MIGRATION AND HABITAT USE OF DACE (LEUCISCUS LEUCISCUS (L.)) IN AN ENGLISH CHALK STREAM

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Submitted for the degree of Doctor of Philosophy, University of St. Andrews

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From Houghton, 1879:

Mr. Manley aptly quotes Drayton as having in his mind the "darting" Dace when he says:-

"Oft swiftly as he swims, his silver belly shows;
But with such nimble flight, that ere ye can disclose
His shape, out of your sight like lightening he is shot."

Little did he know just how far, and how frequently he would shoot, like lightening, out of sight!

However, thanks to the wonders of modern technology, just because he is out of sight, does not necessarily mean that one cannot follow his every move.

Abstract

The dace (*Leuciscus leuciscus* (L.)) is a small, shoaling, rheophilic, lithophilic cyprinid fish, and is an important component of chalk stream ecosystems. Historical recaptures of marked dace in the River Frome suggested that some individuals were mobile, however it was unclear whether these movements occurred predictably in time or space. Migrations, defined as deliberate, temporally predictable translocations in space, allow individuals to exploit new resources, avoid predators and find a mate. However, energy is generally utilised during locomotion, and there are potential costs associated with moving to an unfamiliar environment, including reduced foraging opportunities, and increased predation risk. To be successful, individuals must find food, avoid predation and reproduce. If adult dace can solve these problems efficiently in one section of river, then considering the potential costs associated with migration, it would be most profitable for them to remain in this area.

A range of techniques were used to study the migrations and habitat use of adult dace in the River Frome, covering both daily and seasonal cycles. The movements of 32 radio-tagged dace were tracked over a period covering over 16,000 hours. During this period 6864 radio-locations were made, and radio-tagged fish covered a combined minimum distance of over 109 km. A further 1724 dace were individually or batch marked, of which 128 were recaptured. In addition over 4000 dace were recorded on video as they passed through a fish counter. The daylight habitat use of 377 adult dace was visually observed from the bank, and habitat suitability indices created. The nocturnal habitat use of 11

adult dace was assessed using radio-active isotope tags, which were located on 247 occasions over a period covering 121 "fish nights".

The adult dace observed in this study moved extensively, and their movements were both temporally and spatially predictable, and therefore constituted migrations. Of the 30 fish released at their capture sites, at least 19 moved more than 500m from this site during the observation period. Spawning occurred in millstreams, and was preceded by an upstream migration. After spawning, slow flowing shaded sites out of the main river were selected by at least five out of six radio-tagged dace. A substantial upstream migration was observed in late spring, and diel migrations between separate distinct day and night habitats were observed during the summer. In autumn adult dace moved downstream and formed aggregations in the tidal reaches. Consequently, the hypothesis that dace occupy one section of the river throughout the year was rejected.

Acknowledgments

This work would not have been possible without the continued support and encouragement of my family, in particular my wife Anne-Marie, my parents Anne and Peter, and my sister Michelle. I dedicate this thesis to them.

Special thanks must go to my supervisors Mike Ladle and Anne Magurran, without whose enthusiastic support the project would not have been initiated. Always on hand to offer advice on how the work could be improved, provide constructive criticism where necessary, and never slow to offer assistance with fieldwork or proof reading, Mike can take much credit from the success of this study. Anne provided guidance and support from afar, and her suggestions and comments have helped me to see the bigger picture.

Bill Beaumont requires particular mention, for he has been pivotal throughout the study. Involved in the early "pre-me" days, Bill was fundamental in the early development work which laid the foundations for this study, and his suggestions and assistance during the initial fieldwork were invaluable. Stewart Welton provided a string of constructive and realistic suggestions which helped to keep me on track. In addition he was always available to proof read both chapters and manuscripts, and his help is gratefully acknowledged. I would also like to thank Paul Garner for his help and encouragement throughout the study, and for many interesting and profitable discussions.

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CHAPTER 1

Introduction

1.1 Migration

Mobility, in one form or another, is an essential component of the life of the majority of animals, and is one of the major fundamental differences between plants and animals. The ability of an individual to move allows it to actively exploit new resources, avoid predators and find a mate. The ability to move also results in the individual being faced with a whole suite of decisions, not least where to move to, and when to move. The consequences for the individual of these choices are likely to influence its survival and future fitness, and ultimately exert a substantial adaptive force on the population. At critical stages of the life cycle, one wrong move can result in the death of that individual, and as a result the selective pressures associated with movement, or the lack of it, may be great.

The general meaning of the word migration is to move from one place to another (McKeown, 1984). Many authors have defined the migrations of animals, with each imposing a set of constraints by which migration can be distinguished from other forms of translocation. Baker (1978) provides one of the simplest definitions, when referring to migration as "the act of moving from one spatial unit to another." Some authors suggest that a movement is only a migration when it is seasonal in nature, or involves some form of return component to a previously occupied location (Landsborough Thompson, 1942; Harden-Jones, 1968). Smith (1985) is even more restrictive when describing migrations as "adaptive, long-distance movements that occur predictably in the life cycle of a species." My personal opinion is that many of the arbitrary constraints on the definition only cause confusion, and can result in differentiation between the same basic behaviours occurring on different temporal or spatial scales. For the purposes of this thesis, my own definition of migration with respect to fish is thus:

Migration: a deliberate, temporally predictable translocation in space.

Hence, under this description, juvenile fish drifting downstream with the current from their birthplace, in order to reach suitable habitat, would be considered to be migrating. Likewise a fish which spends the day and night at different locations, moving between those places at dawn and dusk, would be considered to be carrying out diel migrations. Conversely, a drift feeding salmonid, which moves back and forth from a position behind a rock, into the flow to catch prey items, would not be deemed to be carrying out migrations, as such events are not predictable. Similarly, a fish displaced from its initial position by a sudden increase in discharge associated with the opening of a sluice would not be classed as migrating, as the resulting movement would have been unintentional.

For millennia, fish have been known to carry out seasonal migrations, and it seems likely that man has been predicting and subsequently exploiting these migrations for almost as long.

Northcote (1984), provides a classification system for migratory fishes based on the nature of the habitats used for different parts of the life cycle:

1.) **Anadromous** - Freshwater spawning, but spend a substantial proportion of their life in the sea (e.g. Atlantic salmon, *Salmo salar* L.).

2.) **Catadromous** - Marine spawning, but spend a substantial proportion of their life in freshwater (e.g. European eel, *Anguilla anguilla* (L.)).

3.) **Potamodromous** - Freshwater spawning, spend their whole life in fresh water (e.g. dace, *Leuciscus leuciscus* (L.)).

Migration takes many different forms, and is generally most conspicuous, often spectacular, during the breeding season. Consequently, the impressive, large-scale anadromous migrations of the various salmon species, and the remarkable catadromous migration of the European eel have historically received the most attention from researchers. In relative terms, the potamodromous migrations of lacustrine and riverine fishes have, until recently, been ignored. In addition, small-scale migrations, including those related to the diel cycle of light and dark, have been generally overlooked. It is important to obtain detailed information about the movements and behaviour of species in the wild, and the interactions between them, in order to fully understand the community.

The intention of this thesis was to help redress the balance in some small way, by investigating the movements of dace (*Leuciscus leuciscus*), a small, shoaling fish which spends its entire life in flowing freshwater. The dace was selected as an appropriate study species as it is widely distributed throughout Britain and much of Europe, and in terms of biomass is the most important cyprinid in the chalkstreams of southern England (Mann & Mills, 1986). The species was considered to be particularly susceptible to habitat degradation (Mills, 1981, 1982), and anecdotal evidence suggested that dace were in decline in some British rivers. In the River Frome however, the dace population appeared to be stable, and their biology was well understood, making them a good model species (e.g. Mann, 1974; Mann & Mills, 1985, 1986; Mills, 1981, 1981b, 1982). In the

River Frome dace were relatively unaffected by anglers, as the vast majority of landowners operated salmonid fisheries. Neither stocking nor removal of coarse fish was legally practiced, and the system remained relatively simple, with roach (*Rutilus rutilus* (L.)) being the only other common cyprinid of comparable size. Evidence gained from recaptures of marked individuals and from fish counter records, coupled with anecdotal evidence from anglers and personal observations, suggested that at least part of the dace population was mobile to some extent. However it was not known whether these movements were random, or more structured and predictable.

During this study the null hypothesis that the movements of dace are random and unpredictable, and therefore not migrations, was tested. The movements of individual dace were examined in detail using radio-telemetry. Radio-tagged fish were released on a rolling programme throughout the year in order to examine whether or not there are seasonal differences in the magnitude and direction of movements. Additionally, specific periods of interest were examined in greater detail, in order to evaluate the influence of the daily cycle of light and dark on the movement and activity of dace.

The benefits to the fish of carrying out any observed movements that could be regarded as migrations, and the underlying factors governing such migrations are discussed. It was anticipated that during the course of the study many dace would be captured. By marking a sample of those fish, it was possible to gather information about the mobility of the marked individuals from subsequent recaptures. In addition, fish counter data were collected and analysed to investigate the degree to which the daily and seasonal movements of individual radio-tagged dace are representative of other members of the population.

1.2 Habitat use

An understanding of habitat requirements and preferences is required when examining the underlying factors governing and triggering the movements of fishes, and is an essential component of effective fisheries management. The use of habitat by fish can be considered on a number of spatial scales, and several approaches have been adopted. Hermansen & Krog (1984) list the following scales at which riverine fish habitat use in the wild has been considered:

"Superior physical condition" - uses overall physical parameters e.g. discharge, slope and stream order.

"Macro-habitat" - refers to the relative availability of coarse habitat features e.g. riffles, pools and undercut banks.

"Micro-habitat" - involves the measurement of specific environmental characteristics at the focal points of fishes e.g. depth, velocity and substratum composition.

The nature of the habitat selected is likely to reflect many of the fish's needs at a particular point in time. Additionally, the characteristics of the habitat will influence the net energy gain of resident fishes (Sabo *et al.*, 1996), and consequently have the potential to influence the future fitness of those individuals. As the requirements of the fish change, both daily and seasonally, then so too does the relative suitability of different habitats. As a result, differential habitat suitability is a major underlying factor determining the movements and migrations of fishes.

Physical, chemical and biological factors influence the suitability of habitat. Any single habitat may be unsuitable for a variety of reasons, and suitable habitats may become unsuitable due to changes in the prevailing conditions. For example, at certain light intensities a site could be "unsuitable" because of a perceived predation threat, whereas the same site might be actively selected under different light conditions, perhaps for foraging. As a result, there would be a constant, rhythmic shift in the suitability of the habitat according to the diel cycle of light and dark. Longear sunfish (*Lepomis megalotis* (Rafinesque)) preferentially select for both low light intensity and cover, however given a choice, low light and no cover conditions were selected over higher light intensities within cover (Goddard & Mathis, 1997). Metcalfe *et al.* (1997), showed that juvenile stream dwelling salmonids used microhabitats with slower flow velocities as light levels fell, and suggested reduced prey detection distance as the cause. The normal light-dark cycle may be further influenced by changes in water clarity, with increased turbidity resulting in decreased light penetration. Similarly, other variables such as resource availability, degree of instream cover and water velocity also fluctuate temporally (Garner, 1997), and are likely to influence the relative suitability of habitats.

These shifts in suitability are likely to be mirrored by shifts in the use of the habitat by fishes, with each species using those habitats which offer the greatest net profitability. By examining the characteristics of the habitats used by fish under different conditions, it is possible to determine the relative value of each habitat variable, and suggest which components of fish behaviour influence the selection of that habitat. The very act of moving between two habitats, particularly against the flow, carries an obvious energetic cost and in order to be worthwhile is likely to result in a potential benefit to the individual. However, this potential benefit may be the result of biotic factors such as resource depletion or detection of a predator. Consequently, the hypothesis that following a movement, the physical habitat characteristics of the "new" site are not significantly different from those of the "old" site was considered.

There are several methods of observing habitat use by fishes, many of which overlook the propensity of fish to change their behaviour and habitat use when disturbed. In order to establish habitat use by fishes, it is essential to discover their location. This is often carried out by capturing them, using techniques such as electrofishing (Maki-Petays *et al.*, 1997) or netting (Wintersberger, 1996), each of which may be species-biased (Vadas & Orth, 1993). These techniques, however, only provide a rough indication of the general areas selected, or macro-habitats utilised, because the fish almost invariably move during the capture procedure. Trapping can also be used to catch fish, but the trap itself affects the nature of the habitat, and is therefore not suitable for studies of microhabitat selection. Point sample electrofishing provides a more accurate indication of habitat use, but is most suited to small fishes, particularly sedentary species. Direct observation is the simplest and least biased of sampling strategies, particularly in small streams where water clarity is high, macrophyte density low, and water depth less than 1.5 m (Garner & Clough, 1996). However, direct observation cannot be used at night, during turbid water conditions, when macrophyte density is high, or in deep water. Under such conditions radio-telemetry can provide detailed information about fish movements, and can indirectly indicate the location and habitat use of the tagged individuals (Raibley *et al.*, 1997). Therefore, in order to study the habitat selection of fishes under a wide range of conditions, a combination of the most suitable techniques may be required.

Once the location of a fish has been established, details of micro-habitat characteristics can be measured and recorded. Where possible, the habitat characteristics of surrounding areas should also be recorded, in order to provide a relative measure of habitat availability. Those variables which influence habitat selection by fishes are likely to differ between species (Godhino *et al.*, 1997; Prenda *et al.*, 1997), between different sized individuals of the same species (Greenberg *et al.*, 1997; Maki-Petays *et al.*, 1997), and even between individuals of similar size (Bourke, *et al.*, 1997). However, there are components of the habitat, including depth, flow velocity, substratum composition and degree of instream cover, which are likely to influence the habitat selection of all stream fishes, and these should be recorded in all cases. In addition, other factors such as the degree of outstream cover, presence/absence of a shear zone, channel width, and specific aspects of the local environment should also be recorded where appropriate.

1.3 Study species

In all scientific studies of living things it is important to be familiar with existing knowledge of the study species. To this end, a review of existing literature was carried out.

The Dace, *Leuciscus leuciscus* (Linnaeus).

The dace *Leuciscus leuciscus*, formerly *Leuciscus vulgaris*, was first scientifically described by Linnaeus in 1758. It is a member of the carp family, or Cyprinidae, in the Order Ostariophysi. Many authors through the years have mentioned that the dace is also known in some localities as graining, dare or dart (Walton & Cotton, 1653; Houghton, 1879; Tate Regan, 1911; Ensom, 1930; Magri MacMahon, 1946; Travis Jenkins, 1961; Laurence Wells, 1962), however opinions are divided as to how some of the names originated.

Houghton (1879) lists the graining (*Leuciscus lancastriensis*), thought initially to be a separate species occurring in Lancashire, as a mere variety of the dace. Travis Jenkins (1961) states "A Lancashire name for the Dace is "Graining," and in certain localities in both Lancashire and Cheshire the fishermen speak of two varieties, the Dace and the Graining, regarding them as two distinct species". Tate Regan (1911) is sceptical about whether or not the graining is a distinct form and states "I cannot see that the Dace of Lancashire differ in any way from those of other parts of England".

The names dace, dare and dart all appear to originate from an old version of the word "dart", which was given because of "the first impression this lively fish gives to the onlooker - that of sudden quick movement" (Magri MacMahon, 1946). Whether the names are from the French language (Houghton, 1879; Travis Jenkins,

1961) or from English (Tate Regan,1911) is unclear. A full description of one possible origin of the name is given by Houghton (1879): "The word *Dace* appears to have been formed by what philologists term "phonetic decay" from the fuller form of *dart*, a name which, with another synonym of *dare*, is applied to the fish under our consideration. As early as the time of Gesner we learn that this species of *Leuciscus* was called the *Dard* by the Santones and the Pictones (the old names for the inhabitants of the provinces of Saintonge and Poitou), because the fish moves rapidly, like an arrow or "dart"". The French now refer to *Leuciscus leuciscus* as Vandoise, the German translation is Hasel and in Dutch the common name is Serpeling. A full list of the European common names for *Leuciscus leuciscus* is given in Banarescu *et al.* (1971).

The majority of authors refer to the dace as being a "small" species (e.g. Ensom, 1930; Travis Jenkins, 1961; Laurence Wells, 1962; Bagenal, 1970), giving the usual size attained by adults in either length (e.g. Shaw, 1804; Houghton, 1879; Bagenal, 1970; Maitland, 1972, 1977; Beaumont, 1982), weight (e.g. Ensom, 1930) or both (e.g. Tate Regan, 1911 & Travis Jenkins, 1961). Usually reaching not more than 250 mm, in exceptional circumstances dace can attain 300 mm (Bagenal, 1970; Maitland, 1977 & Beaumont, 1982). Mann (1974) lists the ultimate lengths for dace in the River Frome as 265 mm and 275 mm for male and female dace respectively. According to Ensom (1930) "The biggest ever caught weighed 1 lb. 9 oz. and was taken from the Dorsetshire Frome in 1902". Dace grow rapidly in the first two years (Wheeler, 1969), with males growing faster than females, particularly after the onset of maturity (Hellawell, 1974; Mann, 1974). Females appear to outlive the males, and ultimately attain the greatest lengths, the oldest female caught in the Frome study being 11+ years old (Mann & Mills, 1986). Adult dace start to grow in late May and early June, with little growth occurring from November to April (Mann, 1974).

In describing the shape of the dace the most commonly used words appear to be "slender", "slim" and "sleek" (e.g. Tate Regan, 1911; Ensom, 1930; Magri MacMahon, 1946; Laurence Wells, 1962; Wheeler, 1969 and Bagenal, 1970). The head is "comparatively small" (Laurence Wells, 1962), the mouth is "small, slightly below the snout" (Bagenal, 1970), and the angle of the jaw does not reach as far back as vertically below the eye (Wheeler, 1969; Bagenal, 1970).

Most authors agree that the back of the dace is generally a dark shade, but differ in their description of the colour, from steely blue-black (Bagenal, 1970), through dark olive (Ensom, 1930), brownish blue (Houghton, 1879), and bluish green (Magri MacMahon, 1946) to yellowish olive (Shaw, 1804). Wheeler (1969) states that a "living dace gives the impression of being a bright silvery fish" and all are in agreement that the flanks of dace are silver in colour. The belly however seems to cause confusion once again, being described as cream or white (Bagenal, 1970), "silvery to yellowish white" (Wheeler, 1969) and silver (Magri MacMahon, 1946). The discrepancies in authors assessments of the colour of various parts of the dace probably stem, in part, from the ability of a living dace to change colour according to its background. A dace living above a dark substratum rapidly changes to a much lighter shade when captured and placed in a yellow bucket, and quickly returns to its darker state when returned (pers. obs.). There may also be differences in the range of colours of back and belly both between and within populations, with the fish, over a number of generations, having developing a colour most suited to their particular environment. Laurence Wells (1962), describes the eye of the dace as a "brilliant and flashing eye" and goes on to state that it has "yellow as a background over which are glints of red and green".

Dace are gregarious, and are generally found in shoals (Houghton, 1879; Ensom, 1930; Wheeler, 1969), although these shoals are not "usually large and near the surface" as Wheeler (1969) suggests. My observations in the East Stoke Millstream indicate that dace spend a considerable amount of their time in relatively small shoals on or near the substratum (Plate 1.3i).

Dace are indigenous to Britain (Maitland, 1972) and are also found throughout much of Europe (Shaw, 1804; Houghton, 1879; Tate Regan, 1911; Travis Jenkins, 1961; Bagenal, 1970; Maitland, 1977; Mills, 1980; Mann & Mills, 1986; Lobon-Cervia *et al.*, 1996). Lobon-Cervia *et al.*, (1996) describe the dace as a "successful rheophilic cyprinid commonly found in lotic systems" and go on to cite Banarescu, who describes the distribution range of the dace as "the largest area recorded for any cyprinid species which contains or overlaps with the distribution of most other Eurasian freshwater fishes". Where the dace does occur it tends to be abundant (Houghton, 1879; Magri MacMahon, 1946; Bagenal, 1970; Maitland, 1972), and Mann & Mills (1986) state that in terms of population biomass, the dace is the most important cyprinid in the chalk streams of southern England. Several early references mention that dace is absent from both Scotland and Ireland (Houghton, 1879; Tate Regan, 1911; Ensom, 1930) and more recent works state that in Ireland dace are only found in the Blackwater River (Magri MacMahon, 1946). It has been suggested that the dace found in Ireland were in fact introduced, however Travis Jenkins (1961) cites a review of available evidence by Holt, who "is inclined to think that the Dace found in the Blackwater River is really a native species."

Plate 1.3i. Two dace in a Fluvarium tank, positioned just above the gravel substratum.

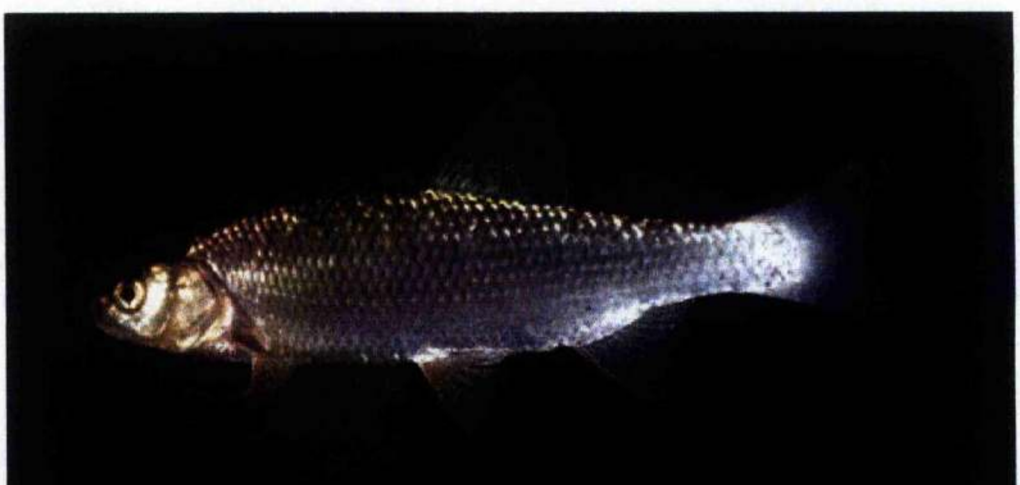

Plate 1.3ii. A typical adult dace, showing the shape and positioning of the fins.

Certainly the distribution of the dace is spreading, and they can now be found in numbers in some of the Scottish lochs and their adjoining rivers, and in some of the lakes in the English Lake District, including Bassenthwaite (pers. obs.). Most of the expansion in the range of the dace and other small fish species in Britain is probably due to anglers, who transport live dace around the country to use as bait for predatory fishes, e.g. pike (*Esox lucius* L.), releasing any unused bait fish after fishing.

Dace are most commonly found in rivers and streams and are said to show a preference for fast-flowing, streamy water (Ensom, 1930; Magri MacMahon, 1946; Travis Jenkins, 1961; Laurence Wells, 1962; Wheeler, 1969; Bagenal, 1970; Maitland, 1972; Mills, 1980; Beaumont, 1982; Mann & Mills, 1985, 1986; Cowx, 1989; Lobon-Cervia *et al*., 1996). Research by Pavlov and Tjurjukov (1995), demonstrated that dace are able to detect the direction of their movements in a water flow by perceiving and analysing positive and negative accelerations by the use of labyrinth organs. Shaw (1804) describes dace as "inhabiting lakes and rivers", Wheeler (1969) suggests that they are "occasionally found in lakes and lowland rivers", and Bagenal (1970) states "When found in lakes it is nearly always near the inflow or outflow where the current is appreciable. They do not occur naturally where the water is still." Dace are however like many other fishes, opportunists, and will use still water if it is profitable for them to do so. I have caught dace in numbers in Bassenthwaite lake a substantial distance from the nearest flowing water, although they presumably move to flowing areas at spawning time. Both Ensom (1930) and Lawrence Wells (1962) state that during the summer dace show a preference for shallow, gravel bedded areas, where they congregate. The preference, in winter, for deeper water mentioned by Ensom (1930) and Magri MacMahon (1946) is probably associated with the reduced water velocities that can often be found in these areas. This might also explain the winter aggregations of dace found in the tidal reaches of some rivers, for example the Frome and the Tees (before the construction of a barrage; pers. obs.), as mean water velocities are known to decrease downstream. Maitland (1977) even suggests that dace are occasionally found in brackish water near river mouths.

The fins of the dace are quite distinctive and have long been used to distinguish dace from small chub (*Leuciscus cephalus* (L.)). The caudal fin of the dace is deeply forked (Shaw, 1804; Houghton, 1879; Ensom, 1930; Bagenal, 1970; Maitland, 1972), and the outer edge of both dorsal and anal fins is concave in profile (Tate Regan, 1911; Ensom, 1930; Magri MacMahon, 1946; Travis Jenkins, 1961; Lawrence Wells, 1962; Wheeler, 1969; Bagenal, 1970; Maitland, 1972, 1977) (Plate 1.3ii). There is disagreement in the literature about how many rays there are in each of the dace's fins, some of which probably stems from individual variation in the fish, and some from differences in the way the rays are classified by the authors. For example the dorsal fin is described as having nine rays by Houghton (1879), seven or eight branched rays by Tate Regan (1911) and Magri MacMahon (1946), seven rays by Wheeler (1969) and ten or eleven rays by Maitland (1977). Wheeler (1969) also gives the formula for the dorsal fin as being III/7, with the III referring to three soft, unbranched rays, making a total of ten, if all rays are counted.

Individual variation between fish is probably the reason that descriptions of fin coloration also seem to differ between authors. Shaw (1804) describes the dorsal fin as being of "a dusky colour" and both he and Ensom (1930) record all other fins being "slightly tinged with red". Conversely, Lawrence Wells (1962) states that the "green of the fins is of a delightful soft shade, sometimes bordering on yellow. Except at the base of the pelvic and pectoral fins there is, as a rule, no red colouring."

The scales of the dace are described as being medium sized (Shaw, 1804; Magri MacMahon, 1946; Beaumont, 1982), with Maitland (1977) being the only author to describe them as large. The number of scales, however, is once again the source of disagreement, with the lateral line being described as having 47 - 54 (Tate Regan, 1911; Ensom, 1930; Magri MacMahon, 1946), 48 - 51 (Wheeler, 1969; Beaumont, 1982), more than 46 (Maitland, 1972), and 49 - 52 (Maitland, 1977). Scales are cycloid in nature (Beaumont, 1982). A rare aberration in the formation of the scales of dace has been noted, where the individual is partially covered with "mirror" scales which are much larger than normal scales (Beaumont, 1982; pers. obs.).

The tooth formation on the pharyngeal bones of dace is 5 + 2 (Maitland, 1972; Beaumont, 1982) or exceptionally 5 + 3 (Wheeler, 1969). Hybrids can be identified by examination of the tooth structure of these bones, although Maitland (1972) lists only two species known to naturally hybridise with dace, those being bleak (*Alburnus alburnus* (L.)) and rudd (*Scardinius erythropthalmus* (L.)).

The timing of dace spawning varies from year to year, and probably differs between regions within the same year. The contradictory reporting in the literature of the breeding period of dace is, almost certainly due, in part, to these variations. However, it seems unlikely that the variation in the timing of spawning is as great as the literature suggests, indeed, if the earliest records are to be believed, then dace have advanced their reproduction by three months. Kennedy (1969) states that "Information in the literature about the spawning of the dace is meagre and sometimes inaccurate." Shaw (1804) states that "spawning time is in the month of June", and the timing is about the same as the chub, according to Tate Regan (1911). Lawrence Wells (1962) writes that dace eggs "are deposited in May or June", and April and May are the spawning months referred to by Magri MacMahon (1946). Any time during the period from March to May is suggested as the spawning season by Ensom (1930), Sterba (1962), Bagenal (1970) and Maitland (1972, 1977). Wheeler (1969) covers most options when stating with reference to dace "It spawns from February to May" commenting that "severe cold in winter or spring will delay spawning into May", and Travis Jenkins (1961) writes that the spawning habits of the dace "resemble those of the Chub, the period being April and May". In fact recent detailed studies suggest that in Britain, dace spawn much earlier in the year than chub, and indeed all other cyprinids. Hellawell (1974), suggested that "observations of the seasonal gonad cycles indicated that spawning occurred in March or April." The recorded times for the spawning of dace in the River Frome, Dorset are "the second half of March" (Mann, 1974), "early spring" (Mills, 1980), and "March or early April" (Mann & Mills, 1986), according to data gathered over a number of consecutive spawning seasons. Mann (1974) reported that "no ripe fish were found in either the Frome or Stour spawning sites in April", suggesting that in the year in question, spawning had been completed during March in these two rivers. Kennedy (1969) states that it is likely that the spawning of dace was delayed by a "spell of unusually cold weather at the beginning of March", and suggests that in other seasons "dace might spawn early in March, possibly even in February."

It is known that the largest females spawn earliest in the season (Wheeler, 1969), with each individual laying a single batch of eggs per year (Mills, 1980, Mann & Mills, 1985). Maturity is reached by both sexes after 4 years of growth (age 3+) (Mann, 1974; Maitland, 1977; Mann & Mills, 1986) but some of the faster-growing, and therefore larger individuals mature one year earlier (Mann, 1974; Mann & Mills, 1986). Maturity in the first year for some and in the second year for the remainder, as suggested by Wheeler (1969), seems unlikely. Males, which constitute 44 % of the River Frome dace population (Mann, 1974), develop tubercles during the breeding season (Magri MacMahon, 1946; Kennedy, 1969; Wheeler, 1969; Bagenal, 1970). The females have no tubercles and were "quite smooth" to the touch, in contrast to the males which feel "rough, like sand-paper" (Kennedy, 1969). Mann, (1974) gives formulae for calculating the fecundity of both Frome and Stour dace. Using the formula for Frome dace it is possible to calculate that a 200 mm female dace would be expected to produce over 7000 (7013) eggs, and a 250 mm female over 16500 (16748) eggs. The figures of "2,500 - 27,500 eggs per female" given by Maitland (1977) represent the extremes of egg numbers (Fig. 1.3i).

The spawning season is recorded as lasting "a month" (Wheeler, 1969), "approximately two weeks" (Mills, 1980) and "over a two or three week period" (Mann & Mills, 1986), and may differ between both years and locations according to conditions. Kennedy (1969) states that spawning of dace "took place on 28 March", a conclusion formed following reports of spawning dace from local anglers, and the fact that all captured fish were ripe on 18 March, and those caught on 1 April were all recently spent. The trigger for the commencement of spawning is probably a combination of factors, including day length and temperature. Mann (1974) states that the "average water temperature at spawning time was 7-8 °C in the Rivers Frome and Stour", and a rise in the daily maximum temperature of the River Frome from 6.6 to 7.9 and 7.5 on consecutive days at the end of March was suggested as the "final trigger for the commencement of spawning" by Mills (1980). The apparently spawning dace reported to Kennedy (1969) by local anglers were sighted on 28 March 1965, "a very warm, sunny day." Dace in central Siberia also spawned just after a rise in water temperature, from 0-2 °C to ~ 6 ° C, which occurred in June (Lobon-Cervia *et al.*, 1996). Although temperature may provide the final trigger, a study of ovarian development in dace artificially exposed to different day lengths at a constant temperature suggested that the primary cue for the timing of reproduction is photoperiod (Brook & Bromage, 1988).

The spawning site studied over a number of years by staff at the IFE River Laboratory was below a small weir in the East Stoke Millstream, with no sites in the main River Frome being found. Lobon-Cervia *et al.* (1996) state that dace "underwent spawning migrations into smaller streams", suggesting that channel size may be an important factor in site selection. The apparent preference of dace for shallow water in which to spawn (Houghton, 1879; Ensom, 1930; Magri MacMahon, 1946; Kennedy, 1969; Wheeler, 1969) may be real, or may be an artefact caused by the requirement for swift flowing water and clean gravel (Maitland, 1977; Mills, 1981; Mann & Mills, 1985, 1986). Kennedy (1969), having discovered numbers of recently spent dace, searched a pool, a riffle and a glide for dace eggs, finding none in either the pool or the glide, and stated "the inference being that the dace had spawned only in the riffle." Winter floods may be an important factor in making "suitable gravel available for dace spawning" (Mills, 1981).

The degree of success, or otherwise, of dace spawning does appear to differ considerably between years, resulting in wide fluctuations in year-class strength (Hellawell, 1974; Mann & Mills, 1986; Cowx, 1988). The reasons for this may differ between systems but in chalk streams the difference in recruitment between years is largely "as a result of the influence of abiotic factors, chiefly water temperature" (Mann & Mills, 1986).

The size of dace eggs is yet another factor over which there is conflicting evidence in the literature, and once again is certainly variable between individuals and populations. Relative measurements with respect to egg size are not particularly useful unless put into context. In stating that the "eggs are small" Magri MacMahon (1946), is in complete opposition to the opinion of Bagenal (1970), who writes that the "eggs are large, about 2 mm in diameter". Whether 2.0 mm eggs are classed as large or small does, of course, depend with what they are being compared, however they are certainly larger than the 1.5 mm eggs referred to by both Wheeler (1969) and Maitland (1972). They are however smaller than those eggs found by Kennedy (1969), which were "2.0 to 2.5 mm in diameter, mostly 2.4 to 2.5 mm". The reason for these discrepancies may lie in the considerable between year and between individual variations in egg size. Mann & Mills (1985) showed that the number of eggs per gram of ovarian tissue decreased with fish length, because "mean egg size (mm^3) increased and not because of a change in the proportion of connective tissue in the ovary." Between the 1976 and 1977 spawning seasons the mean egg size of 200 mm females changed from 1.99 mm^3 to 1.65 mm^3, and within a typical year (1978) egg size increased from 1.35 mm^3 in 170 mm dace to 2.15 mm^3 in a 230 mm female (Mann & Mills, 1985). There is some evidence to suggest that egg size also varies between populations, particularly those exposed to different climatic conditions (Lobon-Cervia *et al.*, 1996) (Fig. 1.3i).

Statements regarding the development time of dace eggs such as the suggestion by Magri MacMahon (1946) that dace eggs "develop quickly", are not particularly helpful without knowing against what the development time is being compared, and may stem from the inaccurate estimates of the timing of dace spawning given in the early literature. In fact, dace eggs develop more slowly than those of other UK cyprinids, taking an average of thirty days in the River Frome, due in part to the lower temperatures encountered early in the year (Mills, 1980). Mann & Mills (1986) state that "The period of egg incubation is strongly correlated with water temperature", and the data collected by Mills (1980) agree quite well with the results of Kennedy (1969), but suggest that at 13 °C, hatching should take place before the 25 days suggested by Wheeler (1969) (Fig. 1.3i).

The adhesive eggs laid by dace are negatively buoyant and attach themselves to the substratum within a short distance of where they are released (Mills, 1981). The "pale orange" (Wheeler, 1969) and "yellow" (Maitland, 1972) colours referred to are probably in reference to the yolk rather than the whole egg. The yolk, referred to as biscuit coloured by Kennedy (1969) was only 1.4 to 1.5 mm in diameter, the perivitelline space being "rather large". The "greyish-white" capsules were "relatively opaque", with the "greyish" eggs becoming "more translucent as development proceeded" (Kennedy, 1969).

As a result of detailed studies into the survival of dace eggs, Mann & Mills (1986) state "From the moment they are released from the parent, dace eggs are vulnerable to several sources of mortality" and estimated that in 1979 the overall mortality from release to hatching at the East Stoke site was in the range 78.2 to 91.4%. In samples, the proportion of dead eggs rose from 4.9% after spawning to 59% after 13 days (Mills, 1981b).

Dace eggs in the River Frome are "tolerant of temperatures as low as 4.1 °C and as high as 13.8 °C, at least for short periods" and the temperature is unlikely to stray outside this range during the incubation period. Flood conditions, associated with heavy rainfall, are common in the River Frome at this time of the year, however Mills (1981) states "Spates are unlikely to affect the survival of dace eggs" and research by Mann & Mills (1986) showed that less than 2% of total egg mortality was caused by eggs being washed away.

The life cycle of River Frome dace (*Leuciscus leuciscus* (L.)).

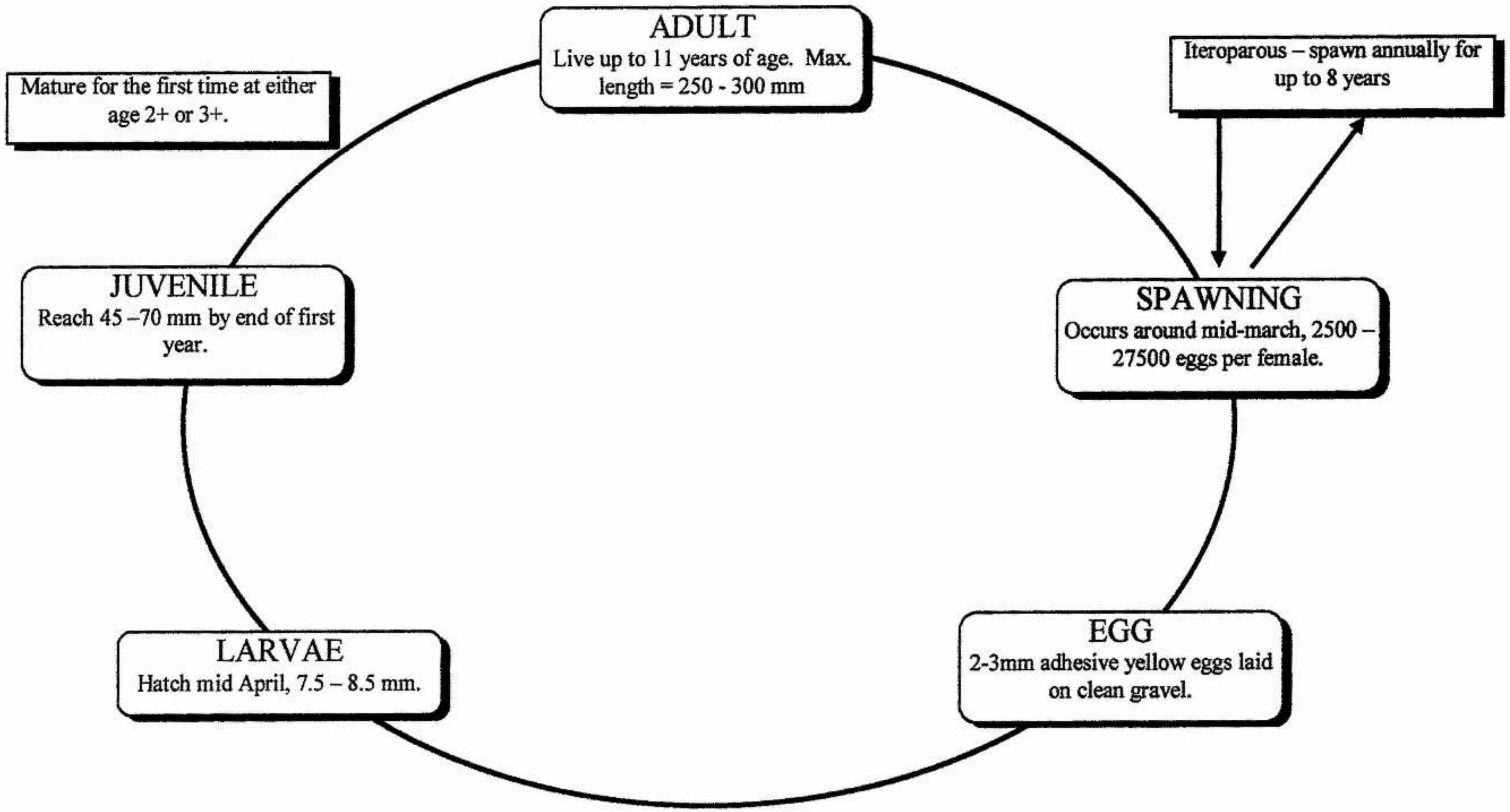

Fig 1.3i The life cycle of dace in the River Frome, giving the approximate size range of each life stage.

A strong correlation between egg survival and substratum composition was found by Mills (1981b), with poor survival in areas of high silt content. Heavy mortality and fungal infection was reported by Mills (1980), following a slight deposition of silt, and may explain the apparent preference of dace for clean gravel spawning sites. The majority of egg mortality was attributed to the effects of silt and other fine sediment, either through unfavorable substratum composition or silt deposition, in either case oxygen starvation was suggested as the cause (Mann & Mills, 1986).

Predation of dace eggs by macroinvertebrates was considered to be a possible cause of mortality, and observations by Mills (1981b) showed that eggs were eaten. However, closer inspection showed that of those invertebrates that could eat dace eggs, most preferred dead ones and those species that ate live dace eggs were relatively scarce. The results suggested that invertebrate predation caused only a five per cent mortality in live dace eggs (Mann & Mills, 1986)

Fish predation was also considered to be a "strong possibilty", but only one egg was found in a mixed species sample of the guts of 17 fish captured at the spawning site (Mann & Mills, 1986). However more detailed studies, throughout the incubation period, and at all times of day, are necessary before fish predation can be ruled out completely.

Dace larvae resemble the larvae of other cyprinids, "being slender and transparent, with a yolk-sac which lies along the belly, and merges with it posteriorly, without a projecting free end" (Kennedy, 1969). Research in Ireland by Kennedy (1969) suggests that the larvae of the dace are easy to identify, as "the eye is pigmented and melanophores are developed on the embryo before hatching" and at 8.6 mm, dace larvae are at least 2 mm longer than the newlyhatched larvae of any other Irish cyprinid. The dace larvae studied by Mann & Mills (1986) were approximately 9 mm long, whereas Wheeler (1969) stated "The alevins measure 7.5 mm at hatching", and I suspect variation between years and between rivers may have led to these discrepancies. Dace larvae first appear in the River Frome from "mid-April to early May" and, being able to swim only at a maximum of 2 body lengths per second, are washed downstream into slow flowing (<20 mm s^{-1}) marginal backwaters where they gather (Mills, 1982; Mann & Mills, 1986). As a result, "water current may play an important role at the time of hatching" (Mills, 1981), and even larger 0 group dace "hold station only if the flow is less than 20 mm s^{-1}" (Mann & Mills, 1986), and in an environment such as the River Frome, the flow regime restricts dace larvae to a "series of discrete backwaters and marginal areas" (Mills *et al.*, 1985).

Feeding in larval dace begins before the yolk-sac is completely absorbed, with the first food items being unicellular algae (Kennedy, 1969), rotifers and diatoms (Mills *et al.*, 1985; Mann & Mills, 1986), before moving on to copepods, cladocerans and chironomids as they grow (Mills *et al.*, 1985).

During the early summer many dace larvae are eaten by invertebrate predators, mainly species of Odonata (Mann & Mills, 1986), and in tank studies most of the predators appear to select smaller larvae (Mills & Mann, 1985). Indirect evidence of heavy losses through predation was provided by very high survival rates of dace kept at low densities in fine mesh cages in the River Frome (Mann & Mills, 1986). The growth of 0 group dace varies from year to year (Mann & Mills, 1986). Assuming that vulnerability is inversely related to fry size, it is possible that rapid growth in warm years could increase the chances of survival (Mills, 1982), however not all the variation in growth can be explained by temperature alone, as "two years of intermediate warmth resulted in widely different growth rates" (Mann & Mills, 1986). Growth rates also appear to vary for fish of the same age in different parts of the river. In a study of dace growth in the River Avon (Hampshire), Gribble (1988), showed that growth rates of 0 and 1 group dace tend to increase with the distance downstream. Conversely the same study showed that the growth rates of 2 group and older dace decrease with distance downstream.

Adult dace are capable of feeding at all depths within the water column, but are most conspicuous when they come to the surface. Walton & Cotton (1653) refer to dace taking flies at the surface, Ensom (1930) records the diet of the dace consisting of "Insects, grubs and flies; worms" and Tate Regan (1911), states "it feeds on insects, shrimps, worms, etc., sometimes leaping at the flies on the surface of the water and sometimes keeping near the bottom". Whether or not plant material constitutes a major part of the diet of the dace probably differs between waters and between times of the year, and may explain the discrepancies in the literature. Wheeler (1969), states that dace "eat a considerable amount of algae and higher plants" Houghton (1879) records that "its food is also partly vegetable in nature" Travis Jenkins (1961) says that it only occasionally feeds on water-plants, and Bagenal (1970) suggests that it only rarely consumes vegetable material.

Dace are known to have "a high feeding diversity" (Cowx, 1989). Whatever the relative importance of plant material in the diet, it is generally accepted that the preferred food of dace is invertebrates, particularly insects, of which Trichoptera and *Simulium* larvae are the most frequently mentioned in the literature (Wheeler, 1969; Bagenal, 1970; Maitland, 1972, 1977; Mann, 1974).

Crustacea are mentioned as being components of dace diet by Travis Jenkins (1961), Wheeler (1969) and Bagenal (1970), however, interestingly, *Gammarus pulex* were only recorded in the diet of Stour dace in two months of the year, comprising only 1 and 0.2 % of the total number of organisms in those months (Mann, 1974). Considering that *G. pulex* are abundant in most chalk-fed streams, it seems likely that if Crustacea were an important component in the diet of dace, the figures for *G. pulex* would have been much higher than those recorded. Similarly, figures for *G. pulex* of 2 % by volume of the diet of two populations of dace in tributaries of the River Wye (Hellawell, 1974), suggest that Crustacea are either relatively uncommon in these rivers, or are not selected by the dace.

Dace in the River Frome only occasionally carry parasites, including tapeworms (*Ligula*) and anchor worms (*Acanthocephala*). In a study of the effects of the eyefluke (*Diplostomum spathaceum*) on the behaviour of the dace, Crowden & Broom (1980) showed that not only was feeding efficiency reduced, but that the infected fish had a tendency to swim near to the surface.

Dace occur in many rivers along with other species, and may form mixed species shoals at times. In particular roach (*Rutilus rutilus* (L.)) and dace are often seen to shoal together, although research by Cowx (1989) on a mixed population of roach and dace suggested "there was little evidence that variability between regions in growth rates of each species resulted from competition for food". Dace are also often perceived to compete with brown trout (*Salmo trutta* L.), and as a result are often culled, although the competition between the species has never been proven (Mann & Mills, 1986). In fact trout are likely to eat small dace, and Lawrence Wells (1962) writes "a trout rarely says "No" to a young dace; if it comes to that, neither does a pike". Ensom (1930) agrees, stating "in the water pike don't argue with them - they eat them". In the River Frome predation by pike is a major contributor to the mortality of dace over one year old (Mann & Mills, 1986). Approximately one third (34%) by weight of the fish prey of Frome pike are dace, and they constitute the principal prey species. Consequently pike consume large numbers of dace (*c.* 1420 ha^{-1} yr^{-1}), with the size of dace eaten increasing with pike size, and no dace becoming too large to be eaten (Mann & Mills, 1986).

1.4 Species description

By drawing information from all the above mentioned literature the following species description can be synthesised:

The dace (*Leuciscus leuciscus* (L.)), also known as the dare or dart is a small, slim, silvery bodied, shoaling member of the carp family, whose name comes from an old word meaning dart, given because of the nature of its movements. It is found throughout most of Britain and mainland Europe, particularly in clear fast flowing streams and rivers in many of which the species is the dominant cyprinid in terms of biomass.

Similar in appearance to small chub (*Leuciscus cephalus* (L.)), the most prominent distinguishing features are the concave outer edges to the dorsal and anal fins of the dace. A lateral line scale count in excess of 46 and a 5 + 2 tooth formation on the pharyngeal bones also identifies a dace. The eye is yellow, and the caudal fin deeply forked, however the colour of the fins appears to vary between populations, and possibly between individuals within the same population.

In the UK adult dace spawn in March and April achieving maturity for the first time in either their third or fourth years of life, and then spawning annually up to their maximum age of 11+. They attach their negatively buoyant, yellow-orange yolked, 1.5 to 2.5 mm spherical eggs to gravel substrata in shallow fast flowing water. The major cause of death to eggs appears to be oxygen starvation caused by fine sediments, but those that survive hatch in around 30 days, with the weakly swimming 7.5 - 9 mm larvae drifting downstream into slow moving marginal backwaters. The fastest growing of these larvae, of which there are more in the warmest years, are better able to avoid predation by invertebrates and fish, and survive to the end of the year, by which time the year class strength has been established.

