13 km. Occurrence in fish pass catches coincide with main spawning periods and may be explained by repeat spawning runs.	Pelz (1985); Philippart *et al.* (1988, 1992, 1993, 1994, 1996); Lanters (1995, 1996); Frederich (1996); Frederich & Ohmann (1996); Prignon *et al.* (1996); Travade *et al.* (1996); Frederich *et al.* (1997) Philippart (1997).
YOY migration	Caught in screens and traps at water intakes. Downstream drift. Diel movements in and out of bays	Penaz *et al.* (1992); Solomom (1992); Baras & Nindaba (in press).
Feeding migration	Diel movements in and out of bays by juveniles to feed.	Baras & Nindaba (in press).
Post-displacement movements & homing	Displaced from spawning site by flood. Washed 3-13 km downstream. Returned to site 1 week later after flood had subsided. Experimentally displaced fish homed from 2 km away.	Frederich (1996); Lucas *et al.* (in press).
Refuge seeking & predator avoidance	Movement into bays to avoid floods. Diel movement of small juveniles into bays to avoid predators.	Pont *et al.* (1998); Baras & Nindaba (in press).
Effects of temperature	Chub only occurs in fish pass on the Elbe at >17 ^{o}C.	Slavík (1996a)
Individual behaviour	Population consists of a static component and a mobile component which fails to accept a home range.	Nicolas *et al.* (1994)

7 Common bream

SUBJECT	NOTES	REFERENCES
Spawning migration	Individuals capable of exceptional movements of up to 59 km. Mostly spawning migrations of up to 10 km occur. After spawning aggregations break down into shoals and return to specific feeding grounds where they rarely move more than 2 km. Substantial but erratic movements of radiotracked individuals also observed in the Grand and Royal Canals, Ireland. Spring peak in occurrence in fish pass catches coincides precedes main spawning period.	Whelan (1983); Pelz (1985); Philippart *et al.* (1988, 1992, 1993, 1994, 1996); Lanters (1995, 1996); Caffrey *et al.* (1996); Philippart (1997); Prignon *et al.* (1996); Travade *et al.* (1996);
Feeding migration	Adults sometimes undergo spontaneous long-distance movements possibly related to foraging movements as in pike mainly move within less than 3 km in home area.	Whelan (1983); Caffrey *et al.* (1996).
Post-displacement movements & homing	Bream returned to their home site after floods. Capable of homing between spawning and feeding sites. Distances of up to 60 km moved by experimentally displaced fish in the Netherlands	Goldspink (1978); Langford (1981); Whelan (1983).
Refuge seeking & predator avoidance	Move from deeper water to marinas and boatyards in winter in the Norfolk Broads	Wortley (1981); Coles (2985); Jordan & Wortley (1985).

8 Dace

SUBJECT	NOTES	REFERENCES
Spawning migration	Highly mobile during spawning season. Radio-tagged fish moved 3.5-14km upstream of Skip Bridge weir to spawn. Occurrence in fish pass catches coincides with main spawning period.	Pelz (1985); Philippart *et al.* (1988, 1992, 1993, 1994, 1996); Lanters (1995, 1996); Lucas & Mercer (1996); Philippart (1997); Prignon *et al.* (1996); Travade *et al.* (1996); Lucas *et al.* (in press)
YOY migration	Caught in screens and traps at water intakes. Diel movements in and out of bays.	Solomon (1992); Baras & Nindaba (in press).
Feeding migration	Regular migrations between discrete day and night feeding and refuge habitats with strong homing between them. Movements in home area characterised by short movements interspersed with long distance movements to new home area. Diel movement of larger juveniles to feed.	Clough & Ladle (1997); Clough & Beaumont (in press); Baras & Nindaba (in press).
Post-displacement movements & homing	Diel homing movements to refuge habitsts for predator avoidance.	Clough & Ladle (1997)
Refuge seeking & predator avoidance	Diel homing movements to refuge habitats for predator avoidance.	Clough & Ladle (1997); Baras & nindaba (in press).
Effects of light	Diel Increased activity at dusk.	 Clough & Ladle (1997)
Effects of temperature	Rapid downstream movement of tagged dace below Skip Bridge weir possibly related to marked drop in April temperature from 9.1-6.1°C	Lucas & Mercer (1996)

9 Roach

SUBJECT	NOTES	REFERENCES
Spawning migration	Spawning shoals migrate each year to use same spawning grounds. Highly mobile during spawning season. Fish ascending Skip Bridge weir moved upstream individually or in groups of 2-4 to spawning areas 0.1-4.5 km upstream of weir.	Diamond (1985); Lucas *et al.* (in press)
YOY migration	Caught in screens and traps at water intakes. Downstream drift. Move into backwaters in response to floods. As grow move from margins to deeper water and then disperse downstream..	Penaz *et al.* (1992); Solomon (1992); Pont *et al.* (1998);
Post-displacement movements & homing	Adults in Lake Årungen home to spawning streams and after drifting to lake subsequent generations also seem capable of homing to the same stream. Found moving upstream through fish pass after floods.	Champion & Swain (1974); Lightfoot & Jones (1979); L'Abee-Lund & Vøllestad(1985, 1987)
Refuge seeking & predator avoidance	Move from deeper water in winter to boatyards and marinas in the Norfolk Broads. Moved habitats at dusk to avoid predators.	Wortley (1981); Coles (2985); Jordan & Wortley (1985); Copp & Jurajda (1993).
Effects of light	Diel Only attempted to cross Skip Bridge weir at night	Lucas & Mercer (1996), Lucas & Batley (1996); Lucas & Frear (1997); Lucas *et al.* (in press)
Meteorological and hydrological effects.	YOY fish move into backwaters in response to flood.	Pont *et al.* (1998)
Water quality effects	Only able to colonise Salford Docks in winter when oxygen levels are high. Move into backwaters of Vltava when oxygen levels high during the day and move out again at night.	Hendry *et al.* (1994); Slavík (in press)

10 Other cyprinids

Bitterling

No published information

Bleak

Occur in fish pass catches suggesting some form of migration particularly during the spawning season (Pelz, 1985; Philippart *et al.*., 1988, 1992, 1993, 1994, 1996; Lanters 1995, 1996; Philippart, 1997; Prignon *et al.* 1996; Travade *et al.* 1996).

