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Factors affecting the dispersal of coarse fish

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ABSTRACT

FACTORS AFFECTING THE DISPERSAL OF COARSE FISH

Globally, freshwater fisheries are faced with numerous impacts that compromise fish populations. A knowledge and understanding of riverine fish movements are crucial for effective management and conservation of populations. However, there is a paucity of information about the spatial behaviour and ecology of wild and stocked cyprinids in floodplain rivers, especially under the influence of elevated flows. This study examined the factors affecting the lateral and longitudinal dispersal of juvenile and adult (wild and stocked) coarse fish in three lowland river catchments, namely the River Trent, the Yorkshire Ouse and the River Roding.

A literature review was carried out to review the influence of floods on riverine ecosystem function and structure, and fish assemblage patterns. In unmodified lowland rivers, floods are characterized by lateral expansion onto floodplains resulting in high levels of habitat heterogeneity, essential for fish refuge, spawning, nursery and feeding. However, anthropogenic alterations to the flow regime and floodplain connectivity have had considerable detrimental impacts on fish populations. The main conclusion of the review was the need to restore and rehabilitate lowland rivers in an attempt to recover natural features or functionality.

The effects of flood timing and magnitude were examined by sampling 0+ fish populations before, during and after floods in the Yorkshire Ouse, a constrained lowland river. Large numbers of eurytopic 0+ fishes were stranded on isolated floodplains when artificial levees ‘over-topped’ in summer (August). By contrast, backwaters provided refuge for high densities of 0+ eurytopic and rheophilic fishes. During floods, small fish were displaced or had lower survival. The results highlight the influence of flood timing on 0+ fish populations, the use of refuge areas and their importance of lowland river rehabilitation.

In the River Trent, 0+ fish populations were sampled in the margins of the main river channel and in ten man-made floodplain waterbodies to evaluate the importance of variable connectivity between these habitats for rehabilitating the riverine-floodplain ecosystem. Fish assemblages compared favourably with studies on unmodified river reaches, i.e. succession of lotic-to-lentic habitat corresponded to a sequence of rheophilic-to-eurytopic-to-limnophilic fish species. Consequently it was concluded that the connection of man-made floodplain waterbodies to the river should incorporate variable, not just high, levels of hydrological connectivity into holistic riverine ecosystem management plans.

Dual-Frequency Identification Sonar (DIDSON) was used to determine the influence of elevated flow on the lateral movements of adult fish between the Yorkshire Ouse and a marina (refuge habitat). Fish activity in the entrance was predominantly during daylight hours. Increased river flow resulted in significantly reduced fish movements, both towards and away from the marina, and fish presence in the entrance, except for larger fish (>30 cm) during the night. This study emphasised the importance of artificial floodplain waterbodies for adult cyprinid fish during winter months.

The influence of environmental variation (flow and temperature) on movements of wild and stocked adult cyprinids is poorly understood, partially because of experimental difficulties. A laboratory study on PIT tagging individual juvenile cyprinids, identified that the method would be suitable for such investigations. In the River Roding, a combination of PIT and radio telemetry was used to compare habitat use, longitudinal movement (timing and direction), site fidelity and survival between wild populations and hatchery-reared fish. Wild cyprinids had high levels of ‘site fidelity’ but highly mobile individuals were present within the population, with movements positively correlated with temperature and flow. During elevated winter flows, wild fish occupied areas of reduced flow to reduce energy expenditure, but some fish performed exploratory movements. Movements of stocked fish were more frequent and longer than for wild fish, particularly just after release, possibly for exploratory purposes. Subsequently, movements of stocked fish were minimal, did not correlate with flow or temperature and the final distributions were more widely dispersed than found in wild fish. Importantly from a stocking perspective, stocked cyprinids had the behavioural and physiological ability to cope with elevated flows. However, differences in movements and habitat use between wild and stocked chub probably had consequences on survival.

1 GENERAL INTRODUCTION

Globally, freshwater fishery managers, including the Environment Agency in England and Wales, are faced with a number of impacts that compromise fish populations. Principle challenges include pollution, flow regulation, channelisation and habitat degradation (see Cowx, 2002), whilst the future includes the threat of climate change. For example, many lowland rivers have been subjected to channelisation and artificial levee construction, that reduce rivers to single-thread channels and isolated from their floodplains (Ward & Stanford, 1995a; Cowx & Welcomme, 1998). Flow stabilization and reduced floodplain habitat have negatively affected fish species highly adapted to the periodic inundation for spawning (Kwak, 1988; Trexler, 1995; Baras & Lucas, 2001; Grift *et al*., 2001a, 2003) and nursery (Gehrke *et al*., 1995, 1999; Modde *et al*., 2001; Grift *et al*., 2003). Such modifications can also have damaging consequences for fishes during flood events, including increasing the severity of conditions in the main channel (Lusk *et al*., 1998; Poff *et al*., 2006*),* preventing fish from using floodplain habitats for refuge (Ross & Baker, 1983; Kwak, 1988), and causing the stranding of fish when artificial levees are ‘over-topped’. Ultimately, human modifications to river-floodplain ecosystems culminate in a high number of endangered fish taxa (for example, Ward, 1998a; Galat *et al*., 1998; Jungwirth, 1998).

The commonly used strategies for addressing these issues and conserving freshwater fish are river habitat improvement and rehabilitation, establishing environmental flows and stock enhancement. River rehabilitation (Cowx & Welcomme, 1998) activities to minimise the potential impacts of river engineering are driven in Europe by the Water Framework Directive (WFD; 2000/60/EEC) and the protection of biodiversity by the Habitats Directive 92/43/EEC, also globally by Agenda 21 of the Rio Convention and the Convention of Biological Diversity. Establishing and enforcing environmental flows (Tharme, 2003; Cowx *et al*., 2004) to mitigate activities that alter hydrological regimes are also integral to national (Catchment Abstraction Management System), European (WFD) and global (International Water Management Institute) initiatives. Stock enhancement (Cowx, 1994, 1998) for conservation purposes should only be carried out after the factors limiting stock recovery have been removed or ameliorated (e.g. water quality improvement or habitat rehabilitation), when they are likely to accrue long-term benefits. In England and Wales, this compensatory action is based on stocking in excess of two million fish per year, from the Environment Agency fish production facilities, plus millions more from fish farms and fisheries. However, the persistence of cyprinids stocked into some rivers appears to be low (Aprahamian *et al*., 2004), and there are doubts about the efficiency of the majority of stocking actions.

Integral to the above rehabilitation and recovery programmes is the underlying relationship between fish dispersal and flows, especially high flows. Furthermore, floods are predicted to increase in frequency and magnitude under the influence of climate change (IPCC, 2002), with a likely concomitant impact on fish populations. Thus, knowledge and understanding of riverine fish movements are crucial for effective management and conservation of populations. However, there is still a paucity of information about the spatial behaviour and ecology of wild and stocked cyprinids in floodplain rivers. For example, little is known about:

- the importance of man-made floodplain waterbodies for juvenile fish (their significance as spawning and nursery habitats);
- the habitats used by juvenile fish before, during (refuge) and after flood events;
- the losses of fish that become stranded on historical floodplain areas following flooding events that breach flood protection structures;
- the lateral movements of adult and sub-adult fish between the main river and floodplain water bodies during winter months and under the influence of elevated flow;
- the short and long-term movements and fate of stocked fish under the influence of environmental variables, especially flow.

Gaps in current knowledge exist because juvenile fishes have not received due attention, but are also partially attributable to historical experimental difficulties of: 1) capturing and identifying the early development stages of fish in the first year of life; 2) observing the movement behaviours of fish in turbid, lowland rivers; and 3) determining the behaviour of individual sub-adult fish. However, recent advances in the capture of fish larvae and their identification (e.g. Pinder, 2001), sonar equipment (e.g. Moursund *et al*., 2003), and tagging and monitoring technology (Lucas & Baras, 2000; Zydlewski *et al*., 2001; Gibbons & Andrews, 2004), have enabled some of these difficulties to be overcome.

The overall aim of the study was to examine the factors influencing the lateral and longitudinal distribution and movement of juvenile and adult (wild and stocked) cyprinid fishes in lowland rivers, and to ascertain the influence of elevated flows on these respective communities; all with a view to conserving and restoring fish stocks by effective management measures. To this end, the study was divided into key topics that are addressed in Chapters 2 to 7. Specific objectives and hypotheses are provided at the start of each chapter.

Chapter 2 reviews current literature documenting the effects and importance of flood and high flow events on species dynamics and fish populations over a river's entire course, with reference to key concepts and principles, longitudinal and lateral connectivity, anthropogenic alterations to the flood pulse and the necessity of rehabilitation programmes.

Chapter 3 investigates the effects of high flow and flood events on the structure and dynamics of the 0+ fish population of the River Ouse (Yorkshire), with particular emphasis on the timing of flooding, the use of refuges (backwaters), and the stranding of fish behind levees after flood waters recede.

Chapter 4 compares 0+ fish populations of the River Trent and numerous man-made floodplain waterbodies with varying degrees of connectivity, with particular emphasis placed upon species composition, community structures and spawning strategies of the fish populations therein.

Chapter 5 investigates the winter-time movements of adult fish between the Yorshire Ouse and a connected marina using a high-definition imaging sonar, with particular emphasis on diel variations in activity and the effects of elevated flow.

Chapter 6 investigates the methods for long-term marking of juvenile cyprinids, with particular emphasis on retention, mortality and growth rates.

Chapter 7 investigates the movement and habitat use of both wild and stocked sub-adult cyprinids in a small river system, with particular emphasis on the influence of temperature and flow, including flood events.

Chapter 8 summarises the information gained from the Chapters 3 to 7 in the context of the literature review in Chapter 2, summarises management implications and provides recommendations for further study.

The information in this report is intended to guide management of river fisheries, in relation to flood defence initiatives and water resources development, and help improve the enhancement and conservation of fish in a future faced with problems such as urban development and climate change scenarios that will affect the functioning of rivers. Specifically, the outputs will inform the future design of river rehabilitation activities and flood alleviation schemes, so as to minimise the potential impacts and maximise the environmental benefits. The study also identifies approaches to maximise the success of future stock enhancement activities.

2 EFFECTS OF FLOODS ON FISH

2.1 INTRODUCTION

River ecosystems provide a wealth of goods and services for society, e.g. attenuation and removal of flood waters, water purification, production of fish and other foods and marketable goods, power, recreation and amenity. Similarly, from an ecological perspective, river ecosystems provide high levels of biodiversity, e.g. aquatic flora, and invertebrate and fish fauna that are highly valued by society for their existence. High flow events are when flow elevations are confined to the main channel and floods are recognised to occur when a river exceeds its bank full level. Severe floods may have long-lasting effects on human populations, via affected man-made structures and disruption to the way of life and commerce. As a result, societies commonly refer to floods as ‘disasters’ (Haeuber & Michener, 1998). However, from an ecological perspective, floods in general should not be considered as ‘disasters’, but as an integral part of the hydrological regime and a beneficial natural disturbance essential for maintaining a biologically diverse and productive ecosystem (Bayley, 1995; Naiman & Décamps, 1997).