Adult dace feed mainly on invertebrates, particularly the insect taxa Trichoptera and *Simulium*, and are themselves prey for piscivorous fishes particularly pike (*Esox lucius* L.), constituting the pike's principal prey species in the River Frome.

1.5 Migration and habitat use of adult dace (*Leuciscus leuciscus* (L.)) in an English chalk stream - the aims of this thesis.

Fish, like other animals, must "solve a number of basic problems" in order to survive. The most important of these are "to find and ingest appropriate food", "to avoid predation", and "to reproduce" (Keenleyside, 1979). The first two of these aims are very much a means to an end, allowing the individual to survive and grow to maturity, at which stage it can pass on copies of its genes to the next generation. Those individuals best equipped to solve these three basic problems are the most successful, and consequently have the highest fitness. Those least well equipped, including those with unsuitable behavioural or morphological traits, are likely to die. This strong selective pressure can result in a population becoming specialised and adapted to specific aspects of its environment. However, there are also generalisations that can be made which hold for individuals of a particular species wherever they occur, e.g. invertebrate feeders or gravel spawners. It seems likely that some aspects of the movements and habitat use of a particular species will be common to that species throughout its range. Other aspects however may be specific to a particular population and may have evolved in response to the particular demands of the local environment.

The River Frome is a typical south of England chalkstream, which is relatively unmanaged and has no significant pollution. Many aspects of the physical and chemical attributes of the river have been studied, and the biology of the fauna and flora has been researched extensively. The fish populations of the river are also relatively unmanaged, with little in the way of angling pressure, and no legal stocking or removal of fish is undertaken. Consequently the fish fauna is relatively simple compared with other south coast rivers, where exotic and non-native species have been introduced. Within the Frome system there are few barriers to migration, and in general most obstructions can be easily passed, either directly, or via millstreams or fish passes.

The River Frome therefore represents a "near-natural" system in which the movements and habitat use of wild, unmanaged fish populations can be examined. Information gathered from research carried out in such a system can be considered baseline data, allowing comparison with other, contrasting systems. Such comparisons can reveal which aspects of migration and habitat use are common across the board, and which are river specific. Such detailed knowledge is essential to our understanding of the behaviour of wild fish populations, and will ultimately allow the response of communities to novel situations to be modeled and predicted.

It is apparent from existing literature that dace generally occur in clear fast-flowing streams, and require clean gravel on which to spawn. Visual observation, electrofishing and fish counter evidence has shown that the East Stoke Millstream is used by adult dace throughout much of the year, suggesting that the available habitat is suitable. In addition the East Stoke Millstream is a known spawning stream, and has been used during a number of consecutive years. By using optimal habitats at appropriate times an individual dace can maximise its lifetime reproductive success, and therefore fitness. If an adult dace can feed efficiently, avoid predation and reproduce in one small area of the East Stoke Millstream, then considering the potential costs associated with moving, it would be most profitable for the individual to remain in the vicinity of the East Stoke Millstream spawning site throughout the year.

Thus the aim of this thesis was to test the following hypothesis:

Adult dace remain in one small section of the river throughout the year.

Encompassed within which are the following component hypotheses:

Movement of adult dace is random and unpredictable and occurs within a limited home range, and therefore does not constitute migration.

Adult dace use habitats with the same physical characteristics throughout the year.

In order to test these hypotheses, the movements and habitat use of adult dace were observed in the River Frome using appropriate techniques. Chapter 2 describes the study area and some of the experimental facilities available at the Institute of Freshwater Ecology River Laboratory. The extent to which movements of wild dace are random and unpredictable was studied using three techniques: radio-telemetry (Chapter 3), mark-recapture (Chapter 4) and fish counters (Chapter 5). The characteristics of the habitats used by adult dace were examined both during the day (Chapter 6) and at night (Chapter 8), and also during the post-spawning period (Chapter 7).

CHAPTER 2

Study area

2.1 River Frome

The River Frome rises at Evershot (NGR ST047576), and flows east through Dorset for approximately 65 km, entering the English channel at Poole Harbour (Casey, 1969). The River Frome catchment covers 300 square kilometres, and comprises mainly rich agricultural land (Casey, 1969). The river is described as a typical medium-sized chalk stream (Crisp *et al.*, 1982); indeed, the most important rock formation in the River Frome basin is chalk, the outcrop of which extends over 46% of the whole catchment (Paolillo, 1969). Chalk streams in Britain are found sporadically throughout the area south of Yorkshire, and east of Dorset.

Chalk is a soft, permeable calcareous rock created in the Upper cretaceous period. Rain falling on chalk rapidly percolates into, and accumulates in aquifers, which may be up to 80 m deep and may retain water for 20 years or more (Ladle & Westlake, 1995). The aquifers act like a sponge and help to regulate the flow, damping the effects of heavy rainfall, and releasing water continuously, even during spells without precipitation. The temperature is also buffered, the groundwater supply being cool in the summer and warm in the winter, relative to air temperatures. Mean monthly temperatures in the Frome range from 6.5°C in January to 17.4°C in July (Crisp *et al.*, 1982). Similarly, the chemical composition of the water is more consistent than in those rivers with a lower percentage input from aquifers. Due to the influence of the chalk, the pH of the River Frome is on the alkaline side of neutral, between 7.5 and 8.5. Water conductivity ranges from 258 to 559 micro siemens per cm, with a median of 518, a mean of 512 and a standard deviation of 33.

The average annual precipitation in the Frome catchment was 38.9 inches (98.8 cm), during the period 1960-67 (Paolillo, 1969). The River Frome, like most chalk streams, responds quickly to precipitation, the vast majority of which falls as rain. Water level starts to rise between 24 and 48 hours after the precipitation event (Paolillo, 1969). The Frome valley is drained by numerous permanent and temporary streams (Paolillo, 1969), those which are dry throughout the whole year, or in the summer only, being known as Winterbournes.

Studies of the discharge of the Sydling water, a tributary of the Frome, at two points 2.5 miles apart showed that there was a considerable influx of groundwater, the discharge more than doubling over this distance (Paolillo, 1969). The groundwater enters the streams through boreholes and springs, and Paolillo (1969) states that 73.6% of the total discharge measured at East Stoke originated as groundwater, a high figure, but one in keeping with the geology of the area. Paolillo (1969) also states that "groundwater in the Frome catchment is of good quality and does not show pollution or saline water contamination." Indeed, in 1975 the Department of the Environment rated the Frome a class 1 river.

At intervals throughout its length the flow of the River Frome splits into narrower channels, usually by the deliberate actions of man, creating millstreams (Fig. 2.1i). Many of these millstreams are now disused, but some retain working hatches, with which the flow down the various sections can be adjusted. Millstreams are typically slow flowing and relatively deep in the upper reaches, becoming generally shallower and faster flowing downstream of the original site of the mill.

Man's influence on the character of the River Frome can also be seen in other areas, usually for reasons of flood defence. Channel straightening, and both bank strengthening and raising, have been carried out in places both to allow flood water to drain away quickly, and to prevent loss of pasture on the outsides of meanders. Weed cutting is also carried out, as deemed necessary by the Environment Agency, as a precaution against summer flooding.

Studies of the fish populations described in this thesis were carried out at the Institute of Freshwater Ecology River Laboratory, at East Stoke, which lies in the lower portion of the Frome basin, about 6 km upstream of the tidal limit (Fig. 2.1i). Here the catchment consists of chalk overlain by Tertiary sand and gravel deposits known as the Bagshot Beds. In this area the river is meandering but fast flowing, having sand and gravel substrata, with depths up to 2 m and widths ranging between 10 and 20 m (Casey, 1969). The mean water velocity upstream of East Stoke was estimated to be around 25 cm s^{-1} by Crisp *et al.* (1982). Ladle & Westlake (1995) give mean water velocities of 4-15 cm s^{-1} inside the dense weed beds, compared to water velocities in excess of 50 cm s^{-1} between them.

The River Frome, like other modified chalk streams flows in a rectangular channel "with a well-developed pool-and-riffle pattern" (Ladle & Westlake, 1995). The river supports a rich flora of in-stream macrophytes, mainly species of both *Ranunculus* and *Potamogeton*. The *Ranunculus* generally grows on the shallow riffle sections, in long oval beds interspersed with clean gravel, whereas *Potamogeton* occurs most commonly in the pools. There are usually two blooms of diatom algae, one in the spring and one in the autumn. The invertebrate community is also rich and varied, with most clean flowing water taxa being represented.

The Study Area - River Frome and tributaries.

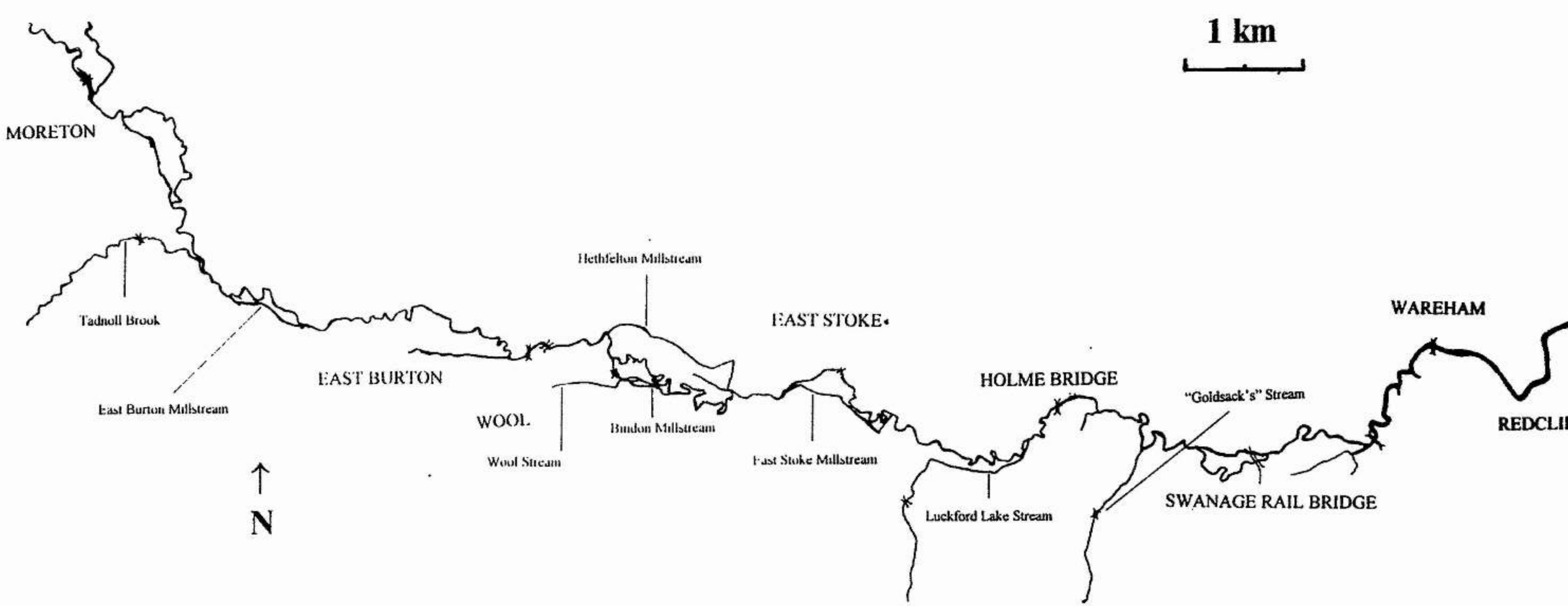

Figure 2.1i Map of the study area, showing the lower River Frome catchment. Towns, bridges, tributaries and millstreams are marked.

The fish community is relatively species poor, compared with other rivers in the south of England. Several species, for example chub (*Leuciscus cephalus* (L.)), barbel (*Barbus barbus* (L.)) and bream (*Abramis brama* (L.)) have established breeding populations in neighboring waterways, such as the Rivers Dorset Stour and Hampshire Avon, but have not been successfully transferred to the Frome. A full species list of fish present in the River Frome is given later in this chapter (2.3).

2.2 East Stoke Millstream

The Institute of Freshwater Ecology River Laboratory is situated on the banks of the East Stoke Millstream, on the site formerly occupied by East Stoke Mill (Fig. 2.1i). The East Stoke Millstream is a side branch of the main River Frome and runs through open pasture for 195 m, before entering the grounds of the River Laboratory. The Millstream then continues downstream for 255 m before entering the Fluvarium (2.4). The section of the Millstream upstream of the Fluvarium is known as the Millhead, and was the capture and release site for the majority of dace tagged during this study.

The Millhead varied between 4 and 8 m wide, and depths generally ranged between 0.2 and 0.6 m. The channel itself was, up until recently, heavily managed, and was trapezoidal in cross section. Away from the margins, the substratum was mainly sand, and normal summer flow velocities were around 0.25 ms^{-1}, with an abundance of in-stream macrophytes, chiefly *Ranunculus* sp. The water height in the Millhead was controlled via three manually operated hatches; the Laminar flow; the Iron hatch and the Eel trap, along with the electronic Fluvarium hatches. Water could also leave the Millhead both to feed the seven experimental channels (Fig. 2.2i, 2.3) and via a pipe which flowed into the Botany pond. The height of the water in the main River Frome also has a significant bearing on the amount of water entering the mouth of the East Stoke Millstream. However the Millhead generally received about one quarter of the total discharge.

Downstream of the Fluvarium, although similar in width, the East Stoke Millstream was more variable in character consisting of fast, gravel-bedded riffles and slower, sandy glides. As further upstream, in-stream macrophytes were locally abundant, however the south bank was wooded along much of its length, unlike the banks of the Millhead. The run-offs from the various hatches and channels rejoined the Millstream, and the combined channels then flowed over an Environment Agency gauging weir and continued downstream, before re-entering the River Frome 700 m downstream of the Fluvarium (Ibbotson *et al.*, 1994).

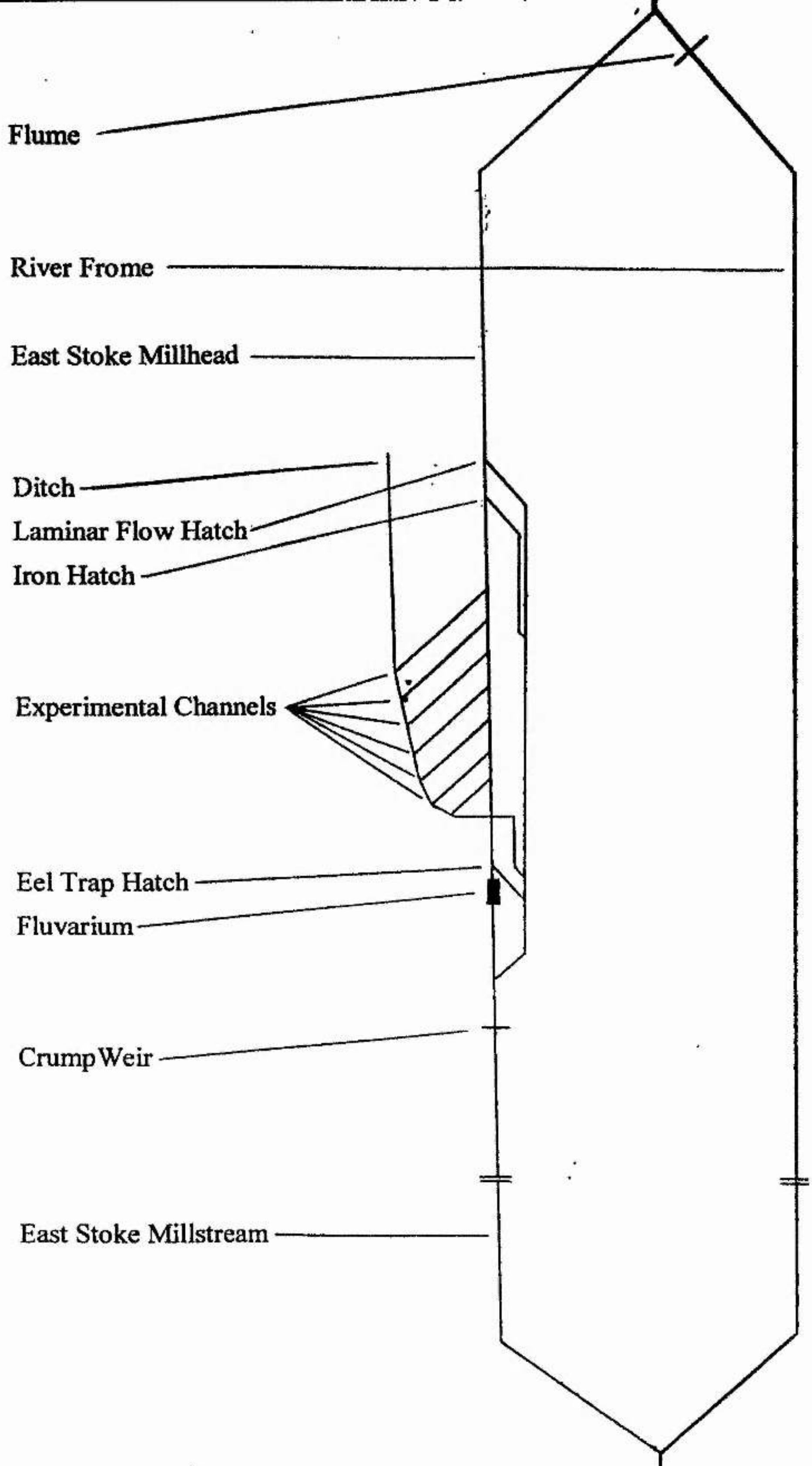

Figure 2.2i. Schematic diagram showing the layout of the East Stoke Millstream and side channels. Water flow is from the top of the page to the bottom. Double lines (=) indicate a distance break. Diagram is not drawn to scale.

2.3 Experimental channels

At frequent intervals, throughout the course of the work, it was necessary to hold dace in captivity, in as near natural conditions as possible, in order to facilitate aspects of their study. One of the most important requirements of keeping dace in near natural conditions was the supply of clean, flowing, oxygenated water. Obviously, the easiest and most natural way to achieve this was to use river water, and such a facility exists at the River Laboratory in the form of seven experimental channels. The 2 m wide channels vary in length from 8 to 20 m, and are fed with water from the East Stoke Millstream, via 0.15 m (diameter) pipes.

The depth of water in the channels was adjusted using dam boards at the downstream end, and mesh screens prevented the fish from leaving the channel. The channels were used to hold fish prior to tagging, for tag retention studies and in order to observe the behaviour of tagged fish. A 2 m wide board was placed over each channel used, in order to provide some cover, and the fish were fed daily with either trout pellets or live food (maggots) when available. Detritus was removed from both the upstream end of the pipes, and the mesh screens as required, usually once a week. Fish favoured the area under the board during the day, and appeared to be most active around dawn and dusk, although torch-lit observations during darkness suggested that the fish moved out from under the board at night, but remained relatively static within the channel until disturbed. The fact that the fish grew whilst in the channel indicated that conditions were satisfactory, and the discovery, during March 1996, of dace eggs on the gravel, suggested that the fish were in good health.

2.4 Fluvarium

Another through-flow facility available at the River Laboratory is the Fluvarium. The Fluvarium consists of two glass sided channels (6 m x 1.4 m x 0.9 m) through which the East Stoke Millstream flows. The Fluvarium is similar in many respects to the stream tank described by Lindroth (1954).

During experiments, the flow through the channels was controlled by electronic hatches at the upstream end of the channels, and water depth within the channels was adjusted using valve boards at the downstream end. The glass sides allowed observations of fish to be made in near-natural conditions. The Fluvarium was used both for tag retention studies, and for examinations of the comparative behaviour of tagged and un-tagged fish. The Fluvarium was also used in order to monitor the downstream migration of juvenile Atlantic salmon, or smolts, which were diverted into the East Stoke Millstream using an acoustic bubble screen, and were counted as they passed through the Fluvarium. A by-product of the smolt counting work was video recordings of the movements of other fish, including dace, which provided a valuable addition to the data gathered from other sources (Chapter 5).

2.5 Species list

The following species are commonly found in the River Frome:

Atlantic salmon	*Salmo salar* L.
Minnow	*Phoxinus phoxinus* (L.)
Dace	*Leuciscus leuciscus* (L.)
Stone loach	*Barbatula barbatula* (L.)
Eel	*Anguilla anguilla* (L.)
Brook lamprey	*Lampetra planeri* (Bloch)
Brown trout / sea trout	*Salmo trutta* L.
Grayling	*Thymallus thymallus* (L.)
Pike	*Esox lucius* L.
Gudgeon	*Gobio gobio* (L.)
Roach	*Rutilus rutilus* (L.)
Three-spined stickleback	*Gasterosteus aculeatus* L.
Thin lipped mullet	*Chelon ramada* (Risso)
Bullhead	*Cottus gobio* L.
Flounder	*Platichthys flesus* (L.)

The following fish species have been recorded in the River Frome, but are not common:

Marine lamprey	*Petromyzon marinus* L.
River lamprey	*Lampetra fluviatilis* (L.)
Sturgeon	*Acipenser sturio* L.
Rainbow trout	*Oncorhynchus mykiss* (Walbaum)

Smelt	*Osmerus eperlanus* (L.)
Carp	*Cyprinus carpio* L.
Tench	*Tinca tinca* (L.)
Rudd	*Scardinius erythrophthalmus* (L.)
Chub	*Leuciscus cephalus* (L.)
Ten-spined stickleback (L.)	*Pungitius pungitius* (L.)
Sea bass	*Dicentrarchus labrax* (L.)
Perch	*Perca fluviatilis* L.

CHAPTER 3

Migrations - radio-tracking

3.1 Introduction

Most animals living in temperate regions change aspects of their behaviour in response to seasonal changes in the prevailing conditions (e.g. barnacle geese, Prop & Vulink, 1992; brown trout, Heggenes *et al.*, 1993; seals, Thompson *et al.*, 1996). Likewise, many animals exhibit alternative behaviours at different times during the daily cycle of light and dark, e.g. the alternation between roosting and foraging in many birds (Eiserer, 1984); the rhythmical dispersal from, and return to a seamount by scalloped hammerhead sharks (Klimley & Nelson, 1984). One possible reaction to an alteration in conditions is migration, where an individual or group searches for an area that is likely to be more suitable under the new conditions. This migration can occur either in response to, or in anticipation of the change, and is therefore predictable.

Rivers are essentially linear systems, which provide a limited diversity of habitat types to resident animals, with the most dissimilar sites generally occurring at opposite ends of the system. Consequently there is often a very gradual change in many of the habitat characteristics of a river from source to mouth, and a fish may have to move a substantial distance in order to take advantage of significantly different habitat.

Although there have been many studies of group dynamics of fish shoals (see Pitcher & Parrish, 1993; Helfman *et al.*, 1997), it is only relatively recently that technological innovations such as radio- and acoustic-tracking have permitted detailed observations to be made of fish activity patterns in natural surroundings. Movements and migrations can now be tracked over periods ranging from minutes to months, including periods of low light intensity, at night or in turbid water conditions.

The majority of research into freshwater fish migration has been carried out with salmonid species (e.g. Gray & Haynes, 1979; Clapp *et al.*, 1990; Young, 1994; Gowan & Fausch, 1996; Armstrong & Herbert, 1997), presumably reflecting their commercial value. Some non-salmonid fishes have been shown to carry out seasonal migrations between different habitats, usually in connection with spawning (e.g. Lindsey & Northcote, 1963; Tyus, 1990; Rodriguez-Ruiz & Granado-Lorencio, 1992; Johnson & Noltie, 1996; Lucas & Batley, 1996). Daily migrations in marine- and lake-dwelling species are well documented (Helfman, 1993); however, there is little information in the literature concerning diel migrations of stream-dwelling species. The propensity or otherwise of stream fishes to migrate, on either a daily or seasonal basis, is an important component of fish ecology, a thorough understanding of which is required in order to effectively manage riverine habitats.

Recaptures of marked individuals, fish counter records, anecdotal evidence from anglers and personal observations have all suggested that in the River Frome, at least some dace are mobile, and move around the river system. However it was not known whether these movements are predictable responses to cyclic changes in conditions.

In order to examine these movements in greater detail, radio-telemetry of individual adult dace was used to test the following hypotheses:

Dace have a limited home range and remain within a short section of river throughout the year.

Dace captured and released in the East Stoke Millhead prior to spawning use the East Stoke Millstream spawning site.

Within their home range, any daily movements are temporally unpredictable, and therefore do not constitute migrations.

3.2 Materials and methods

3.21 Radio-tags

Radio-tracking has been used extensively in the past to monitor the movements of fish, particularly salmonids (Gray & Haynes, 1979; Solomon & Storeton-West, 1983; Webb & Hawkins, 1989). Until recently, little telemetry work had been carried out on non-salmonid fishes, and reviews of fish migration contain few references to the movement patterns of fish other than salmonids, reflecting an "imbalance in the study of fish migration" (Smith, 1991). Some telemetry work has been carried out perciformes and esocids (e.g. Lucas *et al.*, 1991), and on large cyprinids e.g. bream, *Abramis brama* (L.) (Langford, *et al.*, 1979); Colorado squawfish, *Ptychocheilus lucius* Girard (Tyus, *et al.*, 1984); grass carp, *Ctenopharyngodon idella* Val. (Hockin, *et al.*, 1989); tench, *Tinca tinca* (L.) (Perrow, *et al.*, 1996) and barbel, *Barbus barbus* (L.) (Baras, 1995; Lucas & Batley, 1996; Lucas & Frear, 1997). The tags used in these studies however were relatively heavy and only suitable for fish over 1 kg, and therefore of no value for small fish species, such as dace.

Several factors relating to the size of a radio-tag must be considered when planning a radio-tracking study. Catching, tagging, releasing and tracking a fish is time consuming, and in general sufficient data must be collected from each tagged fish in order to make the process worthwhile. In order to gather large amounts of data, tags need to have as long a life as possible. The longer the pulse length and faster the pulse rate of the transmitter, the easier it is to track the tagged fish, but the shorter the life of the tag. The longevity of a tag, and most of its weight, are determined primarily by the size of its battery. A compromise is required so that sufficiently small to be carried by a dace, it still contains a battery large enough to provide sufficient tracking time to gather the required data.

Ross & McCormick (1981) detailed the criteria that should be considered regarding hydrodynamics, smooth anterior aspect and trailing aerial to the tag. Winter *et al.*, (1978) suggest that "the transmitter weight in water should not exceed 1-1.25 % of the fish's weight out of water". With these studies in mind, and following discussions with a local radio tag manufacturer (Biotrack Ltd.) a small waterproof radio-tag was designed and assembled (Plates 3.21i & 3.21ii). Ranges were tested using a Yaesu FT290R receiver and a three-element Yagi antenna.

Technical specifications of the Biotrack SS-2 radio-tag:

Length	17 mm
Width	9 mm
Depth	7 mm
Weight in air	2.3 g
Weight in water	0.9 g
Max. range in air (ground level)	600 m
Max. range in water (ground level, depth 0.5 m)	350 m
Pulse length	20 ms
Pulse-rate	50ppm
Antenna (external)	90 mm
Longevity (weeks) (Hg13 battery)	9-11
Price	£80

Calculations based on a length : weight equation for dace in the River Frome (Mann, 1974), suggested that in order to comply with the maximum weight recommendations of Winter *et al.* (1978), the minimum length of dace that should be tagged with the Biotrack SS-2 tag is 170 - 190 mm for female dace, and 180 - 190 mm for male dace. As identifying the sex of dace at most times of the year is very difficult, it was decided that 200 mm would be the lower size limit for all dace to be radio-tagged.

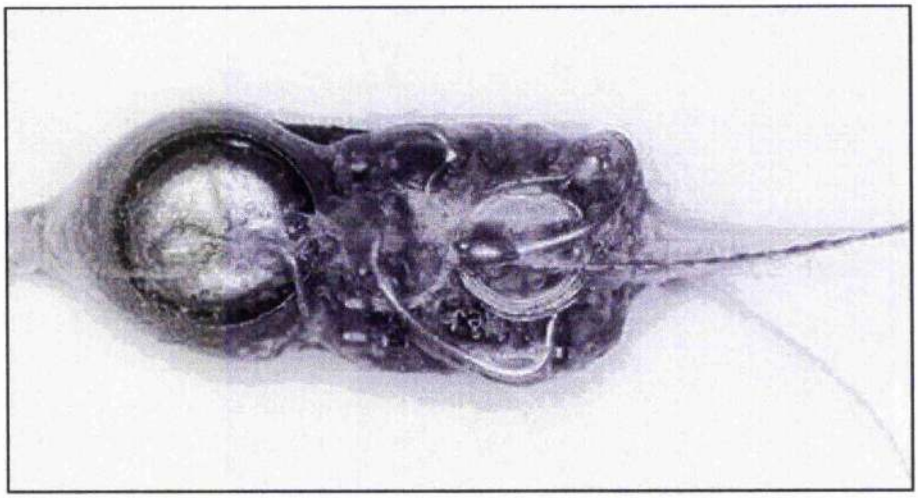

Plate 3.21i. Plan view of a Biotrack SS-2 radio-tag.

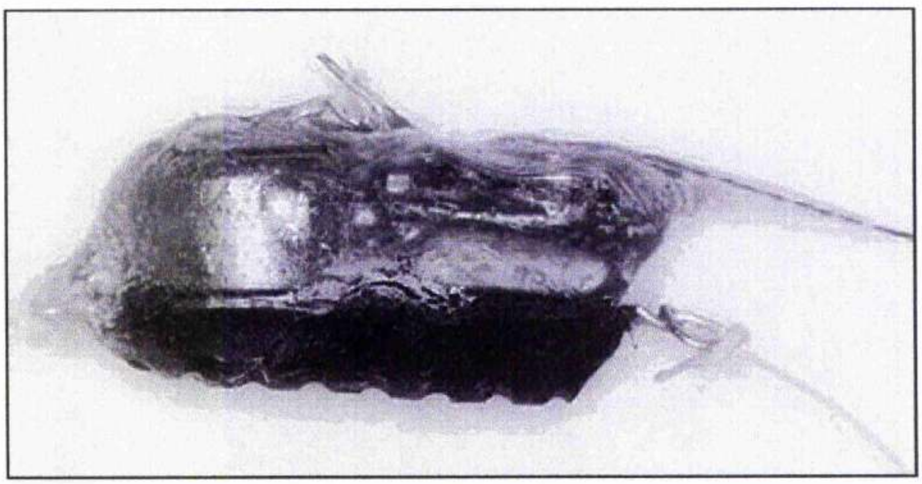

Plate 3.21ii. Side elevation of a Biotrack SS-2 radio-tag, showing neoprene padding and suture attachment loops.

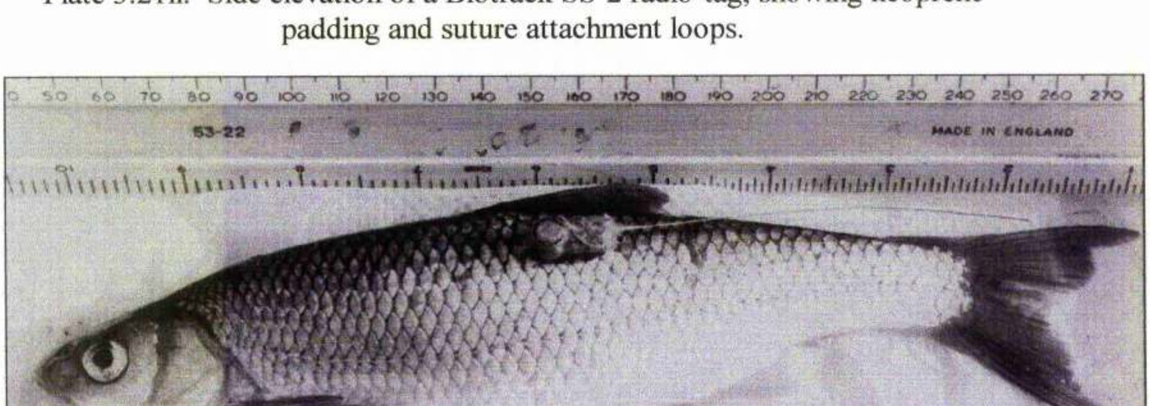

Plate 3.21iii. Adult dace with radio-tag in position.

A 0.9 gram tag therefore represents 0.84% of body weight for a 200 mm male dace, and 0.75% of body weight for a 200 mm female dace, and is well below the minimum percentage weight limit used in other successful studies.

Radio-tags were externally attached to the dorsal musculature of adult dace (Plate 3.21iii) using the technique described by Beaumont *et al.* (1996). The technique essentially involves the insertion of absorbable sutures through the dorsal musculature of an anaesthetised fish, in a position below the internal base of the dorsal fin rays. By pulling the sutures, the radio-tag was positioned snugly against the flank of the fish, before the sutures were tied off, under slight tension, on the opposite flank. This attachment prevents excessive movement of the tag, which otherwise might chafe against the fish, and also allows the tagged individual freedom of movement. As external attachment of transmitters was used, and the data collected was considered useful to the management of the population, a Home Office licence was not required for this procedure.

Fish for radio-tagging were generally captured the day before tagging using rod and line, and were retained in an experimental channel overnight. Recapture from the channel was achieved using a net. A rolling programme of radio-tagged fish releases was selected to allow movement data to be collected throughout the calendar year.

3.22 Receivers

The Biotrack radio-tags used during the study (Chapter 3.21) transmitted signals at frequencies around 173 MHz. In order to detect this signal, a modified Yaesu FT290R receiver was used in conjunction with a three-element Yagi antenna. This particular model of Yaesu receiver was originally manufactured as a marine

VHF radio, but was adapted for radio-telemetry by Argus Electronics (Norfolk), by changing the crystal for one that operates in the 173 MHz waveband. The receiver was powered by 10 rechargeable Ni-Cad cells, the condition of which were checked using a switch on the bottom of the unit which utilised the signal strength meter to show the battery voltage. Many of the dials and switches on the front of the receiver were associated with the signal transmission functions of the pre-modification model, and as a result were redundant. The radio signals were received on the upper side band (USB), and the "MODE" dial was left in this position at all times. The ON/OFF switch also acted as a volume control and was adjusted as required. The frequency of each radio-transmitter in use was set into one of the ten memory pre-sets by pressing the DIAL button and setting the digital display to the required frequency, before selecting the appropriate memory pre-set number with the MEMORY dial, and pressing the M button on the keypad. The memory pre-set frequencies were checked by pressing the MR button and rotating the MEMORY dial through each channel sequentially. The only other function buttons that were frequently used were those which control the STEP and CLAR facilities. The STEP button changed the rate of increment achieved with each click of the frequency dial, from whole units to tenths of units, and back again as required, and was used when locating the bearing of the strongest signal. The CLAR facility was used to temporarily adjust the frequency of any of the pre-sets, and to de-tune the receiver in order to accurately locate a transmitter at close range. The frequency being scanned automatically reverted to the original pre-set value when any other button was pressed, or when the unit was switched off.

3.23 Antennae

There are several 'types' of antennae available for mobile radio-tracking, each having its own strengths and weaknesses. The four most common types are the dipole, loop, "H"-Adcock and Yagi antennae.

1. Dipole - This is a simple antenna often used vertically and mounted on a car roof. In this study a simple dipole was used horizontally on the end of a 20m cable as the antenna for a fixed listening station.

2. Loop - This type of antenna is often attached directly to the receiver. A loop antenna on the end of a pole was used in this study in an attempt to accurately locate 'lost' tags on the river bed, but was later rejected in favour of the de-tuning method (3.24). Loop antennae tend to give reverse bearings, and are most commonly used at frequencies around 27 MHz.

3. H-Adcock - The H-Adcock is a useful antenna, the sensitivity of which can be adjusted by folding in the jointed vertical elements. The H-Adcock used in this study had a 72 cm crosspiece, and 87 cm vertical elements, jointed in the middle, and was used when its compact folded size was anticipated to be an advantage. The bearing is read through the centre of the H, with true and reverse bearings being of equal magnitude. This ambiguity can result in location errors, especially where the river menders extensively.

4. Yagi - Available in a range of sizes having between 3 and 12 elements, Yagi antennae are versatile and accurate. The bearing is read along the line of the handle, so the direction of the tag is discovered by pointing the aerial directly at the strongest signal. The Yagi antenna is described as having a good "front-to-back" ratio, making it easier to distinguish between true and reverse bearings than with other antennae types (Kenward, 1987). The Yagi antenna is used initially with the elements

held vertically, however for accurate location when relatively close to the tag, it should be used with the elements in a horizontal plane. At frequencies in excess of 140 MHz the three element Yagi is the most commonly used antenna for tracking on foot (Kenward, 1987). The 12 element Yagi has a greater range than the 3 element antenna, but it operates over a narrower field.

A three element Yagi, with flexible elements was deemed to be the most suitable antenna for mobile tracking, being light, accurate and providing good range with the 173 MHz radio-transmitters used in the study.

3.24 Radio-tag location

Mobile tracking was used on a regular basis in order to monitor the movements of radio-tagged dace in the River Frome. Tagged fish were located using a bearing triangulation method. When using a Yagi antenna (3.23), the bearing of tag was read as the direction of the strongest signal, as indicated by the relative volume of the 'beep' and the degree of deflection of the meter needle. Three bearings were taken from three different positions, with the intercept of the three bearings being recorded as the position of the tagged fish. The position of the fish was then marked on a sketch map, and a written description of the location was made. This description was created by estimating (pacing) the distance from a position on the bank, adjacent to the position of the fish, to the closest readily identifiable landmark. The distances between the most commonly used landmarks were measured (Table 3.24), and the distance moved by the fish from its previous position to that which it occupied currently was calculated by adding together the appropriate distances.

SITE	DISTANCE (M)	SITE	DISTANCE (M)
MORETON	4500	MEMORIAL SEAT	110
EAST BURTON	2000	DEARN POOL	50
WOOL BRIDGE	600	DUCKS EGG	280
HEDGEMANS HATCHES	1000	WILLOW TREE POOL	80
BINDON MILLSTREAM	1100	FORM CORNER	100
TRYONS HUT	500	POSTS POOL	90
HEDGEMANS POOL	290	UPPER HORSESHOE	100
TOP BOUNDARY	150	THE FROG	110
FIXED STATION	70	LOWER HORSESHOE	90
END OF PATH	170	L-HORSESHOE F'BRIDGE	100
BELHUISH FOOTBRIDGE	140	AFTERNOON POOL	100
IVY BUSH POOL	80	MILLSTREAM F'BRIDGE	100
LAGOON	60	MOORES F'BRIDGE	190
POST	50	BOTTOM BOUNDARY	900
OAK TREE (S. BANK)	80	FISHING HUT	700
EAST STOKE MILLSTREAM	20	LUCKFORD LAKE	500
FISH COUNTER	60	HOLME BRIDGE	1400
ISLAND IN WEIRPOOL	70	GOLDSACKS STREAM	2000
THORN BUSH	150	SWANAGE RAIL BRIDGE	1520
WICKET GATE	270	BYPASS BRIDGE	1320
ROAD BRIDGE	240	WAREHAM QUAY	900
MEMORIAL SEAT		REDCLIFFE	
		TOTAL DISTANCE	**22340**

Table 3.24. Distances between the most commonly used, readily identifiable landmarks within the study area.

In order to test how accurately transmitters could be located, active radio-tags were hidden in the river by one person and searched for by another. To find a hidden transmitter, the operator started at an appropriate position as high as possible above river level, e.g. on a bridge. The receiver was set to the correct frequency, and while holding the Yagi antenna with the elements vertical and the handle horizontal, the operator rotated slowly through 360 degrees, listening for a signal. If no signal was heard the operator moved along the river to another suitable start point, where the process was repeated. If a signal was heard the operator moved off in this direction, in order to obtain an accurate location.

The operator walked along the bank towards the bearing of the strongest signal, until the strongest signal appeared to come from a position perpendicular to the river bank, i.e. neither upstream nor downstream. At this point the antenna was rotated through 90 degrees, so that the elements were horizontal, which reduced the range of the antenna, but increased its directional accuracy. Three bearings were then taken, one from the current position and one each from around five metres upstream and downstream. The position of the tagged fish was recorded as the intercept of the three bearings.

In shallow water, and when the operator is very close to the transmitter, the signal is often extremely strong when the antenna is pointed in all directions, giving a maximum deflection of the meter needle on more than one bearing, thus making it difficult to identify the direction of the strongest signal. In these circumstances the receiver was de-tuned, moving away from the exact frequency of the transmitter using the CLAR facility (3.22). This had the effect of reducing the signal strength, enabling the bearing of the strongest signal to be determined.

In nine out of the ten trials the transmitters were located to within an area of 4 m^2. Visual observations of radio-tagged fish in the river have shown that the majority of radio-locations are equally precise, providing the fish was not disturbed during the tracking procedure.

3.25 Fixed listening stations

Fixed Listening Stations or FLS's are immobile radio-receiver and microprocessor combinations, which automatically switch themselves on after a predetermined interval and scan through each of the ten memory pre-sets checking for radio signals on each frequency.

The FLS's used in this study were manufactured under MAFF licence by Argus Electronics, Norfolk, and comprise an electronics box which includes a microprocessor, a modified Yaesu FT290R radio receiver, a tape recorder, a till roll type printer and a long external dipole antenna. They were powered by 12 volts direct current, supplied by either an internally attached sealed lead acid battery, or by a car or leisure battery through an external power lead. The unit was supplied in a rectangular splash-proof box (0.55 m x 0.30 m x 0.27 m). When deployed in the field, the FLS's were housed in camouflaged wooden boxes (1 m x 0.50 m x 0.40 m). The range at which Biotrack SS-2 radio-tags could be detected by FLS's varied according to water depth and the height and orientation of the dipole antenna, but was typically around 25m.

The chip responsible for switching the FLS on and off (EPROM chip) was available in a number of varieties, of which IFE owned two. The two minute chip, as its name suggests, switched on the FLS every two minutes, as defined by the internal real time clock, and switched it off as soon as each of the ten pre-set channels had been scanned. The five minute chip operated in the same manner but allowed a five minute interval between scans. The two minute chip was useful when used in FLS's that were bracketing a radio-tagged fish that was thought to be likely to move a substantial distance in a short period of time (e.g. a recently released fish), because there was little chance of such a fish getting past, and out of range of a two minute FLS between scans. The five minute chip was more useful when operated in an FLS near to a static radio-tagged fish or in an area regularly frequented by radio-tagged fish. Because the five minute chip initiated the fixed station less frequently per unit time than the two minute chip, the battery life of FLS's containing the longer interval chip was proportionally longer than that of FLS's fitted with the shorter interval chip.

Another factor which affected the battery life was the number of records made by the FLS. When a radio signal was detected by the station the tape recorder was initiated and a ten second recording of the receiver signal was made, before the FLS moved on to the next memory pre-set number. After all ten channels had been scanned, and if any signals had been recorded, the FLS printed out a message showing the time and the channels activated. FLS's containing the two minute chip continued to produce audio and paper records every two minutes for as long as the radio signal was detected, which quickly resulted in a full audio tape and a flat battery. The five minute chip however had a "continued presence" facility that came into operation after 12 consecutive records on the same channel. No more records, either audio or paper, were produced for that channel until the first time a signal was not detected, at which point a "not detected" paper trace was produced, corresponding to a high pitched tone on the audio tape. Further records on this channel were then recorded as before. This facility saved on audio tape, paper and battery power, and was an important consideration when choosing which type of chip to use, and the positioning of FLS's.

A correctly positioned fixed station can supply detailed data on the movements and site preferences of a radio-tagged fish. Alternatively, the fixed station can be used to record whether or not a radio-tagged fish has passed a particular point. If the FLS was powered with a car or leisure battery then ease of access was also an important consideration. If the station was any more than half a mile from the nearest road or track it was easier to make more frequent visits with smaller batteries. Public road bridges provided the easiest access, however these were considered to be the least secure of sites and were avoided where possible. The height above river level was also an important consideration. Although the River Frome is not a particularly "flashy" river, floods can occur at any time of year, and where practical, FLS's were positioned at such a height so as to be above water level during even a large spate. High vertical cliffs on the outside of bends are subject to erosion and can collapse into the river. In these situations FLS's were placed well back from the rivers edge.

Once a location had been chosen the fixed station was positioned and secured, making sure that the lid of the camouflage box could be fully opened, and that it would stay open of its own accord, leaving both hands free. If the box was positioned too close to a wall or tree the lid would not open completely, hindering operations within the box.

The camouflage box was secured in one of a number of ways depending on the availability and suitability of natural or existing anchorage points. All attachments were temporary, allowing relocation or withdrawal of equipment to be carried out with a minimum of effort. The attachments were made secure enough only to discourage the opportunist thief or vandal, as it was considered that the determined thief would return with tools sufficient to breach any practical security measures.

In areas with no natural or existing attachment sites a four foot piece of angle iron provided a suitable anchorage point. The stake was pointed at one end, and had a hole drilled at the other to which a chain was attached. The chain was either permanently attached by breaking a link and welding it through the hole, or temporarily attached using a padlock. The stake was then driven into firm ground with a sledgehammer until only a few inches protruded. This provided a semi-permanent anchorage for the duration of the study. At the end of the study the post was removed with lifting gear, or by placing a horizontal bar through the hole in the stake and lifting vertically.

Natural attachment sites included boulders and the trunks of trees and large shrubs. Existing sites usually took the form of man made structures such as fenceposts, gateposts and parts of buildings. Telegraph poles were avoided because of interference with radio signals. A heavy chain was looped twice around the chosen structure, and padlocked to the camouflage box. The location of the fixed station in relation to fixed points was recorded on a sketch map.

Once the outer camouflaged housing was safely secured in the desired location, the FLS was placed inside and installed. The antenna plug was attached to the port on the rear left side of the waterproof housing, and screwed in tightly. At the opposite end of the antenna wire was a "T" shaped dipole for signal reception. The "T" piece was positioned according to the information required, usually high off the ground in order to maximise the range of the station, and reduce the likelihood of a tagged fish passing without being detected. When more precise measurements of fish location were required appropriate antenna positions were achieved using an active tag and a degree of trial and error.

The FLS's had two battery attachment points. Internal batteries were housed inside the waterproof fixed station housing, in the recess on the right hand side, and were attached using the appropriate spade clip, red for positive, blue for negative. The toggle switch in the back right hand corner of the housing was placed in the INT position when a battery was attached in this manner.

External batteries were much bigger (car or leisure type) and lasted longer than internal cells. They were connected to the fixed station via a lead, the plug of which was screwed into the port on the rear right hand side of the waterproof housing. The crocodile clips on the other end of the lead were attached to the appropriate terminals on the battery, and the toggle switch was set in the EXT position.

Once the battery was connected, the FLS was tested by setting the two toggle switches to the POWER and IDLE positions, and depressing the START button. If the station was functioning correctly the red LED was lit and an idle message printed. If the date and time on the idle message were incorrect, the internal time clock was adjusted using the blue keypad.

The frequencies of the radio-transmitters in use were set into the 10 memory pre-sets as with the mobile receiver (3.22). An audio tape was placed in the tape deck and the RECORD and PLAY buttons depressed. The toggle switch was moved from the IDLE position to RUN, and the START button pressed. A correctly functioning FLS had a lit LED, and produced a high pitched beep every ten seconds, as the memory pre-sets were scanned. When a signal was detected, a short tape recording of the sound was recorded. After each frequency had been scanned, a RUN STARTED message was printed, along with the date, time and a record of those frequencies detected.

3.26 Release cage

Previous unpublished radio-tracking studies of dace at the I. F. E. River Laboratory have demonstrated that dace often show rapid dispersal away from the release site. When two or more radio-tagged fish were released together it was noticeable that the fish rarely stayed in the same shoal, on some occasions traveling away from the release site in opposite directions. The method of release used in these preliminary studies involved introducing the fish into the river from a bin, as soon as they had recovered from the effects of the anaesthetic. Individual fish were often seen to dart away from the release site in different directions, and it appeared unlikely that these fish would remain with, or return to the shoal.

In order to introduce the fish into the river as a shoal, and for them to be given the opportunity to swim away from the point of release as a shoal, a new method of release was devised. The potential for releasing the fish undisturbed, several hours after the tagging event, in order for them to have recovered from any tagging or handling stress was also examined. As a result, a release cage (MK I) was designed.

