TEMPORAL VARIATION IN THE BEHAVIOUR OF PIKE *ESOX LUCIUS* L.

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'Of all the fish that are native to Britain, the pike is the one I would least like to share my bath with.'

Morecombe, Eric. (1984). *On Fishing*. pp. 120. London: Pelham Books Ltd.

ABSTRACT

This thesis examines the behavioural ecology of pike *Esox lucius* L., a widely distributed piscivorous ambush predator, focussing on variations in behaviour at daily, seasonal and annual scales, and discussing the results in relation to community structure, prey behaviour and conservation/management.

Adult pike (n = 30) were radio tagged in the River Frome, Dorset, UK. Home ranges were multi-nuclear in structure, typically extending along several hundred metres of river. Off-river habitats were utilised extensively during winter flooding.

Movement within the home range occurred on a daily basis; interpreted as switching between potential ambush sites. There was evidence for increased activity during dawn and dusk, times when predators may have a competitive advantage, but movements could also occur throughout the day.

The hypothesis that the population consisted of simple 'static' and 'mobile' components (Mann, 1980) was rejected. 'Partial migration' occurred, that is, some individuals ('permanent residents') remained in one area year-round, whilst others ('migrants') moved between putative reproductive and non-reproductive home ranges, separated by several kilometres of river; upstream migration being associated with periods of flooding. Intermediate and 'emigrant' behaviours were also observed, making it unlikely that 'permanent residency' and 'migration' represent two genetically different strategies with equal fitness consequences.

Meanwhile, a study of captive, sibling, young-of-the-year pike, conducted at the Almondbank unit of the Fisheries Research Service Freshwater

Laboratory, determined that habitat use was non-random, and that individual variation in habitat choice occurred; pike positively selecting deeper areas or areas of emergent vegetation. Activity was strongly diurnal and correlated with turbidity.

Overall, this thesis provides an investigation into predator-prey interactions from the point of view of an apex predator, reveals a hitherto unexpected degree of mobility amongst riverine pike, and discusses the potential significance of the demonstrated existence of individual variation in habitat selection and long-term spatial behaviour.

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CONTENTS

INTRODUCTION

To date, behavioural studies of predator-prey interactions in freshwater fishes have focussed on the behaviour of the prey animal. This thesis therefore investigates such behaviours from the point of view of a widely distributed apex predator in freshwater ecosystems, the pike *Esox lucius* L. This species plays a major role in the 'top-down' regulation of prey fish populations, in terms of population structure (He & Kitchell, 1990), behaviour (Wysujack, 2001) and even morphology (Brönmark & Miner, 1992). Consequently studies of the behaviour of this important predator are vital towards achieving an understanding of many aspects of the ecology of freshwater fishes.

Pike spatial behaviour has been shown to be extremely variable both within and between populations (Jepsen *et al.,* 2001). This thesis discusses possible mechanisms underlying the observed diversity of behaviours in the species, following an investigation into the movements of both free-living and captive pike, observed at a variety of temporal scales. In addition to furthering understanding of predator-prey interactions, information on the behaviour and habitat use of pike can also be of practical use, in terms of fisheries management and conservation issues.

The majority of previous studies of free-living pike have been conducted in still waters *e.g.* Diana *et al.* (1977), Diana (1980), Chapman & Mackay (1984b), Cook & Bergersen (1988), Jepsen *et al.* (2000; 2001). Pike however are also important components of river ecosystems, where the environment is often less predictable than lakes, water levels and discharges being in particular subject to large variation. This thesis therefore concentrates on the behaviour of pike in rivers, a habitat in which studies have thus far been relatively scarce.

Fieldwork was conducted in the River Frome, Dorset, UK, an excellent study site due to the relatively unmodified status of the river channel (designated a Site of Special Scientific Interest by English Nature) and the extensive literature available on the ecology of fish in the river, particularly the pike and one of its main prey species, the dace *Leuciscus leuciscus* (L.) (Mann, 1976; 1980; 1982; Mann & Beaumont, 1990; Clough & Ladle, 1997; Clough & Beaumont, 1998; Clough *et al.* 1998). The suitability of the study site was further enhanced by the proximity of laboratory facilities at the NERC Centre for Ecology and Hydrology (CEH), Dorset, the River Laboratory field station[1], and associated environmental monitoring equipment.

When studying highly visible animals living in open, accessible environments, it is often possible to collect a great deal of behavioural data simply by watching the animals for sufficient time *e.g.* Goss-Custard *et al.* (1995). However, the study of animals in less accessible environments presents numerous challenges which must be overcome, foremost among which is often the inability to view animals directly. Aquatic ecosystems form one such habitat, with much, if not all, animal behaviour occurring out of sight, beneath the waters' surface. In the present study, radio telemetry was therefore used as a tool to study the behaviour of free-living pike in the River Frome (Chapters 2 to 7) whilst Passive Integrated Transponder (PIT) tag technology and direct observations were also used to investigate the behaviour of young-of-the-year pike, held at the Almondbank unit of the Fisheries Research Service Freshwater

[1] Owned by the Freshwater Biological Association, with facilities leased by CEH.

Laboratory. The study of these captive fish allowed questions to be addressed which could not answered through studies of wild fish.

The structure of this thesis then is as follows: Chapter 1 introduces the reader to the biology and ecology of the pike; background knowledge of the study species being necessary in order to provide a contextual understanding of the results and discussions presented later. In Chapter 2, the River Frome study area is further described, along with the methods used to capture, radio tag and track pike. The procedures used to collect quantitative data on habitat availability within the study area are also described in this chapter.

An underlying assumption of most telemetry studies is that the behaviour of tagged individuals does not differ from that of untagged conspecifics (White & Garrot, 1990b). The validity of this assumption in the present study is examined in Chapter 3 where evidence from the condition of recaptured animals, direct and indirect observations of fish behaviour, and the long-term survival of radio tagged pike are used to demonstrate that the methods used to tag pike were unlikely to have led to the collection of unrepresentative data.

Chapter 4 uses the locations of seasonally-determined home ranges, together with the results of tracking studies conducted throughout the year, to examine the long-term spatial behaviour of pike in the River Frome. The strategies involved in competition for resources may be reflected in the manner in which a species utilises space, and, within a species a variety of spatial behaviours may occur. The hypothesis of Mann (1980), that the population of pike in the River Frome consisted of both static and mobile components, is specifically examined, and found to be an inadequate description for the variety of spatial behaviours observed in the present study. Instead, a continuum of spatial behaviours including 'permanent resident,' 'migratory' and 'emigrant' categories is proposed, and the long-term spatial behaviours of pike are discussed with reference to partial migration, a widespread phenomenon among many animal taxa in which one fraction of the population is migratory and the other sedentary (Lundberg, 1988).

The diel movements of pike are examined in Chapter 5, the daily cycle of light and dark being a factor that may affect the 'balance of power' between predator and prey. Distinct diel patterns of migration have been reported in adult, juvenile and larval river fishes, and whilst these have been regarded as representing strategies to minimise predation, the diel behaviour of riverine pike has not previously been examined. Data on the diel and diurnal movement patterns of pike are therefore presented, and discussed in relation to the differing strategies available to sit-and-wait predators, the behaviour of prey fish and to optimal foraging theory.

As mentioned previously, rivers can form less predictable environments than still waters. During periods of high discharge, the River Frome is free to burst its banks, and inundate the surrounding meadows, and Chapter 6 describes the habitat utilisation of riverine pike during periods of winter flooding. Off-river habitats were already known to be of importance to pike during the spawning season, and as a nursery ground, but Chapter 6 demonstrates that these areas can also be of importance to adult pike during the winter months, far in advance of the spawning season. Masters *et al.* (2002), written as part of the current study, proposed two hypotheses to explain the observed extensive use of off-river habitats by pike at such times. The 'refuge' and 'feeding' hypotheses are discussed in Chapter 6 in the light of further data collected since the publication of the paper.

Chapter 7 describes attempts to characterise the fine-scale habitat preferences of pike in the River Frome by comparing habitat utilisation (determined from radio tracking and home range analyses) with habitat availability (as recorded during surveys of the river); the aim being to gain a better understanding of the distribution and movements of pike within the river. General conclusions on habitat selection are drawn from the data collected, which are in agreement with the limited previously published information on habitat selection by pike in rivers, and the considerable difficulties involved in collecting fine scale habitat utilisation and availability data for wide-ranging aquatic species are discussed.

Habitat selection by pike is further examined in Chapter 8, which describes a study of captive, sibling young-of-the-year pike, conducted at the Almondbank unit of the Fisheries Research Service Freshwater Laboratory, UK. The experimental set-up provided an advantage over field-based methods of assessing habitat preference as factors such as competition interference, and temporal variation in the proportional availability of habitat could be eliminated. The experiment also provided a unique opportunity to study the behaviour of young-of-the-year pike, fish that are particularly difficult to study in the wild, due to their small size and cryptic nature. Chapter 8 also presents data on the diel activity patterns of these fish, together with the results of continuous visual observations of pike behaviour.

Overall, this thesis provides detailed information on how the behaviour of pike varies with time, over a scale of days to years, together with data on both fine and broad-scale habitat selection in pike. Individual variations in behaviour and the possible underlying causes for the variety of spatial behaviours described for this species are discussed. The thesis is summarised in Chapter 9, where suggestions for future work can also be found.

CHAPTER 1

The biology and ecology of pike

In order to allow the reader to better interpret the results presented later in this thesis, this chapter contains a synthesis of existing literature on the biology and ecology of the study species. Particular attention is paid to the pike of the River Frome, Dorset; this being the location where the fieldwork described in later chapters was conducted.

1.1 TAXONOMY, MORPHOLOGY AND GEOGRAPHIC DISTRIBUTION

The pike is a member of the Esocidae, a group of freshwater fishes inhabiting temperate to cold regions in the northern hemisphere (Raat, 1988). The Esocidae, have been grouped together with the Umbridae (mudminnows) as Esociforms in the Teleost superorder Protacanthopterygii (Helfmann *et al.*, 1997c), however the systematic position of the Esociformes is still debated (Crossman, 1996).

The Esocidae all possess a long body form, with the dorsal and anal fins being placed well to the rear, close to the caudal fin. The flexible body and arrangement of fins in the Esocidae constitutes an adaptation for ambush predation (Webb, 1984a; 1984b; Helfmann *et al.*, 1997d). The snout is long and flattened and the mouth contains teeth on the jaws, vomer, palatines and tongue (Crossman, 1996). The musculature of the Esocidae consists largely of white muscle (Beggs *et al.*, 1980; Webb, 1984b), a muscle type used anaerobically in short-duration burst swimming (Helfman *et al.*, 1997a) suiting the ambush predation tactics of the Esocidae, but reducing the capability for sustained chases of prey (Webb, 1984b).

The Esocidae includes five extant species of the genus *Esox*, these being the pike *Esox lucius* (commonly called northern pike in North America), the muskellunge *Esox masquinongy* Mitchell, the Amur pike *Esox reicherti* Dybowski, the chain pickerel *Esox niger* Lesueur and the redfin and glass pickerels *Esox americanus americanus* Gmelin and *E. a. vermiculatus* Lesueur (Crossman, 1996). The pike is the most widespread of these species, being native to Europe, Asia and North America (Crossman, 1996), whilst the muskellunge and the pickerels are found only in North America, and the Amur pike is native to Russia and China.

Esox lucius is the only pike species occurring in the UK. Pike were restricted to southern and southeastern regions of the British Isles following a period of glaciation 13-15000 years ago, however, in historical times, humans have extended the natural distribution of pike in the UK (Maitland & Campbell, 1992). The species was favoured by medieval aquaculturists who found it suitable for stocking in small ponds, easy to transport and good to eat (Maitland & Campbell, 1992). Pike have also been redistributed as a fish population control measure, for example, in attempts to reduce the numbers of small trout, allowing for the growth of larger specimens (Maitland & Campbell, 1992). The species was introduced to Ireland in the fourteenth or fifteenth century A.D. (Maitland & Campbell, 1992).

Pike occupy both still and flowing freshwater habitats, however, the species can also be found in the brackish waters of the Baltic Sea (Müller, 1986; Westin & Limburg, 2002).

1.2 LIFE HISTORY

The life history of pike has been well studied and is reviewed in detail in the FAO fisheries synopsis of biological data on this species (Raat, 1988).

Pike spawn in the springtime over submerged aquatic vegetation, or in areas where emergent or flooded terrestrial vegetation is present (Fabricius, 1950; Frost & Kipling, 1967; McCarraher & Thomas, 1972; Sukhanova, 1979). In the River Frome, spawning is thought to occur primarily in side channels, with eggs being laid in the main river during low flow years (Mann, 1980; Mann & Beaumont, 1990). The eggs are *ca.* 3 mm in diameter and pale yellow in colour (Balfour Browne, 1905) and become adhesive shortly after being shed from the body of the female allowing them to become stuck to the vegetation over which the pike has spawned (Clark, 1950; Fabricius & Gustafson, 1958; Frost & Kipling, 1967; Raat, 1988). Hatching takes 150 to 155 degree days, after which time the young pike attach themselves to the vegetation by means of adhesive glands in the head (Frost & Kipling, 1967; Braum *et al.*, 1996). Increasing amounts of swimming are seen over the next few days, interspersed with rest periods when the pike attach to vegetation (Frost & Kipling, 1967). The mouth and anus open four and five days after hatching, respectively, with the yolk sac being absorbed and the adhesive glands disappearing around 9 days after hatching (Frost & Kipling, 1967). Feeding on invertebrates begins as soon as the mouth opens, and before complete absorption of the yolk has taken place (Frost, 1954). As the pike fry grow, the diet shifts from crustaceans, to insects, to fish (Frost, 1954; Franklin & Smith Jr., 1963).

Mortality during the egg stage and the first year of life is very high, particularly in the first three months (Kipling & Frost, 1970; Mann, 1980). During their early life, pike are vulnerable to both invertebrate (Le Louarn & Cloarec, 1997) and vertebrate predators, including intra-cohort cannibalistic predation (Kipling & Frost, 1970).

After a period of time spent living in the spawning ground, most pike move to new habitats. Emigration can begin soon after hatching (16 to 20 days being quoted by Franklin & Smith Jr. (1963)), whilst pike are still small, although some fry remain in close proximity to spawning areas until greater sizes ($\geq$ 50 mm) are reached (Franklin & Smith Jr., 1963; Morrow Jr. & Miller, 1998). Most young-of-the-year pike in the River Frome, Dorset, leave side channel spawning areas and enter the main river in the summer (Mann, 1980), but some remain in the channels until the following year, without switching to a piscivorous diet; the fish remaining in the channels having lower growth rates than those that move out into the river (Mann & Beaumont, 1990). Growth of young-of-the-year pike is rapid, with lengths of > 25 cm achievable in the first year (Raat, 1988). The behaviour of young-of-the-year pike is discussed further in Chapter 8.

During their lives, pike can reach considerable sizes, with values of L_∞ of 83 cm for North American pike, 112 cm for European pike and 139 cm for Asian pike (Casselman, 1996), where L_∞ is a measure of projected maximum length, based on the Von Bertalanffy growth equation (Tesch, 1968). Lengths at age of pike from North America and Europe are similar, and much greater than those of Asian pike, although Asian fish have the largest ultimate length (Casselman, 1996). Female pike are on average 7.7% larger at age than males and can grow up to 40% longer (Casselman, 1996). In the River Frome, female pike are generally longer lived than males, with Mann (1976) reporting a maximum age of 12+ for females and 5+ for males, although older males than this were captured during the present study (Chapters 2 and 3).

The onset of sexual maturity varies with location and may occur when pike reach a specific size rather than a specific age, with growth rate determining when this size is reached (Frost & Kipling, 1967). Mann (1976) reported that *ca.* 75% of all pike in the River Stour, Dorset, were mature by the end of their second year of life, with mature age 2+ males and females (mean L_F[1] ♂ = 44.0 cm, mean L_F ♀ = 45.5) being larger than immature males and females of the same age (mean L_F ♂ = 35.6 cm, mean L_F ♀ = 42.9 cm). Ages of first maturity of River Frome pike are similar to those in the nearby River Stour (Mann, 1980).

Pike are very fecund fish with females capable of producing tens to hundreds of thousands of eggs (Billard, 1996). Generally, the number of eggs produced is proportional to the weight of the fish (Carbine, 1944; Frost & Kipling, 1967) although there is considerable variation in fecundity between individuals in the same population (Mann, 1976), between different populations (Billard, 1996) and over time (Craig & Kipling, 1983). Mann (1976) calculated the relationship between fish length and egg number for pike from the River Stour as being:

$$\log_{10} \text{Egg number} = 3.56 \times \log_{10} \text{Length (mm)} - 5.40 \qquad r = 0.88$$

[1] Where L_F = fork length; the length between the forward extremity of the fish and the tip of the median rays of the caudal fin (Lagler 1968).

This relationship between length and fecundity was assumed to be similar for River Frome pike, due to close similarities in growth rate, longevity and age at first maturity between the populations (Mann, 1980). For mature female pike, the ripeness of the fish can greatly affect the relationship between length and weight, with fish weighing more than normal at this time (Mann, 1976) and being noticeably deeper and broader bodied (Figure 1.1).

Pike are known to migrate to spawning grounds prior to spawning taking place, and males are thought to arrive before females, and then remain on the spawning grounds longer (Frost & Kipling, 1967; Lucas, 1992). Pike often home annually to specific spawning grounds (Carbine & Applegate, 1948; Frost & Kipling, 1967; Bregazzi & Kennedy, 1980) with reproductive homing also having been documented in the closely related muskellunge (Crossman, 1990). Studies of allele frequency differences at five microsatellite DNA loci revealed significant differences between spawning populations in a Minnesotan lake, and it was proposed that the observed reproductive isolation would only be expected if most individuals first spawned at the site of their own birth, and returned to that site in succeeding years *i.e.* exhibited both natal-site and spawning-site fidelity (Miller *et al.*, 2001). Discrete populations also appear to occur amongst Baltic pike, with obligate freshwater spawners and brackish water populations, which do not appear to enter fresh water at all (Westin & Limburg, 2002).

Although spawning migrations occur to discrete locations, pike disperse after spawning (Frost & Kipling, 1967) and year round ranges for fish from different spawning sites overlap (Miller *et al.*, 2001). Pike also stray between spawning grounds, with Miller *et al.*(2001) reporting that 1.3% and 4.8% of pike captured at two spawning sites were later captured at the other spawning site.

Figure 1.1 Pike G (Table 2.2) caught on **a)** 27 March 2000 (pre-spawning, L_F = 63.5 cm) and **b)** 6 June 2000 (post-spawning, L_F = 64.0 cm), illustrating the differences in body shape between ripe and spent females. Both photographs were taken prior to this fish being radio tagged and the fish was identified by reference to a 'smolt' tag attached to the dorsal fin (Chapter 2).

a)

b)

Miller (1948) also noted that small numbers of pike caught at a particular spawning ground within a lake, were subsequently recaptured at different spawning grounds, 2 to 5 miles (*ca.* 3 to 8 km) away. Spawning migrations have been reported in rivers as well as lakes, with Ovidio & Philippart (2002) recording upstream migrations of 7.7 ± 6.67 km (mean ± S.D.) in the Rivers Ourthe and Amblève, Belgium.

The spawning behaviour of pike has been studied and described in detail by Clark (1950) and Fabricius & Gustafson (1958). Spawning groups typically consist of one female and up to three males (Clark, 1950; Fabricius & Gusafson, 1958). The spawning act itself is very rapid, lasting less than a second, as the male flaps the caudal fin against the female, before moving the tail to the other side, and raising its paired fins, causing the male to move backwards, during which time the urogenital region of the male is pressed against the female (Fabricius & Gustafson, 1958) (Figure 1.2). Upon being hit by the male, the female sheds a portion of eggs, and the male moves its caudal fin under the female, mixing sperm and eggs together (Fabricius & Gustafson, 1958). These spawning acts are repeated at short intervals, then followed by a period of rest before commencing again (Fabricius & Gustafson, 1958). Individual fish can actively participate in spawning over several days (Clark, 1950).

Figure 1.2 Two pike spawning in the River Frome on 28 March 2001. The female (foreground) is Pike K (Table 2.2).

1.3 FEEDING ECOLOGY AND SPATIAL BEHAVIOUR

Pike are ambush predators, being morphologically adapted to sprint rather than sustained swimming (*op. cit.*). Savino & Stein (1989a; 1989b) found that whilst another piscivorous fish, the largemouth bass *Micropterus salmoides* (Lacapède) switched predatory tactics from searching to ambushing depending upon vegetation density and prey species, pike always employed an ambush mode of predation.

Adult pike are primarily piscivorous *e.g.* Frost (1954), Diana (1979), with prey size increasing with the size of the predator (Mann, 1982). In habitats where prey fish are limited invertebrates can form a significant proportion of the diet (Chapman & Mackay, 1990; Beaudoin *et al.*, 1999), although pike lack the necessary enzymes to digest chitin (Filleul & Le Louarn, 1998). In energetic terms, the contribution of invertebrates to the diet of adult pike in the River

Frome is minor, with fish constituting > 99% of stomach content samples by weight (Mann, 1982).

The stomach contents of pike from the River Frome revealed that young pike (< 4 years of age) ate mostly dace *Leuciscus leuciscus* (L.), gudgeon *Gobio gobio* (L.), minnow *Phoxinus phoxinus* (L.), stone loach *Barbatula barbatula* (L.) and migrating smolts of Atlantic salmon *Salmo salar* L. Larger pike were reported as eating mainly dace, trout *Salmo trutta* L., grayling *Thymallus thymallus* L., eel *Anguilla anguilla* L. and small pike (Mann, 1982).

Although the size of prey selected by pike increases with increasing size of the predator, large pike do take small prey on occasion (Mann, 1976; 1982). Large prey, relative to the size of the pike can be taken, including prey that is too large to swallow completely, and pike can be caught with the tails of their prey still protruding from their mouths (Mann, 1976). In addition to fish, other vertebrates may sometimes be taken by large pike, including frogs, waterfowl and aquatic mammals (*e.g.* Larsen, 1966; Sammons *et al.*, 1994).

Despite their capacity for consuming large food items, prey selected by pike are often below the optimum size predicted from energy/time budgets (Nilsson & Brönmark, 1999). Handling time increases with prey size, as does the associated risk of falling victim to cannibalistic attack or kleptoparasitism whilst handling prey (Nilsson & Brönmark, 1999). Roach have been shown to be preferred over deeper bodied bream *Abramis brama* (L.), handling time being longer for bream than for roach of the same length (Nilsson & Brönmark, 2000). Body depth has been shown to be greater amongst crucian carp *Carassius carassius* (L.) in the presence of pike than amongst predator-free populations; change in body depth being a predator-induced phenotypical change in this species, reducing the risk of predation (Brönmark & Miner, 1992; Pettersson *et al.*, 2000).

Pike are versatile predators and flexibility in feeding is shown by responses to changes in abundance, or availability, of prey. For example, in the River Frome, salmon smolts are preyed on in the spring, and young adult sea trout, returning to the river to breed, in September (Mann, 1982). In Windermere, Arctic charr *Salvelinus alpinus* (L.) were found to be of particular importance to the diet of pike during November and December, when populations of charr enter the shallows to spawn (Frost, 1954).

Perch *Perca fluviatilis* L. is a major prey species for pike in Windermere (Frost, 1954), however, in 1976, disease killed *ca.* 98% of adult perch in the lake (Kipling, 1984). Pike captured later in the year had still shown good growth, and it was assumed that the pike had switched to a diet consisting mainly of trout (Kipling, 1984). Smelt *Osmerus eperlanus* L. and leopard frogs *Rana pipiens* Schreber have also been named as seasonally important dietary components for some pike populations (Ivanova, 1969; Sammons *et al.*, 1994).

Individual specialisation for particular prey occurs, with Jepsen *et al.* (2000) reporting that, after spawning, a few 'specialist' pike appeared to move to areas were they could prey on sea trout smolts, whilst the majority of pike returned to their usual habitats to forage on available prey. Based on stomach content analysis and stable isotope analysis, Beaudoin *et al.* (1999) reported that some individual pike appeared to specialise on an invertebrate diet whereas others were piscivorous.

Pike can have significant effects on the prey fish communities in the areas that they occupy, both in terms of species composition and distribution. He and

Kitchell (1990) studied the fish community in a one hectare lake, with a small inflow channel, collecting groundwater, and an outflow channel connecting to a nearby stream. After a year of pre-manipulation study, pike were introduced to the lake. Decrease of prey fish biomass occurred, due to both emigration and direct consumption, and the mean size of species most vulnerable to predation was also seen to decline (He & Kitchell, 1990).

The effects of pike on prey fish communities have been exploited in order to 'biomanipulate' eutrophic lake systems. The introduction and maintenance of a stock of pike in such a lake can effect changes in the distribution and behaviour of zooplanktivorous fishes, reducing the predation pressure on zooplankton and resulting in increased grazing of phytoplankton, leading to an improvement in water quality (Wysujack, 2001).

The timing of pike feeding and the ecological significance of periods of activity amongst pike are discussed in Chapter 5.

Size classes of pike appear to be ecologically segregated. Grimm and Klinge (1996) proposed that within pike populations a number of length classes could be discriminated according to foraging behaviour and distribution, with these length classes representing ecological subgroups. The proposed groups were:

1) 8 – 15 cm pike: feeding on invertebrates with some piscivory, inhabiting areas of dense emergent vegetation. These pike are capable of occupying areas that are inaccessible to older pike.
2) 15 – 35 cm: Inhabitants of vegetated areas where larger piscivorous pike are also present.

3) Up to 54 cm: Inhabitants of restricted home ranges closely associated with areas of emergent vegetation, submerged vegetation and plants with floating leaves.
4) Up to 44 cm: A subclass that in the presence of larger individuals is strictly tied to vegetation; within reed beds.
5) > 53 cm: no longer strictly bound to vegetation and can wander freely.

Chapman & Mackay (1984a) found that large pike (> 25 cm) were more often found in deeper, unvegetated waters and at macrophyte/open water interfaces than small pike (< 25 cm). This was thought to be due to differences in diet between the size classes, and differences in vulnerability to predatory attack. Similarly, Bregazzi and Kennedy (1980) reported that in Slapton Ley, Devon, UK, small pike were always caught in or near macrophytes and reeds and suggested that the movement of small pike may be somewhat confined.

In lakes, pike are usually found in shallow, vegetated areas, close to shore (Diana *et al.*, 1977; Chapman & Mackay, 1984; Cook & Bergersen, 1988). Pike in rivers have been described as occurring in the river margins and backwaters (Mann, 1976; 1980), and in slow flowing areas (Lamouroux *et al.*, 1999) with bank cover available (Paragamian, 1976). Habitat selection amongst pike is discussed further in Chapters 6, 7 and 8.

When describing the spatial behaviour of animals, the terms home range and territory are frequently used, home range being 'an area repeatedly traversed by an animal' whilst a territory is 'an area defended by an animal' (Kenward, 2001). These terms are not synonymous. Pike are generally not considered to be territorial, although size dependent interference can occur between individuals

(Eklöv & Diehl, 1994). Larsen (1966) found that several pike could be caught together in small areas, with up to four pike of the same size being caught in 30 – 40 m^2 areas of Danish trout streams, although two or more pike of different sizes were never caught at the same time in the same locality. Telemetry studies have revealed that the spatial behaviour of lacustrine pike is highly variable, both within and between populations (Jepsen *et al.*, 2001). Whilst some individuals stay within a restricted area, others move between two or three favoured areas, or wander more freely throughout the lake (Jepsen *et al.*, 2001).

Riverine pike have been shown to be capable of extensive movements, with upstream spawning migrations of 7.7 ± 6.67 km (mean ± S.D.) reported for pike in the Ourthe and Amblève rivers (Ovidio & Philippart, 2002), whilst movements > 100 km, between summer and winter locations, occurred in an Alaskan wetland area (Burkholder & Bernard, 1994). These reports contrast with the results of a mark-recapture study, based in the River Frome, UK, during which most jaw tagged pike remained within the 3 km of study area after release (Mann, 1980). Some pike however dispersed more widely, leading to the proposal that the pike population consisted of both static and mobile components, with the former comprising *ca.* 74% of the population (Mann, 1980). The spatial behaviour of pike is discussed further in Chapter 4.

1.4 FISHERIES

Pike have been valued as a food resource for many centuries (Maitland & Campbell, 1992; Mann, 1996) and commercial pike fisheries exist in several countries, principally in the former Soviet Union, Finland and Canada, with several thousand tonnes being caught annually in each of these countries between

1974 and 1984 (Raat, 1988). Annual catches of 300 to 500 tonnes were reported for Turkey, Germany, Poland and Sweden over the same period (Raat, 1988). The species is also popular with sport anglers and whilst pike caught in North America or mainland Europe may be destined for the table, in the UK most pike are captured on a catch-and-release basis.

In salmonid fisheries, the pike is often unwelcome and culling of pike takes place to reduce predation pressure on the fisheries' target species. Care must be taken however in order that such culls do not become counterproductive. Small pike are often significant predators on salmonids, with cannibalistic larger pike impacting upon the population size of smaller pike. Consequently, selectively removing large pike can remove the predation pressure on smaller pike and actually lead to an increase in the consumption of salmonids (Mann, 1982).

1.5 SUMMARY

1) Pike are a widely distributed species found in a variety of freshwater (and brackish marine) habitats.

2) Pike are piscivorous ambush predators, adaptations for this mode of predation being visible in their body form.

3) Pike spawn in the springtime, in areas of plentiful vegetation. In the River Frome, spawning occurs in side channels, or in the main river itself.

4) After a period of time spent living in the spawning ground, most pike move to new habitats.

5) Most pike in the River Frome are sexually mature by the end of their second year of life, *ca.* $L_F = 45$ cm.

6) Spawning migrations, together with spawning and natal site fidelity have been documented.

7) Ecological segregation of size classes occurs, with smaller pike being closely associated with aquatic vegetation, whilst larger pike are thought to be able to 'wander more freely.'

8) Pike spatial behaviour varies both within and between populations.

9) Although it is a commercially important species in some parts of the world, most UK captures of pike occur during catch-and-release angling, or during directed culls.

CHAPTER 2

Radio tracking pike in the River Frome: General methods

This chapter contains detailed descriptions of the methods used to radio tag and track pike in the River Frome, together with the methods used to record information on habitat. A short description of the method used to internally implant radio tags into pike was included in Beaumont, Cresswell, Hodder, Masters & Welton (2002a). A method of externally attaching miniature radio tags to small pike was developed during the study. This is described below, and is the basis of an article which is currently in press (Beaumont & Masters, in press) (Appendix 3). Ethical considerations associated with the external attachment of electronic tags to fish have been discussed in a Brief Communication (Masters & Beaumont, submitted) (Appendix 4). The development of a protocol for determining seasonal home ranges of pike has been described in Hodder, Masters, Beaumont, Welton, Kenward, Pinder & Gozlan (submitted).

2.1 STUDY AREA

2.1.1 Description of Study Area

The study was based in the River Frome, Dorset, UK, a largely unmodified groundwater fed chalk stream. The river has a meandering main channel and is free to burst its banks under high flows, when water inundates the surrounding meadows. The main study area (SY 8686 and SY 8786), consisted of > 2000 m of river channel (mean width = 14 m), flowing west to east. The meadows surrounding the river form part of a former water meadow system, and as such, several artificial drainage ditches connect with the main river. The East Stoke Millstream also lies within the main study area. The East Stoke gauging weir, at the head of the Weirpool formed a potential barrier to movement, but there were no barriers downstream of the main study area (locations within the river are referred to extensively in Chapter 4, and a map of the main study area is therefore provided as Figure 4.1).

Submerged vegetation in the river consisted mainly of *Ranunculus spp.* and *Potamogeton spp.* Emergent vegetation (*Phragmites australis* (Cav.) and *Glyceria maxima* (Hartm.)) was sparse and mainly confined to the banks. Land use alongside the river consisted mostly of grazed pasture with some wetland, and there was little outstream shade.

In addition to pike, fish species commonly found in the river included representatives of the Salmonidae (Atlantic salmon, brown and sea trout), Thymallidae (grayling), Cyprinidae (minnow, dace, roach *Rutilus rutilus* (L.), Balitoridae (stone loach), Anguillidae (eel) Cottidae (bullhead *Cottus gobio* L.), Pleuronectidae (flounder *Platichthys flesus* (L.)) Gasterosteidae (Three-spined stickleback *Gasterosteus aculeatus* L.) and Mugilidae (thin lipped mullet *Liza ramada* (Risso)) (Clough, 1998).

Environmental information was recorded at the East Stoke weir. Discharge was recorded every fifteen minutes, this data being supplied by the UK Environment Agency. Water temperature was also recorded every fifteen minutes. Daily mean discharges and temperatures were calculated from quarter-hourly records.

2.1.2 Mapping the Study Area

In order to accurately record fish location information, a reliable method of recording fish position was required. A previous radio tracking study conducted in the River Frome used distances to landmarks along the riverbank to describe fish locations (Clough, 1998), however, in order to make best use of current methods for analysing biological location data, a system for recording fish locations as National Grid Coordinates was required. An attempt was made to use hand-held Global Positioning System (GPS) units, which estimate their location based on the time delay in receipt of signals from different satellites (Kenward, 2001), but the error in positioning using the GPS units was found to be larger than the width of the river, and more accurate locations could be recorded simply by taking a map into the field.

A map of the river was created for use in a Geographical Information System (ArcView GIS 3.2, ESRI Inc, Redlands, California). To create the map, the riverbanks, tributaries and adjoining drainage ditches were digitised from aerial photographs of the river, supplied by the Environment Agency. One thousand metre, one hundred metre and ten metre grids were overlaid on the map, and landmarks such as bridges and fences also added.

Over 21 km of river channel and over 7 km of millstreams and tributaries were digitised, running from East Burton (SY 81 87) to Swineham Point (SY 84 87), where the river flows into Poole Harbour. Whilst all tagging was planned to take place in the vicinity of the CEH River Laboratory at East Stoke, upstream and downstream areas were incorporated into the map, to avoiding the need for further digitising at a later stage, should pike move out of the main study area.

After digitising, ground-truthing of the map took place by walking the banks of the river and comparing the actual shape of the river with that on the map. Corrections to the map were made where necessary. Further corrections were made as required during the course of the study, for example following bank erosion that occurred during severe winter flooding.

Sections of the map, overlaid with a 10 m grid, were printed, laminated and bound together, to take into the field in order to record fish positions. In practice it was difficult to record coordinates accurately in straight sections of river. The locations of marker posts, placed along the riverbank at 50 m intervals, were added to the map, to allow fish positions to be determined relative to a point for which the coordinates were known; the posts originally marked the location of transects conducted to estimate the proportion of various habitat types within the river.

2.2 PIKE CAPTURE

In order to tag pike, with either conventional or radio tags, it is first necessary to catch the fish. The two capture methods used during this study were angling and electric fishing.

2.2.1 Angling

Angling had the advantage that a minimum of preparation, equipment and personnel was needed, although capture of pike relied upon the anglers' skill and also upon the hunger state and behaviour of the pike. On several occasions, when attempting to recapture radio tagged pike, experienced anglers failed to catch the fish, even when the location of the pike was exactly known.

Experienced anglers from CEH Dorset volunteered to help catch pike for this project. All anglers held UK fishing licences, and the Environment Agency gave permission for anglers to continue fishing for pike and bait throughout the river coarse fishing close season (15 March to 16 June), providing measures were taken to avoid catching salmon (*i.e.* only live and dead fish baits could be used during the close season).

Angling for pike usually involved the use of dead fish bait, although lures and live bait were used on occasion. Live bait is considered to be the most efficient method of angling for pike; however ethical considerations meant that its use was generally avoided. Only fish caught within the River Frome were used as live bait. Barbless hooks were used to avoid causing excessive damage to the pike. Additionally, anglers were encouraged to use single hooks rather than trebles, the reason being that the location of hooking appears to be a major influence on post-capture survival, with deeply hooked fish being subject to greater mortality (Pottinger, 1995). Deep hooking of pike seemed more common when using paired treble hooks than when using single hooks. Also the time taken to unhook a pike could be much longer when using trebles. Artificial lures are often balanced for use with a pair of treble hooks, therefore the use of lures was avoided, although they were used on occasion, to cover areas where it was impractical to fish with dead bait.

Bait type as well as hook type can also affect post-capture mortality rates (Pottinger, 1995), although this is likely to be associated with the likelihood of deep hooking. Lures present a moving target and are therefore taken at speed by pike (pers. obs.), seemingly increasing the chances of deep hooking. Live bait can also be taken quickly, however pike strike across the body of the bait and subsequently manipulate the prey before swallowing, so when the live bait is on a single hook, through the jaw, pike are not necessarily hooked when first seizing the prey, and the angler needs to wait for the bait to be turned before striking. Dead baits could be taken quickly, or more gently, and the use of a single hook again made deep hooking less likely.

Increased consumption of oxygen during exercise leads to physiological processes in fish that enhance oxygen transport (Ferguson & Tufts, 1992). Even brief exposure to air during this period can lead to increased mortality in angled fish (Ferguson & Tufts, 1992), therefore, pike were returned to the water as quickly as possible following capture, and held in carp sacks (large perforated bags with a zip closure, designed for retaining large fish) prior to tagging. When handling pike, the head of the fish was often covered with wet cloth. This had the apparent effect of calming the fish, making it easier to handle and also potentially reducing the physiological stress experienced by the animal.

2.2.2 Electric Fishing

Electric fishing involves generating an electrical field in the water, which stimulates the nervous system of fishes and induces muscular reaction, drawing fish in to the anode and resulting in immobilisation (Beaumont *et al.* 2002b). To minimise stress to the fish, electric fishing was conducted adhering to the guidelines for best practice, given by Beaumont *et al.* (2002b). Electric fishing required a team of CEH staff members and heavy equipment and therefore needed a greater degree of organisation and planning than angling. In addition it was necessary to obtain the written consent of the Environment Agency before fishing, by completing and submitting form FR2 ‘application to use fishing instruments (other than rod and line) and/or remove fish from inland waters.' English Nature also had to give their approval prior to electric fishing, due to the area around the CEH River Laboratory being designated a Site of Special Scientific Interest. An advantage of electric fishing is that, unlike angling, capture of pike is independent of the pike's hunger state.

2.2.3 The ethics of fish capture

Fish capture is likely to act as a stressor. For ethical reasons, it was important to reduce stress to the animals as much as possible, and minimising stress to the animals also reduces the impact of capture on the subsequent behaviour. Angling, electric fishing and handling of fish can all lead to physiological stress and/or physical damage. Methods of reducing stress to fish during and after capture are detailed in Beaumont *et al.* (2002b), while Pottinger (1995) provides a literature review on fish welfare, focussing on areas associated with angling, including pain perception. General issues relating to fish welfare have been discussed in a recent briefing paper produced by the Fisheries Society of the British Isles (FSBI, 2002). All possible efforts were made to minimise stress in this study.

2.3 DATA RECORDED FROM CAPTURED PIKE

The fork lengths, weights and sexes of captured pike were recorded. Fork length was measured using a retractable tape measure or a measuring board, and weight using a spring balance. The sex of pike was determined by external examination of the urogenital region (Casselman, 1974). Female pike possess many longitudinal folds between the urogenital pore and the anus, with the urogenital region being pink or red in colour, protruding slightly from the body (Casselman, 1974). In males, there is no prominent folding between the two openings, and the colouration is the same light colour as the surrounding skin (Casselman, 1974). During the spawning period, the extrusion of eggs or milt was used to confirm sex.

Scales were removed from the upper flank of the pike, between the dorsal fin and the lateral line, and pike were subsequently aged through examination of these scales. Seasonal patterns of growth are revealed in fish scales through the patterns in the spacing of circuli (concentric ridges running around the scale), circuli being closely spaced during periods of slow growth (winter) and widely spaced during periods of rapid growth (summer) (Tesch, 1968). Pike scales however are difficult to read, possessing many false checks (areas where banding closes and opens up again) (Bregazzi & Kennedy, 1980; Wright 1990). Annual checks in growth can also be difficult to see in older or slow growing pike (Mann, 1980; Mann & Beaumont, 1990). Opercular bones and cleithra (bones in the pectoral girdle) can also be used to estimate the age of pike, however the pike must be killed in order to access these structures (Casselman, 1996).

2.4 EXTERNAL MARKER TAGS

When possible, all pike captured during the study were fitted with individually numbered, external identification tags. Each tag carried a unique number allowing the individual to be identified when recaptured. Radio tagged pike were also fitted with these numbered tags to allow identification of the fish should it be caught by an angler. Two types of numbered tag were used during the study, jaw tags and smolt tags.

Jaw tags have been widely used in studies of pike populations *e.g.* Bregazzi and Kennedy (1980), Carbine and Applegate (1948), Kipling and Frost (1970), Mann (1980; 1985) and Wright (1990). The jaw tag is a flat, numbered, metal strip which is fixed around the maxilla of the pike, in front of a ligament, preventing the tag from moving backwards and slipping off the maxilla (Kipling & Le Cren, 1984). However, these tags were difficult to attach to pike, unless the pike had been anaesthetised. Also, due to the necessity of working in close proximity to the pike's teeth, there was a risk of injury to the person tagging. Whilst this has been a widely used method of tagging pike, there is some evidence that tagging in this way may lead to a subsequent reduction in growth rate. Warner (1971) found that recaptured, jaw tagged, female landlocked Atlantic salmon had grown significantly less than untagged females of identical ages and cycles, presumably through the tag interfering with normal feeding activity, although no such effect was noted in males.

Early in the project, jaw tags ceased to be used, except on anaesthetised pike, and a switch was made to the use of 'smolt' tags. These tags consisted of an individually numbered plastic flag (0.5 x 1.4 cm), which was attached to the dorsal fin of the pike by means of thin line (Figure 2.1). A small puncture was made at the base of the dorsal fin, behind the second fin ray and the attachment line passed through this hole and then securely tied. The attachment lines were not pulled tight to the fin, so as to avoid abrading the fin ray. This tag was simpler to attach than the jaw tag, consequently reducing the amount of time that the pike had to be held out of the water, which served to reduce stress to the fish.

Figure 2.1 An individually identifiable 'smolt' tag attached to the dorsal fin of a pike.

Floy internal anchor tags have also been commonly used during studies of pike *e.g.* Makowecki (1973) and Müller (1986), and have been reported as having no effect on growth rate (Gurtin *et al.*, 1999). These tags consist of a barbed plastic cord, which is fired into the flesh of the fish, using a tagging gun. The plastic cord anchors an external, numbered tag. Floy tags were not used during this study, as specialised tagging equipment would have been needed in the field on each occasion, and this equipment was not available. The amount of equipment needed to attach smolt tags to pike was minimal, and these tags were therefore issued to volunteer anglers during the course of the study.

2.5 FIN CLIPS AND PHOTOGRAPHS

V-shaped fin clips were taken from the right pelvic fin of captured pike, to allowing pike to be identified as recaptures, even if the external marker tag had been shed.

Photographs were taken of both sides of the pike, potentially allowing recaptured individuals to be individually identified, in the absence of an external marker tag, by using the unique pattern of natural markings on the fish (Fickling, 1982).

2.6 RADIO TAGGING

2.6.1 Acoustic and radio telemetry

The two types of telemetry used in studies of fishes are acoustic telemetry and radio telemetry, with transmitters and batteries being sealed into waterproof tags in both cases. In acoustic telemetry, transmitters send out an acoustic signal, which is usually ultrasonic, and can be detected by hydrophones. The angle that the signal is coming from can be determined by listening for the loudest signal received by a directional hydrophone. Distance to the tag can subsequently be determined by triangulation. Radio telemetry is similar, with tags emitting radio signals that can be detected by suitable receivers. Directional antennae are used to establish the angle to the tag, and triangulation is used to work out distance.

Radio telemetry was selected as the appropriate technique to use in this study. As fish were to be tracked in flowing water, signals from acoustic transmitters may have been masked by environmental noise. Acoustic tracking would also have involved repeatedly placing a hydrophone in the water, whereas with radio telemetry no equipment needs to be submerged, making the tracking process simpler. Aquatic vegetation is known to strongly attenuate acoustic signals (Crossman, 1977), making radio telemetry a more suitable technique for areas with dense submerged vegetation such as the River Frome in summer. One disadvantage of radio telemetry is that it is ineffective in high conductivity water, however, conductivity of water in the River Frome was sufficiently low to allow radio telemetry to be used (mean ± S.D. = 547 ± 61 μS cm^{-1} in 2000, CEH unpublished data). The range at which a signal can be detected from a radio transmitter is dependent upon depth (unlike acoustic telemetry) (Mackay & Craig, 1983), but the River Frome was shallow enough to allow radio telemetry to be used (all ≤ *ca.* 5 m during winter flooding).

2.6.2 Radio tags

The main type of tag used in the study was the TW-5 (Biotrack Ltd., Wareham, BH20 5AX, UK) (Figure 2.2) although Biotrack TW-4 (Figure 2.4) transmitters were also used, to a lesser extent (Table 2.1). Each tag transmitted on a unique frequency in the 173 MHz band. In addition to simple radio location, the TW-5 tag could also be used to determine occasions when pike were active, as each tag contained an omni-directional motion sensing switch (Beaumont *et al.*, 2002a). Vigorous activity by the pike caused the switch to close and the tag to transmit at a faster pulse rate. The battery life of the tag was therefore dependent on the amount of time the tag spent transmitting at the more rapid pulse rate. In practice, operational life of the TW-5 tag ranged between 18 months and > two years. TW-5 tags were surgically implanted into the peritoneal cavity of the fish (Appendices 1 & 2), whilst TW-4 tags were attached externally (Appendices 1, 3 & 4).

Table 2.1 Specifications of Biotrack TW-5 and TW-4 radio tags.

Radio tag	TW-5	TW-4
Length	80 mm	17 mm
Width / Diameter	16 mm	9 mm
Weight in air	22 g	2.3 g
Weight in water	7 g	0.9 g
Antenna	internal coil	90 mm external
Battery	2/3 AA lithium thionyl-chloride	Hg13
Tag life	18 months to > 2 years	9 to 11 weeks

Figure 2.2 The Biotrack TW-5 radio tag.

2.6.3 The method used to implant TW-5 radio tags into pike

Surgical implantation into the peritoneal cavity was chosen as the method by which pike would be equipped with TW-5 radio tags (Appendix 1), and after the tagging protocol had been developed, practiced and refined (Appendix 2) the operations proceeded, under Home Office licence, in the manner described below.

Two people were needed to internally implant a tag into a pike, the surgeon and an assistant. The surgeon wore sterile gloves and had to remain 'clean' throughout the procedure. The assistant's duties were to handle the fish, check that maintenance anaesthesia was flowing over the gills, administer an antibiotic injection, and record the time the pike spent in anaesthesia, on the operating table and in recovery. Pike were tagged on the riverbank with all necessary equipment being carried to the pike's location rather than increase the stress to the animal by moving the fish to the equipment.

Between capture and radio tagging, pike were held in carp sacks in the river; each bag being tethered to the bank, with the pike facing upstream inside the bag.

To ensure a suitable tag weight to fish weight ratio, and also to ensure that the physical dimensions of the tag could be accommodated within the peritoneal cavity, only pike of > 50 cm fork length were implanted with TW-5 tags. Mann (1980), based on a sample of 50 pike (length range 20 cm to 94 cm) caught between 1973 and 1977, published a length-weight relationship for River Frome pike. This being:

$$Log_{10}\, W = 3.1129\, Log_{10}\, L - 5.4113$$

where W = weight (g) and L = fork length (mm). Using this equation, a 50 cm long pike would weigh around 978 g, therefore the weight of the TW-5 tag in water (= 7 g) would typically be < 1% of the weight of a 50 cm fish. Data from electric fishing surveys conducted in spring 2003 confirmed that the length-weight relationship published by Mann (1980) could still be applied to pike in the River Frome (CEH unpublished data).

Setting a length limit for tagging rather than a weight limit made it easier for anglers to know when they had caught a pike large enough to radio tag, as not all anglers carried weighing scales. Pike were subsequently weighed as part of the tagging procedure. The smallest pike fitted with an internally implanted tag weighed 1400 g (Pike X, Table 2.2), so in this case the tag weight in water was 0.5% of the wet weight of the fish.

A summary of the method used to internally implant tags into pike appeared in Beaumont *et al.* (2002a). Figure 2.3 shows a tagging operation in progress and the method used is described in full below:

A large plastic bin was filled with river water, until the water level reached the 40 l mark that had previously been drawn on the bin. A small plastic bottle, containing 40 ml of 2-phenoxyethanol, measured in the laboratory, was then added to the 40 l of river water to produce a 1:1000 dilution of the anaesthetic. A second plastic bin was then filled with river water, to act as a recovery tank.

A 5 l plastic bottle was filled with river water, and 2.5 ml of 2-phenoxyethanol added, to form a 0.5:1000 dilution of anaesthetic. The bottle was then hung on a post, near a v-shaped operating table; a hose connecting the bottle to the operating table allowed maintenance anaesthetic to be run over the gills of the fish during surgery. A battery pump and air stone were used to aerate the maintenance solution.

The operating table was covered with damp tissue to avoid damaging the skin of the fish (Brattelid & Smith, 2000), and a sterile green cloth laid down onto a plastic lid alongside the table, within easy reach of the surgeon. The surgeon then put on sterile gloves, and the surgical equipment was laid out on the green cloth with the help of the assistant. Originally, plastic aprons were also worn, but these were discarded as they blew around even in light breezes, getting in the surgeon's way. The surgeon wore a cap during the operations, to prevent dander from falling onto the fish.