Despite the importance of floods to natural ecosystems, many rivers have been subjected to channelisation and artificial levee construction, reducing rivers to single-thread channels and isolating them from their floodplains (Ward & Stanford, 1995a; Cowx & Welcomme, 1998). This has relevance because of the UK’s obligations under the Water Framework Directive to improve the status of fish populations in degraded rivers, i.e. achieving good ecological status may require reconnection of lowland rivers to their floodplains. In addition, flood frequencies and magnitudes are predicted to increase under the influence of climate change (IPCC, 2002), with consequences for riverine ecosystem function, biodiversity and productivity (Gibson *et al*., 2005). Land-use changes may be a greater detriment to riverine fishes than projected climate change, but the combined effect of both factors will further alter the functioning of ecosystems and may lead to local species extinction (Peterson & Kwak, 1999; Gibson *et al*., 2005). Consequently, there is a need for a greater understanding of the effects of floods on fish and the ecological implications of anthropogenic alterations to the flood pulse in ‘flood-dependent’ ecosystems (Bayley, 1995; Sparks, 1995). This knowledge will assist future attempts to manage, protect and rehabilitate river ecosystems whilst maintaining societal needs to protect property and assets from flooding, i.e. minimising human impacts whilst maximising environmental benefits of floods.

The aim of this review is to elucidate the relationships between fish and floods in rivers and the linkages with fish life history strategies, behaviour, assemblage structure and production. More specifically the objectives are to: 1) summarise the concepts and principles associated with floods; 2) consider how high flow and flood events shape stream fish communities, especially in constrained upland reaches; 3) outline the importance of floods, floodplains and floodplain connectivity in lowland rivers; 4) discuss anthropogenic impacts on floods and floodplains; and 5) review current attempts to rehabilitate flow regimes and floodplains, thus increasing ecosystem biodiversity and improving the status of fish populations in degraded rivers.

2.2 FLOOD CONCEPTS

Welcomme & Halls (2004) described the hydrological regime of a flood as a curve with several measurable characteristics (Figure 2.1). Ecologically important components of the flow regime are the amplitude, frequency, seasonal timing, predictability, duration and rate of change of flow conditions (Poff *et al*., 1997; Bunn & Arthington, 2002). Every river system has an individual typical annual hydrological regime, varying with climate, location, geology, topography and vegetation cover (Van der Nat *et al*., 2003; Cowx *et al*., 2004). Winemiller (2004) classified rivers globally based on their annual hydrology as: temperate with aseasonal (seemingly random) flood pulses, temperate with seasonal flood pulses and tropical with seasonal flood pulses. However, this gross classification misses many of the subtleties of local river systems, attributed to local geology, geomorphology, and weather variability (Cowx *et al*., 2004).

Over the last 30 years, development of hydrologic concepts has led to a more detailed understanding and knowledge of riverine ecosystem function, structure and fish assemblage patterns in response to floods. Building from much earlier concepts of longitudinal zonation (e.g. Huet, 1949), the River Continuum Concept (RCC; Vannote *et al*., 1980) described a continuously changing abiotic gradient from headwaters to river mouth structuring the channel biota. However, floods and floodplain dynamics were not considered until a later version of the RCC (Sedell *et al*., 1989). Similarly, the serial discontinuity concept (Ward & Stanford, 1983) recognised the importance of

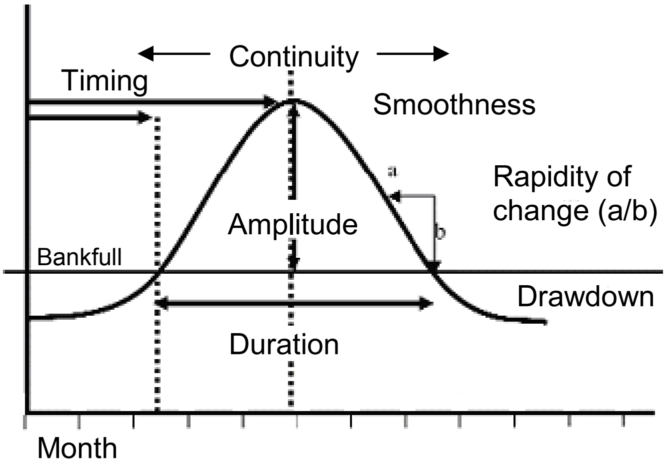


Figure 2.1 Various parameters of a flood hydrograph having biological significance (from Welcomme & Halls 2004).

zonal structure along a water course but ignored floodplain dynamics until Ward & Stanford's (1995b) extended serial discontinuity concept (ESDC). The ESDC described the relative strength of longitudinal, vertical and lateral interactions within a catchment, with the longitudinal (river/river or river/tributaries) pathway being most important in the constrained headwaters, vertical (river bed/aquifer) interactions reaching their maximum importance in the braided middle course and lateral connectivity playing the major role in alluvial floodplain (river bed/floodplains) rivers.

The above concepts largely consider longitudinal processes within a catchment, but the Flood Pulse Concept (FPC; Junk *et al.*, 1989) states that the lateral connection between the river channel and the connected floodplain during periodic inundation is the major driving variable for ecological processes in large tropical and temperate river-floodplain systems (Junk *et al.*, 1989; Bayley, 1991; Tockner *et al.*, 2000b). Junk & Wantzen (2004) provided a summary of how the FPC has been modified, extended and restricted by several authors as knowledge of both rivers and floodplains has increased considerably through studies on the effects of hydrology and hydrochemistry, climate, paleoclimate, biogeography, biodiversity, landscape ecology and wetland restoration and floodplain management in different latitudes and continents. Although the FPC is widely accepted and applied by most river ecologists, it has also been criticised. For example, the Riverine Productivity Model (RPM; Thorp & Delong, 1994) described the role of autochthonous production in the river channel, but also recognised the importance of the riparian zone and lateral connections. Despite this, Walker *et al.* (1995) considered that riverine models are inadequate to describe the functioning of river-floodplain ecosystem. Ultimately, a combination of the RCC, the FPC and the RPM might be a better representation of energy flow in large rivers (Dettmers *et al*., 2001).

Further to these concepts, floods (and droughts) can be considered an environmental disturbance occurring along river corridors (Junk *et al*., 1989; Puckridge *et al*., 1998; Swanson *et al*., 1998; Arscott *et al*., 2002), influencing system structure and function (Resh *et al*., 1988; Townsend, 1989; Poff, 1997; Lake, 2000). Sousa (1984) defined a disturbance as ‘discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.’ Alternatively, White & Pickett (1985) concluded that ‘any relative discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment’ was a disturbance. Although both stated that a disturbance is a discrete event that can be measured by ecological response, for the purposes of this review, the White & Pickett (1985) definition is employed as a working definition because it refers to systems and communities much more generally. Disturbance size, intensity, frequency and predictability determine the community response (Connell & Keough, 1985; Poff, 1992). The intermediate-disturbance hypothesis predicts that species richness will be highest in communities that experience intermediate levels of disturbance (Connell, 1978). Thus rivers with an intermediate (and predictable) level of flooding are expected to provide high diversity, by resetting environmental conditions, interrupting community succession and causing increased habitat heterogeneity for many species with different environmental requirements.

Counterbalancing the theory of disturbance is the principle that a river is a natural fluctuating ecosystem, with unique cycles of chemical matter, energy flux and food chains (Odum, 1969; Odum, 1971; Odum *et al*., 1995). Hence, floods are a completely natural recurring phenomenon essential to the survival of river fauna and flora i.e. rivers are ‘flood-dependent’ ecosystems. Thus, an alternative, and perhaps more appropriate, perspective of the disturbance concept is that the interruption of the flood regime is a disturbance (Bayley, 1995; Sparks, 1995).

2.3 FLOODS IN UPLAND STREAMS

Over evolutionary time, very large floods are regarded are disturbances that exert primary selective pressure for adaptive processes and thereby structure organism evolution (Stanford *et al*., 1996; Richter *et al*., 1997). Arndt *et al*. (2002) suggested that disturbances of the magnitude normal for the environment are an important part of the natural selection process. As a result, individual fish species have different resistances to flooding based on variations in life history, behaviour during floods and morphology. Following a flood, the community structure and ecological response is determined by its resistance and resilience (recovery) (Connell & Sousa, 1983). Reice *et al*. (1990) suggested that fish populations that inhabit unstable stream environments may be in a constant state of recovery from disturbance.

2.3.1 Fish life history adaptations to the hydrological regime

Fish have evolved life history strategies to survive floods based on seasonal timing and predictability, i.e. the synchronization of a life history stage to long-term flow regime dynamics (Poff & Allan, 1995). Although, prior to human intervention upland (and low order lowland) streams were probably choked with wood and had more stable hydrologies. Life history adaptations increase recruitment success by increasing the survival of vulnerable life stages (i.e., eggs, larvae and juveniles) (Seegrist & Gard, 1972). Salmonids excavate egg nests deep enough to minimize scour during elevated flows to a tolerable level (Montgomery *et al*., 1996; DeVries, 1997). The early life stages of some diadromous fish inhabit the marine nvironment in order to avoid exposure to floods (McDowall, 1976). The importance of timing spawning so that fry emergence coincides with seasonal periods of low flood probability appears to be an optimal strategy (Heggberget, 1988; Montgomery *et al*., 1999; Seegrist & Gard, 1972; Erman *et al*., 1988; Hauer *et al*., 1997 Fausch *et al*., 2001). Conversely, floods and high flow events are used as cues for spawning and enabling access to areas of spawning habitat that may not be available at low flows, including anadromous and certain potamodromous species from lowland reaches (John, 1963; Banks, 1969; Alabaster, 1970; Nesler *et al*., 1988; Matheney & Rabeni, 1995; Naesje *et al*., 1995; Katano & Hakoyama, 1997; Swanberg, 1997; Lucas & Baras, 2001; David & Closs, 2002; Ladle, 2002). This is particularly so in intermittent rivers where elevated flows increase longitudinal connectivity and allow access for many species to upstream areas suitable for reproduction and juvenile production (Franssen *et al.*, 2006). Further to this, elevated flows “flush” silted gravels, thus improving the spawning substrate and survival rate of eggs and gravel related larval life stages (Reiser *et al.*, 1989; Wood & Armitage, 1997; Milhouse, 1998). Indeed, cleaning of gravels is an essential service of floods to help maintain the integrity of river substrate for successful fish reproduction.