The cage consisted of a cuboidal wire frame (750 mm x 600 mm x 400 mm) to which was stitched a fine (1 mm) plastic mesh, covering all sides and one end. The other end comprised a coarse wire mesh (20 mm) door which was hinged along its lower axis only. The upper edge of the door was weighted to assist opening. A string (the door string) was attached to the top of the door, and was fed through a wire loop on the top of the frame. This string was used to open and close the door, and was sufficiently long for this process to be carried out remotely. Strings were also attached to the two upper front corners of the cage, by which it was tethered to the bank, in order to prevent the cage being washed downstream.

The release cage was generally positioned with the door facing into the flow, in order that when the door was lowered, the fish, which would normally be facing into the flow, should all see the way out at the same time. This was thought to increase the likelihood that the fish would respond and leave the cage as a shoal. If the release cage was positioned with the door either transverse to the flow or facing downstream, all fish may not see the escape route simultaneously, and each would have to turn before leaving the cage.

Once the fish had been placed in the release cage the door string was kept pulled tight at all times, in order to keep the door firmly closed. The cage was then positioned and tethered to the bank. The door string was tied off on the bank out of full view of the cage, ensuring that the door remained closed. When the pre-determined settling period had elapsed, the fish were released by un-tying the door string and slowly lowering the door, finally letting it gently fall to the river bed under its own weight. The relatively undisturbed fish were then free to swim out of the cage as a shoal.

Although this method was usually effective, a second, improved model (MK II) was designed, following an unsuccessful release event in the summer of 1995, described below:

Adult dace were caught from the Weirpool by angling on the 9th and 10th August, and were retained in an experimental channel (Chapter 2.23). On the 11th August all the fish were recaptured from the channel, weighed, measured and tagged. Three of these fish were radio and visible implant tagged (lengths 251, 240 & 222 mm), the remaining fifteen were visible implant tagged only (length range 163 - 229 mm, mean 197 mm). All fish were transferred to the release cage (MK I) under the Millstream foot-bridge (Chapter 2.1). At 585 mm, the water in this area was the deepest available for some distance, and some overhead shade was afforded by the bridge. The apparent absence of adult dace from the Millhead at the time of release suggested that the habitat was not ideal, having little depth (generally less than 400 mm) and virtually no flow. Small fishes of several species were however abundant throughout the area. Releasing the fish in this area was deemed necessary in order to maintain continuity with previous work.

Some fin damage had occurred during the capture and holding of fish, both pre- and post-tagging. A small amount of damage is always possible when netting fish, however the amount of damage seen in this study was greater than that observed previously, probably due to the unusually long retention in the net. Fish are usually transferred to a bin immediately after capture, but the water temperature was high, and the water would have deoxygenated quickly. Fish were retained in a net prior to, and after tagging in order to supply them with flowing water. The damage was exacerbated by retention in the release cage under sub-optimal conditions, and upon release on the 14th August, at least half of the fish looked unwell, swimming slowly and unsteadily. A group of around ten fish, including one radio tagged fish, left the cage shortly after the door was lowered, and although some showed slight damage as white edges to their fins, their swimming did not appear to be impaired and the fish swam steadily upstream and out of sight.

The two remaining radio-tagged fish, and four visible implant tagged fish emerged more slowly and milled around in a small area upstream of the cage. Their swimming was more erratic than the other fish, and obviously impaired. One of the radio tagged fish swam back into the cage and was removed along with two other visible implant tagged fish which had not left the cage. These fish were transferred to a flowing channel, but were found dead later that day and were removed.

The other two radio-tagged fish were tracked for the rest of the day, each moving up and down the Millhead. Each fish was sighted regularly throughout the day and it became obvious that neither of the fish were behaving as would normally be expected. By late afternoon the signal from each radio tagged fish indicated that the fish were stationary in different weed beds in the Millhead. Two possibilities relating to this behaviour were considered. One possibility was that the injured and exhausted fish had become trapped in the weed bed and had died there. The second was that the fish had selected dense weed cover as a safe place to rest, out of sight of avian predators, and were recovering before moving on. Neither fish showed any movement on the 15th August and both were recovered dead on the 16th August. All recaptured fish were weighed and measured, and had their tags removed, the standard procedure with fish recovered dead.

The MK II plastic cage was larger (1000 mm x 500 mm x 500 mm) than the MK I, and the mesh was coarser, 1 x 5 cm slots, allowing more flow to pass through the cage. A flap was incorporated in the top of the cage, in order that the door could be tied off securely before the fish were placed in the cage (Plate 3.26i). The MK II cage was designed to reduce the possible effects of the cage.

The main aims of the release cage are to allow the fish time to recover from tagging stress, generally settle down, and be released with a minimum of disturbance in a healthy, unstressed condition, with the opportunity to exit as a shoal. This study has shown that retention in the MK I cage for 45 hours under sub-optimal conditions was counterproductive, resulting in the release of stressed and injured fish. In future all handling and retention times should be kept to a minimum. The release cage should be positioned in the most suitable place available that will satisfy the aims of the study, whenever possible in an area shown to be suitable by the presence of adult dace.

Tagged fish were observed exiting both release cages as a shoal on several occasions. The rapid, immediate dispersal away from the release site seen in earlier studies was not observed in fish released from the cage. Retention time in the release cage should be long enough to allow complete recovery, and at least 12 hours, but kept to a minimum to reduce any damage associated with confinement, in no circumstances should retention exceed 48 hours.

Plate 3.26i. MKII release cage, with door half open. By allowing the door to fall to the river bed by remotely releasing the door string, shoals of fish were released into the river with a minimum of disturbance.

3.27 Pike predation

Dace in the River Frome constitute the principal prey species of the pike (*Esox lucius* L.) (Mann & Mills, 1986). It was considered possible that during the course of the study, a pike would eat one or more radio-tagged dace. The aims of this experiment were to examine the effects of predation of a radio-tagged dace by a pike, on signal reception, and to examine the external surface of the tag for damage caused during a period of time in the digestive system.

The damage incurred by the tag during the pike attack, both crush damage and puncture of the waterproof coating, were considered to be chance events, ranging from no effect to complete destruction. Consequently, it was decided to bypass this stage of the predation event and introduce the tag directly into the stomach of the pike.

In order to expose the tag to the same gastric conditions created by such a predation event, it was necessary to insert a dead dace of an appropriate size along with the tag.

A female pike, over one metre in length (Plate 3.27i), was caught by angling from the River Frome on 13 March 1995, and retained in an experimental channel (Chapter 2.23) (Channel 5, 20 m x 1 m x 0.5 m). At 11:45 on 16 March a length of plastic pipe (length 500 mm, diameter 50 mm) was inserted into the throat of the pike and a dead dace (245 mm fork length) fitted with a radio-tag was pushed through the pipe, into the stomach of the pike. The radio-tag was attached to one end of a piece of fishing line, and a small piece of balsa wood was attached to the other. This balsa "float" and attached line were left trailing from the mouth of the pike, in order to monitor the progress of the tag through the digestive system and to aid retrieval of the tag at the appropriate time.

Plate 3.27i. Pike used to test the possible effects on a radio-tag of the predation of a radio-tagged dace. Signal parameters were unchanged throughout the experiment.

The strength of the signal immediately after insertion did not appear to be attenuated by the body of the pike. The signal parameters (strength, frequency and pulse rate) were checked at regular intervals.

The radio-tag was removed from the stomach of the pike at 09:55 on 20 March, by grasping the balsa "float" and gently withdrawing the length of fishing line. Very little pressure was required in order to remove the tag in this way. The pike showed no external signs of discomfort during the retrieval of the tag, and was returned to the East Stoke Millstream immediately after the tag was recovered.

No change in any of the signal parameters was observed during the course of the experiment. Upon examination under a microscope the coating of the tag appeared to be undamaged, apart from two small scratches. These were probably caused during an initial, unsuccessful insertion of the tagged fish into the pike's stomach without the tube, during which the tagged fish was ejected by a flick of the pike's head. The balsa float moved closer to the mouth of the pike on days one and two, but no further progress was seen, indicating that the tag had come to rest somewhere in the digestive tract.

Predation of a radio-tagged dace by a pike during the study, could therefore result in the movements of a pike being tracked, with no change in any of the signal parameters, and hence no remote indication to the tracker. The inserted transmitter was neither regurgitated nor defecated during the study, and it seems likely that a naturally ingested tag could be similarly retained. As a result, all visual sightings of radio-tagged dace should be recorded as evidence of the identity of the fish being tracked. Should any radio-tagged dace apparently show a sudden change in behaviour, favouring habitats normally associated with pike, appropriate efforts should be made to identify the fish being tracked.

3.3 Results

3.31 Fish details

Radio-tracking and other movement data are often presented graphically, and in many ways a chart is a neat and concise technique for presenting such data. However, it can be difficult to portray some of the subtleties of the behaviour of tagged individuals, particularly their position in relation to specific habitat features. As these data often provide clues to the underlying causes influencing the observed movements, they will be presented below for each fish tagged, in the form of a written description.

FISH NUMBER 1995-1

Released 10 February 1995, East Stoke Millhead. Figure 3.3i

The radio-tagged fish, thought to be a female due to its plump condition, initially remained in the release cage for 1 hour, before moving steadily upstream over 700 m to an area of slack water at the mouth of Belhuish ditch, on the outside of a sharp bend. By 13 February the fish had reached Tryon's hut pool, 1500 m upstream of the release point, and was radio-located the following day out of the main channel, in a ditch on the outside of a bend, which is separated from the main river during normal flow conditions. The fish remained in this area for the next four days, before being both visually and radio-located, in a shoal, in the Wool Stream at Bindon, almost 3000 m upstream of the release point, on 19 February. On 24 February, the radio-tagged dace and 29 of the accompanying individuals were captured by electrofishing, weighed, measured, and where possible sexed using external characteristics, before being returned. The radio-tagged fish, now confirmed as being female by its external characteristics, was both visually and radio-located on a daily basis in this area of the Wool Stream, and on each occasion was closely associated with other dace. On 12 March the radio-tagged fish was radio-located in the Bindon Millstream, in a position adjacent to that occupied in the Wool Stream. Under normal circumstances, in order to reach this position, the fish would have had to drop back down the Wool Stream into the River Frome, and enter the Bindon Millstream. However, in this instance a substantial volume of water was overflowing from the Bindon Millstream, and flowing into the Wool Stream, and it seems likely that the fish used this route between the two streams. The tagged fish was radio-located in this area regularly during the next 16 days, among a large aggregation of several hundred dace, some of which appeared to be spawning on gravel in fast flowing water. On 29 March no dace were present in this area, and the radio-tagged fish and 6 untagged dace were visually located 40 m further downstream in the Bindon Millstream. The small group of fish remained in this area for a further twelve days, before the radio-tagged individual, now spent, was recaptured using rod and line on 12 April. The radio-tagged fish was located for the final time on 18 April, at the upstream confluence of the Bindon Millstream and the River Frome.

FISH NUMBER 1995-2

Released 10 February 1995, East Stoke Millhead. Figure 3.3i

This dace remained in the cage for two hours, before moving upstream to the confluence of the East Stoke Millstream and the River Frome. The following day the fish had moved further upstream and occupied a position on the outside of the bend, adjacent to Belhuish ditch. The tagged dace was radio-located out of the main river channel, in Belhuish fen, on 21 February. The fish remained in this area until 25 February, after which the fish was not located until 14 March, by which time it had moved upstream, and was in the same shoal as fish number 1995-1, in the Bindon Millstream. The fish remained in this millstream until 17 March, after which it was not found again.

FISH NUMBER 1995-3

Released 13 February 1995, River Frome, East Stoke. Figure 3.3ii

One of two fish released in the River Frome, this fish remained in the vicinity of the cage for an hour after release, before moving off rapidly downstream, and contact was lost. Despite an extensive search the fish was not re-located until 22 February, when it was discovered in a ditch adjoining a small tributary stream almost 7000 m downstream of the release point. The fish left the ditch, and moved over 200 m further up the tributary on the 28 February, being located in this area for the final time on 5 March.

FISH NUMBER 1995-4

Released 13 February 1995, River Frome, East Stoke. Figure 3.3ii

The second fish released in the main River Frome, this fish also circled the release area before moving rapidly downstream. On the day after release, the fish was radio-located on the outside of sharp bend almost 900 m downstream of the release point. On 16 February, during a flood, the radio-tagged dace was radio-located continuously for one hour in water 60 cm deep, out of the main river channel, swimming around an area, which is a meadow under normal river conditions. The following day the fish was again out of the normal river channel and occupied a position in an incomplete ox-bow lake. On 17 February the fish was found in "Luckford Lake", a tributary stream, almost 1 km upstream of the confluence of this tributary with the main River Frome, 2400 m from the release point. Further radio-locations of this fish were made in this stream up until 28 February, after which time the fish was not found.

FISH NUMBER 1995-5

Released 9 March 1995, East Stoke Millhead.

After exiting the release cage immediately, this fish initially moved downstream 5 m, before moving upstream steadily for a short distance and remaining in this area for the rest of the day. The following day the fish was visually and radio-located in the main River Frome, 200 m downstream of the East Stoke Flume, and it seems likely that the fish moved upstream and out of the East Stoke Millstream, before dropping down the main river. This fish moved gradually downstream during the day, but could not be located the following day. An extensive search of the main River Frome failed to locate this fish until a month later when it was found at the mouth of Goldsack's Stream, over 5500 m downstream of the release point. The fish was radio-located in this area for the final time on 4 May, and was not found thereafter.

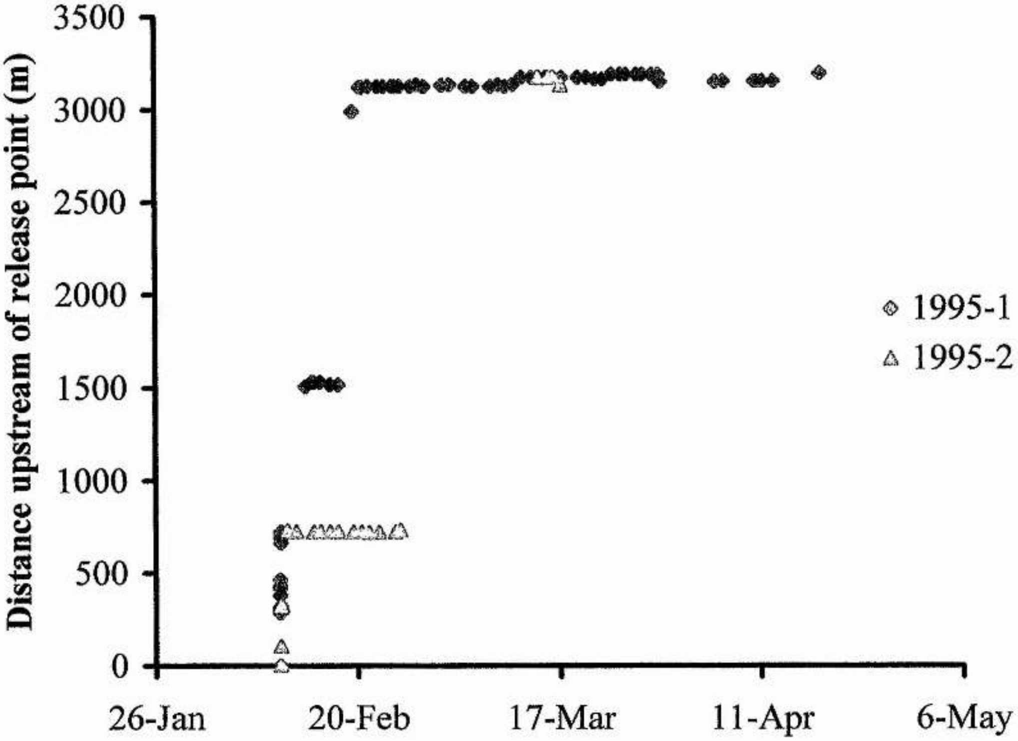

Figure 3.3i. Movements of 2 dace released in the East Stoke Millstream, Feb. 1995

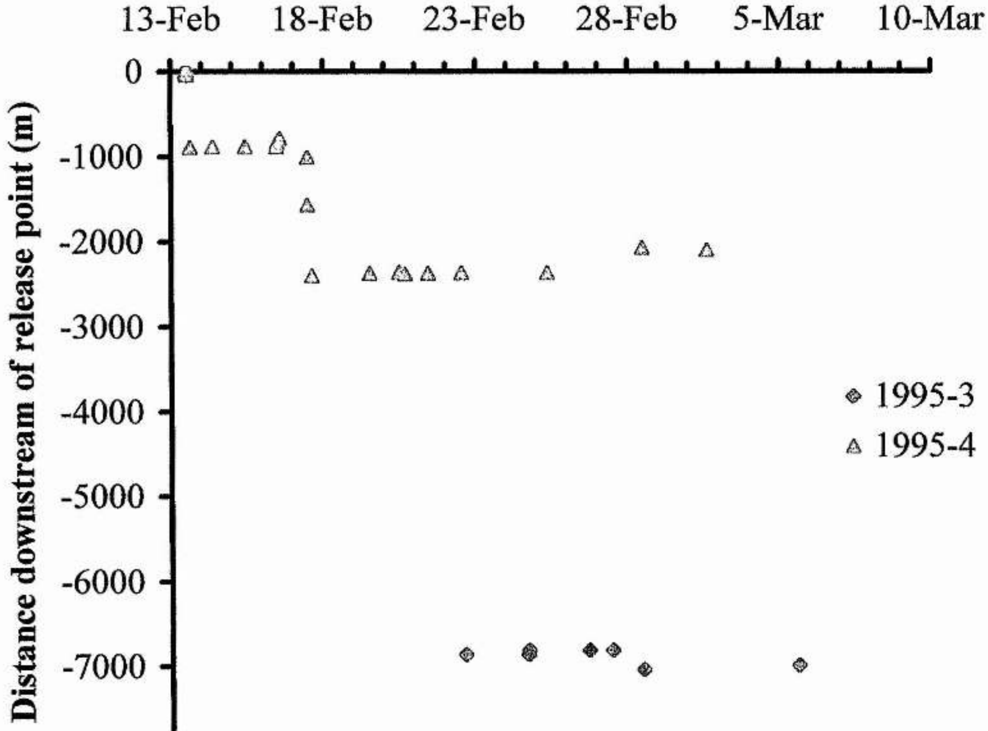

Figure 3.3ii. Movements of 2 dace released in the River Frome, Feb. 1995.

FISH NUMBER 1995-6

Released 9 March 1995, East Stoke Millhead.

The initial movements for this fish were the same as those for fish 1995-5 with which it was released, however it was still present in the East Stoke Millstream the day after release. The fish could not be found the following day, and extensive searches of the main River Frome (Wool to Wareham), East Stoke Millstream and Bindon Millstream, failed to locate the fish, and no further records were made.

FISH NUMBER 1995-7

Released 3 May 1995, East Stoke Millhead.

The fish left the release cage shortly after the door was opened, and was radio-located and visually observed in the East Stoke Millstream regularly over the next few days. During the evening of 9 May, the tagged fish was radio-located in the main River Frome, approximately 300 m upstream of the position it had occupied during the day. The following morning, visual and radio-locations showed that the fish had returned to the same position within the East Stoke Millstream. This diel migration, between the same two distinct, separate sites was observed on four consecutive nights. Thereafter, little movement was observed, and the radio-tag was retrieved from the bed of East Stoke Millstream on 22 May.

FISH NUMBER 1995-8

Released 3 May 1995, East Stoke Millhead.

This fish was also regularly radio-located and visually observed in the East Stoke Millstream during the study and also carried out regular diel migrations between different sites. On the first three nights the tagged fish moved upstream during the evening, and occupied three different positions in the East Stoke Millstream, before returning to the same daytime position by morning. Over the next 8 nights, other smaller diel migrations, including three consecutive downstream dusk movements to the same site were observed. On the evening of 15 May the tagged fish moved upstream around 400 m, and occupied the same position in the River Frome to that previously occupied by fish 1995-7. By the following morning the tagged individual was back near the release point in the East Stoke Millstream, and a regular diel migration between the same two distinct daylight and darkness habitats was observed on each of the following 4 days. The fish was not found after 20 May.

FISH NUMBER 1995-7B

Released 25 May 1995, East Stoke Millhead. Figure 3.3iii.

The fish moved around within the East Stoke Millstream for the first two days after release, using two different sites on a number of occasions. During the evening of 27 May, the radio-tagged fish moved upstream and occupied, throughout the night, the same position in the River Frome used by both fish numbers 1995-7 and 1995-8 (Night site 1). At dawn the fish moved downstream, and was radio-located the following day in the East Stoke Millstream, at the same position used on a number of previous occasions (Day site 1). During the evening the fish once again moved upstream to Night site 1, however at dawn, the fish moved further upstream, and was not located again until 31 May, in a position over 700 m upstream of the release point (Night site 2). The radio-tagged fish remained in this area until dawn on 2 June, at which time it moved downstream and re-entered the East Stoke Millstream, occupying a new position almost 50 m upstream of the release point (Day site 2). During the course of the next 16 days the radio-tagged individual moved between Day site 2, Night site 1 and Night site 2 almost exclusively, with the movements between sites being closely linked with dawn and dusk. There were at least 5 complete diel migrations between Day site 2 and Night site 1, interspersed with three visits to Night site 2. The last record was made on 18 June.

FISH NUMBER 1995-9

Released 6 July 1995, Channels.

This radio-tagged dace was released by lifting the board at the downstream end of the channel in which it was being held. Consequently the fish moved downstream, out of the channel, and through the pipes which carry the channels run-off under the East Stoke Millhead. The tagged fish was observed along with five un-tagged individuals, 5 m upstream of where the channels run-off meets the Eel Trap Pool. The channel at this point was densely vegetated and the fish appeared to be unable to continue downstream easily. Later the same day the radio-tagged fish had moved back upstream and was visually observed and radio-located at the downstream end of the pipes, along with a small shoal of other dace. The following day the radio-tagged fish was radio-located on several occasions, and on each it appeared that the fish was actually inside the pipes under the Millhead. The fish could not be found on 8 July, despite a thorough search both upstream and downstream of the last known position and more widespread searches on each of the following three days also failed to locate the fish. The radio-tagged individual was visually and radio-located in the River Frome on 12 July, along with a shoal of approximately 25 dace and 5 roach, 85 m upstream of the East Stoke Flume. The fish was manually radio-located in this area on each of the next three days. However a Fixed Listening Station (FLS) at this position showed that the fish was not continually present, and another FLS further upstream showed three separate records of the fish, twice at dawn and once at dusk. On 15 & 16 July the radio-tagged fish was radio-located on many occasions in the same position in the East Stoke Millhead, with the fish arriving in the East Stoke Millhead at dawn. The following day the radio-signal was traced to a clump of weed near the edge of the East Stoke Millhead. No dace were visible in the area, and during the course of a closer inspection a pike (*c.* 350 mm, fork length) was disturbed, which moved a short distance upstream. The radio-signal also moved upstream at the same moment, and close observation over the next hour showed that the movements of the pike were now being tracked, suggesting that the pike had eaten the radio-tagged dace. Later that day the pike moved slowly upstream, and occupied a position in the River Frome among dense vegetation, on the outside of a bend. On each of the two following days the pike was radio-located in this area again, however records from FLS's showed that the pike returned to the East Stoke Millstream around midnight on 19 July, leaving again shortly before dawn, and returning to the same position in the River Frome. Radio-signals were stationary at this position on 25 & 26 July, and the radio-tag was recovered from the riverbed on 27 July.

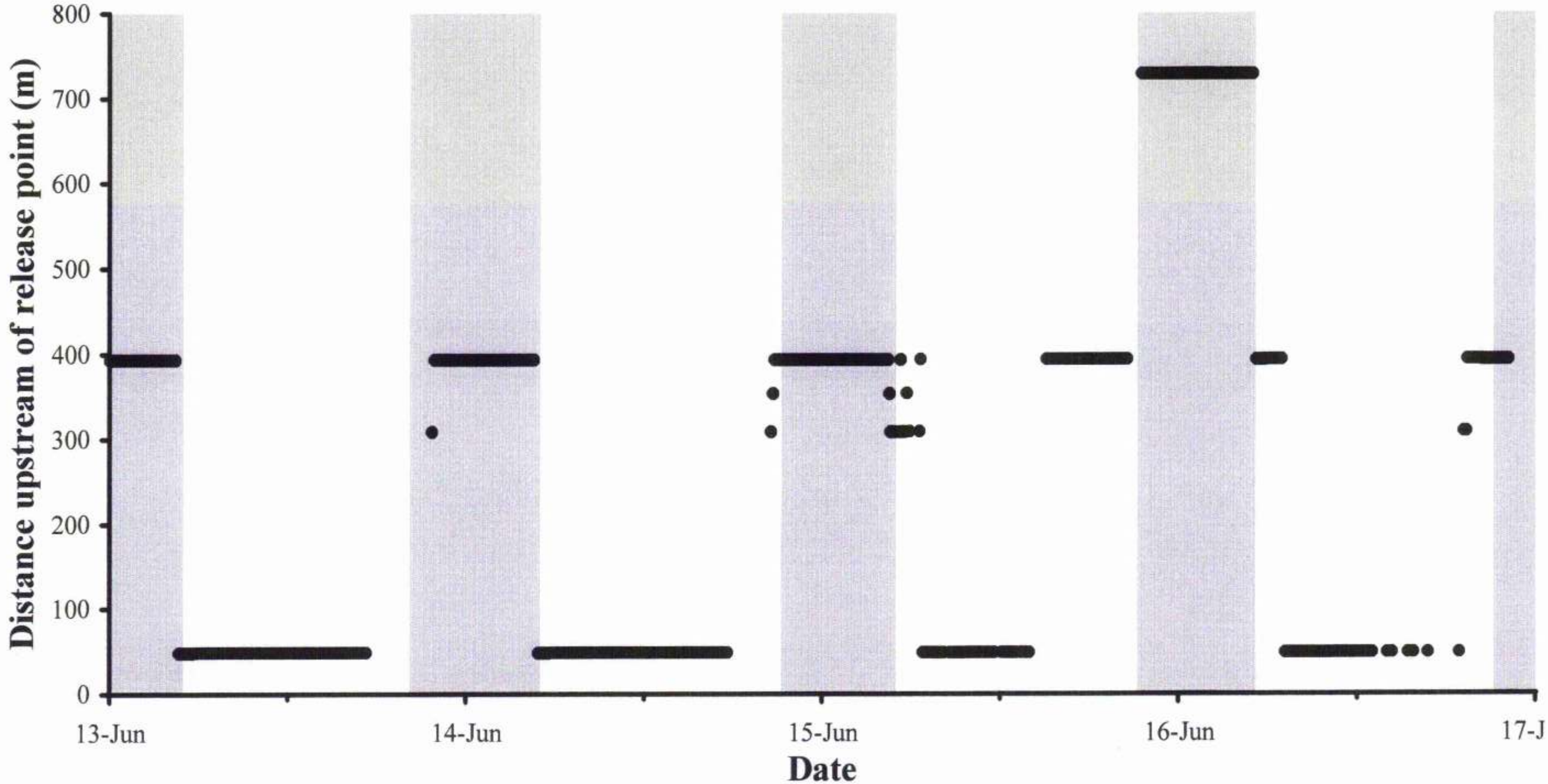

Figure 3.3iii. Diel migration of dace 1995-7b, released in the East Stoke Millhead. Bars represent darkness. Darkness, recorded by an incident light meter, corresponds to a period 30 mins before dawn & 30 mins after dusk

FISH NUMBER 1995-10

Released 11 September 1995, East Stoke Millhead.

This fish was released accidentally when the string holding the release cage door was allowed to become slack. Consequently the fish escaped into the river before the full settling period had elapsed. The tagged individual moved upstream initially, but was still within the vicinity of the release cage two hours after release. The following day the fish was found almost 900 m upstream of the release point, in a fast flowing run. The radio-tagged dace remained in this area until 14 September, and was relocated over 700 m further upstream, on the outside of a sharp bend, on 18 September.

FISH NUMBER 1995-9B

Released 12 September 1995, East Stoke Millhead.

After moving out of the release cage shortly after the door was opened, this fish moved upstream and was visually and radio-located in a shoal with 10 other fish, 15 m upstream of the Iron Hatch. The radio-tagged fish remained in this area for the rest of the day, and was also present on all tracks the following day. On 14 September the radio-tagged individual had moved further up the East Stoke Millstream and was located 31 m downstream of the stile, along with fish number 1995-1b. Over the course of the next 24 days the tagged dace was radio-located regularly, each time being between the Iron Hatch and the stile. The fish was commonly associated with fish number 1995-1b and visual observations showed that the radio-tagged fish were always with other adult dace. At no time during the observation period was the tagged fish observed outside the East Stoke Millhead. The radio-tagged dace was not located on or after 25/10/98.

FISH NUMBER 1995-1B

Released 12 September 1995, East Stoke Millhead.

This fish, released with fish number 1995-9b also spent the majority of the track duration in the East Stoke Millhead. However, the fish did leave the Millhead for an extended period from 10-12 October. During this period the radio-tagged fish carried out a diel migration between a daytime position just upstream of the East Stoke Flume, and the same night position as used by fish numbers 1995-7, 1995-8 and 1995-7b. On 13 October the tagged individual returned to the East Stoke Millhead, where it remained until the last track on 17 November.

FISH NUMBER 1995-2B

Released 23 December 1995, East Stoke Millhead.

Having left the release cage immediately, this dace moved rapidly upstream, covering over 1000 m in the first five hours. The following day the fish was radio-located in the lentic, downstream end of a millstream on the north bank at Bindon. The fish was radio-located on a daily basis in the same section of this millstream up until 22/2/96. In the early part of this period the signal moved in response to bankside disturbance, and on one occasion there was a violent swirl, caused by a large fish, along the bearing of the strongest signal. Later in the study period, deliberate attempts to move the tagged "fish" using disturbance and electrofishing failed, leading to the conclusion that the tag had been shed. The nature of the habitat and responses of the tagged fish to disturbance suggest that the radio-tagged dace may have been eaten by a pike during the early part of the observation period.

FISH NUMBER 1996-6B

Released 21 January 1996, East Stoke Millhead.

After moving rapidly upstream after release, the radio-tagged individual stopped in Belhuish pool, on the outside of a sharp bend, close to the confluence of Belhuish ditch and the River Frome. The fish was radio-located in this area until 27 January, and on one occasion was seen "hiding" in a tussock of grass, in around 40 cm of water on a flooded field margin.

FISH NUMBER 1996-9B

Released 26 January 1996, East Stoke Millhead.

Initially, this fish remained in the release cage despite the door being opened, and was still in the cage on the last track of the day, over two hours after the door was lowered. The following day, the fish was radio-located 1500 m upstream of the release point, on the outside of a sharp bend, adjacent to the mouth of slow flowing field drainage ditch. On 28 January the signal was very weak from the south bank, but still coming from the direction of the pool. On 29 January radio-locations were carried out from the north bank, and revealed that the signal was in fact coming from behind the pool, at a 45 degree angle away from the field drainage ditch. Closer inspection showed that joining the field drainage ditch at right angles, 20 m upstream of the confluence of the ditch and the River Frome, was a small stream, later discovered to be a millstream. Radio-locations and visual observation showed that the tagged individual was in a shoal of several hundred other adult dace, over 150 m up the "Hethfelton" Millstream. The radio-tagged fish moved further upstream within this millstream, and was observed with a large shoal of adult dace in a sharp bend, immediately downstream of an extensive area of riffle. On 22 February the radio-tagged individual was still present on this bend in the "Hethfelton" Millstream, however during the course of tracking the fish, a cormorant (*P. carbo*) appeared in the pool, and was observed eating dace. The radio-tagged individual and several hundred other dace were observed moving upstream, away from the bend at this time. The cormorant quickly became aware of my presence, and regurgitated at least four dace before flying off. After the departure of the cormorant, the tagged dace was radio-located around 200 m upstream of the bend in the "Hethfelton" Millstream. The following day the dace had returned to the bend but was again 200 m further upstream on 25 February. The radio-tagged individual could not be located on or after 27 February, despite a thorough search.

FISH NUMBER 1996-1B

Released 2 February 1996, East Stoke Millhead.

This dace moved immediately downstream upon release, as far as the Fluvarium, and no further movement was observed.

FISH NUMBER 1996-1

Released 15 March 1996, East Stoke Millhead.

Immediately after release this fish headed downstream as far as the small weir in the East Stoke Millhead, before heading upstream to the confluence of the East Stoke Millhead and the River Frome. The following day it appeared at first that the radio-tagged individual had moved downstream to a position immediately below the small weir in the Millhead, however a closer inspection suggested that the strongest signal was coming from a position on the flat face of the weir itself.

As no dace were visible in this extremely unlikely situation, another explanation was required. During an initial search for the tag among the stones at the edge of the weir, the bearing of the strongest signal moved to a position coming out from the bank. It became clear that the fish carrying the radio-tag was in fact underneath the Millhead, in the pipe which carries the channels run-off into the Eel Trap Pool. The fish remained in the pipe until 25 March, after which it was not found again.

FISH NUMBER 1996-2

Released 15 March 1996, East Stoke Millhead.

Unlike fish number 1996-1 with which it was released, this radio-tagged dace moved immediately upstream on release, and was found the following day in the Bindon Millstream, over 3000 m upstream of the release point. On 17 March the radio-tagged individual had moved a short distance and was seen with large numbers of adult dace, at the same position used at the same time the previous year by fish numbers 1995-1 and 1995-2. The following day the fish was no longer present in the Bindon Millstream, and was found on 21 March on the outside of a bend 600 m upstream of the confluence of the Bindon Millstream with the River Frome. The radio-tagged fish was visually observed in the margin of a flooded field later the same day, and an attempt was made to catch the fish using backpack electrofishing equipment. Unfortunately the radio-tagged individual was not caught, however one of the accompanying fish was captured. This fish was tagged with a VI alpha-numeric tag, showing that it was tagged and released in the Bindon Millstream on 23 January 1996. The radio-tagged fish was tracked for the final time on 26 March, 70 m downstream of the bend where the recapture was attempted.

FISH NUMBER 1996-3

Released 5 April 1996, East Stoke Millhead.

After remaining in the release cage for almost six hours after the door was lowered, this fish finally exited the cage and occupied a position 50 m upstream of the cage at 14:15, and was at the same position at 21:35. At 23:20 the fish was radio-located briefly, moving rapidly downstream at the confluence of the Millhead and the River Frome. Ten minutes later the fish had returned to, and was stationary at the previously occupied position. The following day the fish was not present in the East Stoke Millhead, and a thorough search of the main River Frome and East Stoke Millstream, both upstream and downstream of the fish's last known position failed to locate the fish. There were no more records of this fish.

FISH NUMBER 1996-4

Released 13 April 1996, East Stoke Millhead.

The Fluvarium hatches were closed at the time of release, and consequently the Millhead was backed-up, and there was very little flow. The radio-tagged fish moved a short distance upstream before turning and heading downstream, crossing the small weir, which was drowned out by the backed-up water. The radio-tagged fish was visually observed in a loose aggregation with other dace and some salmon smolts (*S. salar*), with all the fish moving around slowly and circling in midwater. On one occasion the radio-tagged individual rapidly moved up in the water column and broke the surface, before returning to a position in midwater. At 19:00 h on the day of release the Fluvarium hatches were opened, and the Millhead started to flow once more. The fish immediately orientated themselves into the flow, and moved to a position just above the substratum, grouping together more cohesively than before. The radio-tagged fish remained in this area until 23:00 h on 16 April, but was located almost 150 m upstream during the early hours of 17 April. Shortly after dawn, the radio-tagged individual moved downstream, crossed the weir and moved through the smolt counter in the Fluvarium, taking up a position 20 m downstream of the bridge in the Iron Hatch run-off. The radio-tagged individual and a mixed size shoal of 16 other dace were recorded on video as they passed through the smolt counter. Later the same day the Fluvarium hatches were once again closed, backing up the water in the Millhead, and resulting in a faster flow in the Iron Hatch run-off. The radio-tagged fish immediately moved downstream to the confluence of the Iron Hatch run-off overflow and the East Stoke Millstream. Over the course of the next four days the tagged dace moved rapidly between these two positions in response to the opening and closing of the Fluvarium hatches.

FISH NUMBER 1996-5

Released 14 May 1996, East Stoke Millhead.

This fish left the cage 2 hours after the door was opened and joined a small shoal of dace 5 m downstream of the release cage. The radio-tagged fish was again in this area the following day, however a Fixed Listening Station (FLS) showed that the fish had moved into the main River Frome during the night. The same diel migration was observed the following day, however there were no further records on the FLS on any of the next three nights. The fish was again detected in the River Frome on both 19 & 20 May, but had returned to the Millhead by the evening of 20 May. The next exit from the Millhead occurred during the evening of 22 May, with the radio-tagged fish moving upstream almost 800 m, and occupying the same position as used by fish number 1995-7b (Night site 2). The tagged individual remained in this area until 25 May, but had returned, by 26 May, to the exact position in the Millhead as previously occupied. Just after midnight on 27 May the tagged dace moved downstream over 50 m, and occupied a position around 20 m downstream of the release point, returning to the previous days position the following dawn. At dusk the fish was radio-located 220 m upstream, again returning to the daylight position at dawn. No substantial diel migrations were observed on either of the following two nights, however another dusk upstream-dawn downstream cycle was observed on the night of 30/31 May. No diel migration was observed the next night, however on each of the following 5 nights the tagged fish moved downstream to the same site during the night, occupying a variety of daytime positions. At dusk on 6 June the fish left the Millhead, and again moved upstream almost 800 m, occupying the same position as on 22-25 May. Several relocations were carried out over the period 7-10 June, before the tagged fish settled in one area during the evening of 10 June. Diel migrations, covering a distance of around 100 m between the same two sites were carried out on each of the following 9 days, with the fish generally spending the night in "Hedgeman's Pool" and moving upstream onto an extensive riffle during the day.

FISH NUMBER 1996-6

Released 13 June 1996, East Stoke Millhead.

Released during darkness, this fish moved rapidly upstream, and had reached a position 315 m upstream of the release point during the first hour. By the following morning the tagged individual had reached a position almost 1000 m upstream of the release point, and was located in this area until the final track on 21 June.

FISH NUMBER 1996-7

Released 24 August 1996, East Stoke Millhead.

Once the fish had exited the release cage it moved upstream a short distance, and occupied a position 37 m upstream of the release point. Just before midnight, and again at dawn, the fish was radio-located a further 28 m upstream, however it had returned to the position used on the previous day sometime between dawn and the next track at 13:35. On 27 August the radio-tagged dace was located, during the day, 85 m upstream of the release point. The fish moved 20 m downstream at dusk, and was again 85 m upstream of the release point at 08:20 the following day. Another short but complete downstream diel migration was observed on 28/29 August. The final observation of this fish was made on 2 Sep.

FISH NUMBER 1996-8

Released 24 August 1996, East Stoke Millhead.

After moving upstream rapidly since release, this fish was radio-located for the final time on 26 August, almost 1600 m upstream of the release point. Extensive searches failed to relocate the fish.

FISH NUMBER 1997-5

Released 12 March 1997, River Frome, Wareham.

Released at Wareham Quay, this fish moved immediately upstream out of range and was not relocated.

FISH NUMBER 1997-2

Released 19 March 1997, East Stoke Millstream.

Having been caught and released at the East Stoke Millstream spawning site this spent (male/female) dace moved upstream towards the Crump weir several times before moving off rapidly downstream and entering the River Frome. The radio-tagged individual was relocated later that day in a large pool over 1500 m downstream of the release point. The day after release, the tagged dace was visually and radio-located in Luckford Lake Stream, a tributary of the River Frome, 448 m upstream of the confluence. The fish was visually and radio-located in this area on a daily basis until 18 April, and on each occasion was associated with other dace, often in large numbers.

FISH NUMBER 1997-3

Released 19 March 1997, East Stoke Millstream.

This radio-tagged dace also approached the weir several times after release before moving off rapidly downstream, exiting the East Stoke Millstream, and pausing for the first time in the same large pool as fish number 1997-2. The following day, this fish was also observed in a shoal of un-tagged dace in Luckford Lake Stream, 32 m downstream of the shoal containing fish number 1997-2. Unlike fish number 1997-2, this dace did not remain in this section of Luckford Lake, but instead gradually moved further upstream within this tributary. This fish was visually observed, and appeared to have a fungal infection on 5 April, and was found dead on 7 April.

FISH NUMBER 1997-4

Released 19 March 1997, East Stoke Millstream.

The immediate post-release behaviour of this fish was the same as fish numbers 1997-2 and 1997-3, stopping for the first time over 1500 m downstream of the release point. The following day this fish had also continued downstream, and was radio-located and visually observed in a large shoal downstream of Holme Bridge. The fish remained in this area until 24 March, before moving still further downstream, and moving into the downstream end of a tributary, "Goldsack's" Stream. Visual observations were not possible in this tributary due to the turbid nature of the water, however when the fish was recovered from "Goldsack's" stream by electrofishing on 8 April, it was found to be in a large shoal of adult dace.

FISH NUMBER 1997-6

Released 19 March 1997, East Stoke Millstream.

This radio-tagged individual behaved in a similar manner to fish numbers 1997-2/3 & 4 with which it was released, however this dace only paused for a short period in the pool 1500 m downstream of the release point. Leaving the other radio-tagged dace with which it was released behind, this fish continued downstream and had reached a position 2950 m downstream of the release point within two hours of leaving the release cage. This fish was not located again, despite a thorough search from East Stoke to Wareham.

FISH NUMBER 1997-1

Released 21 March 1997, Iron Hatch run-off.

Captured and released in the Iron Hatch run-off, this dace moved upstream and spent the majority of the first three days in the Eel Trap Pool, and in a shoal at the downstream end of the pipes carrying the Channels run-off under the Millhead. The tagged individual moved downstream on 24 March, and occupied a number of positions in the Iron Hatch run-off until the last track on 26 March.

FISH NUMBER 1997-7

Released 21 March 1997, Iron Hatch run-off.

This radio-tagged dace also moved upstream on release, and was visually observed and radio-located with a shoal at the downstream end of the pipes which carry the Channels run-off under the Millhead. The following morning the fish was radio-located in the East Stoke Millhead, and was tracked in this area again on both 23 & 24 March. On the morning of 25 March the tagged individual had returned to the Iron Hatch run-off, and was radio-located a short distance upstream of the release point. On 27 March the fish was observed and radio-located in a small shoal at the downstream end of the pipes which carry the Channels run-off under the Millhead, and the tagged individual remained in this area, always with other dace, until 10 April. During the evening of 10 April the radio-tagged dace moved downstream, and occupied a number of different positions in the Iron Hatch run-off until the last track on 17 April.

3.32 Summary

The details of all dace tracks are given in Table 3.3a. Between February 1995 and March 1997 a total of 32 dace were radio-tagged and released. Of these, 22 were released at the same site in the East Stoke Millhead, four in the East Stoke Millstream, two in the Iron Hatch run-off, a side branch of East Stoke Millstream, two in the main River Frome at East Stoke, one was released from the channels, and one in the River Frome at Wareham. All fish were released near their point of capture, except the two fish released in the main River Frome at East Stoke, which were captured in the East Stoke Millstream.

During the study 6864 radio-locations of tagged dace were made, many of which were visually confirmed. Radio-tagged dace were tracked over a period covering 16308 hours, with a mean of 526 ± 162 (95 % C.L.) hours per fish (Table 3.32a). The total minimum distance covered by radio-tagged dace was over 109 km, however this figure is likely to be an underestimate, as some of the lost fish are thought to have moved beyond the study area.

Twenty of the fish were last recorded at a position upstream of their release point, however those which moved downstream tended to cover greater distances, resulting in a negative mean net movement (Table 3.32a). The maximum distance upstream of the release point that a radio-tagged dace was located was 3.8 km and the maximum distance downstream was 7.0 km. The maximum rate of movement recorded was 5.1 km h^{-1}, however the mean maximum rate was much lower at 1.6 ± 0.6 km h^{-1} (95 % C.L.).

Fish No.	Release date	Rel. point	1st m'ment >50m	Total time (h)	No. of Rec's	Total dist. (m)	Net m'ment (m)	Max. range (m) Up	Max. range (m) Down	Max. rate (mh^{-1})
95-1	10/2/95	ESMH	u/s	1604	76	3344	3170	3170	0	1050
95-2	10/2/95	ESMH	u/s	838	37	3240	3130	3170	0	322
95-3	13/2/95	FROME	d/s	482	24	7310	-7040	25	-7040	180
95-4	13/2/95	FROME	d/s	360	27	3093	-2101	10	-2400	395
95-5	9/3/95	ESMH	u/s	1347	17	6413	-5505	300	-5505	4800
95-6	9/3/95	ESMH	u/s	24	12	561	115	135	0	4800
95-7	3/5/95	ESMH	u/s	460	116	4269	21	402	0	5100
95-8	3/5/95	ESMH	u/s	399	761	8409	353	413	-62	2925
95-7b	25/5/95	ESMH	u/s	575	3232	15199	393	728	-72	5100
95-9	6/7/95	CHAN	d/s	478	436	3595	425	710	-150	1788
95-10	11/9/95	ESMH	u/s	403	1013	4545	1965	2210	0	1800
95-9b	12/9/95	ESMH	u/s	1005	65	1951	35	285	-21	216
95-1b	12/9/95	ESMH	u/s	1423	85	2879	95	440	-37	376
95-2b	23/12/95	ESMH	u/s	1414	66	3150	3030	3055	0	1200
96-6b	21/1/96	ESMH	u/s	143	14	845	815	820	0	120
96-9b	26/1/96	ESMH	u/s	719	38	2070	1890	1890	0	1000
96-1b	2/2/96	ESMH	d/s	168	16	99	-99	0	-99	20
96-1	15/3/96	ESMH	u/s	233	27	1067	-45	335	-140	700
96-2	15/3/96	ESMH	u/s	264	21	4500	3680	3790	0	720
96-3	5/4/96	ESMH	u/s	15	24	592	40	311	0	1626
96-4	13/4/96	ESMH	d/s	176	91	840	-110	80	-110	2700
96-5	14/5/96	ESMH	u/s	914	239	11006	1540	1540	-30	675
96-6	13/6/96	ESMH	u/s	180	31	1615	965	1095	0	378
96-7	24/8/96	ESMH	d/s	226	34	434	40	130	0	900
96-8	24/8/96	ESMH	u/s	41	28	1629	1585	1585	0	900
97-5	12/3/97	QUAY	d/s	0	3	65	65	65	0	420
97-2	19/3/97	ESMS	d/s	713	79	3331	-3049	10	-3084	1440
97-3	19/3/97	ESMS	d/s	449	44	4022	-4004	0	-4004	1437
97-4	19/3/97	ESMS	d/s	479	59	4956	-4676	0	-4681	1440
97-6	19/3/97	ESMS	d/s	2	6	2950	-2950	0	-2950	3336
97-1	21/3/97	IH	d/s	129	44	395	-43	51	-65	240
97-7	21/3/97	IH	u/s	645	99	1509	-94	180	-121	360
Total				16308	6864	109883	-6364	26935	-30571	48464
Mean				526	221	3545	-205	869	-986	1563

Table 3.32a. Summary of the movements of all radio-tagged dace. ESMH = Millhead, CHAN = Channels, QUAY = Wareham and IH = Iron Hatch.
u/s & d/s correspond to upstream and downstream respectively.

Of the 30 radio-tagged dace released near their capture sites, 19 (66%) left this reach of the river (> ± 500 m) during the observation period. In addition, a further 3 fish (10%) were lost within 24 hours of release, and were not relocated despite extensive searches. It seems likely that these fish had in fact left the study area. Thus, if the three "lost" fish are excluded, the probability of a fish leaving the reach in which it was released was 0.70 ± 0.18 (95% C.L.). Consequently, the hypothesis that the dace have a limited home range and remain within a short section of river throughout the year was rejected.