Having ensured that all the necessary preparations had been made, the assistant retrieved the pike from the river, weighed the fish, and then placed the pike into the bin containing anaesthetic. When the pike had reached a surgical level of anaesthesia, *i.e.* it no longer responded to external stimuli (Ross & Ross, 1999), the assistant moved the pike to the v-shaped table, turned on the tap on the bottle of 0.5:1000 anaesthetic solution and ensured that the solution was flowing over the gills of the pike. The assistant then injected the antibiotic Baytril into the caudal peduncle of the pike, at a dose of 0.2 ml 1000 g^{-1} fish weight, after having made sure the surgeon's hands were clear of the area. On particularly warm days, or in bright sunshine, the body of the pike was covered with the wet carp sack for protection, leaving enough skin clear for the surgeon to operate.

Figure 2.3 Radio tag implantation being conducted on Pike W on 27 August 2001, showing a) bottle containing aerated maintenance anaesthetic, b) hose for trickling anaesthetic over the gills of the pike c) wet carp sack covering the pike's head d) incision site e) v-shaped table

The surgeon removed enough scales from a small area anterior to and slightly above the left pelvic fin to accommodate the length of the planned incision. The descaled incision area was then cleaned using a specialised fish antiseptic (Tamodine^{TM}, Vetark Professional, Winchester, UK) and wiped with a sterile swab. A scalpel (15T blade) was used to make an incision through the body wall in the cleaned area (approximately 1 cm higher than the pelvic fin, with the posterior end of the incision terminating 2 cm to 3 cm in front of the pelvic fin), the incision being just long enough to accommodate the tag. The tag was gently pushed through the incision and forwards into the body cavity, taking care not to damage the viscera. The wound was then closed using absorbable sutures (Appendix 2) and either a 25 mm or 35 mm curved cutting needle, depending upon the size of pike being tagged. Two to three separate stitches were usually sufficient to close the wound. When suturing, needle holders were used which also included cutting blades ('Gillies' (Kirk, 1978)), allowing the needle to be manipulated and the thread cut using the same instrument. The closed wound was covered with a layer of commercial cyanoacrylate gel adhesive in order to both secure the sutures and provide a watertight seal to the wound. The pike was then transferred to the recovery bin and watched until equilibrium was regained and swimming movements began. After recovery, the pike was released back into the river at, or near, the site of capture, this being considered less stressful than a more prolonged period of post-operative captivity (Crossman, 1977).

During the tagging procedure, an external tag (either jaw or fin) was attached to the pike, a fin clip taken and scales taken from the flank for ageing (those removed from the incision area were discarded). The fork length was also measured and the pike sexed.

In 2002, permission was received from the Home Office for re-tagging of pike to take place. In the larger pike, a second tag could be implanted when the battery of the first tag was running down, without exceeding recommended tag weight to fish weight ratios or excessively filling the peritoneal cavity. This allowed for continued monitoring of the same individual, and was classed as 'continued' rather than 're-use' (re-use of experimental animals not being permitted under the 1986 Act). When re-tagging pike, the incision was made on the opposite side of the fish to the original incision. No attempt was made to remove the original tag, as this would have required longer incisions, prolonged surgery time, and may have required connective tissue to have been cut, had the tag become encapsulated.

2.6.4 Details of pike implanted with TW-5 radio tags

Between May 2000 and July 2002, twenty-five pike ($L_F > 50$ cm) captured by angling or electric fishing, between the Weirpool (SY 386736 86838) and Rushton Pool (SY 387760 86500)(Figure 4.1), were implanted with TW-5 transmitters, using the method described above (Table 2.2). As more pike were captured, the number of radio tagged fish available to be tracked increased. Each tag operated on a unique frequency, allowing individual pike to be identified (Table 2.2). For ease of referral, each pike was also assigned a letter, in alphabetical order, so the first pike tagged became Pike A, the second, Pike B *etc*. Each pike was also given a name, starting with the appropriate letter of the alphabet. Naming pike facilitated communication amongst fieldworkers, as it was far easier for trackers to remember and refer to names than tag frequencies. No Pike D existed, to avoid confusion with dace that were radio tracked in the river during 2000; all dace being identified by names beginning with D, in addition to their individual tag frequency. Once all letters of the alphabet had been used, naming started at A again, and the shorthand for the pike became the first two or three letters of the name. Pike were tagged either by the author, or by one of two members of CEH staff qualified to carry out the procedure. The mean operating time (between removal from initial anaesthesia and placement into the recovery bin) was 9 ± 3 ($\pm$ S.D.) minutes (range: 5 minutes to 14 minutes)(Table 2.2). Surgery should ideally proceed as quickly as possible, and whilst shorter operating times would have been desirable, post-operative survival rates were nevertheless extremely high (Chapter 3).

Table 2.2 Pike captured and implanted with TW-5 radio tags (capture method A = angling, EF = electric fishing). * indicates retagging.

Pike	Sex	Radio Tag Frequency MHz	Date of Tagging	Capture Method	L_F cm	Weight kg	Age	Time in 2:PE (min)	Duration of Surgery (min)	Time to Recovery (min)	Capture location	Releaselocation
A	♀	173.746	24 May 00	EF	86	5.2	5+	6	14	18	SY 386740 86858	SY 386740 86858
B	♂	173.730	24 May 00	EF	71	3.6	4+	3	11	14	SY 387010 86960	SY 387010 86958
*B**		*173.930*	*15 Jul 02*	*A*	*78*	*4.0*	*6+*	*8*	*12*	-	*SY 386746 86865*	*same as capture*
C	♀	173.833	8 Jun 00	A	66	3.0	2+	4	12	9	SY 386978 86925	same as capture
E	♀	173.522	4 Jul 00	A	83	4.5	-	5	8	12	SY 387523 86543	SY 387518 86543
F[1]	♀	173.893	24 Jul 00	A	63	2.0	2+	-	-	15	SY 387494 86600	SY 387492 86600
G	♀	173.904	31 Jul 00	A	66	≈3.0	4+	4	7.5	12.5	SY 387493 86590	SY 387492 86590
H	♀	173.862	23 Aug 00	EF	60	1.7	4+	3	10	15	SY 387430 86594	SY 387431 86594
I	♂	173.972	16 Oct 00	A	87	>5.0	5+	5	5	20	SY 387055 86976	same as capture
J	♀	173.959	30 Nov 00	A	93	8.2	5+	13	6	17	SY 387757 86512	SY 387745 86524
K	♀	173.947	17 Jan 01	A	95	≈8.2	5+	6	6	14	SY 387248 86718	SY 387243 86710
L	♀	173.541	17 Jan 01	A	81	≈4.0	4+	4	7	7	SY 387287 86768	SY 387243 86710
*L**		*173.807 **	*5 Aug 02*	*A*	*79*	*4.2*	*5+*	-	-	-	*SY 387188 86915*	*same as capture*
M	♂	173.988	17 Jan 01	A	64	2.8	1+	4	11	22	SY 387287 86768	SY 387243 86710
N	♀	173.561	22 Feb 01	A	65	1.9	3+	6	6	24	SY 386840 86860	same as capture
O[2]	♀	173.581	1 May 01	EF	60	1.8	4	5	5	-	East Burton[2]	SY 386668 86660
T[2]	♂	173.571	1 May 01	EF	59	1.8	3	5	10	-	East Burton[2]	SY 386668 86660
P	♂	173.530	22 May 01	EF	58	1.7	4+	5	8	8	SY 387480 86540	SY 387495 86552
Q	♂	173.514	22 May 01	EF	69	3.2	4+	5	7	-	SY 387530 86630	SY 387525 86632
R	♂	173.591	22 May 01	EF	60	2.0	3+	7	13	-	SY 387758 86512	SY 387633 86480
V	♀	173.602	31 Jul 01	EF	52	1.7	2+	3	5	5	SY 387091 86982	SY 387091 86976
W	♀	173.505	27 Aug 01	A	63	1.8	4+	5	10	5	SY 387365 86600	same as capture
X	♀	173.591	4 Sep 01	A	54	1.4	3+	5	6	10	SY 387470 86529	same as capture
Y	♂	173.921	8 Nov 01	A	64	2.25	3+	12	9	-	SY 386820 86868	same as capture
Z	♂	173.900	23 Jan 01	EF	55	1.5	-	7	10	10	SY 387716 86600	SY 387720 86556
An	♂	173.561	5 Feb 02	EF	72	3.1	4+	5	11	20	SY 387005 86985	same as capture
Be	♂	173.941	15 Jul 02	A	66	2.8	scarred	5	8	22	SY 386823 86854	SY 386824 86855
Chr	♂	173.856	30 Jan 2003	EF	55.8	1.6	scarred	7	10	-	SY 387005 86985	same as capture
Et	♂	173.668	30 Jan 2003	EF	50.5	1.2	2+	6	5	-	SY 387005 86985	same as capture
Fr	♂	173.682	30 Jan 2003	EF	54.5	1.7	3+	-	6	12	SY 386891 86985	same as capture

1. Captured at East Burton (SY 820 870) on 28 March 2000, transferred to River Laboratory where it escaped from captivity. The pike was subsequently recaptured at East Stoke, radio tagged and released.
2. Captured at East Burton (SY 820 870) on 1 May 2001, and released at East Stoke on the same day, as part of a study on pike homing behaviour (Knight, 2001).

2.6.5 External attachment of TW-4 radio tags

Whilst the internal implantation of the TW-5 tag (Table 2.1) was suitable for pike of $L_F > 50$ cm, this tag could not be used on smaller pike. As implanted tags are permanent, there was also a need to develop a tagging method suitable for short-term studies. During the course of the present study, a method for externally attaching radio tags to small pike was developed, and field trials of the technique took place (Beaumont & Masters, in press) (Appendix 3). Although external attachment of tags is simpler than other methods of tag attachment (Appendix 1) it is still an invasive technique and ethical issues relating to the use of the method were reviewed by Masters and Beaumont (submitted), with particular emphasis on the application of chemical anaesthesia (Appendix 4).

Pike were equipped with external tags by attaching TW-4 transmitters (Table 2.1) to the caudal peduncle; examination of a pike cadaver having shown that needles and sutures could be passed through the fish above and below the spine without damaging major blood vessels or nerves. The spine was considered to be strong enough to prevent suture migration through the tissue and although the tail of the fish is used for propulsion, little flexing was thought to occur within the caudal peduncle itself (W.R.C. Beaumont, pers. comm.).

A mount for the tag was constructed from a rectangular plate of flexible acrylic film (0.75 mm thickness), cut to a length suitable for the size of pike to be tagged; the length of the rectangle being such that it would easily span the spine of the fish. The tag was glued to the acrylic film using cyanoacrylate adhesive. Two holes were then drilled in the acrylic to facilitate passage of needles and sutures when tagging and a neoprene pad was glued to the back. A backing-mount for the other side of the fish was constructed in a similar manner.

Immediately prior to tagging a 3/0 Polyglactin braided (coated VICRYL®) suture with 0.69mm diameter cutting needle was tied through each hole of the mount. These sutures were soluble and were expected to degrade within 8 to 12 weeks in UK river conditions (but see Appendix 2).

The tagging method consisted of sedating a pike in a 1:1000 dilution of 2-phenoxyethanol in river water, then removing enough scales from the caudal peduncle to allow easy passage of the needles. One needle was passed through the dorsal musculature of the caudal peduncle, and one through the ventral musculature, such that the tag would lie against the caudal peduncle with the antenna trailing beyond the caudal fin (Figure 2.4). Each needle was then pushed through the neoprene and holes of the backing-mount, and the backing-mount and tag drawn up tight against the body of the fish. The tag was secured by tying together the sutures and cyanoacrylate adhesive was applied to all knots. The area immediately surrounding the sutures was coated with a mixture of silicon grease and malachite green, to prevent fungal infection (Beaumont *et al.*, 1996).

Figure 2.4 Caudal peduncle area of pike showing position of externally mounted Biotrack TW-4 radio tag.

The method was used in the field on 31 July 2001, when two female pike (Pike S and Pike U in the alphabetical sequence being followed) were captured by electric fishing, and subsequently fitted with externally mounted TW-4 radio tags (Table 2.3). Tagging was rapid (Table 2.3) and after the procedure had been completed, pike were placed in river water to recover. After recovery the pike were released back into the river at, or near, the site of capture; quick release being thought to be less stressful than a period of post-operative recovery in captivity (Crossman, 1977).

Table 2.3 Details of two pike, captured by electric fishing in the River Frome, and fitted with externally mounted Biotrack TW-4 radio tags. A 1:1000 dilution of 2-phenoxyethanol in river water was used as anaesthetic.

Pike	S	U
Radio tag frequency MHz	173.906	173.975
Date of tagging	31 July 2001	31 July 2001
Sex	♀	♀
Fork length cm	52	44
Weight kg	1.2	1.8
Age	3+	2+
Time spent in anaesthetic (min)	4	3
Time taken for surgery (min)	3	3
Time to recovery (min)	7	not recorded
Capture location	SY 386890 86887	SY 386940 86900
Release location	SY 386890 86875	SY 386940 86895

Trials of the tagging method were not performed on captive pike, due to the difficulties previously encountered in keeping this species in captivity. The welfare of Pike S and Pike U was monitored through frequent radio tracking, combined with visual inspection from the bank when possible.

Pike U was located 18 times over around a 10 day period, before apparently moving upstream, into an area of the river which we could not access ('Hedgeman's Stream,' SY 86 86), > 1 km upstream of the release site of this fish. However it is also possible that transmitter failure occurred. During the time that Pike U was being actively followed it was seen on 4 occasions, and no apparent ill effects of the tag were noted.

Pike S was located over 70 times over an 8 week period. The tag was eventually recovered from the riverbed, having become detached from the fish. During the time the tag was attached, Pike S occupied around 120 m of river and was seen visually at least nine times, on one occasion being observed in the process of feeding on another fish. When disturbed, Pike S was often seen swimming away, and swimming appeared unaffected by the presence of the tag. Tag loss probably occurred after degradation of the sutures. Whilst the type of soluble suture used has been shown to persist when used to close incisions in internally tagged pike (Appendix 2), drag caused by the tag may have led to more rapid degradation in this instance.

2.7 RADIO TRACKING

2.7.1 Antennae and receivers

Once tagged fish had been released into the river, they were followed using a hand held radio receiver, connected to a 3-element Yagi antenna (Figure 2.5). Yagi antennae are directional, with the strongest signal being received when the antenna is pointed directly at the tag (Kenward, 2001). The Yagi antenna used (Biotrack Ltd., Wareham, BH20 5AX, UK) had flexible elements, which made it easier to carry and use than antennae with rigid elements. Occasionally an H-Adcock type antenna was also used, particularly when searching for lost fish, as this antenna could easily be mounted onto a long pole to give greater range. The H-Adcock gives a null signal when the two arms of the H are perpendicular to the direction of the tag (Kenward, 2001).

Figure 2.5 Pike being tracked by the author, using a Yaesu receiver and 3-element Yagi antenna.

The most commonly used receivers were the Biotrack BT-256 'Sika' and the Yaesu FT-290. The Biotrack BT-256 receiver was first delivered as a prototype in 2002, and represented a significant advance in technology over the Yaesu. The Biotrack receiver was very light, and had a digital signal strength meter, in addition to producing an audible beep when the radio signal was detected, the beep being louder when the Yagi antenna was pointing directly at the tag. Other desirable features were the large number of channels (n = 999) into which tag frequencies could be pre-set to facilitate tracking, and the search function, which made it was possible to scan through selected frequencies. Prior to the development of the Biotrack receiver, the Yaesu FT-290 had been the most commonly used receiver. The Yaesu receiver included an analogue signal strength meter and up to ten frequencies could be pre-programmed.

Regardless of the receiver used, the basic technique used to find the pike was the same. Once a signal was detected, the direction of the strongest signal was followed until the fieldworker was close to the fish. As the distance to the tag was reduced, the receiver was either de-tuned away from the tag frequency (Yaesu), or the gain was adjusted (Biotrack), to reduce the arc over which the signal could be detected. Once the position longitudinally along the river had been found, the tracker moved five or ten metres up or downstream in order to triangulate the position across the river. With experience, both the volume of the signal and the reading on the signal strength meter could be used as clues to the distance to the fish, with triangulation still being used to fix the fish position. Using the Yagi antenna in a horizontal position has previously been found to decrease the arc over which a signal was received (Clough, 1998). Using the antenna in this manner helped to pinpoint fish locations, although care had to be taken, as even slight turning of the wrist when holding the antenna led to an increase in the signal strength received, which could give the fieldworker a false impression of the fish position.

2.7.2 Information recorded at each fix

Each time a fish location (fix) was determined, a standardised set of data were recorded on a form on the riverbank (Appendix 5). Printed forms taken into the field were covered with matt laminate, waterproofing the form but allowing them to be marked in pencil. Upon returning to the laboratory, forms were photocopied to provide a permanent hard copy record, and the data entered into a spreadsheet. Writing on the laminated form could then be erased and the form reused. Data were recorded in the form of a numerical code (Appendix 5), for ease of subsequent transfer to spreadsheets. Whilst some of the data recorded was not used in subsequent analyses, the form was designed early in the study, to avoid *a priori* assumptions of factors that would be found to affect pike behaviour.

At each fix the date and time were recorded, taking care to include the year, to avoid confusion arising from tags transmitting for >12 months. Where necessary, time was converted to GMT for entry onto the spreadsheet.

The fish location was recorded as a 12-figure national grid coordinate, by referring to a map of the river, also taken into the field. For each fix, the fieldworker also recorded an estimate of the accuracy of that fix (based on signal strength), longitudinally (a) and laterally (b). Thus, a fix was recorded as a rectangle measuring 2a x 2b, centred on the most likely fish position, where both a and b were distances in metres. The fix was also recorded as a position relative to marker posts along the bank (*e.g.* 10 m downstream of post T1, 2 m off south bank). The exact locations of these marker posts were known, allowing the coordinates recorded in the field to be checked against those calculated from the written description of location. Recording both coordinates and location relative to marker posts was necessary, as errors could be made using either method of describing fish location. Describing the fix using both methods allowed mistakes to be identified and corrected.

The signal from each fish was listened to for five minutes, and the number of 'activity events' occurring during this time was recorded, where an 'activity event' was a train of rapid pulses from the tag. Recording activity in this way meant that no distinction could be made between an 'activity event' lasting, for example, 30 seconds and an event lasting 2 seconds, however, counting individual pulses in each event proved impossible and recording the duration of each 'activity event' was difficult when the pike was particularly active. More detailed data from the activity tags were due to be collected as part of a separate CEH study, using data loggers, however manual recording of 'activity events' during tracking was still thought to be of value. Output from the activity tag also allowed the fieldworker to record occasions when the pike was disturbed. If an 'activity event' occurred during a close approach by a fieldworker then the pike was assumed to have been disturbed.

In addition to recording activity events, a note was also made of whether signal strength varied during the five-minute period. Variation in signal strength can occur when the angle between the transmitter and the receiver changes (Kenward, 2001), giving another indication of movement. In practice, variation in the density of aquatic plants around the pike, caused by vegetation waving in the flow, was also seen to alter signal strength.

Details of the environment immediately surrounding the pike (within the rectangle formed by the accuracy estimates of fish position) were recorded whenever possible. During nighttime tracking, such detail could often not be distinguished.

Fish position was recorded as being south or north 'bank', 'midstream', 'bay', 'pool', 'flooded land' or 'ditch'. 'Bank' fixes were recorded when the pike was within 1 m of either the south or north bank, whilst 'bays' were defined as indentations in the bank of the river filled with slack water. 'Pools' were defined as areas of water containing eddies. 'Flooded land' fixes were recorded when pike left the confines of the river during periods of high water, and 'ditch' fixes were recorded when the pike was within one of the several drainage ditches running into the River Frome. 'Midstream' fixes were those in which the pike was > 1 m away from the bank, but not in a 'pool'.

The terms 'bay' and 'pool' were found to cause confusion, particularly amongst anglers, for whom the term 'pool' generally denotes an area of slower, or deeper, water within the river. The term 'bay' could also cause confusion, as the location was only to be recorded as 'bay' if there was no flow in the area. Consequently, the same indentation in the riverbank (*e.g.* a cattle drink) could be recorded as either a 'bay' or a 'pool', depending on the water level in the river at the time. Uniformity over the naming of different habitat types in the river was needed and so all fieldworkers had the various terms explained to them as part of their training.

Flow type for each fix was recorded as 'slack', 'glide', 'turbulent' or 'cascade'. Only the flow at the surface could be seen, as flow meter readings were not taken, to avoid disturbing the fish. Assigning flow types in this way was therefore somewhat subjective. There were no boulders in the study section, and the river flows through level meadows, therefore the 'turbulent' water category did not infer the intensity of turbulence that might be encountered in a higher gradient river. The only place where the 'cascade' flow type occurred was in the discharge from the East Stoke gauging weir. The flow type record for each fix offered an opportunity to check whether 'bays' had been correctly recorded. If anything other than 'slack' water was recorded as being in a 'bay', the fish position was either corrected to 'bank' or 'midstream', or changed to 'unknown'.

It was thought that pike may occupy interface zones, for example holding station in 'slack' water near to a 'glide'. The fieldworker was therefore asked to state whether the fish was within 1 m of another flow type, and to then state the nature of the nearby flow type.

For 'bank' fixes, a record was made of whether or not the bank was undercut.

Vegetation in the vicinity of the pike was categorised as 'submerged', 'emergent', 'floating' or 'overhanging'. 'Emergent' and 'floating' vegetation was described as either 'sparse' or 'dense'. 'Submerged' vegetation was initially recorded the same way, but was subsequently modified to include the relative height of the vegetation in the water column. 'Submerged' vegetation could not be recorded under turbid water conditions, such as often occurred during the winter. 'Overhanging' vegetation was recorded as 'sparse' or 'dense' within 0.5 m of the waters' surface, or 'sparse' or 'dense' > 0.5 m above the water's surface. Confusion could arise when 'emergent' vegetation also hung over the water. 'Emergent' vegetation was not recorded as 'overhanging', even when it shaded areas of river. Overhang came from terrestrial vegetation only. Originally, attempts were made to record whether the pike was in shade, however distinguishing between shade and reflection was difficult and consequently shading was only recorded early on in the study.

Space was provided on the form to record the type of substrate in the vicinity of the fix, though this was rarely possible, due to turbidity and vegetation cover.

Weather and wider environmental conditions were also recorded for each fix. The sky immediately above the fish location was described as being 'clear' or 'overcast', and the percentage cloud cover of the whole sky was estimated. Any precipitation was recorded and the wind speed was categorised as either 'still', 'breeze' or 'windy'. Water level in the river was subjectively assessed as being either 'low', 'normal' or 'in flood' and the water clarity described as 'very turbid', 'intermediate' or 'clear'.

2.7.3 Sampling strategies

Throughout the course of the study, different intensities of tracking were used; each designed to answer different questions about pike behaviour. Tracking is time consuming, and labour intensive and the *pilot*, *home range*, *24 h / diurnal* and *continuous* tracks described below were all conducted with the assistance of CEH members of staff, students and volunteers allowing for a greater volume of data to be collected than I could have achieved working independently. All fieldwork conformed with CEH Health and Safety policies.

Pilot track

A *pilot* track was conducted, during which the locations of Pike A and Pike B (Table 2.2) were determined once an hour, throughout the day and night, between 12 June 2000 and 17 June 2000; tracking being conducted from the riverbank as described above. The aim of the *pilot* track was to determine the minimum number of location records required to estimate a home range, the optimum sampling interval and the most appropriate times of day for sampling (Hodder *et al.*, submitted).

Home range tracks

Home range tracks were performed by recording fixes during the morning, middle of the day and evening, over a period of 13 days; the aim of these tracks being to describe the short-term home ranges of pike.

A protocol for *home range* tracking was developed (Hodder *et al.* submitted) with the analysis being conducted using RANGES V software (Kenward & Hodder, 1996). The procedure by which the *home range* tracking protocol was developed is described below.

The minimum number of location records required to describe the home range of a pike was determined using incremental analysis; this being 'a process of plotting the area of a home range as consecutive locations are added, to determine when sampling further locations will cause little change in area' (Kenward, 2001). The outer minimum convex polygon (MCP) was used to describe the home range during this incremental analysis, where the MCP is 'a polygon in which the linkage distances between peripheral locations sum to a minimum' (Kenward, 2001). As both Pike A and B remained within a relatively straight section of river during the *pilot* track, little of the area of the MCP fell outside of the river channel. Initially, data from the *pilot* track was examined, however incremental analysis showed that the range areas were still increasing at the end of the five-day tracking period, therefore a further period of tracking was conducted, during which locations were recorded three times a day, at dawn, dusk and midday. Sampling at these times provided records during periods when the *pilot* track had revealed the greatest mobility, and also gave the maximum sampling interval possible in daylight hours. Recording locations three times a day showed that range size stabilised after around 40 location records had been collected, therefore subsequent *home range* tracks took place over a 13-day period. Providing gaps in tracking were not too long, pike did not have to be tracked for 13 consecutive days, allowing for breaks in tracking over weekends.

Home range tracks were conducted on a seasonal basis and the number of fish tracked increased over time, as more pike were tagged (Table 2.4). *Home range* tracking was conducted from the riverbank along > 2000 m of the River Frome, from the East Stoke weir (SY 386736 86838) to Rushton Pool (SY 387765 86505) (Figure 4.1). An exception occurred during the March 2001 track, when restrictions were placed on fieldwork to control the spread of foot and mouth disease. At this time, we were not permitted to walk through the meadows adjacent to the river, and so tracking was conducted from an inflatable boat. The boat was rowed from the East Stoke weir, *ca.* 4000 m downstream to Holme Bridge, where it was recovered at a slipway (SY 389058 86676) and then driven back to East Stoke for the next survey. This was a more labour intensive method of tracking than was usually employed as two people were required for each of the three daily tracks, one to operate the radio receiver and one to control the boat.

24 h and diurnal tracks

The *pilot* track suggested a crepuscular pattern to pike activity (Hodder *et al.*, submitted) and a series of *24 h* tracks were planned, which would take place at approximately monthly intervals. During *24 h* tracks, hourly fixes were collected in order to study the diel pattern of movements and to examine whether the diel pattern changed with season. For health and safety reasons, lone fieldwork was not permitted at night, and so two fieldworkers were required during periods of darkness. After three *24 h* tracks had taken place (Table 2.5), it was decided that due to the relative inactivity of pike at night, and the demands placed on staff time, future tracking would commence at least one hour before sunrise and finish at least one hour after sunset. Subsequent tracks, during which hourly fixes were collected between dawn and dusk, are referred to as *diurnal* tracks (Table 2.5).

Diurnal and *24 h* tracks recorded hourly fixes from pike within an 800 m section of river, between the East Stoke weir and the Flood Relief Channel (Figure 4.1). Whilst pike were at times recorded moving over the weir (Chapter 4), no radio tagged pike crossed the weir during *24 h* or *diurnal* tracks. The requirement to locate fish at hourly intervals meant that tagged pike outside of the 800 m section could not be sampled, as it would have been impossible to return to upstream pike within the allotted time.

The number and identity of pike present during each track varied, due to immigration/emigration from the study section, natural mortality and new pike being tagged after the beginning of the study period (to maintain sample size). All tagged pike within the 800 m section were followed on each date in order to provide as large a sample as possible from which to make inferences about the patterns of movement in the pike population. The inclusion of pike that did not reside within the section over the entire study period reduced the potential for bias that might have occurred had only 'resident' fish had been followed.

Continuous tracking

Continuous tracks were conducted to provide an estimate of the degree of error involved in measuring distances between hourly fixes, and to provide a more detailed record of the time pike spent in any one location before moving on. During *continuous* tracking, fixes were recorded at 5-minute intervals, rather than hourly, as was the norm for *24 h / diurnal* tracks. Due to the intensive nature of the tracking, it was only possible to follow one individual at a time. The same fish, Pike L (Table 2.2) was followed during all *continuous* tracks to give an idea of the variation in behaviour of this one individual. It was planned that activity signals from the tag would be recorded during the continuous track, using an Automatic Data Logger (Biotrack Ltd.), with the aim of comparing the activity telemetry with the results of simultaneous location tracking (W.R.C. Beaumont, pers. comm.). Pike L was chosen due to ease of access to the area of river in which this pike usually resided.

A *continuous* track was conducted on 20 June 2002 between 0230 hours and 2200 hours and subsequently a number of shorter *continuous* tracks were performed during which Pike L was followed for *ca.* 4 h, after sunrise or in the middle of the day, with fixes again being recorded at 5-minute intervals (Table 2.6).

Routine tracking

Routine tracking of the pike took place between *home range* and *diel* tracks, the aim of this monitoring being to prevent the occurrence of unexplained disappearances of fish. During the first year of the study, pike at East Stoke were tracked three times a week, however subsequently this tracking intensity was reduced. Locating pike that had migrated away from East Stoke was more time consuming, as extra travel time was required to reach each fish. Consequently, the pike that moved away from East Stoke could not be sampled as intensively as those that remained and fixes were collected from these fish as often as was practical.

Table 2.4 The dates of *home range* tracks, together with the identity of pike included in each track. See Table 2.2 for further details of individual fish.

Track	Date	Pike tracked
1	July 2000	A B C
2	September 2000	A B C G H
3	December 2000	A B C G H I J
4	March 2001	A B C G H I J K L M
5	July 2001	B C H J L M P Q
6	September 2001	B C H J L M P Q V X
7	December 2001	B C H J L M P Q V X Y
8	March 2002	B C H I J L M P Q V X Y

Table 2.5 The dates and durations of *24 h* and *diurnal* tracks, together with the identities of pike followed on each occasion. See Tables 2.2 & 2.3 for further details of individual fish.

Date	Track duration h	Pike tracked
26 Jul 2000	24	A B C
24 Aug 2000	24	A B C
26 Sep 2000	24	A B C
2 Nov 2000	15	A B C I
21 Dec 2000	16	A B C I
31 Jan 2001	16	A B C I
28 Feb 2001	17	A B C I
26 Apr 2001	20	A B C G I N
4 Jun 2001	22	B C L M N O
2 Jul 2001	22	B C L M N O
7 Sep 2001	18	B C L M O S V
3 Oct 2001	16	B C L M O V
30 Oct 2001	15	C L M O P V
28 Nov 2001	16	B C H L M O V Y
20 Dec 2001	15	B C L M O V X Y
29 Jan 2002	15	B C L M O V Y
1 Mar 2002	16	B C I L M O V Y

Table 2.6 The date, start and end times (GMT) of *continuous* tracks of Pike L (Table 2.2), during which fixes were recorded at 5-minute intervals.

Date	Start time (hours)	End time (hours)
	'All-day' track	
20 Jun 2002	0230	2200
	Morning tracks	
28 Jun 2002	0320	0700
03 Jul 2002	0305	0700
15 Jul 2002	0315	0700
17 Jul 2002	0305	0700
25 Jul 2002	0305	0710
26 Jul 2002	0305	0700
	Midday tracks	
26 Jun 2002	1000	1400
2 Jul 2002	1000	1400
5 Jul 2002	1000	1400
10 Jul 2002	1000	1400
18 Jul 2002	1000	1400
22 Jul 2002	1005	1400
24 Jul 2002	1000	1400

2.8 HABITAT SURVEYS

2.8.1 Vegetation and flow

In order to describe the habitat preferences of animals, ideally measures of both habitat utilisation and availability are required (White & Garrot, 1990d). Methods used in this study to estimate utilisation are described in Chapter 7, whilst this section describes the method used to describe the proportional availability of various habitat types within the study area, these habitat types being the same as were recorded at each fix *i.e.* 'sparse' or 'dense' 'submerged', 'emergent', 'floating' and 'overhanging' vegetation and also areas of 'slack' flow, 'glides' and 'turbulent' flow.

The method used to measure habitat availability needed to strike a balance between detail and the time taken to conduct the survey. It was anticipated that rapidly changing proportions of aquatic vegetation would necessitate frequent habitat sampling to take place, and this proved to be the case (Chapter 7).

Initially, a transect based approach was attempted to characterise in-stream habitat. A fieldworker on either bank held a rope across the river, to which an inflatable boat was attached. The boat was drawn across the river, and at three randomly determined points across the river, and at both banks, a fieldworker in the boat took a depth measurement and used an underwater viewer to describe the submerged vegetation. A second person held the boat in place whilst measurements were being taken and recorded the data onto (matt laminated) forms. Transects were performed at 50 m intervals along the river. The transect method was soon discontinued, as it did not provide the degree of resolution needed to quantify habitat availability. However, posts marking the locations of the transect points were left in place and later became useful markers when describing the locations of radio tagged fish.

Sketch mapping subsequently became the preferred method for assessing habitat availability, this being less labour intensive than the transect surveys whilst providing more comprehensive data over a wider area. Two people were required for sketch mapping. While one fieldworker sketched the areas of ‘submerged’ vegetation onto an outline of the river, produced by printing appropriate sections of the digitised map of the river, the other fieldworker similarly sketched areas of ‘emergent’, ‘floating’ and ‘overhanging’ vegetation. A sketch map of flow types was also produced. These sketch maps were then subsequently digitised and imported into ArcView 3.2 GIS, where the area of each habitat type could be determined.

Clear water conditions and bright sunlight were required in order for sketch mapping of submerged vegetation to be possible. Consequently describing the proportional availability of ‘submerged’ vegetation was not possible during winter months, and, during the rest of the year, sampling had to be conducted opportunistically, with poor visibility into the water occasionally causing surveys to be completed without the inclusion of a ‘submerged’ vegetation map (Table 2.7). Sketch mapping of the study area could be completed within one or two days.

Table 2.7 Dates on which habitat sketch mapping of 1) flow type, 2) 'submerged' vegetation and 3) 'emergent'/'floating'/'overhanging' vegetation took place.

	13 Jul 2000	2 Aug 2000	15 Aug 2000	13 Sep 2000	19 Sep 2000	6 Feb 2001	22 May 2001	30 May 2001	5 June 2001	25 June 2001	13 July 2001	26 July 2001	11 Sep 2001	20 Sep 2001	14 Dec 2001	25 Mar 2001
1						✓	✓	✓	✓	✓		✓	✓	✓	✓	✓
2	✓	✓	✓		✓		✓	✓	✓	✓		✓	✓			
3		✓	✓	✓			✓	✓	✓	✓	✓	✓	✓	✓	✓	

2.8.2 Streambed topography

In order to describe depth selection by pike in the river, it was necessary to collect data on the bottom topography of the river. Whilst the actual depth at any one location varies according to discharge/water level, the streambed topography itself will remain the same *i.e.* at all water levels depressions in the streambed will be deeper than shallow riffle areas.

During streambed topography surveys, depths were measured at both banks, and at 2 m intervals across the river, from an inflatable boat attached to a rope stretched across the river. Once a depth transect was completed, the rope was moved 5 m downstream and the measurements repeated. Thus, taking depth measurements was both time and labour intensive, requiring 4 people; this was considered acceptable however as streambed topography surveys did not need to be conducted with the same regularity as vegetation / flow surveys.

A streambed topography survey took place in the summer of 2001, with a further survey being conducted in the summer of 2002, which extended the area of river surveyed and allowed for a greater number of pike to be included in analyses of depth selection. In total, streambed topography was mapped along 1100 m of the river. Water levels were recorded from gauging boards at the upstream end of the study area during the surveys in both 2001 and 2002, allowing depths recorded in 2002 to be adjusted for differences in water level, such that data from the two surveys could be combined. The streambed topography was not thought to have altered significantly between the two years.

Streambed topography data were added to the digitised map of the river as a point coverage in ArcView GIS 3.2. Whilst the exact location of each depth measurement was approximate, due to actions of wind and current pulling the boat off station, the resulting point coverage gave a reasonably detailed map of the overall streambed topography.

CHAPTER 3

The effects of tagging

An underlying assumption of most telemetry studies is that the behaviour of tagged individuals does not differ from that of untagged conspecifics, although formally testing the effects of tags can be difficult (White & Garrot, 1990b). Statements based on superficial observations of the appearance of animals, or their behaviour, show only that the presence of the tag is not overtly deleterious to the animal (White & Garrot, 1990b). During the present study, a 'hands-off' approach was taken, with fish being disturbed as little as possible, and recaptures being rare. Pike were not collected at the end of the study, as the long battery life of the TW-5 tag (Chapter 2) allowed for continued data collection, as part of ongoing studies into the fish of the River Frome (CEH unpublished data). Consequently, few data were available to show that the tagging procedures used did not result in deleterious effects on the study animals. However, the data that are available, from recaptures, direct observations, movements and long term survival of individuals are examined below in order to determine, as far as is possible, the nature and extent of post-tagging effects.

3.1 RECAPTURES OF RADIO TAGGED PIKE

Data from six female and three male pike recaptured on various occasions after tagging were available for analysis. Recaptures occurred either incidentally while angling or electric fishing, when an individual was specifically targeted for retagging, or during displacement experiments (conducted as part of the NERC funded Lowland Catchment Research programme).

3.1.1 Length at age and growth

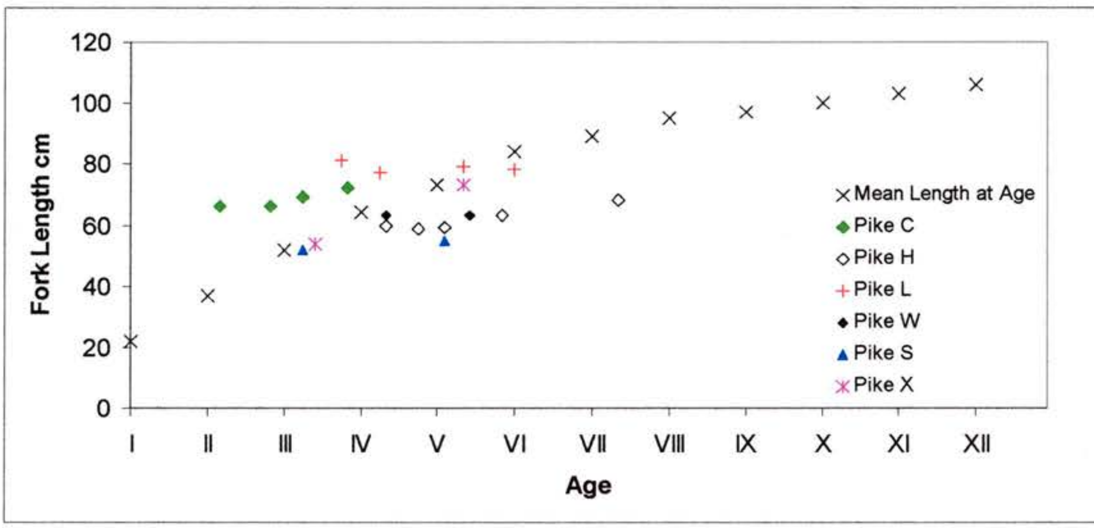
Recaptured pike were aged by examining the patterns of circuli on their scales and the lengths at age of radio tagged fish compared with the mean lengths at age given for male and female River Frome pike by Mann (1976), where the mean length at age for any one age group is the length at the beginning of that particular year of growth (Figure 3.1). The 1^{st} of April was assigned as the date on which the age designation changed, to reflect the time of annulus formation of pike in the River Frome (Mann & Beaumont, 1990). Occasionally, pike were recorded as being shorter on recapture than when first tagged (Figure 3.1), probably reflecting a difference in the way the pike was lying when measured rather than actual changes in fish length. Both Pike C and Pike M showed extremely good 1+ growth (Figure 3.1a and b).

Of the female fish, the length at age of Pike X was very close to the mean values, both on capture and recapture (Figure 3.1a). The growth of Pike S seems much reduced (Figure 3.1a), although this pike was fitted with an external TW-4 tag, which detached from the fish after *ca.* two months (Chapter 2, Appendix 3) and so the lack of growth displayed by this fish during the 22 months between capture and recapture was unlikely to have resulted from this short-term attachment of the tag. Pike C, H, L and W also showed little growth after tagging (Figure 3.1a), but it is not possible to say whether greater growth would have occurred had the tags not been implanted.

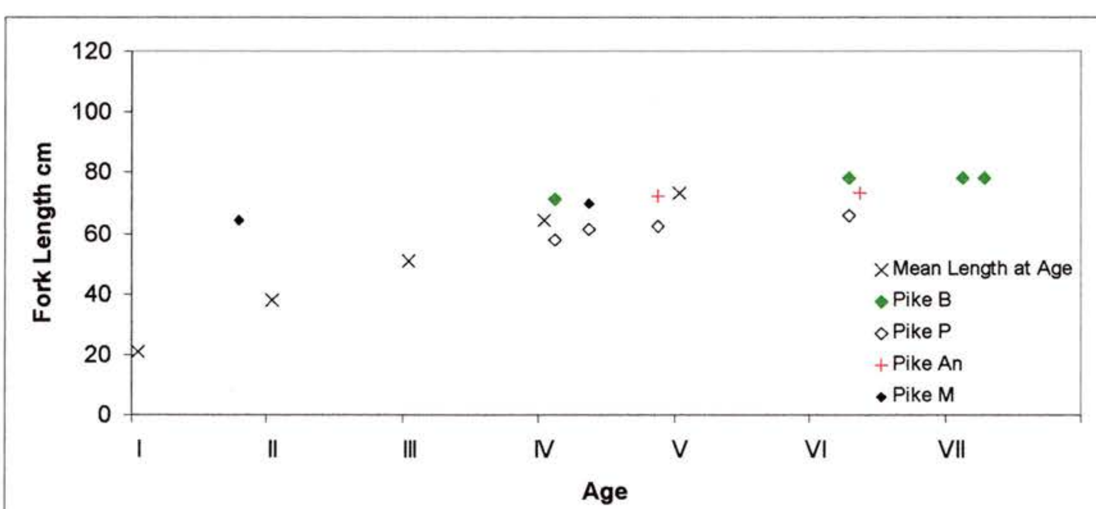
All the male pike tagged were large fish and on recapture several exceeded the maximum age for which mean length data was available (Figure 3.1). Growth appears to have proceeded according to expectation (Figure 3.1).

Figure 3.1 Mean lengths at age for **a)** female and **b)** male River Frome pike, from Mann (1976), together with recorded lengths of radio tagged pike at first capture and subsequent recaptures. For further details of each fish, see Tables 2.2 and 2.3. The first point (chronologically) for each fish shows the length when first radio tagged.

a)



b)



3.1.2 Relative condition factor

The relationship between length and weight of fish can be converted to one of several 'condition factors' and these measures are often used to investigate changes in condition of fishes (Tesch, 1968). Whilst the weight of pike may be greatly affected by stomach fullness, and condition factor changes with reproductive state (Chapter 1), condition factors can still be used to give a general impression of the wellbeing of the fish. Relative condition factors relate the measured weight of a fish to the expected weight for a fish of that length, based on the appropriate length-weight regression. For pike at the time of tagging, and at subsequent recapture, relative condition factors K_n were calculated following the method used by Mann (1976), where:

$$K_n = 100(W_o / W_E)$$

W_o is the observed weight (g) and W_E the expected weight (g), based on the length-weight regression for River Frome pike published by Mann (1980) (Chapter 2). For fish captured after retagging, the weight of the tag was subtracted from the measured weight prior to calculation of K_n.

The relative condition factors of radio tagged pike (Pike An, B, C, H, L, M, P, W and X) did not differ significantly between when they were radio tagged (K_n = 109 ± 17, mean ± S.D.) and their first recapture (K_n = 118 ± 22, mean ± S.D.) (two-tailed paired t-test: d.f. = 8, t = -1.64, P = 0.14). Similarly, there were no significant differences between the relative condition factors of all pike at the time of tagging, and all K_n values from recaptures (two-tailed two-sample t-test: d.f. = 25, t = -0.86, P = 0.40).

While it is not possible to use the relative condition factor to state definitively whether or not deleterious effects occurred for particular individuals, the lack of significant differences between K_n values recorded at tagging and at recapture implies that radio tagging did not lead to gross changes in relative condition factor.

3.2 MORTALITY

During the initial trials of tagging method, one of the three captive pike died shortly after tagging. This pike was already in poor health at the time of tagging, having not fed for *ca.* 1 month since capture. It is likely that death was caused by the prolonged stress of captivity, together with the lack of feeding, with the tagging operation acting as an exacerbating factor (Appendix 2).

The survival of pike that were captured in the river, tagged and subsequently released was good, with some individuals having been tracked for > 3 years (following retagging) at the time of writing. Mortality did occur however. Seven pike died, and, of these deaths, two (Pike R and Pike Et) were attributed to the stresses associated with capture and tagging, due to the short period of time between surgery and fish death (Table 3.1). Radio tags were recovered and in the case of Pike R no remains were found, whereas a few pike scales were found near to the tag of Pike Et. It was possible that tag expulsion, rather than mortality occurred in both cases, but given the lateral placement of the incision and the good healing of incisions seen in recaptured pike, mortality was considered more likely, with scavenging and decomposition accounting for the lack of remains.

Table 3.1 Times between surgery and death for seven pike, radio tagged and released into the River Frome.

Pike	Estimated time of death (after tagging)	Cause of death
E	4 months	natural
G	8 months	natural
K	14 months	natural
N	4 months	natural (intra-specific interaction)
R	15 days	post-tagging mortality
V	17 months	natural
Et	< 1 month	post-tagging mortality

Pike E was tagged on 4 July 2000, leaving the main study area at the end of July and moving to an area 2.5 km to 3 km downstream of its release point. From the end of October through to the end of January, signals were detected from a further *ca.* 3.5 km downstream, being consistently located in a small area on the south bank, from the end of November onwards (Table 3.1). The tag was recovered, and no pike remains were found. Prior to the second major relocation, Pike E was seen in the river, and no obvious signs of disease were noticed. Death from natural causes was assumed.

Pike G performed extensive movements during the winter and spring of 2000 / 2001 (Chapter 4). The signal from the tag was consistently detected near a tree on the bank of the millstream throughout May 2001. In early June water levels dropped sufficiently to allow further investigation and the tag was found buried 10 cm deep in soil at this location. Due to the extensive movements of Pike G, and the time between tagging and presumed death natural mortality was assumed (Table 3.1). Small tooth marks were visible on the casing of the tag, consistent in size with those of mink *Mustela vison* Schreber. The pike was probably either killed by a mink, perhaps whilst in a weakened post-spawning condition, or scavenged after death.

Pike K also ranged over a considerable length of river during the time in which it was tracked (Chapter 4). The tag and some remains were recovered on the bank, although the body was in an advanced state of decomposition. Fox *Vulpes vulpes* (L.) droppings were found nearby, with damaged vegetation and a trail of remains indicating that the fox had dragged the dead, or dying, pike out of slack water alongside the bank. Natural causes were assumed due to the length of time between tagging and death (Table 3.1), and the extensive movements performed by this fish.

Pike V died after intensive tracking had finished, again natural causes were assumed due to the length of time elapsed since tagging (Table 3.1).

Pike N was discovered lying dead on the riverbed (Table 3.1) and the body recovered. Upon examination, the pike was found to have a 20 cm tench *Tinca tinca* (L.) in its mouth (Figure 3.2). A U-shaped bite mark, penetrating into the body cavity, was visible on the left flank behind the operculum. A corresponding abrasion was present on the right flank, the wounds being consistent with a bite mark from a larger pike (Pike N measured L_F = 66 cm at time of death). It is possible that both pike were attempting to attack the same tench, although Pike N could also have fallen victim to a cannibalistic attack, or an attempt at kleptoparasitism (Nilsson & Brönmark, 1999).

Figure 3.2 Pike N, recovered dead from the riverbed on 5 July 2001, with a 20 cm tench in its mouth.

The Freshwater Biological Association and a private fishery owner controlled angling in the main study area and anglers were asked to return any pike caught to the river. None of the mortalities that occurred during the course of the study appeared to be attributable to anglers culling fish.

3.3 WOUND HEALING

Healing of the incisions made during tag implantation operations began rapidly after surgery. Post-mortem examination of a pike that died within a week of surgery (during trials of the tag implantation method, Appendix 2) showed that a layer of connective tissue had already closed over the inside of the incision. Following visual inspection of two further pike, 21 days and 36 days after trial tagging, incisions were noted as being 'well healed' with the skin having formed a total seal over the wound. Post-mortems were not conducted on these two fish.

When the body of Pike N was examined, 4 months after tagging (Table 3.1), the incision site was seen to be well healed and whilst two sutures were still in place, there was no inflammation around the entry sites of the sutures. The radio tag was situated in the posterior end of the peritoneal cavity. There were no internal adhesions to the tag, and there was no inflammation or deformity of the body wall around the tag.

Wound healing was always reported as being good in pike that were recaptured in the river. Over time, the scar healed completely, the only external signs being missing or misaligned scales. Degradation of sutures, however, was not as rapid as had been anticipated, and sutures were often still present when pike were recaptured, at which time they could be removed (Appendix 2). The sutures provided a route for infection to track into the fish and, on occasion, the area around the sutures was reddened and inflamed whilst the incision itself was well healed (Figure 3.3).