2.3.2 Fish behaviour during high flow and flood events

Behavioural adaptations are most necessary in less predictable environments (upland streams), enabling fish to respond directly to individual high flow and flood events to avoid mortality, physical damage or displacement. During elevated flow the creation or existence of refugia and disturbance patches influences organism survival and recolonisation potential (Townsend, 1989). Pearsons *et al.* (1992) reported that fish populations were more stable in physically complex habitats that provide increased availability of flow refugia. Juvenile and adult fish use low-flow refugia near stream banks and in riparian vegetation (Harrell, 1978; Matthews *et al.*, 1996; Jowett & Richardson, 1994; Matheney & Rabeni, 1995; Lusk *et al.*, 1998; Harvey *et al.*, 1999; Brown *et al.*, 2001; Lojkásek *et al.*, 2005; Gillette *et al.*, 2006), rocky shorelines (Deegan *et al.*, 1999; Valdez *et al.*, 2001), large deep pools with low-velocity areas (Brown *et al.*, 2001; David & Closs, 2002), instream interstitial spaces, behind rocks, boulders and woody debris (Tschaplinski & Hartman, 1983; Cunjak & Power, 1986; Hill & Grossman, 1987; Heggenes, 1988; Heggenes & Traaen, 1988; McMahon & Hartman, 1989; Fausch & Bramblett, 1991; Nickelson *et al.*, 1992; Lobón-Cerviá, 1996; Kennedy & Vinyard, 1997; Harvey *et al.*, 1999; White & Harvey, 2001), and off channel areas (Tschaplinski & Hartman, 1983; Brown & Hartman, 1988; Allouche *et al.*, 1999; Bell *et al.*, 2001). Ruetz & Jennings (2000) reported that larval robust redhorse (*Moxostoma robustum* (Cope)) may use the boundary layer as refuge during laboratory swimming tests and since this layer is approximately 1 cm deep it is available to a wide variety of small fish species and early lifecycle stages. Under high-discharge conditions fish are often attracted to areas of low flow because they are energetically less demanding than maintaining a position in faster water, thus avoiding displacement, physical damage and/or mortality.

2.3.3 Morphological advantages of different fish species during high flow and flood events

Despite many studies considering how fishes morphological features affect hydrodynamic performance (review in Fish & Lauder, 2006), the influence of body morphology of species in structuring fish communities of freshwaters with differing hydraulic regimes has been somewhat overlooked. While classical texts (e.g. Lowe-McConnell, 1987) describe convergent trends in morphology among species from similar habitats in widely separated ecoregions, only a few studies have been carried out on the value of these attributes to flood-resistant species. Adams *et al*. (2003) speculated that North American cyprinids use oral grasping during energetically demanding flows, such as floods. Gerstner (2007) found that the suckermouth catfish (*Hypostomus plecostomus* (L.)) uses its oral suction disk to improve station-holding performance, but concluded that the use of other morphological features such as the odontodes (dermal teeth) and fin spines may be equally important. Eel-like fishes (sygnathids, calamoichthyis and mastacembalids) are able to survive high flows and floods by weaving themselves among stones or aquatic vegetation (R.L. Welcomme, *pers. comm*.). The hydraulic basis of position-holding using paired pectoral fins close to the river bed has been established for many species, including salmonids (Arnold *et al*., 1991), cyprinids (Facey & Grossman, 1990), acipenserids (Adams *et al*., 1999) and cottids (Webb, 1989). Tew *et al*. (2002) considered the persistence of a gobiid (*Rhinogobius nantaiensis* (Aonuma & Chen)) before and after a typhoon to be the result of the depressed head of the fish and the modified pelvic fins so it can firmly hold on to bedrock. However, Webb *et al*. (1996) suggested that rather than the hydrodynamic properties of the body alone, behavioral traits associated with benthic fish are the most important determinants of distribution of species in current-swept habitats. Similarly, Ward *et al*. (2003) identified that desert suckers (*Catostomus clarkii* (Baird & Girard)) and bluehead suckers (*Catostomus discobolus discobolus* (Cope)) used their mouths to suck on to the bottom of a swim chamber, whilst speckled dace (*Rhinichthys osculus* (Girard)) positioned their pectoral fins against the bottom, thus reducing energetic expenditure and avoiding displacement, but concluded behavioural responses are more important.

Historic studies considered the nuchal humps (hump behind the head) of benthic species such as razorback sucker (*Xyrauchen texanus* (Abbott)) and humpback chub (*Gila* *cypha* (Miller)) evolved to generate downward force in fast flowing rivers (La Rivers, 1962; Miller, 1946 cited in Portz & Tyus, 2004). However, based on evidence from experiments, Portz & Tyus (2004) argued that in two Colorado River fish these large humps are a result of convergent evolution prompted by predation.

2.3.4 Flood associated mortality

Although fish have evolved life history, behavioural and morphological adaptations to avoid and survive periods of elevated flow, floods can still cause mortality of juveniles and adults. The effects of elevated flow on juvenile fish are directly related to their timing and predictability, and the timing of reproduction and fish size, i.e. elevated flow events are most likely to have a major impact on fish if they occur immediately after spawning. Jensen & Johnsen (1999) suggested that moderate flows at a particularly sensitive stage may cause higher mortality than considerably higher flows at less sensitive stages. For example, elevated flow events can fill interstitial spaces with silt, preventing alevin emergence (Phillips *et al.*, 1975), or scour salmonid redds killing incubating embryos (Elwood & Waters, 1969; Seegrist & Gard, 1972; Erman *et al.*, 1988; Lapointe *et al.*, 2000; Carline & McCullough, 2003). Once emerged, as fish size increases, susceptibility to displacement and mortality declines (Ottaway & Forrest, 1983; Heggenes & Traaen, 1988; Jowett & Richardson, 1989; Nehring & Anderson, 1993; Jensen & Johnsen, 1999; Valdez *et al.*, 2001; Cattanéo *et al.*, 2002), although species specific differences may occur (Crisp & Hurley, 1991; Letcher & Terrick, 1998). The importance of temperature on swimming performance and susceptibility to downstream displacement has also been documented (Heggenes & Traaen, 1988; Jensen & Johnsen, 1999; Ruetz & Jennings, 2000).

The effects of floods on adult fish are less severe or more predictable than on younger and smaller fish (John, 1964; Seegrist & Gard, 1972; Hanson & Waters, 1974; Hoopes, 1975; Tschaplinski & Hartman, 1983; Meffe, 1984; Schlosser, 1985; Fausch *et al.*, 2001). In fact, negligible effects of floods on fish of age 1+ or older have been documented (Elwood & Waters, 1969; Hill & Grossman, 1987; Matthews *et al.*, 1994; Harvey *et al.*, 1999; Jensen & Johnsen, 1999; Lojkásek *et al.*, 2005; Pires *et al.*, 2008), mainly because older fish, with well developed swimming abilities are able to actively avoid areas of high velocities. However, floods of extreme magnitude can cause mortality of adult fish (Allen, 1951; Elwood & Waters, 1969; Seegrist & Gard, 1972;

Weng *et al.*, 2001), although, as with juveniles, vulnerability to flooding may vary between species (Harrell, 1978). Mortality of adult fish during floods mainly occurs in upland reaches because flow variability, intensity of scour and water velocity are inversely related to stream size, i.e. elevated flows are more dramatic in upland reaches. For example, adult fish that inhabit the interstitial spaces of the substratum can be crushed by bed-material transport during floods (Erman *et al.*, 1988; Lusk *et al.*, 1998; Swanson *et al.*, 1998; Natsumeda, 2003; Lojkásek *et al.*, 2005). When landslides combine with floodwaters to produce debris flows (mobile slurry of rocks, soil, water, and trees moving downstream at up to ten m s^{-1} (Roghair *et al.*, 2002)), the effects on stream habitats and fish communities are most severe, potentially causing extreme or complete mortality of all age classes of fish (Lamberti *et al.*, 1991; Roghair *et al.*, 2002; Sato, 2006).

When flood related mortality of fish is not found, fish may still experience reduced growth rates because of invertebrate washout or mortality (Allen, 1951; Elwood & Waters, 1969; Jensen & Johnsen, 1999), reduced foraging efficiency in suboptimal habitat (Deegan *et al.*, 1999), increased activity costs in fast flows and/or reduced foraging efficiency in turbid flood waters (Arndt *et al.*, 2002). In the long-term, floods may modify river habitat structure with cumulative negative effects on fish assemblages. For example, floods can remove the gravel substrates which salmonids and other species use for spawning, or reduce cryptic habitat for sculpins (Cottidae) exposing them to greater predation (Pearsons *et al.*, 1992).

2.3.5 Stream fish population recovery and recolonization after extreme floods

Life history, behavioural and morphological adaptations have evolved by species in environments subjected to frequent disturbances, consequently the species present have evolved the ability to recover quickly (Matthews, 1986; Dolloff *et al.*, 1994). After flood-related mortality, elevated growth rates of both age-0 and adult fish have been reported because of increased food, reduced competition and/or decreased agonistic interactions (Elwood & Waters, 1969; Lamberti *et al.*, 1991; Letcher & Terrick, 1998; Swanson *et al.*, 1998; Roghair *et al.*, 2002). Letcher & Terrick (1998) reported that elevated growth rates altered the direction of a crucial life history trait (parr maturation) in age-0 Atlantic salmon (*Salmo salar* L.), possibly allowing more rapid recovery of salmon populations. Recovery may be aided by the floods providing improved quality of bottom sediments (e.g. flushing of silted gravels) for the surviving fish, thus elevating the survival rate of spawned eggs in the following reproduction period (Dolloff *et al.*, 1994; Harvey *et al.*, 1999; Lojkásek *et al.*, 2005). Stream fish population recovery and recolonisation can also be partly attributed to larger scale migrations from less affected stream reaches (Pearsons *et al.*, 2002; Tew *et al.*, 2002), influenced by a species vagility or colonizing ability (Fausch & Bramblett, 1991).

Floods that combine with landslides and cause debris flows have the most severe effect on fish communities, but Tew *et al.* (2002) could not detect major changes in the cyprinid community composition fourteen months after the debris flows and floods associated with typhoon Herb, Taiwan. Other debris flow studies reported that salmonid populations recovered to higher than pre-flood abundance and density within three to five years (Lamberti *et al.*, 1991; Swanson *et al.*, 1998; Roghair *et al.*, 2002). Additionally, Roghair *et al.* (2002) reported that after a debris flow, high-flow events altered channel morphology and reorganized the stream channel to near-pre-event conditions.