The rolling programme of release ensured that the whole year was covered, with data being collected during each calendar month (Table 3.32b). Diel migrations of radio-tagged dace were only observed during the six consecutive months between May and October inclusive (Table 3.32b). Seven of the twelve fish at liberty during this period exhibited some form of diel migration between two distinct sites, with the movements being closely linked with dawn and dusk. Outside this period no daily migrations were observed. Of the five fish in which diel migrations were not observed, three were lost before nighttime observations were carried out. Therefore the probability of a dace at liberty during the period between May and October inclusive carrying out diel migrations is 0.78 ± 0.28 (95% C.L.). Consequently, the hypothesis that within their home range, any daily movements were temporally unpredictable, and therefore did not constitute migrations was rejected. Further, individual adult dace re-used the same positions on a number of consecutive days. Indeed, each of the three dace released during May 1995 carried out diel migrations between the same two sites in the East Stoke Millhead and main River Frome, despite the fact that these sites are around 400m apart. The probability of an individual fish returning to the same position in the river on two consecutive days or nights by chance alone was extremely small. As the dace were not physically constrained in any way, theoretically any site within swimming distance was available to them. However, if we consider the most restrictive scenario, regarding only those points between the day and night sites as being "available", and set the resolution of "return" as being to within 2 m^2 of the previously occupied position, then the probability of a fish returning to the same site as previously occupied by chance is 1 in the number of 2 metre squares between the two sites. For those dace which migrated between the Millhead and the River Frome, the probability of returning by chance to the same position, ignoring the fact that they had to find and select the mouth of the Millhead (approximately one quarter of the discharge), was therefore 1 in 636. The implication of these observations was that the daily movements of dace were sometimes spatially predictable.

Of the 10 dace captured and released in the East Stoke Millhead prior to the known spawning season, none subsequently visited the East Stoke Millstream spawning site. In fact 5 of these dace moved upstream and entered other millstreams during the pre-spawning period. Consequently the hypothesis that dace captured and released in the East Stoke Millhead prior to spawning use the East Stoke Millstream spawning site has been rejected.

Neither of the dace captured in the East Stoke Millstream and released downstream of the confluence of this millstream with the main River Frome, returned to their capture site.

Fish	**Calendar month**											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1995-1		x	x	x								
1995-2		x	x									
1995-3		x	x									
1995-4		x										
1995-5			x	x	x							
1995-6			x									
1995-7					y							
1995-8					y							
1995-7b					y	y						
1995-9							y					
1995-10									x			
1995-9b									x	x		
1995-1b									x	y	x	
1995-2b	x	x										x
1996-6b	x											
1996-9b	x	x										
1996-1b		x										
1996-1			x									
1996-2			x									
1996-3				x								
1996-4				x								
1996-5					y	y						
1996-6						x						
1996-7								y	y			
1996-8								x				
1997-5			x									
1997-2			x	x								
1997-3			x	x								
1997-4			x	x								
1997-6			x									
1997-1			x									
1997-7			x	x								
Diel?	**x**	**x**	**x**	**x**	**y**	**y**	**y**	**y**	**y**	**y**	**x**	**x**

Table 3.32b. Annual spread of observations of radio-tagged dace. Months during which diel migrations were observed are labelled "y".

At various times of the year dace showed a preference for non-main channel areas, and used tributaries, millstreams, drainage ditches and flooded field margins extensively. At least 18 of the 32 radio-tagged dace studied were located out of the main river channel at some time during the tracking period.

It was considered that the direction of the first movement of a tagged dace upon exiting the cage might provide an indication of the fish's motivation, and assist in focusing searches when searching for missing fish. The first movement of radio-tagged dace after being released was upstream on 23 out of 32 occasions (72%), however this may have been influenced by the fact the release cage itself was always positioned facing into the flow. For this reason the direction of the first single post-release movement in excess of 50 m was tested as an indicator of the last known position of the fish. If there was no correlation between the direction of the first movement in excess of 50 m and the last known position of the fish, the expected probability that they would be in the same direction would be 0.5. On 26 out of 32 occasions the direction of the first movement over 50 m was an accurate indication of the last known position of the fish, giving a probability of 0.81 ± 0.14 (95% C.L.).

3.4 Discussion

Dace were highly mobile and capable of moving around the river system rapidly. Their movements were temporally and sometimes spatially predictable. Particular areas of the river were used by many of the radio-tagged fish released, whereas others were not occupied, except in transit. The presumed implication of these observations is that some sections of the river were more suitable for dace than others. It was also apparent that the relative suitability of each habitat changed throughout the year, with some sites only being used at certain times of year.

From radio-tracking results, the year of adult River Frome dace was separated into at least three distinct, unequal sections, during each of which the behaviour of the fish was different:

Pre-spawning, mid-January to mid-March.

Fish released during this period frequently left the main river channel during periods of high flow. Movements were generally into smaller channels, particularly millstreams, most frequently upstream of the release point. Electrofishing in spawning streams during February and early March showed a predominance of males. Radio-tracking showed that some females moved in, spawned and left quickly, in either an upstream or downstream direction. Spawning occurred in fast flowing water on coarse gravel and pebbles. Diel migrations did not occur at this time of year. Angling records showed that the fish did feed during this period, and both males running milt, and females with the ovipositor visible, were caught on rod and line.

Late spring - early autumn, late March to mid-October.

During daylight dace occupied areas of moderate water velocity (*c.* 20 cm s^{-1}), with sand and gravel substrata and little or no instream cover. At or shortly before dusk the dace frequently moved to another position within the river, where they remained throughout the night. At dawn the dace regularly returned to the exact position occupied the previous day. These diel migrations were punctuated by rapid, generally short relocations. All annual growth was confined to this period (Mann, 1974) indicating a net energy gain, and suggested that the diel migration may be related to feeding.

Late autumn - winter, Mid-October to mid January.

Large numbers of dace aggregated in the slower flowing reaches of the river, particularly the tidal section. Angling catches showed that the dace continued to feed, even at very low water temperatures, however they grew very little between November and April (Mann, 1974). Diel migrations were not observed at this time of the year. During floods some adult dace left the main channel and occupied positions which were either dry or boggy during normal flows. These positions were most commonly on the outsides of bends, and were characterised by low water velocities.

The direction of the first single post-release movement in excess of 50 m was an accurate indication of the last known position of a tagged individual on significantly more occasions than would be expected by chance. Careful monitoring of the movements of tagged individuals during the early post-release period can provide information about the motivation of the individual. When fish are lost, particularly during the early post-release period, the tracker is often faced with a dilemma of where to initiate the search. The last known position is an obvious starting point, however in a linear system such as a river, the decision to go upstream or downstream is often a difficult one. The data gathered during the immediate post-release period can assist in the decision making process. Consequently, continuous tracking during the first 24 hours after release is considered to be a worthwhile use of time in future studies.

Migrations of radio-tagged dace between two distinct sites, with the movements closely linked with dawn and dusk, were observed during all months between May and October inclusive, but not outside this period. Presumably the potential benefits of such a daily migration outweigh the costs. Possible factors influencing differential habitat use of this type include differences in predation pressure, temperature, oxygen and food availability between sites. It appears that neither site, on its own, meets all the requirements of the dace during a complete 24 h cycle. Meek (1916) suggested that cyprinids exhibit an alternation between relative passivity during the day and activity at night. Helfman (1993) stated that "many fishes appear to separate the day into an active, food gathering phase and a relatively inactive, resting phase that is intimately linked with predator avoidance." It seems possible therefore that dace move to feeding areas at night, and return to resting areas during the day.

In a study of River Frome dace, Mann (1974) stated that "minimal growth occurred from November to April". The fact that all growth in dace is limited to the same period during which they undergo diel migrations may suggest that the diel migration is linked, in part at least, to food gathering. However, enhanced foraging opportunities at a particular site cannot be the only factor driving the observed diel migrations. If this were the case, remaining at the more profitable site for the whole of the 24-h cycle would result in a greater net energy gain than would be achieved by leaving and returning. Instead, there must be another contributory factor influencing the relative suitability of the two sites.

One possibility is a difference in the degree of predation risk between sites. The major predatory threat to adult dace in the River Frome is provided by pike, with dace being the most common food items found in the guts of pike in the Frome (Mann, 1982). Pike use both stalking and ambush techniques to capture prey, are generally accepted as being visual predators, and are consequently most active during daylight (Diana, 1980; Cook & Bergersen, 1988; Lucas *et al.*, 1991). If the nocturnally used sites are both more profitable in terms of food availability, and carry a higher risk of predation, then it is possible that dace might use these sites during the period when the threat of predation is diminished, i.e. at night. They could then spend the period when the predation threat is at its highest, i.e. during the day, at a "safer" location. Large piscivorous fish are assumed to affect habitat selection and food intake of prey fish (Damsgard & Ugedal, 1997). Such trade-offs between foraging and predation risk could increase the lifetime fitness of the individual by reducing the number of encounters between the potential prey fish and an active predator.

Determining the sex of a live dace was very difficult during the majority of the year. From about mid-January onwards the males started to develop tubercles all over the body. These tiny white lumps, particularly noticeable on the head and gill covers, also grew on the edges of the scales, giving the fish a distinctly rough feel, and dull appearance. The body shape of male dace however appeared to remain the same throughout the year. Female dace did not develop tubercles, and produced more mucus than normal, resulting in a smooth, slippery feel and a shiny appearance. Unlike males, adult female dace changed shape as they developed their eggs, becoming deeper bodied and often "barrel chested" in appearance (pers. obs.). Immediately prior to spawning the ovipositor could be seen protruding from the abdomen. After spawning males quickly lost their tubercles, and consequently their rough feel. Initially, spent females remained deeper bodied than the males, however having deposited their eggs, their abdomens became noticeably flaccid. During the remainder of the year, from mid-April to mid-January, male and female dace could not be reliably differentiated using external characteristics, and consequently no conclusions regarding sexual differences in dace migration can be made from fish tracked during this period.

The use by dace of non-main channel habitats was widespread, with radio-tagged fish moving out of the main channel during periods of high flow, at spawning time, during the post-spawning period and during diel migrations. River management techniques such as bank re-enforcement, straightening, dredging and weed cutting can all affect the availability and accessibility of such areas. Similarly water abstraction will alter the hydrology of the catchment, and could ultimately impact upon the fish populations by influencing the character and availability of existing non-main channel habitats.

During periods of high flow dace often moved out of the main river channel into field drainage ditches, fens, tributaries and other flooded areas, probably to avoid being displaced downstream. Many of the areas used during such conditions would be completely dry during summer low water conditions, and consequently are unlikely to be considered important fish habitat if viewed at this time. Management practices that affect the high water availability of such areas are likely to impact upon the dace population.

The apparent preference of dace for clean gravel areas in millstreams for spawning is interesting, especially considering that such areas were created by, and are maintained by man. Although similar clean gravel areas are available in tributaries, it is possible that the buffering influence of the main river results in a more stable flow, temperature and chemical regime in millstreams than can be found in tributaries. It seems likely that the conditions found in man-made millstreams are similar to those that occur in naturally braided sections of the main river. If the historical preference of dace was for clean gravel areas in naturally braided sections of rivers, it is possible that since current management techniques have reduced the incidence of such areas in the River Frome, the most suitable clean gravel areas are now found in millstreams. If the existing, now disused millstreams were allowed to fall into disrepair, become choked with weed, and ultimately dry up, it seems likely that this would have an impact on the subsequent spawning success of dace in the River Frome.

CHAPTER 4

Migrations - mark-recapture

4.1 Introduction

The marking of animals probably started as means of proving ownership, and as early as the 13th century, falconers marked their birds with name plates or bands for this purpose (McFarlane *et al.*, 1990). More recently the tagging of animals has been used for many other purposes, and providing a suitable marking technique is selected, information can be gathered relating to stock identity, movements, migration, abundance, age, growth, mortality, behaviour and stocking success (McFarlane *et al.*, 1990).

Mark-recapture, also referred to as capture-mark-recapture and capture-recapture, is a technique which is generally used to assess the size of populations. The accuracy of the estimate is likely to be influenced by the number of recaptures, the timing and location of recapture efforts, the degree of mixing of the marked individuals within the population, and the effects of the tag itself, or the attachment technique, on the behaviour or survival of the individual. Other limitations are frequently imposed by the marking technique itself, with batch marking often being the only viable technique for large numbers of individuals. In addition, the retention rate of tags or marks must be known before accurate population estimates can be made.

The majority of early mark-recapture experiments were based on the assumption that all individuals have the same catchability. More recent studies of population size have allowed for the eventuality that individuals have different capture probabilities (Chao, 1987).

A by-product of the mark-recapture population estimate technique can be the provision of information relating to the seasonal migrations of animals; indeed much of our knowledge of the long distance movements of animals comes from tagging studies (Hilborn, 1990). The technique is however limited for direct studies of migration in that, by definition, the marked individuals must be recaptured. Consequently, marked animals are only ever recaptured in areas where the recaptures are attempted, placing an obvious potential bias on the results. In addition, the release and recapture sites provide limited information, serving only as snapshots in time, and although the route between the two positions can sometimes be inferred, the timing and rate of migrations are generally not accurately discovered using this technique (although see: Hilborn, 1990; Xiao, 1996). Subsequent recaptures can continue to provide information into the future, but the potential impact of repeated capture on the migration of the individual must be considered. However, providing the limitations of the technique are accepted, valuable information relating to the migration of the marked individuals can be gathered, and aspects of the mobility of the population can be inferred.

A slight variation on the mark-recapture theme is the attachment of an externally visible tag to an animal. In this situation the individual does not necessarily need to be recaptured in order to be recognised, providing the external mark or tag is sufficiently conspicuous to be identified by the observer. Such resightings can provide ongoing multiple "recapture" information on "seasonal movements and site tenacity of individual fish." (Matthews & Reavis, 1990). Unfortunately, the more conspicuous a tag or mark is, the more likely it is to have an impact on the behaviour and survival of the individual, thus potentially biasing the results.

Another variation involves the use of passive integrated transponders or PIT tags. These electronic tags have no power supply of their own, but are energised when brought into close proximity with a reader. Once energised the tag emits a signal, which carries a unique code. The alpha-numeric code, specific to that tagged individual, is displayed on the LCD screen of the reader. The animals are captured and tagged, usually internally, with PIT tags, before being released. At a later date the identity of the tagged individual can be determined, when the PIT tag comes into close proximity with a PIT tag reader. The way in which the PIT tag and reader and tag are brought into proximity is likely to vary between animals, and may or may not involve the recapture of the individual. For example pit tag readers can be installed into the bed of shallow streams, and will detect those tags present in wild fishes which swim close to the substratum.

Although it is unclear exactly when fish were first marked for the purpose of identification, Walton & Cotton (1653) refer to ribbons being tied to the tails of juvenile Atlantic salmon (*Salmo salar*), and that these fish returned as adults, to the streams where they were first captured. Though a fictional work, the technique of marking and recapturing fish was also referred to in 20,000 Leagues Under The Sea (Verne, 1869). Mark-recapture studies of fishes can reveal information about movement, mortality and growth rate (Parker *et al.*, 1990), and variations of the mark-recapture method have been used to examine the riverine migrations of fishes including Atlantic salmon (Calderwood, 1902); smallmouth bass, *Micropterus dolomieui* (Munther, 1970); cutthroat trout, *Oncorhynchus clarki* (Heggenes *et al.*, 1991); roach, *Rutilus rutilus* (L'Abee-Lund & Vollestad, 1987); longnose gar *Lepisosteus osseus* (Johnson & Noltie, 1996) chinook salmon, *Oncorhynchus tshawytscha* (Achord *et al.*, 1996); and grayling, *Thymallus thymallus* (Kristiansen & Doving, 1996). In addition, the movements of 14 species of stream fishes in Missouri were examined by Funk (1957), from reports of tagged fish recaptured by anglers, and the home ranges of three North American stream fishes were estimated by Hill & Grossman (1987), using mark-recapture data.

There are many ways in which tags and marks can be used in order to make fishes identifiable, and these can be divided into 5 main groups:

1. Internal tags or marks
2. External tags or marks
3. Electronic tags
4. Genetic marks
5. Chemical marks

Each group of marks has its own subdivisions, and each technique has both advantages and disadvantages. It is only by weighing up the advantages and disadvantages of each type of mark for the application in question that the most suitable technique can be selected. The relative merits of the marking techniques used in this study are discussed in turn.

Appropriate marking techniques were selected in order to examine the overall hypothesis that the movements of marked dace are similar to those of radio-tagged dace.

4.2 Fin clipping

Introduction

Of all the fish marking techniques, fin clipping has been far the most popular (Stott, 1968), and has been used as a means of identification for over 100 years (McFarlane *et al.*, 1990). Calderwood (1902) refers to fin clipping studies in Scotland as early as 1829. The advantages of the technique include speed of application, permanence, low cost and a lack of adverse affects (Welch & Mills, 1981). Conversely however, O'Grady (1984), having followed the progress of clipped and un-clipped brown trout (*Salmo trutta*) released into Irish lakes, concluded that "even a single fin clip can seriously reduce survival and also retard the growth of fish." It is likely that the negative effects associated with the clipping of fins will vary between species, and could also differ between waters, individuals, fins and types of clip, thus influencing the relative suitability of the technique.

There are several ways in which a fin can be treated in order to make the fish identifiable, either as part of a batch, or as an individual. The re-growth characteristics of the fin are likely to be species specific, vary between individuals, and differ between fins. Complete removal of the fin close to the body of the fish usually prevents re-growth of any kind, and the resulting scar identifies marked fish from those individuals which are missing fins through abnormal development (Stuart, 1958). Partial removal, particularly where the proximal third of the fin is left intact, usually results in complete regeneration of the fin. However this re-growth is generally at a slight angle to the original orientation of the fin rays, and a noticeable joint can be felt between the original and re-grown portions. Individual identification can also be achieved by clipping individual fin rays in a particular sequence, and a number of combinations are possible if more than one fin is used (Welch & Mills, 1981).

Materials and methods

MARK RETENTION

In order to test the relative retention of fin clips and Elastomer tags, a group of 39 dace marked with both an anal fin-clip and two Elastomer marks, were retained in an experimental channel, and examined at intervals. The fish (size range 154 - 269 mm) were tagged on 1/3/96, and examined on 20/3/96, 12/4/96 & 18/12/96.

FIELD STUDY

An annual fin-clipping study of spawning dace in the East Stoke Millstream, has been undertaken by I.F.E. staff over a number of consecutive years. This study involved the removal of the distal portion (approximately two thirds) of one of the paired fins (pectoral and pelvic), on a four year rotation (Table 4.1). The marked fin quickly regenerated (2-3 months), but was still identifiable because the rays of the re-grown fins were noticeably kinked at the site of the clip. In subsequent years, by catching and examining a sample of fish for fin-clips it was possible to assess the relative proportions of individuals returning to the East Stoke Millstream having spawned there previously, and those spawning in the East Stoke Millstream for the first time (Plate 4.2i). In consequence, an unknown number of existing fin-clipped fish were likely to be already present in the study area.

Plate 4.2i. Examining the left pelvic fin of a dace for a fin clip. Clips appear as a noticeable kink in the fin ray, which can be felt as a ridge between the fingers.

Fin Clipped	Code	Year
Right Pectoral	RXC	1990, 94
Left Pectoral	LXC	1991, 95
Left Pelvic	LPC	1992, 96
Right Pelvic	RPC	1993, 97

Table 4.1. The four year rotation of paired fin clipping.

During the course of the present study, the annual fin clipping of spawning dace was continued, though on a much reduced scale. In addition, all fish tagged with visible implant alpha numeric (VI) tags also had the distal two thirds of the anal fin removed, in order to distinguish those tagged with VI tags from those without. A by-product of both fin-clipping studies was that should any of the fin-clipped individuals be recaptured elsewhere, at any time of the year, it was possible to gain information about the mobility of dace. To this end, all subsequent re-captures of fin-clipped dace were recorded. As fin clips are only batch marks, a limited amount of information can be gleaned from each recapture. However as all the marked fish were released in one area, any recaptures outside this area were worthy of note. Consequently, the hypothesis that dace which spawn in the East Stoke Millstream remain in the vicinity of this spawning site throughout the year was tested.

Results

MARK RETENTION

Full details of the retention of fin-clips and Elastomer marks by fish retained in an experimental channel are given in section 4.4 (this Chapter).

FIELD STUDY

In total 1014 fish (1005 dace and 9 roach) were fin-clipped during the study and released back into the river at the point of capture. Anal fin-clipped fish were all captured and released in the vicinity of East Stoke. All of the fish having one or other of the paired fins clipped were captured and released in the lower portion of the East Stoke Millstream at spawning time. Although no specific efforts to recapture the marked fish were made, a total of 88 fin-clipped fish (88 dace and 2 roach) were recaptured during the study, with 8 of the fish (all dace) having two fins clipped, making a total of 96 clip recoveries.

On four occasions during the course of the study (18 & 20/12/96, 6 & 7/3/97), a total of 27 dace were recaptured by angling from the tidal reaches of the River Frome, at Wareham, 6 km downstream of the release point. Of these, 1 had an anal fin clip, showing that it had been in the vicinity of East Stoke at some time during the previous year and 3 had one of the four paired fins clipped, indicating that each of these fish had been present in the East Stoke Millstream during a particular spawning season. One fish had both an anal fin clip and a left pelvic fin clip (Table 4.2).

As part of the ongoing study of spawning, 31, 286 & 278 dace were captured from a known spawning site in the East Stoke Millstream during March 1995, 1996 & 1997 respectively. A small percentage of each sample of fish had existing fin-clips (Table 4.2). An additional spawning site in the Bindon Millstream, over 3 km upstream of East Stoke was discovered by radio-tracking. Samples of spawning and pre-spawning dace were collected from this stream during March 1995, January 1996 and March 1996, with a small percentage of these fish also having clipped fins (Table 4.2).

It seems unlikely that the clipped fish mixed randomly within the population, particularly as the release dates were staggered over a long period of time. However, the proportions of fish displaying a clip were similar for each of the sites examined (mean = 5.9 % +/- 3.2 %, range 0-20 %), despite their differing geographical distances from the release point. On this basis, if random mixing is assumed, it is possible to carry out a very crude population estimate from those recapture data where the total number of accompanying individuals is known (Table 4.2).

Location	Date	No. of dace	Paired fin-clips	Anal fin-clips
ESMS	Mar-95	31	2	0
ESMS	Mar-96	286	6	11
ESMS	Mar-97	278	8	3
Bindon	Mar-95	176	15	0
Bindon	Jan-96	136	3	4
Bindon	Mar-96	55	0	7
Wareham	Dec-96	17	2	2
Wareham	Mar-97	10	2	0
	Total handled	989	38	27
	Clips recovered	65		
	%	6.6		
	Total clipped	737		
	Population	11214		

Table 4.2 Summary of recaptured fin-clipped dace where the total number of accompanying individuals is known.

A dace with a fully re-grown left pelvic fin-clip, indicating that it was present in the East Stoke Millstream during March 1996, was recaptured over 7 km upstream of East Stoke in the East Burton Millstream, during April 1998.

4.3 VI tagging

Introduction

Visible implant alpha-numeric tags (VI tags) are small (2mm x 1mm), thin pieces of plastic film, manufactured by Northwest Marine Technology, Inc. Each of the tags carries a three character alpha numeric code, comprising either two letters and one digit or two numeric and one alphabetical character. There are several colour combinations of both characters and background. Each code can be used to identify a fish either as an individual or as part of a batch.

The VI tag was designed to be externally visible and able to be read in situ. In order for these tags to be read they must be implanted into transparent tissue, for example between the fin rays, or into clear adipose tissue, with the most suitable location differing between fish species (Haw *et al.*, 1990). The VI tag "has the potential to become increasingly popular, since it provides a means of individual or batch identification of fish which causes minimal tissue damage during application" (Farooqi *et al.*, 1995).

The concept of the subcutaneous insertion of vinyl tags for fish identification was first described by Butler (1957). VI alpha numeric tags, in their current form, were introduced by Haw *et al.* (1990), and have since been used to tag several fish species including lake trout, *Salvelinus namaycush* and Atlantic salmon, *Salmo salar* (Kincaid & Calkins, 1992); brook trout, *Salvelinus fontinalis* (Bryan & Ney, 1994); juvenile reef fishes (Buckley *et al.*, 1994); five species of galaxiids, *Galaxias* spp. (Crook & White, 1995); Arctic charr, *Salvelinus alpinus* (Farooqi et al., 1995); brown trout, *Salmo trutta* (Niva, 1995); cutthroat trout, *Oncorhynchus clarki* (Wenburg & George, 1995) and Atlantic salmon, *S. salar* (Moffett *et al.*, 1997).

Several different tagging locations have been tested, including the preoperculum (Crook & White, 1995), anal fin (Wenburg & George, 1995) and adipose eyelid (Haw *et al.*, 1990; Farooqi *et al.*, 1995 & Niva, 1995). Tag retention appears to vary widely between sites, and between species. It also seems likely that fish size could influence tag retention. For these reasons, a suitable clear tissue site for VI tagging dace was required, as was data relating to the effect of fish size on tag retention.

The primary hypothesis of the VI tagging study was that the seasonal movements of VI tagged fish were similar to those of radio-tagged fish. It was also considered that sufficient data may be collected to allow a secondary hypothesis, that the fish captured and released along with the radio-tagged fish all remain together, as part of the same shoal, to be tested.

Materials and methods

TAGGING TECHNIQUE

The tags were supplied in gel strips containing one hundred tags and were inserted using a special injector supplied by the manufacturer. The injector was loaded by pushing the needle into the gel, taking one tag into the hollow point. The tag was removed by twisting the injector through ninety degrees and withdrawing. The hollow needle containing the tag was then pushed into the selected clear tissue site at a shallow angle, and the plunger of the injector depressed, forcing the tag out of the needle. The needle was withdrawn, leaving the tag embedded in the tissue of the fish

(Plates 4.3i & 4.3ii). Care was taken to ensure the tag was inserted the correct way up, as the characters were legible on one side only.

RETENTION STUDY

In order to assess the relative suitability of VI tagging as a technique for marking dace, a number of trials involving small numbers of captive fish were carried out.

In a preliminary study 5 dace and 3 roach were tagged with VI alpha numeric tags in the post-ocular adipose tissue on 18/11/94, and were retained in an experimental channel (see chap 2.3). Five more dace were tagged in the pre-ocular adipose tissue on 5/12/94, and retained in another channel. In another small study, started on 21/12/94 and designed to eliminate potential channel effects, five dace were tagged in the pre-ocular adipose tissue (mean fork length 210 mm), and five dace were tagged in the post-ocular adipose tissue (mean fork length 201 mm), with all ten fish being retained together in an experimental channel. The fish were recaptured from each of the channels at intervals, weighed and measured, and examined for the presence and legibility of a visible implant alpha-numeric tag.

In order to examine the effect of fish size on the retention rate of visible implant tags, 47 dace of mixed sizes (range 128 - 248 mm fork length) were tagged with VI alpha numeric tags in the pre-ocular adipose tissue on 23/11/95, and transferred to an experimental channel. All the fish were recaptured on 24/1/96, and were weighed, measured, and examined for the presence of a VI tag. The mean lengths of the two groups of fish, those which had retained the tag and those which had shed the tag, were then calculated and compared.

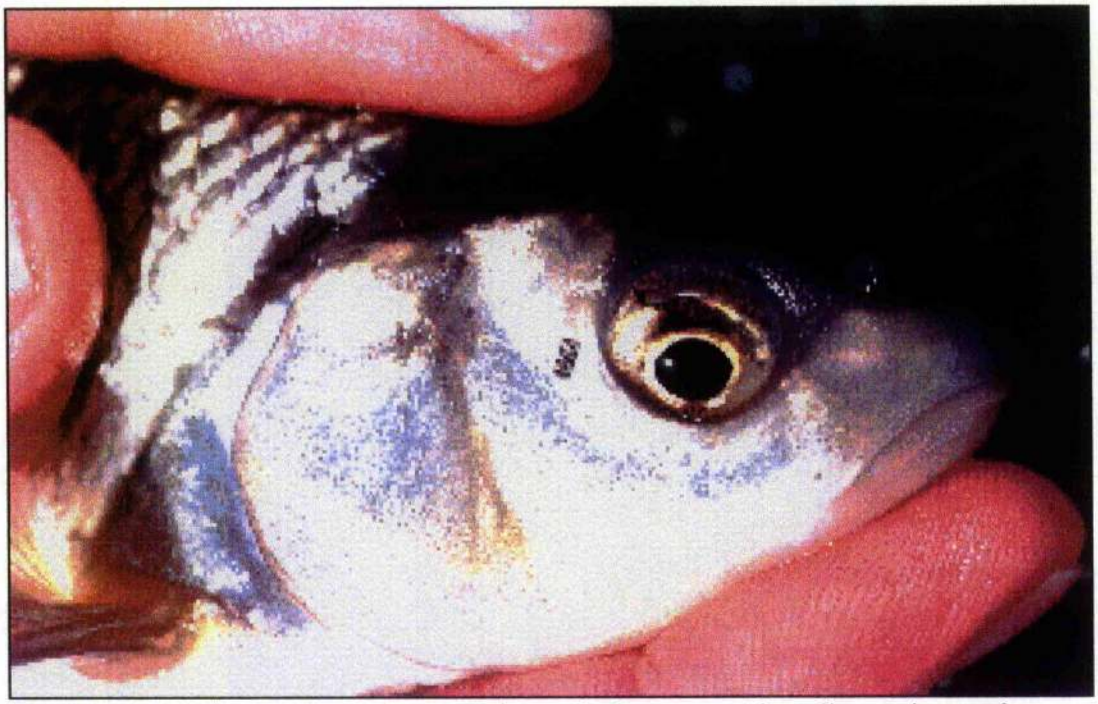

Plate 4.3i. Visible implant alpha-numeric tag in the post ocular adipose tissue of a dace.

Plate 4.3ii. Close-up of visible implant alpha-numeric tag No. D36 in the post ocular adipose tissue of a dace.

FIELD STUDY

As dace are a shoaling species, when radio-tagged fish were released it was considered that in order for them to behave normally, they should be released with a shoal. Evidence that shoaling fish have the cognitive ability to recognise and preferentially associate with familiar individuals is well documented (Magurran *et al.*, 1994; Griffiths, 1997). During the course of the study radio-tagged individuals were frequently observed, and on all occasions were in the company of other dace. However it was unclear whether or not the accompanying individuals were those with which it was first captured and released. To this end fish released with radio-tagged individuals were marked with VI tags.

In order to gain supplementary information about the movement and shoal fidelity of dace in the wild, several additional batches of VI tagged fish were released on a rolling program between 9/2/95 and 23/8/96. The length, weight and location of all subsequent recaptures was recorded.

Results

RETENTION STUDY

The numbers of fish used in the preliminary trials (5 dace and 3 roach) were too small to provide reliable results, however the trials did show that VI tags inserted in the post-ocular adipose tissue are retained, for short periods at least, by both dace and roach, and suggested that retention rate may be higher in roach than in dace after the first two months (Fig. 4.3i). The five dace tagged in the pre-ocular adipose tissue and retained in a separate channel, escaped during a flood event. One of these fish, however, was recaptured, with the tag still in place, on 29/3/95 in the Bindon Millstream, 5.8 km upstream of the point from which it escaped.

In a separate study, all five of the dace tagged in front of the eye had retained their tags at the end of the three month study period, whereas of the five tagged behind the eye, only two had retained their tags after three months (Fig. 4.3ii). Again, the results gathered from such a small sample size can serve only as a guide to the relative retention rates between the two positions.

Of the 47 dace of mixed sizes tagged in the pre-ocular adipose tissue on 23/11/95, more than half (25) had shed their tags after two months. However the mean length of the group that had shed their tags was significantly less than the mean length of those that had retained their tags (*t*-test $p < 0.001$, $df = 45$) (Fig. 4.3iii). In all, twenty eight of the dace tagged measured less than 200 mm (fork length), with all bar four of this group shedding their tags within two months. Conversely, 17 of the 19 dace 200 mm and over had retained their tags at the end of the two month study period.

FIELD STUDY

In total 703 fish were tagged with VI alpha numeric tags between 5/12/94 and 11/4/96, of which 692 were dace, with 10 roach (*R. rutilus* (L.)) and 1 rudd (*Scardinius erythropthalmus* (L.)). Thirty one different fish, all dace, were recaptured between 29/3/95 and 13/4/96, with one fish being re-captured on two separate occasions (Table 4.3). The length of time between release and recapture varied between 2 and 218 days, with a mean of 72 days. Fifteen of the recaptures were within the same area of the river where the fish was released after tagging, with a further nine occurring upstream, and eight downstream of their original release point (Table 4.3).

All bar one of the recaptures of VI tagged dace between January and the end of the spawning season, at the end of March, occurred in either the East Stoke Millstream or the Bindon Millstream, the exception being caught along with a spent radio-tagged fish in the main River Frome near the end of March, having been tagged in the Bindon Millstream the previous January. All recaptures of VI tagged dace after the end of the spawning season occurred in the East Stoke Millhead (Table 4.3). These recaptures partially reflect the targeting of recapture efforts, however, angling results suggest that adult dace were generally absent from the East Stoke Millhead during the period around spawning time. Observations also showed that the large aggregations of dace found in the Bindon Millstream from January onwards were absent from mid-April onwards. These data suggest that there are temporal shifts in habitat use by dace, specific aspects of which will be discussed in later chapters.

Despite issuing an information sheet to local anglers, detailing the position of the VI tag, no reports of VI tagged fish have been received to date.

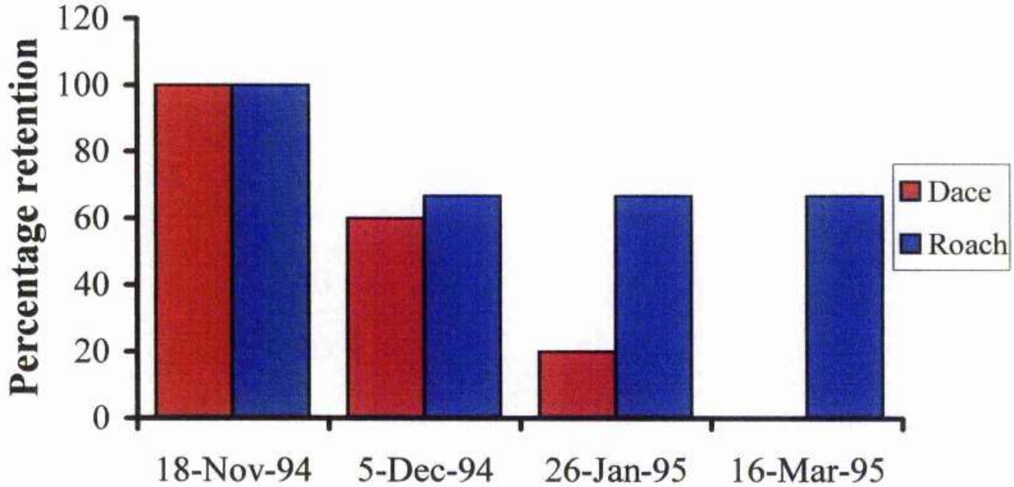

Figure 4.3i. Retention of VI tags in roach and dace.

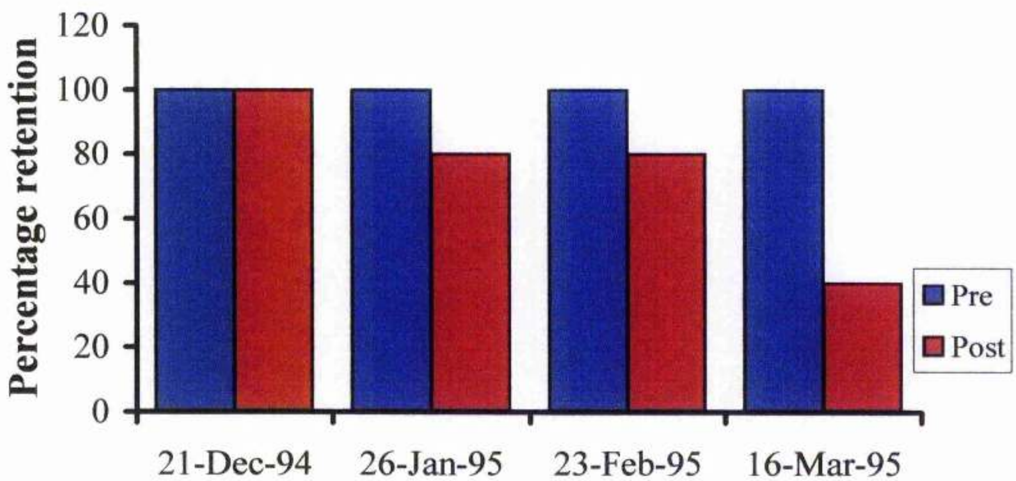

Figure 4.3ii. Retention of VI tags in the pre- and post-ocular adipose tissue of dace.

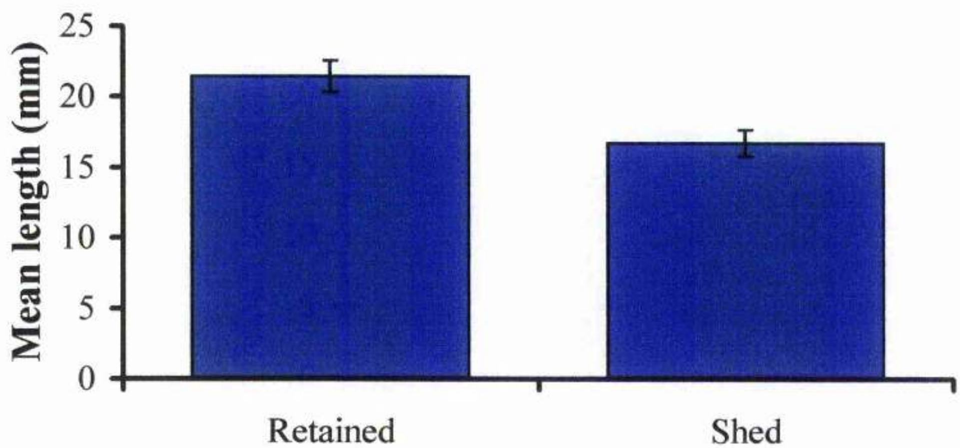

Figure 4.3iii. Mean (+/- 95% C.L.) lengths of dace retaining and shedding VI tags.

Release date	VI tag	Position	L. (mm)	Wt. (g)	Release location	Recapture date	L. (mm)	Wt. (g)	Recapture location	Time (Days)
5-Dec-94	D90	Post	223	169	CHAN.	29-Mar-95	224	138	BMS	114
9-Feb-95	D78	Post	195	96	ESMH	29-Mar-95	195	81	BMS	48
24-Feb-95	D48	Post	218	127	BMS	29-Mar-95	214	125	BMS	33
24-Feb-95	D47	Post	235	165	BMS	29-Mar-95	225	135	BMS	33
1-Mar-95	D26	Post	213	143	ESMH	29-Apr-95	212	155	ESMH	59
24-Mar-95	D18	Pre	233	151	ESMS	29-Mar-95	233	148	BMS	5
29-Mar-95	UF0	Pre	220	151	BMS	2-Nov-95	232	*	ESMH	218
17-Oct-95	E39	Pre	163	60	ESMH	2-Nov-95	156	*	ESMH	16
17-Oct-95	E42	Pre	217	140	ESMH	28-Mar-96	*	*	ESMS	163
2-Nov-95	E62	Pre	223	*	ESMH	28-Mar-96	223	*	ESMS	147
2-Nov-95	E64	Pre	162	*	ESMH	30-Nov-95	164	54	ESMH	28
2-Nov-95	E65	Pre	165	*	ESMH	1-Dec-95	166	58	ESMH	29
2-Nov-95	E85	Pre	167	*	ESMH	28-Nov-95	170	65	ESMH	26
2-Nov-95	E91	Pre	227	*	ESMH	1-Mar-96	225	155	BMS	120
2-Nov-95	E92	Pre	220	*	ESMH	28-Mar-96	220	*	ESMS	147
2-Nov-95	F11	Pre	169	*	ESMH	1-Dec-95	170	57	ESMH	29
2-Nov-95	F19	Pre	250	*	ESMH	28-Mar-96	252	*	ESMS	147
2-Nov-95	F41	Pre	229	*	ESMH	28-Mar-96	230	*	ESMS	147
2-Nov-95	F69	Pre	251	*	ESMH	23-Jan-96	246	*	BMS	82
3-Nov-95	F92	Pre	229	150	FLUV	28-Mar-96	228	*	ESMS	146
3-Nov-95	F96	Pre	224	210	FLUV	28-Mar-96	244	*	ESMS	146
3-Nov-95	F97	Pre	231	169	FLUV	30-Nov-95	231	172	ESMH	27
3-Nov-95	H23	Pre	206	135	FLUV	23-Jan-96	205	*	BMS	81
19-Jan-96	V97	Pre	207	114	ESMS	18-Mar-96	206	*	ESMS	59
23-Jan-96	H92	Pre	239	*	BMS	1-Mar-96	239	196	BMS	38
23-Jan-96	H93	Pre	204	*	BMS	1-Mar-96	204	114	BMS	38
23-Jan-96	H95	Pre	218	*	BMS	1-Mar-96	218	141	BMS	38
23-Jan-96	A02	Pre	167	*	BMS	22-Mar-96	165	52	MR	59
23-Jan-96	A06	Pre	180	*	BMS	1-Mar-96	181	85	BMS	38
23-Jan-96	A47	Pre	164	*	BMS	1-Mar-96	161	56	BMS	38
28-Mar-96	E92	Pre	220	*	ESMS	9-Apr-96	223	134	ESMH	12
11-Apr-96	N13	Pre	225	134	ESMH	13-Apr-96	*	*	ESMH	2

Table 4.3 Details of all VI tagged fish recaptured from the wild during the study period. CHAN. = experimental channel, ESMH = East Stoke Millhead, BMS = Bindon Millstream, ESMS = East Stoke Millstream, FLUV = Fluvarium & MR = Main River

4.4 VI elastomer tagging

Introduction

Dyes, paints and pigments have been used in a number of different ways to mark aquatic animals since the early part of the century, when paint was first used to mark invertebrates. (McFarlane *et al.*, 1990). In a review of around 900 published works, McFarlane *et al.* (1990) state that aquatic marking studies using dyes and pigments were the second most common type, after those using physical tags, and comprised 14% of the total.

Granulated fluorescent pigments were first used by Jackson (1959), who applied the marks to 10 different fish species using compressed air. Further studies were carried out with 3 species of Pacific salmon, *Oncorhynchus gorbuscha, O. kisutch* and *O. nerka* and rainbow trout, *Salmo gairdneri* (Phinney *et al.*, 1967); coho salmon, *O. kisutch* (Phinney & Mathews, 1969), pink salmon, *O. gorbuscha* (Hennick & Tyler, 1970), brook stickleback, *Culaea inconstans* (Moodie & Salfert, 1982); cutthroat trout, *O. clarki* (Nielson, 1990) and Atlantic salmon, *Salmo salar* (Moffett *et al.*, 1997).

The technique of marking fish using a subcutaneous injection of a coloured substance was first tested in the 1950's on cutthroat trout (Bond & Culver, 1952) and on bluegill sunfish, *Lepomis macrochirus* (Al-Hamid, 1954), before being further developed for trout by Kelly and Loeb (1964). The technique has subsequently been used with five different species of warmwater fishes (Arnold, 1966), and with brown trout *Salmo trutta*, brook trout *Salvelinus fontinalis* and winter flounders *Pseudopleuronectes americanus* (Kelly, 1967).

Visible implant elastomer (VIE) tags are small pieces of fluorescent material which are injected, as a liquid, into clear tissue sites of fish. After a short period (a few hours) the liquid hardens into a pliable, rubbery solid. The material fluoresces brightly when illuminated with ultra-violet light. VIE tags have been used on five species of juvenile reef fishes (Buckley *et al.*, 1994), and on juveniles of both bull trout, *Salvelinus confluentus* and cutthroat trout *Oncorhynchus clarki* (Bonneau *et al.*, 1995).

Six colours of elastomer are available. By careful planning, using several different colours and sites, individual identification can be achieved. Elastomer tags can also be used to batch mark large numbers of fish.

Materials and methods

The elastomer material arrived from the manufacturer, Northwest Marine Technology Inc., in two joined tubes, one containing the coloured liquid part and the other a colourless hardener. The correct amount of each of these liquids was expressed from the tubes using the special gun provided, and was automatically mixed in the spiral nozzle. The elastomer material was then loaded into a 0.3 cc syringe fitted with a 29 gauge needle.

TAGGING TECHNIQUE

Anaesthetised fish were tagged with elastomer by inserting the needle at a shallow angle into the selected clear tissue area. The syringe plunger was then depressed and the needle slowly removed, leaving a small amount of elastomer behind. Any material that leaked out of the insertion was wiped away, in order to prevent the formation of a trailing portion, which once hardened, could increase the likelihood of the mark being shed.

RETENTION STUDY

In order to test tag retention, on the 1st March 1996, 39 dace were weighed, measured and marked twice with elastomer, once in the clear pre-ocular adipose tissue, and once between the first and second rays of the dorsal fin. The fish were retained in an experimental channel (see chap 2.23), and examined at intervals, for the presence of elastomer.

Recapturing the tagged dace from the channel was not always easy, and it was possible for the fish to remain hidden within the channel, even when most of the water had been drained out. In addition, some mortality occurred, and although all dead fish discovered were recorded, it is possible that some of the dead fish were taken by animals before being found. It is also possible that some of the fish escaped, and others could have been taken, particularly by herons (*Ardea cinerea*) or mink (*Mustela vison*) which are frequently seen in the area. Consequently, the number of fish remaining in the channel at any one time was unclear, and numbers did fall during the course of the experiment, making calculation of total mark retention impossible. Accordingly, the number of fish with each type of mark visible was calculated both as a percentage of the number of fish initially released, and as a percentage of the number of fish captured during each sampling.

Plate 4.4i. Orange elastomer tag between the second and third anal fin rays of a dace.

FIELD STUDY

Large aggregations of adult dace form in the tidal reaches of the River Frome from autumn onwards (pers. obs.). These aggregations persist through the winter, and large numbers of dace are still present during late February and early March, in the lead up to spawning. There are substantial areas of gravel immediately upstream of Wareham road bridge (SY 98 NW 924872), and it has been suggested by local anglers that dace spawn on these gravel areas. However, being tidal in nature, the water flow frequently changes direction, and is commonly turbid. In addition, the salinity of the water is also likely to be subject to wide fluctuations. Consequently, the suitability of this particular site for the spawning of dace is questionable.

From mid to late March (Mann, 1974), dace have spawned on a clean gravel bedded riffle in the East Stoke Millstream over a number of consecutive years (Mills, 1981, pers. obs.). During the spawning period, mark-recapture experiments have shown that there is a constant turnover of fish, with some leaving the spawning stream and others arriving (W. Beaumont, pers. comm.). It is possible that those dace shoals arriving in the East Stoke Millstream from mid to late March were formed, in part, of individuals which had over-wintered in the tidal reaches of the river. In order to test this hypothesis, dace captured by angling during the winter and early spring in the tidal reaches of the river, were batch marked with VIE tags in between their second and third anal fin rays, and returned (Plate 4.4i). If any of these dace were to move upstream to the East Stoke Millstream to spawn, it is possible that they would be recaptured during the annual electrofishing survey of spawning dace within this stream.

Results

RETENTION STUDY

As expected, the percentage of the original fish being recaptured with each type of mark reduced with time, giving values, after 292 days, of 77, 72 and 64 % for anal fin-clip, pre-ocular elastomer and dorsal elastomer respectively (Fig. 4.4i). After 19 and 42 days, all fish recaptured from the channel showed all three marks, and an anal fin clip was visible on all fish after 292 days in the channel (Fig. 4.4ii). The pre-ocular and dorsal fin elastomer tagged fish recaptured after 292 days showed 93 and 83 % retention respectively (Fig. 4.4ii). No fish lost both of their elastomer tags. There was no significant difference in elastomer retention between the two tissues after 292 days ($P = 0.67$, Fisher exact test).

FIELD STUDY

Due to unfavourable weather conditions, only a small number of dace were caught in the tidal reaches of the River Frome between 18/12/96 and 7/3/97, of which 27 were marked with VIE tags between the 2nd and 3rd anal fin rays. On March 18 1997, 267 spawning dace were captured from the East Stoke Millstream, of which 1 male (160 mm, fork length), had been VIE tagged between the 2nd and 3rd anal fin rays.

Although a population estimate based on one recapture is at best extremely crude, the suggested figure of 7209 between Wareham and East Stoke (10.7 km) compares favourably with the previous estimate of 11214 between Bindon and Wareham (13.3 km) (Chapter 4.2).