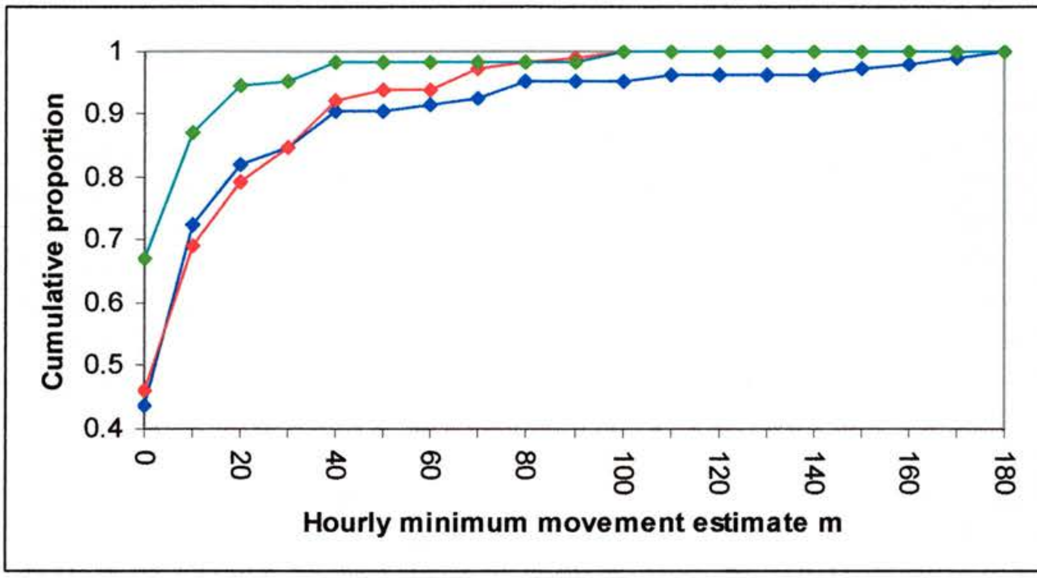
Figure 3.3 The incision area through which a radio tag was implanted into Pike W. Surgery took place on 27 August 2001 and this photograph was taken over a year later, on 5 September 2002. The coated VICRYL® sutures are still in place, although the knots have loosened. Inflammation and infection around the sutures is visible, but the incision itself is well healed.

3.4 RECOVERY TIME FOLLOWING SURGERY

Periods of post-operative recovery are required after the attachment of radio tags to fish, allowing them to recover from the stress of capture and surgery. Capture by angling causes physiological stress to fish, with recovery occurring within 24 – 72 h of capture (Pottinger, 1995). Short-term behavioural modifications can also occur following capture and release (by angling or electric fishing), although the duration of behavioural modification following stress is shorter than the period required for physiological recovery (Pottinger, 1995).

In the present study, although pike were monitored (for welfare reasons) in the days following surgery, data collection did not begin until ten days after tag implantation to allow pike behaviour to return to normal following recovery from capture and tagging; the ten day time period being derived from observations made during the *pilot* track (Chapter 2), when, in addition to Pike A and B, Pike C was also followed. Whilst Pike A and Pike B had been radio tagged 2 weeks prior to the start of the *pilot* track, Pike C had been radio tagged just four days previously (Table 2.2). The minimum distances moved between successive hourly fixes were estimated for all three pike (as described in Chapter 5) and movement appeared reduced for Pike C as compared to the other two fish. During the *pilot* track, the proportion of occasions when hourly minimum movement estimates equalled 0 m was 0.67 for Pike C, compared to 0.44 for Pike A and 0.46 for Pike B (Figure 3.4). Additionally, Pike C performed fewer longer distance movements than Pike A or B (Figure 3.4). Due to the apparent reduced movement of Pike C, the results from this fish were excluded from any analysis involving the *pilot* track. Continued monitoring showed that after a period of 10 days, Pike C began using a home range comparable in size to those of Pike A and B (Welton *et al.*, 2000). Similarly, Diana (1980) found that pike with surgically implanted transmitters did not move for up to five days after the tag was implanted.

Figure 3.4 The cumulative proportions of all hourly minimum movement estimates for Pike A (◆), Pike B (◆) and Pike C (◆) during the *pilot* track.



3.5 DIRECT OBSERVATIONS OF PIKE BEHAVIOUR

On each occasion when radio tagged pike were directly observed in the river, pike appeared to be swimming normally. Pike P, Pike L and Pike K were all seen participating in spawning activity during the course of the study, and long distances (> 1 km) were swum by several fish on occasion, in both upstream and downstream directions.

3.6 DISCUSSION

The 'hands-off' approach taken in the present study meant that few data were available to analyse for tagging effects, but the observed long-term survival and extensive movements of radio tagged pike, together with data on growth rate and relative condition factor and the participation of radio tagged fish in spawning behaviour combine to suggest that the adverse effects of tagging were minimal. Therefore, after a suitable recovery period, the behaviour of radio tagged pike could be considered to be representative of the population.

Post-tagging mortality was extremely low, with only two out of the 28 pike implanted with TW-5 tags dying soon after surgery.

Comparing the growth of radio tagged pike with that which would be expected amongst untagged pike was difficult due to the large amount of variation in length at age and growth rate. For example, the growth of Pike S appears to be poor, but as this pike was fitted with an external transmitter that detached two months after tagging it is unlikely that this poor growth is entirely attributable to the presence of the tag and may instead represent slow 'natural' growth. On an individual basis, it is difficult to comment on whether growth has been reduced compared to what could have been achieved had the fish not been tagged. The study of growth rate is further complicated by the fact that as relatively large, older individuals, the growth rate of pike $L_F > 50$ cm is slowing down and so any natural growth would only involve small changes in length.

Sutures often remained after the wound itself had healed, and could serve as a route for infection to track into the fish. Systematic recapture of pike and removal of sutures, some months after surgery, is worth considering in future studies.

Further support for the assumption that the behaviour of radio tagged individuals did not differ from that of untagged fish comes from Jepsen & Aarestrup (1999), who compared the growth rates of radio tagged and dye marked pike. Tagging proceeded using a method similar to that in the present study, although mid-ventral incisions were made, tags were smaller (15 mm × 45 mm, weight in air = 14.5 g) and external antennae were used. Dyed pike were marked using a PanJet innoculator, a needleless system for injecting coloured dye under the skin. The two groups of pike came from the same population and were caught, handled and anaesthetised in the same way before being released into the environment for *ca.* 1 year and then recaptured. Neither group of pike showed a significant change in condition factor (calculated as 100 WL^{-3}, where W = body weight g and L = total length cm) from initial capture to recapture and no significant differences in growth rate were found between the groups. Radio tagging did not appear to cause any more severe effects, in terms of growth than Panjetting, a far less invasive technique. There may however have been a short-term adverse effect on growth rate amongst radio tagged pike, that was subsequently compensated for (Jepsen & Aarestrup, 1999). The similarities between the tagging methods used by Jepsen and Aarestrup (1999) and those used in the present study suggest that only small effects on growth would be expected as a result of the implantation of TW-5 radio tags.

3.7 SUMMARY

1) Long-term survival and growth of tagged fish occurred.

2) Mortality attributable to the radio tagging procedure was very low (two out of 28 fish).

3) Relative condition factors did not differ significantly between radio tagged and untagged fish.

4) Wound healing was good, although suture degradation was not as rapid as anticipated, and systematic recapture of pike and removal of sutures is worth considering in future studies.

5) Data collection began ten days after surgery to allow time for pike behaviour to return to normal.

6) After a suitable recovery period, there were no reasons to suppose that the behaviour of radio tagged pike differed from that of untagged pike.

CHAPTER 4

Long-term spatial behaviour of riverine pike

The strategies involved in competition for resources may be reflected in the manner in which a species utilises space. Whilst some animals compete for resources by exploitation *e.g.* loriicarid catfish (Power, 1984), others display territorial behaviour, defending the resources in a particular area against invaders *e.g.* male pomacentrid damselfish (Helfman *et al.*, 1997e). Within a species, different behavioural strategies may occur, including a variety of spatial behaviours, and such differences can be viewed as being the product of three mechanisms; a variable environment, phenotypic differences and the behaviour of other individuals (Magurran, 1993).

The spatial behaviour of animals may vary depending on resource availability (Helfman *et al.*, 1997e) and competition may occur if resources become limiting. Resources of importance to pike include areas of suitable habitat, for feeding or reproduction, and pike have been shown to display a variety of spatial behaviours both within and between populations (Mann, 1980; Jepsen *et al.*, 2001).

In this chapter, remote methods of observation are used to investigate the long-term spatial behaviour of the pike, with a view to investigating the diversity of patterns of space use of this versatile top predator in a riverine environment; a habitat in which the species has been relatively poorly studied. In addition to the inherent ecological interest of such a study, the information obtained is also of practical value for effective fisheries management and conservation.

4.1 INTRODUCTION

Pike are the top predators in many aquatic ecosystems and have been shown to display a variety of spatial behaviours both within and between populations (Jepsen *et al.*, 2001). Mark-recapture and telemetry techniques have both been employed in the study of pike spatial behaviour, although the majority of studies have concentrated on lacustrine, rather than riverine pike *e.g.* Bregazzi & Kennedy (1980), Chapman & Mackay (1984b), Cook & Bergersen (1988), Diana (1980), Diana *et al.* (1977), Jepsen *et al.* (2001), Kipling & Le Cren (1984), Mackay & Craig (1983).

The limited number of telemetry studies of riverine pike show that a high degree of mobility can occur, although detailed description of spatial behaviour has been lacking. Langford (1979) found that the 'home ranges' of six pike in the River Thames were 2.3 ± 0.7 km (mean ± S.D.) in length (the distance between the furthest upstream and furthest downstream locations), although the duration of the tracks was not reported. Recently, Ovidio & Phillipart (2002) have described pike performing upstream spawning migrations of 7.7 ± 6.67 km (mean ± S.D.) in the River Meuse basin, Belgium, and Gerlier & Luquet (1999) reported radio tagged pike occupying between 0.40 km and 12.26 km of the River Ill, France. Interpretation of the results presented by Gerlier & Luquet (1999) is however complicated, due to differences in release strategy and the length of time over which pike were tracked in this preliminary study. Extreme long-distance movements (> 100 km) between summer and winter locations were observed in an Alaskan wetland area (Burkholder & Bernard, 1994).

Classic studies of riverine pike, which described a propensity for limited movement, *e.g.* Mann (1980), together with the adaptations of pike for fast-start swimming (Helfman *et al.*, 1997d) and the species preference for areas of slack water (Lamouroux *et al.*, 1999) have led to reports of extensive movements in rivers being viewed as paradoxical (Ovidio & Philippart, 2002). However, from the results of telemetry studies, it appears that large-scale movements can and do occur.

Mann (1980) interpreted the results of a mark-recapture study of jaw tagged pike in the River Frome to suggest that there were both static and mobile components to the population. Pike were marked and released along the whole length of the study area and the data were corrected, following Stott (1967), to allow for the greater chance of pike in the centre sections being recaptured. The results suggested that the overall pattern of distances between capture and release sites could be described using two overlapping normal distributions, with widely different standard deviations. The pike from the population with the lowest standard deviation were termed static, and comprised *ca.* 74% of the population. Based on Figure 1 in Mann (1980), the vast majority of recaptures of static pike would be expected to occur within 250 m up or downstream of the original capture location. Mobile pike (*ca.* 26% of the population) were those from the normal distribution with the greater standard deviation, and more than half of the recaptures of this component would be expected to take place > 250 m up or downstream of the release site; the release site still being the place where recapture was most likely (Mann, 1980).

In this chapter the long-term spatial behaviours of fifteen pike are presented and discussed, the overall study area being the same as that of Mann (1980). The hypothesis that the pike population consists of components exhibiting alternative behavioural strategies (Mann, 1980) is specifically examined and the results are discussed in terms of the possible ecological significance of the observed behaviours; the simultaneous, sympatric, existence of different strategies being of interest as it suggests that variation may occur due to phenotypic differences, or in response to the behaviour of other individuals, rather than being a response to environmental variation (Magurran, 1993).

To date, descriptions of the long-term spatial behaviour of radio tagged fish have tended towards simple descriptions of the overall length, or area, of river utilised, *e.g.* Lyons & Lucas (2002), but a greater understanding of space use can be achieved if distinctions are made between core areas of intensive use, and areas which are infrequently visited (Hodder *et al.*, submitted). Consequently, in this chapter the spatial behaviour of radio tagged pike is described through reference to the locations of seasonally determined cluster polygon (C_{tx}) home ranges, together with the locations of positional fixes recorded throughout the year. Records of pike movement from an automatic fish counter in the river are also presented.

4.2 METHODS

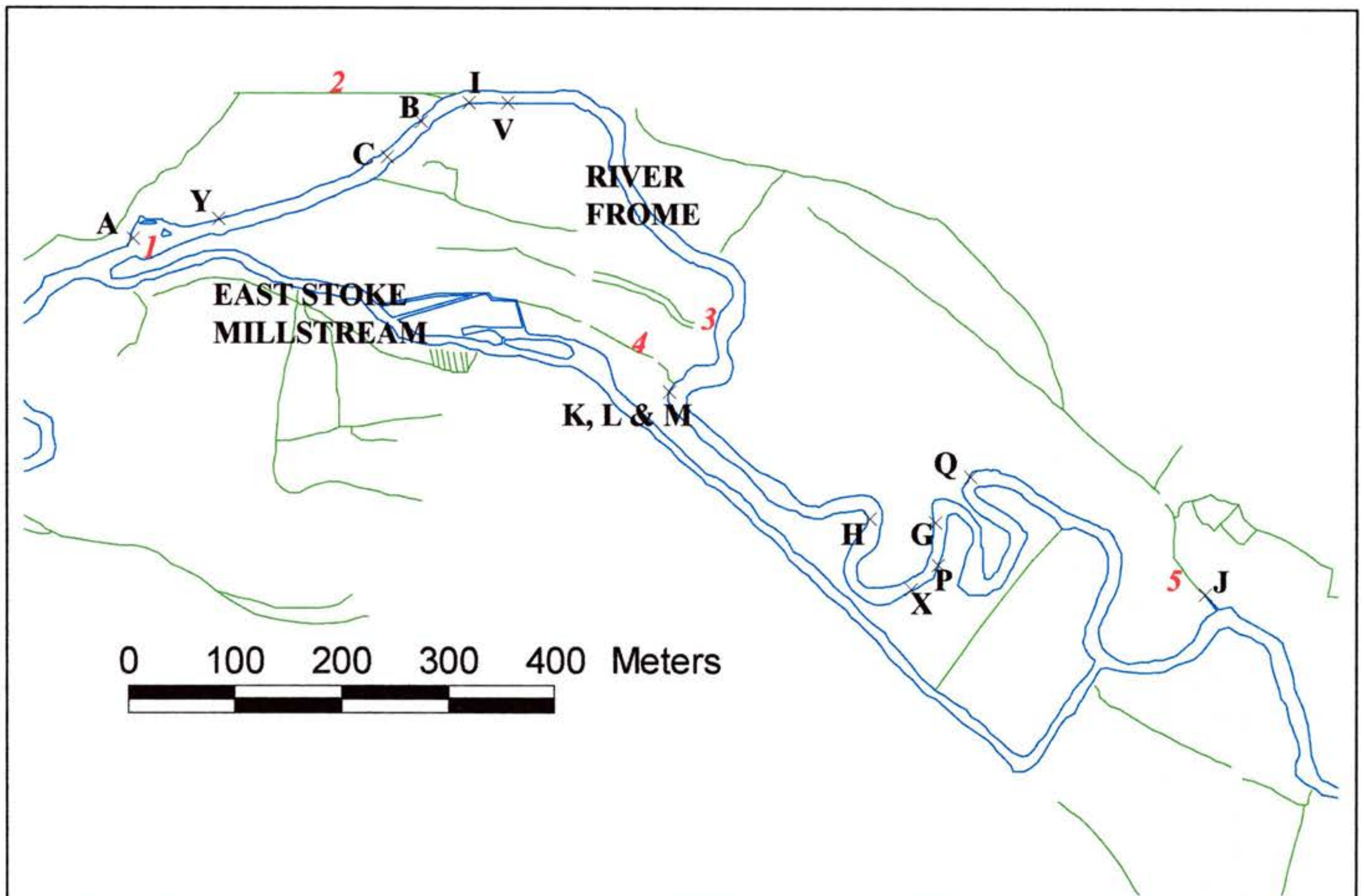
4.2.1 Fish counters

A resistivity fish counter, used to study the migration and population status of Atlantic salmon, is maintained on the River Frome at East Stoke (SY 386736 86838), being situated on a gauging weir at the upstream end of the Weirpool (Figure 4.1). A video camera, looking down on to the water, is located, vertically, above the weir; the area being illuminated by red lights at night. Tapes from this camera were viewed by CEH staff in order to identify and measure fish passing over the weir. Video recorders were set up to place an 'alarm event' on the videotape when the counter detected a fish. During these alarm events the tape recorded at normal speed, whilst, outside of alarm events, the tape ran on a time lapse system. When viewing tapes, the tape was usually fast-forwarded to an alarm event and just that short section of tape watched, the time between alarm events only being viewed occasionally, to verify the accuracy of the counter. The fish counter was designed to detect the movements of adult salmon, and, as such, only fish greater than 45cm in length were detected. As not all of each tape was watched, movements of fish less than 45cm in length were not recorded.

Fish seen passing over the weir were identified to species level, where possible, and measured, by reference to the known spacing of the fish counting electrodes on the bottom of the weir, these being visible on screen. Pike were identified by the distinctive 'duck-bill' shape of their head when viewed from above, and by the rearward placement of the dorsal and anal fins.

Videos were only watched when the water was clear enough to see fish, and when the bottom of the weir was clean. When conditions were such that fish could not be seen, videos were not recorded and only electronic records of fish movement exist. Whilst it is possible to identify a high proportion of eels based on the voltage pattern produced by the electronic counter (Beaumont *et al.*, 1986), it is not possible to distinguish between other species in this manner.

Figure 4.1 Capture locations for each pike (A, B, C *etc.*) within the main study area. Locations referred to in the text are *1* – Weirpool (East Stoke weir), *2* – Railway Ditch, *3* – Hummock Ditch, *4* – Flood Relief Channel, *5* – Rushton Ditch.



4.2.2 Radio telemetry

Quantification of the areas utilised by animals can be achieved through home range analysis (White & Garrot, 1990a), where home range is defined as an area repeatedly traversed by an animal (Kenward 2001). CEH researchers (as part of a NERC funded project) studied the area and structure of the pike home ranges, in relation to differing flow levels, in a paper submitted to the *Journal of Fish Biology*, on which I am second author (Hodder *et al.*, submitted). Ranges were found to be mostly multinuclear, with a median of two activity centres (Hodder *et al.*, submitted). Whilst the CEH study concentrated on home range area and structure, I used data from the same fish to describe the actual locations of home ranges over time, making an oral presentation on the subject at the Fifth Conference for Fish Telemetry held in Europe and submitting a manuscript for the conference proceedings (Masters *et al.*, submitted). Fieldwork was conducted both by myself, and by CEH staff members, students and volunteers, allowing for a greater volume of data to be collected than could have been achieved by working independently.

Home ranges can be determined using a variety of techniques (White & Garrot, 1990c; Kenward, 2001). In studies of riverine fishes, the terms 'home range' or 'linear home range' are often used to describe the distance between the furthermost upstream and downstream fixes, with home range areas being calculated by multiplying the longitudinal distance between fixes by the mean stream width (Minns, 1995). To avoid confusion with more detailed home range analysis techniques, Hodder *et al.* (submitted) termed the area of river thus calculated as the Maximum Linear Displacement (MLD). The MLD gives a measure of the total area of river available to the fish, but it is difficult to visualize longitudinal movements along the river using units of area; therefore in the analysis below I describe fish locations using units of distance, introducing the terms Total Maximum Linear Displacement (TMLD) and Maximum Core Displacement (MCD).

Whilst the distance between the furthest upstream and downstream fixes gives a measure of overall mobility, if excursive movements occur, using this measure alone can lead to an exaggerated impression of the length of river regularly utilized. More detailed information can be gained by examining both the distance between furthermost upstream and downstream fixes, and the distribution of core centres of activity.

Analysis

Of the 25 pike fitted with internal transmitters during this study, sufficient data were available from 15 to investigate long-term spatial behaviour, these fish having been tracked for between 8 and 20 months (Table 4.1). Long-term spatial behaviour was described by reference to the locations of fixes recorded during *home range* and *routine* tracks (Chapter 2). A modified version of RANGES V (Kenward & Hodder, 1996) was used to calculate home ranges, and for measuring distances along the midline of the river.

Table 4.1 Data collected for the 15 pike used to investigate long-term spatial behaviour. 'No. days' refers to the number of days between tagging and the last fix recorded for each fish. L_F is the fork length at time of capture. The key to the numerical code for home range tracks is given in Table 2.4

Pike	Date tagged	Sex	L_F (cm)	No. fixes	No. days	Present in home range tracks
A	24 May 2000	♀	86	295	1276	1 to 4
B	24 May 2000	♂	71	471	773	1 to 8
C	08 Jun 2000	♀	66	500	748	1 to 8
G	31 July 2000	♀	66	172	243	2 to 4
H	23 Aug 2000	♀	60	401	689	2 to 8
I	16 Oct 2000	♂	87	239	633	3, 4 and 8
J	30 Nov 2000	♀	93	296	581	4 to 8
K	17 Jan 2001	♀	95	111	417	4
L	17 Jan 2001	♀	81	324	544	4 to 8
M	17 Jan 2001	♂	64	310	542	4 to 8
P	22 May 2001	♂	58	225	416	5 to 8
Q	22 May 2001	♂	69	218	416	5 to 8
V	31 Jul 2001	♀	52	232	346	6 to 8
X	4 Sep 2001	♀	54	166	316	6 to 8
Y	8 Nov 2001	♂	64	130	240	7 and 8

Maximum Core Displacement (MCD)

Convex cluster polygon (C_{tx}) home ranges were calculated for every individual in each *home range* track, after removal of outlying fixes; defined as those within the upper five percent of the distribution of distances between neighbouring fixes (Hodder *et al.* 1998; Kenward, 2001; Kenward *et al.*, 2001). C_{tx} home ranges (Figure 4.2) showed the multinuclear structure of the pike home ranges, minimized the area of bank included within the home range and were stable with low numbers of fixes, thus making the technique superior (for the purposes of this study) to other types of home range estimator, such as Minimum Convex Polygons, Ellipses or Kernal contours (Welton *et al.*, 2000, Kenward, 2001).

To describe the location of the C_{tx} home ranges, a 'centre' was determined for each cluster polygon. For each fix within a cluster polygon, the distance along the midline of the river was measured between the fix and the original capture location for that fish. The mean distance from the capture location for all the fixes within each cluster was then calculated, this mean distance being termed the cluster 'centre' (Figure 4.2). The use of a single home range centre, based on a kernel density function, was considered, but was found to be unsuitable due to the multinuclear structure of many pike home ranges.

Maximum Core Displacement (MCD) was calculated for each individual, where MCD was the distance between the furthest upstream and downstream cluster centres, in all *home range* tracks combined (Figure 4.3).

Outlying fixes

The distance from the capture location, along the midline of the river, was calculated separately for each of the fixes that were excluded from the C_{tx} ranges. Similarly distances from the capture location were calculated for all fixes collected between the dates of *home range* tracks.

Total Maximum Linear Displacement (TMLD)

For each of the 15 pike, the Total Maximum Linear Displacement (TMLD) was calculated, over the entire period of time during which each pike was tracked; TMLD being the distance between the furthest upstream and furthest downstream locations, as measured along the midline of the river, regardless of whether or not the fixes were part of a C_{tx} range (Figure 4.3). Spearman's rank correlations were used to look for relationships between TMLD and pike length, TMLD and the number of fixes obtained for each pike and between TMLD and the number of days between the first and last fixes for each pike.

Figure 4.2 An example of C_{tx} home ranges (—), showing tight clustering around groups of fixes (×), and minimal expansion of the range outlines outside of the river channel (—). The location of cluster 'centres' (**o**) on the midline of the river (—) are also illustrated. Fixes and ranges displayed are those recorded for Pike J during the March 2002 home range track.

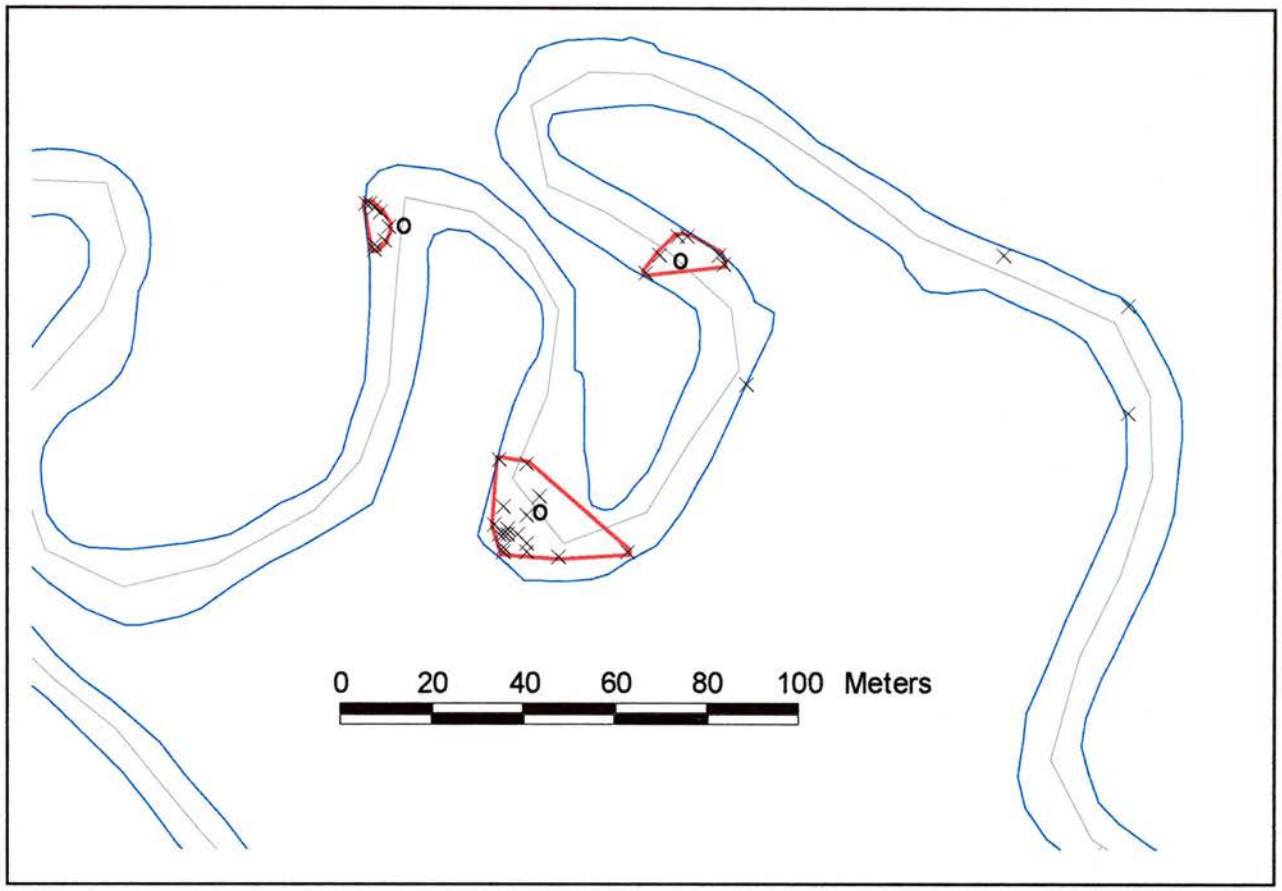
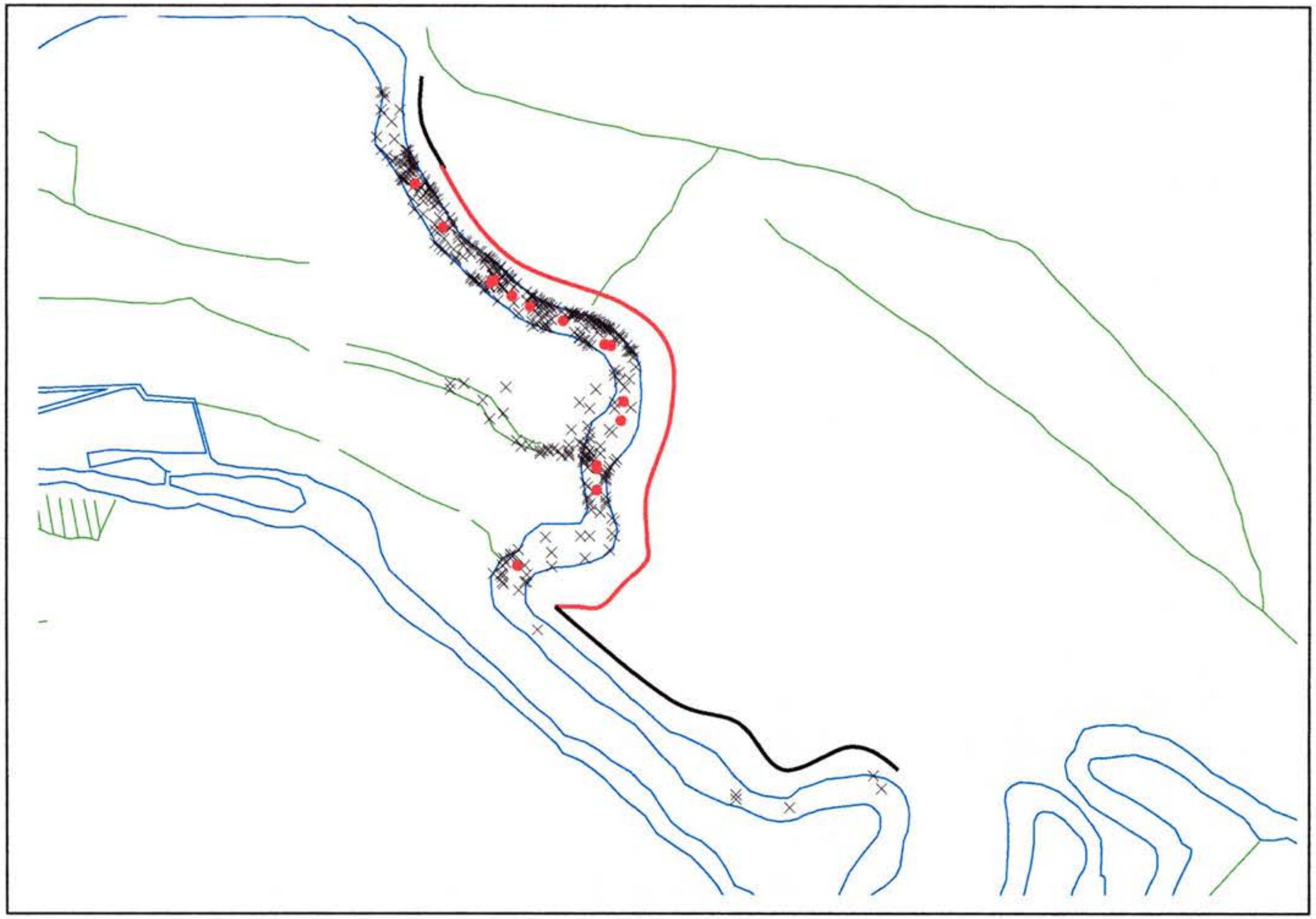


Figure 4.3 All individual fixes (×) for Pike M, together with the locations of 'cluster centres' (•), illustrating the Total Maximum Linear Displacement (TMLD)(———) and Maximum Core Displacement (MCD) (——).



Range Shift Indices (RSI)

MCD and TMLD were calculated by measuring distances along the midline of the river. Fixes that were the same distance from the capture location could however still be in different places, for example, on the north or south banks of the river, therefore Range Shift Indices (RSI) were calculated, in order to provide a measure of the extent to which individual pike were utilising the same areas within the river over time.

C_{tx} range outlines were imported into ArcView GIS 3.2 (ESRI Inc., Redlands, USA) and examined for overlaps. The RSI was then calculated for each individual as:

RSI = number of 'track pairs' where overlap occurred / total number of 'track pairs'

For example, if a pike had been tracked during March, July, September and December *home range* tracks, and overlaps occurred between March and July C_{tx} ranges, but not between any other pairing of tracks, then the Range Shift Index would be one (the number of 'track pairs' where overlap occurred) divided by six (the total number of 'track pairs') (RSI = 0.17). Where no overlaps occurred between cluster polygons from any pair of tracks, RSI = 0. Where overlaps occurred between cluster polygons from all pairings of tracks, then RSI = 1.

Use of side channels

In order to describe linear movement of pike along the river channel itself, when fixes occurred in side channels, the location of the fix was described as the distance between the capture location and the point where the side channel connected to the river. By this method, a fix, for example, 10 m downstream of the capture location and 10 m along a drainage ditch, could not be confused with a separate fix, 20 m downstream of the capture location.

To give an indication of the extent of side channel utilisation, in every *home range* track, the proportion of fixes occurring within the side channels was determined for each fish and a median value then calculated from all pike during that track.

Side channel utilisation during winter flooding was examined in more detail by Masters *et al.* (2002) and this subject is considered further in Chapter 6.

4.3 RESULTS

4.3.1 Fish counters

Data from videos recorded during 1997 and 1998 were examined for records of pike movement. CEH staff had viewed 122 days of tape, recorded between April and September 1997 and 184 days of tape, recorded between March and November 1998 (Table 4.2).

Low numbers of pike were recorded moving over the fish counter in both 1997 (n = 12) and 1998 (n = 5). Eight of the 1997 records occurred during April, but in 1998 no pike were seen in this month (Table 4.2).

Table 4.2 The number of pike seen on video records from the East Stoke salmon counter in 1997 and 1998, together with the direction of movement (upstream or downstream) and *V*, the number of days for which video records were available in each month.

		March	April	May	June	July	August	September	October	November
1997	*V*	0	22	31	11	24	31	3	0	0
	u/s		4	2	1	1				
	d/s		4							
1998	*V*	11	19	29	9	29	27	29	28	3
	u/s	2			2			1		
	d/s									

4.3.2 Radio telemetry

During the period of time in which the 15 pike were tracked, mean discharge in the River Frome was somewhat variable, with relatively high discharges occurring during autumn/winter 2000/2001 (Table 4.3). Mean water temperatures ranged between *ca.* 8 °C in winter and *ca.* 16 °C in summer (Table 4.3).

There were no correlations between Total Maximum Linear Displacement and either the length of time for which a pike was tracked (r_s = 0.37, n = 15, P = 0.18), or the number of fixes recorded for each fish (r_s = -0.05, n = 15, P = 0.85), therefore the observed variation in TMLD was not simply a reflection of the different datasets. There was a significant positive correlation between TMLD and the fork length of pike (r_s = 0.69, n = 15, $P < 0.01$), however TMLD could vary widely between similarly sized fish, for example, Pike C and G both measured 66 cm at capture although TMLDs were 781 m and 2694 m respectively (Table 4.1, Figure 4.4, Figure 4.7).

Using the data from all pike and all *home range* tracks, the mean length of C_{tx} ranges, as measured along the midline of the river, was 36 ± 4 m (± S.E.), making the cluster centre a suitable measure of location to describe long term spatial behaviour, over the scale of the river.

Examination of the distribution of cluster centres along the river for each fish allowed pike to be categorised according to the type of spatial behaviour they had displayed. There were no obvious differences in spatial behaviour between males and females, with both sexes appearing in all categories containing more than one fish.

Table 4.3 Mean daily discharge and water temperatures for the River Frome, summarised for 3-month periods, (means ± S.E.).

	Water temperature °C	Discharge m^3s^{-1}
2000		
Apr-May-Jun	13.0 ± 0.3	6.2 ± 0.3
Jul-Aug-Sep	15.9 ±0.1	2.6 ± 0.1
Oct-Nov-Dec	8.7 ± 0.2	11.3 ± 0.7
2001		
Jan-Feb-Mar	8.1 ± 0.2	13.3 ± 0.4
Apr-May-Jun	12.5 ± 0.4	5.5 ± 0.3
Jul-Aug-Sep	16.0 ± 0.2	2.1 ± 0.0
Oct-Nov-Dec	9.6 ± 0.3	3.4 ± 0.1
2002		
Jan-Feb-Mar	8.6 ± 0.2	5.6 ± 0.2
Apr-May-Jun	13.3 ± 0.2	3.7 ± 0.1
Jul-Aug-Sep	15.6 ± 0.2	2.8 ± 0.1

'PERMANENT RESIDENT' PIKE

Pike B, C, H, M, V and Y were categorised as permanent residents, as they displayed a high degree of site fidelity, with Maximum Core Displacements (MCD) of 275 ± 175 m and Total Maximum Linear Displacements (TMLD) of 645 ± 446 m (means ± S.D.)(Figure 4.4).

Short-term excursions outside of their main area of residency (as defined by the MCD) were recorded for three of these fish. Pike B and C were located *ca.* 1000 m and *ca.* 500 m downstream of their capture locations during a week in February 2001, and for *ca.* 3 weeks in November 2000, respectively. A more prolonged excursion was performed by Pike H, which stayed between 165 and 420 m downstream of its capture location between mid-December 2000 and early February 2001. Following these excursions, all three fish returned to their usual areas of residency. Pike B performed another excursion in Autumn 2001, when for *ca.* 1 month this fish could not be found in the main study area.

For most permanent residents, there was a high degree of overlap between cluster polygons in different tracks (mean Range Shift Index = 0.85)(Table 4.4).

Figure 4.4 Locations of cluster centres (×) in each home range track, for all **'permanent resident'** pike, relative to their release point. Furthest upstream (┬) and furthest downstream (┴) fixes, over the entire tracking period, are also shown for each individual. Distance between furthest upstream and downstream fixes = Total Maximum Linear Displacement (TMLD). Distance between furthest upstream and downstream cluster centres = Maximum Core Displacement (MCD).

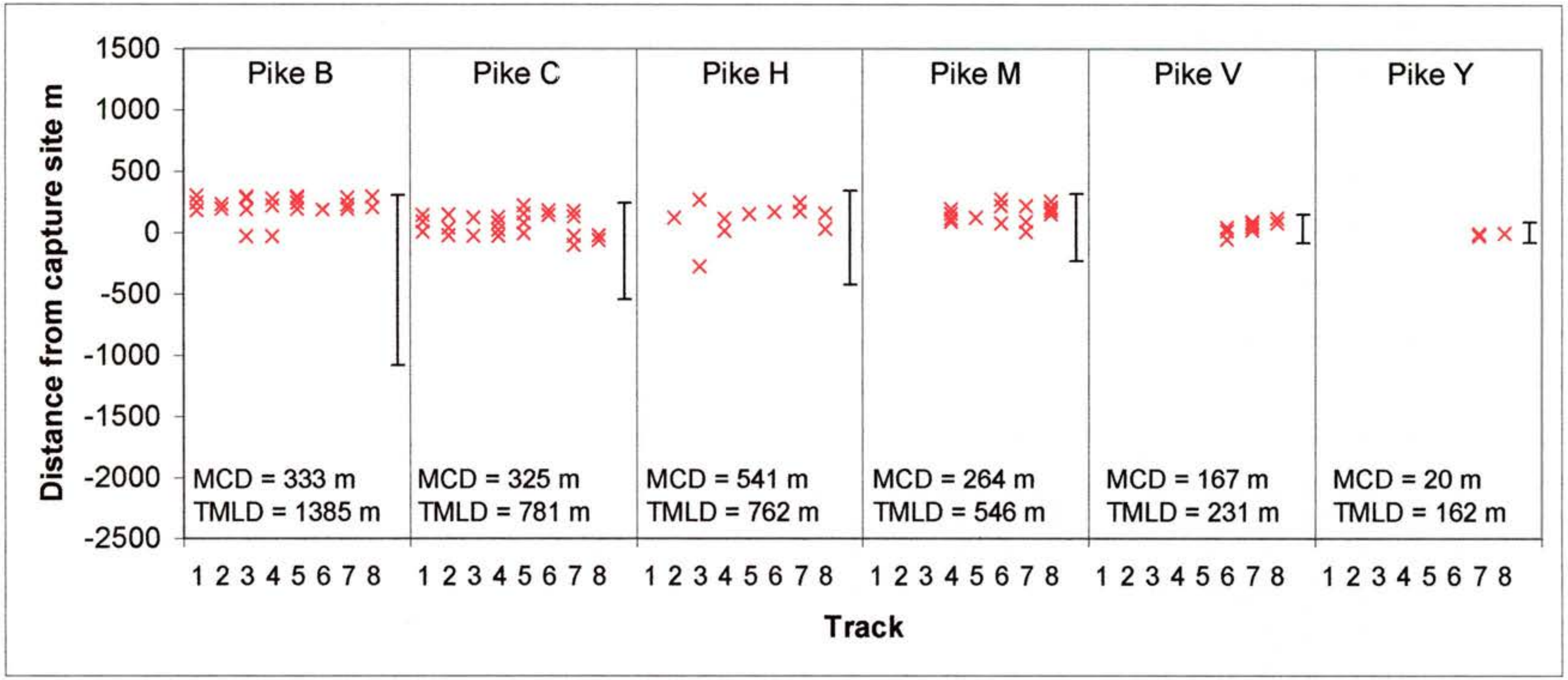


Table 4.4 Range Shift Indices for each pike.

	'Permanent Resident'						'Migratory'		'Emigrant'	Pike with indistinct patterns of behaviour					
	B	C	H	M	V	Y	I	K	A	G	J	L	P	Q	X
RSI	0.96	0.96	0.52	1.00	0.67	1.00	1.00	n/a	1.00	0.00	0.50	0.60	0.50	0.67	0.00

'MIGRATORY' PIKE

Two pike utilised widely separated areas of river at different times of the year (Figure 4.5a, 4.5b). Total Maximum Linear Displacements were 5643 m for Pike I and 2857 m for Pike K. Pike K was only present in the main study area during the March 2001 *home range* track, consequently a Range Shift Index could not be calculated for this fish.

Despite Pike I being absent from the main study area for around 8 months, fixes in spring 2002 were very similar in location to those recorded during the autumn/spring period of 2000/2001. Using data from December 2000, March 2001 and March 2002 *home range* tracks, Maximum Core Displacement for Pike I was 27 m and the Range Shift Index 1.0 (Table 4.4).

Whilst downstream in 2001 and 2002, fixes ranged over 562 m and 349 m of river for Pike I and K respectively, these distances being comparable to TMLD values of permanent resident pike (Figure 4.4) Both pike returned to the same downstream areas in 2002 (Figure 4.5a, 4.5b).

Both fish frequented known spawning grounds whilst residing in the main study area, and Pike K was observed spawning in the Hummock Ditch (Figure 1.2, Figure 4.1) in March 2001. The pike were not followed continuously when moving between upstream and downstream locations, however, a signal was detected from Pike K around the area of the Hummock Ditch (Figure 4.1) on the day after the pike had been seen spawning, and the fish was subsequently found > 2000 m downstream, one and a half hours later.

The timing of the movements of Pike I and K were broadly seasonal in nature; but discharge also appeared to be a factor, with both pike moving upstream during a flood in February 2002 (Figure 4.5a, 4.5b), although the short flood events in October and December 2001 did not result in upstream movements by either pike. Downstream movement took place later in the year for Pike I than for Pike K during both 2001 and 2002 (Figure 4.5a, 4.5b).

'EMIGRANT' PIKE

After release, Pike A appeared to be a 'permanent resident' for *ca.* 11 months (Figure 4.6). During this time, overlaps occurred between cluster polygons in all home range tracks (Range Shift Index = 1.0, Table 4.4), whilst Maximum Core and Total Maximum Linear Displacements were 336 m and 342 m respectively.

Large movements occurred in spring 2001, when between 30 April and 22 May, Pike A was found in Rushton Ditch (Figure 4.1), an oxbow 1000 m further downstream (SY 88 86) , and a side channel *ca.* 1000 m upstream of the release site (SY 86 86). After this, the pike relocated to an area between 2000 m and 3000 m upstream of the release site. There were no repeated seasonal patterns to the movements of Pike A and the flood in February 2002 did not prompt a return to the main study area.

Whilst moving upstream, Pike A swam over the East Stoke gauging weir. Further upstream movement may have been blocked by the Bindon Abbey weir (SY 85 86), with the pike being found in the pool below this weir, *ca.* 2800 m upstream of the capture location, on numerous occasions.

Figure 4.5 Distance from capture location (×) over time for the two **'migratory'** pike a) Pike I and b) Pike K, together with mean daily discharge (—).

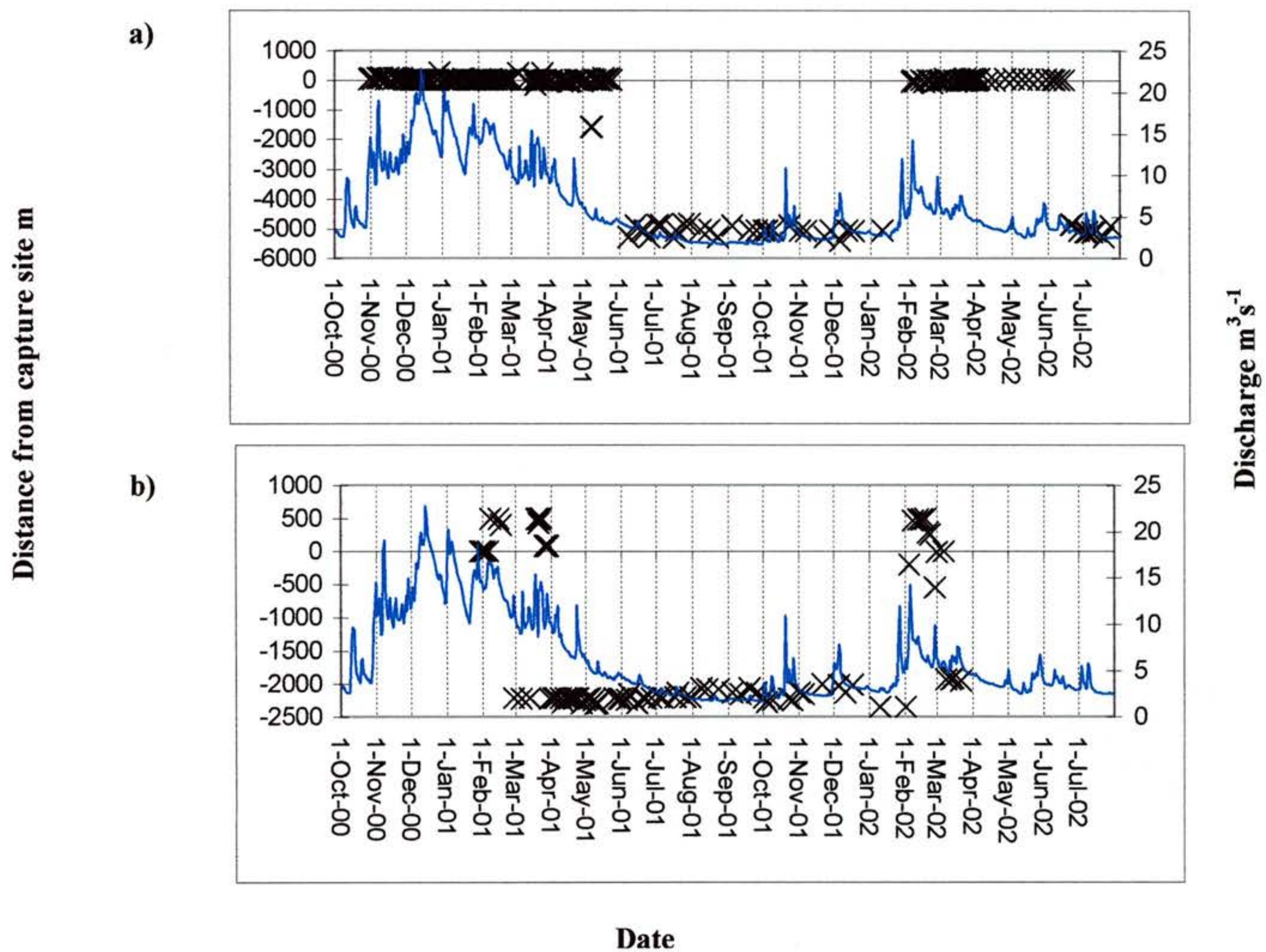
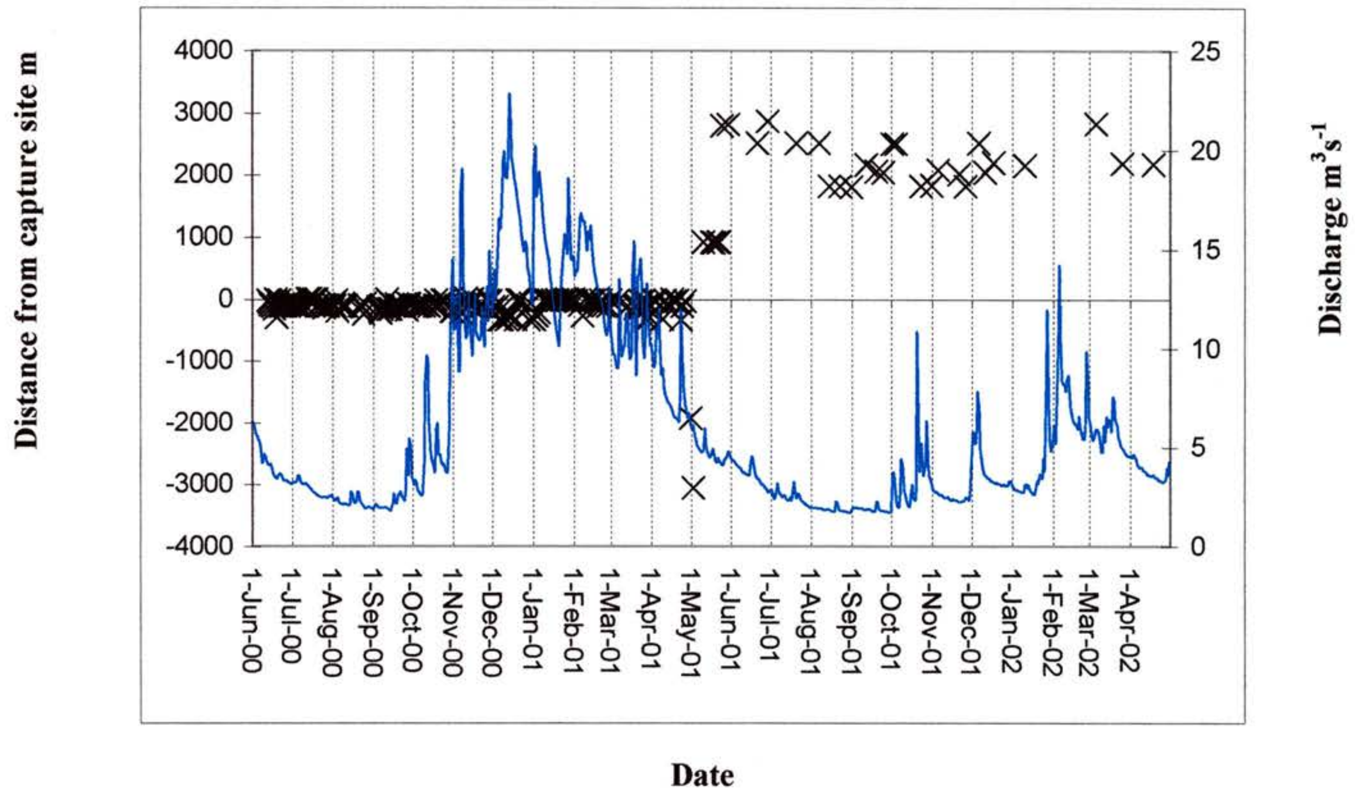


Figure 4.6 Distance from capture location (×) over time for the **'emigrant'** Pike A, together with mean daily discharge (—).