2.4 FLOODS IN LOWLAND RIVERS

The importance of floods and floodplains for fish reproduction and recruitment in low gradient rivers dates back in Europe at least as far as Antipa (1921, 1928). Floods are characterized by lateral expansion onto floodplains (Welcomme, 1979), thus, floodplains extend from a river's low-water mark to the high-water mark; they are ecotones between terrestrial and aquatic environments (Ward *et al.*, 1999). The complex gradient of aquatic and riparian habitats collectively contributes high structural diversity (Welcomme, 1979; Junk *et al.*, 1989; Amoros & Petts, 1993). The habitat heterogeneity of floodplain river ecosystems is not only maintained but is often increased by erosional and depositional processes during floods (Moore & Gregory, 1988; Reeves *et al.*, 1995; Mertes, 1997; Schroeder & Savonen, 1997; Junk *et al.*, 1989, Ward, 1997; Salo, 1990; Ward *et al.*, 2002a, c). For example, fluvial action may create fish habitats through the formation of channels, backwaters, standing water bodies and marshes (Figure 2.2; see Amoros *et al.*, 1982, for a functional classification of floodplain water bodies). During periods of low flow, succession towards terrestrialization re-shapes habitats over time. Major flood events ('flood pulses' *sensu* Junk *et al.*, 1989) rejuvenate parts of the aquatic network, compensating for the ongoing reduction of ecological connectivity (Amoros, 1991), but even small water level fluctuations ('flow pulses' *sensu* Tockner *et al.*, 2000b) can lead to major habitat changes (Van der Nat *et al.*, 2003). The balance between rejuvenation (erosive flooding) and terrestrialization processes sustains a constantly changing mosaic of habitats in riverine floodplains (Ward, 1998a; Ward & Tockner, 2001), each characterized by a distinct fish species assemblage (Copp, 1989).

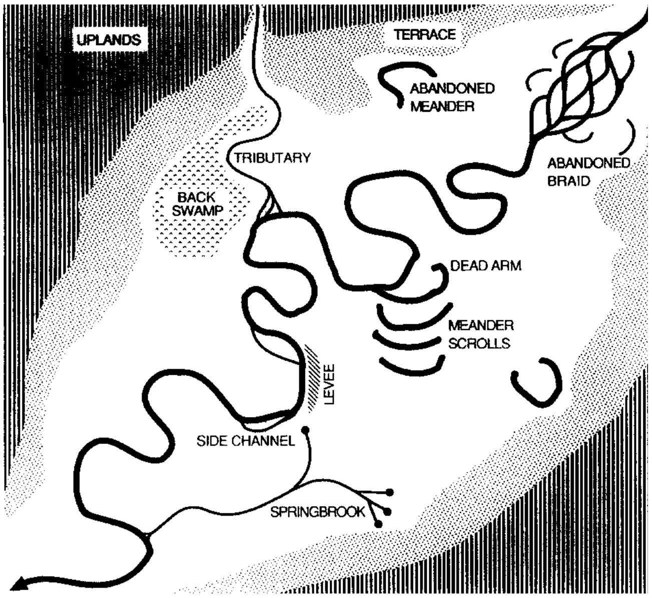


Figure 2.2 Geomorphic features of river-floodplain systems (from Ward 1998a).

Floods also play an important role in connecting various landscape patches. During floods, the floodplain shifts from a fragmented and lentic system to a connected and primarily lotic system, thus reducing environmental heterogeneity (Ward, 1998a; Tockner *et al.*, 2000a, b; Ward & Tockner, 2001; Ward *et al.*, 2002a, b, c; Thoms *et al.*, 2005) (Figure 2.3), determining the availability of isolated aquatic habitats to fish. Flooding, therefore, enhances hydrological and ecological connectivity between the main river channel and the floodplain. Thus, lateral connections are essential for the functioning and integrity of floodplain–river ecosystems (Amoros & Bornette, 2002). The FPC states that the lateral connection between the river channel and the connected floodplain during periodic inundation is the major driving variable for ecological processes, biotic interactions and productivity (Junk *et al.*, 1989), making floodplains of large rivers among the most productive landscapes on Earth (Tockner & Stanford, 2002; Welcomme, 2001). Waidbacher (1989) found a positive relationship between hydrological connectivity and fish species richness in European aquatic floodplain habitats. Tockner *et al.* (1998) identified that fish diversity peaked in highly connected habitats on a Danube floodplain, but other fauna and flora attain different peak species richness along the lateral connectivity gradient (Figure 2.4).

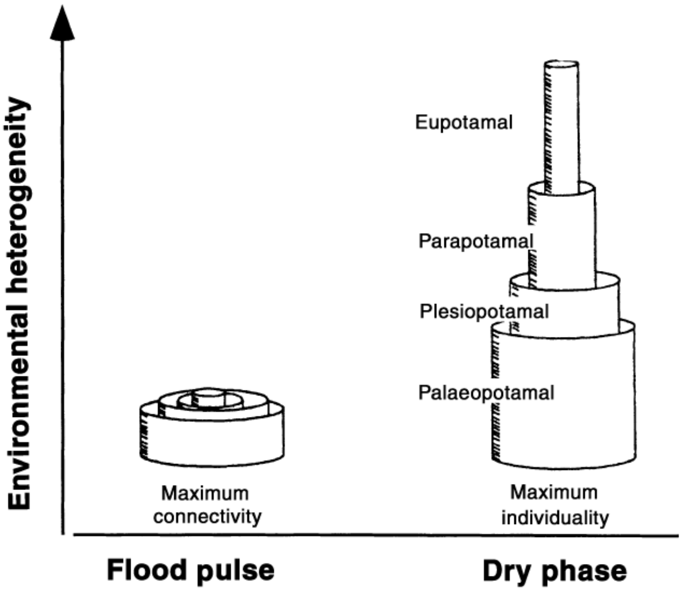


Figure 2.3 A conceptual model depicting how floodplain water bodies, that exhibit essentially uniform conditions during the period of inundation, re-establish their individuality during the dry phase (based on a modification of the telescoping ecosystem model of Fisher *et al.*, 1998). Eupotamal refers to the main channel or side channels with both upstream and downstream connections to the main channel; parapotamal refers to side channels with only downstream connections to the main channel; plesiopotamal refers to a former braided channel that is connected only during high flow; and palaeopotamal refers to former meander loops that are reconnected with the main channel only during floods. (From Ward & Tockner, 2001).

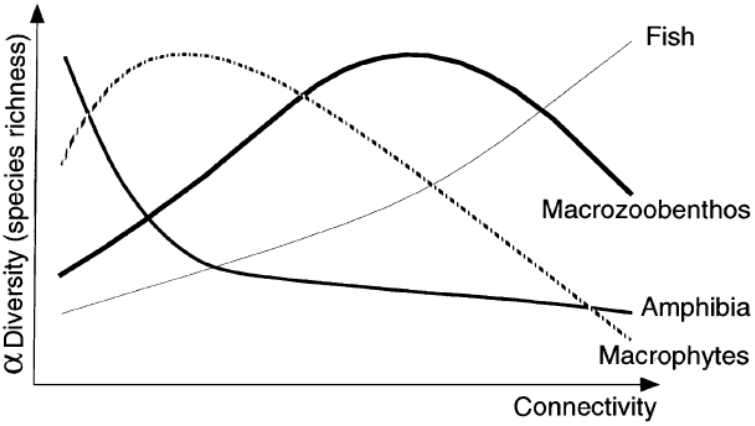


Figure 2.4 Diversity patterns of different biota in relation to river connectivity in a Danube floodplain, Austria (modified from Tockner *et al.*, 1998, from Amoros & Bornette, 2002).

Floodplain habitat heterogeneity and high hydrological connectivity, driven by the flood pulse, leads to high levels of productivity and biodiversity (Ward & Stanford, 1995a; Ward, 1998a; Tockner *et al*., 2000a; Amoros, 2002; Robinson *et al*., 2002; Ward *et al*., 2002a, c; Sommer *et al*., 2004b). River-floodplain connectivity during floods, allows fish to disperse freely and take advantage of different floodplain habitats for refuge, spawning, nursery and feeding. After the flood waters recede, the mosaic of many different aquatic habitats, at different succession stages, contain different fish assemblages, which are further structured by abiotic and biotic interactions. These processes are discussed in more detail in the following section.

2.4.1 Floodplain habitat for fish spawning

In rivers with a seasonal flood pulse (predictable timing), spawning of many fish species coincides with floods; thus fish are able to exploit relatively predictable habitats and resources on the floodplain (Welcomme, 1985; Junk *et al*., 1989). Welcomme & Halls (2001) summarised the reproductive behaviour of tropical river fish into three main categories - fish that spawn in the channel, marginal spawners and parental care species. For European floodplain rivers, spawning, nursery and adult habitat requirements have led to the formation of six guilds: rhithralic, rheophilic A, rheophilic B, eurytopic, stagnophilic and anadromous species (Schiemer & Waidbacher, 1992; Schiemer *et al*., 2004) (Figure 2.5). However, Schiemer & Waidbacher (1992) classification was based on a modified river, thus tropical rivers are perhaps more representative of the diversity of spawning strategies found in unmodified lowland rivers. Further to this, reproductive strategies can be classified according to where particular species preferentially deposit their eggs (Balon, 1975). In natural floodplain systems this diversity in spawning requirements often leads to lateral zonation of fish reproduction, with a sequence of rheophilic-to-eurytopic-to-limnophilic fish species corresponding with a lotic-to-lentic succession of habitat (Copp & Peňáz, 1988; Copp, 1989; Copp *et al*., 1991, 1994).

In temperate rivers, seasonal temperature changes and photoperiod influence spawning, thus the timing of connectivity is crucial (Sparks *et al*., 1990; Junk, 1999; Bartosova & Jurajda, 2001). In catchments with substantial snow-covered uplands (e.g. mainland Europe (Schiemer *et al*., 2004, Buijse *et al*., 2002, Raat, 2001)), temperate seasonal floods result from elevated temperatures and rainfall causing snow melt (Winemiller, 2004). Floodplains bordering snow-melt rivers provide a temperature advantage as shallow depths promote early seasonal warming via solar radiation (Modde *et al*., 2001; Jackson, 2004). In rivers with an aseasonal flood pulse, i.e. when the flood pulse can be decoupled from the temperature pulse (e.g. United Kingdom and Australia), high temperatures trigger spawning during low flows, causing Humphries *et al.* (1999) to propose the 'low flow recruitment hypothesis'. However, Molls (1999) found adult bream (*Abramis brama* (L.)) develop permanent stocks in oxbow lakes on the River Rhine because of the irregularity of connection, thus giving bream a reproductive advantage over other species. As discussed for fish in upland streams, high flow and flood events of irregular timing in lowland rivers can be highly detrimental, i.e. if elevated flows occur immediately after spawning, larvae and juveniles are highly susceptible to displacement and mortality (Harvey, 1987; Simonson & Swenson, 1990; Mann & Bass, 1997; Mion *et al*., 1998; Thieme *et al*., 2001; Nunn *et al*., 2007b).