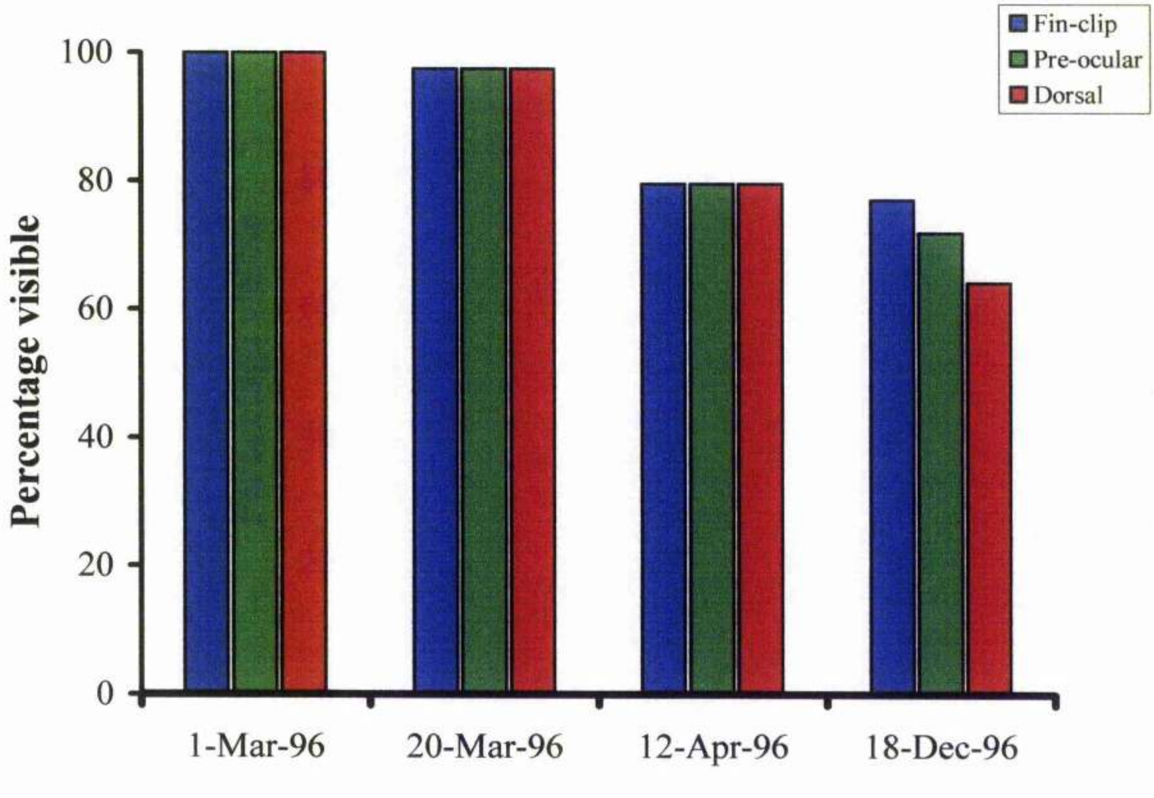

Figure 4.4i Percentage of the fish initially tagged showing each type of mark.

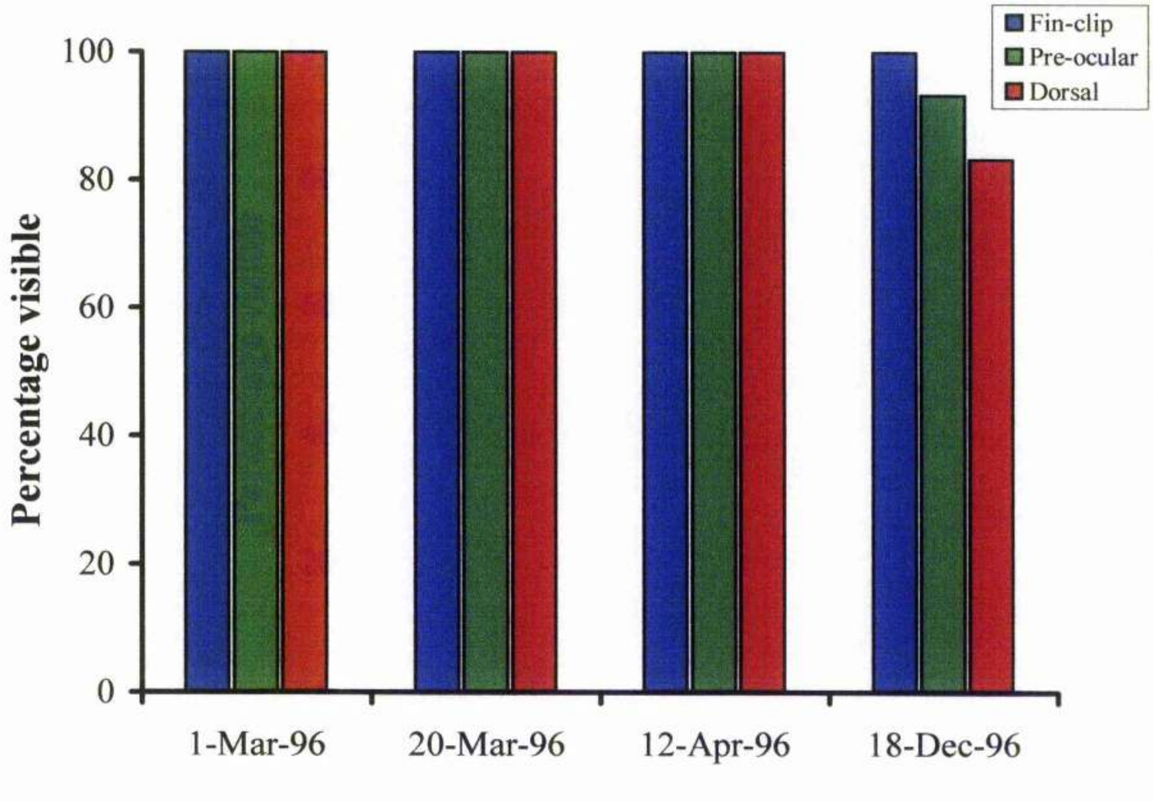

Figure 4.4ii Percentage of the fish recaptured showing each type of mark

4.5 Discussion

The recapture of marked individuals did provide some valuable data, despite the fact that specific attempts to recapture marked fish were limited, with the vast majority of the recaptures being made during attempts to catch fish for other purposes. Considering the degree of effort, and the relatively low numbers of individuals handled, the number of recaptures of marked fish was surprisingly high, suggesting that the dace population is relatively small. However, great caution must be exercised, as there exists within this particular study a substantial potential for bias. A proportion of the recaptures were made at specific sites only discovered by following the movements of a radio-tagged individual. Indeed, some of the recaptures were of fish released with radio-tagged individuals, and others of fish released at the same site within a short space of time. The mark-recapture study was not primarily designed in order to be able to make an accurate population estimate, and consequently this is not possible from the existing data. However the recaptures of fin-clipped fish did provide sufficient data for a very approximate estimate to be made.

FIN CLIP FIELD STUDY

The fin-clipping study provided further evidence that dace are highly mobile, with fin-clipped fish being caught at each of the two most remote sites from the release point, as well as at other sites in between. The hypothesis that dace which spawn in the East Stoke Millstream remain within the vicinity of this site throughout the year can therefore be rejected. Further, the discovery of marked fish at other spawning sites during the known spawning season indicates that although some individuals return to the same site in subsequent years, spawning site fidelity is not a feature of the whole dace population.

Dace in the River Frome attain a maximum age of at least 10 years (Mann, 1974 pers. obs.), and could therefore, in theory at least, have one of the paired fins clipped on 10 separate occasions. On a four year rotation therefore, any fish 4+ years or older showing a particular clip, could have been clipped in one of two years.

The crude population estimate, based on the recaptures of fin-clipped fish, contains a number of biases which will affect the accuracy. Random mixing of the clipped individuals within the population cannot be assured, although the data do suggest that there is substantial movement through the system. Size assortive shoaling, and differences in seasonal behaviour are likely to occur between mature and immature dace. Adult dace were the main focus of the study and were specifically targeted. As a result the smaller size classes are probably under-represented in the crude population estimate. Conversely, some of the recaptures of fin-clipped fish were made at the release site, a short time after release, and others were recaptured in association with the radio-tagged fish with which they were released. Consequently, these recaptures do not conform to random mixing, and are likely to result in an overestimate in the numbers of individuals in the larger size classes.

VI ALPHA NUMERIC TAG RETENTION

VI alpha-numeric tags are retained for short periods in the adipose tissue around the eye of dace, with the thicker pre-ocular tissue providing better retention than the post-ocular tissue. Retention appears to be strongly size related, with larger individuals retaining tags for longer periods than small ones. Recaptures of anal fin-clipped fish from the field suggest that long term retention of VI tags is very low, thus limiting the usefulness of the technique with dace.

VI ALPHA NUMERIC TAG FIELD STUDY

VI tagged and anal fin clipped dace initially released in the East Stoke Millhead were recaptured at both Bindon and Wareham. The observed migration of radio-tagged dace from the East Stoke Millhead to the Bindon Millstream before spawning (Chapter 3) was mirrored by VI tagged and anal fin clipped dace in this study. Marked dace were highly mobile, and were found at each of the two sites furthest from the release point. The primary hypothesis, that the seasonal movements of VI tagged fish were similar to those of radio-tagged fish can be accepted.

The vast majority of tagged dace recaptures occurred around spawning time, and it was therefore impossible to test the secondary hypothesis, that the fish captured and released along with the radio-tagged fish all remained together, as part of the same shoal. The fact that dace are known to aggregate to spawn meant that it was impossible to determine whether the VI tagged fish had remained together throughout, or had in fact re-joined at the spawning site.

ELASTOMER RETENTION

Retention of VIE tags was high in both the pre-ocular and dorsal sites, with no fish losing both marks during the course of the study. Consequently, elastomer tagging appears to be a suitable technique for batch-marking large numbers of individuals, at least for dace. If the retention rate of VIE tags in other fins is similar, or if a number of other suitable sites can be found, individual identification of a small number of fish can be achieved. In addition, by using a coding system, involving the use of several different sites, and more than one colour of elastomer, a substantial number of unique codes could be created.

ELASTOMER FIELD STUDY

The recapture in the East Stoke Millstream of a VIE tagged spawning dace, caught and released during the winter in the tidal reaches of the river at Wareham, suggests that at least some of the large aggregations of dace observed in the tidal river from autumn onwards move upstream to spawn in the spring. The fact that only one of the 27 dace released was recaptured is hardly surprising, considering the abundance of other potential spawning sites, and the fact that there is a large turnover of fish within the spawning stream. However the fact that one of a small number of marked individuals was recaptured from such limited recapture effort, coupled with the discovery of aggregations of spawning fish in other millstreams, may be further evidence of the relative importance of such sites. Millstreams by their very nature are capable of being influenced by the actions of man (e.g. adjustment of hatches) and are subject to a variety of management practices (e.g. weedcutting, dredging). Any such anthropogenic influences, either before, during or after spawning are likely to affect reproductive success, and could ultimately impact upon the dace population as a whole.

CONCLUSIONS

Mark-recapture studies can provide important information relating to the seasonal migrations of fishes, as long as a suitable marking technique is selected. In studies where the intention is to catch fish from a number of different sections of the same system at intervals, a batch marking technique offering good retention can provide gross movement data, from which aspects of the mobility of the whole population can be implied. The use of individually identifiable tags and codes additionally produces specific information about the movement and growth of individuals, and can potentially provide more accurate estimates of the rate of fish movement.

The retention of VI alpha-numeric tags fell over time, and differed between different sizes of dace. Consequently VI alpha-numeric tags are of limited value for long term field studies of dace, but can provide details relating to the movements of larger individuals in the short term.

VIF tags show good long-term retention in dace, both in the dorsal fin and pre-ocular adipose tissue. They are therefore suitable for large batch marking programmes, and are unlikely to have the mortality and growth problems that have been recorded for fin-clips (O'Grady, 1984). Use of several colours of Elastomer and a number of different tagging locations, it would also be possible to individually mark a large number of fish.

Population estimates of riverine fishes from mark-recapture data can be difficult to establish due to the mobility of the fish, size related differences in tag retention and behaviour, and the potential for non-random mixing within the population. However providing all the potential biases are identified and accepted, and by using a variety of different techniques, an approximate figure can be arrived at.

Fin clipped dace were recaptured at each of the two most remote sites sampled (Wareham and East Burton), showing that at least some of the population move extensively and do not remain in the vicinity of the East Stoke Millstream throughout the year. Some dace marked at the East Stoke spawning site were recaptured in other millstreams during subsequent spawning seasons, indicating that at least some of the dace population do not remain faithful to one spawning site for life. Marked individuals released before spawning in the East Stoke Millhead moved upstream to the Bindon Millstream, as did radio-tagged fish (Chapter 3). A proportion of those dace aggregated in the tidal reaches of the River Frome moved upstream in the spring to the East Stoke Millstream spawning site. Consequently, the overall hypothesis that the movements of marked dace are similar to those of radio-tagged dace has been accepted.

CHAPTER 5

Migrations - fish counters

5.1 Introduction

The staff of the I.F.E. were involved in the development of a unique system for counting young Atlantic salmon or smolts, as they migrated downstream to the sea. The system was designed to divert the fish from the main River Frome into the East Stoke Millstream using an acoustic bubble screen, and focus them through a fish counter and a glass-sided observation channel. In this way, the need to trap or handle the fish during this delicate transitional phase of their life cycle was avoided. This was the first system of its kind.

A by-product of this smolt counting study was a record of the movements of other fish species within the vicinity of the counter. It was possible to record the size, direction and timing of the movements of all fishes passing the counter, except during very turbid conditions. Consequently, the hypothesis that the direction and timing of dace movements are random and unpredictable on both daily and seasonal scales was tested by examining the differences between the numbers of dace passing the counters in each direction during specific periods.

5.2 Materials and methods

In order to produce the bubble screen, compressed air was pumped through an array of perforated pipes on the river bed. The air was forced through the holes, forming a dense curtain of bubbles as they rose to the surface. Sound (50 – 600 Hz), covering the most sensitive part of a smolt's hearing range (approx 200 Hz), was generated by transducers and entrained within the bubble curtain. The 24 m bubble screen was angled upstream across the river, from the mouth of the East Stoke Millstream. This had the effect of diverting smolts and presumably other fish from the main river into the Millstream.

Water from the East Stoke Millstream flowed downstream and through the Fluvarium, which consists of two glass sided channels. The fish were ultimately directed using wire mesh screens, so that they first passed through an array of automatic resistivity fish counters and then through a narrow (200 mm) gap between a white screen and the glass side of the channels. A camera, connected to a time lapse video recorder, was focused through the glass, and any fish moving through the Fluvarium were recorded on video. All fish passing through the Fluvarium were counted by the resistivity counters, with the sizes and species being ascertained from the video.

In 1996 a new, purpose-built, smolt counter was constructed in a side branch of the East Stoke Millstream, immediately downstream of the laminar flow hatch. By including video records gathered from the adult salmon counter in the River Frome at the East Stoke Flume, all possible routes of passage, both upstream and downstream, were covered with cameras.

By watching the video recordings it was possible to identify the species of each fish on the screen. For the two horizontal counters (i.e., not the vertical overhead adult counter), it was then a relatively simple matter to measure, on screen, an object of known size (e.g. a graduated ruler), and calculate a conversion factor to correct the on screen measurement to actual fish length.

The conversion factors for each counter were different, and monitor specific. For example, on one particular VDU screen, an object of 100 mm in the Fluvarium appeared as 13 mm on the screen, and the same object in the new smolt counter measured 12 mm on the screen. Therefore, when using that particular monitor the actual size of fish passing through the counters was calculated by multiplying the size on the screen by either 7.69 or 8.33 for the Fluvarium and new smolt counter respectively.

As a by-product of the smolt counting, the numbers, size and movements of dace in the vicinity of the various counters, were obtained. These data were collected and analysed for the periods during which the smolt counter was operated, in order to examine the degree to which dace movements are predictable.

5.3 Results

In spring 1996 the smolt counters in the Fluvarium were run almost continuously over the period between 1st April and 31st May. During this period 939 dace were counted passing through the smolt counter. On this occasion, as the data had been gathered purely as a by product of the smolt counting work, the size and direction of movement of dace was not recorded. The number of dace passing through the counter during any 24 hour period ranged from 0 to 169, with a mean of 15.4 (Fig. 5.3i). By examining the number of dace moving during each half hour period, it became clear that the majority of the movement occurred during the afternoon and evening, with virtually none at night. Eighty four percent of the dace passing the counter did so in the third of the day between 14:00 and 21:59 (Fig. 5.3ii). The mean number of fish moving per half hour during this period (0.79 +/- 0.23) was significantly greater than the mean number of fish moving during either the period between 22:00 and 05:59 (0.13 +/- 0.04, *t*-test $P<0.001$, df = 15), or the period between 06:00 and 13:59 (0.04 +/- 0.03, *t*-test $P<0.001$, df = 15).

Results from autumn 1996 showed that of the 288 dace recorded on video between 25 October and 22 November (22 days of observations), 166 (58%) actually passed *through* the counter. The majority (73%) of these fish were small (< 15 cm), however of those which were 15 cm or over (adults), a significant proportion (n = 44, 73%) were travelling in a downstream direction (χ^2 1df = 13.07, P = 0.0003). Migration through the counter was again greatest during the late afternoon and early evening, with more than half of the total number of dace passing during the four hours between 14:00 and 18:59 (Fig. 5.3iii).

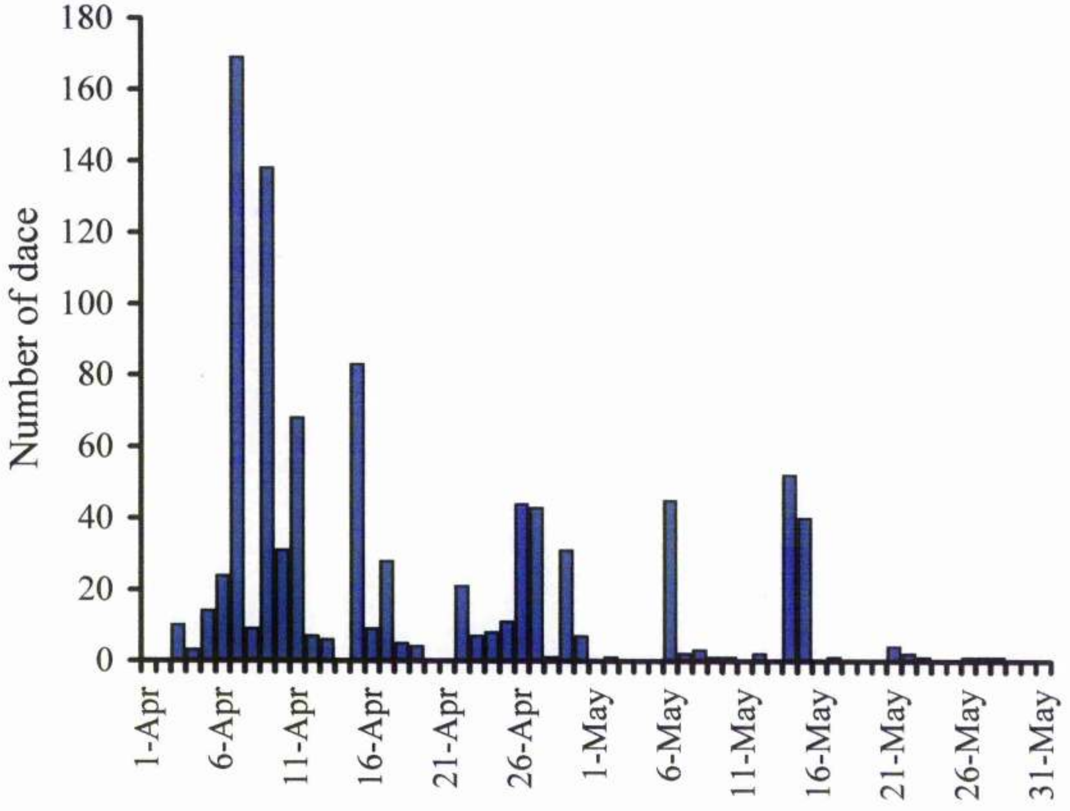

Figure 5.3i. Daily movement of dace through the smolt counter during spring 1996

Figure 5.3ii. Diel timing of dace movements through the smolt counter, spring 1996.

Charts illustrating the net movement of both large and small dace show an upstream migration at dusk and a downstream migration around dawn, although the numbers of fish are quite small (Figs 5.3iv & 5.3v). In spring 1997, the sizes of dace passing through the three counters were not recorded, however the direction of passage was, and yielded interesting results. Of the 3186 dace which passed through the counters during 52 days in April and May, 89% were travelling in an upstream direction. When the daily movement totals of dace were plotted over time, two major periods of migration became apparent, between 23 April and 3 May (11 days), and from 9 to 17 May (9 days) (Fig. 5.3vi). During these 20 days (<39% of the total time), 92% (2916 fish) of the dace passed through the counters. During the first period (<22 % of the total time) 2409 dace (76% of the total fish) were recorded, of which 97% were travelling in an upstream direction. The majority (60%) of these upstream relocations occurred between 16:00 and 21:00 h. During the second period 507 dace passed through the counters, however, unlike the previous period, 45% of these dace were travelling in a downstream direction (Fig. 5.3vii). The proportion of fish moving upstream was significantly higher during the first period compared to the second (χ^2 1df = 799.8, P<0.001). The net daily movement of dace over three hourly periods between 9 and 17 May suggested that the number of fish moving upstream and downstream were similar during all but two periods (Fig. 5.3viii), with a net upstream movement of 89 fish between 16:00 and 18:59, and a net downstream movement of 40 fish between 04:00 and 06:59. The proportion of fish moving upstream through the counter varied significantly throughout the day (χ^2 7df = 101.88, P<0.001). The estimated proportion moving upstream between 16:00 and 18:59 is 94%, with confidence intervals of 87% to 98%. The estimated proportion moving downstream between 04:00 and 06:59 is 76%, with confidence intervals of 65% to 85%.

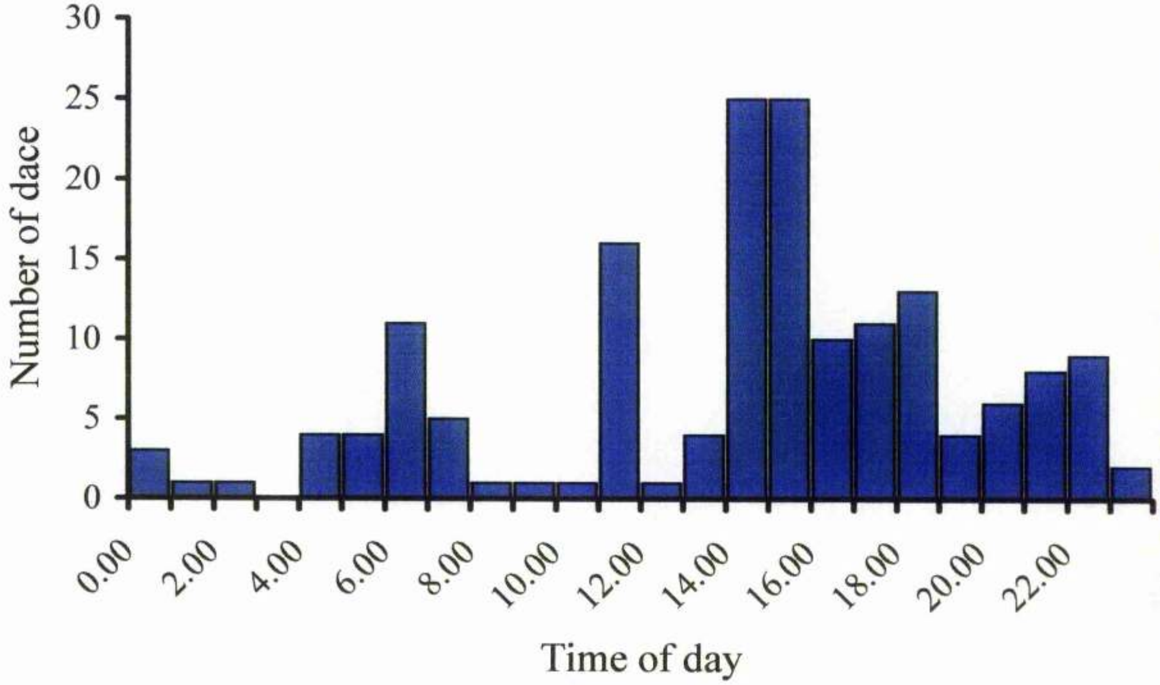

Figure 5.3iii. Diel timing of dace movements through the smolt counter during autumn 1996.

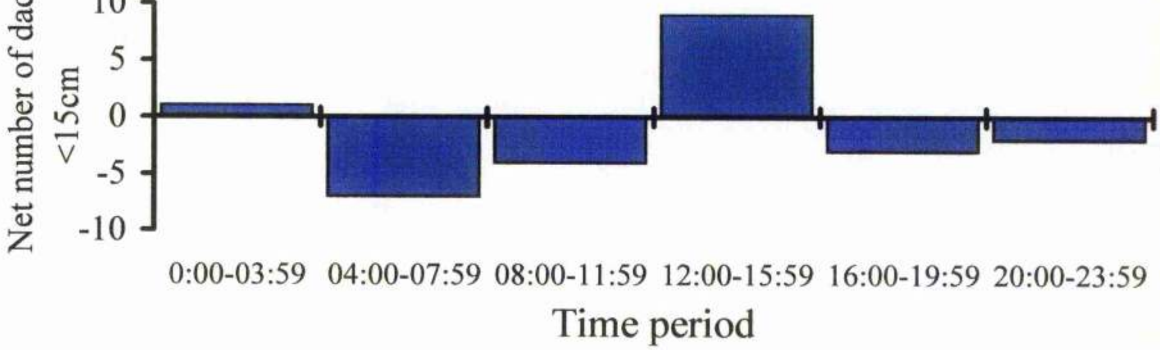

Figure 5.3iv. Net movement of small dace through the smolt counter during autumn 1996. Positive numbers represent a net upstream movement.

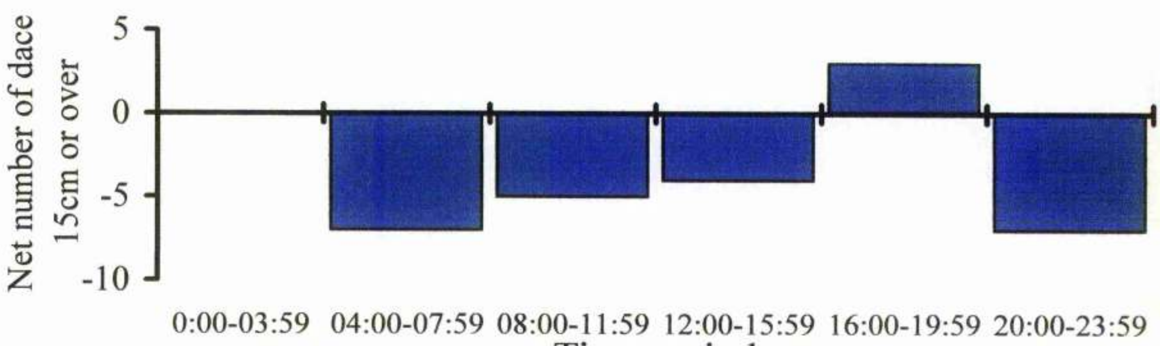

Figure 5.3v. Net movement of large dace through the smolt counter during autumn 1996. Positive numbers represent a net upstream movement.

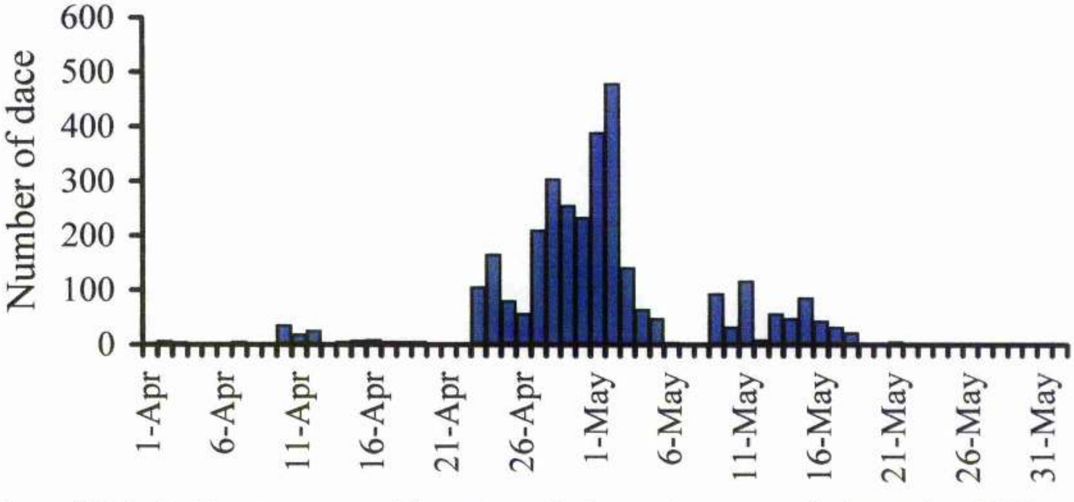

Figure 5.3vi. Daily movement of dace through the smolt counter during spring 1997.

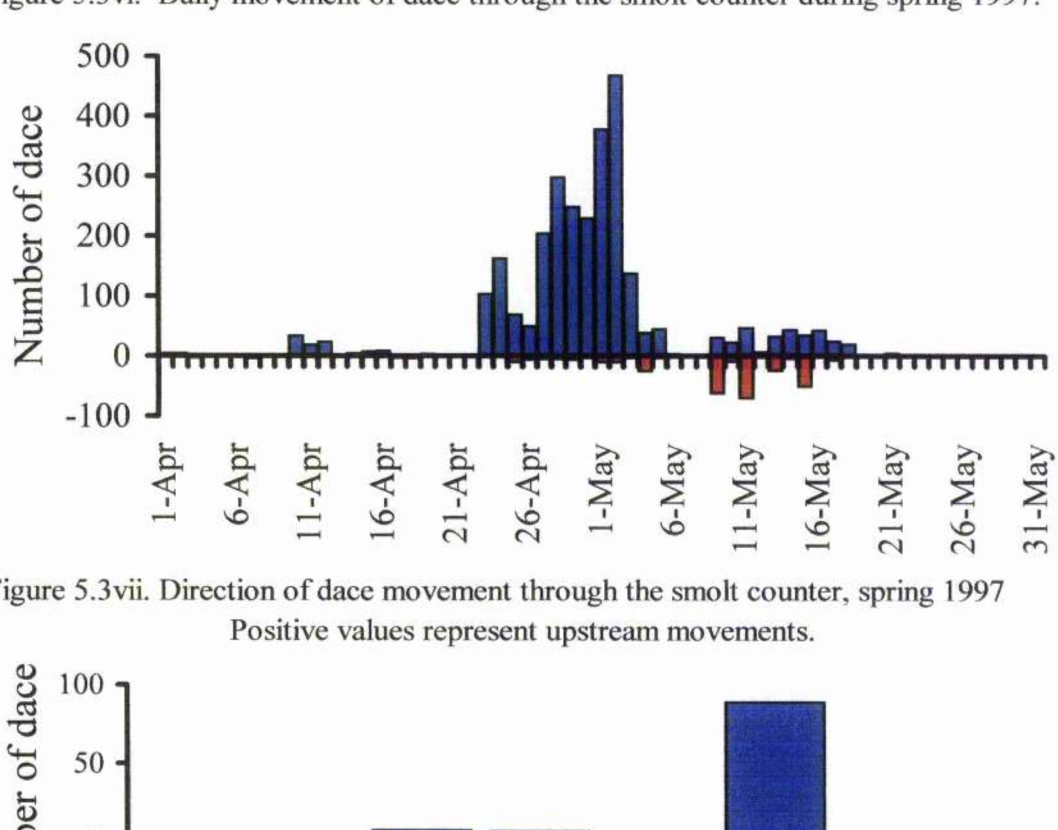

Figure 5.3vii. Direction of dace movement through the smolt counter, spring 1997
Positive values represent upstream movements.

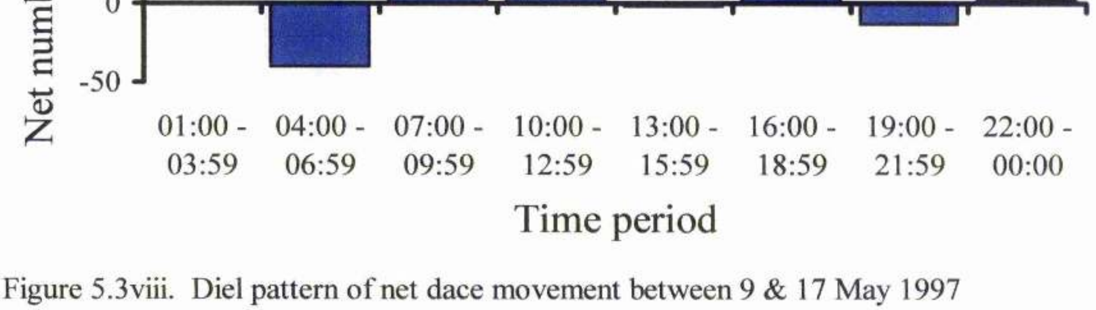

Figure 5.3viii. Diel pattern of net dace movement between 9 & 17 May 1997
Positive values indicate a net upsteam movement.

5.4 Discussion

The timing and direction of dace movement through the East Stoke Millstream smolt counter was predictable on both daily and seasonal scales. Consequently, the hypothesis that the direction and timing of dace movements are random and unpredictable on both daily and seasonal scales has been rejected.

In addition the observed migration of large numbers of untagged dace support those the observations of both radio-tracking (Chapter 3) and mark-recapture (Chapter 4) studies, and reduce the probability that migrations observed during these studies were caused, or influenced by the tagging and handling process.

The results from spring 1996 showed that, at this time of year the vast majority of dace movement occurred during the afternoon and evening. Adult dace in the River Frome spawn in the second half of March (Mann, 1974; pers. obs.). The movement of dace through the East Stoke Millstream smolt counter may have represented a re-distribution of dace through the system, following the aggregations for spawning, however there appeared to be a delay between the end of spawning and the redistribution of adult dace. Whether or not the spent dace remained in the vicinity of the spawning grounds after the completion of spawning was unclear at this point (see Chapter 7). As no size or direction data were recorded for dace passing in spring 1996, no further comments can be made.

The spring 1997 data also showed that the majority of the movement occurred in the evening, and that most of the fish passing the counters at this time of year were travelling in an upstream direction. Two distinctly different periods of movement were observed over the course of the spring 1997 counting period. During the first period almost all of the dace passing through the counters did so in an upstream direction, and the numbers of fish involved suggested a widespread migration of a substantial proportion of the population. Again there appeared to be a gap between the completion of spawning, around the end of March, and the observed upstream migration. Consequently, a radio-telemetry study of the migration and habitat selection of adult dace during the immediate post-spawning period was carried out (Chapter 7). The observed upstream relocational migration of dace around the end of April coincides with the beginning of a substantial increase in the abundance of invertebrates. Monthly samples taken within the study area show a 13 fold increase in the numbers of drifting invertebrates between the end of April and the end of June (pers. obs.). It is possible that increasing day length and/or temperature act as the trigger for dace to anticipate this predictable increase in food availability, and respond by migrating to areas which allow them to make most efficient use of the resource.

The second period had roughly equal upstream and downstream components, and involved fewer fish. As no size data were available, the possibility that the net movements of dace of different size classes were in opposite directions cannot be ruled out. However, as the net movement of dace around dusk was in an upstream direction, it is also possible that the observed pattern reflected a diel migration of those individuals resident in the vicinity of the counters, especially as diel migrations are a noted feature of dace behaviour in the River Frome at this time of the year (Chapter 3; Clough & Ladle, 1997).

Dace lengths were recorded during the autumn 1996 smolt counting period, and these data suggested that fish in different size classes showed different behaviours at this time of the year. Although relatively low numbers of fish were observed during the autumn 1996 smolt counting period, there appeared to be differences in the net migrations of fish of different sizes. For fish of 150 mm or less, the numbers travelling in each direction were almost equal. The majority of dace over 150 mm however, were travelling in a downstream direction, which was supported by anecdotal evidence suggesting that adult dace carried out a downstream migration in the autumn.

Overwintering migrations of fish to the lower reaches of rivers has been documented (Northcote, 1978). Large aggregations of adult dace are known to form in the tidal reaches of rivers during the winter including the River Tees, prior to the construction of a tidal barrage-barrage (I.F.E. unpublished data, pers. obs.), the River Stour (A. Pinder, pers. comm.), and the River Frome (pers. obs.). Although some dace were present in the tidal reaches of these rivers throughout the year, there appeared to be far fewer during spring and summer and it seems likely that these aggregations were formed, in part at least, of fish which had spent the summer months further upstream within the catchment. Under normal flow conditions the tidal reaches of rivers appear to be generally more turbid in nature than sections further upstream (pers. obs.). Although gravel areas can be found in the tidal reaches, the constant variation in flow direction and salinity, coupled with exposure during low spring tides and silt deposition at the top of the tide, probably results in such areas being unsuitable for the spawning of dace. It seems likely, therefore, that in those rivers where large aggregations of dace form in the tidal reaches during winter, an upstream migration of adult dace will occur in the spring, in order to find clean gravel on which to spawn. It is also possible that such an upstream migration of adults compensates for the downstream drift of juveniles, which might otherwise be carried out to sea.

CHAPTER 6

Diurnal habitat use

This section of work was carried out in collaboration with P. Garner, and the results have been published: Garner, P. & Clough, S. (1996). Habitat use by dace, *Leuciscus leuciscus* (L.), in a side channel of the River Frome, England. Fisheries Management and Ecology 3, 349-352.

6.1 Introduction

The characteristics of the habitat selected by an individual fish will affect, among other things, the risk of predation and the availability of food. By selecting superior habitats a fish can gain a competitive advantage over conspecifics, which can ultimately result in the individual having a higher fitness.

In recent times there has been a growing interest in the way non-salmonid fishes utilise and select their habitat (Baras, 1997), resulting in the development of habitat suitability curves for some species. In order to assess the habitat use of fish it is necessary to discover their location, with direct observation being one of the simplest and most efficient techniques.

During much of the summer, the water of the River Frome is very clear, allowing observers, during suitable light conditions, to see the substratum throughout much of the study area, particularly in the East Stoke Millstream. At this time of the year, dace inhabited sections of the East Stoke Millstream, and if approached carefully, could be observed without disturbance.

During daylight the fish remained relatively static within the river channel, utilising specific areas for extended periods, often several weeks. During June, adult dace had been observed in the same short sections of the East Stoke Millstream on a number of different days, and recognisable individuals were observed occupying the same area of the channel on consecutive days. The implication of this persistent habitat use is that the dace are, in effect, continually re-selecting the same area, suggesting that it represents suitable habitat. Further, dace resident in this area during the day are known to carry out diel migrations, often moving several hundred metres, before returning to the same position at dawn (Chapter 3, Clough & Ladle, 1997). It seems reasonable to suggest that this continual re-selection of the same daylight position implies that it is the most suitable habitat in the vicinity. Whilst there is evidence that some fish consistently use breeding sites which have been traditionally used, rather than continually selecting the most suitable habitats (Warner, 1988), it is likely that the areas occupied, whilst not necessarily optimal, still represented suitable habitat. Indeed, in terms of daytime habitat of dace, the benefits of familiarity with the local environment may outweigh the benefits of occupying another site, due to the increased risk of predation or loss of foraging opportunities associated with the searching and familiarisation period.

It was, however, unclear which factors influence the habitat selection of dace, or whether sites were chosen randomly. Therefore in order to examine the daylight habitat selection of dace, visual observation was used to test the hypothesis that during daylight, dace use habitats in the same proportion as they are available, i.e. their habitat "selection" is random.

6.2 Materials and methods

In order to examine which factors make a site suitable for use during daylight, dace were observed *in situ*, without disturbance. Only dace over *c*. 10 cm were included in the study, as fish of this size could be easily distinguished from roach (*Rutilus rutilus* (L.)), the only cyprinid of comparable size present. Between 11.00 h and 14.00 h on the 23rd June 1995, two observers walked slowly along the north bank of the East Stoke Millstream, utilising bank-side cover to avoid disturbing the fish. Whenever a dace was observed, a detailed sketch and written description were made of the fish's position relative to fixed objects, both within the channel and on the bank. Any fish that appeared to be moving or which became agitated during the period of the observation were excluded. The whole 500 m of the East Stoke Millhead was searched.

Habitat use data were then recorded by returning to each of the previously sketched fish positions. Water depth and focal point velocity (8 cm above the substratum) were measured at each point. In accordance with the Instream Flow Incremental Methodology (IFIM) (Bovee, 1986), the degree of instream cover and composition of the substratum was estimated over an area of 10 cm radius around the recorded fish position. Habitat availability was assessed by taking 20 randomly spaced transects along the length of the Millhead, with measurements being taken at 1 m intervals along each transect, starting a random distance out from the bank. Habitat use and availability were calculated as the percentage frequency of occurrence in each category of habitat variable. Habitat suitability was calculated as the proportion of habitat used by the dace relative to that which was available (Bovee, 1986) (Fig. 6i).

6.3 Results

A total of 377 sets of habitat measurements were taken, corresponding to the positions of the 377 adult dace that held station during the period of observation. All of the dace observed appeared to be just above the substratum. Dace selected water of between 40 and 60 cm deep. Water depth use was significantly different than water depth availability (χ^2_{6df} 126.49, $p < 0.001$). Water velocities between 10 and 40 cm s^{-1} were used. Water velocity use was significantly different than water velocity availability (χ^2_{4df} 46.64, $p < 0.001$). Instream cover was generally avoided. Instream cover use was significantly different to instream cover availability (χ^2_{4df} 203.23, $p < 0.001$). There was a preference for sites with a sand substratum. The use of substratum was significantly different from the availability of substratum (χ^2_{2df} 54.70, $p < 0.001$).

Within the study area the fish were highly aggregated, and the majority were members of two large shoals containing 235 and 107 individuals respectively. The degree to which shoal membership affects habitat use is unknown, although the shape of the shoals appeared to correspond to the distribution of particular habitat types. Dace only appeared to occupy areas where all the habitat variables were within the observed range, with those areas apparently similar apart from being shallower, or weedier, not being used.

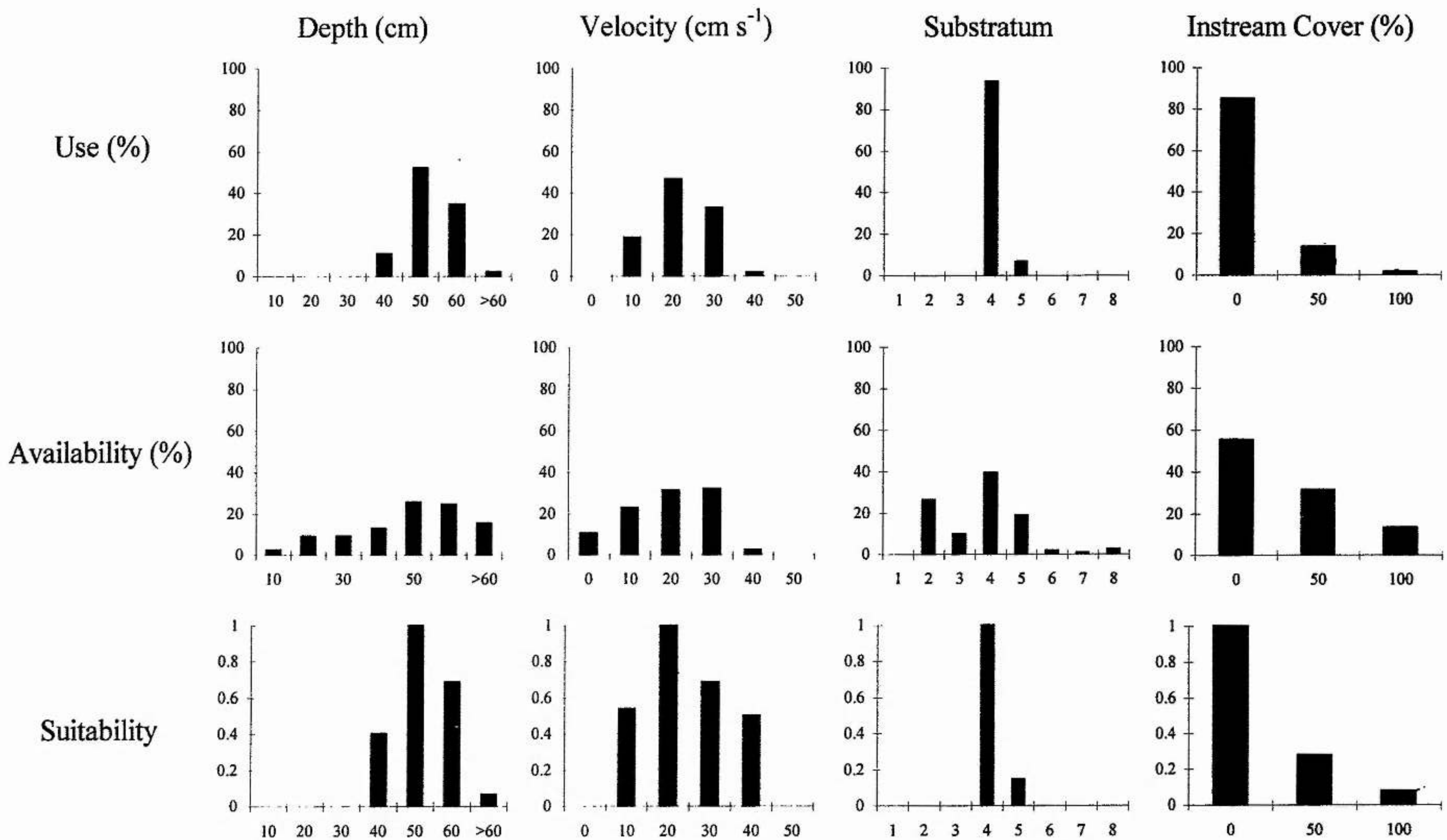

Figure 6i. Habitat suitability indices for dace in the East Stoke Millstream (daylight). Suitability was calculated as the proportion of habitat used relative to that available. Substratum categories: 1 = leaves, 2 = silt, 3 = mud, 4 = sand, 5 = gravel, 6 = pebbles, 7 = boulders, 8 = bedrock.

6.4 Discussion

Adult dace appeared to have specific preferences for areas with particular habitat characteristics, and used these areas in a greater proportion than they were available. Consequently the hypothesis that during daylight, dace use habitats in the same proportion as they are available, i.e. their habitat "selection" is random, has been rejected.

The characteristics of the habitat used by dace are similar in many respects to those postulated by Armitage and Ladle (1991), differing only in the preference for shallower water than predicted. The data suggest that during the daylight hours of summer, adult dace tend not to use water shallower than 40 cm, with diminishing use over 60 cm. There was only a limited amount of water over 60 cm available in the upper Millstream, and it is possible that these were little used due to unfavourable water velocity or degree of instream cover. By avoiding areas shallower than 40 cm it is possible that dace reduce the threat from avian predators e.g. herons.

The apparent preference for sand substrata could be an artefact of the selection of water velocities around 20 cm s^{-1}. However, it is also possible that camouflage against the substratum in order to reduce the threat from predators, could be a significant factor in substratum selection. Indeed the preference for areas with little or no instream cover could also be associated with predator avoidance. In the River Frome, adult dace are the most common food items of the pike (Mann, 1982). One of the most conspicuous characteristics of the pike is its association with aquatic vegetation (Raat, 1988). Pike usually employ either the "ambush" or the "stalking" method of prey capture (Keenleyside, 1979). The ambush technique is characterised by the pike concealing themselves in and around vegetation, waiting until a prey fish is within range, before using rapid acceleration to rush out from cover, seizing the prey fish. The stalking strategy involves the pike finning gently forward into range, before striking. By avoiding areas of dense instream cover, it may be possible for the dace to reduce the predation threat from any pike using the "ambush" strategy. Similarly, by selecting a position with a clear view of their surroundings, the dace were more likely to see the approach of a stalking pike.