PIKE WITH INDISTINCT PATTERNS OF BEHAVIOUR

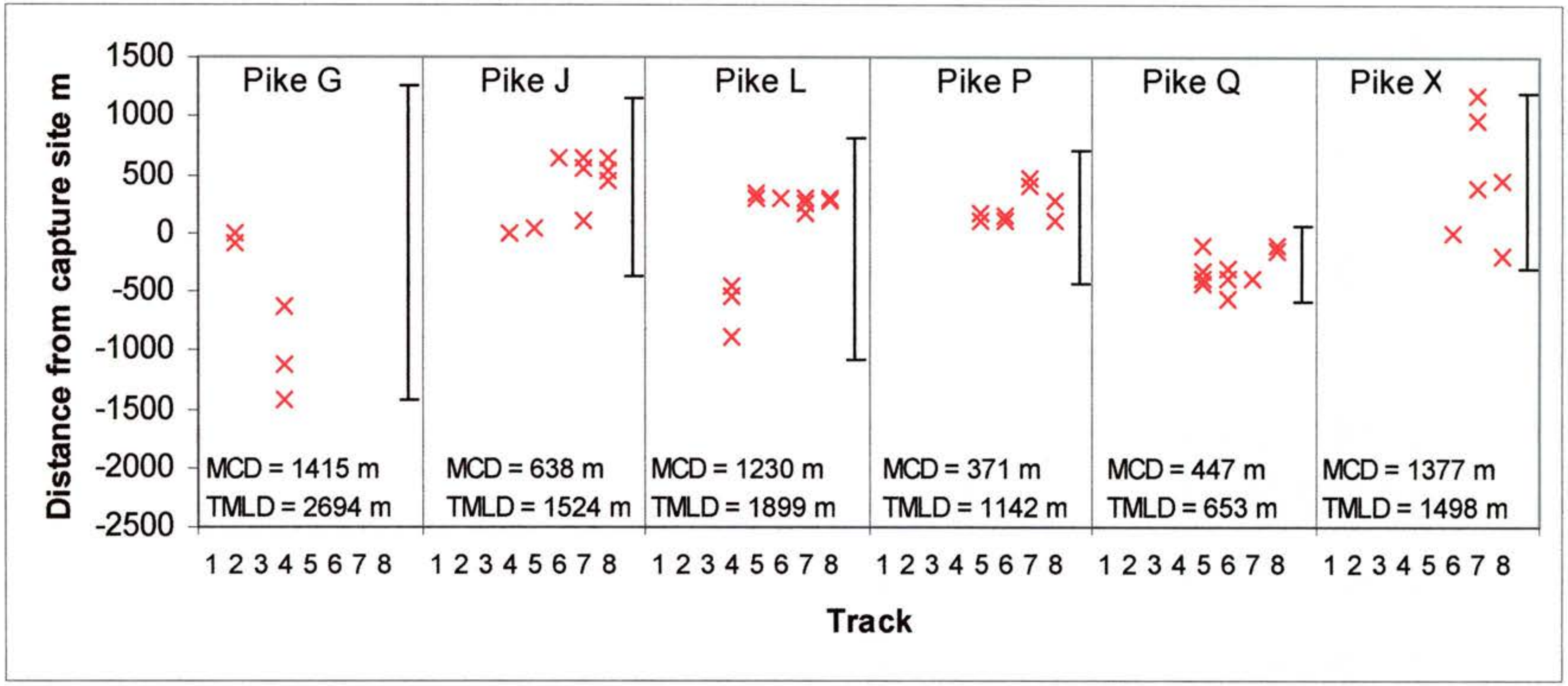
Pike G, J, L, P, Q and X could not be fitted into the above categories, however, of these fish Pike J and Q appeared similar in behaviour to permanent residents, but were excluded from this category due to their having widely dispersed C_{tx} home ranges, which were not utilised consistently throughout the period of tracking (Figure 4.7, Table 4.4).

The spatial behaviour of Pike L was also similar to that of permanent residents, however, this fish originally resided over 500 m further downstream than the locations occupied in subsequent *home range* tracks (Figure 4.7), and the RSI for this pike was relatively low (Table 4.4). It is not possible to say whether these differences in locations of ranges were due to excursive, emigrant or reproductive behaviour.

The behaviour of Pike P appeared similar to that of the two migratory pike, although upstream and downstream locations were separated by hundreds rather than thousands of metres. During winter and spring, Pike P resided around the Flood Relief Channel and Hummock Ditch, however during the summer, locations were closer to the capture location (Figure 4.1, Figure 4.7). The Range Shift Index for Pike P was relatively low (Table 4.4). Pike X was frequently found far upstream of its release site during the winter and spring of 2001/2002, although core ranges were widely dispersed at this time (Figure 4.7). No ranges overlapped between successive tracks for this pike (Table 4.4). The lack of subsequent year's data for both Pike P and Pike X precludes comment on the repeatability of the observed patterns.

Pike G moved downstream during the winter and spring of 2000 (Figure 4.7). Cluster centres were widely dispersed during the March 2001 track and no overlaps occurred between cluster polygons from different home range tracks (Table 4.4). Fixes collected after March 2001 showed Pike G ranging widely in a similar manner to that exhibited by Pike A prior to relocation, however the death of Pike G in spring 2001, precluded comment on whether the movements seen were repeated annually.

Figure 4.7 Locations of cluster centres (×) in each home range track, relative to their release point, for pike with **'indistinct patterns of behaviour'**. Furthest upstream (┬) and furthest downstream (┴) fixes, over the entire tracking period, are also shown for each individual. Distance between furthest upstream and downstream fixes = Total Maximum Linear Displacement (MLD). Distance between furthest upstream and downstream cluster centres = Maximum Core Displacement (MCD).

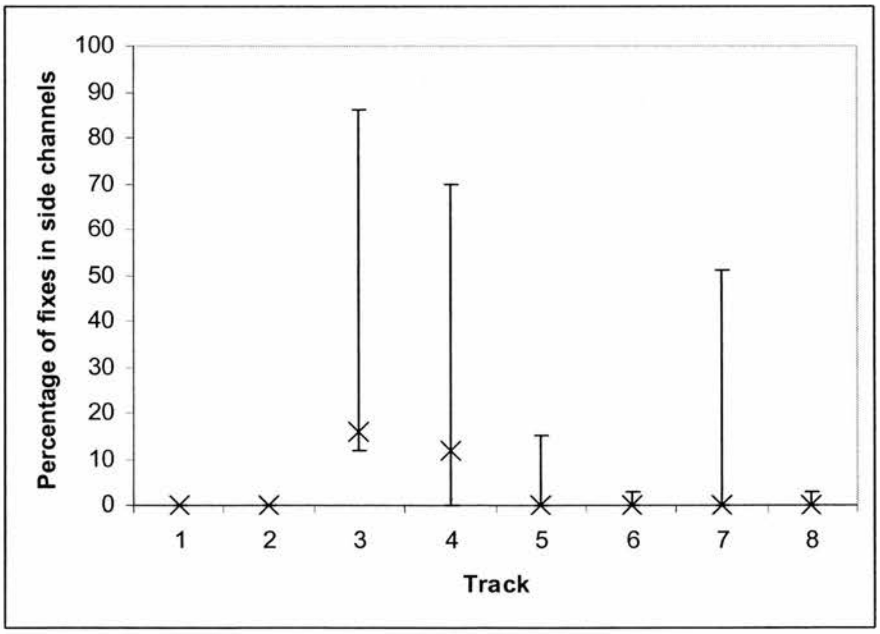


Utilisation of side channel habitats

Of the fifteen pike tracked in this study, only two (Pike X and Y) were never found in side channels either during or between *home range* tracks.

No pike were found in side channels during July and September 2000. Pike were often found in side channels during the December 2000 and March 2001 home range tracks, with generally lower percentage utilisation occurring in subsequent tracks, although over 50% of the fixes for one pike occurred within a ditch in December 2002 (Figure 4.8).

Figure 4.8 The median percentage of fixes occurring in side channels in each home range track together with maximum and minimum values recorded from individual pike.



4.4 DISCUSSION

Very low numbers of pike were detected on the CEH salmon counter, suggesting that either the weir forms a barrier to migration, or migration over the weir is naturally infrequent. Whilst radio tagged pike have been observed crossing the weir on occasion (*e.g.* Pike A), none has naturally done so regularly or repeatedly (CEH unpublished data). Due to the low numbers of pike seen, fish counter records were not examined in any greater detail. Although fish counters do not constitute a reliable method for studying pike movements in the River Frome, their use in other systems could potentially be informative, for example, during the anadromous spawning migration of Baltic pike (Müller, 1986).

Radio telemetry revealed that the variety of spatial behaviours found amongst River Frome pike was more complex than that proposed by Mann (1980), and pike could not be split simply into static and mobile groups. Whilst the 'permanent resident' category roughly corresponded with the idea of a static group, the term was avoided as it implies a lack of movement whereas, in reality the pike move between several intensively used core areas, and also perform excursive movements. Indeed, extensive movement between core areas can occur on a daily basis (Chapter 5).

The spatial behaviour of the pike population in the River Frome may represent a partial migratory strategy, this being a widespread phenomenon among many animal taxa, ranging from insects to higher vertebrates, in which one fraction of the population is migratory and the other sedentary (Lundberg, 1988). Before discussing partial migration further, it should be noted that whilst the predictable and synchronous movements of Pike I and K led to their categorisation as 'migrants,' in order for a behaviour to truly be categorised as migration the strategy must be of adaptive value (Lucas & Baras, 2001), and the adaptive significance of the strategy exhibited by these two pike remains to be tested. The observations were however consistent with the pike undertaking a spawning migration; the locations frequented whilst upstream being known spawning areas, and spawning of Pike K actually being observed.

Under the 'two pure strategies' hypothesis, migratory and non-migratory behaviours represent genetically determined strategies, with precisely equal average fitness (Lundberg, 1988).

The data suggest that the 'two pure strategies' hypothesis appears unlikely in this instance. A continuum of spatial behaviours seems to exist amongst riverine pike, with 'permanent residents' at one extreme (year-round occupation of a particular area) and 'migratory' individuals at the other (temporally and spatially separated seasonal home ranges); pike between these extremes occupying more dispersed ranges, or migrating over shorter distances. Although a series of categories of behaviour has been proposed ('permanent resident,' 'migratory,' 'emigrant'), the compartmentalisation should not be regarded as rigid and inflexible, as patterns of spatial behaviour exist which do not fit the proposed categories. These instances should not be regarded as exceptional results but as examples of the fluid nature of pike spatial behaviour, and the versatility of the species. The variation in spatial behaviour observed within individuals (*e.g.* Pike A) further suggests that the existence of 'two pure strategies' cannot explain the observed variety of spatial behaviour.

The variety of spatial behaviours observed may instead reflect the existence of different 'conditional strategies' with individuals possessing the ability to adopt either the 'migratory' or the 'permanent resident' option, or to become 'emigrants', depending upon the environmental conditions they encounter (Alcock, 1993).

Under the conditional strategy hypothesis individuals have the flexibility to adopt whichever tactic will yield the highest fitness gain given their competitive status; socially dominant individuals being in a position to select the better of the available strategies whilst subdominants 'make the best of a bad job' by adopting an option with lower fitness gains (but where the fitness benefits are still greater than those associated with unsuccessful attempts at dominance) (Alcock, 1993).

Such a situation appears to occur amongst juvenile Atlantic salmon, where good competitors are territorial, and the optimum strategy for some poorer competitors is to live in non-defended areas, or in the gaps between the territories of other fish (Metcalfe, 1998). Competitive ability may be phenotypically determined, therefore under the 'conditional strategy' hypothesis individual differences in behaviour may arise both as a result of phenotypic differences, and by the response of an individual to the behaviour of others (Magurran, 1993).

Whilst a variety of spatial behaviours has been described, explanations for the observed behaviours must of necessity be speculative at this stage. In blackbirds *Turdus merula* L., a species whose migratory behaviour appears to be explained by the conditional strategy hypothesis, there is a significant tendency for migrants to become residents the following season, rather than the reverse, indicating that age, or some correlated trait is an important condition for residency (Lundberg, 1988). The two migratory pike however were both large, relatively old, fish (Table 2.2), and a significant relationship between fork length and TMLD was found amongst the pike as a whole. Small pike are thought to be more confined to aquatic vegetation than larger pike, which are thought to be able to occupy a wider range of habitats (Grimm & Klinge, 1996). Due to the indeterminate growth of fishes, the largest fish will tend to be the oldest in the population. Therefore it appears unlikely that pike switch from a migratory to a resident strategy with increasing age, in the manner of blackbirds.

It is possible that the excursive movements by 'permanent residents' on occasion lead to relocation, if better conditions (in terms of prey availability, vegetative cover or competition) are discovered, although at present there is no way of knowing whether the excursions represent genuine 'discovery dispersal' (Begon *et al.*, 1990). Excursive movements may on occasion be related to discharge, many of the excursions seen in the present study occurring during times of flooding, whilst Langford (1979) noted that flood flows could lead to the 'displacement' of pike. The behaviour of Pike A was unusual in that several side channels (known or potential spawning grounds) were visited. The timing of these visits (early May) suggests that the excursive behaviour of this fish may have been associated with reproductive activity.

Miller *et al.* (2001) demonstrated the existence of natal homing amongst pike and due to the lack of a distinct spawning migration it may be that 'permanent residents' stay within the vicinity of their natal spawning site for their entire life, but that migratory and more mobile pike disperse, possibly to reduce intra-specific interaction (competition, risk of cannibalism *etc.*) or as a result of environmental factors, such as displacement during flood flows. The hypothesis that 'permanent residents' remain in the vicinity of their natal spawning site is one that can be tested experimentally (see below). The timing of any such dispersal is uncertain, although Mann (1980) suggested that age 0+ and

1+ pike may disperse more widely than older pike in the River Frome. Whilst young pike are thought to be restricted to areas of dense vegetation (Grimm & Klinge, 1996) this does not necessarily imply that the young pike will occur only in small areas. During summer months extensive growths of dense submerged vegetation can occur in the River Frome (Chapter 7), the continuity of which may facilitate the dispersal of the young fish. In this way, pike may establish remote home ranges, returning to their natal sites to spawn, before again 'homing' to their non-reproductive home ranges. The dispersal may be 'conditional,' being density dependent or in some way related to the competitive ability of the individual. Dispersal away from the spawning grounds may therefore represent the 'best of a bad job' for some pike, implying that 'migratory' pike may be poorer competitors than 'permanent residents.' The large size and relative age of the two migratory pike discovered in this study however implies that these were not subdominant, at least at that stage of their life history. Having lived successfully in an area away from the natal spawning ground, individuals may return to this area of known quality following spawning, rather than risking the less familiar habitat near the ditch. Alternatively, the 'migrant' behaviour may only arise amongst large pike, once they have reached a 'size refuge' at which they can explore the environment in relative safety. Flexibility within individuals clearly occurs however, with 'emigrant' pike apparently exploring new areas before resettling, and even 'permanent residents' showing excursive behaviour. The possibility of individual differences in habitat selection (Chapter 8) or dietary preference (Beaudoin *et al.*, 1999; Jepsen *et al.*, 2000) should also not be discounted as potential mechanisms leading to a variety of spatial behaviours in some instances.

Whilst pike are 'specialised' in terms employing a fast-start mode of ambush predation (Savino & Stein, 1989a), they are 'generalists' in terms of the range of species they consume (Mann, 1982), although some dietary specialisation may occur between individuals (*op. cit.*). In fishes, 'trophic breadth' may be correlated with behavioural and functional versatility or flexibility (Liem, 1984), with behavioural adaptations extending to include a diversity of spatial behaviours. Such versatility is likely to be a distinct advantage to predators which are 'generalists' in terms of diet, as it will allow for adaptation to a wide variety of intra and inter-specific factors, such as competitor density, risk of predation, differing anti-predator strategies amongst prey species *etc.*

Territory size can vary with the availability of resources, smaller territories commonly occurring when resources are more concentrated (Hixon, 1980), and a similar situation may occur with home ranges. Differences in prey distribution or habitat patchiness may therefore lead to different spatial behaviours being adopted in different areas of the river, with the more dispersed home ranges occurring in areas of lower resource availability. Lack of information on resource availability in different parts of the river, and the relatively low number of pike tagged precludes comment on whether resource availability in different parts of the river influences spatial behaviour. During winter months, large aggregations of dace occur in the lower River Frome, particularly in the tidal section (> 6 km downstream of the main study area) (Clough, 1998) and it was thought that pike might migrate to feed upon these aggregations, however no such movements were noted during the present study.

Habitat surveys could not be conducted in the downstream areas occupied by 'migrant' pike, due to constraints of time and access, but, superficially, the habitat in the downstream areas did not appear to differ greatly from that available in the main study area.

The small number of radio tagged pike that were classed as 'migrants', together with the low numbers of pike detected on the CEH salmon counter, suggest that the 'migratory' strategy is relatively rare in the River Frome (although an extrapolation of the proportion of behaviours from 15 animals to the population should be treated with appropriate caution). The situation appears to be different in the River Meuse basin, Belgium, where Ovidio & Philippart (2002) radio tagged eight pike, all of which were reported as having performed upstream spawning migrations, followed by downstream, post-spawning movements. The same authors conducted a further study of the seasonal movements of pike in the Meuse basin, during which six radio tagged pike were tracked for 149 to 349 days (Ovidio & Philippart, submitted)[1]. All six pike were described as migrating away from their capture location to spawning sites < 1 km to > 15 km distant, despite the capture area itself being a known spawning ground. Outside of the spawning period the patterns of spatial behaviour appear similar to those seen in the River Frome, with pike appearing to occupy multi-nuclear home ranges (Ovidio & Philippart, submitted). After spawning, the pike all moved away from their spawning grounds, but only one of the six returned to the area it had occupied prior to spawning. Although the numbers of pike tagged by Ovidio & Phillipart (2002, submitted) were low, the results suggest that the proportion of pike employing the migratory strategy may vary between rivers.

[1] This work was presented at the Fifth Conference for Fish Telemetry held in Europe, 2003, and has been submitted for publication in the Conference proceedings. The results are quoted with the kind permission of the authors.

Other interesting differences in behaviour were observed; River Meuse pike spent only five to 25 days on the spawning grounds, much shorter than the times observed for the two migratory pike in the River Frome, and migration was apparently not confined to times of increased discharge, but also occurred during flows close to the mean annual discharge for the river (Ovidio & Philippart, submitted).

Although pike have been shown to occupy home ranges, the extent to which territorial defence occurs remains unknown at present. Size dependent interference competition, kleptoparasitism, agonistic displays and fighting behaviours have been observed in pike held in aquaria (Fabricius & Gustafson, 1958; Eklöv & Diehl, 1994; Nilsson & Brönmark, 1999; Nilsson *et al.*, 2000), but due to the difficulties associated with directly viewing fish in the wild, the incidence of such behaviours under natural conditions cannot easily be determined. Pike do not defend an exclusive outer territory, such as the entire TMLD, as overlaps from up to five other radio tagged fish can occur within an individual's C_{tx} core range, and, on several occasions (outside of spawning activity) pike have been found very close together, in locations where they would have been clearly visible to one another (Hodder *et al.*, submitted). The possibility remains that the actual site occupied by pike at any one time may be defended against incomers, with smaller pike avoiding larger, potentially predatory, pike. Larsen (1966) noted that up to four pike of similar size could be found within 30 – 40 m^2 of river, but that two pike of different sizes were never caught at the same time in the same locality. At spawning time, intra-specific interaction may be more aggressive than at other times of year, with scars and bite marks commonly occurring on pike of both sexes at this time (pers. obs., M. Ovidio, pers. comm.).

In addition to being of general ecological interest, an understanding of the spatial behaviour of animals is important for their management and conservation. Clearly, side channels are of great importance to pike under certain conditions and the conservation value of these habitats should therefore be recognised. The exact reasons for the frequent utilisation of these habitats are at present unknown. Although these areas are used for spawning, utilisation also occurs far in advance of the recognised spawning period for this species. Whilst most pike utilised the ditches nearest to the areas where they normally resided, the two migratory pike both moved several kilometres upstream during a flood in 2001, swimming past numerous side channels before arriving in the main study area. Off-river habitat use is discussed further in Chapter 6.

In terms of population structure, it appears that although spawning site fidelity occurs, straying can also occur, which, together with the fact that pike may visit several spawning areas during the spring (*e.g.* Pike K) suggests that each side channel does not hold a unique, genetically distinct, spawning population and that the spawning ground for pike may consist of a number of separate areas, in close proximity to one another. In combination with the apparent behavioural flexibility of individuals, this suggests that the loss of one particular spawning site may not lead to a loss of genetic diversity within the population, providing that suitable alternative sites still exist nearby. The effects of varying the number of spawning sites, and thus the density of juveniles in these areas, would have on the proportion of 'permanent resident,' 'migratory' or 'emigrant' pike cannot be predicted at present.

Through the use of radio telemetry, varying patterns of spatial behaviour have been discovered in other fish species, *e.g.* paddlefish *Polyodon spathula* (Walbaum) (Zigler *et al.*, 2003), Mary River cod, *Maccullochella peelii mariensis* Rowland (Simpson & Mapleston, 2002) and nase *Chondrostoma nasus* L. (Huber & Kirchofer, 1998), and it is being increasingly recognised that fish populations are comprised of individuals, capable of displaying a variety of patterns of behaviour. Ecological parameters are often described by reference to means or medians, and a measure of variability, such as standard deviation or interquartile range, however, a single summary statistic can mask considerable individual variation (Magurran, 1993). With the diversity of spatial behaviours observed in this study, providing a single mean and standard deviation to describe the longitudinal distribution of pike would clearly have been misleading. Variability in movement behaviour among individuals in a population of fish is considered an important ecological behaviour in the long-term maintenance of fish populations, with 'mobile' individuals providing the means to colonise new areas (Stott, 1967), and potentially leading to gene flow between spawning grounds (Simpson & Mapleston, 2002). Furthermore, individual variation in behaviour can influence population dynamics and speciation (Magurran, 1993). Through the study of the movements of individuals, detailed, accurate, data on spatial behaviour can be obtained. However, large samples and appropriate experimental designs are required before such individual-based information can be reliably incorporated into population scale models.

4.5 FURTHER WORK

To fully understand the incidence and significance of the various strategies within the population, it is essential to learn more about the movements of smaller pike than those that were tagged during the present study. Ideally pike need to be followed throughout their lives.

The development of techniques for the external attachment of miniature radio tags to pike gives researchers the opportunity to track juveniles, all previous telemetry studies having been conducted on adult pike. In May 2003, one juvenile pike (L_F = 22 cm) was caught by electric fishing and successfully fitted with a Biotrack TW-4 tag, using the method described by Beaumont & Masters (in press) (CEH unpublished data). Tagging more pike of this size is clearly desirable, and could be used to test whether these fish have more restricted home ranges than adults, or whether dispersal occurs amongst smaller fish, as proposed by Mann (1980). Tagging of smaller fish is also required to determine whether the 'migratory' strategy occurs in this, more vulnerable, size class of pike.

The minimum size of currently available radio and acoustic tags restricts the lower size limit of fish that can be tagged to around 15 cm (Lucas, 1999). Even if miniaturisation eventually produces a tag capable of being fitted to fish below this size, battery life of such a tag will be short; the smallest tags currently available (0.35 g to 0.50 g) having battery lives of 1 to 3 weeks (Kenward, 2001). Due to the effects of tagging, the amount of time during which valid data could be collected would be even shorter. Passive integrated transponder (PIT) tags offer a method of tagging young-of-the-year pike (Chapter 8). PIT tags transmit a unique code upon interrogation by a suitable detector (Lucas, 1999). The tags are small (12 mm x 2.12 mm, weight in air 0.1 g) and can be internally implanted in fish from 6 cm upwards, enabling individuals to be identified throughout their lives.

Young-of-the-year (and older) pike are currently being implanted with PIT tags in the River Frome, as part of the NERC funded Lowland Catchment Research (LOCAR) programme. PIT tag detectors are being installed within existing side channels, to automatically record the passage of tagged fish, potentially providing a great deal more information than would be possible through periodic recaptures alone. Young-of-the-year pike are also being PIT tagged in the River Meuse basin, as part of a separate study (Ovidio & Philippart, submitted).

Assuming pike are tagged on their natal spawning grounds, it should be possible to determine whether natal homing occurs, and recaptures can also be used to determine the dispersal of the tagged fish away from the spawning grounds. Comparing and contrasting the results of tracking studies from these two different river systems may shed further light on the versatility of riverine pike, and the adaptive significance of the various spatial behaviours that have been observed.

The influence of habitat quality on pike spatial behaviour is an area worthy of further study. By holding radio tagged pike in enclosed systems and experimentally manipulating prey or habitat availability, the effects of variation in these factors on spatial behaviour could be investigated, although such experiments would require appropriate licensing. Generally, more concentrated home ranges might be expected with greater resource availability (Hixon, 1980), whilst a more wandering strategy, akin to that seen in some lacustrine pike, *e.g.* Diana *et al.* (1977), Lucas *et al.* (1991), might be expected under conditions of lower resource availability. The influence of competitors could also be studied by introducing more pike into the system.

The behaviour of the migratory pike, and of residents following excursions, demonstrates that pike are able to home to specific areas of the river. The mechanism by which this is achieved is at present unknown, although the fact that both migratory pike returned upstream during flood conditions makes it unlikely that visual cues are used, at least for long term migration. At such times, the river becomes extremely turbid, with visibility being reduced to < 10 cm (pers. obs.).

Olfaction provides a possible means by which pike could navigate long distances, and pike may home using olfactory cues in a manner similar to that discovered in salmon (Helfman *et al.*, 1997b). The importance of olfaction in homing behaviour is soon to be investigated by displacing radio tagged pike from their known home ranges in the River Frome, transporting them to novel sites, and comparing their homing behaviour with that of similarly translocated pike that have had their nares temporarily plugged with petroleum jelly (R.E. Gozlan, pers. comm.). By introducing pike into new areas, investigation of how pike explore these areas and of how multinuclear home ranges become established may also be possible (R.E. Gozlan, pers. comm.).

4.6 SUMMARY

1) Automatic fish counters are not an appropriate method of studying pike spatial behaviour in the River Frome, due to the low number of pike movements recorded.

2) Through examination of the locations of seasonally-determined home ranges, in addition to radio tracking fish throughout the year, a continuum of spatial behaviours was revealed. Rather than a split into simple 'static' and 'mobile' categories, 'permanent resident' and 'migrant' behaviours occur, with pike between these two extremes occupying more dispersed home ranges, or migrating over shorter distances. 'Emigrant' behaviour was also observed.

3) There were no obvious differences in spatial behaviour between males and females.

4) There was a significant positive correlation between the fork length of pike and the Total Maximum Linear Displacement (the distance between the furthermost upstream and downstream fixes over the entire period of time during which the pike was tracked), although wide variation could occur between similarly sized fish.

5) Due to the apparent continuum of behaviours, and the observed variation within individuals, the 'partial migration' of the pike population does not appear consistent with the 'two pure strategies' hypothesis. 'Conditional' strategies may be occurring, but further work is required to investigate the incidence and significance of the different spatial behaviours observed.

6) Spawning site fidelity and straying were observed, movements between different side channels during a spawning season suggesting that spawning grounds consist of a number of separate areas in close proximity to one another.

7) Side channels appear to be of great importance to pike, a subject returned to in Chapter 6.

CHAPTER 5

Diel movement patterns of riverine pike

During interactions between predators and their prey, temporally variable environmental factors may influence the chances of successful predation events occurring. The daily cycle of light and dark is one such factor that may affect the 'balance of power' between predator and prey. During dawn and dusk, aquatic predators have a competitive advantage over prey; a predator in shade potentially being able to detect prey fish swimming in open water at a greater distance than the predator can itself be detected (Helfman, 1981; Cerri, 1983; Pitcher & Turner, 1986). Additionally, schooling, which has an anti-predator function (reviewed in Pitcher and Parrish (1993)) breaks down at low light intensities, and this can lead to individual prey fish being exposed to a greater risk of predation (Dobler, 1977).

Distinct diel patterns of migration have been reported in adult, juvenile and larval river fishes, and these are thought to represent strategies to minimise predation risk, with fish moving between feeding locations and either diurnal or nocturnal refuges *e.g.* Baade & Friedrich (1998), Clough & Ladle (1997), Copp & Jurajda (1993), Borcherding *et al.* (2002). However the diel behaviour of pike, an apex predator, has not previously been examined in rivers. In this chapter, the daily movement patterns of pike are described and discussed in relation to the behaviour of prey fish. The daily movement patterns of pike are further discussed in relation to the strategies available to sit-and-wait predators, and also to optimal foraging theory.

Sections of this chapter have been included in a paper submitted to the *Journal of Fish Biology* (Masters *et al.*, submitted b), whilst results from the manual recording of activity event data were included in Beaumont, Hodder, Masters, Scott & Welton (submitted).

5.1 INTRODUCTION

Diel patterns of migration have been reported in numerous riverine fishes (*op. cit.*) and movements between locations often occur around sunrise and sunset, a time when predators have a competitive advantage over prey (*op. cit.*). Rapid movements can occur, for example, around sunrise and sunset. Radio tagged dace have been followed moving distances of 260 m in < five minutes, between diurnally occupied unvegetated areas, putative refugia, and nocturnally occupied feeding sites, downstream of riffles (Clough & Ladle, 1997).

Pike are generally regarded as displaying either crepuscular (Malinin, 1970) or diurnal (Diana, 1980) peaks in activity, with nocturnal inactivity (Malinin, 1970; Diana, 1980; Mackay & Craig, 1983; Lucas *et al.*, 1991). Jepsen *et al.* (2001) reported that pike in Lake Ring, Denmark, were predominantly nocturnal during June and July, however, positional fixes were collected at 6 h intervals and movement assessed as the distance between successive fixes. Movement could therefore have occurred during dawn/dusk periods rather than during the hours of darkness.

Pike employ an ambush mode of predation (Savino & Stein, 1989a), but within the broad category of ambush, or sit-and-wait predation, a variety of foraging strategies may be employed by different species. The goshawk *Accipiter nisus* L. for example employs a mode of predation described as 'short-stay perched hunting,' in which the goshawk scans its surroundings from a perch, before moving onto another if prey (such as woodpigeons *Columba palumbus* (L.)) are not detected, repeating the process at fairly short intervals (Kenward, 1982). In contrast, the pit viper *Gloydius shedaoensis* Zhao feeds on migratory birds, often favouring one ambush site, usually a tree branch, for the entire bird migration period (Shine & Li-Xin, 2002). The benefits of employing either strategy may depend upon factors such as prey encounter rate and the energetic cost of movement. Within rivers, moving between potential ambush sites may be particularly energetically expensive, especially if moving in an upstream direction. Due to the adaptations of the pike for rapid acceleration rather than sustained swimming (Webb, 1984a), prior to the commencement of the study it was hypothesised that such costs would prove unacceptable to pike, and that, within rivers, only limited movements would occur, with pike remaining in one small area on a daily basis (Welton *et al.*, 2003). Considerable movements were detected during the *pilot* track however, and frequent relocations were observed, with successive hourly fixes being separated by distances of up to 250 m on occasion (Welton *et al.*, 2000). Consequently, the hypothesis that pike display limited movements on a daily basis, remaining at a single location in the river, was rejected.

Hodder *et al.* (submitted) used the straight-line distances between consecutive hourly fixes collected during the *pilot* track (Chapter 2) to demonstrate significant differences in mobility throughout the diel cycle, with median distances moved being 13 m at both dawn and dusk, compared with 4 m during the day and 1 m at night. Hodder *et al.* (submitted) defined dawn and dusk as being between 1 h before and 2 h after sunrise, and dusk 2 h before and 1 h after sunset. Dawn and dusk time periods therefore covered the whole period of changing light intensity at the interfaces between day and night.

In this chapter, the *pilot* track data are further examined to test the hypothesis that pike follow a regular patrol route. The results of an intensive sampling strategy, with a high degree of spatial and temporal resolution, are also presented, and are used to test the whether the summertime crepuscular activity of pike (Hodder *et al.*, submitted) persists throughout the year.

5.2 METHODS

In all subsequent analyses, a modified version of RANGES V (Kenward & Hodder, 1996) was used to calculate straight-line distances between successive fixes, inter-fix distances measured along the midline of the river and distances between pike location records and fixed points.

5.2.1 *Pilot* track

During the *pilot* track in June 2000, location data for Pike A and Pike B (Table 2.2) were recorded at hourly intervals over five consecutive 24 h periods (Chapter 2) and these data are used to test the hypothesis that pike follow a regular patrol route. The straight line distance along the midline of the river was calculated, between each pike location record and a fixed point (the East Stoke gauging weir). The location of a pike at any particular fix could then be expressed as a distance from the weir and the pike locations on successive dates examined for any regularity of pattern. Neither pike passed over the weir during the *pilot* track.

5.2.2 *Continuous* tracks

During the *pilot* track and subsequent *24 h* and *diurnal* tracks, fixes were collected at hourly intervals (Chapter 2). A gap of one hour between fixes meant that a greater number of pike could be included in each track than would have been possible with a shorter sampling interval, whilst significant diel movement patterns could still be revealed (Hodder *et al.*, submitted). However, with an hourly sampling interval the actual distances moved by the fish are likely to be underestimated. Ovidio *et al.* (2000) suggested the use of models to estimate true distances moved from tracks with different sampling intervals. The possibility of similarly correcting hourly data was investigated by comparing distances calculated from five-minute interval tracking of pike with distances calculated from the same data, sampled to give an hourly inter-fix interval.

Thirteen *continuous* tracks, each of four hours duration, were conducted, during which one positional fix for Pike L (Table 2.2) was recorded every five minutes (Table 2.6, Chapter 2). *Continuous* tracks were conducted between 0300 hours and 0700 hours or between 1000 hours and 1400 hours, these time periods being chosen in order to sample activity during both dawn and day time periods. The 0300 hours to 0700 hours track extended beyond the dawn period as defined by Hodder *et al.* (submitted) (Section 5.1) consequently *continuous* tracks from this time period are subsequently referred to as morning tracks. Personnel constraints did not allow for *continuous* tracking to take place in the evening at this time.

As described in Chapter 2, for each fix, the fieldworker also recorded an estimate of the accuracy of that fix, longitudinally (a) and laterally (b) where both a and b were distances in metres.

The minimum movement estimate (MiME), an estimate of the shortest distance that could have been moved between successive fixes, was calculated by adding the largest error value (a or b) from the first of a pair of fixes to the largest error value (a or b) from the subsequent fix, then subtracting this combined error value from the straight line distance between fixes. Exceptionally, when a pike swam around one of the few bends in the study section of river, the straight line distance clearly underestimated the actual distance swum, and the distance along the midline of the river was used in place of the straight-line distance between the two fixes.

In addition to calculating MiMEs for successive five-minute interval fixes, MiMEs were also calculated for the data sampled at hourly intervals, starting with the first fix of the track. By summing the MiME values from both five-minute and hourly sampling intervals, two estimates were obtained for the total distance moved during each *continuous* track, allowing comparisons to be made between the movement estimates obtained by the different sampling intervals.

Five-minute period minimum movement estimates were also used to describe movement activity within each time period, and to compare movement activity between time periods.

Activity during morning and day *continuous* tracks was further investigated using motion-sensing telemetry. The TW-5 radio tag contains an omni-directional motion-sensing switch, connected to a microcontroller which sets the transmitter pulse rate (Beaumont *et al.*, 2002a). The regular pulse interval (1.3 s) switches to a noticeably shorter pulse interval when the fish is actively moving (Beaumont *et al.*, 2002a). Whilst the output from the tag can be recorded using automatic data loggers (Beaumont *et al.*, 2002a; Beaumont *et al.*, submitted), a method was also developed by which fieldworkers could record motion-sensing data during manual tracking. During each five-minute interval of *continuous* tracking, the number of 'activity events' that occurred was recorded, where an 'activity event' was defined as a period of time when the tag was transmitting at the faster pulse rate. Whilst the information recorded using this method was somewhat limited, more detailed manual recording of activity data (counting the actual number of rapid pulses or recording the duration of 'activity events') was found to be impractical under fieldwork conditions.

For each of the *continuous* tracks, the proportion of five-minute periods containing 'activity events' was determined, and these proportions were then compared between morning and day time periods using a Mann-Whitney test. The actual numbers of 'activity events' occurring in five-minute periods during all morning and day tracks were also compared using a Mann-Whitney test.

The duration of periods of inactivity were compared between morning and day tracks, using a Mann-Whitney test, where inactivity was defined as a five-minute period containing no 'activity events'. The exact timing of 'activity events' was not recorded, so minimum estimates of the time interval between events were used. For example, if for three successive five-minute periods the number of 'activity events' recorded were one, zero and one, the minimum time interval that could have passed between 'activity events' would have been five minutes (with the 'activity events' occurring at the end of the first five-minute period and the beginning of the second).

5.2.3 *24 h* and *diurnal* tracks

The discovery of a crepuscular pattern during the *pilot* track (Hodder *et al.*, submitted) led to the monthly series of *24 h / diurnal* tracks being executed, during which fixes were collected at hourly intervals from pike within an 800 m section of the River Frome. The aim of these tracks was to study the diel pattern of movements and to examine whether diel pattern changed with season. The method used during *24 h / diurnal* tracks is described in full in Chapter 2.

Analysis of 24 h and diurnal tracking data (26 July 2000 to 28 February 2001)

Three *24 h* and five *diurnal* tracks were conducted between 26 July 2000 and 28 February 2001. On each date, minimum movement estimates (MiMEs) were calculated between successive hourly fixes for each of three to four pike (Table 5.1). In order to avoid compounding any potential errors, correction factors were not applied to hourly MiMEs, the results of comparisons between distance estimates obtained from five-minute and hourly sampling intervals during *continuous* tracking having shown a high degree of variability (Sections 5.2.2 & 5.3.2).

Using data pooled from all fish, for each date, the median MiME was calculated during dawn, day and dusk time periods, where dawn and dusk were defined as in Hodder *et al.* (submitted) (dawn = 1 h before to 2 h after sunrise, dusk = 2 h before to 1 h after sunset). For the three *24 h* tracks, median MiMEs were also calculated for the night time period. For each date on which tracking took place, minimum movement estimates were compared between time periods using non-parametric tests (Kruskal-Wallis or Mann-Whitney).

Table 5.1 The dates and durations of *24 h / diurnal* tracks (26 July 2000 to 28 February 2001), together with environmental information and the identity of pike followed.

Date	Track duration (h)	Mean water temperature °C	Mean discharge m^3s^{-1}	Pike tracked
26 Jul 2000	24	15.3	2.5	A B C
24 Augt 2000	24	17.2	2.1	A B C
26 Sep 2000	24	14.7	4.9	A B C
2 Nov 2000	15	not recorded	11.4	A B C I
21 Dec 2000	16	9.5	16.5	A B C I
31 Jan 2001	16	not recorded	14.7	A B C I
28 Feb 2001	17	7.2	11.2	A B C I

Analysis of diurnal tracking data (26 April 2001 to 1 March 2002)

Greater experience of tracking techniques amongst fieldworkers made it possible to increase the number of pike followed in later *diurnal* tracks, thus allowing more detailed analyses of the diurnal patterns of movement throughout the year. Six to eight pike were included in *diurnal* tracks between April 2001 and March 2002 (Table 5.2). Each of the ten tracking sessions conducted during this period being categorised as having occurred in one of four seasons (Table 5.2). Due to the increased sample size, more appropriate statistical techniques could be used than was possible when analysing early *24 h* and *diurnal* tracks. Sample size was now sufficient such that movement data calculated from individual fish could be compared between seasons and between time periods using non-parametric techniques, whereas for tracks which involved lower numbers of fish (26 July 2000 to 28 February 2001) individual data were pooled prior to analysis. Non-parametric techniques were used as the large number of occasions when pike did not move in an hour rendered data non-normal, even after transformation. As the analysis of data collected during these later *diurnal* tracks was based on results from individuals, the potential existed to use two-way tests (*e.g.* Friedman test), to investigate variability amongst individuals, as well as differences between time period or season. Such tests were not conducted however, as the number of observations of an individual fish within a season was felt to be too low to allow valid comments on individual variability.

Table 5.2 The dates and durations of *diurnal* tracks (26 April 2001 to 1 March 2002), together with environmental information and the identity of pike followed.

Date	Track duration (h)	Mean water temperature °C	Mean discharge m^3s^{-1}	Season	Pike tracked
26 April 2001	17	11.1	7.2	Spring	A B C G I N
4 June 2001	20		4.1	Summer	B C L M N O
2 July 2001	20	17.8	2.6	Summer	B C L M N O
7 September 2001	15	15.5	1.9	Summer	B C L M O S V
3 October 2001	15	14.3	3.2	Autumn	B C L O V
30 October 2001	13	13.0	3.3	Autumn	C L M O P V
28 November 2001	12	7.6	2.4	Winter	B C H L M O V Y
20 December 2001	12	6.5	3.2	Winter	B C L M O V X Y
29 January 2002	13	9.6	5.3	Winter	B C L M O V Y
1 March 2002	14	7.6	6.0	Spring	B C I L M O V Y

The minimum movement estimate (MiME) was calculated for each hour, for all pike, during each of these *diurnal* tracks, using the method outlined above (Section 5.2.2). As with data from earlier *24 h* and *diurnal* tracks, correction factors were not applied to hourly MiMEs due to the high degree of variability found between distance estimates obtained from five-minute and hourly sampling intervals during *continuous* tracking (Sections 5.2.2 & 5.3.2). Minimum movement estimates were classed as having occurred during one of the three time periods; dawn, day or dusk (Hodder *et al.*, submitted).

To examine whether the amount of time a pike spent immobile varied with time period or season, the proportion of hours when no movement occurred (MiME = 0 m) was calculated, within each time period, for all pike during every track. These data were compared between time periods within a season, and between the same time period across the seasons, using Kruskal-Wallis or Mann-Whitney tests.

The scale of movements was examined by calculating the mean MiME in each time period, for all fish, on each tracking date. Within each season, the means from all fish were compared between time periods using a Kruskall-Wallis test. The mean MiME values from each time period were also compared, between the seasons, using Kruskal-Wallis tests.

Within seasons, where a pike was tracked on more than one occasion, the mean proportion of hours when no movement occurred, and the mean MiME, were both calculated from all observations of the fish within that season.

5.2.4 *Home range* tracks

During *home range* tracks, three positional fixes were recorded for each pike on each date, over a thirteen-day period (Chapter 2). Tracking took place in the morning (in the two hours after sunrise), in the evening (in the two hours before sunset) and midway between these two times, therefore fixes were recorded in the dawn, day and dusk periods as defined by Hodder *et al.* (submitted). Whilst only one fix was recorded for each fish in each time period, the level of activity within the population could be compared between time periods by making use of the motion-sensing properties of the TW-5 radio tag. Each time a fish equipped with a TW-5 tag was found, the signal from the tag was listened to for a five minute period and the number of 'activity events' heard was recorded. where an 'activity event' was defined as a period of time when the tag was transmitting at the faster pulse rate (Section 5.2.2).

Within each *home range* track, the proportion of fixes during which 'activity events' were recorded was determined separately for each individual pike. With the exception of the July 2000 track (*home range* track number 1), the proportions of fixes during which activity occurred were then compared between time periods (dawn, day, dusk) using Kruskal-Wallis tests. The July 2000 track was not examined in this way due to the low number of pike (n = 3) followed during this track (Table 2.4).

Similarly, within each *home range* track, and for each pike individually, the mean number of activity events heard in each time period was calculated. Mean numbers of activity events were then compared between time periods, within each *home range* track, using Kruskal-Wallis tests, with the exception of the July 2000 track (*home range* track number 1), when the number of fish followed ($n = 3$) was too low to allow these tests to be performed.

Activity event data were not recorded during March 2001 (*home range* track number 4), as at this time, tracking was being performed from a boat due to restrictions placed on fieldwork to prevent the spread of foot and mouth disease (Chapter 2). Fixes had to be recorded as the fish were passed and a five-minute listening period could not be conducted under these conditions.

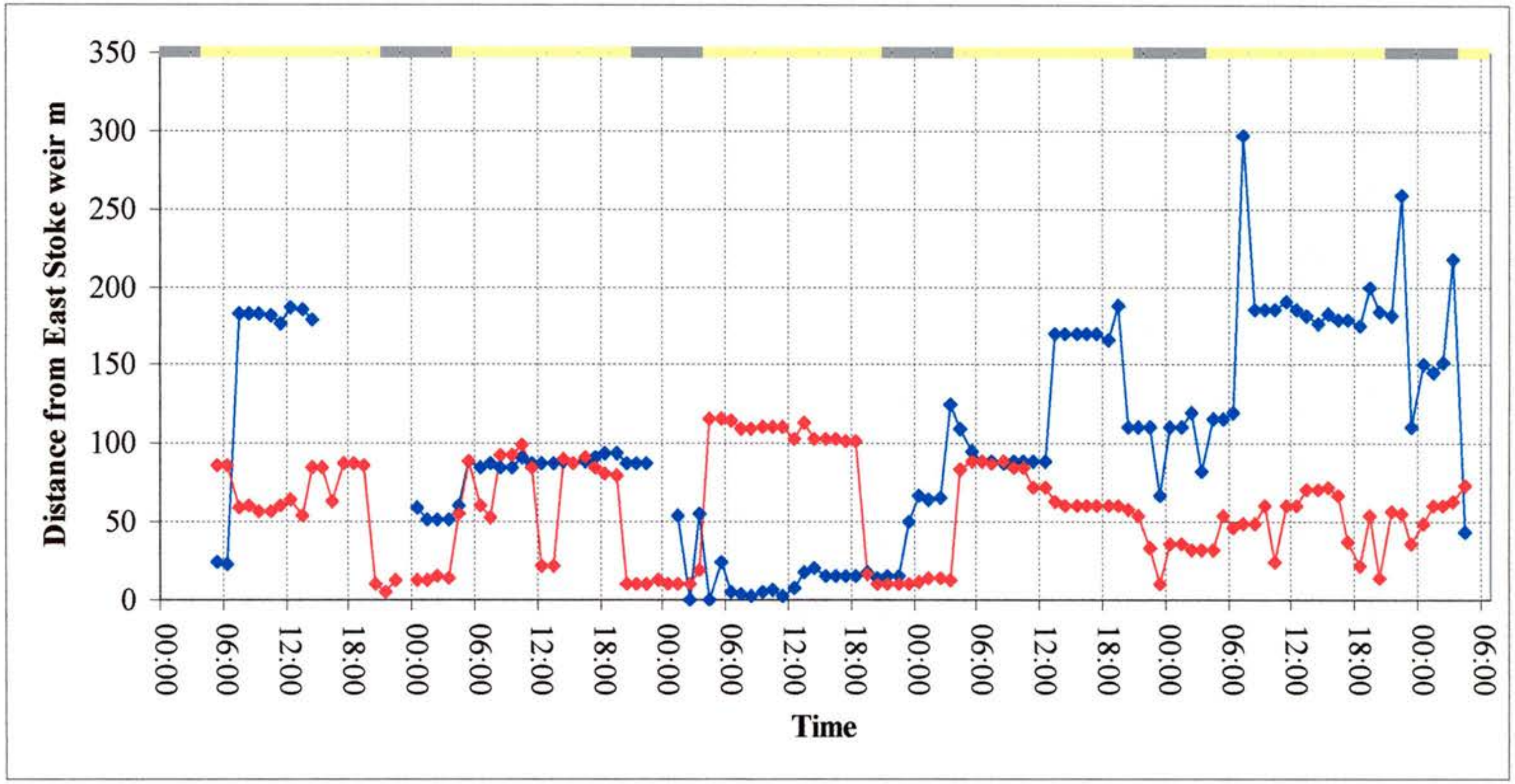
5.3 RESULTS

5.3.1 *Pilot* track

During the *pilot* track (12 to 17 June 2000) daily mean water temperature was 16.3 ± 0.1 °C (± S.E.) and daily mean discharge 4.0 ± 0.02 m^3s^{-1} (± S.E.). Sunrise occurred at 0354 hours and sunset at 2022 hours.