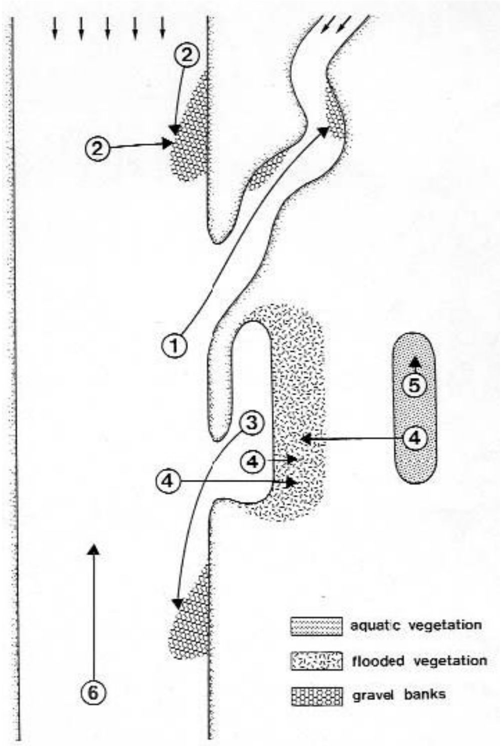


Figure 2.5 Schematic presentation of main habitat requirements of six fish guilds. Circles: preferred habitats of adults; arrows: spawning and nursery sites. 1: rhithralic, 2: rheophilic A, 3: rheophilic B, 4: eurytopic, 5: stagnophilic and 6: anadromous species (modified after Schiemer & Waidbacher, 1992, from Schiemer *et al*., 2004).

Further to these key principles, globally there are many studies that report adult fish spawning is synchronized with flooding periodicity to ensure larvae develop on the floodplain (Lowe-McConnell, 1975; Guillory, 1979; Halyk & Balon, 1983; Ross & Baker, 1983; Tyus, 1987; Kwak, 1988; Sabo *et al*., 1991; Sabo & Kelso, 1991; Peňáz *et al*., 1992; Gehrke, 1992; Turner *et al*., 1994; Sparks, 1995; Agostinho & Zalewski, 1995; Killgore & Baker, 1996; Fernandes, 1997; Gomes & Agostinho, 1997; Poizat & Crivelli, 1997; Sommer *et al*., 1997; Winemiller & Jepsen, 1998; Sparks *et al*., 1998; Modde *et al*., 2001; Sommer *et al*., 2001a, b; Jurajda *et al*., 2004; Barko *et al*., 2006; Lojkásek *et al*., 2005). Ward *et al*. (1999) emphasized that fish movements to floodplain spawning and nurseries areas, are crucial for the recruitment and sustainability of fish populations.

2.4.2 Floodplain habitat for fish nursery

The FPC suggests that fish spawning coincides with floodplain inundation because nutrient release stimulates production of phytoplankton and zooplankton, thus providing abundant food resources for newly hatched larvae (Junk *et al*., 1989) in tropical and temperate rivers (Bayley, 1995). Sommer *et al*. (2001a) used bioenergetic modelling to show that feeding success of young chinook salmon (*Oncorhynchus tshawytscha* (Walbaum)) was greater in the Yolo Bypass floodplain than in the Sacramento River, resulting in higher growth rates. Stimulation of macrophyte growth also provides spawning substrate for many species and cover for young fish. Inshore zones (connected secondary channels and oxbow lakes) are also of high value as fish nursery areas (Grift *et al*., 2001b; Simons *et al*., 2001), because they are areas of high structure, low flow and significant food production (i.e. the Inshore Retention Concept; Schiemer *et al*., 2001) (Figure 2.6). Thus, inundated floodplain habitats enable young progeny to take advantage of abundant food resources, refuge from velocity and shelter from predators. However, high levels of tannins, decaying plant matter and resultant low dissolved oxygen, may severely impact larval fish abundance and diversity (Gehrke *et al*., 1993; Lusk *et al*., 1998; Swales *et al*., 1999; Fontenot *et al*., 2001). In the latter context, Gehrke (1990) demonstrated that golden perch, (*Macquaria ambigua* (Richardson)), larvae may actively avoid inundated floodplain areas if water quality is unsuitable.

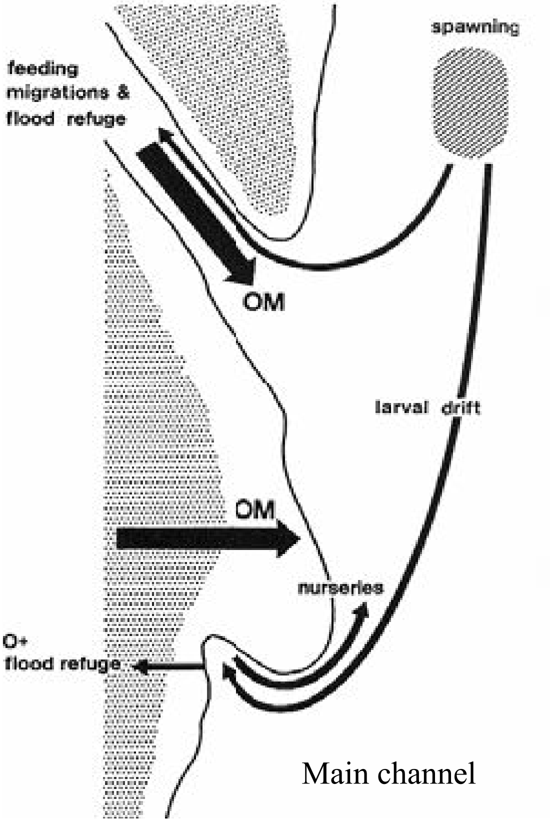


Figure 2.6 Schematic representation of quality criteria of inshore zones with respect to their value as fish nurseries for species that spawn in the main channel. The scheme indicates the river shoreline with a connected backwater and gravel bar (hatched). Stippled area = terrestrial vegetation; OM = organic material (from Schiemer *et al.*, 2001).

2.4.3 Flood intensity and duration

In rivers with seasonal flood pulses (predictable timing), inundated floodplains provide benefits to both adult and juvenile fish, but these benefits are dependent on the magnitude and duration of the flood pulse (Junk *et al.*, 1989). Welcomme & Halls (2004) reviewed the influence of the hydrological regime on fisheries, and detailed that floods of greater amplitude increased the area for spawning sites, food and shelter for the fish, whilst duration influences the time available for fish to grow and shelter from predators. These principles apply to rivers globally; large floods of long-term duration increase fish species richness and abundance in both temperate (Jurajda *et al.*, 2004; Modde *et al.*, 1996) and tropical (Gomes & Agostinho, 1997; Agostinho *et al.*, 2000) floodplain systems. However, different species respond differently to different types of flood regime (Welcomme & Halls, 2004; Welcomme *et al.*, 2006). For example, floodplain fish feeding on flooded tropical floodplain forests and grasslands were dominant groups in years with large floods (Goulding, 1980; Agostinho & Zalewski, 1995). Similarly, Jurajda *et al.* (2004) identified that long-term flooding increased the abundance of phytophilous and phytolithophilous species (Balon, 1975), and suggested that flooded vegetation provided food and shelter, thus increased growth and reduced predation. Floods of short duration or low amplitude are most detrimental if spawning involves nest building and adhesive eggs because of the risk of desiccation (Humphries *et al.*, 1999). Therefore, hydrological variability of the flood pulse can have a marked influence on the year class strength of fishes, causing annual variation in species assemblages.

2.4.4 Floodplain habitat for fish refuge during floods

Floodplain connectivity plays an important role in determining the severity of conditions in the main channel during floods (Poff *et al.*, 2006). Lojkásek *et al.* (2005) noted that the resistance of stream ecosystems to destructive effects caused by floods increases from upper stream sections towards the lower ones with developed floodplains. However, as documented for fish in upland streams, the relationship between flood timing and fish size is crucial (Harvey, 1987; Mann & Bass, 1997), but behavioural adaptations of fish determine their survival during flood events. Many studies report the movement of fish onto inundated floodplains (Guillory, 1979; Ross & Baker, 1983; Kwak, 1988; Bell *et al.*, 2001), and migrations into floodplain waterbodies (Sedell *et al.*, 1990; Molls & Neumann, 1994; Allouche *et al.*, 1999) for refuge during floods, especially in vegetated and depositional floodplain habitat with negligible velocity (Grift *et al.*, 2003; Schiemer *et al.*, 2004; Schwartz & Herricks, 2005). Humphries *et al.* (2006) hypothesized that slack water refuges provide juvenile fish with energetic advantages, primarily related to the poor swimming capabilities of these fish. If elevated flows occur at times when metabolic capacity is low (low temperatures) and hence the capability of fish to withstand elevated current velocity is low; under these circumstances availability of low current refuge areas may be crucial. However, fish can become stranded on the floodplains that dry-up when flood waters recede (Bain *et al.*, 1988; Brown *et al.*, 2001; Ortlepp & Murle, 2003; Lojkásek *et al.*, 2005), or they take up residence in isolated floodplain waterbodies until they are liberated during future a flood event. In the former case there is a net loss to recruitment in that period; whether this affects year class strength depends on the intensity of the stranding and loss of the cohort.

2.4.5 Floodplain water bodies during low flows

As water levels drop, fish migrate back to the river, providing food for river-resident piscivores (Fernandes, 1997), or fish are concentrated in isolated floodplain water bodies. In tropical floodplains, 10–70% of fishes are found only in floodplain waterbodies variously connected to the main channel (Welcomme, 1985). Lateral differences in floodplain waterbodies environments produce differences in species distributions associated with physiological and morphological adaptations between fishes (Dudgeon, 2000; Welcomme *et al.*, 2006). Welcomme (1985) documented that assemblage characteristics of fishes were reflected by the size of floodplain waterbodies, with larger fish inhabiting larger floodplain pools. Abiotic variables such as pH, oxygen, turbidity, depth and macrophyte cover affect isolated water body fish assemblages in perennial tropical (Rodriguez & Lewis, 1997; Tejerina-Garro *et al.*, 1998; Suarez *et al.*, 2001; Petry *et al.*, 2003a, b, c; Hoeinghaus *et al.*, 2003; Pouilly & Rodriguez, 2004) and temperate floodplains (DeAngelis *et al.*, 1997; Grift, 2001; Winemiller *et al.*, 2000; Feyrer *et al.*, 2004). Biotic variables such as predator/prey interaction (Rodriguez & Lewis, 1997; Suarez *et al.*, 2001) and disease risk (DeAngelis *et al.*, 1997; Bartosova *et al.*, 1999) are also strong determinants of assemblage composition. For example, at the end of the dry season in the River Orinoco, air-breathing predators dominate the community composition in isolated floodplain waterbodies with low dissolved oxygen (Rodriguez & Lewis, 1994). Stochastic floods produce different disturbance and colonization regimes to perennial rivers, which strongly influence fish species assemblages (Zeug *et al.*, 2005), although, similar relationships between assemblage structure and physicochemical characteristics occur during isolation (Zeug *et al.*, 2005; Arthington *et al.*, 2005). Floodplain waterbodies can eventually desiccate causing mortalities of all fish present (Lusk *et al.*, 1998). Ultimately, abiotic and biotic (predation and competition) controls over fish in floodplain water bodies can cause localized extinctions of species intolerant of conditions and/or modulate recruitment of juveniles to riverine populations.