Common carp

No published information

Crucian carp

No published information

Goldfish

No published information

Grass carp

Movements in British canals consist of short distance movements (<10 m) within restricted feeding habitats together with longer distance movements (>20 m) between such areas (Hockin *et al.*, 1989)

Gudgeon

Capable of homing after displacement (Stott *et al.* 1963). Occur in fish pass catches suggesting some form of migration particularly during the spawning season (Pelz, 1985; Philippart *et al.*., 1988, 1992, 1993, 1994, 1996; Lanters 1995, 1996; Philippart, 1997; Prignon *et al.* 1996; Travade *et al.* 1996). Populations consist of a static component and a mobile component which fails to accept a home range (Stott, 1967).

Ide

Found in fish passes in the Netherlands (Winter, 1996; Winter & van Densen, in press).

Minnow

Minnows may undertake spawning migrations in May moving between 250 m and 1 km. Capable of homing to home range after spawning, displacement and avoidance of pollution. Move into side streams to avoid floods. Population consists of a static component and a mobile component (Pitcher, 1971; Kennedy & Pitcher, 1975; Goldspink, 1977; Kennedy, 1977; Slavík, unpubl. data).

Rudd

No published information

Silver bream

Occur in fish pass catches suggesting some form of migration particularly during the spawning season (Pelz, 1985; Philippart *et al.*, 1988, 1992, 1993, 1994, 1996; Lanters 1995, 1996; Philippart, 1997; Prignon *et al.* 1996; Travade *et al.* 1996).

Tench

No published information

11 Stone loach

Individuals with enlarged gonads found crossing weirs in River Sheaf (Axford, pers. comm.).

12 Spined loach

Downstream spawning migration in March / April, spawning in June followed by upstream migration in July. Distances of 200-800 m travelled (Slavík & Rab, 1995, 1996).

13 Wels

May move short distances in spring (Lelek, 1987; Cowx & Welcomme, 1998).

14 Sticklebacks

Three-spined stickleback has three forms: (i) *trachurus* is anadromous; (ii) *leirus* and *semi-armatus* are freshwater only. Adult *trachurus* migrate in spring to freshwater. Spawn in the lower reaches of streams. Nine-spined stickleback may be anadromous. Anadromous three-spined stickleback intolerant of freshwater in late summer and migrate towards sea. Movements of stickleback in Black River, Alaska in May could be due to avoidance of high discharge and low temperature caused by the June snowmelt (Wootton, 1976; McDowall, 1988; Harvey *et al.*, 1997).

15 Bullhead

Bullhead are normally considered solitary and territorial. They may, however, migrate to deeper water to spawn (Mills & Mann, 1983). Crisp *et al.* (1984) and Crisp & Mann (1991) provided evidence to suggest that bullhead in Cow Green Reservoir, Teesdale over-wintered in the reservoir and migrated to afferent streams to spawn. Upstream movements occur in German rivers in May and June (Bless, 1990). Dispersal movements may be correlated with higher population densities (Dunhower *et al.*, 1990).

16 Perch

Populations consist of a static component and a mobile component which may fail to accept a home range. The mobile component forms a higher proportion of the population when habitat is unsuitable (Bruylants *et al.*, 1996).

17 Zander

Fickling & Lee (1985) showed that zander displayed movements of up to 38 km although the reason for such movements was unknown. Zander occur in large numbers in fish pass catches in continental Europe indicating some form of migratory behaviour (Pelz, 1985; Philippart *et al.*, 1988, 1992, 1993, 1994, 1996; Lanters 1995, 1996; Philippart, 1997; Prignon *et al.* 1996; Travade *et al.* 1996).

18 Ruffe

No published information. Anecdotal reports of winter aggregations in boatyards in Fenland, East Anglia.

19 Mullets

Mullets were described as catadromous by McDowall (1988). Hickling (1970) suggested that thin-lipped mullet migrated 200-330 km upstream in some Moroccan and French rivers. Within the UK, thick-lipped mullet may occur in estuaries and rivers around the whole country; golden-grey mullet and thin-lipped mullet tend to be restricted to southern rivers and the latter is most common in freshwater (Maitland & Campbell, 1992). Most movements into rivers are by adults during spring and summer for feeding purposes, moving back to sea in autumn. Juveniles are also abundant during summer in estuaries.

20 Sea bass

Young bass often enter estuaries and may penetrate freshwater for feeding and predator evasion purposes, mainly in the south of England and Wales. Estuaries and river mouths provide important nursery areas, especially in summer (Pickett & Pawson, 1994). Juveniles and sub-adult fish return to the sea to spawn.

21 Flatfish

Flounder may often be present in freshwater in the lower reaches of rivers (McDowall (1988) and were described as the 'River flounder' by Berg (1962). Young feed in brackish or freshwater then migrate to the sea as adults to spawn (Nikolskii, 1961; Berg, 1962). Rivers are important as nursery and feeding grounds and may also provide refuge from predators (Summers, 1979, 1980; Kerstan, 1991).