During the 120 h of tracking, there was an indication that Pike B favoured a particular location at night; the same stretch of river being visited on the first three nights, although Pike A did not appear to favour a particular nocturnal location (Figure 5.1). Whilst both pike made repeated use of certain stretches of river during daylight, there was no consistent pattern to the areas visited (Figure 5.1). Consequently, the hypothesis that pike follow a regular patrol route is rejected, although it appears that particular areas of river may be favoured at certain times.

Figure 5.1 The distance from the East Stoke weir of fixes recorded for Pike A (◆) and Pike B (◆), as measured along the midline of the river, during the *pilot* track (12 to 17 June 2000). The duration of day (—) and night (—) was determined by reference to sunrise and sunset times. Fixes have been joined by lines for ease of viewing; however the lines do not necessarily represent the path travelled between fixes.



5.3.2 *Continuous* tracks

Consistent with the results of Hodder *et al.* (submitted), Pike L appeared to move greater distances (as calculated using a five-minute sampling interval) during morning *continuous* tracks (mean = 104 m) than during day tracks (mean = 7 m) (two tailed two-sample *t*-test, assuming unequal variance: $n_{\text{morning}} = 6$, $n_{\text{midday}} = 7$, $t = 2.33$, $P = 0.07$). Within each time period however, considerable variation occurred in distances moved. During both time periods, there were occasions when Pike L remained stationary throughout the entire track (Figure 5.2). Minimum movement estimates (MiMEs), of 0 m over a five-minute period were common, comprising 87 % and 96 % of MiMEs in the morning and day respectively (Figure 5.3). Relatively long distance movements were found to occur (Figure 5.3), a minimum movement estimate of 105 m in five minutes occurring on one morning, this movement taking place in a downstream direction.

Significantly higher proportions of five-minute periods contained 'activity events' during morning tracks (median = 0.57) than during day tracks (median = 0.31) (Mann-Whitney test: $n_{\text{morning}} = 6$, $n_{\text{midday}} = 7$, $W = 59.0$, $P = 0.02$). The median number of 'activity events' recorded from during five-minute periods in the morning (median = 1 'activity event' minute^{-1}, interquartile range = 0 to 4) was also significantly higher than during the day (median = 0 'activity events' minute^{-1} interquartile range = 0 to 1) (Mann-Whitney test: $n_{\text{morning}} = 290$, $n_{\text{midday}} = 389$, $W = 117851$, $P < 0.0001$). Periods of inactivity were significantly longer during day (median = 15 minutes) than during morning *continuous* tracks (median = 7.5 minutes) (Mann-Whitney test: $n_{\text{morning}} = 42$, $n_{\text{midday}} = 44$, $W = 1409.5$, $P < 0.001$).

Figure 5.2 Estimates of the total distance moved, derived from five-minute sampling intervals, during morning and midday *continuous* tracks of Pike L.

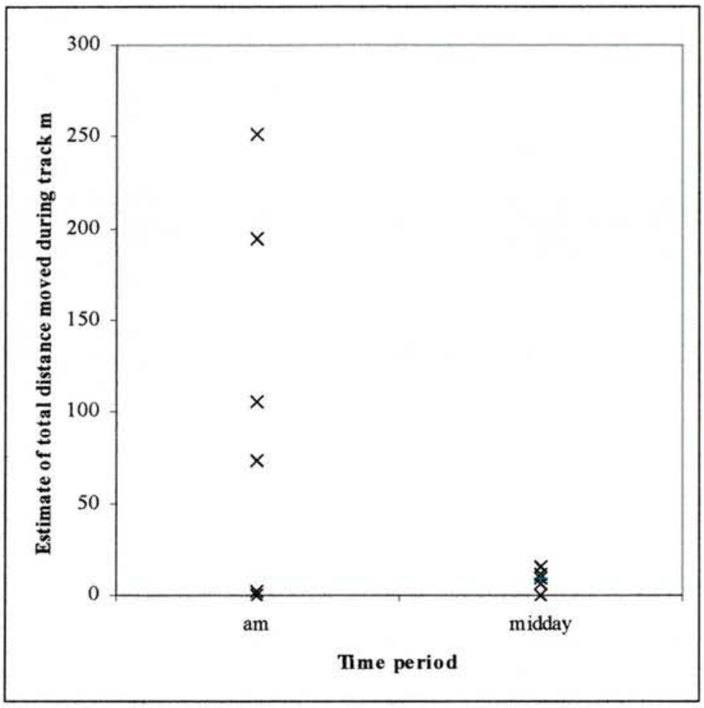
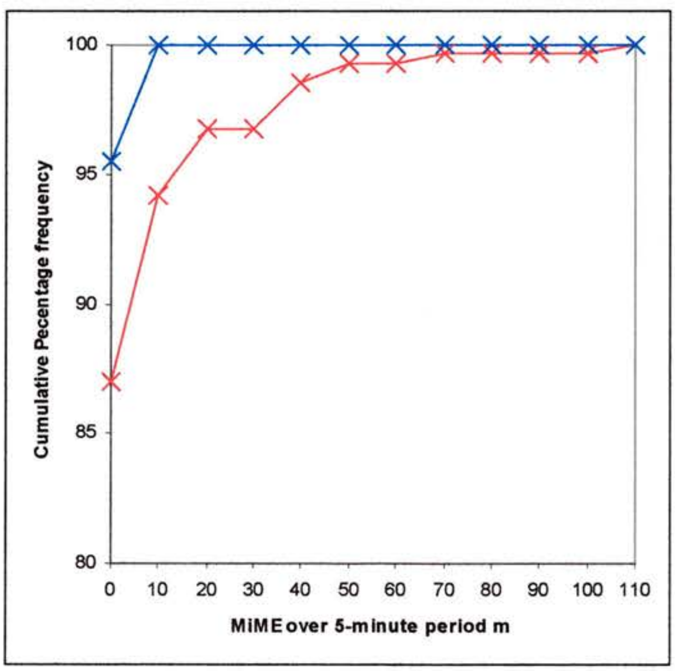


Figure 5.3 Percentage cumulative frequency graph, showing five-minute minimum movement estimates (MiMEs) from morning (×) and midday (×) *continuous* tracks.



During afternoon *continuous* tracks, estimates of total distance moved were significantly smaller when an hourly sampling interval was used than when a five-minute interval was used (one-tailed paired t-test: d.f. = 6, t = 2.59, P = 0.02). Similarly, the difference between distances estimated using hourly and five-minute sampling intervals approached significance during morning *continuous* tracks (one-tailed paired t-test: d.f. = 5, t = 1.71, P = 0.07). The difference between total distance estimates derived from the two sampling intervals was very variable; the estimate derived from the hourly sampling interval being 57 ± 23 % (mean ± S.D.) of the value obtained from five-minute sampling.

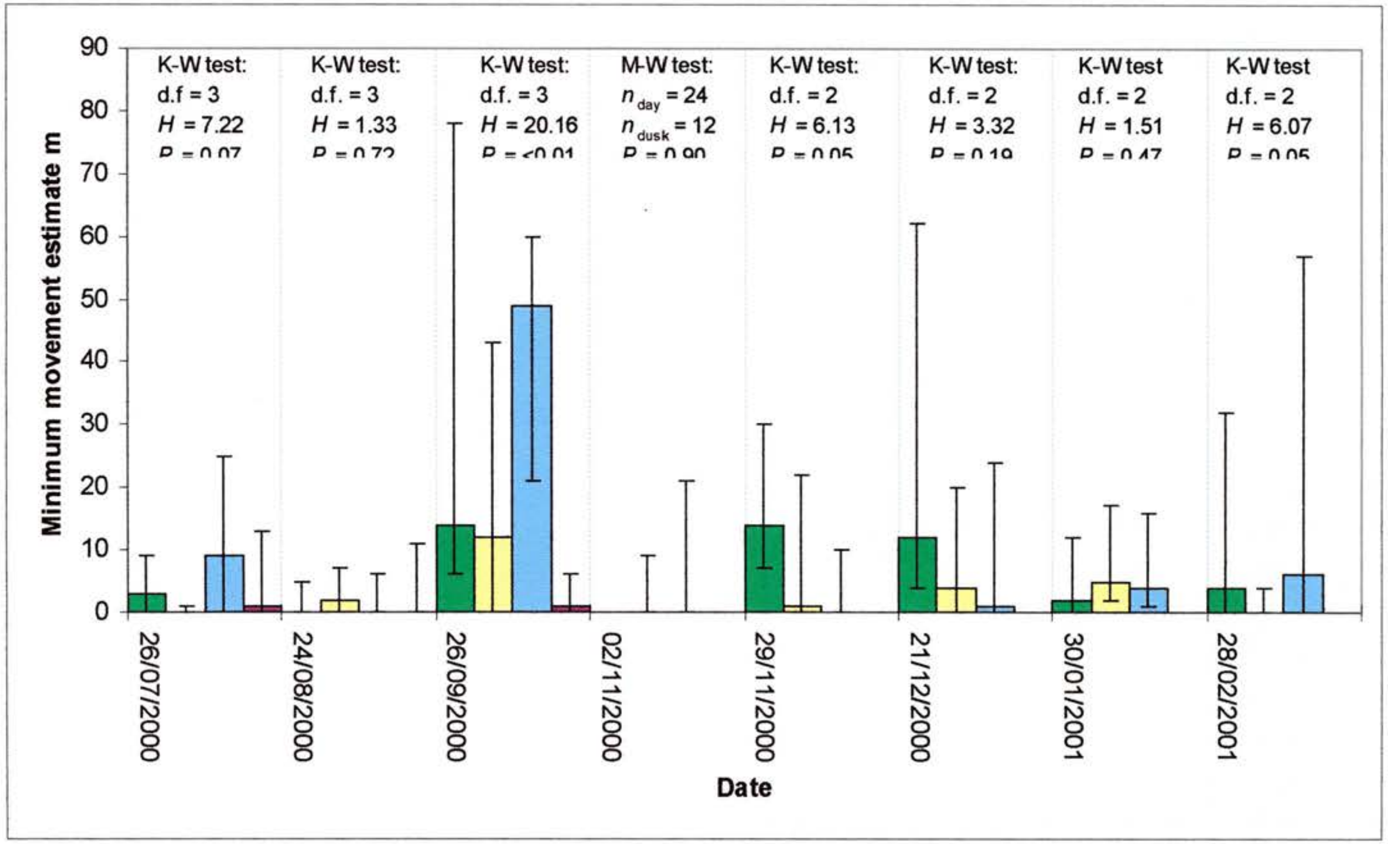
5.3.3 *24 h* and *diurnal* tracks

Analysis of diurnal tracking data (26 July 2000 to 28 February 2001)

Significant differences in minimum movement estimates (MiMEs) occurred between time periods on 26 July 2000, 26 September 2000, 21 December 2000 and 28 February 2001, when greater movements occurred during the dawn or dusk periods than either during the day or the night (Figure 5.4). Generally, little movement occurred overnight during the three *24 h* tracks (Figure 5.4). However, there were some nocturnal movements, with Pike C moving 181 m throughout six hours of night on the 26 July 2000 track, and Pike A moving 119 m during seven hours of night on the 24 August 2000 track.

As during the *pilot* track, relatively large movements were recorded, with the maximum MiMEs from all tracks ranging between 73 m (2 November 2000) and 304 m (28 February 2001). Furthermore movement seemed to occur

Figure 5.4 Median values of hourly minimum movement estimates (MiMEs), together with interquartile ranges, during dawn ( ), day ( ), dusk ( ) and night ( ) for three *24 h* (26 July 2000 to 26 September 2000) and five *diurnal* (2 November 2000 onwards) tracks. The results of Kruskal-Wallis and Mann-Whitney tests for differences between time periods on each date are also shown.



throughout the year (Figure 5.4). Of particular note was the continued occurrence of relatively large minimum movement estimates throughout the period of elevated discharge, and extensive flooding, which occurred over-winter in 2000/2001 (Table 5.1, Figure 5.4). The behaviour of pike during winter flood events is revisited in Chapter 6.

Analysis of diurnal tracking data (26 April 2001 to 1 March 2002)

From all data collected during *diurnal* tracking, between 26 April 2001 and 1 March 2002, minimum movement estimates (MiMEs) between successive hourly fixes ranged between 0 m and 281 m (median = 2 m, interquartile range = 0 m to 8 m). Pike often did not move between successive hourly fixes. Overall, 44% of MiMEs equalled 0 m during these tracks.

Median values for the proportion of occasions when MiME = 0 m in any one time period ranged between 0.2 and 0.5 (Figure 5.5). There appeared to be a general trend for higher proportions of 0 m MiMEs during the day (Figure 5.5). Differences between the proportion of 0 m MiMEs in the three time periods occurred in the autumn (Kruskal-Wallis: d.f. = 2, $H = 6.96$ $P = 0.03$)(Figure 5.5), with the proportion during the day being significantly greater than during dusk (Mann-Whitney: $n_{\mathrm{day}} = n_{\mathrm{dusk}} = 7$, $W = 72.0$, $P = 0.01$), and the difference between dawn and day proportions approaching significance (Mann-Whitney: $n_{\mathrm{day}} = n_{\mathrm{dawn}} = 7$, $W = 38.5$, $P = 0.08$). The differences between the proportion of 0 m MiMEs in the three time periods were not significant in the other three seasons (Figure 5.5). There were no significant seasonal differences in the proportion of 0 m MiME's within time periods (Kruskal-Wallis: all d.f. = 3, dawn: $H = 0.31$, $P = 0.96$, day: $H = 2.03$, $P = 0.57$, dusk: $H = 4.22$, $P = 0.24$) (Figure 5.5).

Significant differences in distances moved occurred between time periods in the summer (Kruskal-Wallis: d.f. = 2, H = 6.94, P = 0.03), with distances moved during dawn being greater than during the day (Mann-Whitney: n_{dawn} = n_{day} = 8, W = 96.0, P < 0.01) (Figure 5.6). No significant differences in distances moved occurred between time periods in spring, autumn or winter (Kruskal-Wallis: d.f. = 2, 0.62 < H < 0.75, P > 0.05)(Figure 5.6). No significant differences occurred in distances moved during dawn (Kruskal-Wallis: d.f. = 3, H = 4.87, P = 0.18) day (Kruskal-Wallis: d.f. = 3, H = 0.48, P = 0.92) or dusk (Kruskal-Wallis: d.f. = 3, H = 1.24, P = 0.74) time periods (Figure 5.6).

Figure 5.5 The median proportion of hourly inter-fix distances, with interquartile range, during which minimum movement estimates (MiMEs) were 0 m, during dawn ( ), day ( ) and dusk ( ), in each of the four seasons, calculated from individual pike. The results of Kruskal-Wallis tests within each season are also shown. Data are from *diurnal* tracks conducted between 26 April 2001 and March 2002.

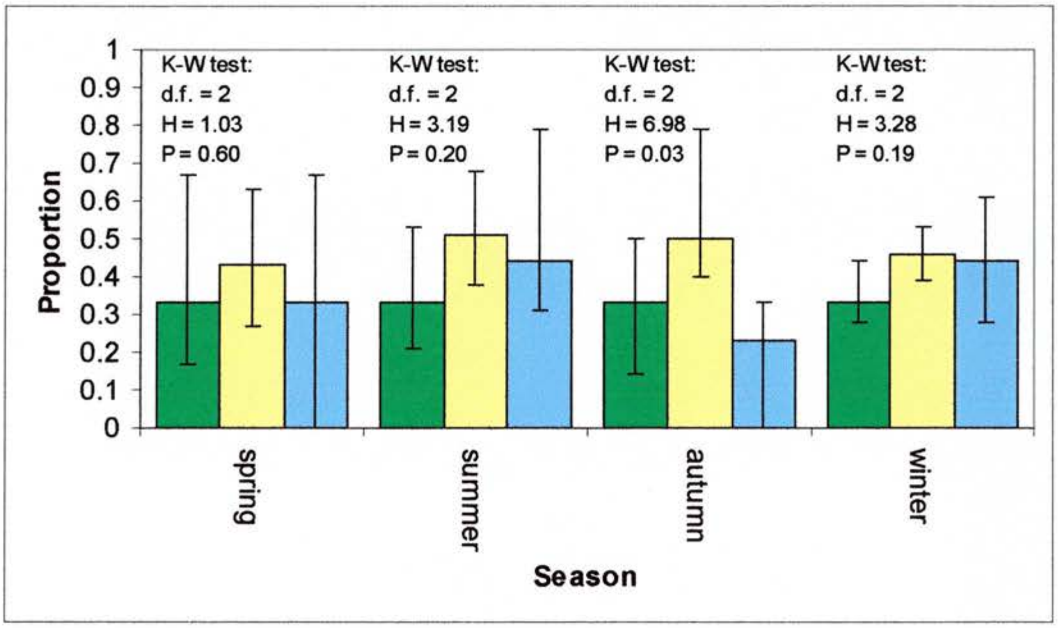
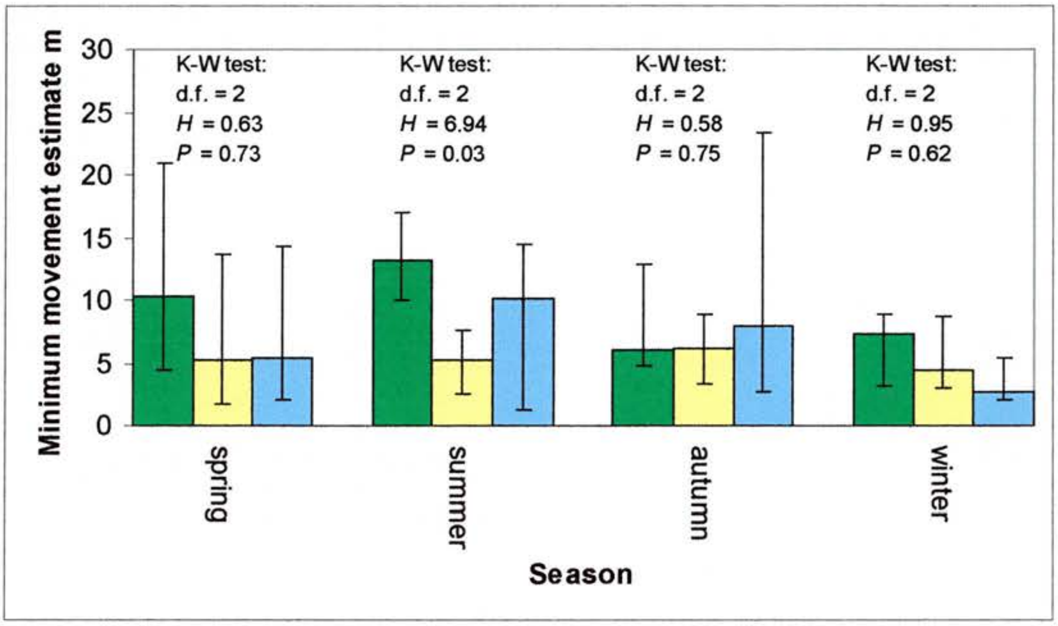


Figure 5.6 Median values (and interquartile ranges) of the mean Minimum Movement Estimates as calculated from hourly positioning of individual pike, during dawn ( ), day ( ) and dusk ( ), in each season. The results of Kruskal-Wallis tests conducted between time periods are given for each season. Data are from *diurnal* tracks conducted between 26 April 2001 and March 2002.



5.3.4 *Home range* tracks

The modal number of activity events recorded, from all *home range* tracks combined, was 0, (median = 0, interquartile range = 0 to 1, maximum = 40) with no activity events occurring during 74% of fixes.

Whilst there appeared to be a trend towards lower proportions of activity events occurring during the day, as compared to during dawn or dusk, no significant differences occurred between the proportion of five-minute periods containing activity events in different time periods (Kruskal-Wallis tests: all d.f. = 2, $0.13 < H < 3.86$, $0.15 < P < 0.94$) (Figure 5.7). Similarly, there also appeared to be a trend towards lower median numbers of activity events being recorded during the day, with Kruskal-Wallis tests returning notably low P values for the differences between time in December 2000 ($P = 0.13$) and July 2001 ($P = 0.08$) tracks (*home range* tracks 3 and 5)(Figure 5.8). However, no significant differences occurred between the number of activity events recorded in each time period, for any of the tracks (Kruskal-Wallis tests: all $P > 0.05$)(Figure 5.8).

Figure 5.7 The median proportion (with interquartile ranges) of five-minute periods containing activity events during morning ( ), midday ( ) and evening ( ) in each *home range* track, calculated from individual pike. The dates of *home range* tracks are shown in Table 2.4. The results of Kruskal-Wallis tests for differences between time periods during each track are also shown.

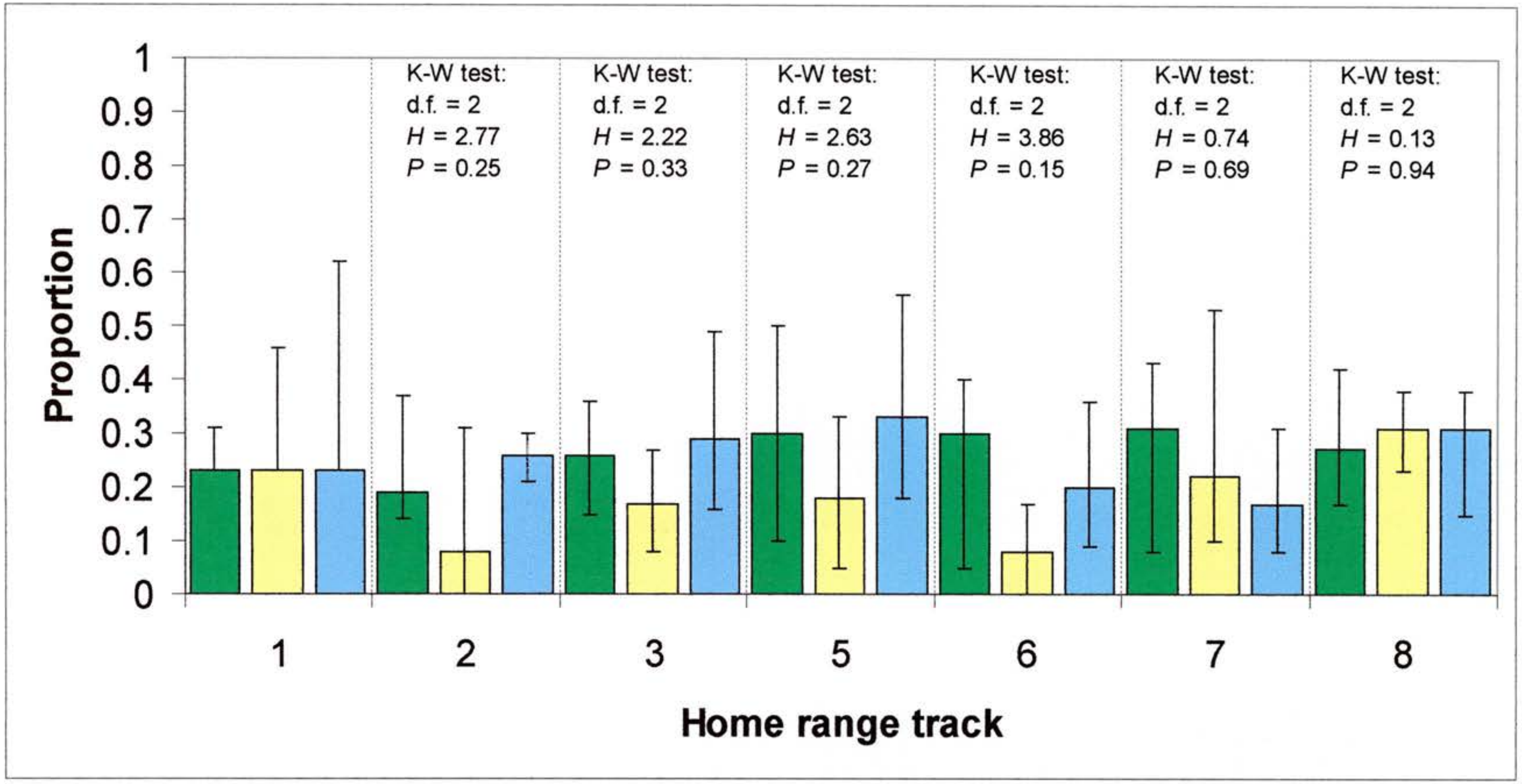
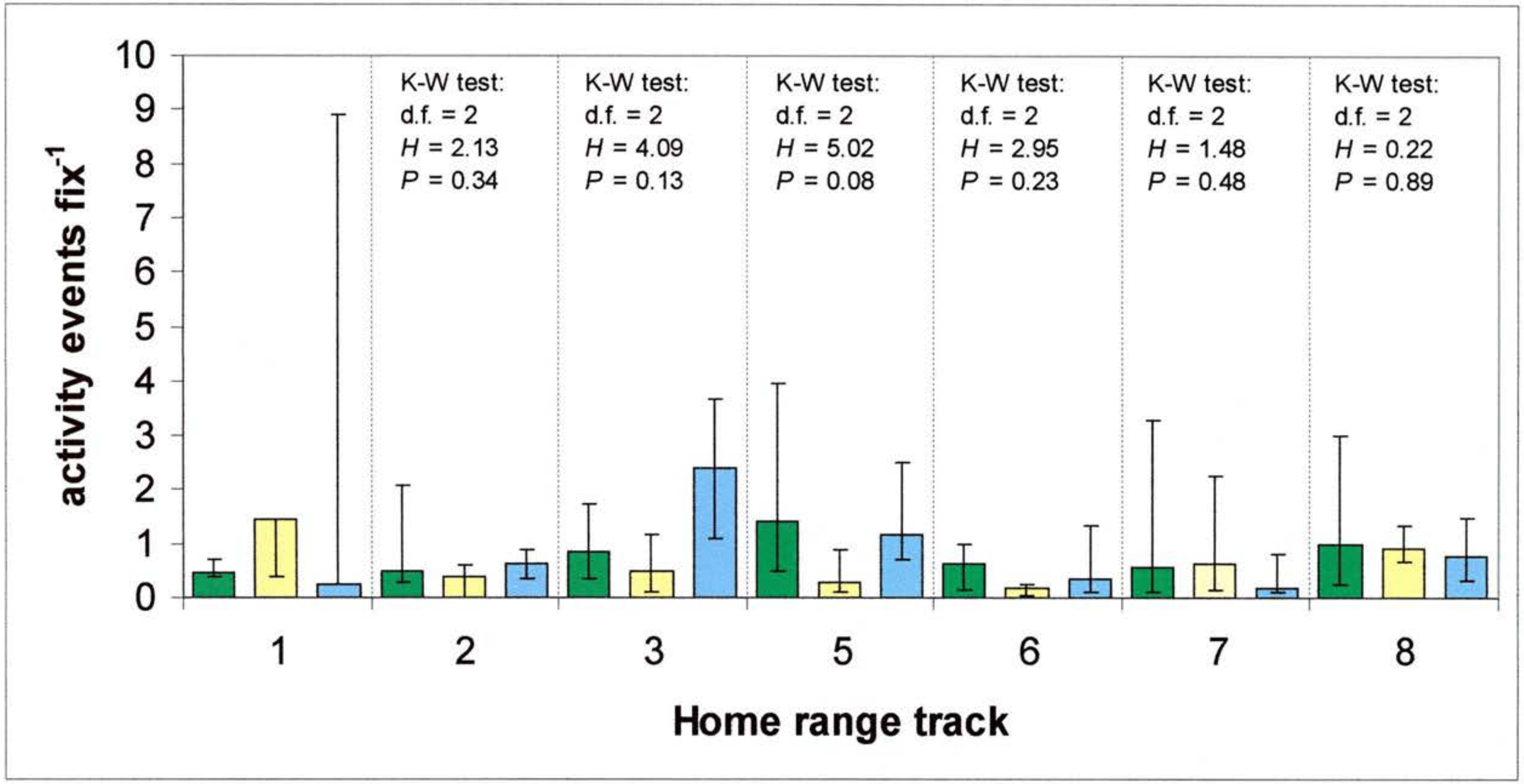


Figure 5.8 The median numbers of activity events (with interquartile ranges) occurring during five-minute periods during morning ( ), midday ( ) and evening ( ) in each *home range* track, calculated from individual pike. The dates of *home range* tracks are shown in Table 2.4. The results of Kruskal-Wallis tests for differences between time periods during each track are also shown.



5.4 DISCUSSION

Continuous and *24 h / diurnal* tracking confirmed that rather than remaining in one place on any one date, as had been predicted prior to conducting the *pilot* track (Welton *et al.*, 2003), pike instead frequently relocate. During *pilot*, *diurnal* and *24 h* tracking, minimum distance estimates of up to several hundred metres were recorded between successive hourly fixes, whilst during *continuous* tracking a maximum distance of *ca.* 105 m was moved in one five-minute period. 'Permanent resident' pike have been shown to have maximum core displacements (MCD) of 275 ± 175 m (mean ± S.D.), where the MCD is the distance between the furthermost upstream and downstream activity core 'centres' (Chapter 4). Thus, it appears that, on any one date, movements between activity cores within the multinuclear home range can occur, and that a substantial portion of the MCD may be visited.

Based on the analysis of movements during the *pilot* track, the hypothesis that pike followed a particular patrol route was rejected, although there were indications that certain areas of river could be favoured at times.

The observed pattern of movements resemble the 'short-stay perched hunting' strategy of the goshawk (Kenward, 1982), and probably represent an active hunting strategy, with pike moving between several potential ambush sites. The pattern of frequently relocating during a diel cycle continued throughout the year, including during periods of elevated discharge. During the whole study, instances occurred where some pike remained immobile at times when others were moving large distances. This complicated the analyses and made the detection of statistically significant differences in movement patterns difficult, although broad patterns could be seen.

Tracking throughout the year showed that the movement patterns distinguished in the summer (Hodder *et al.*, submitted) persisted throughout the year. From the later *diurnal* tracks, neither the distances moved during each time period (dawn, day, dusk) or the proportion of occasions when pike did not move differed significantly with season and there was no evidence of a phase shift in the timing of pike activity (with crepuscular peaks in activity in the summer and a diurnal peak in the winter) as reported by Kaukoranta & Lind (1975) and Cook & Bergersen (1988). The analysis of minimum movement estimates from *continuous*, *24 h* and *diurnal* tracks showed a trend for increased movements in the dawn and dusk periods as opposed to during the day. The data also showed that movements could occur throughout the day, and were not confined to dawn and dusk time periods alone.

Analysis of motion-sensing telemetry from *continuous* tracks also showed increased morning activity, although the apparent trends towards crepuscularity seen from the *home range* track 'activity event' data were not significant.

This discussion proceeds to examine the factors which may drive the observed diel patterns of movement, before finishing with a consideration of the utility of manual methods of recording motion-sensing telemetry.

5.4.1 The daily movement patterns of riverine pike.

Assuming that relocations on any particular date do indeed represent movements between potential ambush sites, then pike may move to a new site if **a)** prey are not detected, **b)** the predator is detected by its prey **c)** a successful predation event occurs **d)** intraspecific interaction occurs or **e)** the fish is disturbed by something else.

a) Prey are not detected: If prey are not detected then the decision over whether to stay at a particular potential ambush site may be influenced by the overall prey density and by the encounter rate between predator and prey. In environments with different food availabilities, bluegills *Lepomis macrochirus* Rafinesque, were shown to stay in patches for longer periods of time when the overall food availability was lower (Wildhaber *et al.*, 1994). In the experiment, patch quality within environments also varied, and the bluegills were found to stay in better quality patches longer than in poorer quality patches (although the time spent at a good patch in a poor environment was still longer than that at a good patch in a good environment) (Wildhaber *et al.*, 1994). The time a pike spends in any one location before moving on to another potential ambush site may similarly depend upon the prey density and the encounter rate of the predator with the prey.

The quality of a potential ambush site could vary temporally, due to prey fish migrations (Clough & Ladle, 1997) or to the increased chance of predators being detected during daylight (Pitcher & Turner, 1986). The chance of a successful predation event occurring, and hence 'patch quality' may be correspondingly reduced during the day, relative to during dawn or dusk. If patch quality does indeed vary temporally in this manner then this may in part account for the tendency towards less movements occurring during the day, with pike staying longer at ambush sites during this time of reduced 'habitat quality', as compared to during dawn or dusk.

b) the predator is detected by its prey: Relocation of pike may also occur following detection of the predator by the prey. Pike are 'fierce predators' as defined by Brown *et al.* (1999), in that prey behaviour can be modified once a predator is detected. For example, during the early stages of an attack by a stalking pike, minnows may make close approaches to the predator, and this behaviour may serve to inhibit attacks, by informing the predator that it has been detected (Pitcher & Parrish, 1993). Display behaviour by Thompson's gazelles *Gazella thomsoni* Günther, initiated by predator detection, has been shown to often result in predatory cheetah *Acinonyx jubatus* (Schreber) abandoning their hunt (Caro, 1986), whilst, in the marine environment, 'mobbing' of white sharks *Carcharodon carcharias* (L.) by cape fur seals *Arctocephalus pusillus pusillus* (Schreber) may reduce the shark's hunting effectiveness and motivation near the mobbing site (Stewardson & Brett, 2000). Detection may similarly lead to hunting being abandoned amongst pike, perhaps prompting relocation.

c) a successful predation event occurs: Following a successful predation event, pike have been shown to become immobile (Lucas *et al.*, 1991; Beaumont *et al.*, 2002a) and the mobility of pike, on a daily basis, may therefore be state-dependent. Pike which do not move very far on any particular date may be in the process of digesting prey, although amongst sit-and-wait predators immobility is not necessarily synonymous with inactivity, as the predator may immobile but be waiting in ambush. A pike which is immobile and digesting prey may require a different habitat to one that is actively searching for prey, for example, it may prefer areas of slack water to minimise energetic costs associated with swimming. However, following feeding with dead fish bait, radio tagged pike were seen to remain within the same general area, and not relocate (W.R.C. Beaumont, pers. comm.). Within the river, it is likely that pike could move into areas of reduced water velocity using small scale movements, either horizontally or vertically, which could be below the tracking resolution of the equipment used in this study.

d) intraspecific interaction occurs: The food intake of a predator depends in part on competition and its susceptibility to interference (Goss-Custard & Sutherland, 1997). Large pike were the apex predators within study section, therefore competition and interference can be assumed to have been intra rather than interspecific. Pike in the river were shown to possess overlapping home ranges, and up to five radio tagged pike could be found within an individuals C_{tx} core home range (Chapter 4, Hodder *et al.* (submitted)). Indeed, this result is likely to underestimate the actual degree of overlap between home ranges, due to the presence of untagged pike in the study section. On occasion whilst tracking, similarly sized pike were found very close together on several occasions (outside of the spawning season), even when they would have been clearly visible to one another (Hodder *et al.*, submitted). Despite these observations, due to the occurrence of cannibalism, kleptoparasitism and size-dependent interference amongst pike (Eklöv & Diehl, 1994; Nilsson & Brönmark, 1999), it is likely that the distribution of pike within the river is directly influenced by interaction between individuals to some degree. Larsen (1966) noted that whilst up to four pike of the same size could be caught in areas of 30-40m^2, two or more pike of different sizes were never caught at the same time and in the same locality. Post-mortem examination of Pike N demonstrated that even relatively large pike (L_F = 66 cm at time of death) can fall victim to intraspecific attack (Chapter 3). Despite the observed overlap of home ranges in this study, pike distribution between potential ambush sites within the river is therefore likely to conform to a despotic distribution, where subordinate individuals maximise their food intake by occupying 'sub-optimal' habitat, rather than competing directly with 'dominant' (larger) individuals, even if the 'dominant' individuals do not specifically defend territories. The observed overlap in home ranges together with the extent of movements on a daily basis, make it likely that pike will come into contact with one another, and the arrival of a significantly larger pike at a locality may prompt a smaller pike to relocate.

e) The fish is disturbed by something else: Disturbance by factors such as grazing cattle, people walking along the bank *etc.* could also potentially cause a pike to relocate. When disturbed, pike sometimes appear to 'freeze' in place at first, and may then either slowly swim out of sight, using their fins for propulsion, or perform a rapid swimming motion, involving beating the tail (pers. obs.). When tracking fish equipped with TW-5 radio tags, it was possible to tell when the fish swam rapidly away following disturbance, as the motion-sensing tags switched to the more rapid pulse rate. Often, pike would not swim far following disturbance and on occasion could also be seen to return to the spot from which they had been disturbed (pers. obs.). Such reaction to disturbance probably reflects a predator evasion response. For the duration of the study, the pike in the river were the apex aquatic predator, although in July 2003, after fieldwork had concluded, an otter *Lutra lutra* (L.) was seen on videos recorded at the CEH salmon counter on the East Stoke weir. Throughout their geographic range pike are also exposed to terrestrial and avian predators, and people must themselves also be considered as a predator on the species.

Whilst some concentration of movement during the dawn and dusk period was observed, movements were not restricted to these time periods, and could also occur during the day. Furthermore, movement within the dawn and dusk time periods was not restricted solely to the periods of rapidly changing light intensity associated with sunrise and sunset, but took place over a more extended period of time. The rapid movement of prey, such as dace, at sunrise and sunset (Clough & Ladle, 1997) suggests that the fish are seeking to minimise their exposure to predation risk during the risky 'twilight' period. If pike movements are indeed related to hunting behaviour, then it appears that hunting does not solely occur during dawn and dusk, and that prey fishes may therefore be at risk throughout the day. Dobler (1977) examined the correlation between the feeding time of pike and the dispersion of a school of sunbleak *Leucaspius delineatus* (Heckel), finding that pike fed more during evening hours, at light levels where the school of sunbleak gradually dispersed. Food consumption was determined by counting the number of sunbleak remaining in the study aquaria at hourly intervals, and fish were not watched continuously, therefore there was no measure of pike activity, or feeding efficiency, throughout the day. Conversely however, Grellner (1975), cited in Dobler (1977), found that pike fed on crucian carp *Carassius carassius* (L.) chiefly in the day time. The crucian carp did not show such a marked tendency to form schools as the sunbleak. It appeared then that the pike were willing and able to feed during the day, but that the schooling behaviour of the sunbleak acted as an effective defensive mechanism during daylight hours. The risk of falling victim to predation during the day therefore appears to drive prey species into partitioning their time between feeding and refuging behaviours. The effectiveness of the diurnal anti-predation strategies of prey fish may lead to a temporal reduction of 'food availability', in turn bringing about a reduction in activity amongst pike during the day. Daytime immobility may also be brought about by successful feeding during the dawn period, followed by reduced movements whilst successful pike are digesting prey.

5.4.2 The utility of manual methods of recording motion-sensing telemetry

The output from the motion-sensing TW-5 radio tag can be recorded automatically or manually, a prototype automatic data logging (ADL) system being used as part of a CEH study into the predatory behaviour of pike (Welton *et al.*, 2003). Whilst the technology worked, and detailed records of pike activity were built up over several days, the mobility of pike on a 24 h time scale meant that radio tagged fish often moved outside of the detection range of the equipment (Beaumont *et al.*, submitted). Another limitation of the ADL was that it could only listen to one tag at a time.

Manual recording offers an alternative method of recording motion-sensing telemetry data, which does not require further investment in expensive, specialised equipment and software. During the present study, manual recording of 'activity event' data was sufficient to reveal significant differences in activity between morning and day periods during *continuous* tracks, although during *home range* tracks no significant difference were seen.

Activity event data were recorded in five-minute blocks in both *continuous* and *home range* tracks, the number of these blocks from the *continuous* tracks combined (n = 679) being greater than from any of the seven available *home range* tracks (n = 318 ± 155, mean ± S.D.). Significance differences between time periods in *home range* tracks may have been achieved had a larger number of fish been included, or if the tracks had extended beyond thirteen days (thus increasing the number of five-minute periods available for analysis). Significant differences may also have been found had a longer sampling interval than five-minutes been used. From *continuous* tracking data, periods of inactivity lasted significantly longer in the day (median = 15 minutes) than in the morning (median = 7.5 minutes). Therefore, extending the period of time over which activity events were recorded, to *e.g.* ten minutes, could lead to a proportionally larger increase in the number of activity events recorded in the morning than in the day.

Extending the time over which activity was recorded, the number of fish tracked or the duration of tracks was not attempted during *home range* tracks as the activity event data were being recorded as supplementary data to a fieldwork protocol primarily aimed at establishing the short-term home ranges of pike (Chapter 2). Any increase in the number of fish or the time over which activity events were recorded would have led to an increase in the length of time required to collect fixes from all fish, such that sampling could not be completed within the desired time period. Extending the duration of the survey was not possible in this instance, due to personnel constraints.

In addition to the results from motion-sensing telemetry presented in this thesis, Beaumont *et al.* (submitted) manually collected 'activity event' data during a *24 h* track, using the method described above. The number of 'activity events' per hour, pooled from all pike, showed peaks in activity around dawn and dusk demonstrating that although Automatic Data Logging can be useful for building up detailed records from individual fish, manual data collection provides a useful 'low-tech' alternative for studying activity from a larger sample of individuals (Beaumont *et al.*, submitted).

5.5 FURTHER WORK

This study has demonstrated that pike in the River Frome are capable of moving throughout their home range on a 24 h time scale, and that, diurnally, frequent relocation often occurs. Questions remain however as to the exact causes and benefits of this behaviour, and over the extent to which environmental factors can influence the diel pattern of movements.

Further work is required to demonstrate whether pike favour different locations at different times, or whether different behaviours (such as hunting or digestion) occur in different areas. During the *pilot* track, Pike B appeared to have a favoured nighttime location, although Pike A did not exhibit similar behaviour, and neither pike appeared to follow a regular patrol route. Further tracking, continued over consecutive 24 h periods, would be required to answer this question. Longer periods of tracking may also be able to determine whether diel patterns of movement vary between individual fish. More detailed analyses of habitat selection by pike than were possible during the present study (Chapter 7), possibly including measures of prey availability at different sites, would also be of value.

Relating the movements of pike to optimality theory is also an area worthy of further research. Wildhaber *et al.* (1994) showed that the time bluegills spent at a particular patch varied according to the quality of the overall habitat and the quality of the patch within the habitat, and similar rules may govern pike behaviour. If so, then the patterns of diel movements of pike might be expected to vary between habitats, depending upon prey availability. This could be tested experimentally using ponds or enclosures stocked with known densities of pike and prey fish, although such experiments would need to comply with the terms of the Animals (Scientific Procedures) Act 1986. Alternatively, experiments could be conducted using small captive pike, fed on a diet of earthworms, with these experiments being able to address questions such as the effect of prior experience on the amount of time pike stay in any particular patch; Wildhaber *et al.* (1994) having found that the time bluegills spent at a patch could be influenced by prior experience, at least when differences in prey availability were large. Between different water bodies differences in community structure, prey density, prey morphology and prey behaviour may all potentially influence food availability for pike. Replicated studies in a number of water bodies would be of value here, for example, in the Dorset Stour, near to the River Frome, minnows are the most numerically abundant fish species (Mann, 1976) and it would be interesting to compare the diel activity patterns of pike in these two neighbouring rivers.

The possibility of pike being distributed according to a despotic distribution was discussed above. The interactions between individual pike could be further tested by simultaneous tracking of a number of individuals (Hodder *et al.*, submitted). In order to avoid interference from untagged pike, such studies might be best performed in enclosed waters, stocked with pike and prey at known densities, or could perhaps be performed using captive young-of-the-year pike *e.g.* Hawkins *et al.* (in press).

A combination of positional radio tracking and motion-sensing / physiological telemetry should be used to test the hypothesis that the extent of daily movements is state dependent, particularly during the day when food availability may be reduced as an effect of predator avoidance behaviours amongst prey fishes. This would require intensive tracking however, and would require pike to be monitored constantly in order to determine feeding periodicity.

Whilst simple motion-sensing telemetry may be sufficient for the task, heart-rate telemetry offers another possibility (Lucas *et al.*, 1991), although the short battery life of such equipment means that behaviour may still be affected by the stresses of capture and tagging during the monitoring period. The maintenance requirements of pike vary seasonally, with lower rations required over winter (Johnson, 1966), and although large movements have been demonstrated to occur throughout the year, temperature induced differences in metabolic activity would be expected to lead to variable feeding periodicity and longer digestion times, which may alter the duration of any post-prandial immobility. Larger sample sizes, or tracking over successive dates, coupled with motion-sensing or physiological telemetry would be required to investigate the interaction of temperature, metabolism and mobility.

The present study only involved tracking pike of $L_F > 50$ cm, however, small pike are thought to be more restricted in habitat use than larger pike, due to the risk from cannibalistic predation (Bregazzi & Kennedy, 1980; Chapman & Mackay, 1984a), and these pike may therefore show a more restricted pattern of diel movements. This can be tested in the field now that techniques have been developed for attaching external radio tags to small pike (Beaumont & Masters, in press). Determining activity patterns of young-of-the-year in the wild remains problematic, and may best be investigated using captive pike (Chapter 8).

Having determined the broad nature of the diel movements of pike in the river throughout the year, the influence of environmental factors on pike movement could be investigated through more focussed radio tracking studies. Water temperature may affect the scale of movements, such as has been observed in pikeperch *Sander lucioperca* (L.), where distances moved correlated positively with temperature (Jepsen *et al.*, 1999). Reduced light intensity during the day (caused by cloud cover) or bright, moonlit nights may extend the 'twilight' period during which predators have an advantage over prey, which might be reflected in pike movements. The influence of illumination is difficult to study however, as, although light levels can be recorded in the field, the light level as perceived by individual fish will vary according to their position in the river, and will also be influenced by turbidity. The exact relationship between light level and movement may therefore be better examined experimentally, under controlled conditions. Whilst nocturnal movements were rare during *24 h* tracking, they were found to occur on occasion, and nocturnal activity has also been detected through automatic monitoring of the output of motion sensing tags (Beaumont *et al.*, submitted). Young-of-the-year pike appear to 'sleep' overnight (Chapter 8), but on bright, moonlit nights light levels may be such that pike are still able to see their prey, and under these conditions hunting may continue. Further tracking throughout the night, coupled with readings from low intensity light meters, capable of distinguishing between moonlit and moonless nights, would enable the nocturnal behaviour of pike to be better described.

Turbidity is another factor that could influence pike movements in the river. In lakes, pike have been reported moving offshore to clearer water at times when wave action caused increased turbidity in the littoral zone (Chapman & Mackay, 1984; Cook & Bergersen, 1988). Pike home ranges in the River Frome increase in size during periods of flooding (Hodder *et al.*, submitted), and riverine pike utilise side channel and flooded field habitats under such conditions (Gerlier & Luquet, 1999; Masters *et al.*, 2002), although further investigation is required to explain the function of this behaviour (Chapter 6). Pike have been observed moving between main river and off-river habitats on a daily basis during winter flooding (Chapter 6) and the pattern of daily movements during floods may therefore differ from those occurring under normal flow conditions. Off-river habitat use by pike during winter flood events is examined in detail in Chapter 6.

5.6 SUMMARY

1) Rather than remaining in one place in the river, pike often frequently relocate on a daily basis, with these movements persisting throughout the year.

2) Daily movements commonly cover substantial portions of the pike's core home range.

3) The movements are reminiscent of the hunting strategy of an avian ambush predator, the goshawk.

4) Whilst there is some evidence for increased movements occurring during dawn and dusk periods, movements can also occur throughout the day. Further work is required to determine the incidence of nocturnal activity.

5) Manual recording of motion-sensing telemetry has the potential to provide a simple method of assessing variation in activity levels within a population.

6) Further work is required to determine whether pike favour specific areas for specific activities, to determine the precise relationship between feeding and mobility, and to investigate the significance of intraspecific interactions on the daily movements of pike.

CHAPTER 6

Habitat utilisation by pike during winter flooding

European floodplains have been described as 'a highly interesting and nearly vanished biotope' with most of the ecological adaptations to the environment being unknown (Reimer, 1991). The River Frome provides an excellent location for studying the behaviour of fish in floodplains as although the plain itself has been modified from its natural state, the main channel of the river has not been straightened and the river is free to burst its banks under high flows. The land surrounding the river consists largely of a disused water meadow system, with associated drainage ditches and side channels (Armitage *et al.*, 2002).

Off-river habitat was known to be of importance to pike during the spawning season, and as a nursery ground (Mann, 1980; Billard, 1996), however the first indication that such habitat was of importance to adult pike in the River Frome, outside of the spawning season, occurred during a diurnal track on 29 November 2000. On this date, when discharge was 2 m^3s^{-1} above bank-full level, fieldworkers found Pike I within the Railway Ditch (Figure 4.1), over 180 m from the confluence with the main river channel. Tracking continued throughout the period of flooding in 2000 / 2001 and the opportunity was taken to use results from *diurnal*, *home range* and *routine* tracking to describe habitat utilisation by pike during winter floods. The extent to which these habitats were utilised outside of the spawning season was an important new discovery and the results were presented at the Fourth Conference on Fish Telemetry in Europe, Trondheim, 2001, and published in the journal *Hydrobiologia* (Masters *et al.*, 2002).

Two hypotheses were proposed to explain the observed extensive use of off-river habitats (Masters *et al.*, 2002). Under the 'refuge' hypothesis, pike would seek out areas of slower flowing water to shelter from the high flows in the main river channel, whilst under the 'feeding' hypothesis, pike would leave the main river channel to exploit feeding opportunities in flooded fields and ditches (Masters *et al.*, 2002). The possibility that the observed movements into off-river habitats were related with spawning or pre-spawning behaviour was also discussed (Masters *et al.*, 2002).