2.5 ANTHROPOGENIC IMPACTS ON FLOODS AND FLOODPLAINS

Many studies document the extent to which regulated rivers deviate from a pristine state (see Cowx, 2002). Dynesius & Nilsson (1994) found that dams, reservoirs, inter-basin diversions and irrigation strongly or moderately affected 77% of the flows from the 139 largest rivers in the northern third of the world. In a more recent global overview of large river systems, Nilsson *et al*. (2005) found that over half (172 of 292) were affected by dams. Construction of dams for flood control or hydroelectric power generation imposes serial discontinuities (Ward & Stanford, 1983, 1995b), alters the natural flow (and flood) regime (*sensu* Poff *et al*., 1997), and can result in dramatic loss of ecological integrity and spatial heterogeneity (Toth *et al*., 1995; Schmidt *et al*., 1998; Molles *et al*., 1998; Jungwirth *et al*., 2000; Schiemer, 2000; Snyder *et al*., 2003; Thoms, 2003). Alterations to the flow regime are considered to be the most detrimental human alterations to freshwater ecosystems (Stanford *et al*., 1996; Poff *et al*., 1997).

Flow regulation, channelisation, and artificial levee construction (Ward, 1998a; Amoros & Bornette, 2002) reduce rivers to single-thread channels, with shortened shoreline length and isolated from their floodplains and lentic waters (e.g. oxbows and pools) (Petts *et al*., 1989; Ward & Stanford, 1995a; Neumann *et al*., 1996; Cowx & Welcomme, 1998; Tockner & Stanford, 2002; Thoms, 2003; Schiemer *et al*., 2004). Man-made levees completely separate the former floodplains from erosive, scouring flood flow, thus preventing the creation of new floodplain waters, reducing rejuvenation and accelerating terrestrialization of existing water bodies (Tockner & Bretschko, 1996; Ward, 1998b) (Figure 2.7). Up to 90% of European and North American floodplains are ‘cultivated’ and therefore functionally extinct (Tockner & Stanford, 2002).

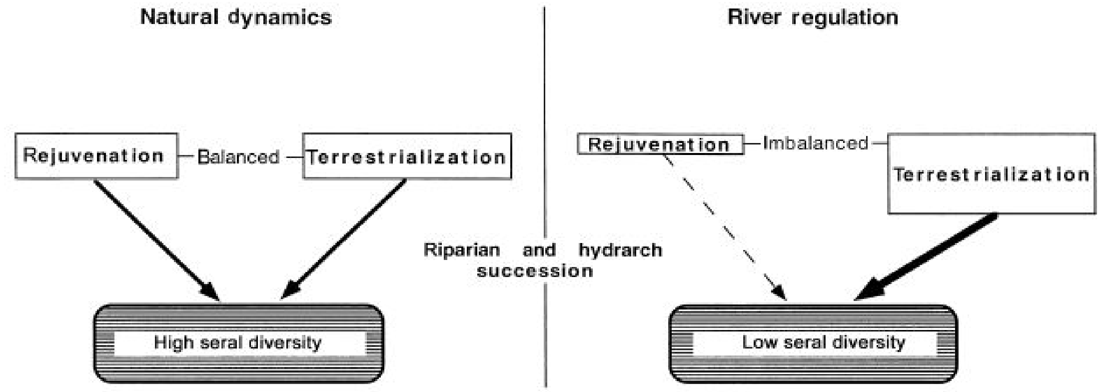


Figure 2.7 The diversity of succession stages in natural and regulated riverine landscapes as a function of the relationship between rejuvenation and terrestrialization processes (from Ward & Tockner, 2001).

Since floodplain habitat heterogeneity and high hydrological connectivity, driven by the flood pulse, leads to high levels of productivity and biodiversity, most human alterations are likely to cause a reduction in biodiversity and productivity of both the main river channel and its accompanying floodplain waterbodies, by reducing lateral connectivity, altering succession trajectories and disrupting seasonal water level fluctuations (Figure 2.8). Thus, in ‘flood-dependent’ ecosystems the prevention of floods is considered a disturbance (Bayley, 1995; Sparks, 1995).

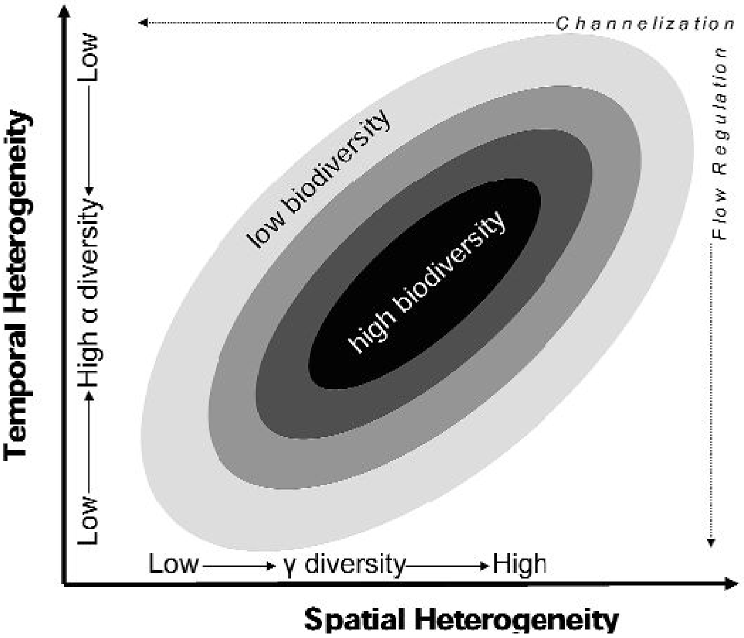


Figure 2.8 Conceptual model illustrating the importance of spatiotemporal heterogeneity in maintaining biological diversity in floodplain rivers. Anthropogenic alterations such as channelization and flow regulation are expected to result in compromised heterogeneity; direction of impact is indicated by dotted lines (Arrington & Winemiller, 2004).

Nilsson *et al.* (2005) stated that human modifications to the hydrologic regime and floodplain connectivity are impacting fish communities globally. Where natural flash floods are regulated by upstream dams, stabilized flows often favour alien fish species, which prey on and compete with native fish (Meffe, 1984; Moyle & Light, 1996a, b; Reid & Brooks, 2000) or are better able to tolerate the harsher conditions in the modified environment. Aarts *et al.* (2004) reported that ecological fish guilds are unevenly affected in heavily regulated rivers as rheophilic species have become (very) rare because their lotic habitats have been lost or degraded, but the floodplain transversal succession gradient in fish community resembled that of natural rivers, because plesiopotamal and paleopotamal lakes are still present in regulated river–floodplain systems. Flow stabilization and reduced floodplain habitat have been reported to affect fish species highly adapted to the periodic inundation for spawning

(Kwak, 1988; Trexler, 1995; Baras & Lucas, 2001; Grift *et al*., 2001a, 2003), nursery (Gehrke *et al*., 1995, 1999; Modde *et al*., 2001; Grift *et al*., 2003), flow refuge (Bischoff & Wolter, 2001) and also affect food web structure (Power *et al*., 1996). The loss of floodplain habitat also has a knock-on effect on in-channel species. The absence of flooding in regulated sections of the upper River Paraná, Brazil, has had adverse effects on many fish species due to lack of access to out-of-channel habitat, resulting in increased predation in the channel (Agostinho *et al*., 2001). The composition of the fish fauna in dammed channels changes from a rheophile-dominated assemblage to eurytopic forms (Schiemer & Waidbacher, 1992). Schiemer & Zalewski (1992) suggested that the RCC might be more appropriate than the FPC, for describing the functioning of floodplain rivers restricted to channel by levees, based on the dominant role of longitudinal processes. Welcomme *et al*. (2006) propose the use of environmental guilds as indicators of fish assemblage responses to hydrological, morphological and functional changes in a river.

It is important to consider the potential for a lag time between abiotic changes and abiotic adjustments, since floodplains respond slowly to anthropogenic impacts, i.e. it is easy to underestimate the extent of degradation. Hence, apparent high biodiversity in regulated floodplains may often be a relict of former conditions (Tockner & Stanford, 2002). For example, Tockner & Bretschko (1996) suggested the high invertebrate diversity in a regulated section of the Danube, Austria, is a transitional state related to the high spatial heterogeneity, but is ultimately succeeding toward terrestrialization. Additionally, subtle effects of modifications and schemes may have been, and may remain, undetected (Craig *et al*., 2004). Alternatively, alterations in population structure caused by environmental change may be difficult to detect in rivers exposed to numerous detrimental impacts. For example, environmental degradation produces very similar effects to fishing pressure, i.e. altering population structure by replacing larger, long-lived “K” selected species with smaller, short-lived “r” selected ones (fishing-down; Welcomme, 1999).

Ultimately human modifications to the river-floodplain ecosystem culminate in more fish taxa becoming endangered and a loss of species diversity (for example, Ward, 1998a; Galat *et al*., 1998; Jungwirth, 1998; Collares-Pereira *et al*., 2002). Robinson *et al*. (2002) suggested that the complex life cycles of many fauna of intact riverine landscapes infers that species loss translates to a loss in evolutionary trajectories of morphology, physiology, behaviour and complex life cycles. Tockner & Stanford (2002) emphasized the urgent need to preserve intact floodplain rivers and restore impacted systems to prevent extinctions of species and ecosystem services.