In a study of barbel, Baras (1997) suggested that one aspect determining the suitability of a habitat is the presence of at least 10 resident fish. Whilst this seems reasonable for a gregarious species, the fact that an individual chooses not to occupy a particular habitat, and citing the lack of conspecifics as the reason, could be considered to be circular logic. Indeed, the lack of resident individuals from an area may in fact suggest that the habitat is unsuitable or sub-optimal. If the presence of at least 10 conspecifics is a major aspect determining habitat suitability, then an individual or small group introduced into a new system with no existing population of that species, would not settle in one area, but instead continually search for others of their kind.

The observation that the shape of the dace shoals appeared to correspond to the availability of suitable habitat is an interesting one. This suggests that at some stage it will become more profitable for groups or individuals to leave the main shoal in search of new habitats, rather than occupy fringe positions with sub-optimal suitability. It has been demonstrated that cyprinids in larger shoals find food faster than those in smaller shoals (Pitcher *et al.*, 1982). It seems reasonable to suggest that for a given food supply there will be an optimal shoal size, where the mean energy gain per individual is at its highest. In the wild situation however, the amount of available habitat may result in the shoal size being maintained below the optimum, constrained by habitat availability, rather than food supply.

Whilst the habitat suitability indices produced in this study were a real reflection of the habitat selection of those individuals present, it should be noted that many of the factors influencing their choice of habitat are in constant flux on both a daily and seasonal scale. Changes in any one of these factors is likely to influence the relative suitability of the habitat. Indeed, it has been demonstrated that adult dace have different, distinct day and night habitats, and carry out regular diel migrations between the two sites (Clough & Ladle, 1997; Chapter 3). The same daytime site under identical conditions could become "unsuitable" if appropriate nighttime habitat became unavailable. Consequently, the suitability of a particular daytime habitat cannot be viewed in isolation, but instead as one component of a much wider suite of daily and seasonal habitat requirements.

CHAPTER 7

Post-spawning habitat use

I was assisted in this study by P. Garner, and by D. Deans who helped with radio-tracking and measurement of habitat variables. The results have been published: Clough, S., Garner, P., Deans, D. & Ladle, M. (1998). Postspawning movements and habitat selection of dace in the River Frome, Dorset, southern England. Journal of Fish Biology 53, 1060-1070.

7.1 Introduction

Spawning is a critical stage in the life cycle of fishes, often involving a substantial amount of physiological and energetic investment (Jobling, 1994). Spawning migrations are documented for many fishes, including some cyprinids, e.g. redside shiners (Lindsey & Northcote, 1963), roach (L'Abée-Lund & Vollestad, 1987), Colorado squawfish (Tyus, 1990) and barbel (Lucas & Frear, 1997); however, the movements and behaviour of iteroparous species *after* spawning has generally been neglected. Condition (K) of adults usually reaches its lowest value during the immediate post-spawning period, and it can take several weeks or months to recover from the energetic expenditure imposed by gamete production and spawning activity (Mann, 1974; Jobling, 1994). Spawning and spent fish are likely to be susceptible to disease and predation (Wootton, 1984), and mortality rates are often elevated (Pitcher & Hart, 1982). Consequently, the behaviour and habitat selection of spent fish immediately after spawning is likely to be a factor in their survival and future fitness.

Spawning of dace occurs earlier in the year than in any other UK cyprinid, usually from mid to late March in the River Frome (Mann, 1974, Chapter 1). Dace are iteroparous, females in the River Frome mature for the first time at either age III or IV (Mann, 1974), and may spawn annually for up to seven years (Mann & Mills, 1985), with fecundity and egg size increasing with length (Mann, 1974; Mann & Mills, 1985). Further, larger eggs result in bigger larvae, and it has been hypothesised that larger dace larvae are more likely to survive, being better able to avoid predation than smaller ones (Mann & Mills, 1985). Those females which survive to the following year could therefore significantly influence both the number of eggs laid, and the survival of progeny in future spawning seasons. In many species, larger males have reproductive advantages over smaller ones (Milinski, 1993), and it seems reasonable to suggest that older, larger male dace are at least as likely as smaller individuals to fertilise eggs. As a result, male fish that survive post-spawning have the potential to contribute significantly to the numbers of eggs fertilised the following year. Mills & Mann (1985) suggest that without the contribution of repeat spawning individuals, some dace populations "would be in great danger of extinction", due to the substantial variability in year class strength, and the potential for several consecutive years of poor year classes.

Extensive mark recapture experiments, over a number of years, in the vicinity of the East Stoke Millstream spawning site (I.F.E. unpublished data), have shown that there is a constant turn-over of fish during the spawning period, with some, presumably spent individuals, leaving the area and others, as yet un-spawned, arriving. However, it is not known where the spent individuals that leave the spawning area go, or what type of habitat they subsequently select.

Thus, the aim of the study was to determine the post-spawning movements and habitat selection of dace in the River Frome during this important period.

Dace, unsurprisingly, reach their minimum relative condition (K_n) immediately after spawning (Mann, 1974), however they attain maximum K_n by June/July (Mann, op. cit.). In order to move from minimum to maximum condition in such a short space of time the dace must obtain a substantial amount of food. Consequently, radio-telemetry was used in order to test the hypothesis that dace leave the spawning area immediately after the spawning period, and select post-spawning habitats in order to maximise their food intake, and replace the resources used up during spawning.

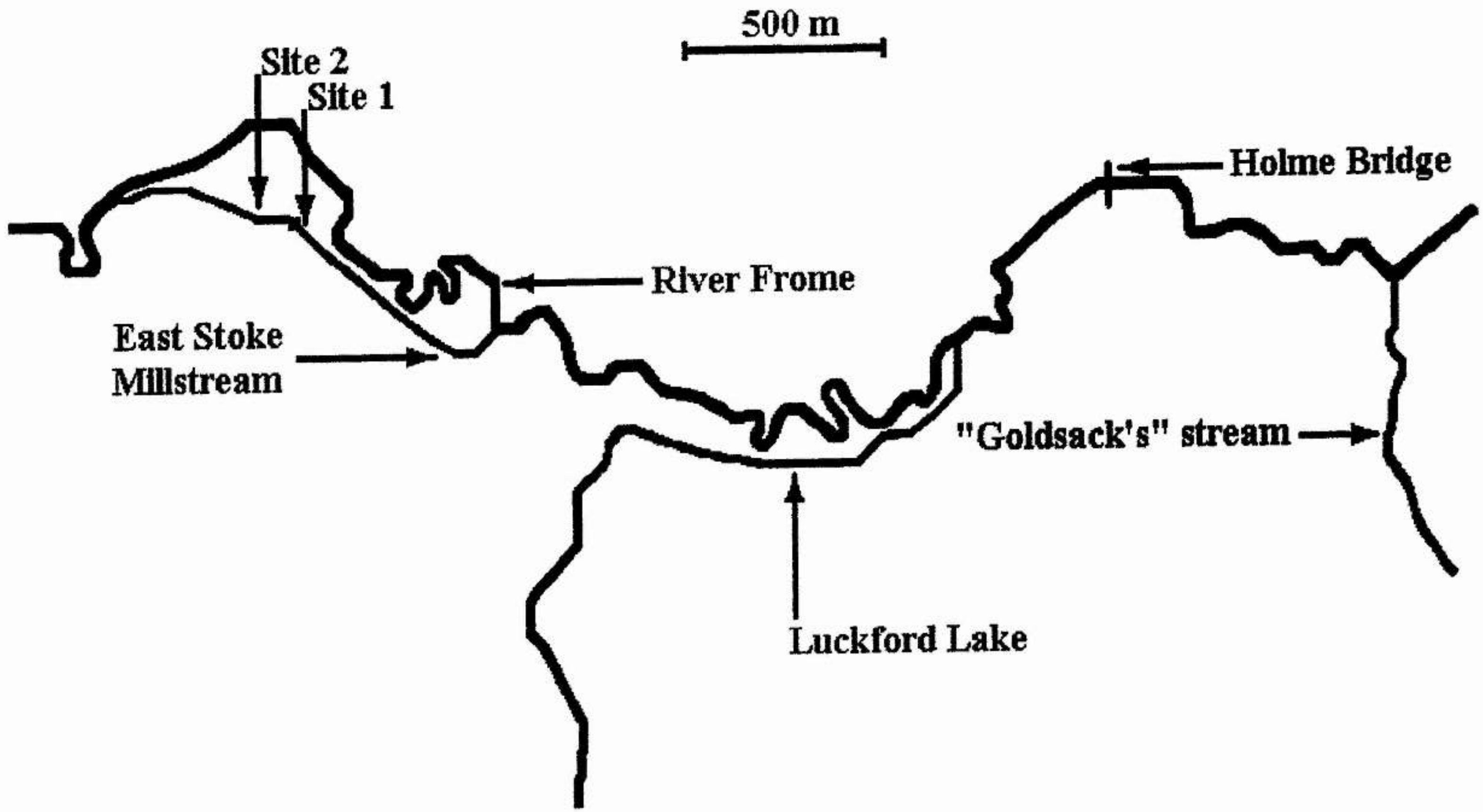

Figure 7i. Map of the area used by post-spawning dace. Site 1 is a known spawning site. Site 2 is a suspected spawning site.

7.2 Materials and methods

Study area

The capture and release sites of post-spawning dace were in the East Stoke Millstream (Fig. 7i, Sites 1 & 2). The shallow, gravel-bedded riffle (Fig. 7i, Site 1) downstream of a Crump weir has been used by spawning dace over a number of consecutive years (NGR SY869869) (Mills, 1981; pers. obs.). All fish had unrestricted access to the main River Frome throughout the study period, at either the upstream or downstream end of the East Stoke Millstream.

Radio-tracking

Post-spawning migrations and habitat selection were determined using radio-telemetry and visual observation. On 17 and 18 March 1997, 233 dace were caught by electrofishing at two sites in the East Stoke Millstream (Fig. 7i). All dace were measured (fork length, L_F), sexed where possible, using external sexual characteristics, and had the distal portion (approximately two thirds) of their right pelvic fin removed, as part of an ongoing annual marking programme. In addition, adult females were classified as either ripe, part spent, or spent. A mixed size group of 20 dace from each capture site, including those individuals selected for tagging, were retained in mesh cages at their respective capture sites prior to tagging, the remainder being returned immediately. Six dace, 3 males (247 mm, 252 mm & 263 mm) and 3 spent females (235 mm, 243 mm & 244 mm), were externally tagged with Biotrack SS-2 radio-tags using the technique described by Beaumont *et al.* (1996). Each radio-tagged fish was assigned a number (1 to 7), according to the relative frequency of its radio-tag, with fish 1 having the lowest frequency. A transmitter with a frequency corresponding to position 5 was already active as part another study and the name "fish 5" was therefore omitted to avoid confusion. The radio-tagged fish and fin clipped individuals were retained in a release cage at their respective capture sites for 24 hours.

On 19 March 1997, four of the six radio-tagged dace, three males, (fish numbers 2, 4 & 6) and one female (fish number 3), were released remotely with a minimum of disturbance (Clough & Beaumont, 1998), 10 m upstream of the fast flowing gravel-bedded spawning site (Fig. 7i, Site 1). On 21 March 1997, the remaining two radio-tagged dace, both females (fish numbers 1 & 7) were released in the same manner 140 m upstream of the weir, 80 m upstream of a fast flowing gravel-bedded riffle, a suspected spawning site (Fig. 7i, Site 2). After release, the fish were tracked continuously, in order to monitor any immediate post-release migration, until a time when they were considered to have temporarily "settled". Thereafter, the fish were accurately located, using triangulation of the radio-signal, on two occasions each day, once in the morning and again in the evening. Some additional position fixes were obtained during darkness, in order to detect any diel shifts in position, which are known to occur in dace at other times of the year (Clough & Ladle, 1997; Chapter 3). Wherever possible, triangulation of the position of a radio-tagged fish was complemented with visual observations, with both the exact location of the tagged individual, and an estimate of the number of accompanying fish being recorded.

Previous studies indicated that hidden transmitters could be consistently located to within an area of approximately 4 m^2 in the East Stoke Millstream (Chapter 3), however visual observations in smaller streams during the present study suggested that the majority of fish radio-locations were more accurate than this, and were frequently within an area of 1 m^2.

Habitat measurements

In order to determine the habitat selection of dace, habitat measurements were taken only from "residence sites", and not from those areas used by radio-tagged fish for brief periods, or in transit. Residence sites were classified as positions occupied by an individual fish on at least two consecutive observations > 4 hours apart. The implication of the utilisation of a particular position for extended periods is that the fish are deemed to have had adequate time to actively select the most suitable habitat from that available (Bovee, 1986; Garner & Clough, 1996; Chapter 6). Habitat variables; substratum composition (modified Wentworth scale), depth (m), water velocity ($m\ s^{-1}$) and instream cover (% stream bed area), were recorded for each residence site. The degree of shading by outstream cover at each site was also estimated as the proportion of the sky obscured, which would otherwise be visible from the fish's position (i.e., that above bank level). The degree of shade was assigned a value of either zero, one-quarter, half, three-quarters or one.

Measurements were taken within 48 hours of a fish's first known arrival at a site, and were repeated after each subsequent week of residence, in order to take into account any changes in the habitat over time. When sites were re-used, a new set of habitat measurements were taken if more than 1 week had elapsed since the previous set were recorded. One week was chosen as a suitable interval between samples, compromising between the need to gather current habitat data and possible disturbance to the fish. Environmental variables, discharge ($m^3\ s^{-1}$), air and water temperature (^{o}C) and incident light (relative units) were continuously monitored near the release sites.

It was considered that, due to the direction and effects of the flow, the area upstream of the fish was likely to impose a greater influence on the fish's choice of position, than that which was downstream. In the absence of a standard methodology, a sampling protocol, which took into account the effects of the flow, was designed. Consequently, in order to determine the habitat characteristics of each area selected, seven sets of habitat measurements (A to G) were taken, in a "kite shaped" pattern, the whole area being referred to as the "zone of influence" (Fig. 7ii). The fish position (E), determined by both triangulation and visual observation where possible, occupied the intersect of the axes of the kite, with the longer portion being orientated into the flow (Fig. 7ii). By taking measurements in this way, an assessment of the habitat characteristics in the vicinity of the fish was gained, with measurements being taken from the area considered most likely to affect the fish's habitat selection.

Tests for differences in depth or velocity for each surrounding position (A, B, C, D, F, G) relative to the corresponding values for the exact fish position (E) were carried out using t-tests, based on the mean difference in value (e.g. E minus A) for each fish, with the number of fish giving the true degree of replication. However, the mean difference values for each fish were based on an average of 26 observations (range = 7-56 observations). Thus, though there are few degrees of freedom, each fish's mean is based on numerous observations, making their statistical distribution more likely to be normal.

At the end of the study period fish 4 and 7 and a sub-sample of the accompanying dace were captured by electrofishing, inspected for fin clips and had their gut contents and gonads examined.

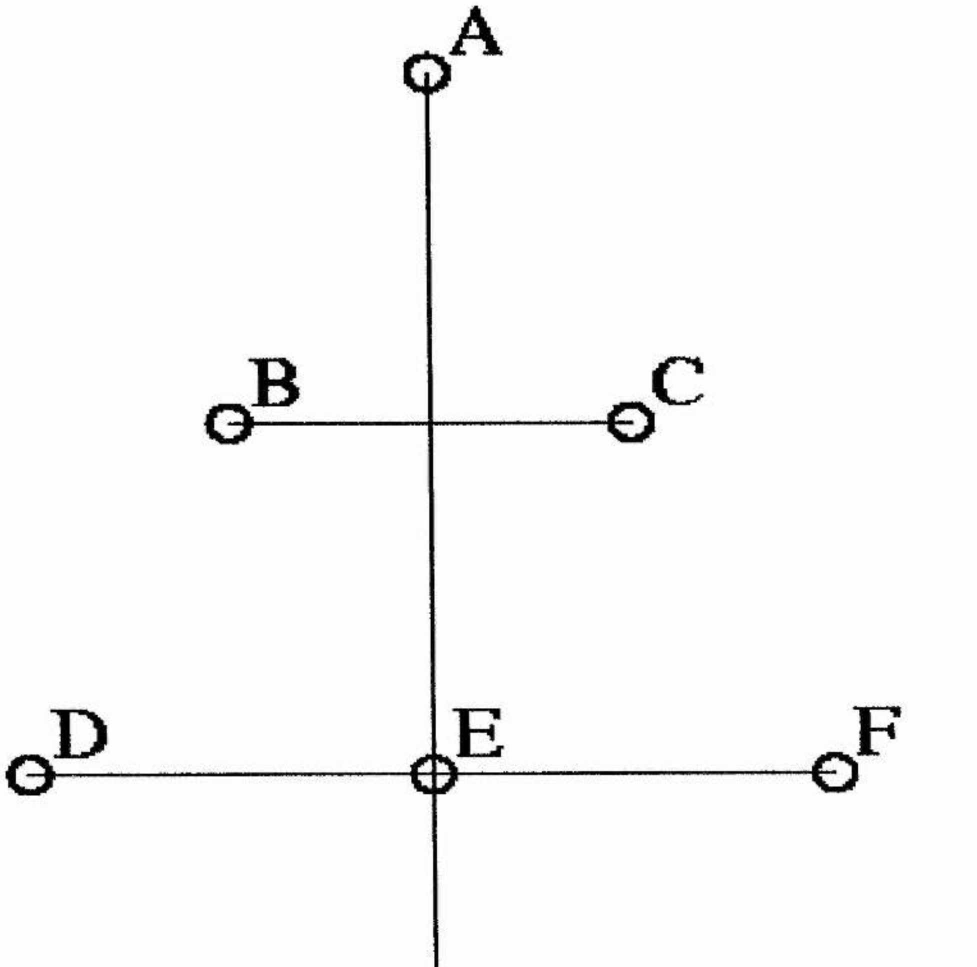

Figure 7ii. Diagrammatic representation of the "zone of influence". Position E corresponds to the exact position occupied by the fish.

7.3 Results

Movements of radio-tagged dace

The four fish released below the weir on 19 March 1997 showed the same immediate post-release pattern of behaviour, swimming upstream towards the weir several times, before moving rapidly downstream 25 minutes after release, and exiting the East Stoke Millstream (Fig. 7iii). Contact with all four fish was regained in a large pool in the main River Frome, 1560m downstream of the release point, 65 minutes after leaving the vicinity of the release cage. At 1745 hours, fish 6 left this pool, and headed rapidly downstream, while the other three fish remained in the pool. Contact with fish 6 was maintained until 1815 hours, whereupon it had reached and become stationary at a position 2950 m downstream of the release point. The continued presence of the other three fish was recorded at 1825 hours. On returning to the previously recorded position of fish 6, no signal was detected, and despite continued tracking downstream, the fish was not located again that evening. A thorough search from the release site to the tidal reaches of the river, including the lower portions of all tributaries and side streams, failed to re-locate fish 6, and no further contact was made during the study.

Fish 2 and 3 were located on 20 March 1997 in Luckford Lake, a tributary stream of the River Frome, 448 and 416 m upstream of the confluence respectively. (Figs. 7iii, 7iv & 7v). Visual observations showed that each fish was in a shoal, being accompanied by approximately 150 and 50 other adult (> 150 mm) dace respectively. Thereafter, each fish was visually observed on a daily basis. In all cases, the tagged individual was associated with other dace.

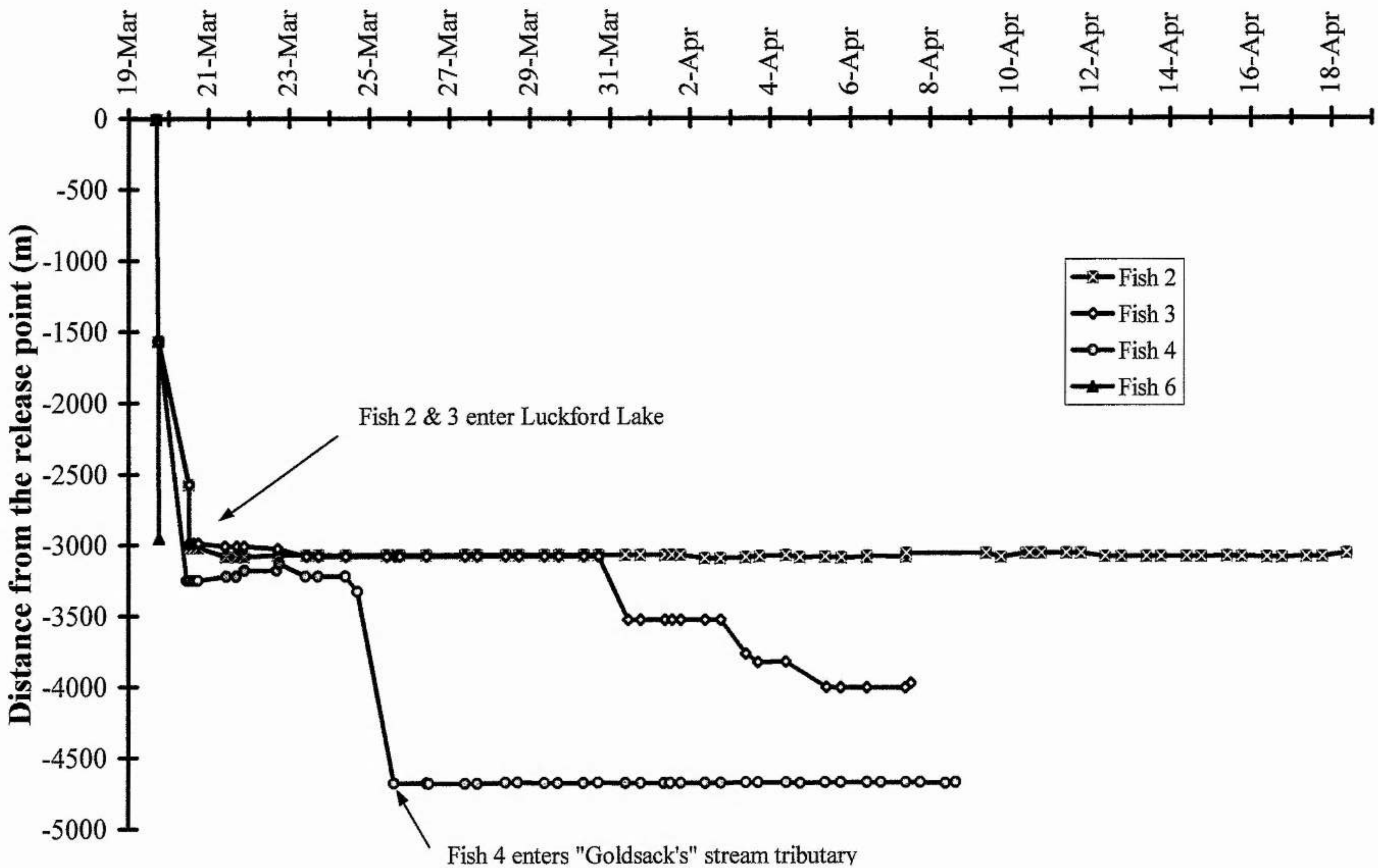

Figure 7iii. Movement of the dace released at site 1. Negative values refer to positions downstream of the release point. Upstream movements in tributaries increase the distance from the release point, and are shown as such.

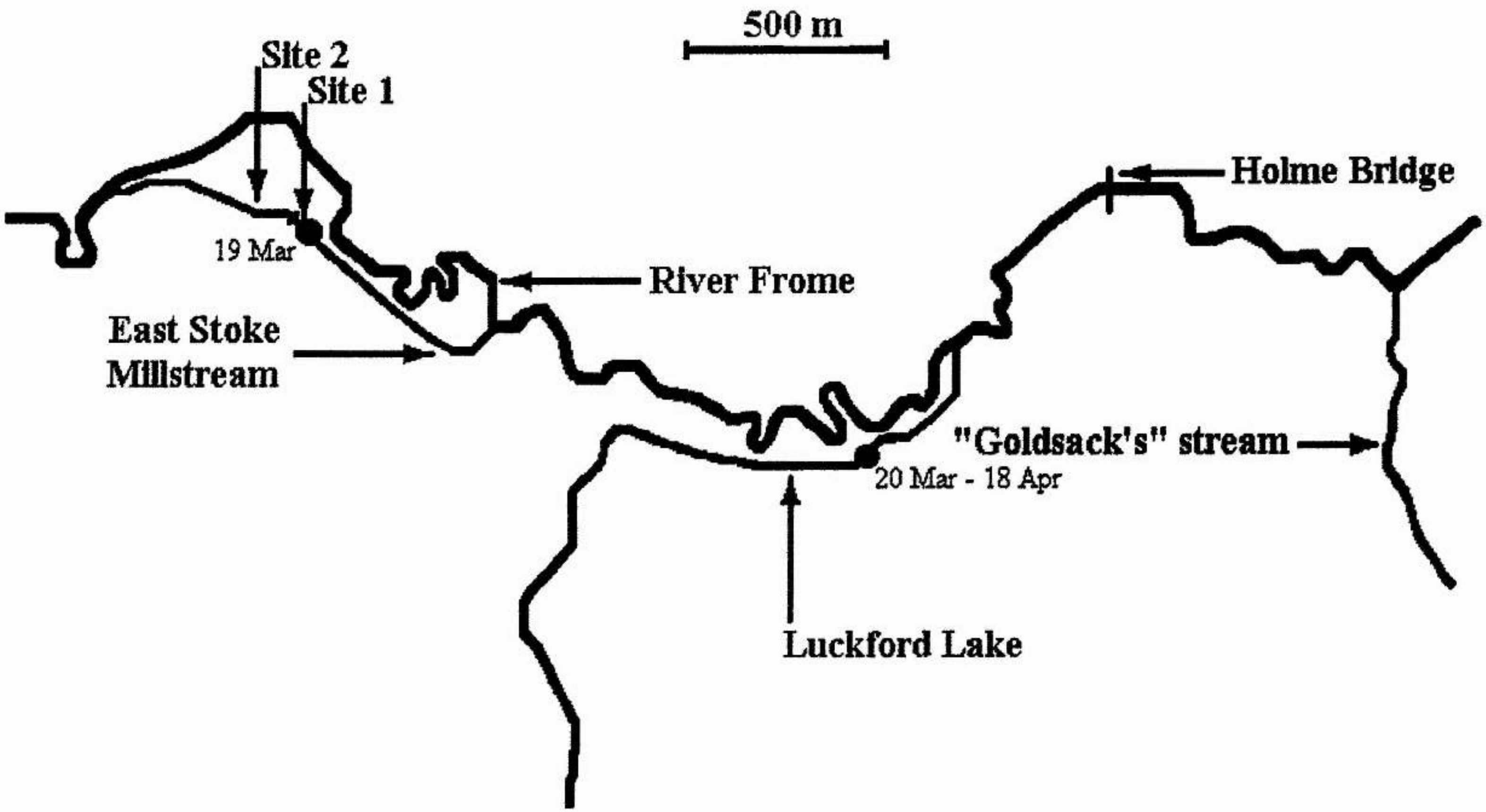

Figure 7iv. Map showing the post-spawning movements of fish 2.

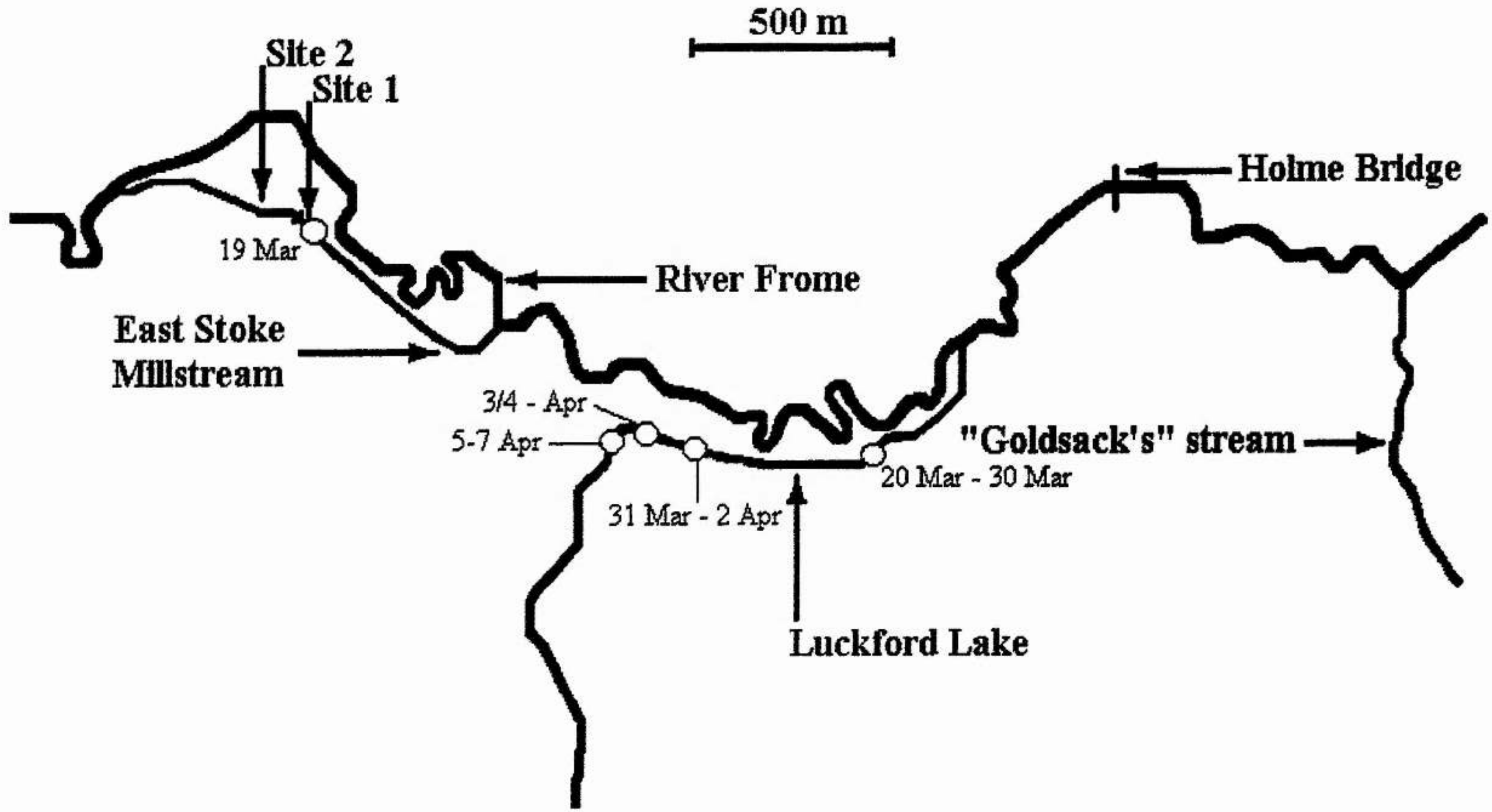

Figure 7v. Map showing the post-spawning movements of fish 3.

Fish 2 remained in the same area of Luckford Lake until observations were terminated on 18 April 1997(Fig 7iv). Fish 3 slowly progressed further up Luckford Lake reaching a maximum distance of 1435 m up this tributary, over 4000 m from the release point (Fig 7v). It was observed on 5 April 1997 with 7 other dace, all smaller than itself, and both it and two of the other dace appeared to have fungal infections. Fish 3 was found dead on 7 April. On examination, the fish was almost completely covered in fungus, apart from the area surrounding the tag attachment site. This area was free of infection, presumably due to the fungicidal action of the malachite gel, which in accordance with the suggestions of Beaumont *et al.* (1996), had been applied at the time of tagging, of which some was still evident.

On 20 March 1997, fish 4 was located in the River Frome, a short distance downstream of Holme Bridge (Fig. 7vi). The following day this fish was visually observed in an area of slack water immediately downstream of one of the bridge pillars, 3220 m downstream of the release site, in a shoal containing approximately 200 other dace. The fish remained in the vicinity of the bridge for 4 days, before moving downstream 1340 m and entering the lower end of an unnamed tributary, referred to as "Goldsack's" stream, on 25 March 1997 (Fig. 7vi). No visual observations were possible in this tributary, due to the turbid nature of the water throughout the study period. Fish 4 remained in the same section of this tributary until it was removed by electrofishing on 8 April 1997, whereupon it was found to be accompanied by several hundred other dace. Of the 11 accompanying dace captured, 8 were adult females, of which only one was spent. Few identifiable food items were found in the gut contents of any fish at this site, and six of the guts were completely empty.

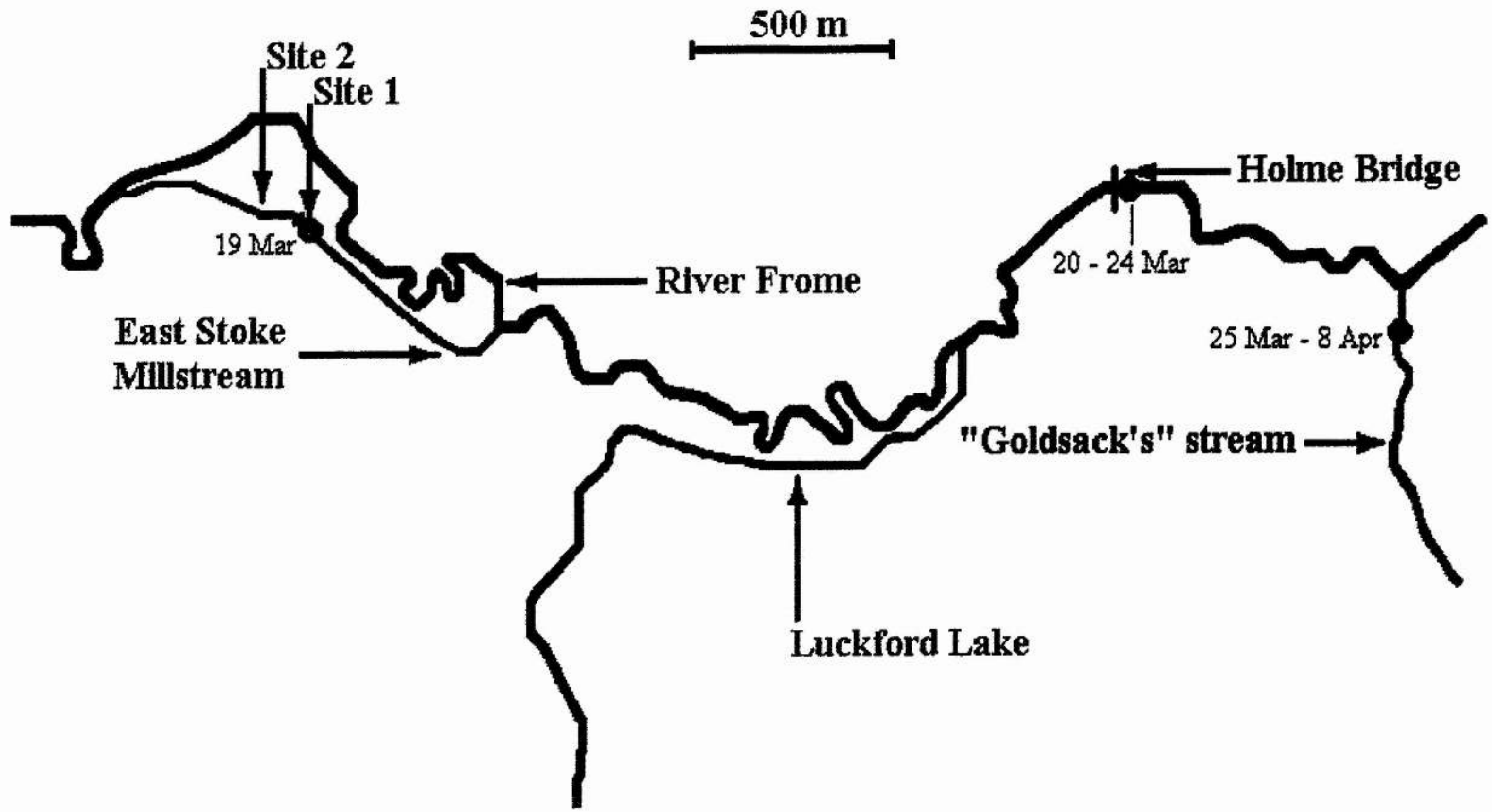

Figure 7vi. Map showing the post-spawning movements of fish 4.

The two fish (1 & 7) released at Site 2 on 21 March 1997 moved upstream initially, remaining at different sites within 50 m of the release cage for the rest of the day (Fig. 7vii). Fish 1 was both radio-located and visually observed within the vicinity of the release cage regularly up to 26 March 1997, always in the company of other dace. The fish was never recorded more than 65 m downstream or more than 55 m upstream of its release point, although it did move around extensively within this area, frequently re-using the same sites. Fish 1 was not found on or after 27 March 1997 despite a thorough search covering several kilometres, both upstream and downstream of its last known location.

Fish 7 was also frequently radio-located and visually observed in the vicinity of the release point, on all occasions with other dace, and occupied some of the same positions used by fish 1. Contact with fish 7 was maintained until 17 April 1997 when the fish was recaptured by electrofishing, along with 5 other dace. During the 27 days following release, fish 7 was never located more than 180 m upstream or 125 m downstream of the release point. The five dace captured with fish 7 were all spent females. All fish contained food. Two of the accompanying fish had fin clips, indicating that they were part of the group captured on 17 & 18 March 1997.

Diel migrations were not detected in any of the post-spawning dace, either in the main River Frome, or any of the tributaries or side streams.

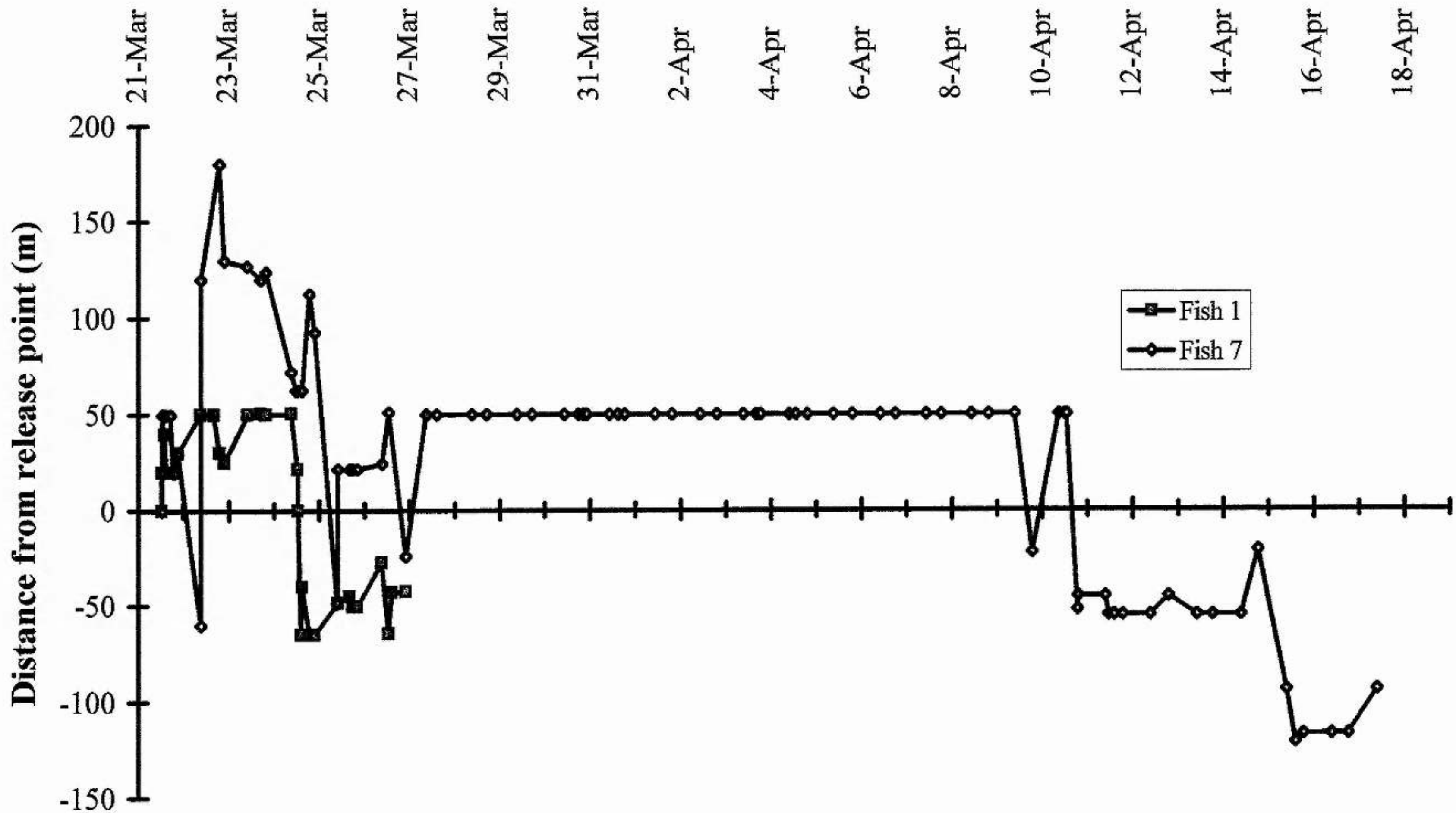

Figure 7iv. Movements of the two fish released at site 2. Positive values correspond to positions upstream of the release point.

Habitat characteristics

In total, 213 sets of habitat measurements were recorded from 39 different sites used by five of the radio-tagged fish. The mean number of sets of habitat data per fish was 42.6, and ranged from 17 to 68. Only three of the sites (7.7%), used on nine separate occasions (4.2%) were in the main river, the rest being in tributaries and side streams. This behaviour was observed despite at least four of the six fish moving from the East Stoke Millstream into the River Frome soon after release, and all fish having unrestricted access to the main River Frome.

Substratum within the zone of influence tended to be either leaves (code 1) or silt (code 2), however those substrata recorded at the exact position of the fish (E) were most commonly silt (code 2), accounting for almost half of the records (Fig. 7viii). Water velocities within the zone of influence at the residence sites ranged from 0 to 0.61 m s^{-1}, with a mode of 0.00 and a median of 0.01 m s^{-1}. At the position used by the fish (E), water velocity varied from 0 to 0.57 m s^{-1}, with a mode of 0.00 and a median of 0.02 m s^{-1}. Over 85% of sites used had a water velocity less than 0.10 m s^{-1} (Fig. 7viii). Depths within the zone of influence ranged from 0.10 m to 1.39 m (median = 53), whilst depth at position E ranged from 0.17 to 1.13 m (median = 54)(Fig. 7viii). Instream cover was generally absent within the zone of influence, with 87% of the sites having zero instream cover. Similarly, 75% of the positions used by the fish had no instream cover (Fig. 7viii). Almost eighty percent of the sites used were at least half shaded by outstream cover (Fig. 7ix).

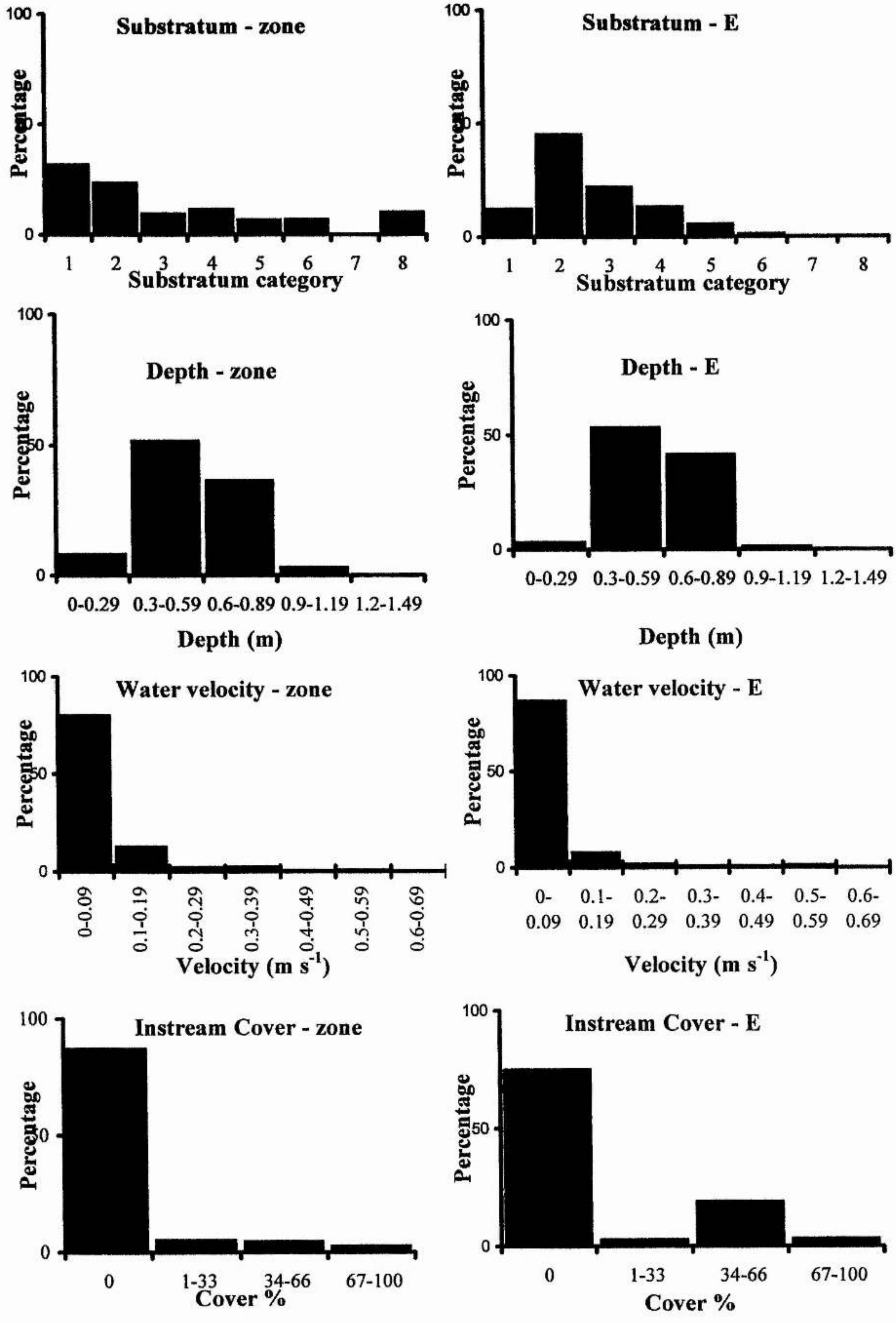

Figure 7viii. Habitat characteristics found at the fish position and within the zone. Substratum categories: 1=leaves 2=silt 3=mud 4=sand 5=gravel 6=pebbles 7=boulders 8=bedrock.

For all five fish, t-tests showed that depth at E was significantly greater than at A ($p = 0.04$, $t = 3.00$), and was also greater than depth at B ($p = 0.07$, $t = 2.47$), D ($p = 0.11$, $t = 2.01$) and G ($p = 0.06$, $t = 2.56$). Of the 30 possible comparisons (5 fish positions (E), six surrounding positions), the depth at E was greater than all except three, those being position C and F for fish 4, and position C for fish 7.

Velocities at all positions were generally low (mean = 0.06 m s^{-1}), however the velocity at E for all five fish was significantly lower than at A (t-test, $p = 0.03$, $t = -3.43$). It is noticeable that two of the three positions that were deeper than at E (fish 4, positions C & F and fish 7, position C), also had a higher flow velocity. By re-examining the raw data, it became apparent that a substantial proportion of the habitat measurements taken for fish 4 and 7 corresponded to positions immediately downstream, and slightly to one side of areas where the stream flow was focused through pipes. As a result, the measurements at positions C & F were in a direct line with the outfall from the pipe, potentially explaining the increased depths and velocities found at these positions.