Observations of off-river habitat use continued throughout the course of the present study (up to spring 2003). This chapter presents the work of Masters *et al.* (2002), conducted as part of this Ph.D. study, and discusses the various hypotheses in the light of further data collected since the submission of the paper.

6.1 INTRODUCTION

The body of the pike is adapted for rapid acceleration to facilitate ambush predation (Webb, 1984a) and consequently pike are regarded as being poorly adapted for sustained swimming. Jones *et al.* (1974) evaluated the swimming performance of fish, in relation to their ability to negotiate culverts up to 100 m in length. The relationship between fork length and the ability to move 100 m in 10 minutes at different water velocities was determined for 11 species of fish, and pike of all sizes (up to 50 cm) were found to require lower water velocities (*ca.* 10 to 20 cm s^{-1}) to negotiate this distance in the allotted time than the other species tested (Jones *et al.*, 1974). Pike are generally regarded as occurring within slow flowing stretches of river; Lamouroux *et al.* (1999) studied habitat use of fish in large streams of southern France, catching pike most often in areas where water velocity was < 0.05 m s^{-1}.

Environmental variation in rivers is less predictable than that which pike could be expected to encounter in lakes, particularly with regard to the water levels and discharge. Through their ability to live in a variety of different water bodies, pike clearly display a high degree of adaptability (Jepsen *et al.*, 2001) and the species may therefore be expected to show adaptations to cope with the environmental conditions encountered during flood events. Studies of pike in rivers have been limited, however Langford (1979) reported that acoustically tagged pike in exposed positions in the River Thames (UK) could be 'displaced' during strong flood currents, particularly downstream of weirs.

Off-river habitats, and side channels in particular, are known nursery grounds for fish, and recently, the invertebrate communities of these areas have also begun to receive attention, in terms of their contribution to overall floodplain diversity (Armitage *et al.*, 2002). To date though, research on off-river habitat use amongst fishes has largely been concentrated in tropical countries; many European rivers having been altered from their natural state by the construction of artificial embankments and/or damming (Reimer, 1991). Despite these recent modifications, European floodplains formerly occupied large areas, and although flooding is less regular and predictable than in the tropics, fish may still be adapted to use such habitats (Reimer, 1991).

During autumn/winter 2000 / 2001, high rainfall caused the River Frome, a relatively unmodified system, to be in flood for >50% of the time. Radio tagged pike were tracked throughout the period of flooding and were often found in side channels or over flooded fields, in addition to the main river channel. Later periods of flooding provided further opportunities to study off-river habitat use amongst pike. The incidence of, and possible reasons for, such off-river habitat utilisation are examined below.

6.2 METHODS

6.2.1 Radio tracking during floods

Radio tracking during daylight hours continued to be performed by solo fieldworkers during periods of flooding, although extra safety precautions were taken at this time. Life jackets were worn at all times when radio tracking during floods. A member of CEH staff was notified by mobile telephone whenever a tracking session finished and the fieldworker had returned safely to the River Laboratory Field Station. When dawn tracking was being conducted, fieldworkers were asked not to begin walking along the riverbank, or across flooded fields, until it was light enough to see. Similarly, fieldworkers were requested to leave the water meadows prior to it becoming dark during evening tracks.

Particular care needed to be taken near the riverbank, even after floodwater had receded, as considerable erosion occurred during periods of flooding, and many sections of bank became undercut.

6.2.2 Autumn/winter flooding 2000/2001

Flows in the river rarely fell below bank-full level between November 2000 and February 2001. Location data between September 2000 (prior to the onset of flooding) and February 2001 were available from up to seven pike, five

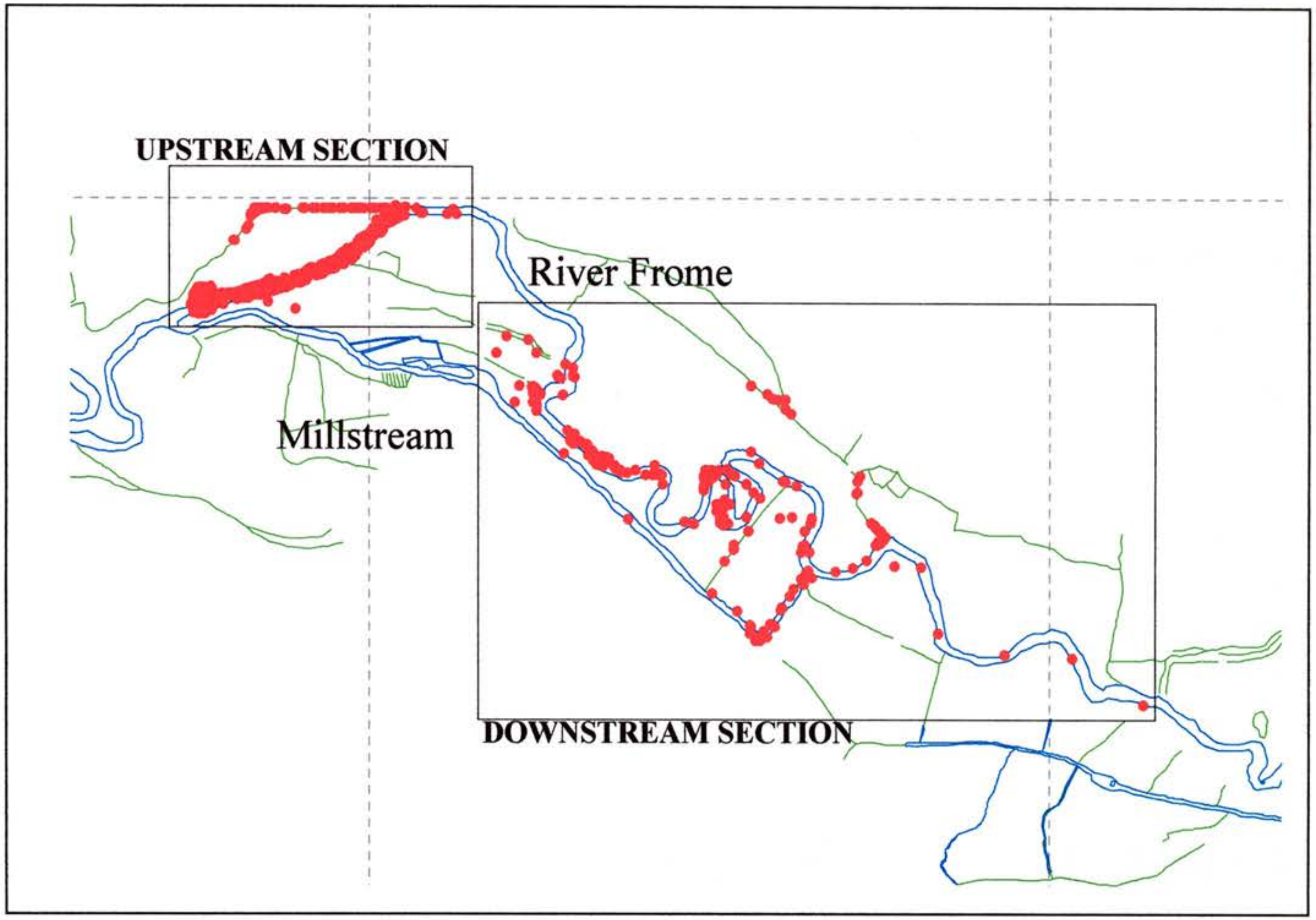
(Pike A, B, C, G and H, Table 2.2) having been tagged between May and August 2000, whilst one pike was tagged in October 2000 and one in November 2000 (Pike I & J respectively, Table 2.2). Data from the ten days following tag implantation were excluded from analysis (Beaumont *et al.*, 2002a).

Two reaches of river within the main study area (SY 86 86 and SY 87 86) were defined from their character (Figure 6.1). The upstream section was straighter than the downstream section, with fewer pools per unit length. Flooding occurred at 10 m^3s^{-1} in the downstream section as opposed to 11 m^3s^{-1} upstream. Mean daily discharge (midnight to midnight) was calculated from hourly data provided by the UK Environment Agency for the East Stoke weir, immediately upstream of the study site.

Between September 2000 and February 2001, location data for fish in both sections was available from both *routine* tracking and from *home range* tracks 2 and 3 (Chapter 2, Table 2.4). The upstream section contained the 800 m section of river in which *24 h / diurnal* tracking was conducted (Chapters 2 and 5), five such tracks occurring between September 2000 and the end of February 2001 (Table 2.5).

The location of each pike was recorded as being either in the main river channel, over flooded land, in one of the drainage ditches or in the millstream (at this time the millstream had little flow, due to an upstream obstruction). For pike in the main river, fixes were taken from the riverbank as described in Chapter 2. When pike were in flooded fields, the position of the fish was fixed by triangulation from several points within the field. When pike were in ditches, fixes were generally taken from the bank of the ditch, but sometimes, due to difficulty of access, fixes had to be taken from a greater distance away.

Figure 6.1 The positions of all fish fixes (●) between September 2000 and February 2001. 1 km NGR squares are overlaid on the map for scale.



The relationship between the proportion of fixes outside of the main river channel and mean daily flows greater than bank-full level were examined using Spearman rank correlations (with corrections applied for tied values (Zar, 1974)), separately for upstream and downstream sections. Data for these correlations was drawn from the whole time period between September 2000 and February 2001, and therefore covered several individual flood events. Data were included from *routine*, *home range* and *24 h / diurnal* tracks. The proportion of fixes outside of the main river channel formed an estimate of the proportion of time spent outside of the river channel on that day, better estimates being obtained by the more intensive sampling periods.

During the period of time when data from all seven pike were being collected (14 December to 28 February), the proportion of fixes in each habitat category was calculated for each individual pike, and the relationship between the size of the pike (L_F at time of capture) and the proportion of fixes outside of the main river examined with a Spearman rank correlation.

Fixes were plotted onto a digitised map of the river using ArcView GIS 3.2. For all fixes occurring outside of the main river channel, the distance to the nearest riverbank was then measured. The relationship between distance from the nearest riverbank and discharge above bank-full level (grouped into 1 m^3s^{-1} intervals) was examined using Spearman rank correlations, separately for fixes within flooded field and drainage ditch habitats. The discharge above bank-full level was calculated by subtracting the bank-full level for the upstream or downstream section from the actual discharge on that date, allowing upstream and downstream data to be combined.

6.2.3 The proportion of 'bank' and 'midstream' fixes

The proportion of 'bank' to 'midstream' fixes was calculated for each pike in every *home range* track, using only fixes recorded within the main river channel. 'Bank' fixes were those where the most likely position of the fish was within 1 m of the nearest bank, with midstream fixes being those where the most likely fish position was > 1 m away from the nearest bank. The proportions of 'bank' fixes were compared between *home range* tracks 2 to 8 using a Kruskal-Wallis test, the results from *home range* track number 1 being excluded due to only three pike having been tracked on this occasion (Table 2.4). A Spearman rank correlation was used to investigate whether the proportion of 'bank' fixes could be related to discharge (with the discharge value used being the mean of mean daily discharge values recorded throughout the period of the *home range* track).

6.2.4 Electric fishing of side channels

Following observations having been made of pike entering drainage ditches during winter flooding in 2000 / 2001, it was planned to sample these side channels during winter flood events in 2001 / 2002, using electric fishing; the aim being to sample the fish community and to determine the reproductive condition of any pike caught. However, discharge remained comparatively low throughout this period (see Figure 4.5), and so electric fishing took place after only minor flooding on 23 and 28 January 2001 (Table 6.1). Sampling also took place during more extensive flooding on 5 and 6 February 2001 (Table 6.1); this being the flood that was associated with the return of the two migratory pike to East Stoke (Chapter 4).

Sampling was conducted using Electracatch WFC4-20 electric fishing apparatus. The Railway and Rushton Ditches were waded on both occasions in January, whereas in February, deeper water meant that the Railway Ditch needed to be fished from the bank, and, due to the presence of flood water along sides of the ditch, only the 100 m nearest to the river could be fished. Fishing of the Hummock Ditch and the Flood Relief Channel in February was conducted whilst wading and also from an inflatable boat. Due to the narrow width of the channels, a single anode was used at all times.

Table 6.1 Dates of electric fishing of side channels connected to the River Frome, together with mean daily water temperature and mean daily discharge, as measured at the East Stoke gauging weir. Channels fished: 1) Railway Ditch 2) Rushton Ditch 3) Hummock Ditch 4) Flood Relief Channel.

Date	Channels fished				Water Temperature	Discharge
	1	2	3	4	°C	m^3s^{-1}
23 Jan 2001	✓	✓			8.8	3.4
28 Jan 2001	✓	✓			10.0	7.1
5 Feb 2001	✓		✓	✓	9.6	14.2
6 Feb 2001				✓	8.2	10.4

6.3 RESULTS

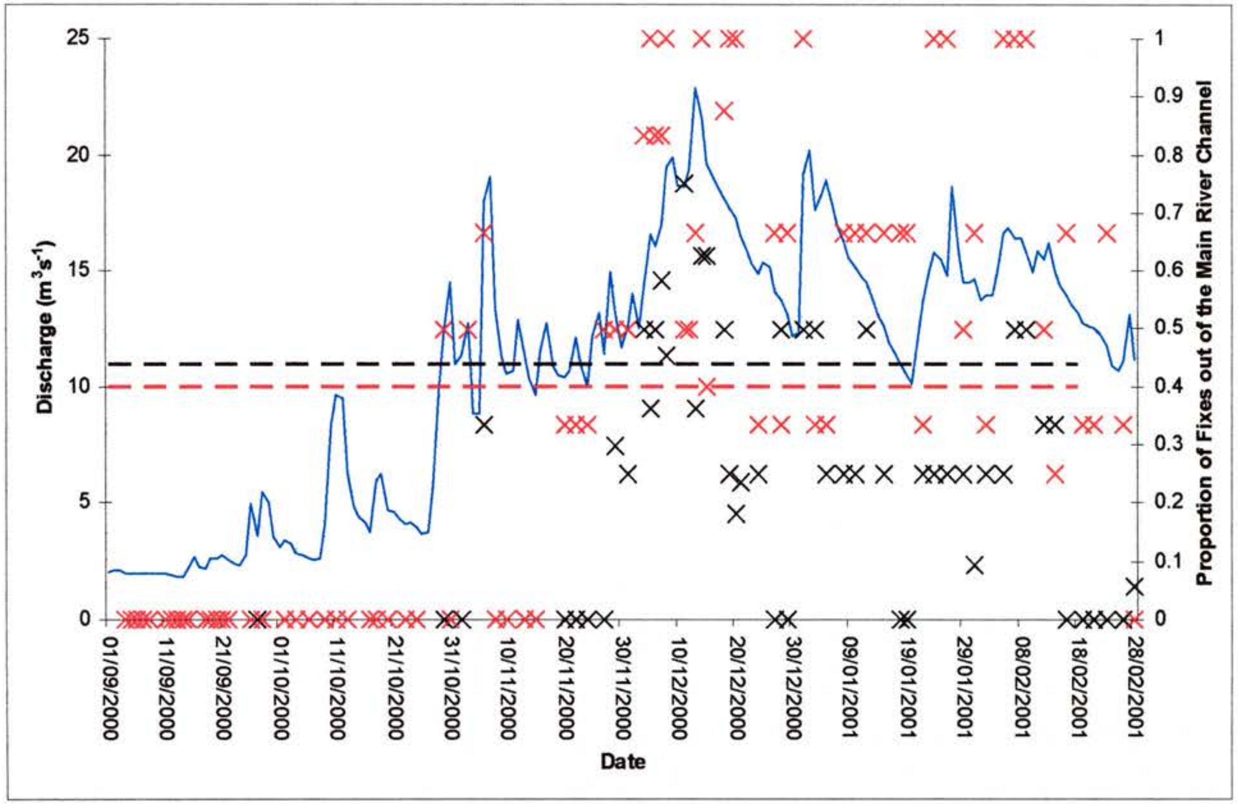
6.3.1 Autumn/winter flooding 2000/2001

Between September 2000 and February 2001, 1106 positional fixes were recorded on the seven radio tagged pike, with fixes occurring in the main river, side channels and over flooded fields (Figure 6.1).

Discharge data showed several peaks in flow, after each of which river levels fell, although discharge remained high (>10 m^3s^{-1}) until the end of February (Figure 6.2). During the first floods of the year, in September and October, water levels did not rise sufficiently high to overflow the banks in either section (Figure 6.2). The entrances to most drainage ditches in both sections were connected to the river at all times and were therefore accessible to pike, however, no pike left the main channel (Figure 6.2). During November it was more common to find pike out of the river in the downstream section than in the upstream section, whilst from December onwards, some pike were always found out of the main river channel in either section with, typically, a quarter to one half of upstream fixes and one third to all downstream fixes being outside the main river (Figure 6.2). Whilst radio tracking, untagged pike were seen in flooded fields on a number of occasions, implying that the behaviour of tagged pike was not unrepresentative.

In both upstream and downstream sections there were significant positive correlations between mean daily flows greater than bank-full level (upstream = 11 m^3s^{-1}, downstream = 10 m^3s^{-1}) and the proportion of fixes outside of the main river channel (upstream: $r_s = 0.72$, $n = 52$, $P < 0.01$, downstream: $r_s = 0.51$, $n = 56$, $P < 0.01$).

Figure 6.2 The proportion of fixes of pike, in both upstream (×) and downstream (×) sections, that were outside of the main river channel on each tracking day, together with mean daily discharge (m^3s^{-1})(—), as calculated at the East Stoke gauging weir. Includes data from *routine*, *home range* and *24 h / diurnal* tracks. Bank-full discharge levels in upstream (– –) and downstream (– –) sections also shown.



For pike in flooded fields, 79% of fixes were within 10 m of the nearest riverbank, with the maximum distance from the nearest riverbank being 86 m (median= 3 m, interquartile range = 1 m to 9 m). For pike in ditches, only 18% of fixes occurred within 10 m of the ditch mouth, and the maximum recorded distance for a pike was 282 m from the ditch mouth (median = 52 m, interquartile range = 13 m to 139 m). There was a significant positive correlation between discharge above bank-full level and the mean distance that pike were found from the main river channel in flooded fields ($r_s = 0.89$, $n = 10$, $P < 0.01$) whilst the corresponding positive correlation between discharge above bank-full level and distance along drainage ditches approached significance ($r_s = 0.50$, $n = 12$, $P < 0.10$)(Figure 6.3 and 6.4).

During the period when data were collected from all seven pike (14 December to 28 February), individual differences existed between the proportions of fixes in each type of habitat category (Table 6.2). In the upstream section, pike rarely used flooded fields or ditches, with the exception of Pike I, which was recorded in a drainage ditch for >50% of fixes. In the downstream section, habitat use was more varied, with Pike G and Pike J using all available habitat categories, and Pike H being found in flooded fields more than any other pike. During this time period, discharge exceeded the bank-full level for 95% of the time in the upstream section, and for 100% of the time in the downstream section (Figure 6.2). There was no correlation between the length of pike (L_F at time of capture) and the proportion of fixes out of the main river ($r_s = 0.27$, $n = 7$, $P > 0.05$).

Figure 6.3 Mean, maximum and minimum distances from the nearest riverbank, for all pike in flooded fields against discharge above bank-full value (m^3s^{-1}). Upstream and downstream sections combined.

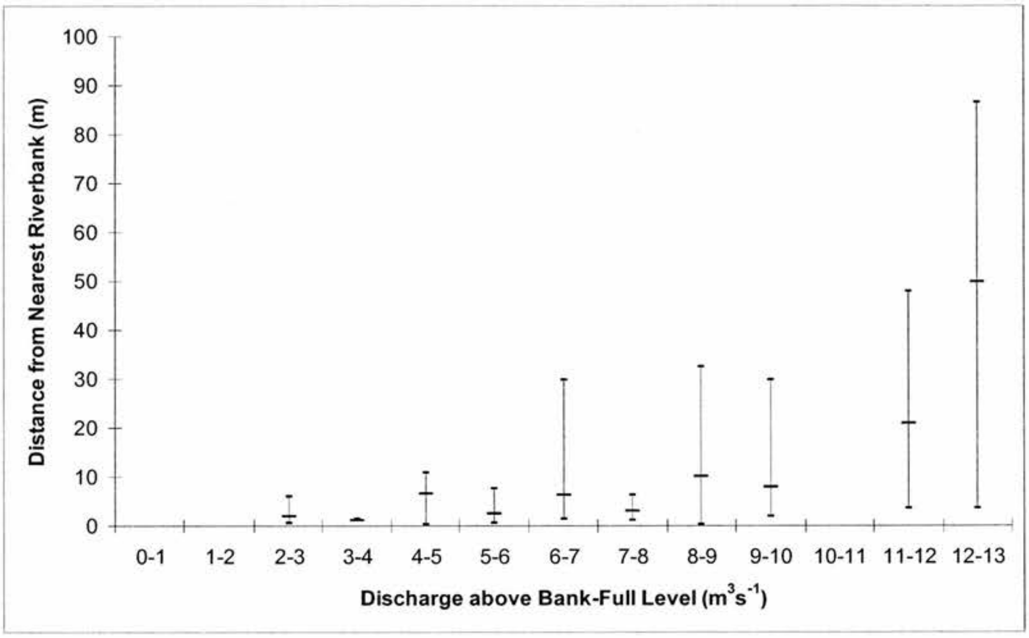


Figure 6.4 Mean, maximum and minimum distances from the ditch entrance, for all pike in ditches against discharge above bank-full value (m^3s^{-1}). Upstream and downstream sections combined.

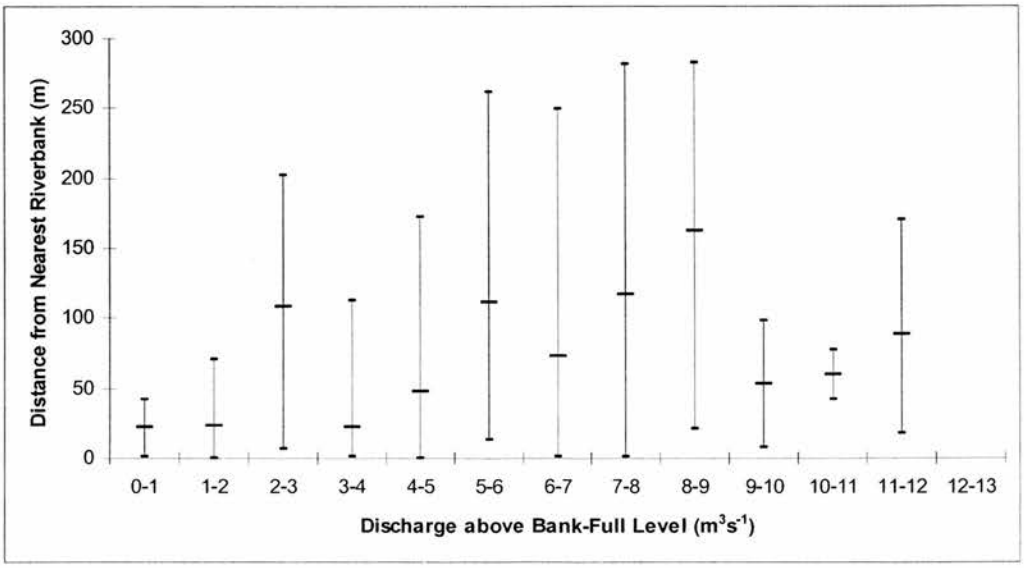


Table 6.2 The proportion of fixes recorded in each habitat category for each individual radio tagged pike, during the period when all pike were tagged (14 December 2000 to 28 February 2001). For further details on individual fish (fork length at time of capture, sex etc.) see Table 2.2.

	Upstream section				Downstream section		
Pike	A	B	C	I	G	H	J
Main River	0.94	0.94	0.88	0.45	0.21	0.66	0.11
Flooded Field	0.00	0.01	0.06	0.02	0.15	0.29	0.17
Ditch	0.06	0.04	0.07	0.52	0.26	0.05	0.66
Millstream					0.38	0.00	0.06

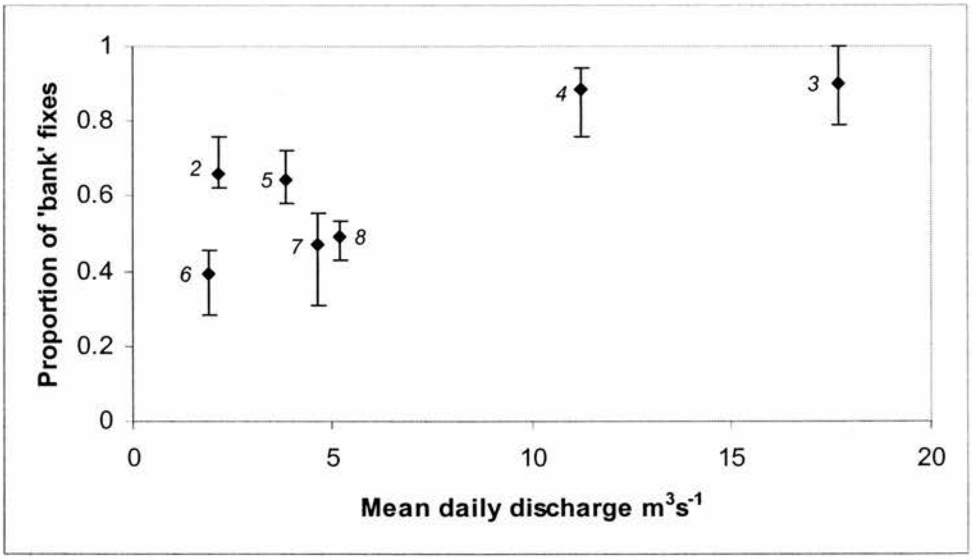
During the September *home range* track (*home range* track number 2), all pike remained within the main river channel, despite ditch habitat, and the millstream being accessible at this time. During the December *home range* track (*home range* track number 3), all habitat categories were accessible, and all were utilised by pike, with pike often being found in several different habitat categories during a single day.

Pike remained within the main river channel during the *24 h / diurnal* tracks at the end of September and in early November when discharge was below, and marginally above, bank-full respectively. During the next four *diurnal* tracks, some fixes always occurred outside of the main river channel, and individual pike were recorded moving between different habitat categories. During high flows however, pike could still be active in the main river channel (Chapter 5), and during the *diurnal* track of 21 December 2000, when discharge was 5.5 m^3s^{-1} above bank-full in the upstream section, Pike A swam >600 m (sum of hourly minimum movement estimates, Chapter 5) between 0500 hours and 2000 hours. This represented a move from the upstream end of the seasonally-determined linear home range, to the downstream end, and then a return to the upstream end again (where the seasonally-determined linear home range refers to the distance between the furthermost upstream and downstream fixes collected during the December *home range* track).

6.3.2 The proportion of 'bank' and 'midstream' fixes

Significant differences occurred between the proportions of 'bank' fixes occurring in *home range* tracks two to eight (Kruskal-Wallis: H = 48.37, d.f. = 6, P < 0.001). There was no clear seasonal pattern, the high proportions of bank fixes (*ca.* 90%) occurring during December 2000 and March 2001 (*home range* tracks 3 and 4), contrasted with the relatively low proportions (*ca.* 50%) in December 2001 and March 2002 (*home range* tracks 7 and 8) (Figure 6.5). There appeared to be a relationship between the proportions of 'bank' fixes and mean daily discharge (Figure 6.5). Although the correlation between these two variables was only significant at the 10% level (Spearman rank correlation: r_s = 0.68, n = 7, P = 0.09)(Figure 6.5), pike appear to occupy midstream areas less frequently under higher discharges and 'bank' habitats seem to be important areas for pike in the river during winter flooding.

Figure 6.5 The median proportion (with interquartile range) of 'bank' fixes (♦) during each *home range* tracks *2* to *8* (Table 2.4) against mean daily discharge.



6.3.3 Electric fishing of side channels

Seven species were either seen or caught during electric fishing of the side channels during January and February 2001, these being pike, perch, minnows, eels, common carp *Cyprinus carpio* L., bullhead and lamprey (not identified to species level)(Appendix 6). Perch and carp are both scarce in the River Frome, but both were caught in Rushton Ditch on 23 January 2001, although the carp was diseased and in poor condition.

On the 23 and 28 of January none of the radio tagged pike were within the side channels, however a large pike was caught, radio tagged and released back into Rushton Ditch , this being Pike Z (Table 2.2). Radio tagged pike were caught around the end of the Railway Ditch on 5 February 2002, whilst Pike I was seen but not caught, and another large pike was caught and radio tagged (Appendix 6). Large pike were also caught in the Hummock and Flood Relief Channels at this time, including radio tagged fish (Appendix 6). The only other fish found in the side channels at this time however were eels and small minnows; larger cyprinid species such as dace were absent (Appendix 6).

None of the pike caught on 23 or 28 January were running milt or eggs, whilst in early February, three pike were running milt, although for two of the three the milt was recorded as being watery. On 5 February, the genital opening of Pike C (♀) was swollen, a condition that occurs towards spawning time (Casselman, 1974), although the pike was not running eggs. When caught on 6 February, Pike H (♀) appeared to be very thin and had the appearance of a post-spawning fish, although it was also possible that this pike was in a generally poor condition.

6.4 DISCUSSION

The use of radio telemetry has allowed valuable data to be collected on the habitat usage of pike during winter flooding and it is clear that off-river habitats are important to pike during winter flooding events. Information on habitat use of fishes throughout the year is of importance to fishery and river management. Studies of the effect river management schemes have on pike populations have concentrated on the loss of off-river habitat as spawning grounds (Boet *et al.*, 1999), however Masters *et al.* (2002) concluded that the potential importance of such habitat to pike populations throughout the winter period should not be overlooked. The pike population of the River Ill, France, was also noted to use off-river habitats (tributaries, ditches, flooded fields and side arms)(Gerlier & Luquet, 1999).

Masters *et al.* (2002) proposed both refuge and feeding hypotheses to explain the use of off-river habitats during winter flooding. Under the refuge hypothesis, pike would be seeking out areas of slow flowing water to shelter from the high flows in the main channel, whilst under the feeding hypothesis, pike would be leaving the main river channel to exploit feeding opportunities in flooded fields and ditches.

Pike did not appear to be confined to areas outside of the main river during floods, but could move about freely in the river at these times, even though the relationship between the proportion of 'bank' fixes and discharge suggests that pike in the river were selecting areas sheltered from the flow; slack water areas being associated with the banks under these conditions.

During *home range* tracks each pike used a variety of the habitat categories available, often being found in several different habitat categories during the course of a single day. Similarly, during *24 h / diurnal* tracks, pike were observed moving into and out of ditches, and were also seen to be active in the main river during major flooding. It is however possible that off-river habitat is used as a refuge in between foraging excursions to the main river. In larger river systems with higher discharges, off-river refugia may be of greater importance than in the relatively small River Frome.

Masters *et al.* (2002) concluded that the feeding hypothesis was a more likely explanation of the observed habitat selections, with pike exploiting feeding opportunities in the flooded fields and drainage ditches.

Reimer (1991) studied the use of floodplains by fishes in the River March, Austria, and after analysing the stomach contents of fish caught in gill nets, suggested that cyprinid species were moving out onto flooded fields to feed. Radio tracking of dace in the River Frome also showed that this species will leave the main channel of the river under flood conditions, and can be found far into fields (Clough, 1998). Wheeler (1998) suggested that an important consequence of seasonal flooding was the increase in foraging space available to adaptable and generalist feeders, noting that various cyprinids, and trout, take advantage of terrestrial insects which become locally abundant during seasonal flooding. Species which move out onto the floodplain were termed 'flood exploitative' by Ross and Baker (1983), who hypothesised that populations of such fish may be favoured during high discharge years as their use of seasonally abundant resources may lead to an increase in the amount of energy available for reproduction.

In flooded fields, the observed positive correlation between discharge and distance from the river bank may be due to pike following prey species into newly inundated areas; fresh sources of terrestrial prey being in the most recently flooded areas, further from the river bank. Frogs, newts and earthworms, in addition to fish, have also been recoded in the stomachs of fish caught in floodplains (W.R.C. Beaumont, pers. comm.; Reimer, 1991).

The positive correlation between discharge and the distance pike could be found along side channels approached significance. If pike were solely using these ditches as refugia from high discharge in the river, then there appears to be no reason why they should swim further along the channel at higher discharges, flow characteristics being superficially similar along the whole length of the channel. Masters *et al.* (2002) suggested that the correlation may again be related to the behaviour of prey fish: as discharge increases, floodwater may wash terrestrial sources of food into the ditch, with this terrestrial input occurring further along the ditch as water level increases, causing prey fish to swim further from the main channel, with these prey in turn being followed by pike.

During winter flooding in the River Frome, the water becomes extremely turbid, with minimum Secchi depths of 0.35 m (pers. obs.), however on the flooded fields and in the side channels, the slower flowing water led to silt being deposited, with a corresponding decrease in turbidity. Pike are regarded as being primarily visual predators (Raat, 1988), therefore conditions for capturing prey may be more favourable in the fields and side channels than in the turbid main river.

If the feeding hypothesis is correct, then pike may be viewed as a 'flood exploitative' species (Ross & Baker, 1983) Whilst individual variation was seen in the amount of time spent off-river, and in the type of habitats selected, both male and female fish were seen to make use of off-river habitats. Any enhanced feeding opportunities during winter flooding may be of particular importance to adult female pike, in which, unlike males, gonad development takes place throughout the winter period (Mann, 1976).

Whilst Masters *et al.* (2002) favoured the feeding hypothesis, further work conducted after the paper was accepted for publication made this explanation seem less likely. Electric fishing of ditches during flood conditions failed to find any concentrations of likely prey fish in these areas, with the exception of eels.

Masters *et al.* (2002) reported that large migrations (> 1 km) occurred during the spring of 2001, with these migrations being performed by pike that had used side channels during the winter. The large scale spring movements initially appeared to be different phenomena to the more localised movements which occurred during winter flooding and therefore the use of off-river habitat was regarded as being unlikely to be related to spawning.

Continued tracking placed the observed movements into a broader context. It became clear that two of the pike which moved large distances in the spring (Pike I and K), regularly migrated between two distinct areas of river and that the timing of upstream migrations, whilst broadly seasonal in nature, also appeared to be cued by increased discharge (Chapter 4). In spring 2002, these pike both swam several kilometres upstream, under flood conditions, to reach the areas near which they had been originally captured, bypassing many suitable refugia on the way. These upstream movements, performed against flood discharges, offer further evidence against a simple refuge hypothesis.

The upstream movements of Pike I and K appeared to be spawning migrations, with the pike possibly displaying either spawning site or natal site fidelity (Chapter 4). The migratory behaviour of these fish suggests that the concentration of pike within and around side channels during periods of flooding may be related to spawning, or pre-spawning behaviour, even though such movements take place well in advance of the recognised spring spawning period for pike in the River Frome (Mann, 1976). The hollow appearance of Pike H when captured in February 2002 suggested the possibility that pike spawning was occurring earlier than had previously been expected. In Windermere, pike spawn at temperatures > 6°C (Frost & Kipling, 1967), and mean daily water temperatures exceeded this value throughout much of the winter of 2000 / 2001 when off-river habitats were commonly utilised.

In order to investigate whether spawning activity was taking place earlier than expected, between January 2003 and March 2003, when water levels were generally high (January, February and March mean daily discharges = 15.0 m^3s^{-1}, 13.9 m^3s^{-1} and 11.1 m^3s^{-1}), individual radio tagged pike were 'observed' whilst in side channels, or the main river, and the side channels themselves were also watched for spawning pike. 'Observation' consisted of listening to the output of the tag (typically for 45 minutes to 1 hour) whilst standing near to the fish location in order that any spawning activity would be seen, but not so close that the fish would be disturbed. No spawning or interaction between pike was observed during these periods (18 observer hours in total), although similar observations, made in spring 2001 and 2002, had resulted in spawning behaviour being observed.

In 2003 CEH staff conducted numerous electric fishing surveys of the side channels, as well as the main river, as part of the NERC funded Lowland Catchment Research (LOCAR) programme. Whilst some males caught in

January were running milt, females were described as being full of eggs but not running, until early April, when two spent females were caught in the main river, near to the Flood Relief Channel (R. Gozlan, pers. comm.).

From the observations of pike within ditches and the results of electric fishing carried out in 2003, when discharge was generally high, it seems unlikely that spawning does occur over the winter period, despite the external appearance of Pike H in February 2002. The return of migrant pike to potential spawning areas does however indicate that the association with side channels may be related to pre-spawning activity. Both male and female pike have been seen utilising side channels during winter flooding, and the fish have also been seen swimming in and out of the channels on a daily basis. The behaviour therefore cannot simply be explained by pike setting up breeding territories, which they then hold until the spawning season.

Individual variation occurs in the proportion of time spent in various off-river habitats, and the number of side channels visited by pike can also vary. The migrant Pike K for example was on occasion found within three separate side channels, whilst Pike I was almost always in the vicinity of the Railway Ditch. Individual variation was also seen during *home range* tracking in December 2001, when < 5% of fixes occurred in side channels for ten of the eleven pike being tracked. For one pike however (Pike Q), 51% of fixes were within a side channel. Such periods of residence in off-river habitats also occurred in the River Ill, with both short (1 - 4 days) and long (41 -146 days) duration incursions being noted (Gerlier & Luquet, 1999).

In conclusion, although off-river habitat is clearly of great importance to pike, even outside of the actual spawning period, the reasons that pike utilise these habitats remain uncertain at present. The refuge and feeding hypotheses are not mutually exclusive, and it could be that in different circumstances pike leave the river to rest or to feed. Similarly, the utilisation of these areas during pre-spawning activity would not preclude the possibility of the areas being used as refugia or foraging locations at different times.

6.5 FURTHER WORK

A better understanding of the reasons off-river habitats, particularly side channels, are used is needed to be able to understand the ecology of riverine pike, and to properly assess the conservation value of these areas. As mentioned in Chapter 4, young-of-the-year pike are currently being implanted with PIT tags in the River Frome, as part of the Lowland Catchment Research (LOCAR) programme, and PIT tag detectors are being installed within existing side channels to automatically record the passage of tagged fish. In addition to young-of-the-year pike, all > 0+ pike captured are also being implanted with PIT tags, as are all other coarse fish species in the river.

Through the results of automatic PIT tag monitoring it should be possible to demonstrate how individual pike partition their time between river and side channel habitats, and to gather evidence to support or refute the feeding hypothesis by analysing the movements of prey species.

Continuous monitoring of the activity of pike within side channels, using the motion sensing TW-5 tag and automatic data logging (ADL) equipment would also help to determine whether pike are feeding within the ditches, and could also potentially identify spawning activity (Beaumont *et al.*, submitted). Sites where the ADL can be deployed during flood conditions are however limited, as the equipment has to be placed above the level of flooding to prevent water from damaging the electronics. The utility of the ADL system during flooding may be further restricted by the mobility of pike, which have been seen to move between river and off-river habitats during a single day. It is quite likely therefore that pike would often swim out of range of the ADL listening station.

6.6 SUMMARY

1) During winter flooding, pike frequently utilise off-river habitats, such as side channels and flooded fields, and can be found up to several hundred metres away from the river channel.
2) The proportion of pike utilising off-river habitat, and the distance from the main river channel (in flooded fields and side channels) are both positively correlated with discharge above bank-full level.
3) Individual differences exist between the proportions of time that different pike spend in particular habitats.
4) Pike were not restricted to off-river habitat during flooding although, within the river, bank-side habitat may be utilised more often at these times. Activity, including upstream migration, occurs within the river even during periods of heavy flooding.
5) Further work is required to determine whether the incidence of off-river habitat utilisation by pike is driven by refuging, feeding or reproductive behaviour.

CHAPTER 7

Habitat selection within the river

To gain a better understanding of the distribution and movements of pike within the river, attempts were made to characterise fine-scale habitat preferences in the River Frome by comparing habitat utilisation, determined from radio tracking and home range analyses, with habitat availability, as recorded during surveys of the river.

My involvement consisted of training and supervision of CEH staff, co-ordination and planning of the various surveys, data collection and digitising of habitat sketch maps. The majority of subsequent analyses were carried out by CEH staff, as part of a project running concurrently with this Ph.D. study (Welton, Hodder, Beaumont, Masters, Pinder & Kenward, 2003; Hodder, Masters, Beaumont, Welton, Kenward, Pinder, Gozlan, submitted); the appropriately cited methods and results being summarised below for completeness and ease of reference.

7.1 INTRODUCTION

An understanding of habitat use is critical towards the understanding of the ecology of a wildlife species, as habitat provides food and cover essential for the population to survive (White & Garrot, 1990d). Pike generally prefer shallow vegetated areas (Diana *et al.*, 1977; Chapman & Mackay, 1984a; Cook & Bergersen, 1988); vegetation being required to provide cover from which to ambush prey, and in turn to provide a refuge from predation (Casselman & Lewis, 1996). Versatility in habitat selection occurs however (Chapman & Mackay, 1984b), and large pike are thought to be less 'tied' to vegetation than smaller fish (Chapter 1; Grimm & Klinge, 1996). Very dense vegetation appears to be suboptimal, especially for larger pike, whilst the boundary zones between vegetated areas and open water may form important ambush sites (Casselman & Lewis, 1996).

As with most aspects of pike biology and ecology, habitat selection studies have concentrated on lacustrine pike, with comparatively little work being conducted in rivers. In the Dorset Stour, electric fished pike were almost always caught among *Iris* and *Scirpus* reed beds[1] along the margins of the river (Mann, 1976), whilst in the River Frome, pike were described as being caught mostly along the river margins or in backwaters, and only rarely in mid-river (Mann, 1980). Similarly, Paragamian (1976) working in the Plover River, Wisconsin, reported that pike were usually caught in vegetated areas, of low water velocity, with bank cover available. Lamouroux *et al.* (1999) described pike as having a significant preference for slow flowing areas of rivers.

The present study aimed to compare habitat utilisation by pike, determined from individual fixes and from home range analyses, with habitat availability in order to comment on habitat selection by riverine pike. Sketch maps of the distribution of various habitat types within the river, together with the results of streambed topography surveys, were used to determine habitat availability (Chapter 2).

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[1] Probably *Iris pseudacorus* L. and *Scirpus lacustris* L. (now *Schoenoplectus lacustris* Palla)(P. Scarlett, pers. comm.).

7.2 METHOD

7.2.1 Available habitat

The proportional availability of habitat types within the river was assessed through mapping surveys conducted from the river bank (Chapter 2). During these surveys, areas of 'sparse' and 'dense' 'submerged', 'floating', 'emergent' and 'overhanging' vegetation, together with flow type ('turbulent', 'glide', 'slack') were sketched onto an outline of the river. The sketch maps were subsequently digitised and the total areas of each habitat type calculated using ArcView GIS 3.2.

Difficulties encountered when assessing habitat availability

Difficulties were encountered when estimating the availability of the different habitat types in the river. Initially, transect surveys were conducted, but due to the unexpected mobility of pike, these were found to not produce the degree of resolution needed and sketch mapping was subsequently performed (Chapter 2). The proportions of aquatic vegetation could change rapidly, such that more than one map was generally needed to describe habitat availability during any particular *home range* track. Mapping could only be conducted on sunny days when the water was clear, as otherwise 'submerged' vegetation could not be seen. Due to the turbidity of the river during winter months, sketch mapping of 'submerged' vegetation could not be conducted year-round.

7.2.2 Utilised habitat

Radio tracking

At each fix, when visibility allowed, information was recorded on the occurrence of 'submerged', 'floating', 'emergent' and 'overhanging' vegetation within the rectangle around the likely fish position formed by the accuracy estimate (Chapter 2). Flow type was recorded and the substratum noted if visible (Chapter 2). The location of the fish relative to the banks was also recorded, with 'bank' fixes being those that occurred within 1 m of the nearest bank, and 'midstream' fixes being those > 1 m from the nearest bank.

Utilised habitat was also estimated by overlaying cluster polygon (C_{tx}) home range outlines onto habitat sketch maps and determining the proportions of each habitat type within the polygons (Welton *et al.*, 2003).

Direct visual observation

During the majority of the study, the immediate surroundings of radio tracked pike were described from the bank, but during the summer of 2002 I attempted to investigate fine-scale habitat selection by pike in greater detail.

Direct visual observation by snorkelling was attempted, with a fieldworker on the bank directing the snorkeller to the location of a radio tagged pike; the aim being for the snorkeller to view the fish and record accurate information about its location, including factors which were impossible to determine from the bank, such as depth in the water column and the angle to the flow. The method was however found to be of little use, as it was heavily biased towards the observation of pike in relatively open, shallow water; pike in deeper areas and/or amongst submerged vegetation being impossible to see. Consequently the method was discontinued.

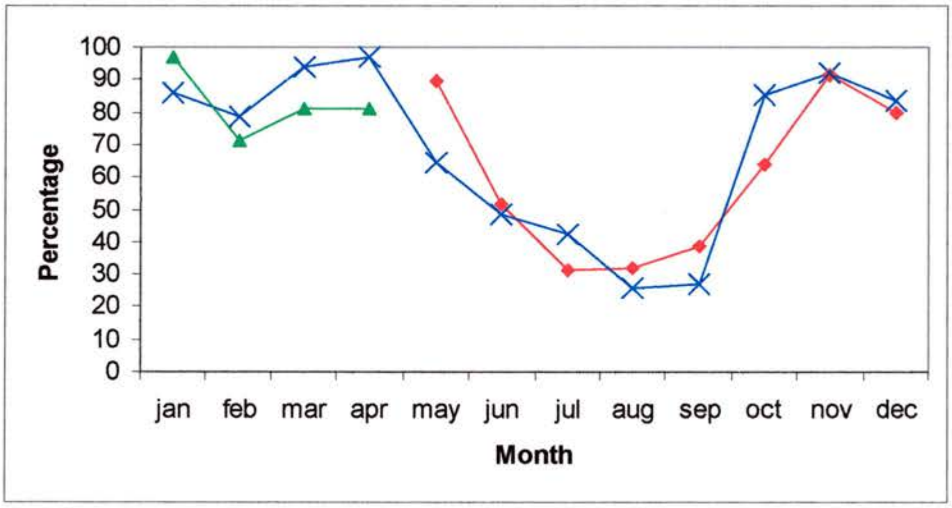
Previously, attempts had also been made to directly view radio tagged pike in the river by using a pole-mounted underwater video camera. The camera was moved slowly towards a radio tagged pike, whilst the picture from the camera was viewed live using a miniature television set on the river bank. This method also proved to be impractical, due to the difficulty of seeing cryptic pike amongst the dense submerged vegetation of the river, and was consequently abandoned.

Difficulties encountered when assessing habitat utilisation

As with describing the availability of different habitat types, describing the exact habitat that pike were utilising was problematic. When recording information from fixes, despite being able to accurately locate the radio tags, the fish itself was only very rarely seen. The rectangle described by the accuracy estimates placed around the fish location (Chapter 2) could easily contain different species and densities of vegetation, together with unvegetated areas, and it was not possible to say which of the particular habitat types the fish was actually in. Also, whilst radio tracking from the bank, only the two-dimensional location of the pike could be determined, it being impossible to estimate the vertical position of the pike within the water column. The immediate environment around the pike could be quite different, depending upon its depth. For example, a pike under a mat of flowering *Ranunculus spp.* could be amongst the floating vegetation at the water's surface, lying on bare substratum on the riverbed, or at any depth in between. Furthermore, the river was often too turbid to be able to describe the submerged vegetation at any particular fix. Sixty-three percent (5300) of all 8433 fixes recorded between May 2000 and April 2002 (when regular tracking ended) had 'unknown' recorded as the submerged vegetation type, with the proportion of 'unknowns' higher in winter than in summer months (Figure 7.1).

Describing habitat utilisation by overlaying home range areas onto habitat maps was also problematic. The proportion of the various habitat types could change rapidly, such that each map provided only a 'snapshot' of habitat availability. The habitat types within any particular C_{tx} home range cluster polygon could vary temporally, even within the 13 day period of a *home range* track. White and Garrot (1990d) recommend against this approach, stating that any errors in the home range estimate will be carried over into subsequent habitat analysis.

Figure 7.1 The proportion of fixes for which submerged vegetation was recorded as being unknown during each calendar month in 2000 (◆), 2001 (×) and 2002 (▲). Data from all 7709 fixes collected during *routine*, *24 h*, *diurnal* and *home range* tracks between May 2000 and April 2002.



7.2.3 Selection for vegetation and flow types

Welton *et al.* (2003) used data collected during *home range* tracks and concurrent habitat mapping to examine habitat selection. Four different comparisons between utilised and available habitat were made, for each fish in every *home range* track, these being:

a) Comparing the proportion of a habitat type within a fish's 'reach' with the proportion of that habitat type in the study area as a whole (where the 'reach' is defined as the area of river between the furthermost upstream and downstream fixes during the *home range* track).
b) Comparing the proportion of a habitat type within the cluster polygon home range of a fish with that available within the study area as a whole.
c) Comparing the proportional use of a habitat type for a fish, as recorded at each fix, with the availability of that habitat type within the fish's 'reach'.
d) Comparing the proportional use of a habitat type for a fish, as recorded at each fix, with its availability within the C_{tx} cluster polygons.

Utilised habitat was then compared with available habitat for each fish and a Jacobs' '*D*' score calculated, using the formula:

$$D = U - V / [U + V - 2UV]$$

Where U = proportion used, V = proportion available. The Jacobs' '*D* ' score provides an unbiased symmetrical index, giving values between -1 and +1, negative values indicating relative avoidance and positive values relative preference (Jacobs, 1974; Kenward, 2001). For each habitat type, the median Jacobs' index was then calculated from all fish and Wilcoxon rank tests used to test whether the distribution of the Jacob's indices for any particular habitat type differed significantly from zero *i.e.* whether relative preference or avoidance was occurring (Welton *et al.*, 2003).