2.6 REHABILITATION OF FLOW REGIMES AND FLOODPLAINS

Much of the knowledge about the structure and function of river-floodplain landscapes is based on research in the tropics on unregulated rivers (Junk *et al*., 1989). However, it is believed that unchanged temperate rivers functioned in a comparable way to tropical river-floodplain rivers (Welcomme, 1995), although differences in climate can influence some seasonal processes. Brown (2002) stated that if river restoration is to have an ecological, as opposed to ‘cosmetic’ design, it is necessary to question what the natural river-floodplain state was and whether this state can be recreated. Ecological conditions of rivers before channelization are poorly known, (for example, the Kissimmee River; Trexler, 1995), although, with sufficient hydrologic variation, unmodified reaches can remain intact (Sparks *et al*., 1990; Poff *et al*., 1997; Richter *et al*., 1997). Inadequate data from pristine natural systems constrain the capability to restore river-floodplain systems. Additionally, Hauer & Lorang (2004) questioned, “Can a reasonable amount of natural functionality be restored while also allowing traditional human uses of the river and its floodplains?” this is particularly true where re-establishment of natural floodplain functioning compromises societal values, property and economic investment. Consequently, restoration of aquatic habitats towards pristine conditions is considered a utopian view (Cowx *et al*., 2004). Tockner & Stanford (2002) and Schiemer *et al.* (1999) suggested restoration projects could serve as large-scale field experiments for a better understanding of the dynamics and complexity of riverine floodplains. Hauer & Lorang (2004) suggested recovery towards a “normative” condition, allows many, if not most, of the historical natural resource uses of rivers to occur within historical ranges of variation, but this is compromised in large urban areas where such adjustment is not feasible.

Restoration strategies should not focus on a single taxonomic group or species (Sparks, 1995; Tockner *et al*., 2000a), because different faunal groups have different environmental requirements, i.e. different taxonomic groups peak in performance at different positions along the connectivity gradient (Tockner *et al*., 1998). However, flagship species can highlight key issues and progress in addressing these. For example, nase (*Chondrostoma nasus* (L.)) has become a key conservation species for highlighting the environmental conditions of large European rivers (Schiemer *et al*., 2003). Conservation plans that target only one species, e.g. *Anaecypris hispanica* (Steindachner), but incorporate habitat protection and improvements can confer wider benefits to ecosystem health and allow a wider diversity of species to flourish (Collares-Pereira & Cowx, 2004). Cowx & Welcomme (1998) suggested rehabilitation of rivers for fish should involve reinstating lateral and longitudinal connectivity, recreating habitat diversity and channel morphology, improving flow regimes for fisheries purposes and improving water quality problems. In many cases, the removal of dams to improve longitudinal connectivity is not possible, and water quality no longer limits riverine fish populations, certainly in Europe (Van Dijk *et al*., 1995; Cals *et al*., 1998; Nienhuis & Leuven, 2001; Raat, 2001). Hence, riverscape management and rehabilitation strategies should focus on restoring hydro-geomorphological dynamics to increase spatio-temporal heterogeneity (Amoros & Bornette, 2002).

Tockner *et al*. (1998) suggested restoration of the integrity of the hydrograph is the most vital step in restoring rivers. Several studies have attempted to model environmental flows regimes necessary to protect or restore river ecosystems, for example the RVA (Range of Variability Approach; Richter *et al*., 1997), the DRIFT methodology (Downstream Response to Imposed Flow Transformations; King *et al*. 2003), and others (Arthington & Pusey, 2003; Arthington *et al*., 2003; Richter *et al*., 2003; reviewed in Tharme, 2003; Cowx *et al*., 2004). Re-regulating flows by rescheduling dam releases, to simulate the range of natural intra- and interannual variation of hydrologic regimes (magnitude, timing, duration, variability and frequency), "naturalizes" regulated rivers (*sensu* Poff *et al*., 1997), thus protecting native biodiversity and the evolutionary potential of aquatic, riparian and wetland ecosystems (Richter *et al*., 1996, 1997; Stanford *et al*., 1996; Poff *et al*., 1997). Stanford *et al*. (1996) argued that flows should be re-regulating so that the river performs most of the geomorphic restoration of floodplain habitats, instead of using heavy equipment to engineer artificial solutions. Bischoff & Wolter (2001) documented that habitat diversity increased in the River Oder in response to a very large flood, and they suggested that more large floods could enhance fish recovery in this highly regulated system. In the Kissimmee River (Florida, USA), restoration of a more natural hydrologic regime has resulted in increased growth rate and maximum size of largemouth bass (*Micropterus salmoides* (Lacepède)) (Arrington & Jepsen, 2001). Many studies have also documented the benefits of dam release floods for enhancing native fish populations over non-native fish (Meffe & Minckley, 1987; Marchetti & Moyle, 2001; Valdez *et al*., 2001; Brown & Ford, 2002; Schultz *et al*., 2003), primarily because of varying behavioural responses during flood events (Meffe, 1984; Ward *et al*., 2003).

Cowx & Gerdeaux (2004) suggested the necessity of recreating functional habitats for spawning, feeding, nursery (growth) and resting (self protection) areas, and the connectivity between these habitats, so improving the ecological functions of the river system (Schiemer *et al*., 1999). As a result, levees should be set back, lowered or removed; secondary channels created and isolated oxbows reconnected (Van Dijk *et al*., 1995; Cals *et al*., 1998; Tockner *et al*., 1998; Simons *et al*., 2001; Lusk *et al*., 2001, 2003). These processes have the capacity to restore floodplains, backwaters and floodplain water bodies, reinstate hydrological connectivity and increase habitat complexity (Gore & Shields, 1995; Stanford *et al*., 1996; Aarts *et al*., 2004). Such restoration or rehabilitation efforts may only be necessary in limited reaches to maintain the fishery and biodiversity, i.e. the “string of beads principle” (Cowx & Welcomme, 1998).

Artificial floodplain ponds (borrow pits excavated during dyke construction) connected to the main channel function as excellent fish spawning, nursery, feeding, winter and shelter habitats, replacing habitat lost during river regulation (Sabo & Kelso, 1991; Staas & Neumann, 1996), especially if coupled with controlled flooding of the floodplain habitat (Jurajda *et al*., 2004). Grift *et al*. (2003) observed fish habitat use in man-made secondary channels (rheophilic fish) and reconnected oxbow lakes (eurytopic fish) was comparable to (semi-)natural floodplains, with different water bodies having complementary values, emphasizing that future floodplain rehabilitation should focus on water bodies diverse in habitat type. Simons *et al*. (2001) also concluded that man-made secondary channels function as a biotope for riverine fish species, including the more demanding rheophilic species. Sommer *et al*. (2002) reported that floodplain restoration improves floodplain connectivity during low flows with benefits for splittail (*Pogonichthys macrolepidotus* (Ayres)) reproduction in dry years. In addition, restoring seasonal hydrology and increasing river floodplain connectivity reduces the impacts of non-native fish and benefits native fish (Gutreuter *et al*., 1999; Sommer *et al*., 2001b; Sommer *et al*., 2004a; Barko *et al*., 2006), although, the opposite has also been reported (Heeg *et al*., 1980; Heeg & Breen, 1994; Bruwer *et al*., 1996; Scheerer, 2002).

Tockner & Stanford (2002) stated that natural uses of floodplains far outweigh the value of human activities that constrain floodplain structure and function. Not only are such statements unrealistic (socio-economic constraints), they also fail to incorporate the benefits of floodplain structure and function to humans; floodplains store huge amounts of water and change the flood pulse from short, devastating peak discharges to lower discharges of longer duration, i.e. floodplains are natural flood control structures that can provide human flood protection benefits. Brenner *et al*. (2003) reported that ecologically sensitive flood control structures enhanced fish recruitment and diversity along the rivers Rhine and Meuse. In addition, Poff (2002) outlined a successful example of non-structural flood controls managed for wildlife habitat on Charles River, USA, at a cost of less than 10% of the projected cost of the originally proposed dam and levee project. Since the impact of floods on human habitation are the driving forces in river corridor and floodplain management, there is an urgent need to ensure that such soft engineering flood protection methods that are sensitive to fisheries are integral to future human flood management strategies. Consequently, ecologists need to play a major role in providing education and leadership of the benefits of the natural hydrological regimes and associated habitat within catchments, to both humans and biodiversity (Collares-Pereira *et al*., 2002).

2.7 CONCLUSIONS

Floods are an essential component of the hydrological regime that influence riverine ecosystem function and structure and fish assemblage patterns throughout the catchment. In upland streams, floods are hydrological disturbances influencing the evolution of fish species life history, behavioural and morphological adaptations. Floods of irregular timing and magnitude can cause mortality of juveniles and adults; but in upland streams the species present generally have evolved the ability to recover quickly. In more lowland reaches, floods are characterized by lateral expansion onto floodplains resulting in high levels of habitat heterogeneity, essential for fish refuge, spawning, nursery and feeding. As reported for upland reaches, in temperate aseasonal rivers, floods of irregular timing can cause mortality of juveniles, but variations in magnitude and duration can have significant influence on species assemblages in seasonal rivers. Anthropogenic alterations to the flow regime and floodplain connectivity cause a reduction in biodiversity and productivity of both the main river channel and its accompanying floodplain waterbodies. Rehabilitation efforts should reinstate lateral and longitudinal connectivity by restoring a more natural hydrologic regime and recreating functional habitats, i.e. recovery towards a “normative” condition, thus providing human flood protection whilst maximizing ecological benefits.

3 EFFECTS OF FLOODS ON 0+ CYPRINID FISHES IN A CONSTRAINED LOWLAND RIVER: EVIDENCE FOR BACKWATER AND FLOODPLAIN REHABILITATION

3.1 INTRODUCTION

Connectivity between rivers and their floodplains is essential for the functioning and integrity of floodplain ecosystems (Amoros & Bornette, 2002). River-floodplain connectivity allows fish to disperse freely and take advantage of different floodplain habitats for refuge, spawning, nursery and feeding (Chapter 2). However, many rivers have been subjected to channelisation and artificial levee construction, reducing them to single-thread channels and isolating them from their floodplains (Ward & Stanford, 1995a; Cowx & Welcomme, 1998). Reduced floodplain habitat have been reported to affect fish species highly adapted to the periodic inundation for spawning (Kwak, 1988; Trexler, 1995; Baras & Lucas, 2001; Grift *et al*., 2001a, 2003) and nursery (Gehrke *et al*. 1995, 1999; Modde *et al*., 2001; Grift *et al*., 2003). Such modifications can also have adverse consequences for fishes during floods, because of increased severity of conditions (e.g. increased water velocity and bed load transport) in the main channel (Lusk *et al*., 1998; Poff *et al*., 2006), prevention of fish using floodplain habitats for refuge (Ross & Baker, 1983; Kwak, 1988), and the stranding of fish when artificial levees are ‘over-topped’. This is of particular importance to 0+ fishes because of their poor swimming capabilities (Harvey, 1987; Humphries *et al*., 2006). Furthermore, abiotic factors are increasingly being recognised as an important factor causing inter-annual variability in the recruitment success of cyprinid fishes (Nunn *et al*., 2007b). However, relatively little is known about the habitat use of 0+ fishes before, during and after high flow and flood events (but see Bischoff & Wolter, 2001) in relation to the timing of such events. This issue is of particular importance since flood frequency and magnitude are predicted to increase under the influence of climate change (IPCC, 2002). Additionally, climate change is predicted to interact with existing riverine alterations and further impact ecosystem functioning (Peterson & Kwak, 1999; Gibson *et al*., 2005).