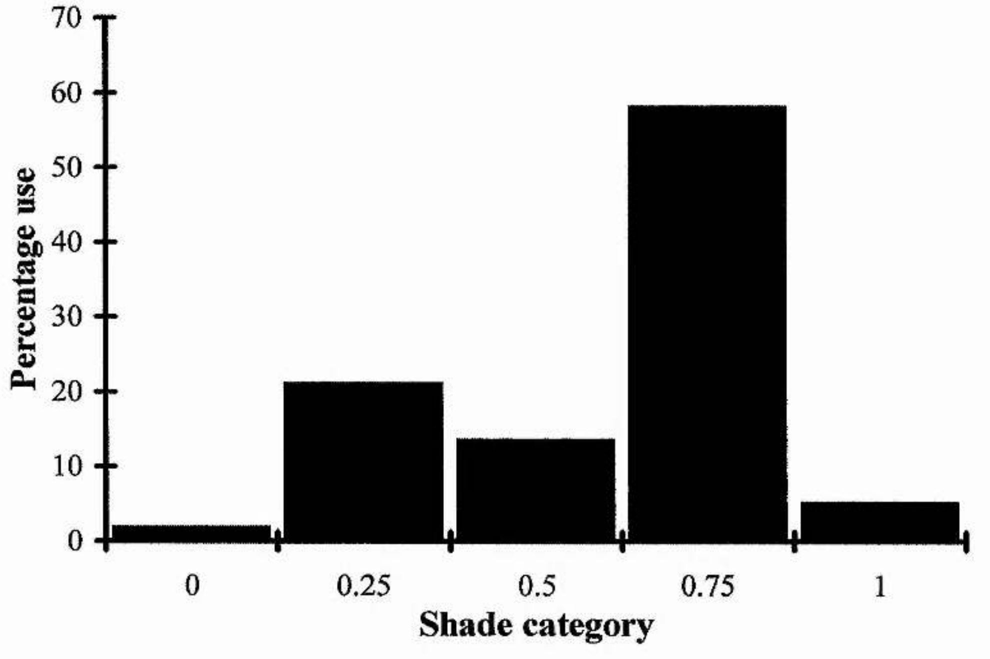

Figure 7vi. Proportion of the sky above bank level obscured from the fish by outstre
cover at each of the sites used by radio-tagged dace. The majority of the
and tributaries within the study area were unshaded.

7.4 Discussion

At the end of the spawning period, the tagged dace did indeed leave the spawning area, however they did not appear to move to areas with a rich food supply. Consequently the hypothesis that dace leave the spawning area and select post-spawning habitats in order to maximise their food intake, and replace the resources used up during spawning, has been rejected.

MIGRATIONS

Of the four dace released at Site 1, all showed the same immediate post-release pattern of behaviour. The observation that all the fish approached the weir on several occasions before heading off downstream may suggest that their initial motivation was to move upstream. It is possible that had the weir not been present the fish would have continued to move upstream. Whether or not the weir represents a physical barrier to the upstream movements of dace is unclear, as none of the radio-tagged fish appeared to attempt to ascend.

The fact that the fish left the East Stoke Millstream shortly after release suggests that this habitat was not optimal for spent dace. Having entered the main River Frome, the four fish moved rapidly downstream and at least three moved into the lower reaches of tributaries, where they remained. This suggests that there was little, if any, suitable habitat between the release point and the first tributary, and that the combination of habitat characteristics available in the downstream ends of such tributaries, i.e. relatively slow flow, shade and a general absence of instream macrophytes, were selected by post-spawning dace. The discovery that each radio-tagged fish was associated with other adult dace, often in large numbers, is a further indication that these sites are preferentially selected. These data are supported by an observation made by Mann & Mills (1986), who caught fin-clipped dace, initially captured and marked at the same spawning site as in this study (Fig 7i, Site 1), in the lower reaches of another tributary, Tadnoll Brook, shortly after release.

The two radio-tagged dace released at Site 2 also showed the same immediate post-release pattern of behaviour as each other, but different to that displayed by the fish released at Site 1. Both fish remained in the vicinity of the release point, suggesting that the habitat characteristics in this area were suitable. As the same capture, tagging and release techniques were used for both groups of fish, it seems likely that the observed differences in the immediate post-release behaviour were a consequence of differences in the accessibility of suitable habitat types.

Dace constitute the major food items of pike in the River Frome (Mann, 1982). During late March and early April, pike spawn in small, densely vegetated side channels and ditches connected to the main River Frome (Mann, 1980). It seems possible that predator avoidance is a factor in the apparent selection for the generally un-vegetated downstream ends of tributaries.

The discovery of ripe female dace in "Goldsack's" stream on 8 April 1997 was curious. Mann (1974) never found ripe dace at any spawning site during April in either the Frome or Dorset Stour. In this study, of the 88 adult female dace caught on 17 and 18 March 1997, 60% were spent. In contrast, of the eight adult female dace caught on 8 April, seven were ripe. The reasons for this are unclear, however the turbid nature of the water in this tributary could be a factor. Dace eggs are known to be particularly sensitive to silt deposition, and in the

River Frome the majority of egg mortality was attributed to the effects of silt and other fine sediments (Mills, 1981; Mann & Mills, 1986). It is possible that spawning in "Goldsack's" stream had been delayed, in response to the turbid conditions.

Aggregations of spent dace in the downstream ends of tributaries after the known spawning season may, in the past, have been taken as an indication that the tributary had been used as a spawning site. However, the data presented here suggest that at least some of the dace found in the lower ends of tributaries at this time are likely to have spawned elsewhere. Indeed, there is no evidence to suggest that any of the dace present in either of the tributaries actually spawned there, and the presence of ripe female dace after the end of the spawning season, in the downstream end of one of them may in fact indicate the unsuitability of that particular site for spawning.

Some fish species are known to change their behaviour in accordance with the daily cycle of light and darkness (Helfman, 1993). These diel patterns are known to be disrupted during the cold-water periods of the year and a "relative breakdown of normal patterns" has been observed around the spawning period (Helfman, op. cit.). During May and June, dace in the River Frome show a diel migration between different, clearly defined day and night-time habitats (Clough & Ladle, 1997). It was hypothesised that neither site on its own met all the requirements of the dace during a complete 24-h cycle, and that the migration may represent a trade-off between feeding and predation threat (Clough & Ladle, op. cit.). Diel migrations were not observed in any of the post-spawning dace, the inference being that the selected site met all the requirements of the fish during the complete 24-h cycle. The relatively high numbers of individuals observed in small areas of these tributaries, coupled with low water velocities and hence a limited supply of drifting food, suggests that there were either abundant food supplies at the positions occupied, or that feeding was of low priority to the fish. Few identifiable food items were found in the guts of the fish captured in the tributaries (mean < 1 item per fish), with 66% of the guts being completely empty. This suggests that the fish were not aggregated in these areas in order to take advantage of a rich supply of food. The possibility that having missed their normal window for spawning, the ripe female dace were re-absorbing their eggs, thus reducing the need to feed, should not be overlooked. However, it does not explain the lack of food items in the guts of male and spent female dace, unless the advantages of remaining as part of a large shoal outweigh the benefits of searching for food at this time of the year.

Two of the most common food items of dace in the River Frome are the larvae of *Simulium* spp. and Trichoptera, particularly *Brachycentrus subnubilus* Curtis (pers. obs.). The two most common species of *Simulium* within the study area, *S. ornatum* Meigen and *S. lineatum* (Meigen), both pupate in early April, and larvae are scarce at this time (Ladle *et al.*, 1977). Similarly, *B. subnubilus* larvae pupate during April (Gunn, 1985). As a result, during the post-spawning period few of either of these food items are available to the dace. It is possible that, in the virtual absence of two of their major food items, it is not profitable for dace to actively search for food.

HABITAT

The majority of the River Frome and its tributaries in this study lie within areas of grazed pasture, and as a consequence have little outstream shade and extensive areas of aquatic plants. After spawning, dace chose slow flowing, shaded sites out of the main river channel, perhaps selecting low velocity areas in order to minimise energy expenditure, and opted for positions with little in-stream cover, possibly to minimise the risk of ambush attacks from pike. The apparent preference for shaded sites is interesting, particularly as such sites are comparatively rare within the study area, and may be linked with predator avoidance, with the outstream cover obscuring them from the view of avian predators. Alternatively, the presence of shade inhibits the growth of instream macrophytes, and the apparent selection of shaded areas may be an artefact of the preference for areas with little or no instream macrophyte cover.

Within the chosen areas the individual fish frequently selected the deepest and slowest flowing positions available. The observed selection of shallower areas, however, when water velocity was greater in the deepest sections, e.g. at the mouth of a pipe, suggests that relative depth is less important than the preference for low water velocities.

During the low flow conditions of summer, dace in the East Stoke Millstream occupy positions with a water velocity between 0.10 and 0.40 m s^{-1} (81% > 0.15 m s^{-1}) (Chapter 6, Garner & Clough, 1996). The preference of post-spawning dace to aggregate in areas with slower water velocities (0.00 - 0.61 m s^{-1}, 80% < 0.1 m s^{-1}), and apparent selection of the slowest flowing positions within these areas 0.00 - 0.57 m s^{-1}, 87% < 0.1 m s^{-1}), suggests that energy conservation is an important factor.

In view of the nature of the areas selected by post-spawning dace, the unavailability of two major food items, and the apparent lack of food in the guts, it is suggested that energy conservation and predator avoidance may take precedence over feeding at this time of year.

Fish, including cyprinids, appear to be able to adapt to feast-and-famine conditions by showing marked growth spurts, known as compensatory growth, when food supplies are increased following a period of starvation or food restriction (Jobling, 1994). Providing food supplies are adequate, the energy reserves of fish are replenished during the post-spawning period, and weight gain may be rapid (Jobling, op. cit). However, this does not appear to occur during the immediate post-spawning period in dace. Mann (1974), referring to River Stour dace, states that "spawning delayed the maximum K_n (relative condition) of mature dace until June/July." If this is also the case in River Frome dace, then in order to reach this maximum value of relative condition, a substantial amount of food, over and above normal maintenance rations, must be consumed after the end of the spawning period. Monthly drift samples taken in the study area show a 13 fold increase in the daylight numbers of drifting invertebrates between the end of April and the end of June (S. Clough, pers. obs.), and large numbers of early instar *S. ornatum, S. lineatum* and *B. subnubilus* larvae appear during May. In order to take advantage of these substantial increases in food availability, it is anticipated that the observed post-spawning behaviour will not persist. Instead, it is proposed that the dace will re-locate within the system (Clough & Beaumont, 1998), occupy daylight areas with similar characteristics to those described in Chapter 6, and begin diel migration behaviour (Chapter 3, Clough & Ladle, 1997). The expected change in behaviour is likely to be timed to coincide with the increase in food availability, and result in compensatory growth, allowing the fish to reach maximum relative condition (K_n) by early summer.

CHAPTER 8

Nocturnal habitat use

The fieldwork for this study was carried out with the assistance of Nicholas Brown, an MSc. Student from Middlesex University. Nicholas helped by carrying out some of the nocturnal observations and assisted with the collection of habitat data.

8.1 Introduction

The activity and habitat use of many stream fishes changes over time, both daily (Tyus, 1991; Sempeski & Gaudin, 1995; Clough & Ladle, 1997; Roussel & Bardonnet, 1997) and seasonally (Baras, 1995; Cunjak, 1996; Lucas & Batley, 1996; Ridgway & Shuter, 1996). Models of fish habitat suitability must take into account all these changes in habitat utilisation in order to be fully effective.

Observations of diurnal habitat use during the summer showed that dace in the East Stoke Millstream have specific preferences for particular habitat types (Chapter 6; Garner & Clough, 1996). During the same period, radio-telemetry showed that at least some members of the shoals observed during the day, moved to different sites around dusk. Another migration at dawn was frequently seen, with the fish 'homing' to the same area they had occupied the previous day (Chapter 3; Clough & Ladle, 1997). This behaviour suggests that during the summer, adult dace have separate, distinct daylight and darkness habitat preferences. In order to understand the possible benefits to the fish of such a diel migration, it was necessary to establish the habitat characteristics of both the diurnally and nocturnally used sites. In addition, detailed information regarding homing accuracy, behaviour and activity at each site, was required in order to elucidate the potential gains of such behaviour to the individual.

Several techniques can be used to examine habitat use by fish, of which many overlook the propensity of fish to change their behaviour when they are disturbed. Of the non-intrusive methods, visual observation from the bank is the simplest and least biased, particularly in small shallow streams where water clarity is high and macrophyte density low (Garner & Clough, 1996). Direct observation, however, cannot be used in deep water and, even where the water is shallow, observations cannot be made at night or in turbid conditions. Either radio- or sonic-telemetry can be applied to most situations, however the exact location, position in the water column, orientation and activity of the tagged individual can be very difficult to determine using these techniques. In addition the size of the transmitters precludes their effective use with fish under 18 cm (fork length).

Bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*), marked with polymer implants, have been observed during darkness, with the use of a fluorescent light (Bonneau *et al.*, 1995). Similarly, visual observations at night, using a flashlight, have been carried out on fish in the littoral zones of lakes (Rossier, 1997), and in a river, on juvenile grayling *Thymallus thymallus*, (Sempeski & Gaudin, 1995). However, when this technique was tested with adult dace (*Leuciscus leuciscus* (L.)) in the East Stoke Millstream, the fish rarely stayed in one position when the light was directed into the water, instead moving out of the beam, often rapidly (S. Clough, pers. obs.). The impact of the fleeing fish, or the light, on those individuals not directly in the beam was unknown. As a result a limited amount of data could be collected using this technique, and the interpretation of such data was uncertain.

Light emitting, luminous tags, visible during darkness, have been used to study the movements of nocturnally active animals, including bats (Gifford and Griffin, 1960; Bulcher, 1976), badgers *Meles meles* (Cheeseman and Mallinson, 1980), rats *Rattus norvegicus* (Hardy and Taylor, 1980) and foxes *Vulpes vulpes* (Macdonald, 1978) and are "often adequate for making systematic observations of animals which live in the open" (Kenward, 1987). By attaching to a fish a luminous tag, which is visible during darkness, observations of the movements, habitat selection and behaviour of the individual can be made without disturbance from the observer.

In all studies of tagged animals it is essential that the tag itself, and the attachment used, have a minimal effect on the behaviour of the tagged individuals. Thus the aims of this study were fourfold:

- Design and test both radio-active isotope tags, and a suitable attachment technique for use with fish.
- Discover how easily an isotope tagged fish can be located in the field.
- Examine the nocturnal habitat use and activity of adult dace under natural and near-natural conditions.
- Test the hypothesis that the habitats occupied by dace during darkness are randomly selected.

8.2 Materials and methods

STUDY AREA

Field observations were carried out in the upstream portion of the East Stoke Millstream, the "Millhead". The discharge of the Millstream can be adjusted using a variety of hatches, and was continuously monitored close to the study area.

Observations were also carried out in the near-natural conditions of a Fluvarium (Chapter 2), through which a portion of the flow of the East Stoke Millstream passes.

Environmental variables, discharge ($m^3 s^{-1}$), air and water temperature (°C) and incident light (relative units) were continuously monitored near the release site.

TAG DESIGN

Betalights® are sealed glass cylinders, internally coated with phosphor, and filled with tritium gas. The products of the radio-active decay of the tritium bombard the phosphor, activating it, and causing it to emit light. Betalights® are available from the manufacturer (Saunders-Roe Ltd.) in a range of shapes, colours and brightness. For the purposes of this study, green cylinders (30 mm x 3 mm), with a brightness rating of 400 microlamberts were selected. Luminous isotope tags were constructed by placing a short (6 mm) section of heat-shrink tubing over each end of a Betalight®, leaving approximately half of the tubing protruding past the end of the glass cylinder. Heat was then applied, causing the tubing to shrink and grip the Betalight®. Whilst still hot, the protruding sections of tubing were flattened against the bench, producing a small tab at either end of the cylinder (Fig. 8.2i). Each tag was made individually identifiable by the addition of further short sections of shrink tubing at different positions along the cylinder. By using different combinations of bands of four widths (2, 4, 6 & 8 mm), unique codes were created. The weight of prepared isotope tags varied a little according to the number and size of shrink tubing bands that were added. The weight in air of 10 prepared tags was 4.4g, giving a mean individual weight of 0.44g.

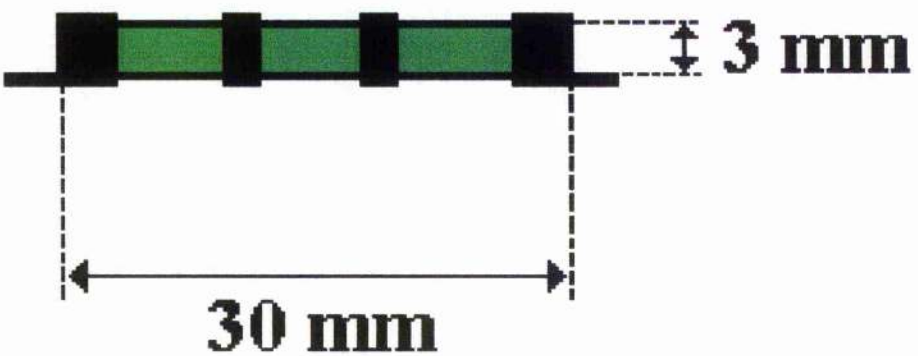

Figure 8.2i. A prepared Betalight® radio-active isotope tag.

VISIBILITY

In order to test visibility in the field, six tags, each with a different combination of bands, were attached to a cork board by pushing pins through the tabs at either end of the tag. The cork board was anchored to the river bed in flowing water 0.8 m deep, one of the deepest sections within the study area. After dark, an independent observer, positioned on the river bank adjacent to the board, recorded the position of each tag visible, and the number, size and position of any visible bands, both with the naked eye and with the use of binoculars (magnification 8 x 24).

ALGAL GROWTH

It was considered that algae might grow on the tags, thus reducing their visibility, and that tags with bands of shrink tubing may be more susceptible to algal growth than those without bands due to the provision of an attachment site by the band. In an attempt to prevent the growth of algae, one set of three isotope tags (0, 2 & 4 bands) was coated with silicone grease and another set with a silicone grease and copper sulphate (a known algicide) mixture. The two sets of tags were attached to rubber bungs along with an identical set of untreated isotope tags to act as controls. The bungs were then fixed to the river bed in shallow running water in a line perpendicular to the flow. The relative brightness of the tags during darkness was recorded at the start of the experiment, after three weeks, and after six weeks. After six weeks the bungs were recovered and the tags examined for growth of algae.

ATTACHMENT TECHNIQUE

Prior to attaching the tags, fish were anaesthetised with Benzocaine to a level at which they no longer responded to external stimuli. Isotope tags were attached to the dorsal surface of adult dace using 2 sutures (Ethicon Coated Vicryl size 3/0, 26 mm curved reverse cutting needle), with one being attached to each shrink tubing tab at either end of the tag. The rear suture was attached to the fish immediately anterior, and slightly (approx.1 mm) to one side of the origin of the first dorsal fin ray. The front suture was attached one tag's length toward the head of the fish, from the position of the rear suture. Sutures emerged approximately one third of the total body depth down the left flank of the fish, and were tied together, so that the tag was pulled snugly against the fish, leaving no slack. A fungicidal gel, comprising malachite green and silicone grease (Beaumont *et al.*, 1996) was carefully applied to the attachment site, ensuring the tag was not obscured.

In any study using externally attached tags it is essential that the tag weight is as small as possible in relation to the weight of the fish, to minimise both the impact on the fish of transporting the tag, and the load at the attachment site. In this study, in order to be able to comfortably fit a prepared tag between the dorsal fin and the head, only fish over 160 mm (fork length) were used. Prepared tags, with shrink tubing tabs, weigh 0.44 g in air. Therefore a prepared isotope tag represents 0.85 and 0.74 % of the body weight of 160 mm male and female dace respectively, based on a length : weight relationship for River Frome dace (Mann, 1974).

FLUVARIUM OBSERVATIONS

In order to examine the comparative behaviour of tagged and untagged dace both visual and video observations were carried out in the near-natural conditions of a Fluvarium. The Fluvarium tank consists of a glass sided channel (6 m x 1.4 m x 0.9 m) through which river water flows, governed at the upstream end by electronic hatches and by valve boards at the downstream end. The glass sides allowed observations of fish to be made. The tank was set up using a series of bricks and artificial river plants, so that a range of habitats and flow patterns was available. In order to allow night-time observations of both the tagged and untagged dace, the tank was continuously illuminated using 4 red strip lights, situated immediately above the tank, approximately 2 m above water level. The glass roof of the Fluvarium building ensured that the normal light-dark sequence was maintained. Three individually identifiable, isotope-tagged dace (170, 209 & 167 mm fork length) were placed in the Fluvarium tank, along with 8 untagged dace of mixed sizes (range 120-210 mm). Direct observations were carried out both during the day and at night, with the position of all visible dace being marked on two scale drawings of the tank. One showed the fish's position within the tank (horizontal component) and the other described the position of the tag relative to the substratum (vertical component). From the scale drawings it was possible to calculate which areas were used most frequently by the fish, and examine the inter-individual distances of tagged fish at different times of the day. In addition, video observations were carried out by focusing a video camera on one specific section of the tank, and recording for three hours. Untagged fish were not visible on the video recordings, and individual identification of tagged dace was not possible due to a lack of definition. In addition, only fish near to the glass were visible, and all records corresponded to a narrow section of the tank nearest to the glass (approx. 20 cm). Each video tape was viewed by haphazardly selecting a starting position near the beginning of the tape, and recording the distance from the downstream end of the tank, height above the substratum, and activity of all fish visible over a two-minute period. This process was repeated at 15 minute intervals until the end of the tape was reached. Different sections of the tank were observed on different nights, with the whole tank being covered.

FIELD OBSERVATIONS

All dace in this study were captured from the East Stoke Millstream, using rod and line. In total twelve dace coded A - L (mean fork length = 180 mm, range = 168-231 mm) were tagged with individually coded isotope-tags. Dace in the

River Frome are known to be highly mobile, periodically relocating within the river system (Clough & Beaumont, 1998). Consequently, the fish were captured, tagged and released in three separate batches (9/8, 9/9 & 30/9/97) to ensure a spread of observations. After tagging, each batch of dace was transferred, along with a shoal of untagged dace, to a release cage (1 m x 0.5 m x 0.5 m) (Chapter 3), from where they were released remotely with a minimum of disturbance (Clough & Beaumont, op. cit.) after a settling period of 6-10 hours.

The addition of a tag to the body of a fish can result in the fish having "negative buoyancy". In an experiment on roach (*Rutilus rutilus*), negatively buoyant fish denied access to the surface took 112 hours to completely regain neutral buoyancy, whereas all individuals with unrestricted access to the surface completely compensated for the negative buoyancy within 7 hours (Evans & Damant, 1929). To this end, the release cage was positioned in water slightly shallower than the depth of the cage, in order to allow the tagged dace unrestricted access to the surface.

The post-release positions of each tagged dace were recorded on a detailed sketch map with specific reference to both numbered posts and static riparian features (e.g. bushes). A written description of each recorded location was made, and in addition a small, labeled peg was inserted into the bank on a hypothetical line which passed through the position of the fish, and was perpendicular to the main direction of the flow. For the purposes of the analysis, the longitudinal position of each fish was calculated as the distance in metres from the mouth of the release cage to the peg, along the north bank. In addition, the latitudinal (across the river) position of the fish was assigned a code, where code 1 corresponded to the fifth of the river's width closest to the south bank, and code

5 represented the fifth of the river's width closest to the north bank. The remaining three fifths of the width were classified as codes 2, 3 & 4 accordingly. The wetted width within the study area ranged between 4 and 5 m, and as a result, each code represented between 0.8 and 1 m of channel width.

Once located, the activity of each fish was observed closely for five minutes, with the magnitude of any movements being recorded. Movements were classified as either "none" (< 0.1 m), "short" (0.1 - 0.5 m), "longer" (> 0.5 m), or "relocation" (> 5 m). The degree of activity over the observation period was then assigned a code between 1 and 6, according to the following scale:

Activity code	Degree of movement
1	None
2	< 3 short movements
3	3 or more short movements
4	< 3 longer movements
5	3 or more longer movements
6	Relocation

HABITAT MEASUREMENTS

In order to determine the habitat selection by isotope tagged dace, habitat measurements were made at each of the positions used by the fish. Habitat variables; substratum composition (modified Wentworth scale), depth (m), water velocity (m s^{-1}) and instream cover (% stream bed area), were recorded for each site used. Measurements were taken within 48 hours of a fish's first known arrival at a site, and when sites were re-used, a new set of habitat measurements were taken if more than 1 week had elapsed since the previous set were recorded, to allow for temporal changes in the habitat characteristics.

In order to determine the habitat characteristics of each area selected, seven sets of habitat measurements (A to G) were taken, in a "kite shaped" pattern, the whole area being referred to as the "zone of influence" (Clough *et al.*, 1998; Chapter 7). The fish position (E), determined by visual observation, occupied the intersect of the axes of the kite, with the longer portion being orientated into the flow. It was considered that, due to the direction and effects of the flow, the area upstream was likely to impose a greater influence on the fish's choice of position, than that which was downstream. By taking measurements in this way, an assessment of the habitat characteristics in the vicinity of the fish was gained, with measurements being taken from the area considered most likely to affect the fish's habitat selection. The relative depth and velocity characteristics within a given zone of influence were examined by subtracting the depth and velocity values for each position (A, B, C, D, F, G) from the corresponding values for the exact fish position (E). A positive value indicated that depth or velocity was greater at E than at the comparative position. Significance was tested, using a *t*-test of the mean difference between positions.

8.3 Results

VISIBILITY

The six tags attached to the cork board in 0.8 m of water were clearly visible from the bank, and the glow given off could be seen up to 10 m away. With the naked eye the positioning and relative width of the three widest types of band (4, 6 & 8 mm) were recorded correctly, however the narrow bands (2 mm) were not visible. There was also slight confusion in determining the width of bands that were positioned very close together (gap width <1mm). With binoculars, all codes were recorded correctly, however a comment was recorded that the narrow bands were very difficult to see.

ALGAL GROWTH

All isotope tags appeared duller after three and six weeks than at the start of the experiment, however there appeared to be no difference in relative brightness between the treatments. Algal growth on the tags attached to rubber bungs was 100% on the exposed surface of all treatments after six weeks in shallow flowing water.

Recapture of three tagged fish 31, 69 and 89 days after release showed that algae had grown on the tags. However, the growth consisted of a very thin layer, and although brightness is likely to have been reduced, it was considered that the code on each tag would still have been identifiable.

FLUVARIUM OBSERVATIONS

Visual and video observations in the Fluvarium suggested that the behaviours of tagged and untagged fish were equivalent, with no unnatural or unusual behaviour being observed.

Observations showed that during daylight both tagged and untagged fish grouped together just above the substratum in one small section of the tank, approximately 1 m^2 in area. The same section was used on each day of observation, and apart from occasional short excursions, usually by groups of three or four fish, very little movement was observed. At night, the fish were generally more spread out, and occupied two different sections of the tank, each approximately 1.5 m^2 in area. Visual observations showed that each of the tagged fish returned to the same position which it had previously occupied on each night of observations. As during daylight, the fish were usually close to the substratum (Fig. 8.3i), and very little activity other than maintaining station was observed. Tagged fish were significantly closer together during the day (t-test, $p < 0.001$, $df = 14$), with the mean distance between the tagged fish during daylight being 0.47 m, compared with 1.07 m at night (Fig. 8.3ii).

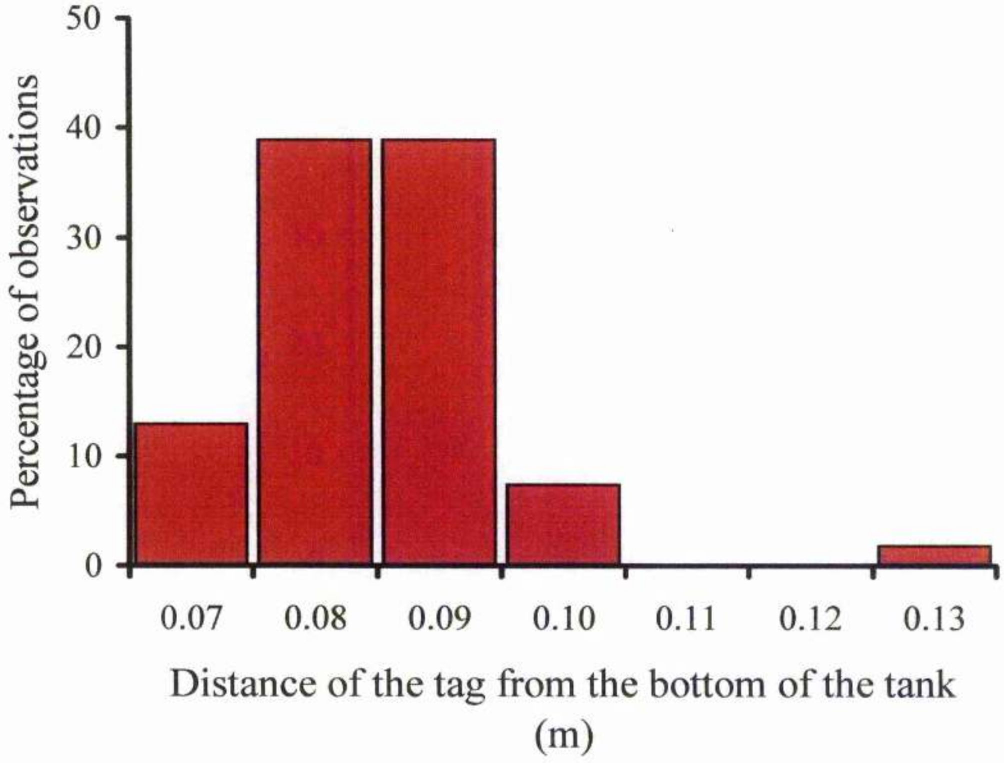

Figure 8.3i. Distance of the tags up from the bottom of the tank during darkness.

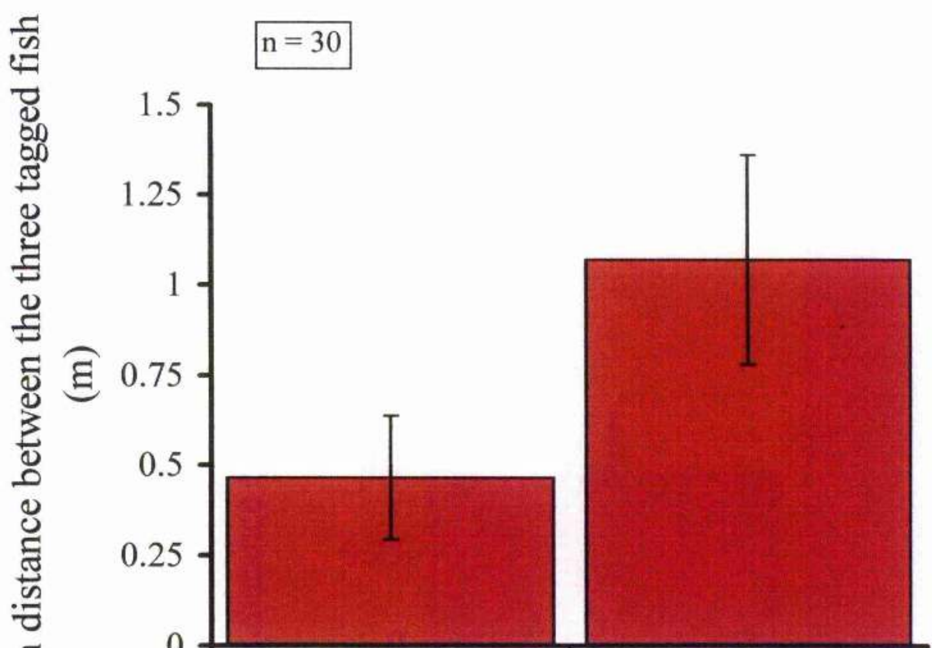

Figure 8.3ii. Mean distance between the tagged fish during daylight and darkness

FIELD OBSERVATIONS

In the river, isotope tagged dace were observed on a total of 247 occasions over a period covering 121 "fish nights" between 9/8/97 and 3/10/97, totaling over 20 hours of observation. Some dulling of the tags was noted, and this was thought to be due to the growth of algae.

Individual dace frequently re-used the same areas on consecutive nights (Fig. 8.3iv). Of 72 different "fish nights" of observations where a return was possible (i.e. excluding the first night of observation) the fish occupied the same area as on the previous observation on 44 (61%) "fish nights". Of these, 70 % were also in the same latitudinal position within the channel.

Daylight observations were particularly difficult, however on the vast majority of occasions when the tagged fish could not be located during the day, the observers can confidently say that they were no longer present at the position used during the night. Indeed, dace were only found at the same location during the day as occupied on the previous night on 10 occasions, despite these sites being the starting place for the search. When the tagged dace were located during daylight, they were always with other dace. In addition, there was further evidence that dace have separate daylight and darkness habitats, as reported elsewhere (Clough & Ladle, 1997; Chapter 3) (Fig. 8.3iii, 12-17 Sep).

Three of the tagged fish were re-captured, two after the end of the observation period. In each case some algae had grown on the surface of the tags, however the attachment was sound. The recaptures of two of the fish were close to the study area, however the third was reported by an angler, and was captured in the tidal reaches of the River Frome, 69 days after release and over 6 km downstream of the release point.

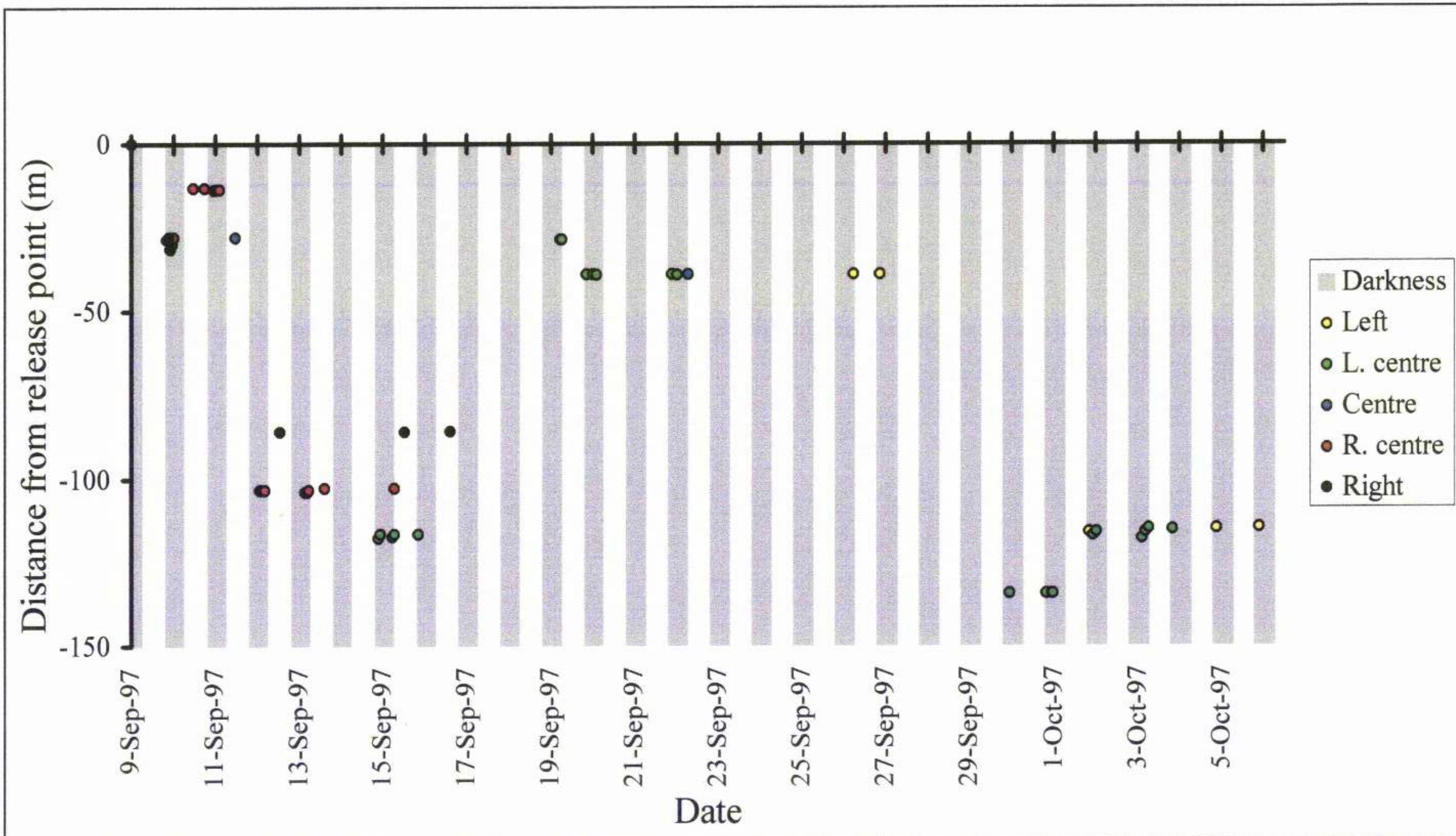

Figure 8.2iii. The post-release movements and position within the channel of fish F. Movements downstream of the release point are shown as negative values.

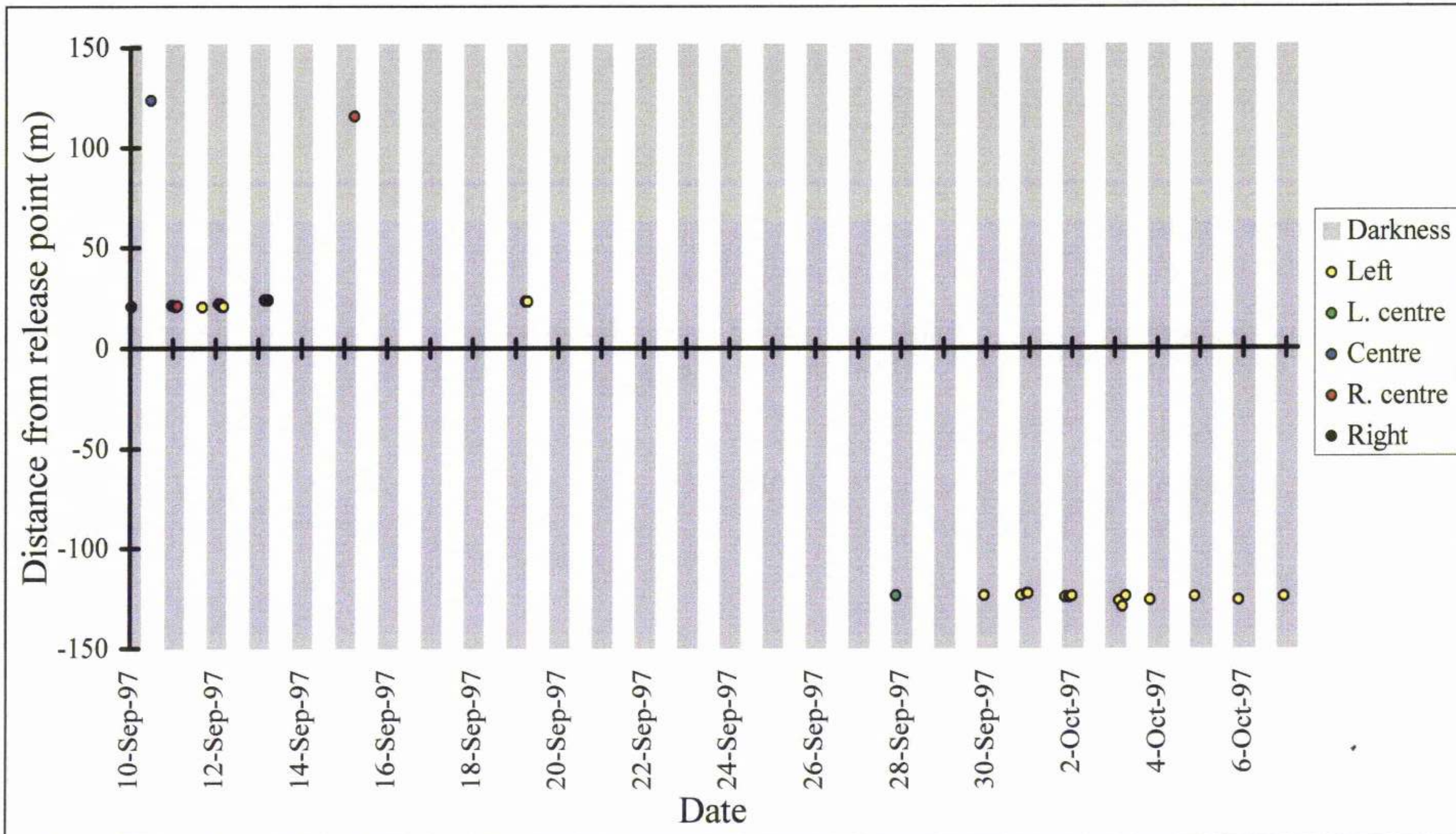

Figure 8.2iv. Post-release movements and position within the channel of fish E. Movements downstream of the release point are shown as negative values.

This re-capture supports suggestions that the aggregations of adult dace found in the tidal reaches of the River Frome consist, in part at least, of individuals that spend the summer in the vicinity of East Stoke (Chapter 5; pers. obs.).

Activity was generally low in all cases, with the modal activity code being 1 (the lowest value) in three of the five time periods studied. By treating the six movement codes as six ordered categories which can therefore be ranked, a Kruskal-Wallis one way analysis of ranks showed that median activity score was significantly greater in the hour before dawn than in the other time periods (χ^2 4df = 19.9, P = 0.001, adjusted for tied scores).

HABITAT

The habitat characteristics within the zone of influence were, in general, very similar to those found at the exact fish position (Fig. 8.3vi). Although 7 of the 8 substratum categories were represented within the zone of influence, substratum was most commonly sand (4) and gravel (5), accounting for 84% of the observations. Depths within the zone ranged from 0.04 to 1.20 m with a mean of 0.60 m, and water velocity ranged from 0 to 0.9 m s^{-1}, with a mean of 0.11 m s^{-1}. There was little instream cover within the zone, with over 65% of positions having zero cover, and 82% of sites having less than one third of their area covered with aquatic vegetation (Fig. 8.3vi).

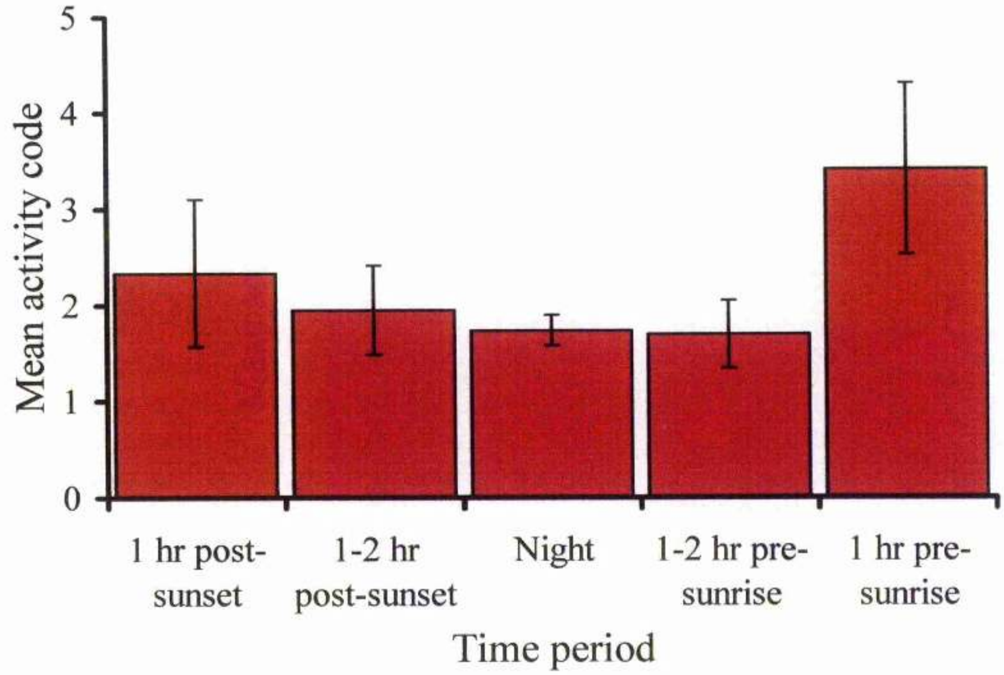

Figure 8.3v. Activity during five periods of the night. (Movement code 1 = none, 2 = <3 short, 3 = 3 or more short, 4 = <3 long, 5 = 3 or more long, 6 = relocation.

At the exact position used by the fish (E), substratum was most commonly sand (4) and gravel (5), accounting for almost 91% of the observations, with only 5 of the 8 possible categories being used. Depths ranged from 0.17 to 0.95 m, with a mean of 0.59 m. Water velocities ranged from 0 to 0.26 m s^{-1}, with a mean of 0.11 m s^{-1}. Instream cover was even more sparse at the fish position than elsewhere within the zone, with 76% of sites having zero cover, and 90% having less than one third macrophyte coverage.

The mean differences in depth for each fish were negative for 9 out of the 11 fish for positions A & B and 6 out of 11 for position C. These data suggest that in the positions selected by dace at night, the water upstream of the fish was generally deeper than at the exact fish position. Conversely, the mean difference in depth was positive for 10 and 9 out of eleven fish for positions D and F respectively, suggesting that the water at either side of the fish was shallower than at the exact fish position.

By treating the mean differences between the fish position (E) and positions within the zone (A, B, C, D, F, G) for each of the 11 fish as 11 independent observations, paired t-tests showed that depth was significantly greater at A than at E ($p = 0.02$, $t = -2.87$), and significantly shallower at both D ($p = 0.01$, $t = 3.00$) and F ($p = 0.02$, $t = 2.94$), than at E. Of the other positions, G was shallower, and both B and C were deeper than E, though not significantly ($p = 0.07$, $t = 2.03$; $p = 0.08$, $t = -1.92$; and $p = 0.26$, $t = -1.19$ respectively).

The water velocity at E was significantly greater than at both D ($p = 0.02$, $t = 2.83$) and F ($p = 0.008$, $t = 3.28$). Negative values for the mean difference between both E & A, and E & G, suggest that water velocity may have been higher at these two positions than at E, however the differences were not significant ($p = 0.24$, $t = -1.26$ and $p = 0.10$, $t = -1.80$ respectively).

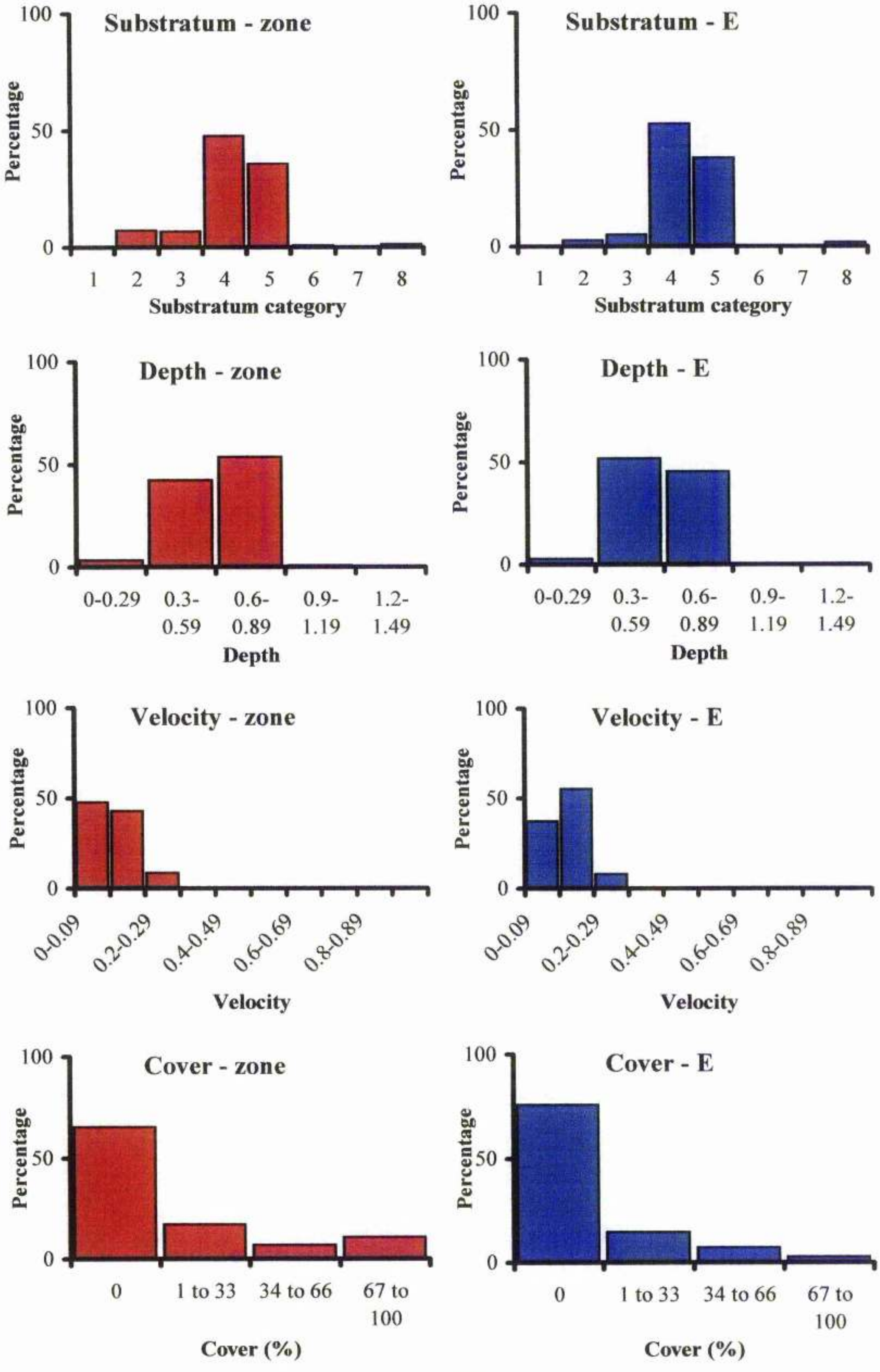

Figure 8.2vi. Habitat characteristics at the fish position (E), and within the zone of influence. Substratum categories: 1 = leaves, 2 = silt, 3 = mud, 4 = sand, 5 = gravel, 6 = pebbles, 7 = boulders, 8 = bedrock.