7.2.4 Selection for depths

Streambed topography data, collected during depth surveys (Chapter 2) were available for 16 ranges recorded for nine pike (Hodder *et al.*, submitted). The mean depth within the C_{tx} home ranges were calculated from the individual depth measurements within these areas and compared with the mean of depth measurements within the entire 'reach,' for each fish in every *home range* track, using a paired *t*-test (Hodder *et al.*, submitted). Depth measurements were taken directly from the point coverage containing the depth data and were not adjusted for water level during the *home range* tracks; they therefore represent relative rather than absolute depths.

In certain areas of river, the C_{tx} home ranges of several pike overlapped. The mean depths within these areas of overlap were calculated and the relationship between mean depth and the number of overlapping home ranges examined using a Pearson's correlation (Hodder *et al.*, submitted), depth values being relative rather than absolute, as before.

7.3 RESULTS

Studying fine scale habitat selection within the river proved to be more difficult than anticipated. As explained in the method, considerable difficulties were encountered in determining both habitat utilisation and availability.

7.3.1 Available habitat

The numbers of sketch maps available that recorded 'submerged' vegetation, 'emergent'/'floating'/'overhanging' vegetation and flow categories were 10, 12 and 11 respectively (Welton *et al.*, 2003). 'Emergent', 'floating' and 'overhanging' vegetation formed low percentages of the area mapped, generally being restricted to occurring along the banks, whilst 'submerged' vegetation generally formed a higher percentage of the available vegetative cover (Table 7.1). 'Floating' vegetation could occur midstream in summer, when submerged macrophytes grew up to the surface (Welton *et al.*, 2003). In general more vegetative cover was recorded in summer months but there was considerable annual variation between the percentage cover in the same month *e.g.* submerged vegetation covered 82% of the area mapped in July 2000, but only 24% of the area mapped in 2001 (Welton *et al.*, 2003). The principal flow type within the river was described as 'glide,' smooth-flowing water (Table 7.1). 'Slack' water was restricted to the margins in spring, autumn and winter, but occurred midstream in summer months, in association with mats of floating vegetation (Welton *et al.*, 2003).

Table 7.1 *Redrawn using data from* Welton *et al.* (2003): Percentage cover of vegetation summarised from 12 sketch maps of out-stream vegetation and 10 sketch maps of submerged vegetation. Low overhanging vegetation was defined as ≤ 0.5 m and high overhanging vegetation as ≥ 0.5 m from the water level. a = 'absent', s = 'sparse', d = 'dense'. Flow type 1 = 'slack,' 2 = 'glide,' 3 = 'turbulent.'

	Vegetation type and density															Flow type		
	Submerged			Emergent			Floating			Low Overhang			High Overhang					
% Cover	a	s	d	a	s	d	a	s	d	a	s	d	a	s	d	1	2	3
Minimum	10	3	1	90	0	0	88	0	1	93	0	0	95	0	0	3	65	3
Median	**67**	**10**	**12**	**97**	**1**	**1**	**96**	**1**	**3**	**97**	**1**	**2**	**99**	**0**	**1**	**5**	**87**	**6**
Maximum	88	46	87	99	4	8	99	3	11	100	4	4	100	2	4	22	93	26

7.3.2 Selection for vegetation and flow types

Comparisons of habitat availability within the 'reach' (the area of river between the furthermost upstream and downstream fixes during the *home range* track) was not significantly different from that available in the whole study area, with the exception of flow categories, where there was a relative preference for 'glides' within reaches, and a corresponding relative avoidance of 'turbulent' flows (Figure 7.2a).

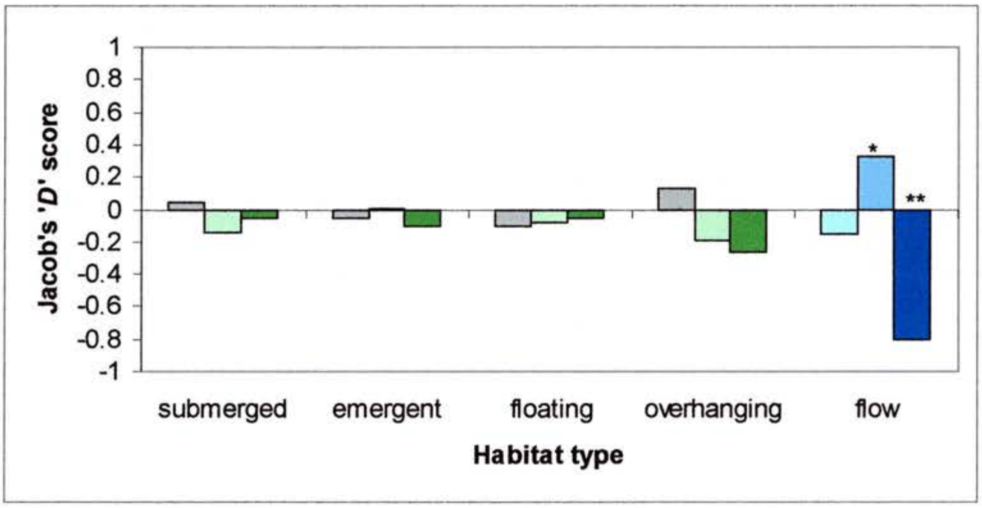
There was apparent avoidance of 'emergent', 'floating' and 'overhanging' vegetation within the C_{tx} home range, as compared to availability within the whole study area. However, these habitats all occur along the river margins and so any cluster polygon that does not include the same proportion of bank habitat as is generally available will necessarily show avoidance of these habitats (Figure 7.2b).

For utilisation determined at individual fixes, compared to availability within both the 'reach' and the C_{tx} range, significant relative selection occurred for habitats including 'submerged,' 'emergent', 'floating' and 'overhanging' vegetation and relative avoidance of open areas of water, devoid of cover (Figure 7.2c & 7.2d). Within 'submerged' and 'emergent' vegetation, selection was for 'dense' and 'sparse' categories respectively, whereas for 'floating' and 'overhanging' vegetation both 'sparse' and 'dense' categories were selected (Figures 7.2c & 7.2d).

Amongst the flow categories, for utilisation as determined at individual fixes, compared to availability within both the reach and the C_{tx} range, significant relative selection occurred for areas of 'slack' water (Figures 7.2c & 7.2d).

Figure 7.2 *Redrawn from data in* Welton *et al.* (2003): Median values of Jacob's '*D*' scores for pike for 'absent' ( ), 'sparse' ( ) and 'dense' ( ) categories of vegetation, and 'slack' ( ), 'glide' ( ) and 'turbulent' ( ) flow types in the River Frome. Significance of Wilcoxon's rank tests, testing that *D* scores are different from zero, are indicated, where * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

7.2a) U = proportion in reach, V = proportion in entire study area



7.2b) U = proportion in C_{tx} home ranges, V = proportion in entire study area

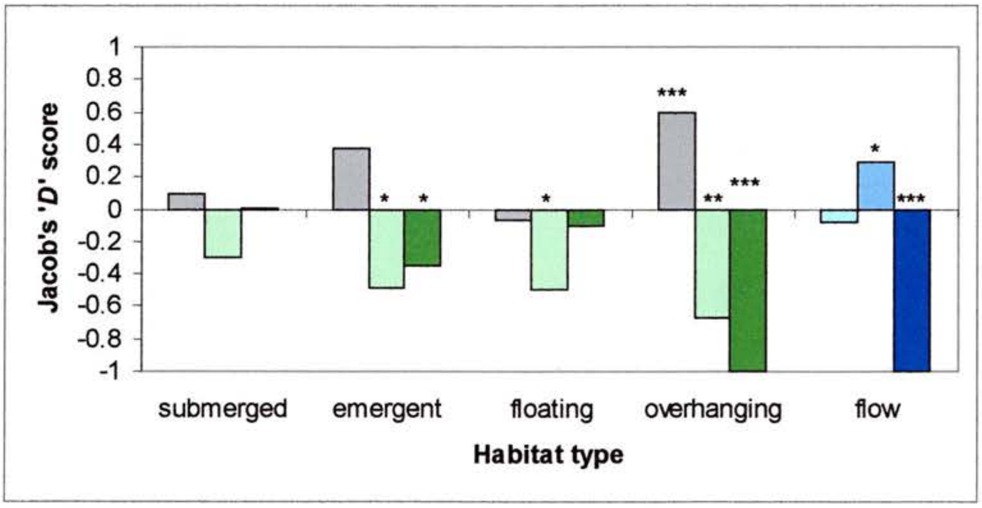
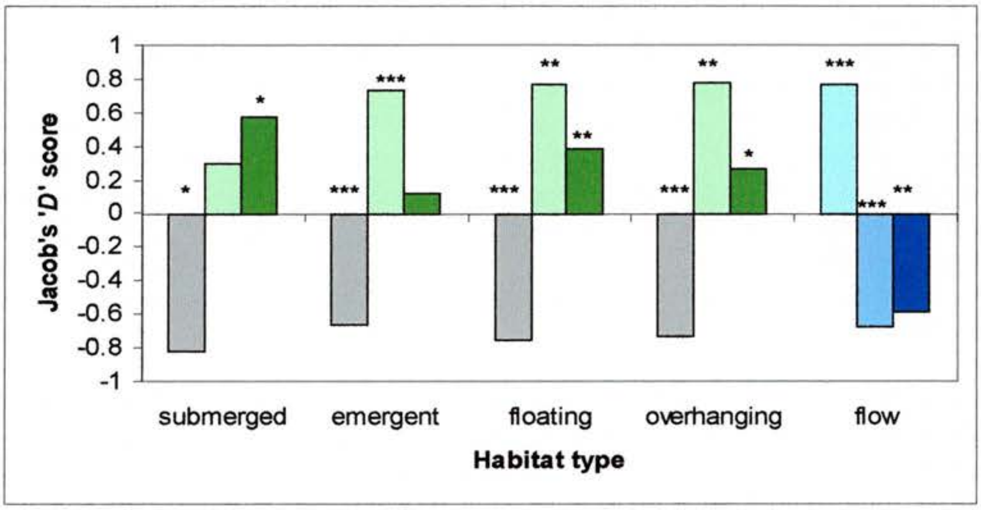
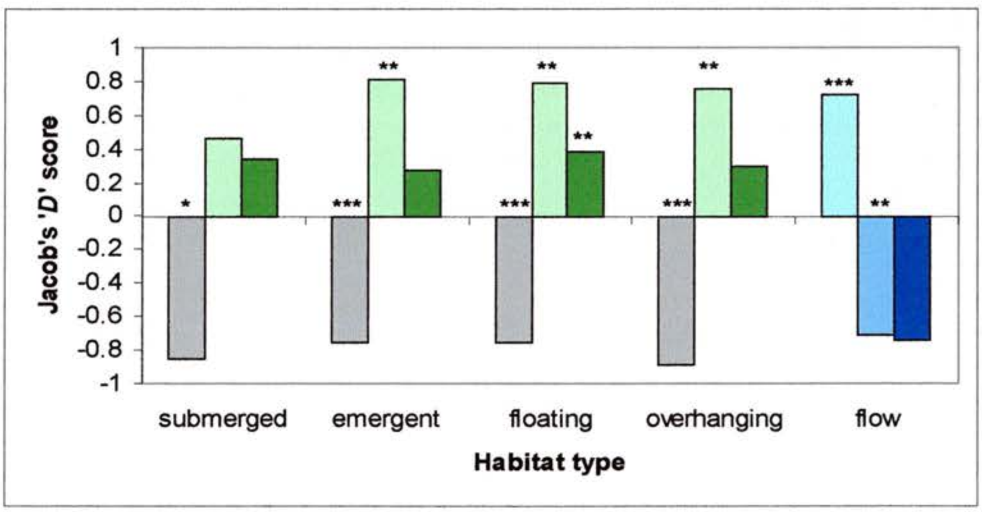


Figure 7.2 continued

7.2c) U = proportion determined from fixes, V = proportion in reach



7.2d) U = proportion determined from fixes, V = proportion in C_{tx} home ranges.

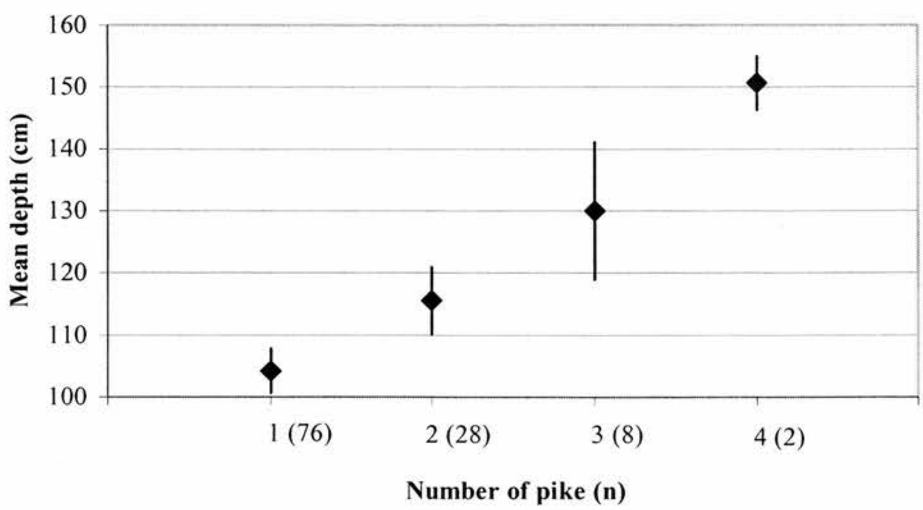


7.3.3 Selection for depths

Cluster polygons generated during C_{tx} home range analysis showed that core areas of activity tended to be located around deeper areas of the river channel (Hodder *et al.*, submitted); areas defined by the C_{tx} ranges being significantly deeper (0.16 ± 0.05 m difference, mean ± S.E.) than the depths within the reaches (paired t-test: t = 3.35, $n = 9$, $P = 0.01$)(Hodder *et al.*, submitted).

Areas where more C_{tx} home ranges overlapped tended to be deeper than areas where fewer ranges overlapped (Pearson's correlation: r = 0.99, d.f. = 3, $P <$ 0.01)(Figure 7.3) (Hodder *et al.*, submitted).

Figure 7.3 *Reproduced from* Hodder *et al.* (submitted): The relationship between the degree of overlap between pike C_{tx} home ranges and mean (± S.E.) depth. On the x-axis, one pike indicates zero overlaps, two pike one overlap *etc.* with the number of records for each value shown in brackets. Mean depths were calculated from streambed topography survey data (Chapter 2) and therefore represent relative rather than absolute depths.



7.4 DISCUSSION

As with lacustrine pike, a general preference was seen for vegetated areas over bare areas. Deeper areas within the river were preferred and areas of slack water were also selected. The results of habitat analyses conducted as part of the present study are in general agreement with the limited, previously published information on habitat selection by pike in rivers (*op. cit.*).

Due to the inaccuracies involved in the various methods described above, the results should be treated with caution and regarded as showing general patterns only. Particular caution should be taken in interpreting the degree of selection for 'emergent', 'floating' and 'overhanging' vegetation, due to the often low availability of these habitat types. With only low proportional availability (Table 7.1), a low number of fixes in these locations could lead to apparent high levels of preference.

The lack of independence between habitat types should also be taken into account when interpreting the habitat selection results. For example, 'slack' flows often occur alongside banks, and contain 'floating' vegetation and the habitat records cannot be used to distinguish which factor pike are selecting for, whether the 'slack' flow, the 'floating' vegetation or the 'bank'. Equally, observed preferences for 'emergent' and 'overhanging' vegetation could in fact be due to pike preferentially locating near banks (Chapter 6) rather than selecting the vegetation type itself.

Throughout the year, 30% to 90% of fixes occur within 1 m of the bank, with higher proportions of 'bank' fixes occurring during periods of high discharge (Chapter 6). By comparing utilisation of 'bank' habitat with availability within the 'reaches' of 15 pike, Cooper (2003) demonstrated that pike were positively selecting 'bank' habitat during the summer, percentage availability ranging between 11 % and 18 % of the reach, whilst utilisation ranged between 75% and 100%. This selection may be due to the presence of slack flows and vegetation, although banks can also themselves provide shade; a pike hovering in shade may benefit from being able to detect approaching fish before it can itself be detected (Helfman, 1981).

Despite the positive selection for 'bank' habitat, 'midstream' areas were also commonly used. During times when there is plentiful submerged vegetation pike appear to be able to find localised patches of 'slack' water in the middle of the river, by sheltering amongst or behind vegetation. During summer months, pike often seemed associated with mats of floating vegetation, such as flowering *Ranunculus spp.* with these mats often being 'midstream' (> 1 m away from the nearest bank). As the signal from the radio tag provided no information on the depth at which the pike was located, it was not possible to determine whether pike were immediately beneath the floating vegetation at the surface, or at greater depth, sheltered from the flow by the mass of vegetation upstream. Mats of floating vegetation may represent high quality habitat for pike as in addition to providing shelter from flow, the mats also provide overhead shade, with pike in such locations able to accrue the benefits associated with such cover (Helfman, 1981).

Within the vegetation categories, preferences for dense submerged and sparse emergent vegetation were seen. Whilst 'emergent' vegetation may provide good cover, high densities of emergent plants may impede mobility, or may be physically inaccessible to larger pike (Grimm & Klinge, 1996) and this may serve to explain why significant positive selection for 'dense emergent' vegetation did not occur. 'Submerged' vegetation provides a different physical structure from 'emergent' vegetation, and pike may be able to occupy denser stands of this vegetation type. It may be easier for pike to occupy vegetation which trails in the horizontal plane (such is the case for many submerged macrophytes) rather than more vertical emergent vegetation, with good vision and mobility being possible in horizontal structures (Welton *et al.*, 2003).

In the aquatic environment, prey may be particularly conspicuous when viewed from below, backlit against the sky, whereas cryptic predators may be particularly difficult to view from above, particularly during dawn and dusk periods (Helfman *et al.*, 1997f). Consequently, occupying the deeper areas within the river may prove advantageous to pike. Both the strong positive correlation between the number of pike found in an overlap area and the mean depth of that area, and the fact that C_{tx} ranges were significantly deeper than the area defined by the reach, showed that pike tended to congregate in the deeper parts of the study area. The river is relatively shallow throughout the study area, the median depth recorded during streambed topography surveys in the summer of 2001 and 2002 being 0.85 m (interquartile range = 0.55 m to 1.25 m). Whilst deeper areas could contain many overlapping C_{tx} ranges, without simultaneous tracking it was not possible to determine whether areas of overlap were routinely occupied by more than one pike at the same time (Hodder *et al.*, submitted).

Areas of 'slack' water were positively selected. However, as with boundary zones between vegetated areas and open water (Casselman & Lewis, 1996), there may also be advantages in occupying boundary areas between flow types. A pike in an area of 'slack' water, but near to a 'glide', for example, would benefit from the reduced energy expenditure in station keeping afforded by being in slow flowing water, but would still be able to view the faster flowing river, where prey, such as drift feeding dace and salmonids may be more common. The proportional availability of interface areas between different flow types could not be estimated from habitat sketch maps, however the flow type at the surface was recorded at each fix ('slack', 'glide' or 'turbulent'), along with the presence of any other flow type within 1 m of the probable fish location. Cooper (2003) reported that out of a total of 176 fixes of pike tracked in the River Frome during the summer of 2002, 90 fixes (51%) were in locations where another flow type was located within 1 m of the pike, with pike being in 'slack' water and near 'glides' for 85 fixes and in 'glides', but near 'slacks' for five of these fixes.

The percentage of cover of submerged vegetation available in 13 pike 'reaches' determined during *home range* tracking in July and September varied between 18% and 94% (median 46%). However, no correlation between percentage cover in the 'reach' and the area of 'reach' existed, *i.e.* range sizes neither increased nor decreased in response to the changing availability of submerged vegetation (Hodder *et al.*, submitted). An adjustment of space use with the availability of submerged vegetation may have been expected, however an absence of such a relationship suggests that the requirements for cover may have been met in all cases, such that aquatic vegetation never became a limiting factor in range size (Hodder *et al.*, submitted).

7.5 FURTHER WORK

Whilst general conclusions on habitat selection could be drawn from the data collected during the present study, considerable difficulties are involved in describing fine-scale habitat selection amongst widely ranging aquatic species. Consequently, further studies of habitat selection by pike may be best conducted on captive individuals, where conditions can be controlled such that the exact location of the pike may be determined (perhaps using combinations of radio telemetry, PIT tagging and direct visualisation), and the habitat types offered can be controlled to 'tease out' the factors important to pike. Work of this nature would have to take into account the difficulties associated with successfully keeping pike in captivity. Large pike require large aquaria, particularly if the fish are to be presented with a variety of habitats. Furthermore, feeding large pike in captivity is problematic. Whilst some can be induced to take dead fish bait, not all will do so (J.D. Armstrong, pers. comm.), and the feeding of live prey to predators would require a license under the Animals (Scientific Procedures) Act 1986. Small pike can be kept successfully in captivity, and their habitat preferences studied (Chapter 8), but the results of selection studies on small pike cannot necessarily be applied to larger pike, due to changing habitat requirements associated with increasing fish size (Chapter 1; Grimm & Klinge, 1996).

The fish tracked in the present study were all large pike ($L_F > 50$ cm). Despite the difficulties associated with habitat selection studies of wild fish, a study of small pike, testing the hypothesis that these fish are more closely associated with vegetation than larger pike, could make a considerable contribution towards the understanding of the ecology of the species. Such a study could be conducted by externally attaching miniature radio tags to small pike (Beaumont & Masters, in press).

The possibility of using experimental manipulations to study habitat selection in the wild also exists, for example, through the provision of artificial structures within the river. Under such conditions, however, the difficulties associated with determining exact locations for pike would remain.

7.6 SUMMARY

1) As with lacustrine pike, selection for vegetated areas occurred, with significant relative selection occurring for habitats including 'emergent', 'overhanging', 'floating' and 'submerged' vegetation, and relative avoidance of open water areas.
2) Within 'submerged' and 'emergent' vegetation, selection was for 'dense' and 'sparse' categories respectively, whereas for 'floating' and 'overhanging' vegetation some selection for both 'sparse' and 'dense' categories occurred.
3) There was significant relative selection for areas of 'slack' water.
4) Core areas of activity tended to be located around deeper areas of the river channel, whilst areas where more C_{tx} home ranges overlapped tended to be deeper than areas where fewer ranges overlapped.
5) The availability of different vegetation and flow categories within the river varied on a seasonal basis and between years, but range sizes neither increased nor decreased in response to changing availability of submerged vegetation.

CHAPTER 8

Habitat selection and diel activity of sibling young-of-the-year pike

Studies of captive animals can offer insights into behaviour that are impossible to obtain in the field. This is particularly true of studies of habitat selection, or studies of small, cryptic animals. Fieldwork based sampling of habitat selection by animals is complicated by factors such as competition interference, which can result in only a fraction of the population occupying the areas they would choose if free to do so (Krebs & Davies, 1993). Additionally, practical difficulties exist in determining proportional utilisation and availability of habitat types (Chapter 7) and sampling techniques themselves may also lead to bias in results. When studying the distribution of juvenile pike using the point abundance by electric fishing method (PASE), Brosse *et al.* (2001) described fish as being mainly found in 'shelter habitats;' probably as a result of disturbance caused by the fieldworker.

Radio or acoustic telemetry offer means of collecting information on habitat utilisation with less opportunity for bias than visual (or capture) based methods, assuming that habitat selection by the tagged animals is representative of that amongst the population. However, the technique can only be applied to relatively large fish, due to limitations imposed by minimum tag sizes and tag to fish weight ratios, the lower size limit for fish that can be tagged currently being around 15 cm (Lucas, 1999). Whilst the behaviour of free-living adult pike has therefore been studied extensively (see previous chapters), little is known about the behaviour of 0+ pike, these being particularly difficult to study due to their small size, assumed solitary nature, cryptic colouration and association with aquatic vegetation.

Although habitat selection studies on pike may be best carried out on captive animals, there are considerable difficulties associated with keeping large pike in captivity (Chapter 7, Appendix 2). In the present chapter, the distribution and movements of individual young-of-the-year pike are examined, under standardised conditions to provide information on habitat selection, and also to increase knowledge on the behaviour of 0+ pike. Specifically, two hypotheses are tested, these being that habitat use and the timing of activity are both non-random.

This work was conducted in collaboration with Dr J.D. Armstrong of the Fisheries Research Services and Professor A.E. Magurran of the University of St Andrews and sections of the current chapter have been submitted for publication in the *Journal of Fish Biology*.

8.1 INTRODUCTION

As adults, pike tend to be associated with vegetation (Chapter 7) and this association is also seen during the first year of life, when moderately dense vegetation can reduce vulnerability to predation, as well as providing suitable sites from which to ambush prey (Casselman & Lewis, 1996).

The early lives of many pike are spent in the spawning areas, where the young fish are vulnerable to intra-cohort cannibalistic predation (Grimm & Klinge, 1996; Skov *et al.*, 2003). After migration from spawning to nursery habitats (Chapter 1), the young pike become vulnerable to cannibalism from older year classes. Some 0+ pike overwinter in the nursery areas (Mann &

Beaumont, 1990) and these may become vulnerable to cannibalism from older fish during winter flooding, when riverine pike make use of these areas (Chapter 6). Pike use increasingly deep water throughout their first year, although in late summer individuals appear to be distributed across a wider range of depths (Casselman & Lewis, 1996).

Data on the effect of light intensity on 0+ pike behaviour is sparse: Skov *et al.* (2002) reported different distributions of 0+ pike between open water and structured habitats during the day and night. In clear water, without prey, pike appeared to be located in complex habitat by day and open water at night (Skov *et al.*, 2002). Adult pike are generally regarded as moving least at night, and may have single, diurnal peaks in activity or peaks around dawn and dusk (Chapter 5). The activity pattern can also vary throughout the year, with crepuscular peaks in the summer and a single diurnal peak during the winter (Chapter 5).

In the present study, the distribution and movements of individually identifiable, sibling, young-of-the-year pike were examined in an indoor glass-sided canal, to test the null hypotheses that 1) distribution between habitat types and 2) the timing of activity were random.

8.2 METHOD

A brood of pike was reared in captivity at the Almondbank unit of the Fisheries Research Service Freshwater Laboratory, UK. All pike were full siblings, the progeny of one male and one female caught in Loch Freuchie, Perthshire (56° 3' N 3° 5' W) in spring 2002. After hatching, the pike were kept in unstructured glass aquaria, under ambient light supplemented by artificial illumination. The pike were initially fed on *Daphnia*, and then on a diet of earthworms as they became larger. The fish were graded by size as they grew and experiments were conducted using the largest group of fish ($L_F = 21.2 \pm 1.0$ cm; mean ± S.D.), which were comparable in length to wild 0+ pike at the same time of year (Raat, 1988). All 16 pike used in the experiment had previously been implanted with PIT tags (U.K.I.D. Systems, Riverside Industrial Park, Caterall, Preston, Lancashire, PR3 0HP) for husbandry purposes; PIT tags being small (12 mm x 2.12 mm, weight in air 0.1 g) transponders, encapsulated in glass which emit a unique code when interrogated by a detector, allowing for the individual identification of fish. PIT tags were implanted into the peritoneal cavity of pike (anaesthetised using benzocaine) via a mid-ventral incision, just anterior of the pelvic fins. Following tag insertion, the wound was covered with Cicatrin antibiotic powder (The Wellcome Foundation Ltd, Greenford, Middlesex, UB6 0NN) and Orahesive adhesive powder (Convatec Limited, Deeside).

Experiments were conducted in four identical arenas (7.5 m long by 1.6 m wide) in a glass-sided canal. Metal grilles, covered with wooden boards, separated the arenas. The boards prevented pike from rubbing against the grilles and ensured visual isolation between the arenas. Fish were viewed from within a dark hide that ran the length of the canal. Each arena was divided notionally into five sections, landscaped to provide a variety of habitat types for the pike, and flat-bed PIT tag detectors (Armstrong *et al.*, 1996) were placed at the boundaries of adjacent sections. PIT tag detections were automatically logged. Each section had a gravel/cobble substratum. The sections in each arena were (upstream end first):

S1 (Shallow 1) – a shallow section (depth = 20 cm) containing 17 bamboo canes planted in the substratum to simulate a reed bed; **S2** (Shallow 2) – a shallow section (depth = 20 cm) containing no shelter apart from a short length of tube (6" PVC pipe fitting) placed on the substratum; **Pool** – a deeper area (depth = 44 cm) in which a 17 cm wide wooden beam, parallel to the glass side and 36 cm from the substratum, provided overhanging cover; **S3** (Shallow 3) = similar to S2; **S4** (Shallow 4) – similar to S1 but with only 10 bamboo canes.

Excluding the areas over the PIT tag detectors, S1 and S4 each comprised 13% of the surface area of each section, with S2 and S3 each comprising 24% of the surface area. The pool comprised 27% of the surface area. Water was refreshed by a trickle feed from the nearby River Almond and velocity was too low to measure.

Single pike were placed in each of the four sections for 7 – 8 d, between 8 October and 4 November 2002, giving a total of 16 replicates over a 4-week period (Table 8.1). During this time water temperatures in the canal varied naturally between 1.3° C and 10.3° C (mean daily average water temperature = 6.2 ° C).

Pike were not fed whilst in the canal, in order to standardise hunger level among individuals, and to avoid simply recording behaviour during digestion, when pike are predominantly inactive (Lucas *et al.*, 1991). As pike were placed in a novel environment where they were not fed, and where predators were absent, the inherent behaviours of individual fish guided their assessment of potential prey availability and predator risk in the different habitats (Hawkins *et al.*, in press).

Table 8.1 The dates of each of the four weekly experiments, together with PIT tag identification numbers and fork lengths of each pike.

Week	Arena	Tag	L_F (cm)
1 (8 - 15 Oct)	1	B9C5	21.0
	2	A2C8	22.0
	3	B7A5	21.7
	4	9OEA	21.8
2 (15 – 22 Oct)	1	B3BE	20.0
	2	AA92	21.3
	3	A83C	21.5
	4	AC5B	21.4
3 (22 – 29 Oct)	1	AFE7	20.5
	2	AC06	20.2
	3	AO5C	21.2
	4	B996	19.5
4 (29 Oct – 4 Nov)	1	AA2F	22.0
	2	AOCE	23.3
	3	9981	20.2
	4	9801	22.2

Lights (400 Watt Philips SON Agro bulbs (6000 lux) suspended 1.6 m above the gravel surface every 1.8 m along the canal) were switched on or off incrementally over a ten minute period, between 06:30 and 07:00 and 17:00 and 17:30. The precise time varied in accordance with natural variation in day length.

8.2.1 Settling time

The time pike took to settle in the arenas was examined by using records from the PIT tag monitoring system as an index of movement. In order to use PIT tag detections in this way, it was necessary to remove repeat detections from the dataset, which occurred when a pike remained near a detector for an extended period of time. Accordingly, any records for an individual pike for which the interval between consecutive detections, over the same detector, was < 1 minute were removed. All of the remaining records were termed 'new detections.'

To establish the veracity of using these 'new detections' as an index for movement, visual observations of occasions when pike changed sections during 13 separate, 2 h periods of continuous observation, were compared with PIT tag records. The number of new detections for each PIT tag detector was compared with the number of visual observations of pike passing over that detector. Out of 69 new detections, two did not correspond with a visual record, as the pike came within range of the detector without passing over. On one occasion, the PIT tag system missed a fish movement which was observed visually.

New detections were grouped into day (07:00 to 17:00) and night (18:00 to 06:00) categories, depending upon the hour in which they occurred. Detections occurring between 06:00 and 07:00, or between 17:00 and 18:00, were not placed into either day or night categories, due to variation in the level of illumination in the sections during this time.

To examine the duration of any settling period, the median number of new detections h^{-1} were calculated for the first, second, third *etc.* day and the first, second, third *etc.* night of the experiment, using pooled data from all 16 pike.

8.2.2 Habitat use

Throughout the experiment, arenas were visually examined at hourly intervals during daylight, and the section in which the pike was located was recorded. Additionally within the pool section, the number of times when pike were observed beneath the overhang was also recorded. From the hourly data (collected after the settling period) χ^2 analyses were conducted for each pike, to determine whether habitat use was non-random (Neu *et al.*, 1974; White & Garrot, 1990d), at a Bonferonni adjusted significance level of α" = 0.05 / 16. Where non-random use occurred, Bonferroni confidence intervals were calculated around the proportion of records in each habitat type, to estimate where significant selection or avoidance occurred (Neu *et al.*, 1974; White & Garrot, 1990d), the interval being as follows, with α = 0.05 and k, the number of habitats, = 5,

$$\hat{p}_i - z_{(1-\alpha/2k)}\left[\frac{\hat{p}_i(1-\hat{p}_i)}{n}\right]^{1/2} \leq p_i \leq \hat{p}_i + z_{(1-\alpha/2k)}\left[\frac{\hat{p}_i(1-\hat{p}_i)}{n}\right]^{1/2}$$

where p_i is the observed proportion of locations in habitat type i, n is the sample size (number of observations) and $z_{(1-\alpha/2k)}$ is the upper standard normal variate corresponding to a probability tail area of $(1-\alpha/2k)$. If the confidence interval generated includes the availability proportion, then significant preference or avoidance cannot be said to have occurred.

An overall test of the presence of habitat selection by the population was calculated by summing the χ^2 statistics and degrees of freedom from all 16 pike (White & Garrot, 1990d). Pike locations recorded at hourly intervals were assumed to be independent, as during thirteen 2 h periods of continuous observation, a median of 1.5 section change events h^{-1} took place (first quartile = 0, third quartile = 3) where a section change event was a five-minute period during which the pike moved between two or more chambers.

A χ^2 test was conducted, to determine whether pike were preferentially located beneath the overhang, rather than being randomly distributed within the pool.

8.2.3 PIT tag records

Diel pattern of activity

To examine the diel activity pattern of the pike, the mean number of new detections recorded during each hour was calculated for each individual fish, after the settling period. Consequently, for each hour, there were 16 values for the mean number of new detections in that hour, one for each pike, allowing comparisons to be made between the distributions of these mean values at different times in the diel cycle; new detections being grouped into day (07:00 to

17:00) and night (18:00 to 06:00) categories, depending upon the hour in which they occurred.

Correlations of activity with environmental factors

The temperature of water drawn from the river into the canal was recorded continuously throughout the experiments. Turbidity in the canal was related to discharge in the River Almond, with spates resulting in more turbid water being drawn in. Daily discharge data from the Almondbank gauging station (56° 25' N 3° 30' W) were used as an indicator of relative turbidity in the canal. Spearman's rank correlations were used to examine relationships between activity, and both water temperature and discharge, where activity was the total number of new detections from all fish.

8.2.4 Continuous visual observations

Pike were selected at random and observed for 2 h, either in the morning (≈07:00 to 09:00), midday (≈11:00 to 13:00) or evening (≈15:00 to 17:00). As the canal was illuminated by artificial lights, variation in light level between the three time periods was minor, thus the terms dawn and dusk are avoided. Observations were conducted only after the end of the settling period.

In addition to morning, midday and afternoon observations, attempts were made to observe pike during the hours of darkness using night vision equipment however the short attenuation distance of infra-red light in water, together with the lack of close focussing capability, meant that the fish could not be viewed at night.

Following initial observations of the pike, a series of behaviour categories was described (Table 8.2). The number of occasions each behaviour type was observed was recorded, during five minute periods, throughout each continuous observation. Distinguishing between 'fin' and 'body' swims could be difficult. When recording the number of 'waves,' if the pike flexed twice without a pause between each flexing, this was recorded as one 'wave' behaviour, rather than two; two or more 'waves' being recorded if there was a perceptible return to 'station keeping' between each 'wave' event.

For each of the three time periods, the overall proportion of five-minute periods containing a particular behaviour category was calculated, from all fish combined. Due to the low number of observations, no statistical tests have been conducted to compare the proportions of each behaviour category between time periods, or between fish.

Table 8.2 Behaviour categories recorded during continuous observations of pike.

'Immobile'

Fish in contact with substratum. No fin movement.

'Station keeping'

Fish not in contact with substrate. Maintaining position by means of small fin movements (typically dorsal and pectoral).

'Wave'

Whilst station keeping, fish slowly flexes body from pelvic fins back to tail.

'Fin Swim'

Movement (including vertical movements or turning), using fins for propulsion but not involving flexing of the body.

'Body swim'

Forward propulsion resulting from both fin movements and flexing of the body. Often followed by a short glide.

8.3 RESULTS

8.3.1 Settling time

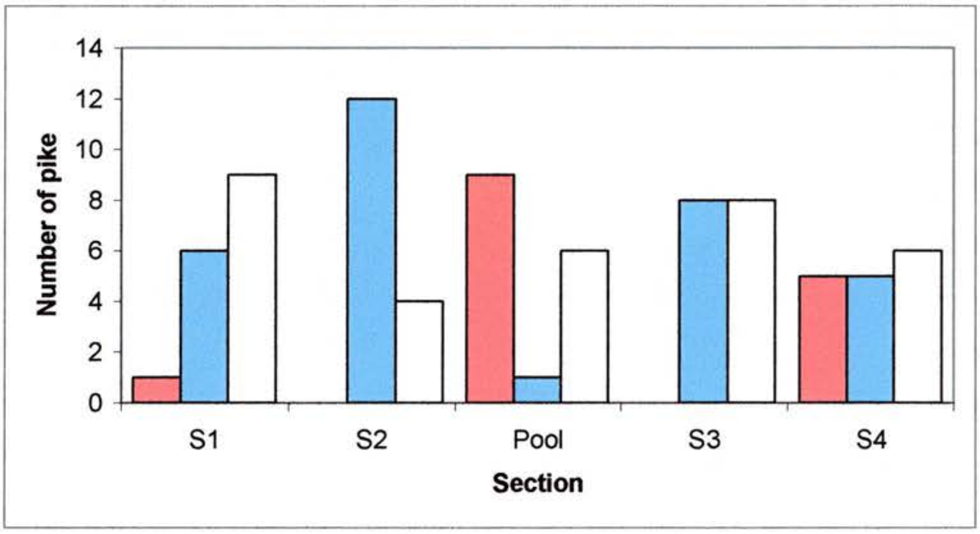
From the records of the PIT tag monitoring system, a median of two new detections h^{-1} was seen to occur on both the first and second days (using data pooled from all fish). On subsequent days, the median numbers of new detections h^{-1} equalled zero. Pike were therefore regarded as settling for the first two days of each experiment, with habitat, movement analysis and continuous observations all therefore beginning on the third day of each week. The median number of new detections h^{-1} was zero during all night periods.

8.3.2 Habitat use

Between 21 and 35 (28.1 ± 4.6, mean ± S.D.) records of location within the arena were available for each pike. High turbidity in the flume prevented visual observations on some occasions. Overall habitat use was non-random (χ^2 = 678.5, d.f. = 64, $P < 0.001$), with every pike individually also showing non-random selection of habitat (χ^2 = 16.7 to 79.6, all d.f. = 4, all $P < 0.003$). Overall, pike were recorded in S1, S2, pool, S3 and S4 during 11%, 6%, 53%, 8% and 23% of observations respectively (where the sections formed 13%, 24%, 27%, 24% and 13% of the available area).

Amongst the pike where significant positive selection for particular habitat types occurred, this selection was either for the pool (n = 9), section S1 (n = 1) or section S4 (n = 5) (Figure 8.1). No pike showed positive selection for more than one habitat. 12 pike and 8 pike respectively, avoided sections S2 and S3, and no pike showed positive selection for these sections (Figure 8.1). Pike were never observed sheltering inside the lengths of tubing provided in these two sections.

Figure 8.1 The number of pike showing significant preference (■), significant avoidance (■), or no significant preference or avoidance (□) for each habitat type.



Pike were recorded as being beneath the overhang during 85% of the 239 observations of pike in the pool. Only 9% of the volume of the pool lay beneath the overhang, therefore, within the pool, pike were recorded under the overhang far more often than would have been expected by chance ($\chi^2 = 1707$, d.f. = 1, $P <$ 0.001).

8.3.3 PIT tag records

Diel Pattern of Activity

Mean values of the number of new detections during each hour of the day (07:00 to 17:00) were higher than during each hour of the night (18:00 to 06:00), when few new detections occurred (Figure 8.2). The median value of the mean numbers of new detections for each pike, was 0 in eleven out of the twelve night time hours (Figure 8.2); therefore data from this time period were not examined for variation. During the day, the median values of the mean numbers of new detections for each hour, ranged between 0.8 and 2.53 (Figure 8.2). There were no significant differences in the mean numbers of new detections occurring during different hours of the day (Friedman test: $S = 13.7$, d.f. = 9, $P = 0.133$), however there were significant differences in activity between pike (Friedman test: $S = 68.6$, d.f. = 15, $P < 0.001$).

When the activity of individual pike was further examined, it was seen that the variation in activity between individuals may have been attributable to some variation in conditions between replicates, as instances of greater activity occurred in weeks three and four of the experiment than in weeks one and two (Figure 8.3).

Figure 8.2 The median value, with interquartile ranges, of the mean number of new detections, calculated for each hour (n = 16 pike).

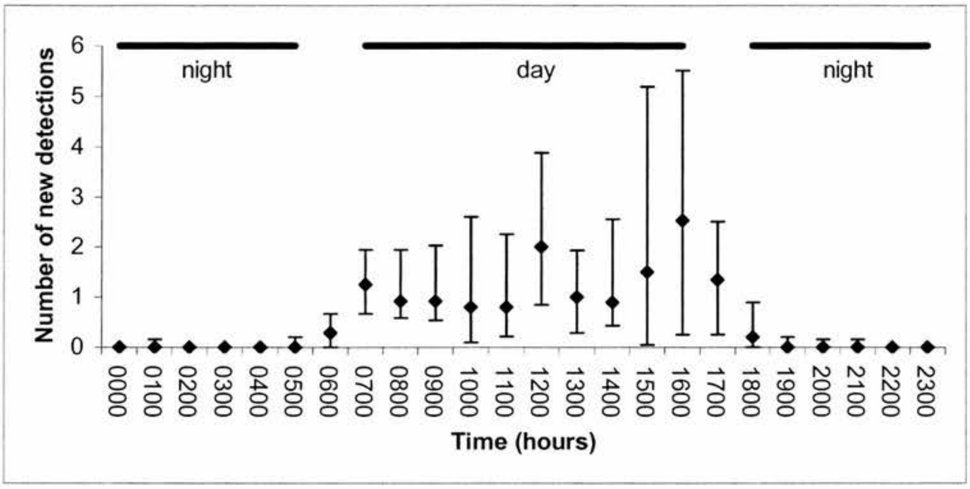
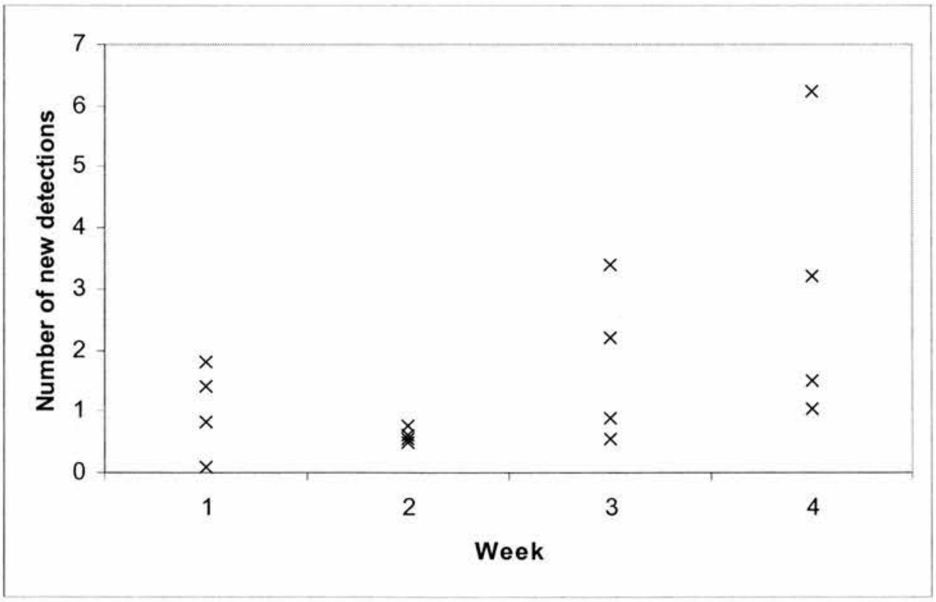


Figure 8.3 Median values of the mean number of new detections in all daylight hours, for each pike, in weeks one to four.



Correlations of activity with environmental factors

The total number of new detections during the daytime (after settling, pooled from all fish) was positively correlated with the discharge of the River Almond ($r_s = 0.58$, $n = 19$, $P = 0.01$) but not with water temperature ($r_s = 0.38$, $n = 19$, $P = 0.11$). Discharge was higher during week three and week four of the experiment than during week one and week two, whilst water temperature was highest in the first week (Table 8.3). The lowest discharges and temperatures both occurred in week two (Table 8.3).

Table 8.3 Daily average water temperatures (mean ± SE) recorded in the canal and discharge of the River Almond (mean ± SE) during each week of the experiment.

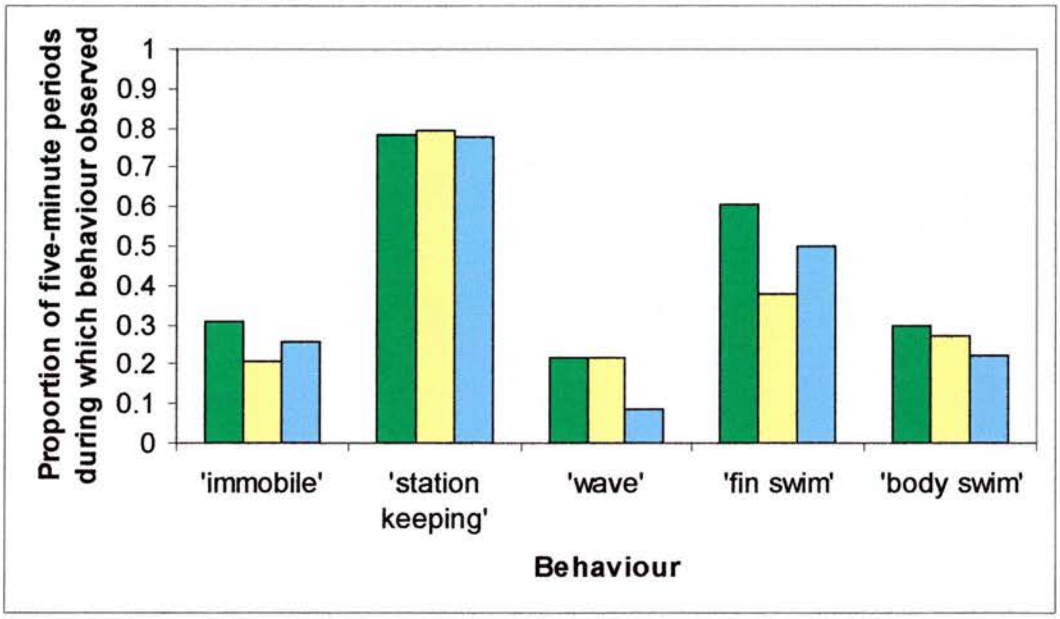
Week	1	2	3	4
Daily water temperature °C	8.4 ± 0.4	4.1 ± 0.7	5.4 ± 0.2	6.9 ± 0.7
Daily discharge m^3s^{-1}	13.2 ± 4.7	7.8 ± 4.7	13.4 ± 2.3	15.1 ± 5.2

8.3.4 Continuous observations

Two-hour continuous observations were conducted in the morning (n = 4), the midday (n =5) and evening (n = 4) time periods. More continuous observations were planned, but these had to be abandoned when high turbidity prevented pike from being viewed continuously.

The proportions of behaviour categories observed during five-minute periods, pooled from all observations during the morning, midday and evening observations appear very similar (Figure 8.4).

Figure 8.4 The overall proportions of five-minute periods containing each behaviour type during morning (■),midday (■)and evening (■) continuous visual observations.



'Station keeping' was the most commonly observed behaviour, occurring in around 80% of all five-minute periods during morning, midday and afternoon.

'Fin swimming' was more common than the more rapid 'body swimming' (Figure 8.4). Distinguishing between 'fin' and 'body' swims could be difficult, particularly when a movement involved a transition between swimming types.

The 'immobile' behaviour, where pike rested motionless on the substratum occurred in a similar overall proportion of five-minute periods from all three time periods (Figure 8.4), but the pattern of occurrence of this behaviour category differed between the time periods. During morning observations, 'immobile' was always the first behaviour category recorded, with the pike switching to 'station keeping' between 5 and 25 minutes after the lights switched on. All but two of the 49 midday and evening five-minute periods containing the 'immobile' behaviour occurred on the 19 and 20 October, when daily average water temperatures were 3.3°C and 1.9°C respectively, low in comparison to those recorded throughout the whole duration of the experiment (Table 8.3).

The 'wave' behaviour occurred in all time periods, with the number of 'waves' occurring within a five-minute period ranging between one and six, although, as noted in the method, some of these 'wave' behaviours would have involved more than one flexing of the body.

8.4 DISCUSSION

Overall, pike selected relatively deep habitat, and areas of overhang within that habitat. However, there was significant variation among individuals and some fish selected shallow reed habitat. There was a clear avoidance of habitat including shelter in the form of tubes. Activity was strongly diurnal and therefore broadly similar to patterns observed in studies of adult pike. Activity varied among individuals and correlated with turbidity.

Since substantial variation in preference exists within a single sibling group, the present study suggests that a substantial proportion of the variation in habitat use by wild pike, *e.g.* depth selection amongst 0+ pike, (Casselman & Lewis, 1996) could be a product of individual differences. The fish were held in a common environment and therefore the variation cannot readily be attributed to rearing history.

Differential behaviours can arise through different competitive abilities amongst fish. For example, amongst Atlantic salmon, the optimum strategy for some poorer competitors is to live in non-defended areas or in the gaps between the territories of other fish, rather than attempting to hold a territory themselves (Metcalfe, 1998). The pike used in the experiment were graded by size as they grew (in order to reduce cannibalism amongst the brood), with the pike used in the experiment being the largest available. These fish were therefore all good competitors and the variation in habitat use is unlikely to be associated with inherent differences in competitive ability amongst the fish.

In nature, variations in habitat selection can have profound consequences for life histories. For example, in the River Frome, Dorset, UK, a proportion of 0+ pike remain in the spawning channels for the whole of the first year, where they grow slowly, feeding on invertebrates, whereas those that migrate to the main channel have a piscivorous diet and a more rapid growth rate (Mann & Beaumont, 1990).

The three habitat types in the experiment provided distinctly different types of cover. Reeds gave good cover from the side, but pike were clearly visible from overhead, whereas overhead cover, but little side cover, was provided by the overhang in the pool. Overhangs also provide shade from which a predator can gain a visual advantage over approaching prey and predators, detecting them before it is itself detected (Helfman, 1981).

Whilst there were no predators in the present study, their absence does not remove the anticipated risk of predation. Avoidance of potentially dangerous habitats even in the absence of predators is an inherent behaviour (Metcalfe *et al.*, 1998) and laboratory-reared fish from wild parents retain this anti-predator behaviour (Metcalfe *et al.*, 1987; Magurran, 1990).

The overall selection for pools suggested that overhead cover from avian predators was generally of most intrinsic importance. Although the reed bed sections provided no overhead cover, densely vegetated areas may act as a physical barrier to larger pike, restricting their mobility and foraging efficiency (Bry, 1996). Consequently, although providing limited shelter from birds, the reed bed sections may have provided relatively effective shelter from one of the most dangerous aquatic predators. Of the two sections simulating reed beds, more pike showed positive selection for S4, which contained 10 canes, than for S1, which contained 17 canes. Less dense reed beds may be preferred, so that the mobility of the 0+ pike is not impaired.

Despite providing good cover, from both from the side and overhead, the tubes in sections S2 and S3 were never seen to be occupied in this study, although pike have been seen occupying tubes in the absence of other forms of shelter (J.D. Armstrong, pers. comm.). It seems likely that the pike perceived their mobility and/or visual field to be impaired by the shelters, such that the chances of escaping a predator, or of detecting prey, would be compromised. Additionally, tubes may form good shelters for eels, which in nature occupy diurnal residences such as burrows, or cavities inside stone walls (Baras *et al.*, 1998). The tubular shelters may therefore have been avoided due to an inherent assessment of the risk of predation in these locations.

The diurnal activity of the 0+ pike was consistent with vision being the primary sense involved in prey capture (Raat, 1988). During dawn and dusk periods, pike have a competitive advantage over their prey (Pitcher & Turner, 1986) and increased activity may occur at these times (Malinin, 1970; Mackay & Craig, 1983). A more accurate simulation of dawn and dusk than was possible with the experimental apparatus employed would be required to establish clearly whether there is a crepuscular pattern to the activity of 0+ pike.

Discharge of the River Almond served as a proxy for turbidity in the arenas, with increasing turbidity occurring during spates. There was a positive correlation between discharge and activity, and the generally greater activity of pike during weeks three and four correlates with increased turbidity at these times. Pike may employ a more active hunting strategy during periods of reduced visibility, as sufficient cover for hunting may be provided by the opacity of the water, whilst low visibility gives greater protection from avian predators, allowing pike to venture out of refugia (Skov *et al.*, 2002). However, both Cook & Bergersen (1988) and Chapman & Mackay (1984b) found adult pike in lakes were distributed further offshore in windy conditions, when wave action brought about increased turbidity near-shore, although the depths selected by pike did not change. This suggests that pike avoid turbid areas, although other parameters, such as turbulence may be the causative factors. Masters *et al.* (2002) reported adult pike using flooded field and drainage ditch habitat during winter flooding of the River Frome and noted that the slower flowing water in these habitats led to silt deposition and a corresponding decrease in turbidity. A search for clearer water then may also be a factor in explaining the observed correlation between turbidity and activity in 0+ pike.

The prevalence of the 'immobile' behaviour early in the morning, together with the low number of PIT tag detections at night, suggests that this behaviour may occur over night, although this could not be confirmed due to the difficulty of conducting nocturnal observations. When 'immobile,' pike were noticeably more difficult to disturb than at other times, suggesting that the 'immobile' behaviour represents a period of 'sleep'; lack of response to disturbance having been documented amongst other 'sleeping' fishes (Marshall, 1972). The 'immobile' pike commonly rested with their pelvic and lower caudal fin in contact with the substratum, and the fish were often difficult to see whilst 'immobile' due to their cryptic colouration. Such colouration may serve as a passive defence mechanism at a time when pike are potentially more vulnerable to predators. The occurrence of the 'immobile' behaviour throughout the day during periods of low water temperature is interesting, suggesting short periods of relative cold may result in pike 'sleeping' for a greater proportion of time than would otherwise be the case.

The function of the 'wave' behaviour is at present unknown. Pike have low heart rates at cold temperatures (maximum *ca.* 30 beats per minute^{-1} at 5°C (Armstrong, 1986)) which, coupled with the small size of the ventricle, suggests that there is little blood flow around the body (J.D. Armstrong pers. comm.). Whilst the body of the pike consists of 55% to 60% muscle (Webb, 1984a), the majority of this is unvascularised white muscle, as in the closely related muskellunge (Beggs *et al.*, 1980). It is possible then that the slow, exaggerated movement seen during 'wave' behaviour, is involved in aiding blood flow around the body. Alternatively, a 'station keeping' pike may be alert to the possibility of prey coming within ambush range, and if such an event occurred, the muscles would need to operate efficiently despite the fish having been inactive for some time. The 'wave' behaviour may therefore be involved in maintaining the fish in a state of readiness and be analogous to the 'warming up' stretches performed by human athletes prior to exercise.

8.5 FURTHER WORK

This study has demonstrated the occurrence of individual differences in behaviour within a single family of pike. However, further studies with more families would be needed to assess the extent of within-family variation in the population as a whole. Observations should also be extended over a greater period of time to confirm that the individual differences observed are not simply an artefact resulting from the length of each experiment; extending the experiment to longer than one week will be complicated by a need to feed the pike. As the present study was conducted on single pike, which were not fed for the duration of the experiment, the effects of adding potential competitors to the arenas, or of introducing food, remain to be studied. Similarly, the experiments were performed in the absence of predators. With appropriate licensing, the effect of model predators on habitat selection could be studied.

An experimental set-up, similar to that used in the present study, could potentially be used to investigate patch residency times in habitats between/within which food availability differs, contributing to the understanding of the diel / diurnal movement patterns of pike (Chapter 5). A suitable food delivery system would have to be devised, in order that pike could be fed without disturbance.

Although a strongly diurnal pattern of activity was seen, given the crepuscularity often reported for this species (*op. cit.*), it is unfortunate that the lighting system used could not simulate extended periods of 'twilight.' Studying the relationship between light level and activity in the wild is difficult (Chapter 5), and so, providing that illumination could be adequately controlled, studies of captive pike could be of value in determining the relationship between illumination and mobility. Viewing pike at night remains problematic, but locations within the arenas, at least, could be determined if pike were fitted with small, luminous markers *e.g.* Betalights (SRB Technologies (UK) Ltd., 6 Portland Business Centre, Datchett, Berkshire, SL3 9EG) (Clough, 1998).

Further investigation of the various behaviours categorised during the study is also warranted. The function of the 'wave' behaviour remains to be determined. Given experimental equipment that allows for the simulation of dawn and dusk periods, and an adequate sample size, the proportional occurrence of the different behaviour categories could be examined at different times of day. Comparisons between individual fish could also potentially be made.

8.6 SUMMARY

1) Habitat use was found to be non-random, with the deepest areas being preferred overall.

2) Individual variation in habitat choice occurred. Of the 16 pike tested, nine selected the pool habitat and six the artificial reeds. No pike showed positive selection for more than one habitat.

3) Within the pool there was a strong preference for areas with overhang.

4) Activity was predominantly diurnal, in common with observations of larger pike.

5) Individual variation in the level of activity occurred and this variation was positively correlated with turbidity.

CHAPTER 9

Summary and future directions for research

9.1 SUMMARY

The aim of this thesis has been to investigate predator-prey interactions from the point of view of a widespread, versatile, apex predator; the pike. Studies of riverine pike have, to date, been relatively scarce and fieldwork therefore took place in the River Frome, Dorset. A study of captive young-of-the-year pike provided further information on habitat utilisation, diel behaviour and individual variation in the species.

In the river, pike were shown to display a high degree of mobility at each of the temporal levels at which they were studied, contrasting with the *a priori* expectation that the fish would occupy small, preferred areas, such as a single pool within the river (Welton *et al.*, 2003; Beaumont *et al.*, submitted).

Pike were shown to move between different locations in the river on a daily basis. Whilst there was some evidence for increased movements during dawn and dusk periods, movements could also occur throughout the day; movements between locations being interpreted as occurring between different potential ambush sites, with satiated pike being more likely to remain stationary (Chapter 5). Prey species therefore appear to be at risk from pike throughout the day, leading to prey partitioning their time into refuging and feeding behaviours. As with adult pike, young-of-the-year fish were also found to be diurnally active (Chapter 8).

On a seasonal basis, pike were seen to occupy multinuclear home ranges, typically extending along several hundred metres of river (Chapter 4), with the daily activity representing movements between nuclei within the home range. On any one date, pike were capable of moving throughout their entire seasonal home range, even under flood conditions. Pike were commonly found in deeper water; they also showed positive selection for bank-side areas, regions of slack flow and plentiful aquatic vegetation (Chapter 7). Work on habitat selection by young-of-the-year pike revealed individual variations in habitat preference (Chapter 8).

Radio tracking pike over the course of several seasons, or years, revealed a variety of spatial behaviours. The hypothesis that the pike population consisted of 'static' and 'mobile' components (Mann, 1980) was rejected. Instead, the existence of a continuum of spatial behaviours, containing 'permanent resident,' 'migratory' and 'emigrant' categories was proposed (Chapter 4). 'Migratory' pike appeared to be performing spawning migrations, and moved between the same upstream and downstream areas in successive years. Although broadly seasonal in nature, these movements were also associated with periods of flooding. Migration of these pike was not obviously related to the migration of prey species, and, superficially, habitat did not appear to differ between the upstream and downstream locations.

The long-term spatial behaviour of River Frome pike can therefore be discussed in relation to the phenomenon of 'partial migration', in which one fraction of the population is migratory whilst another remains as residents. The apparent continuum of spatial behaviours, together with the observation of 'emigrant' behaviour, suggests that the 'migrant' and 'permanent resident' categories of behaviour result from 'conditional' factors, rather than representing two distinct, genetically determined strategies (Chapter 4).

Off-river habitats, particularly side channels, were found to be of great importance to the pike population of the River Frome, not just during the spawning period and early life history, but also during periods of winter flooding. Pike do not appear to be simply seeking refuge from high flows, and the behaviour may instead be related to movements of prey species out of the main river and onto the floodplain. However, the association between the upstream movements of 'migratory' pike and the onset of flooding, together with the absence of prey fish in side channels during electric fishing surveys, suggested that the observed utilisation of side channels may have been related to pre-spawning behaviour.

9.2 FUTURE DIRECTIONS FOR RESEARCH

From the suggestions for further work highlighted individually in Chapters 4 to 8, it is clear that there are three broad directions in which future work should proceed, these being:

a) An extension of the study of pike movements in the River Frome to include the smaller size classes.

Begon *et al.* (1990) state that 'phases of dispersal or migration are crucial in the life history of all organisms' and that 'the extent of dispersal of individuals and populations in nature is usually the most difficult part of the life history to measure.' This may be particularly true of species living in environments where direct observation of individuals is impossible.

Currently knowledge of the movement and dispersal of small pike is very limited, but techniques are now available to extend the study of pike spatial behaviour into the smaller size classes; this being vital towards answering fundamental questions raised by the discovery of the 'partial migration' phenomenon amongst River Frome pike. Specifically, the questions of whether 'permanent resident' pike are indeed remaining close to their natal spawning ground throughout their lives, and whether 'migrant' pike are performing natal homing need to be answered. Methods available to address the questions include externally attaching miniature radio tags to small pike (Beaumont & Masters, in press) and the recapture and automatic detection of pike implanted with passive integrated transponder (PIT) tags. Pike in the River Frome are currently being implanted with PIT tags, to study off-river habitat use as part of the NERC funded Lowland Catchment Research (LOCAR) programme; a collaborative research project between CEH Dorset and the University of Durham being a direct product of the present study. Radio tracking of small pike is also planned as part of the LOCAR research.

b) Further investigation into the significance of off-river habitat to the pike population.

By automatically logging the movements of PIT tagged pike, and similarly tagged prey species into and out of side channels, it will be possible to further study off-river habitat use by fishes in the River Frome, and to investigate the 'refuge' and 'feeding' hypotheses discussed in Chapter 6, as well as the possibility that the occurrence of pike in these habitats is a pre-spawning behaviour, such a study being a part of the work of the LOCAR programme. It will also be possible to automatically collect information on the frequency with which side channel habitats are occupied by individually identifiable pike.

c) Studies of how 'decision making' at the individual level influence the spatial behaviour of pike in different environments.

Differences in spatial behaviour have been described between populations, with some pike occupying multinuclear home ranges (Mackay & Craig, 1983; Jepsen *et al.*, 2001; Ovidio & Philippart, submitted) whilst others occupy an area for a time before relocating (Diana *et al.*, 1977; Mackay & Craig, 1983; Cook & Bergersen, 1988), and still others show less structured spatial behaviour still, with pike moving freely throughout the lake (Diana, 1980; Chapman & Mackay, 1984b; Jepsen *et al.*, 2001). Although Jepsen *et al.* (2001) concluded that the reported differences in behaviour were probably genuine, and not simply artefacts resulting from different sampling strategies, little work to date has explored the underlying reasons for the observed variations in spatial behaviour.

In addition to the effects of phenotypic variation and the behaviour of other individuals, individual variation can also arise through behavioural responses to different environmental conditions (Magurran, 1993). Pike appear to have an in-built adaptability, and further research into the conditions which bring about the variety of spatial behaviours in this species would be of considerable interest. Pike may operate by a series of 'rules' which govern their behaviour at each temporal scale, through which different spatial behaviours arise depending upon circumstance. A valuable future direction for research then would be to link individual behaviour, on a daily basis, to long-term spatial behaviours as observed in different populations. For example, where prey are sparsely distributed, pike would be expected to remain longer at any one potential ambush site than in prey dense environments (Chapter 5), whilst overall home range/territory size would be expected to be larger than in an environment with greater food availability (Chapter 4). In prey dense environments then, pike may be expected to relocate more frequently than where prey is sparse, but to occupy smaller areas overall. Such a hypothesis could potentially be tested either through comparative studies between water bodies, or through stocking of sufficiently large experimental areas with known densities of pike and prey, and then following pike movements using telemetry, although difficulties would undoubtedly be encountered in controlling for factors such as vegetation density, prey community composition *etc.* Similar investigations could also potentially be conducted using young-of-the-year pike, these fish being easier to keep in captivity than adult fish (Chapter 8). Appropriate licensing would be required in all such studies.

Further studies of the behavioural ecology of pike, with an emphasis on predator-prey interactions between pike and juvenile Atlantic salmon are currently being conducted by the University of St Andrews and the Fisheries Research Service. Whilst perhaps not directly addressing the issues arising from the present study, the research will further increase the understanding of fundamental aspects of freshwater ecology, and will no doubt in turn lead to many other suggestions for future research.

In conclusion, the study of aquatic ecology can metaphorically, and often literally, be described as an attempt to distinguish detail from the broad outlines visible through turbid water. Through the application of both direct and remote methods of observing the behaviour of an apex predator, this study has revealed intriguing details of the ecology of fish in rivers. Future research will no doubt continue to increase the clarity with which predator-prey dynamics in freshwater ecosystems can be viewed.

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APPENDIX 1.

The variety of attachment methods available when radio tagging fish.

Acoustic or radio tags are generally attached to fish in one of three ways, either externally, internally in the stomach or internally in the body cavity (Mellas & Haynes, 1985). Ideally, a tagged fish should behave no differently than an untagged fish. To this end, the weight of the tag in water should not exceed 1 to 2 % of the weight of the fish to be tagged (Laird & Stott, 1978; Ross & McCormick, 1981).

External tags are generally attached to anaesthetised fish using sutures or wire passed through the dorsal musculature of the fish, either alongside or behind the dorsal fin (Kenward, 2001). Whilst wire forms a permanent attachment, soluble sutures may be used to ensure that the tag falls off the fish after the battery has expired (Beaumont *et al.*, 1996). External tags can increase the energy expenditure of the fish as the surface of the tag can cause significant drag, reducing swimming performance *e.g.* Counihan & Frost (1999). If sutured onto the outside of the fish, drag caused by the tag can result in significant abrasion around the suturing sites (McCleave & Stred, 1975), this abraded area being vulnerable to infection, particularly by aquatic fungi (Ross & McCormick, 1981; Mellas & Haynes, 1985) however, passing attachment lines through narrow, flexible plastic tubing inserted into the body of the fish can reduce this problem (Herke & Moring, 1999). Prophylactic measures can be taken against fungal infection, for example, by applying the fungicide malachite green, mixed with silicone grease, around the area of tag attachment (Beaumont *et al.*, 1996). The effects of external tags can include an increased susceptibility to predation, increased sensitivity to environmental stress and reduced growth rates (Ross & McCormick, 1981). Entanglement in aquatic vegetation can also potentially be a problem (Ross & McCormick, 1981). The behaviour of fish can also be altered by the presence of an external tag, for example, coral grouper *Plectropomus leopardus* (Lacapède), in aquaria, were observed spending a lot of time rubbing the tag area against the substratum (Zeller, 1999). The adverse effects of external tags can be minimised by using small tag sizes, suitable attachment techniques and streamlining tags where possible.

Intragastric implantation of tags is a quick and simple method for tagging carnivorous fishes (Lucas & Johnstone, 1990), however the technique is best suited for short term studies, as the tag may be regurgitated after a short period of time (Lucas & Johnstone, 1990; Zeller, 1999). Implanting a transmitter in this way may lead to changes in behaviour by the fish. Stomach fullness may control appetite, so a transmitter implanted in the stomach may potentially lead to a reduction in foraging activity by the fish, although a reduction in feeding was not reported for cod *Gadus morhua* L. implanted with intragastric tags (Lucas & Johnstone, 1990). Although the problem of drag, associated with external tags, can be eliminated, intragastric tags are still capable of reducing swimming performance (McCleave & Stred, 1975), and again the minimum possible tag size should be used.

Acoustic or radio tags can be internally implanted into the peritoneal cavity of fishes (Hart & Summerfelt, 1975). Many peritoneal radio tags have an external antenna, which requires a hole to be pierced into the side of the fish, allowing the antenna to trail externally (Jepsen & Aarestrup, 1999), however fully encapsulated tags with an internal coiled antenna are also available (such as the Biotrack TW-5 used in this study). Whilst external antennae increase the range of the signal, passing an antenna through the body wall can potentially lead to infection, and may possess other disadvantages associated with externally attached tags; for example, entanglement with aquatic vegetation.

Peritoneal tagging has the advantage of eliminating external drag, but the major disadvantage is the invasive nature of the procedure, although stress to the animal can be minimized through the use of appropriate anaesthetics, sterile surgical equipment and prophylactic doses of antibiotics. Internally implanted tags are suitable for long-term studies, as tag retention is good. Expulsion of tags can occur however, through the incision site, through the hole made for an external antenna (Bunnell & Isely, 1999), or even through passage into the gut (Baras & Westerloppe, 1999). As with external tags, fungal infection may occur following surgery (Mellas & Haynes, 1985). Whilst problem of increased drag is eliminated, tags should still be kept to the minimum possible size to avoid adverse effects to the fish.

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APPENDIX 2

Developing a method for the internal implantation of TW-5 radio tags into pike.

Implanting radio tags into fish is a technique regulated by the Animals (Scientific Procedures) Act 1986, in that it is a scientific procedure which may have the effect of causing pain, suffering, distress or lasting harm. Consequently, this study was carried out under licence from the Home Office. Prior to commencing the study, Modules 1 to 4 of the Institute of Biology courses were completed, which provided training on legal, ethical and practical matters, relating to working with animals under the 1986 Act. In addition to myself, two members of CEH staff were authorised to carry out the tagging procedure.

A significant effort was made to ensure that the procedure was performed in as humane a manner as possible, minimising adverse effects to the animal, for both ethical and experimental reasons; it being desirable for tagged fish to behave no differently than untagged fish. Internal implantation of tags into fish is a technique which has been in use since the 1970's (Hart & Summerfelt, 1975) and has been used specifically on pike since at least 1980 (Diana, 1980) and on muskellunge *Esox masquinongy* since at least 1977 (Crossman, 1977). Therefore there was a large body of literature to draw on, to assist in developing a tag implantation protocol.

Prior to carrying out tagging on live fish, techniques were practiced on dead rainbow trout *Oncorhynchus mykiss* (Walbaum) and pike cadavers. Practising on dead fish allowed different incision locations to be tried, and different suturing techniques to be practised. At first, in order to avoid cutting across muscle blocks, a dorso-ventral incision was made, however flexing the fish was found to reopen the wound; a problem that did not occur when an anterior-posterior incision was made. In the following trials, and all actual taggings, anterior-posterior incisions were used. The incision was made on the side of the body, in front of and slightly above the pelvic fin (approximately 1 cm higher than the pelvic fin, with the posterior end of the incision terminating 2 cm to 3 cm in front of the pelvic fin). A mid-ventral incision has more typically been used when tagging pike, *e.g.* Jepsen and Aarestrup (1999), however it was felt that a mid-ventral incision would lead to a greater chance of tag expulsion, through the weight of the tag pushing down on the incision site. With the lateral incision position, care had to be taken not to make the cut too high up the body, to avoid cutting through the ribs. The incision needed to be only 2 to 3 cm long to allow the tag to be inserted.

The choice of methods available for closing incisions includes suturing, stapling and gluing (using cyanoacrylate adhesive). A good method of wound closure was found to be the use of combination of soluble sutures and adhesive. The sutures acted to pull the flesh together, whilst the adhesive formed a watertight seal over the incision site. Staples were not used as, although they can be applied quickly, thereby reducing stress to the animal, they are permanently attached to the fish, unlike soluble sutures (Swanberg *et al.*, 1999). Single sutures were chosen over alternative suturing techniques, such as sub-cutaneous stitching and mattress stitching (Kirk, 1978), due to their simplicity, and therefore the speed at which suturing could be performed. A failure in one of the more complex suture techniques could also potentially lead to a longer length of wound re-opening. In mammals it can be desirable to suture skin and muscle separately, however this was considered impractical in pike due to the very thin skin. Hart and Summerfelt (1975) actually found that healing was impaired when the skin and muscle of flathead catfish *Pylodictis olivaris* (Rafinesque) were sutured separately.

When tagging pike in the field, sutures made of 2/0 (3 metric) polydioxanone monofilament (PDS® II) were used at first, however subsequent examination of pike that had been radio tagged and released into the river showed that the suture material could still be present over a year after tagging. For example, Pike C still retained one suture when captured on 31 July 2001, despite having been tagged over a year previously on 8 June 2000. When pike were recaptured, and the incision wounds were healed, sutures were cut and removed. The long-term presence of sutures is undesirable as sutures can act as a track for infection to enter the fish. Consequently for pike tagged later in the study incisions were closed using 2/0 (3 metric) Polyglactin braided (coated VICRYL®) sutures. Although these sutures are braided, rather than monofilament, thereby increasing the risk of infection tracking into the wound, coated VICRYL® sutures had previously been shown to degrade in 8-12 weeks in UK river conditions (W.R.C. Beaumont, pers. comm.), and it was felt that the solubility of these sutures compensated for the increased possibility of infection tracking into wounds. A recapture of a radio tagged pike subsequently showed however that coated VICRYL® sutures could also remain in the pike for over a year (Pike W, tag implanted on 27 August 2001, fish recaptured on 5 September 2002, when two sutures were removed).

Pike needed to be anaesthetised prior to tagging, and the choice of anaesthetic to be used was carefully considered. Of the many possible anaesthetics, 2-phenoxyethanol (2:PE) was chosen. This chemical has bactericidal and fungicidal properties making it particularly suitable for surgical procedures (Burgess, 1997). Some anaesthetics (*e.g.* metomidate) can act to suppress the corticosteroid stress response in fish (Thomas & Robertson, 1991). Whilst this may be desirable when handling fish, the corticosteroid response appears to be essential for resistance to severe physical trauma, therefore an anaesthetic that did not suppress the stress response was thought to be more appropriate for tag implantation.

Once the techniques to be employed had been developed and practiced, the tagging procedure was performed on two live, captive, pike under the supervision of a local vet (Table I). The pike had been captured by electric fishing at East Burton (SY 381 869) on 28 March 2000, as part of a pike removal exercise conducted for a local fishery owner, and had been kept in a shallow outside channel at the CEH River Laboratory since that date. Radio tagging took place on 20 April 2000. The outside channel was the best holding area that was available, however, the channel was too shallow for the pike, and despite cover being provided, neither pike fed when presented with either static or moving dead baits. Feeding attempts had to be performed using dead prey fish, as feeding live vertebrate prey to captive predators is forbidden under the Animals (Scientific Procedures) Act 1986. Whilst a proportion of captive adult pike will respond to dead bait, not all will do so (J.D. Armstrong, pers. comm.). Due to the lack of feeding, both pike were in general poor health prior to tagging. One of the pike also contained eggs, and peritoneal tagging of gravid females is generally avoided. On 5 May 2000, a further practice tagging was conducted on another captive pike (Table I), this pike having been captured during electric fishing on the CEH River Laboratory site on 25 April 2000, after which the pike was transferred to the outside channel.

Following the tagging operations conducted on 20 April 2000, the vet made a number of recommendations. The first pike tagged (173.895) was thought to take too long to recover (Table I). This pike was anaesthetised using a 1:1000 dilution of 2:PE, and the same concentration of anaesthetic was run over the gills of the fish during surgery, to ensure a suitable state of anaesthesia was maintained. All subsequent operations used a 0.5:1000 dilution for maintenance anaesthesia, whilst keeping a 1:1000 dilution for the initial anaesthetic. The tags used on 20 April had been disinfected using Industrial Methylated Spirits, but after this date, radio tags were gas sterilised. It was also recommended that all instruments be re-sterilised after use. We were also advised to administer a prophylactic dose of the broad-spectrum antibiotic Baytril (Bayer plc., Bury St. Edmonds, UK) to each fish, at a dose of 0.2 ml 1000 g^{-1} of fish weight, to help combat any post-operative bacterial infection.

The smaller of the two pike tagged on 20 April 2000 (Table I) became infected with fungi and was treated in a bath of malachite green on 26 April 2000, however the fish was found dead the following day. It is likely that death was caused by the prolonged stress of captivity, together with the lack of feeding, with the tagging operation acting as an exacerbating factor. A post-mortem was performed on this pike. Although the muscle had not healed since tagging, an unbroken layer of connective tissue was found beneath the incision. Attempts to feed the two remaining pike continued to be unsuccessful, even after moving them to a large (1.40 m × 0.90 m × 6.00 m), landscaped tank in the CEH

Fluvarium, and these two pike were killed to prevent prolonged suffering (in accordance with the Animals (Scientific Procedures) Act 1986).

Table I Pike implanted with Biotrack TW-5 transmitters whilst kept in captivity in an outside channel at the CEH River Laboratory.

Radio tag frequency MHz	173.895	173.862	173.906
Date of capture	28 March 2000	28 March 2000	25 April 2000
Date of tagging	20 April 2000	20 April 2000	5 May 2000
Sex	♀?	♀	♀?
Fork length cm	68	56	55
Weight kg	2.9	1.9	1.6
Time spent in 2:PE (min)	*ca.* 5	2	*ca.* 10
Time taken for surgery (min)	2	4	5
Time to recovery (min)	*ca.* 10	0.5	not recorded

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APPENDIX 3

A method for the external attachment of miniature radio tags to pike *Esox lucius* L.

W.R.C. BEAUMONT & J.E.G. MASTERS

In press as a 'Management and Ecological Note' in *Fisheries Management and Ecology.*

In previous telemetry studies of pike *Esox lucius* L., radio and acoustic transmitters have been either implanted into the body cavity of the fish (*e.g.* Beaumont, Cresswell, Hodder, Masters, Welton 2002) or mounted externally on the fish (Armstrong, Lucas, Priede & de Vera 1989; Herke & Moring 1999). Implanted tags have several advantages over externally mounted ones in that the possibility of weed entanglement is lessened and swimming is less likely to be affected. The size of the tag however can preclude using internal tags on small fish, as, unless trailing external antennas are used, tag size is relatively large. This makes tagging of small fish a problem both with respect to minimum recommended tag size (Winter, Keuchle, Siniff & Tester 1978) and the physical space available for the tag in the fish's peritoneal cavity. Whilst in some studies implanted tags have been ejected from the peritoneal cavity (Lucas 1989; Baras & Westerloppe 1999), implanted transmitters are designed to be permanently retained by the fish. Intragastric implantation of tags has been used for tagging carnivorous fish, however the tag may be regurgitated after a short period of time

(Lucas & Johnstone 1990). Implanting a transmitter in this way may also lead to changes in behaviour by the fish. Stomach fullness may also control appetite, a transmitter implanted in the stomach may therefore potentially lead to a reduction in foraging activity by the fish; especially if the tag to stomach size ratio is large. Although the problem of drag, associated with external tags, can be eliminated, intragastric tags are still capable of reducing swimming performance (McCleave & Stred 1975), and the minimum possible tag size should be used.

For short-term studies and studies using smaller fish therefore, temporary, external attachment of transmitters may be a more suitable attachment method. This is a less severe procedure for the fish, and has the added benefit of being simpler for the person performing the procedure. In fish studies, external transmitters are often attached through the dorsal musculature, with sutures passing underneath the dorsal fin rays to secure the tag (Beaumont, Clough, Ladle & Welton 1996). This attachment location in pike is difficult however, due to the posterior placement of the dorsal fin, and the broad back of the fish. Armstrong *et al.* (1989) and Herke and Moring (1999) described methods for externally attaching of transmitters to pike, but both methods resulted in a very ungainly tag attachment. Recent availability of small, powerful transmitters (*e.g.* Biotrack SS-2) allowed a novel method for external tag attachment to be developed for this species. Potential sites for tag attachment were investigated with respect to minimal impact upon the fish's swimming ability, likelihood of weed entanglement and the fish morphology. Previously described tag attachment sites (*op cit*) were considered unsuitable because of the problems noted above and suture migration through the muscle tissue possibly resulting in premature tag loss (addressed to some extent by Herke & Moring (1999)). It was decided that the lateral side of the fish, just anterior to the caudal fin, would be the optimum position for the tag. Although the fin is used for propulsion, little flexing occurs in this area (personal observation) and a relatively large, flat area exists, allowing a modified version of the attachment method described by Beaumont *et al.* (1996) to be used. The spine of the fish prevents suture migration yet is robust enough not to be damaged by the sutures. Dead pike were dissected to ensure no vital blood vessels or nerves would be affected by the choice of tag site. All work was carried out in accordance with the UK Animals (Scientific Procedures) Act 1986.

To prepare the mount for the tag, a rectangular plate of flexible acrylic film (0.75 mm thickness) was cut to a length suitable for the size of pike to be tagged. The length of the rectangle was cut to easily span the spine of the fish. The tag was glued to the plate using cyanoacrylate adhesive so the antenna would trail to the rear of the fish. Two holes were then drilled in the acrylic to facilitate passage of needles and sutures when tagging, and a neoprene pad was glued to the back. A backing-mount for the other side of the fish was constructed in a similar manner. Immediately prior to tagging a 3/0 Polyglactin braided (coated VICRYL®) suture with 0.69 mm diameter cutting needle was tied through each hole of the mount. These sutures are soluble and degrade in 8 to 12 weeks in UK river conditions (Beaumont *et al.* 1996). Enough scales were removed from the caudal peduncle to allow easy passage of the needles. The tagging method consisted of passing one needle through the dorsal musculature of the caudal peduncle, above the spine and major blood vessels, and one through the ventral musculature, similarly avoiding the spine and blood vessels, such that the tag would lie against the caudal peduncle with the antenna trailing out beyond the caudal fin (Fig. 1). Each needle was then pushed through the neoprene and holes of the backing-mount, and the backing-mount and tag drawn up tight against the body of the fish. The tag was secured by tying together the sutures and cyanoacrylate adhesive applied to all knots. The area immediately surrounding the sutures was coated with a mixture of silicon grease and malachite green in order to prevent fungal infection (Beaumont *et al.* 1996).

Two female pike, Pike S (fork length (FL) 52.0 cm 1.2 kg) and Pike U (FL 43.5 cm, 1.8 kg) were captured by electric fishing, and subsequently tagged with SS-2 transmitters, on 31 July 2001. The pike were lightly anaesthetised in a 1:1000 dilution of 2-phenoxyethanol, which has both antibacterial and antifungal properties. Tagging was rapid, the procedure taking 3 minutes for each fish, after which they were placed in river water to recover. After recovery (around 10 minutes) the pike were released back into the river; quick release of these fish being thought to be less stressful than a period of post-operative recovery in captivity (Crossman 1977). Trials of the tagging method were not performed on captive pike, due to the difficulties previously encountered in keeping this species in captivity, where they became inactive and reluctant to feed, even when provided with large tanks and plentiful cover (Beaumont *et al.* 2002). The welfare of Pike S and Pike U was monitored through frequent radio tracking, and visual inspection from the bank when possible.

Pike U was located 18 times between 31 July and 8 August 2001. On 10 August 2001 a signal was heard from upstream of the study area. The pike could not be located in subsequent searches and it was suspected that the pike swam into a stream > 1 km upstream from the release site which we could not access, however it is also possible the transmitter failed. During the time this pike was being actively followed it was seen on 4 occasions, and no apparent ill effects of the tag were noted.

Pike S was located over 70 times between 31 July and 26 September, 8 weeks later, when the tag was recovered from the riverbed, having become detached from the pike either on 25 or 26 September. During the time the tag was attached, Pike S occupied around 120 m of river and was seen visually at least nine times, on one occasion being observed in the process of feeding on another fish. When disturbed, Pike S was often seen swimming away, and swimming appeared unaffected by the presence of the tag.

It was concluded that attaching small radio transmitters to the caudal peduncle of pike is an appropriate technique that could be applied in future telemetry studies of this, and similar, species. External attachment has the disadvantage of causing drag, which may increase the energetic expenditure of fish, consequently the tag size should be kept to the minimum. Also, with external tags there is a risk of entanglement with aquatic vegetation, particularly for pike, which show a particular affinity for this type of habitat (Raat 1988). Frequent observations of the pike involved in this trial did not suggest that entanglement occurred, with the loss of the tag on Pike S probably being caused by degradation of the sutures.

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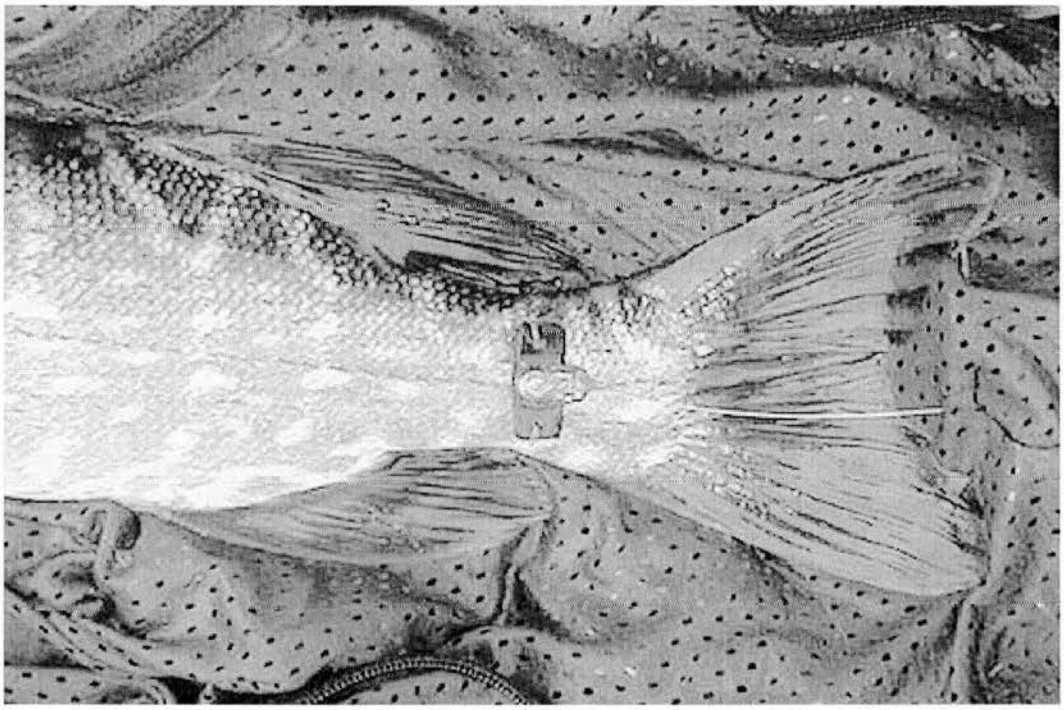
Figure 1: Caudal peduncle area of pike showing position of radio tag



APPENDIX 4

Ethical considerations relating to the external attachment of electronic tags to fish.

J. E. G. MASTERS & W.R.C. BEAUMONT

Submitted as a 'Brief Communication' to the *Journal of Fish Biology*

The external attachment of electronic tags to fish is a common procedure, and although simpler than other attachment methods, it is still an invasive technique. Ethical issues relating to the use of the method are reviewed, with particular emphasis on the application of chemical anaesthesia.

Key words: electronic tags, ethics, anaesthesia.

Electronic tags are frequently employed in studies of fish behaviour. Surgical implantation of tags was reviewed by Jepsen *et al.* (2002), and whilst such methods are suitable for permanently attaching tags to many species, external attachment is often preferable for short-term studies and studies using smaller fish: although the possibility of entanglement in weed should be considered (Beaumont & Masters, in press). External tagging is simpler and quicker than most internal tagging (Thorsteinsson, 2002), however, it still remains an invasive technique, and researchers should acquaint themselves with both the national or regional legal requirements for undertaking such work, summarised in Thorsteinsson (2002), and with the ethical guidelines of the journal for which the work is intended. It should be noted that the experience of surgeons has been shown to affect post-operative survival rates amongst internally tagged fish (Cooke *et al.*, 2003) and considerable practice is also advisable prior to attaching external transmitters to fish.

A commonly used procedure for external tagging consists of anaesthetising the fish and then passing needles through the musculature, in order to create a firm attachment *e.g.* Beaumont *et al.* (1996), however a recent paper raised the issue of whether anaesthesia is an absolute requirement during such procedures (Cooke, 2003).

The primary reason for sedating fish prior to tagging is to minimise the stress and pain experienced by the animal. Sedating the fish also reduces the risk of muscle damage through sudden movements of the fish during the operation. Similarly, mechanical damage may occur to unanaesthetised fish during handling, although delicate fish such as cyprinids or salmonids may be more prone to scale loss and abrasion than robust fish such as centrachids. Risks to the researchers using sharp needles on unsedated fish should also not be overlooked.

Furthermore, chemical anaesthesia may incur other benefits such as analgesia (Ross & Ross, 1999) and the suppression of the physiological stress response (Thomas & Robertson, 1991). Stress responses to tagging have been shown to differ between species however, and ideally quantification of these responses should take place prior to the commencement of any field based study (A. Moore, CEFAS, pers. comm.). Certain chemical anaesthetics (*e.g.* 2-phenoxyethanol) also have mild antibacterial and fungicidal properties, which may help to reduce the risk of infection.

Sedation or light anaesthesia (Stage 1, Plane 2) (Ross & Ross, 1999) is generally sufficient to allow external tagging to take place, and this can be achieved using minimum exposure to chemicals (administered in aqueous solution as inhalation anaesthesetics). External tag attachment is generally sufficiently rapid to allow fish to be tagged without the need for water or maintenance anaesthetic solution to be flushed over the gills.

One concern when using anaesthesia is that the time taken to recover may affect the natural behaviour of the fish (Cooke, 2003). In order to avoid anaesthesia (or the effects of capture and tagging) affecting recorded behaviours, sufficient time should be allowed for anaesthetic to clear from the body of the fish, equilibrium to be regained, buoyancy adjusted and the fish to recover from the physiological stresses associated with capture and tagging. Consequently, data are generally recorded from tagged fish after an appropriate recovery period has taken place. The decision over whether to release fish back into the environment as soon as possible or whether full recovery should occur in captivity is one which requires careful consideration (Jepsen *et al.*, 2002). Even if data are not to be analysed immediately following release, fish should still be tracked during this time, in order to monitor their recovery.

Stress, through the action of corticosteroids, may reduce immunocompetence and may also affect reproduction by altering the levels and patterns of reproductive hormones that influence maturation (Barton & Iwama, 1991). Particular caution should therefore be taken when considering tagging during the reproductive period, potentially a time of naturally increased physiological stress, associated with, for example, competition for mates or reduced feeding opportunities resulting from the guarding of offspring (Helfman *et al.*, 1997).

Considerations regarding potential harm to organisms eating previously anaesthetised fish (and thus the requirement for a post-anaesthesia holding period) may also be a consideration regarding the decision of whether to use an anaesthetic; these considerations should not however lead to non-use where other considerations recommend their use.

Thorsteinsson (2002) states that 'although the use of anaesthetics in some cases may be unwanted due to their detrimental effects on the physiology and behaviour of the fish, considerations of animal welfare will in most cases prohibit tag attachment to unsedated fish if surgery is involved.' Similarly, the 'guidelines for use of fishes in field research,' published by American research associations state that procedures must avoid pain or stress to the fishes, consistent with sound research design, and that procedures that may cause more than momentary or slight distress should be performed with appropriate sedation (Anonymous, 1988). Sufficient evidence does not yet exist to support a general recommendation that the external attachment of radio transmitters should be conducted without the use of anaesthetics. It should also be remembered that the choice of anaesthetics that can be used may be governed by national legislation, for example, in the United Kingdom, only MS-222 is authorised for use on fish; if any other anaesthetic is to be used, specific approval is required under the terms of the Animals (Scientific Procedures) Act 1986.

Whilst the ratio of tag weight to fish weight has received much attention, with most researchers ensuring that tag weight in water does not exceed 2% of the wet fish weight (Jepsen *et al.*, 2002), the mechanical attachment method used should also be considered carefully. External tags are attached using either sutures, *e.g.* Beaumont *et al.* (1996), or stainless steel wire *e.g.* Cooke (2003).

From an animal welfare point of view, it may be preferable to use soluble sutures rather than wire for short term studies as these will allow the tag to be shed after the duration of the experiment, or as the fish grows. Every effort should be made to remove wire attached tags at the end of the study period.

Researchers may also wish to consider recapturing all externally tagged fish irrespective of the attachment technique, towards the end of the battery life of the transmitter. This will enable measurements of fish growth and condition factor to be made, whilst also allowing the tag to be recovered. Recovery of tags would also serve to negate the charge that biologists are 'littering' the environment with spent tags, and removes the risk of tags and batteries being consumed by predators or scavengers after the conclusion of the experiment. The benefits of recapture however, would have to be carefully weighed against the risk of further stress, or mortality, to the fish.

In conclusion, externally attached electronic tags are valuable tools for studying fish behaviour. Whilst the ability of fish to 'suffer' when exposed to adverse affects is still the subject of debate, injury or the experience of other harmful conditions is a cause of concern for the welfare of individual fish (FSBI, 2002). Prior to employing such techniques therefore, the methods to be used should be thoroughly examined from an ethical point of view. Zeller (1999) provides a good example of the process involved in evaluating the relative utility of a variety of anaesthetic and tag attachment methods. Further guidance can be found online at the FAO fish telemetry website (Baras *et al.*, 2003).

We would like to express our thanks to the many colleagues with whom we have discussed the issues addressed in this paper. Jerome Masters was in receipt of the Freshwater Biological Association Frost Scholarship.

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APPENDIX 5

An example of the form on which field notes were made whilst radio tracking.

Notes													
Substrate (? =-9 mud=1 silt=2 sand=3 grav-sand=4 gravel=5)													
Overhang Veg > 0.5m (? =-9 zero=0 sparse=1 dense=2)													
Overhang Veg < 0.5m (? =-9 zero=0 sparse=1 dense=2)													
F. Veg.(unknown=-9 zero=0 sparse=1 dense=2)													
E. Veg. (unknown=-9 zero=0 sparse=1 dense=2)													
SubVeg(?=-9,zero=0,sparse<0.5=3,s>0.5=4, dense<0.5=5,d>0.5=6)													
Undercut bank (yes=1 no=2 n/a or unknown=-9)													
Other flow type (slack=0 glide=1 turb=2 cascade=3)													
Another flow type within 1m (yes=1 no=2)													
Flow at fish location (slack=0 glide=1 turb=2 cascade=3)													
Fish position (S=1 N=2 midstream=3 bay=4 pool=5 flooded land=6 ditch=7)													
Visibility (dark=0 dawn/dusk=1 day=2)													
Turbidity (0=very turbid 1=intermediate 2=clear)													
River cond (low=1 2=normal 3=flood)													
Wind (still=0 breeze=1 windy=2)													
Precipitation (dry=0 L.rain=1 H.rain=2 hail=3 snow/sleet=4)													
% cloud (whole sky)													
Clear (1) or Overcast (2)													
Time													
Date													
Fish disturbed (yes=1 no=2)													
Change in signal strength (yes=1, no=2)													
Extra beep events (steady=0, fast x 1 =1 etc)													
Fieldworker position (S=1, N=2 or S&N=3)													
Fieldworker													
Across													
Along													
YYYYYY													
XXXXXX													
Fish Name													

591 Xena
921 Yoda
900 Zebedee
561 Anakin

746 Alice
730 Boris
833 Chica
862 Hannah
972 Isaac
959 Julia
541 Lisa
988 Mark
581 Orla
530 Pete
514 Quentin
602 Victoria

APPENDIX 6

Fish caught during electric fishing of side channels in January and February 2001.

Date	Location	Species	L_F cm	Notes
23 Jan 02	Rushton Ditch	common carp	58.0	diseased
				Mouth & pectoral fins rotten.
		perch	15.2	
		perch	15.8	
		perch	16.1	
		perch	17.1	half of caudal fin missing
		pike	10.8	scales not taken
		pike	17.0	
		pike	31.8	
		pike	34.5	
		pike	37.9	bite mark on side
		pike	52.1	bitten and in poor condition
				Puncture wound in belly.
		pike	54.6	Radio tagged – Pike Z
		bullhead	5.6	scales not taken
		bullhead	6.2	scales not taken

<u>other</u>

0+ minnows

10 eels seen

1 pike *ca.* 25 cm seen but not caught

Date	Location	Species	L_F cm	Notes
23 Jan 02	Railway Ditch	pike	26.3	
		pike	26.9	
		<u>other</u>		
		lots of 0+ minnows		
		3 eels		
		1 lamprey		

Date	Location	Species	L_F cm	Notes
28 Jan 02	Railway Ditch	pike	26.?	Caught on 23 Jan 02 so not measured.
		<u>other</u>		
		2 eels		
		lots of 0+ minnows		

Date	Location	Species	L_F cm	Notes
28 Jan 02	Rushton Ditch	pike	23.1	
		pike	29.4	
		pike	11.1	
		<u>other</u>		
		2 eels		
		lots of 0+ minnows		

Date	Location	Species	L_F cm	Notes
5 Feb 02	Railway Ditch	pike	72	Pike C. At end of railway ditch fork. Genital opening swollen. Not running eggs.
		pike	72	Radio tagged. Pike An.
		Pike	70	Not radio tagged. Running white milt. Scar on one side. Fitted with smolt tag 0490.

<u>other</u>

Pike disturbed at end of railway ditch – probably Pike I

One more pike seen but not caught

eels

1 minnow

Date	Location	Species	L_F cm	Notes
5 Feb 02	Hummock Ditch	pike	62	Pike P. Inflammation around suture. No scissors – not removed. Running watery milt.

<u>other</u>

eels, particularly in the lower part of the Hummock

eels on the flooded field

Date	Location	Species	L_F cm	Notes
5 Feb 02	Flood Relief Channel	pike	37	not tagged. Running watery milt

<u>other</u>

Very large pike seen but not caught (just d/s of footbridge over channel)

eels

Date	Location	Species	L_F cm	Notes
6 Feb 02	Flood Relief Channel	pike	30.2	not scaled
		pike	35.4	scarred both sides behind pectorals
		pike	63.0	Pike H. Looked very thin but scar well healed.
		pike	33.2	scarred in front of dorsal fin - looked like a pike bite.
		<u>other</u>		
		lots of tiny minnows seen		
		eels		