8.4 Discussion

VISIBILITY

Betalight® radio-active isotope tags are effective tools for monitoring the behaviour and habitat use of fishes in shallow, clear water at night. By using individually identifiable codes on each tag, with both bands, and gaps between bands, of at least 4 mm wide, it is possible, in the field, to distinguish between tagged fishes with the naked eye.

Fish tagged with Betalight® tags are difficult to locate during the day, and once located, individual identification is more difficult than at night. The observations that were carried out during the day showed that the tagged individuals were always associated with other dace, often in large numbers, in positions away from instream cover. This suggests that on those occasions when tagged dace were not found during the day it was simply due to the fact that they were more difficult to locate visually, rather than because the fish had become cryptic, or were associated with cover. In addition, the observer was more visible to the fish during the day, and on some occasions the fish was disturbed during the searching process. Consequently, when the fish was discovered it was either moving, or was likely to have moved away from its initial position. For obvious reasons, the location and habitat use of such apparently disturbed fish was not recorded. A combination of both radio- and isotope tags would allow both rapid fish location and accurate position fixing during either daylight or darkness, and is suggested as the most suitable technique for future studies. Indeed, if the saddle used by Beaumont *et al.* (1996) were to be replaced by an isotope tag, or incorporate a Betalight®, both radio-locations and direct nocturnal observations could be made following a single tagging procedure.

ALGAL GROWTH

During summer and autumn, at least, algae grows on the outer surface of Betalight® tags. Neither of the two treatments tested resulted in a reduction in the growth of algae compared with the untreated control, and other techniques may be required for long term studies. However, growth of algae on tags attached to fish did not preclude their identification during the course of this study, and is likely to differ both seasonally and between study sites.

FLUVARIUM OBSERVATIONS

Direct observation indicated that the behaviours of tagged and untagged fish in near-natural conditions were equivalent, and suggested that observations of tagged individuals in the wild would provide valid data.

The fact that little activity was observed during either the day or the night may be an indication that the fish feed by collecting drifting food items, and therefore do not need to move extensively. Alternatively, the lack of activity may suggest that active food gathering periods are short in duration, and were generally outside the periods of observation.

It has been suggested that dace form large shoals near the surface (Wheeler, 1969), and they have also been described as "mid-water generalist feeders" (Allan, 1986). During this study all dace observed, both in the Fluvarium and in the field, remained close to the substratum at virtually all times. It appears that though they may visit the surface occasionally to feed on emerging insects, the vast majority of their time is spent close to the river bed.

Some fish schools are known to break up at night, re-forming at dawn, and a number of hypotheses as to why this might occur have been postulated

(John, 1964). John (op. cit.) showed a gradual decline in the schooling of *Astyanax mexicanus* (Fillipi) with reductions in illumination, and suggested this "relationship may be a general pattern amongst fishes." There is general agreement that visual signals are important in shoal formation and group cohesion (Guthrie & Muntz, 1993), and it has been suggested that without vision fish do not school (Breder, 1959). Conversely, Pitcher *et al.*, (1976) demonstrated in captivity that fish blinded with opaque eye covers could shoal, whereas such "blind" fish which also had the lateral line cut at the opercular could not, thus confirming the role of the lateral line in schooling. There were however differences in the schooling behaviour and reaction times of blinded fish compared with the untreated individuals, leading Pitcher *et al.*, (op. cit.) to conclude that it is unlikely that such blind fish could school in the wild. Consequently, Pitcher (1979) suggested that schooling is maintained by the interaction of both visual and lateral line information. Visual signals can be ineffective at night or in murky water (Smith, 1991), and is seems possible that inter-individual distance at night is governed more by the lateral line sense than by vision. Auditory communication (Moulton, 1960) and olfaction (Keenleyside, 1955) have also been suggested as potential means by which groups of fish can stay together when vision is impaired.

Alternatively, the observed spacing patterns may be a deliberate action in response to a change in the prevailing conditions. If the fish's major predators are diurnally active, the fish may shoal less tightly following a perceived or expected reduction in predation threat. Similarly, if the fish were drift feeding, the observed spacing pattern may have been selected in order for each individual to maximise its own prey encounter rate, thus making more efficient use of a widely spaced food supply. This could be tested in the Fluvarium by setting up two identical throughflow tanks, one supplied with a widely spaced food supply, and the other with a much narrower, more focused food supply. If the fish were deliberately spacing themselves in order to make best use of the resource, the inter-individual should be reduced when the food supply is not evenly spaced.

FIELD OBSERVATIONS

Dace are capable of "homing" precisely to previously used positions, and frequently re-use the same sites within the river channel on consecutive nights. Dace regularly moved to different locations during the day, returning to the previously occupied position the following night. It seems reasonable to suggest that remembering the location of a previously used site, or at least recognising it, and moving to it at a particular part of the diel cycle, is likely to be of some potential benefit to the individual. A detailed knowledge of the local environment should be of assistance in both predator avoidance and prey capture, and is likely to influence the fitness of an individual (Braithwaite *et al.*, 1996).

In the River Frome, pike constitute the major predator of the dace (Mann, 1982). Pike are generally accepted to be diurnal predators, with vision forming an integral part of their two major hunting strategies, stalking and ambush (Keenleyside, 1979). Similarly, avian predators such as herons and cormorants are generally accepted to be diurnally active, often roosting in trees during darkness (pers. obs.). Of the nocturnally active predators, eels rarely grow to sufficient size to catch and kill adult dace, and although some sea trout (*Salmo trutta* L.) undoubtedly attain a size at which they could pose a seasonal threat to adult dace, fish of such size are comparatively rare in the River Frome, and the East Stoke Millstream is unlikely to represent an ideal habitat for them. Mink are known to present within the study area, and are nocturnally active. However, they were most commonly encountered on the more remote sections of the main River Frome, and infrequently in the vicinity of the East Stoke Millstream (pers. obs.). In consequence, it is not considered that predator avoidance is a major factor governing the nighttime habitat selection of dace.

Dace are known, at times, to feed on drifting invertebrates (pers. obs.). The numbers of invertebrates drifting at night is generally higher than the numbers drifting during the day, with a substantial peak around dusk, and a smaller peak at dawn (Elliott, 1965; pers. obs.). It is possible that dace select their nighttime positions in order to take advantage of this increase in food availability, returning to locations that have proved profitable in the past.

Dace are most active during the hour before sunrise, and carry out a number of short rapid movements immediately prior to re-locating around dawn. It is possible that these movements are associated with active feeding, and possibly coincide with peaks in the availability of drifting invertebrates. A smaller peak in activity was observed at dusk, with the apparent reduction in the degree of activity possibly being related to the greater abundance of drifting invertebrates at this time (Elliott, 1965; pers. obs.).

Tank studies have shown that goldfish (*Carassius auratus* (L.)) are able to locate previously profitable areas by referring to familiar visual landmarks (Douglas, 1996). Dace move towards and leave their nighttime positions before dusk and at dawn (i.e. during daylight), and appear to be relatively inactive during darkness. This may be an indication that visual cues, which are likely to be ineffective during darkness, are the major factors in patch location. It may be possible to test this by displacing tagged dace during darkness. Any post-displacement return to the previously used position would implicate cues other than visual. Failures to return, however, would not necessarily prove vision alone was involved, as the displacement event could prevent the tagged fish returning, rather than the fish being unable to locate the pre-displacement position.

Repeated use of particular, specific positions may also suggest some degree of territoriality, or a dominance hierarchy within the population. If this is the case, the removal of a strong competitor from a particularly profitable patch may result in a weaker competitor moving into the vacated habitat. However, this would be extremely difficult to test in the field, with only a small proportion of the population tagged.

HABITAT

The habitat characteristics of the areas selected by dace at night are interesting. The reduced mean depth and slower mean flows found at D and F compared with E, are perhaps to be expected in a trapezoidal channel, as their relative positions, either side of the fish make it more likely that on occasion their position will be on the sloping bank of the channel. However it is also possible that the fish prefer to position themselves closer to one bank or the other, than in the middle of the channel.

The observation that the water at A was significantly deeper than at E was however quite unexpected. It is possible that a slight up-slope provides a foraging advantage, by concentrating the drifting invertebrates in the lower layers of the water column into a narrower band. If this was the case, a dace positioned on such an up-slope would encounter more drifting food items than one positioned on a flat, level section of the stream bed. In a similar way, such gentle up-slopes may be regions where there is a significant increase in the numbers of drifting invertebrates settling out of the drift.

The dace however were generally inactive when in these positions, and active, mobile foraging during the middle of the night can therefore be ruled out. Examination of the temporal variation in gut contents of dace might provide an insight into whether dace take up such positions in order to "drift feed", and if so, the degree to which feeding occurs at dusk, at dawn or through the night.

The relative importance of such gentle up-slopes of the substratum in the nighttime habitat selection of dace could be tested by creating, in the field, a selection of otherwise identical habitats with a variety of gradients, with some level, and some sloping in each direction. Use of such "up-slope" sites in a proportion greater than can be expected by chance alone would be further evidence that these positions are preferentially selected by dace, and further examination of the potential benefits to the individual of occupying such sites would be warranted.

CHAPTER 9

Discussion

9.1 Migration

Adult dace were highly mobile and moved extensively around the river system, on both daily and seasonal scales. The null hypothesis, that adult dace remain in one small section of the river throughout the year, has been rejected. The movements of adult dace were both temporally, and in some circumstances spatially predictable. Consequently the component hypothesis, that the movement of adult dace is random and unpredictable, and therefore does not constitute migration, has also been rejected.

Radio-telemetry (Chapter 3) showed that adult dace migrate around the river system, and use specific sections of the river in response to predictable changes in the prevailing conditions. These changes occurred on both a daily and seasonal basis, as did the migrations of dace. During autumn and winter floods adult dace left the main river channel and occupied positions in drainage ditches and on the flooded field margins, sometimes hiding among vegetation. Spawning occurred during mid-March on clean gravel, particularly in millstreams, and was generally preceded by an upstream migration. During the summer months adult dace regularly carried out diel migrations between specific sites, with the movements being closely linked to dusk and dawn.

Mark recapture data (Chapter 4) suggested that the size of the dace population within the study area was relatively small. However, the fact that some of the population were fitted with radio-tags could be a substantial source of bias. The recapture of a marked fish in the East Stoke Millstream, initially caught, tagged and released in the River Frome at Wareham, showed that at least some of the dace which aggregated in the tidal reaches of the River Frome during winter moved upstream to the East Stoke Millstream to spawn.

Fish counter data (Chapter 5) showed that there was a net downstream movement of adult dace during autumn. This observation is supported by anecdotal evidence which suggests large aggregations of dace form in the tidal reaches of the river at this time of year. In addition, during April and early May there was a substantial upstream migration of adult dace, with the vast majority of fish migrating during the evening.

9.2 Habitat use

At different times of the year adult dace occupied a variety of habitats, the physical characteristics of which were different, and presumably reflected many of the fish's needs at that point in time. Consequently the component hypothesis that adult dace use habitats with the same physical characteristics throughout the year, has also been rejected.

In summer, during the day (Chapter 6) adult dace formed shoals in areas with sand substrata, little instream cover and a flow velocity of around 20 cm s^{-1}. Visual observation suggested that the fish did not actively search for food in such areas, but did occasionally investigate drifting items. The shape of the shoals appeared to correspond to that of the available habitat, with dace being absent from areas which did not match the preferred criteria. It seems likely that habitat availability can influence shoal size in dace.

At night in summer and early autumn (Chapter 8) individual dace frequently moved to the exact position used on previous nights. The mean water depth at these nocturnally used positions was significantly shallower than the mean depth at positions 1 m upstream of the fish, and consequently fish which selected these positions occupied a slight up-slope in the river bed. Activity was greatest during the period immediately before dawn, with a smaller peak shortly after dusk. These peaks in activity may have been related to corresponding peaks in the number of drifting invertebrates (pers. obs.), and it is possible that dace which occupied "up-slopes" were able to feed more efficiently on these drifting food items.

Slow flowing, shaded sites out of the main river channel were selected after spawning (Chapter 7), particularly the downstream sections of tributaries. Within these areas dace avoided instream cover, and selected the deepest and slowest flowing positions. Few food items were found in the guts of dace captured in these areas, and it seems unlikely that adult dace were aggregated in order to feed. Instead it is possible that energy conservation and predator avoidance were important factors at this time.

9.3 Annual cycle of events

Using the data gathered during this study, the year of adult River Frome dace was separated into at least four distinct, unequal sections, during each of which the fish migrated predictably in order to use specific habitats (Figure 9.3i).

The four sequential sections were:

1. Pre-spawning, mid-January to mid-March.

2. Post-spawning, mid-March to end of April.

3. Summer / early Autumn, May to mid-October.

4. Late Autumn / Winter, mid-October to mid-January.

Details of the characteristic movements and habitat use associated with each of these periods are given in Figure 9.3i. The figure is intended only as a guide to the behaviour of a proportion of the adult dace population of the River Frome.

A YEAR IN THE LIFE OFAN ADULT RIVER FROME DACE

Pre-spawning, mid-January to mid-March

Dace moved upstream into smaller channels, particularly millstreams. Electrofishing showed a predominance of males. Radio-tracking showed that some females move in, spawned and left quickly. Spawning occurred around the middle of March in fast flowing water on clean gravel and pebbles.

Post-spawning, mid-March to end of April.

Adult dace aggregated in shaded, slow flowing sites out of main river channel, particularly downstream ends of tributaries, and fed little. Here they selected the deepest and slowest flowing positions, with silt substrata away from instream cover. During April and May, adult dace move upstream in shoals.

Autumn/Winter, Mid-October to mid January

Many adult dace moved downstream during autumn, and large numbers aggregated in areas of slower flow, particularly the tidal section. Angling catches showed that the dace continued to feed even at very low water temperatures, but grew little between November and April. Diel migrations were not observed at this time of the year.

Summer/Autumn, May to mid-October

During daylight dace occupied areas of moderate flow, with sand and gravel substrata and no instream cover. Around dusk they moved to another position, where they remained throughout the night. At dawn the dace regularly returned to the exact position occupied the previous day. All annual growth was confined to this period suggesting that the diel migration may be related to feeding.

Figure 9.3i. The annual cycle of events in the year of an adult River Frome dace.

9.4 Species description - updated

In the light of the findings of this thesis, the description of a dace given in the introduction has been updated. The additional information only relates directly to the dace population of the study area. However, it was expected that some of the observed behaviours would hold true for all dace, and that many others would be relevant to all populations of chalkstream dace, particularly those exposed to similar physical, chemical and biological conditions (Chapter 9.7). The sections which have been added are highlighted:

The dace (*Leuciscus leuciscus* (L.)), also known as the dare or dart is a small, slim, silvery bodied, shoaling member of the carp family, whose name comes from an old word meaning dart, given because of the nature of its movements. It is found throughout most of Britain and mainland Europe, particularly in clear fast flowing streams and rivers, in many of which the species is the dominant cyprinid in terms of biomass.

Similar in appearance to small chub (*Leuciscus cephalus* (L.)), the most prominent distinguishing features are the concave outer edges to the dorsal and anal fins of the dace. A lateral line scale count in excess of 46 and a 5 + 2 tooth formation on the pharyngeal bones also identifies a dace. The eye is yellow, and the caudal fin deeply forked, however the colour of the fins appears to vary between populations, and possibly between individuals within the same population. Dace are known to feed throughout the water column, but spend the vast majority of their time on or near the substratum.

Males grow white tubercles, are rough to the touch, and in the Frome, move upstream to the spawning grounds from mid January onwards, with the plumper, mucous covered females arriving closer to spawning time. Adult dace spawn in March and April achieving maturity for the first time in either their third or fourth years of life, and then spawn annually up to their maximum age of 11+. In the River Frome, spawning takes place on clean gravel substrata in millstreams, and is usually completed during March. They attach their negatively buoyant, yellow-orange yolked, 1.5 to 2.5 mm spherical eggs to gravel substrata in shallow fast flowing water. The major cause of death to eggs appears to be oxygen starvation caused by fine sediments, but those that survive hatch in around 30 days, with the weakly swimming 7.5 - 9 mm larvae drifting downstream into slow moving marginal backwaters. The fastest growing of these larvae, of which there are more in the warmest years, are better able to avoid predation by invertebrates and fish, and survive to the end of the year, by which time the year class strength has been established.

After spawning adult dace move to slow flowing shaded sites out of the main river channel, particularly the downstream ends of tributaries. Within these areas they take up the deepest positions available, away from instream cover. Here they remain, feeding little, until late April or early May when they leave these habitats and move upstream, usually during the evenings.

From May onwards, during the day adult dace occupy areas of river with a sand substratum, little instream cover and a water velocity of around 20 cm s^{-1}. Around dusk they move to a different site, usually a position where there is a slight rise in the river bed, and remain relatively inactive at this position throughout the night. Shoals of dace break down around dusk, and appear to be generally less cohesive at night, with greater inter-individual distances. At dawn the dace move again, with individuals frequently returning to the exact position occupied the previous day. This diel migration may represent a trade off between foraging and predator avoidance. An individual may use the same sites on a number of consecutive days and nights, before relocating within the system, with diel migrations recommencing at the new position. Diel migrations continue throughout the summer months, before the adult dace migrate downstream during autumn, forming large aggregations in the tidal reaches of the river.

Adult dace feed mainly on invertebrates, particularly the insect taxa Trichoptera and *Simulium*. In the River Frome the cased caddis *Brachycentrus subnubilus* was the most common food item. Despite their abundance, and propensity to drift, *Gammarus pulex* did not form a substantial part of the diet of River Frome dace. Adult dace are themselves prey for piscivorous fishes particularly pike (*Esox lucius* L.), constituting the principal prey species of the pike in the River Frome.

9.5 Relative merits of the techniques used

Radio-tracking is a useful technique, which can provide accurate movement data of tagged individuals in relatively shallow, low conductivity water. Visual observations and fish counter records have shown that the movement of the tagged individual can often be extrapolated to that of the shoal with which it is associated.

The external attachment of radio-transmitters and other percutaneous tags is a suitable technique for short term studies only. Towards the end of one of the longer tracks a small amount of abrasion was seen at the attachment site. It is possible that this would affect the behaviour of the individual, thus biasing the results. For studies in excess of three months surgically implanted tags would be more suitable. For short term studies however, the reduced recovery times associated with non-surgical techniques, coupled with an appropriate method of release is likely to increase the validity of short-term tracks (Clough & Beaumont, 1998).

Any further miniaturisation of radio-tag components will allow smaller and smaller individuals to be tracked. In addition, advances in the encapsulation of transmitters for use under water may also assist in the miniaturisation process. The way forward could be in a wider use of physiological tags, such as heart-rate monitors and electromyogram tags, which not only indicate the position of the individual, but can also relay data relating to the fish's current physiological state.

The present study has shown the degree to which a small, shoaling, riverine cyprinid fish species migrates within the river system, both on a daily and seasonal basis. Many of the migrations are carried out in order to solve the three basic problems referred to by Keenleyside (1979), i.e. to find enough to eat, to avoid being killed and to ultimately reproduce successfully. However it is not clear which aspects of the observed behaviour are specific to the dace population of the study area, and which are common to dace in other systems.

Multi-species radio-tracking studies are rare. The majority of existing studies have focused on one particular problem facing a single species, with the interactions between co-existing species being generally neglected.

Dace and roach often form mixed shoals in the River Frome (pers obs). By tagging both roach and dace at the same time, the degree of niche overlap between the species could be assessed. Any behavioural mechanisms to reduce competition, thus allowing co-existence, could be examined in the wild situation. The relative impact of existing management practices on each species, for example weedcutting could be assessed, and the likely impact on the fish populations of a change in these practices could be modeled.

Dace constitute the major food items of both small and large pike in the River Frome (Mann, 1982). By monitoring the movements of both predator and prey at the same time, the extent of the interaction between the two species could be assessed. In particular, the diel timing of activity and habitat use of each species could be examined in order to assess the likely encounter rate.

Fish counters with video validation can provide detailed data relating to the number and size of migrating fishes, information which is often ignored. In river systems with several comparable cyprinid species, identification in all but the best of viewing conditions could be difficult. However, it is possible that computerised image analysis could hold the key and increase the automation of such systems.

Mark recapture is a useful technique, which takes on a whole new dimension in the study of fish migration when individuals can be identified. Growth rates can be assessed, as can site and shoal fidelity and partner choice. Providing a suitable tag attachment site can be found in which retention is good, VI alpha-numeric tags can provide detailed information about individuals, with VI Elastomer tags serving as an excellent batch mark PIT tags are a relatively new application for marking fishes, and their use is likely to increase. The use of "flat-bed" PIT tag readers built into the bed of natural and artificial streams could provide interesting data on the diel and seasonal movements of small riverine fishes.

9.6 Implications of the ecological strategy

Adult dace solve the three basic problems referred to by Keenleyside (1979), i.e. finding enough to eat, avoiding predation and reproducing, by moving extensively, using a variety of different habitats at appropriate times, and often returning exactly to those sites which have proved profitable in the past. It seems likely that other shoaling riverine cyprinids faced with the same problems will solve them in a similar fashion, and migration among such fishes is likely to be widespread. The construction of weirs and impassable barriers has obvious implications for such mobile fish populations. Indeed, the significance of the effects of river obstruction on riverine fishes has probably been underestimated (Lucas *et al.*, 1998). Current fish pass design generally targets adult salmonids, and the usefulness of such structures to migratory non-salmonid fishes is unknown. The installation of an impassable barrier, without appropriate ameliorative measures is, to the fish populations, equivalent to the destruction of all habitat beyond the barrier. It seems unlikely, in the current climate, that such destruction of habitat would be sanctioned by the authorities, and nor should equivalent measures which have the same net effect.

Without a constant stream of freshwater potentially bringing new resources, it seems likely that some stillwater fishes too, will need to migrate in order to find sufficient food, and to avoid predators. Shoaling species, in particular, for example roach (*Rutilus rutilus*) and bream (*Abramis brama*), might separate their day in similar fashion to dace, using specific parts of the available habitat at appropriate times.

The fact that dace re-used specific areas, and the speed at which they moved between sites might suggest that not only do they recognise particular previously occupied sites, but also that they know the route between them. It is possible that adult dace have detailed cognitive map of their local environment, which enables them to find and re-use sites which have been profitable in the past. However it has been argued that no animal has been conclusively shown to have a cognitive map (Bennett, 1996). It has been suggested that juvenile Atlantic salmon use multiple cues in order to help them to solve spatial tasks (Braithwaite *et al.*, 1996), and that goldfish use the visual angle of a familiar landmark to locate previously profitable sites (Douglas, 1996). It seems reasonable to suggest that dace may also be able to utilise external cues in order to move rapidly between "home" sites.

Homing in fishes is well known, especially in salmonids (e.g. Tallman, 1994; Youngson *et al.*, 1994; Pascual *et al.*, 1995). The homing of non-salmonid fishes has been studied in some species, however these studies are usually limited to homing to previously used spawning sites (Tyus, 1985; Tyus, 1990), or the return of fish which have been displaced (e.g. Stott *et al.*, 1963; Margenau, 1994; Parker, 1995). The discovery of a regular daily homing of a small, shoaling, riverine cyprinid therefore represents a major advance in our understanding of the use of space by such animals.

The concept of animals occupying a home range has been researched in detail. Early work on riverine fishes suggested that they occupied limited home ranges, where they remained for extended periods (Gerking, 1953; 1959). Later studies with roach (*Rutilus rutilus*) and gudgeon (*Gobio gobio*) led Stott (1967) to conclude that river populations were divisible into mobile and static components, with around two thirds of the populations of these fishes remaining within home ranges, and the remainder wandering more widely.

Linfield (1985) proposed an alternative concept to home range theory with respect to riverine cyprinid populations. The alternative hypothesis was based on a perception of cyprinid communities as "totally mobile populations influenced predominantly by river flow characteristics and behavioural responses to flow and seasonal temperature factors." In a study of the movements of dace in the River Frome Clough & Beaumont (1998) suggested that the overall movement patterns observed supported Linfield's alternative concept of range theory, but added that individual fish take up residence in defined areas for periods of days or weeks. The migration of dace described in this thesis support the findings of Clough & Beaumont (1998), and suggest that the application of a home range to dace needs to be considered on a variety of temporal scales, ranging from daily home range to annual home range, possibly even lifetime home range.

9.7 Relevance of the findings to other systems

Whilst some of the aspects of dace behaviour observed during this study are likely to be specific to the River Frome dace population, others may well be true for all dace. Indeed identifying which aspects of behaviour have evolved in order to solve those problems particular to specific environments, might enable us to model the responses of populations to novel situations.

The most efficient way to test this would be to repeat the study with another dace population which inhabits a river with substantially different characteristics. An acidic, flashy upland river produced primarily by surface run-off with a sparse growth of instream macrophytes would provide a suitable contrast to the rich, stable, groundwater fed environment found in a chalkstream.

I would expect an upstream migration to spawn would still be seen in such rivers, as this would help to counterbalance the downstream drift of juveniles. Millstreams however may not be found on such rivers, and consequently other clean gravel spawning sites would be used. If dace do have a preference for smaller channels in which to spawn it seems likely that suitable conditions could be found in tributaries, however the more consistent physical and chemical characteristics found in naturally braided sections of the channel may be preferred if available. Re-use of the same spawning sites in consecutive years may not be an option in such rivers, due to the significant alteration to the distribution of bed sediments which can occur during winter floods. However, where suitable clean gravel areas do persist between years, I would expect the dace to re-use the same sites that were used in the past.

The use by dace of slow-flowing shaded sites out of the main channel after spawning may also be characteristic of chalk-fed streams. The availability of macrophyte free, slow-flowing reaches is likely to be greater in other rivers, and consequently post-spawning behaviour might be less specific.

Diel migrations between two distinct habitats have been noted during the summer months for River Frome dace (Chapter 3), and are thought to represent a trade-off between feeding and predator avoidance. These diel migrations may well be driven by the specific conditions found in chalkstreams, and might not occur in rivers with different characteristics. However, providing the invertebrate populations behave in a similar fashion, i.e. drifting mainly at dawn and dusk, then I would expect the crepuscular peaks in activity seen in chalkstream dace to be apparent in populations in other systems.

The downstream migration of adult dace to slow-flowing reaches of the River Frome during autumn is thought to be either in response to, or anticipation of a predictable increase in flow. Consequently, as these seasonal increases in discharge are seen in virtually all temperate rivers, I would expect dace to respond in a similar fashion wherever they occur.

In the River Frome, and in other rivers, dace form mixed shoals at certain times of the year with roach (*Rutilus rutilus* (L.)) of a similar size. It is unclear whether or not those roach which form mixed shoals with dace during the summer months also carry out diel migrations between separate, distinct day and night habitats. However, I would suggest that as there is considerable overlap in the diet of these fishes, and that they are each vulnerable to many of the same predators, the potential benefits of carrying out a diel migration might also apply to roach. If this was the case, I would suggest that during the summer months, a regular diel migration between two distinct habitats would also be found in roach.

Similarly, those fish species which occupy a similar niche to dace in rivers where dace are absent may well behave in a similar fashion, especially if they are exposed to diurnal predators which hunt using the stalking and ambush techniques.

9.8 The way forward.

"It is virtually impossible to predict the next 25 years of research in aquatic ecology and behaviour with any accuracy. However, by identifying those areas that are the current frontiers of the discipline it is possible to guess at the most likely research developments over the next decade" (Dill, 1987). Dill goes on to say "the research programme most likely to be productive in the near future is that of behavioural ecology, which studies, among other things, animal decision making in an ecological context." More than a decade on from these statements, it is still unclear in exactly which field the major advances will occur, however there can be little doubt that since those statements were made, studies of behavioural ecology and decision making in fish have substantially increased our understanding of this fascinating field of study.

It is for this reason that I feel there is an ever-increasing requirement for such studies, the vast majority of which have been conducted in captivity, to be complemented by studies of the behaviour of fishes in their natural environment.

There can be little doubt, for example, that if a dace and a pike (appropriately sized) were placed in a tank, the dace would try to avoid being eaten by the pike, and the pike would attempt to eat the dace, and I suspect that ultimately the pike would be successful in its quest. This is the likely outcome because the unnatural conditions have deprived the dace of several of its anti-predator mechanisms, most notably schooling, fleeing and avoidance.

However in the field, a much more complex environment, both predator and prey have many more options available, even before the two fish come into contact.

By studying the behaviour of fishes in their natural environment against the backdrop of the inevitably more detailed behavioural research carried out under laboratory conditions, real advances in our understanding can be achieved, with the wild fish themselves determining which aspects of their behaviour are the most worthy of closer inspection. Subsequent research can then focus on those aspects of fish behaviour which have the greatest impact on the daily lives of wild fishes, and provide valuable information for interested parties.

In addition, current models of fish habitat suitability need to be greatly improved, not least to take into account spatial and temporal variability in the habitat use of fishes, on both daily and seasonal scales. Only then will scientists and managers have the detailed information necessary to predict and model the responses of fish populations to novel conditions, and carry out effective fisheries management and conservation.

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Appendix 1. – Dace gut content data.

Date	Fork length (cm)	algae	*Brachycentrus subnubilus*	*Potamopyrgus jenkinsi*	*Theodoxus fluviatilis*	*Aphelochierus aestivalis*	*Simulidae spp.*	Maggots	Others	Total
21/10/95	14.8	0	0	0	0	0	0	0	0	**0**
21/10/95	16.8	0	0	0	0	0	0	0	0	**0**
21/10/95	11.5	0	7	0	0	0	0	0	0	**7**
21/10/95	11.4	0	8	0	0	0	0	0	0	**8**
21/10/95	16.3	y	1	0	0	0	0	0	0	**1**
21/10/95	16.7	0	0	0	0	0	0	0	0	**0**
21/10/95	16.4	y	3	0	0	0	0	0	0	**3**
21/10/95	15.6	0	0	0	0	0	0	0	0	**0**
21/10/95	16.3	0	12	0	0	0	0	0	0	**12**
21/10/95	19.8	0	0	0	0	0	0	0	0	**0**
23/10/95	16.0	y	1	0	0	0	0	0	0	**1**
23/10/95	15.8	y	1	0	0	0	0	0	0	**1**
23/10/95	15.2	y	2	0	0	0	0	1	0	**3**
23/10/95	23.3	0	0	0	0	0	0	0	0	**0**
23/10/95	19.4	0	1	0	0	0	0	0	0	**1**
23/10/95	14.8	0	0	0	0	0	0	0	0	**0**
23/10/95	15.6	y	0	0	0	0	0	0	0	**0**
23/10/95	14.7	0	0	0	0	0	0	0	0	**0**
23/10/95	12.8	y	5	0	0	0	0	0	0	**5**

Date	Fork length (cm)	algae	*Brachycentrus subnubilus*	*Potamopyrgus jenkinsi*	*Theodoxus fluviatilis*	*Aphelochierus aestivalis*	*Simulidae spp.*	Maggots	Others	Total
24/10/95	11.4	0	4	0	0	0	0	0	1	**5**
24/10/95	13.9	0	14	0	0	0	0	0	0	**14**
24/10/95	15.2	y	0	0	0	0	0	0	1	**1**
24/10/95	12.7	0	0	0	0	0	0	0	0	**0**
24/10/95	15.2	0	0	0	0	0	0	0	0	**0**
24/10/95	15.4	0	1	0	0	0	0	0	0	**1**
24/10/95	15.8	y	4	0	0	0	0	0	1	**5**
24/10/95	15.6	y	0	0	0	0	0	0	0	**0**
24/10/95	20.9	0	0	0	0	0	0	0	1	**1**
24/10/95	20.9	y	1	0	0	0	0	0	0	**1**
10/1/96	12.1	0	0	0	0	0	0	0	0	**0**
10/1/96	14.9	0	0	0	0	0	0	0	0	**0**
10/1/96	15.0	0	0	0	0	0	0	0	0	**0**
10/1/96	15.1	0	0	0	0	0	0	0	0	**0**
10/1/96	15.3	0	0	0	0	0	0	0	0	**0**
10/1/96	14.2	0	3	0	0	0	0	2	1	**6**
10/1/96	15.5	0	0	0	0	0	0	0	0	**0**
10/1/96	16.6	0	0	0	0	0	0	2	2	**4**
10/1/96	15.6	0	1	0	0	0	0	23	3	**27**
10/1/96	17.4	0	0	0	0	0	0	0	0	**0**
10/1/96	17.5	0	0	0	0	0	0	0	0	**0**
10/1/96	17.6	0	0	0	0	0	0	12	1	**13**

Date	Fork length (cm)	algae	*Brachycentrus subnubilus*	*Potamopyrgus jenkinsi*	*Theodoxus fluviatilis*	*Aphelochierus aestivalis*	*Simulidae spp.*	Maggots	Others	Total
10/1/96	17.9	0	2	0	0	0	0	2	2	**6**
10/1/96	23.6	0	2	0	0	0	0	5	2	**9**
18/10/96	15.0	0	28	5	0	0	0	0	0	**33**
18/10/96	14.0	0	3	80	6	0	0	0	0	**89**
18/10/96	18.0	0	80	1	0	0	0	0	0	**81**
18/10/96	21.8	0	2	1	0	1	0	0	0	**4**
18/10/96	23.2	0	1	0	5	1	0	0	0	**7**
18/10/96	26.2	0	1	4	8	2	0	0	0	**15**
18/10/96	19.5	0	19	0	0	9	0	0	0	**28**
18/10/96	24.7	0	0	0	0	0	0	0	0	**0**
18/10/96	20.0	0	4	0	0	0	0	0	0	**4**
18/10/96	20.0	0	0	0	0	0	0	0	0	**0**
18/10/96	20.0	0	0	0	0	0	0	0	0	**0**
18/10/96	17.0	0	0	12	0	0	0	0	0	**12**
18/10/96	17.9	0	1	1	0	0	0	0	1	**3**
18/10/96	19.4	0	0	0	0	0	0	0	0	**0**
18/10/96	19.0	0	9	0	0	0	0	0	0	**9**
18/10/96	15.0	0	1	140	0	0	0	0	0	**141**
18/10/96	16.0	0	0	0	0	0	0	0	0	**0**
18/10/96	19.8	0	0	0	0	0	0	0	0	**0**
18/10/96	16.8	0	2	0	0	0	0	0	1	**3**
18/10/96	15.9	0	0	0	0	0	0	0	0	**0**

Date	Fork length (cm)	algae	*Brachycentrus subnubilus*	*Potamopyrgus jenkinsi*	*Theodoxus fluviatilis*	*Aphelochierus aestivalis*	*Simulidae spp.*	Maggots	Others	Total
18/10/96	16.6	0	54	0	0	1	0	0	0	**55**
18/10/96	14.9	0	8	0	0	0	0	0	0	**8**
18/10/96	15.6	0	35	14	8	0	0	0	0	**57**
18/10/96	15.7	0	1	0	0	0	0	0	0	**1**
18/10/96	15.8	0	86	0	0	0	0	0	0	**86**
18/10/96	16.6	0	35	0	0	0	0	0	0	**35**
18/10/96	15.1	0	3	0	0	0	0	0	0	**3**
18/10/96	16.2	0	31	15	4	1	0	0	0	**51**
18/10/96	15.5	0	0	0	0	0	0	0	0	**0**
Totals			**477**	**273**	**31**	**15**	**0**	**47**	**17**	**860**

Appendix 2. – Drift sample data.

		Water		Time			Water velocity			Volume	Debris			Invertebrates		
Date	Site	Depth (m)	Period	In	Out	Hr's	Start	End	Mean	Filtered (m^3)	Dry wt. (g)	g/hour	g/m^3	Total	Per hour	Per m^3
14/5/97	ESMH	0.81	Day	12:08	12:21	0.22	0.47	0.46	0.47	98.07	2.25	10.38	0.02	53	245	0.54
14/5/97	Frome	0.76	Day	11:59	12:15	0.27	0.22	0.17	0.20	50.62	1.86	6.98	0.04	75	281	1.48
14/5/97	ESMH	0.82	Dusk	21:53	22:06	0.22	*	*	*	*	2.00	9.23	*	134	618	*
14/5/97	Frome	0.77	Dusk	21:45	22:00	0.25	*	*	*	*	1.52	6.08	*	171	684	*
15/5/97	ESMH	0.84	Night	0:15	0:26	0.18	*	*	*	*	1.28	6.98	*	166	905	*
15/5/97	Frome	0.76	Night	0:10	0:21	0.18	*	*	*	*	0.74	4.04	*	128	698	*
15/5/97	ESMH	0.83	Dawn	5:10	5:21	0.18	*	*	*	*	1.23	6.71	*	99	540	*
15/5/97	Frome	0.76	Dawn	5:04	5:15	0.18	*	*	*	*	0.80	4.36	*	78	425	*
15/5/97	ESMH	0.80	Day	11:50	12:08	0.30	0.44	0.41	0.43	124.11	3.82	12.73	0.03	86	287	0.69
15/5/97	Frome	0.74	Day	11:42	12:01	0.32	0.21	0.18	0.20	60.11	2.14	6.76	0.04	88	278	1.46
21/5/97	ESMH	0.80	Day	12:00	12:29	0.48	*	*	*	*	6.66	13.78	*	393	813	*
21/5/97	Frome	0.75	Day	11:47	12:23	0.60	0.22	*	*	*	2.85	4.75	*	187	312	*
22/5/97	ESMH	0.87	Day	11:53	12:06	0.22	*	*	*	*	1.43	6.60	*	89	411	*
22/5/97	Frome	0.79	Day	11:45	12:00	0.25	*	*	*	*	0.86	3.44	*	44	176	*
24/6/97	ESMH	0.62	Day	11:30	11:46	0.27	*	*	*	*	4.67	17.51	*	315	1181	*
24/6/97	Frome	0.68	Day	11:59	12:15	0.27	*	*	*	*	1.43	5.36	*	240	900	*
24/6/97	ESMH	0.68	Dusk	22:07	22:19	0.20	*	*	*	*	0.58	2.90	*	68	340	*
24/6/97	Frome	0.76	Dusk	22:12	22:26	0.23	*	*	*	*	0.23	0.99	*	174	746	*
25/6/97	ESMH	0.68	Night	1:01	1:20	0.32	*	*	*	*	0.22	0.69	*	220	695	*
25/6/97	Frome	0.73	Night	1:11	1:30	0.32	*	*	*	*	0.19	0.60	*	239	755	*
25/6/97	ESMH	0.70	Dawn	3:41	3:56	0.25	*	*	*	*	0.02	0.08	*	39	156	*
25/6/97	Frome	0.72	Dawn	3:47	4:02	0.25	*	*	*	*	0.10	0.40	*	54	216	*

		Water		Time			Water velocity			Volume	Debris			Invertebrates		
Date	Site	Depth (m)	Period	In	Out	Hr's	Start	End	Mean	Filtered (m^3)	Dry wt. (g)	g/hour	g/m^3	Total	Per hour	Per m^3
16/5/96	ESMH	0.77	Dawn	4:27	4:42	0.25	0.5	0.45	0.48	115.60	6.97	27.88	0.06	27	108	0.23
16/5/96	Frome	0.81	Dawn	4:27	4:42	0.25	0.6	0.55	0.58	139.93	4.40	17.60	0.03	24	96	0.17
5/6/96	ESMH	0.77	Day	14:41	15:06	0.42	0.49	0.45	0.47	190.63	3.70	8.88	0.02	71	170	0.37
5/6/96	Frome	0.77	Day	14:55	15:20	0.42	0.53	0.47	0.50	202.80	3.82	9.17	0.02	192	461	0.95
5/6/96	ESMH	0.78	Dusk	22:05	22:20	0.25	0.47	0.46	0.47	113.16	1.70	6.80	0.02	155	620	1.37
5/6/96	Frome	0.89	Dusk	22:10	22:25	0.25	0.51	0.54	0.53	127.76	1.90	7.60	0.01	583	2332	4.56
6/6/96	ESMH	0.78	Dawn	4:05	4:20	0.25	0.5	0.46	0.48	116.81	1.34	5.36	0.01	2	8	0.02
6/6/96	Frome	0.89	Dawn	4:12	4:27	0.25	0.5	0.51	0.51	122.90	1.60	6.40	0.01	566	2264	4.61
23/4/97	ESMH	*	Day	*	*	*	*	*	*	*	2.04	*	*	20	*	*
23/4/97	Frome	*	Day	*	*	*	*	*	*	*	1.20	*	*	19	*	*
30/4/97	ESMH	0.74	Day	11:55	12:25	0.50	0.45	0.36	0.41	197.12	9.72	19.44	0.05	29	58	0.15
30/4/97	Frome	0.66	Day	12:14	12:40	0.43	0.29	0.26	0.28	116.00	2.20	5.08	0.02	45	104	0.39
30/4/97	ESMH	0.70	Dusk	21:10	21:30	0.33	0.52	0.49	0.51	163.86	8.70	26.10	0.05	79	237	0.48
30/4/97	Frome	0.64	Dusk	20:56	21:16	0.33	0.3	0.26	0.28	90.85	4.41	13.23	0.05	79	237	0.87
30/4/97	ESMH	0.73	Night	23:54	0:09	0.25	0.5	0.47	0.49	118.03	5.16	20.64	0.04	178	712	1.51
1/5/97	Frome	0.64	Night	0:18	0:28	0.17	0.26	0.22	0.24	38.94	3.33	19.98	0.09	134	804	3.44
1/5/97	ESMH	0.73	Dawn	5:30	5:45	0.25	0.51	0.46	0.49	118.03	5.06	20.24	0.04	63	252	0.53
1/5/97	Frome	0.64	Dawn	5:22	5:37	0.25	0.29	0.25	0.27	65.71	2.05	8.20	0.03	62	248	0.94
1/5/97	ESMH	0.72	Day	12:00	12:20	0.33	0.48	0.37	0.43	137.90	9.94	29.82	0.07	57	171	0.41
1/5/97	Frome	0.64	Day	11:48	12:10	0.37	0.29	0.17	0.23	82.09	1.68	4.58	0.02	23	63	0.28
7/5/97	ESMH	0.80	Day	12:00	*	*	0.42	*	*	*	*	*	*	*	*	*
7/5/97	Frome	0.72	Day	11:52	12:08	0.27	0.28	0.2	0.24	62.30	0.47	1.76	0.01	35	131	0.56
8/5/97	ESMH	0.80	Day	11:53	12:10	0.28	0.4	0.34	0.37	102.05	2.80	9.88	0.03	28	99	0.27
8/5/97	Frome	0.72	Day	11:44	12:02	0.27	0.27	0.21	0.24	62.30	1.98	7.43	0.03	37	139	0.59

Date	Site	Water Depth (m)	Period	Time In	Time Out	Hr's	Water velocity Start	Water velocity End	Water velocity Mean	Volume Filtered (m^3)	Debris Dry wt. (g)	Debris g/hour	Debris g/m^3	Invertebrates Total	Invertebrates Per hour	Invertebrates Per m^3
15/12/95	ESMH	*	Day	12:55	14.55	2.00	*	*	*	*	4.60	2.30	*	7	4	*
15/12/95	Frome	*	Day	13:05	15:05	2.00	*	*	*	*	19.80	9.90	*	9	5	*
15/12/95	ESMH	*	Night	19:00	21:00	2.00	*	*	*	*	6.70	3.35	*	15	8	*
15/12/95	Frome	*	Night	19:05	21:05	2.00	*	*	*	*	18.90	9.45	*	39	20	*
19/1/96	ESMH	*	Day	9:35	11:35	2.00	0.5	0.5	0.50	973.44	27.80	13.90	0.03	12	6	0.01
19/1/96	Frome	*	Day	10:00	12:00	2.00	0.5	0.5	0.50	973.44	6.90	3.45	0.01	5	3	0.01
19/1/96	ESMH	*	Dusk	15:50	17:50	2.00	0.5	0.5	0.50	973.44	35.30	17.65	0.04	16	8	0.02
19/1/96	Frome	*	Dusk	15:55	17:55	2.00	0.5	0.5	0.50	973.44	7.80	3.90	0.01	8	4	0.01
29/2/96	ESMH	*	Day	12:30	12:45	0.25	1	1	1.00	243.36	131.60	526.40	0.54	16	64	0.07
29/2/96	Frome	*	Day	12:40	14:40	2.00	<0.25	<0.25	*	*	3.00	1.50	*	7	4	*
15/3/96	ESMH	0.88	Day	12:30	12:55	0.42	0.7	0.66	0.68	275.81	38.00	91.20	0.14	4	10	0.01
15/3/96	Frome	0.78	Day	12:45	13:10	0.42	0.69	0.66	0.68	273.78	16.80	40.32	0.06	7	17	0.03
15/3/96	ESMH	0.90	Night	20:37	20:57	0.33	0.67	0.67	0.67	217.40	85.04	255.12	0.39	37	111	0.17
15/3/96	Frome	0.80	Night	20:49	21:09	0.33	0.65	0.65	0.65	210.91	14.90	44.70	0.07	24	72	0.11
8/5/96	ESMH	0.76	Day	11:45	12:05	0.33	0.5	0.45	0.48	154.13	7.90	23.70	0.05	21	63	0.14
8/5/96	Frome	0.79	Day	11:57	12:17	0.33	0.55	0.5	0.53	170.35	8.20	24.60	0.05	15	45	0.09
9/5/96	ESMH	0.79	Night	23:50	0:10	0.33	0.45	0.4	0.43	137.90	10.60	31.80	0.08	133	399	0.96
9/5/96	Frome	0.81	Night	0:02	0:22	0.33	0.55	0.5	0.53	170.35	8.25	24.75	0.05	48	144	0.28
15/5/96	ESMH	0.74	Day	11:39	11:59	0.33	0.5	0.4	0.45	146.02	8.20	24.60	0.06	0	0	0.00
15/5/96	Frome	0.79	Day	11:50	12:10	0.33	0.6	0.55	0.58	186.58	7.70	23.10	0.04	37	111	0.20
15/5/96	ESMH	0.76	Dusk	21:45	22:05	0.33	0.5	0.45	0.48	154.13	12.20	36.60	0.08	59	177	0.38
15/5/96	Frome	0.81	Dusk	21:32	21:52	0.33	0.6	0.55	0.58	186.58	7.65	22.95	0.04	68	204	0.36
15/5/96	ESMH	0.76	Night	23:28	23:43	0.25	0.50	0.45	0.48	115.60	8.40	33.60	0.07	101	404	0.87
15/5/96	Frome	0.81	Night	23:35	23:50	0.25	0.6	0.55	0.58	139.93	6.50	26.00	0.05	60	240	0.43