The aim of this study was to determine the effect of high flow and flood events of varying timing and magnitude on 0+ cyprinids in a constrained lowland river, assess the significance of these effects and suggest mitigative measures, if necessary. This was achieved by sampling the 0+ fish populations of the Yorkshire Ouse in: (1) the main river channel on a fortnightly/monthly basis; (2) backwaters during high flow and flood events; and (3) areas of water isolated from the main river channel behind levees after flood waters receded. Specifically, the objectives were to compare the community structure, density and size composition of 0+ fish species in the main river with those in backwaters and on floodplains during / after high flow and flood events.

3.2 MATERIALS AND METHODS

3.2.1 Study area

The Yorkshire Ouse (Figure 3.1), north-east England, is one of the UK's largest single-thread rivers and has been isolated from its floodplain by channelisation and levee construction. The river drains 10 000 km^2 of predominantly rural catchment, has an average width of 50 m and a depth of 3-4 m, and water quality is generally good (Neal & Robson, 2000). Precipitation run-off from the Pennines often results in elevated river levels and out-of-bank floods, such as in August, October and December 2004, March, May and December 2006, and January 2007 (Figure 3.2).

3.2.2 Surveys of 0+ fish

Sampling was carried out at eight river sites, six backwater sites and five floodplain sites (Table 3.1). The river sites were in the margins of the main channel in areas devoid of large woody debris, in water $\leq$1.5 m deep, where water velocity was slow and where 0+ fishes tend to aggregate. 0+ fish populations were surveyed at river sites approximately at intervals of between 14 and 30 days from April 2004 to February 2007, inclusive, in daylight hours. The exception was during June and July 2006 when no sampling was undertaken because of an outbreak of Viral Hemorrhagic Septicaemia (VHS) at a fish farm within the catchment. Backwaters were areas of slack water that were sampled during high flow events and floods, and consisted of plateaus between the main river channel and the levees (B1, B2 and B3), a 'backed-up' tributary (B4), a slipway between two buildings (B5) and a bay downstream of some large marginal willows (*Salix* spp.) (B6). Four of the floodplain sites flooded via levee overtopping, of which two (F1 and F2) drained through underground drains, one (F5) drained via a 'flap-gated' ditch but left a substantial area of isolated water, and one (F3) emptied

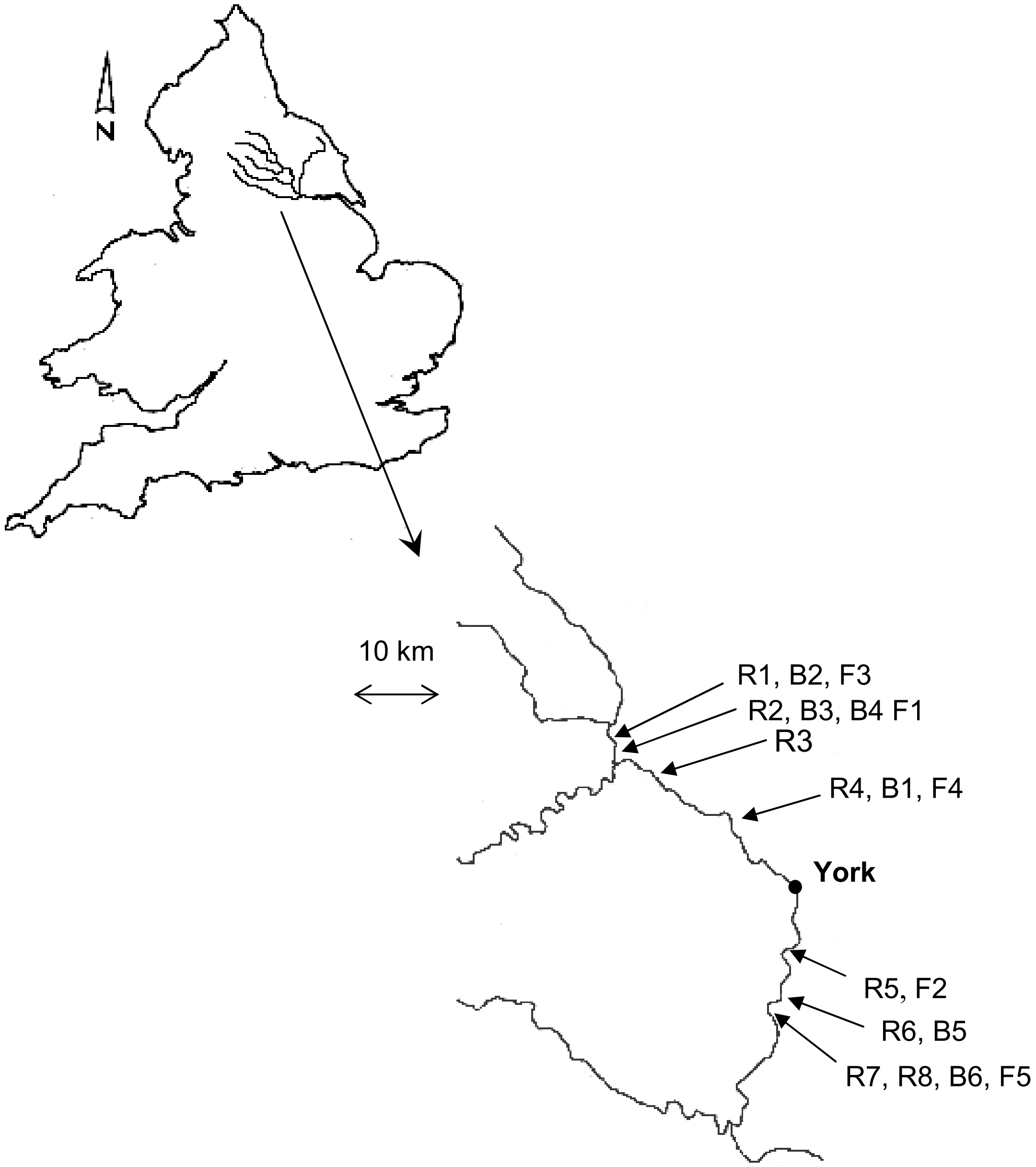


Figure 3.1 A map of England showing the location of the Ouse catchment, and a more detailed catchment map showing river, backwater and floodplain sampling sites. Site codes are as in Table 3.1.

through a sluice with any residual water extracted by pump. The fifth floodplain site (F4) was flooded by a manually-operated sluice (upstream end) and drained through a sluice (downstream end) after river levels receded, with any residual water extracted by pump. After floods, sampling on floodplains began as soon as areas of water became isolated from the main river channel. All samples were collected using a micromesh seine net (25 m long by 3 m deep, 3-mm hexagonal mesh) that was set in a rectangle parallel to the bank by wading. The seine net captured larvae as small as 5 mm, although its efficiency was reduced for fish smaller than ~15 mm (Cowx *et al.*, 2001). Captured fish were identified to species (Pinder, 2001), separated into six larval (L1-L6)

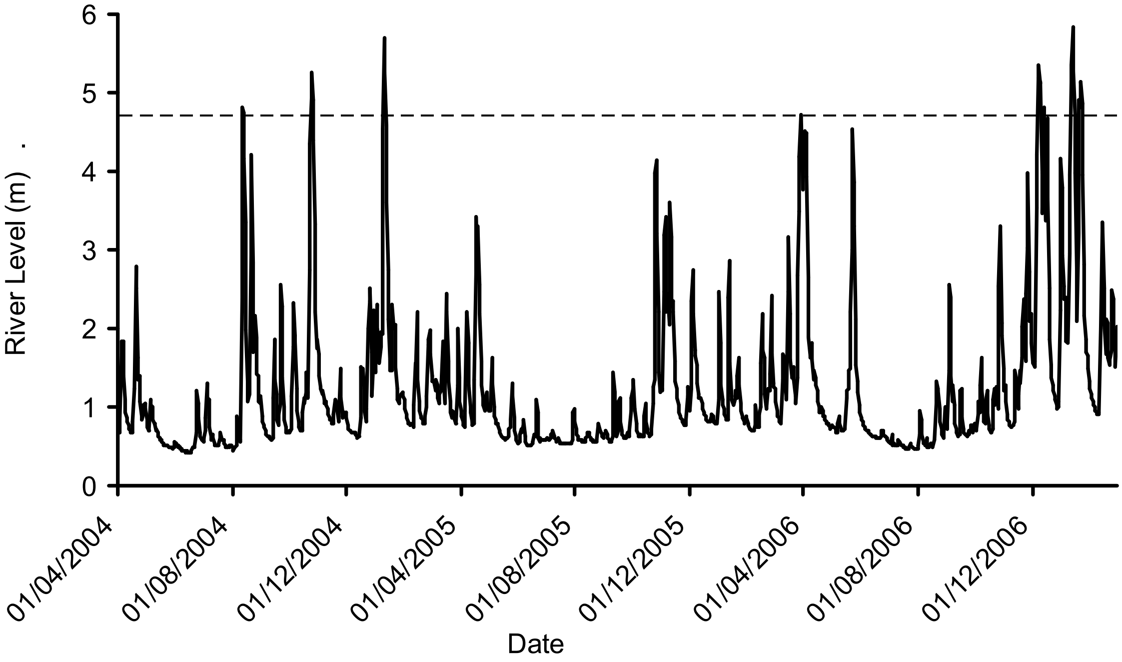


Figure 3.2 Mean daily river level (m) of the Yorkshire Ouse at Skelton from April 2004 to February 2007. River level when ‘out-of-bank’ floods occur (– – –).

and one 0+ juvenile (J) developmental step (Copp, 1990; Peňáz, 2001), and measured for standard length (SL, nearest mm).

3.2.3 Data analysis

For each site sampled, the frequency of occurrence and relative abundance of each fish species was calculated from all the surveys (Hynes, 1950), and the Shannon-Wiener diversity index (*H’*), species richness, Pielou’s measure of evenness (*J*) (Washington, 1984) and relative density (fish m^{-2}) of 0+ fishes (all species combined) was calculated for each sampling occasion. Frequency of occurrence of a given species was defined as the number of surveys in which the species occurred, expressed as a frequency of the total number of surveys in which fish were captured. Relative abundance of a species was defined as the percentage of total catches (numbers) in all surveys comprised by the given species.

Mann-Whitney *U*-tests were used to test the null hypothesis that mean H’, richness, *J* and density of 0+ fishes for all surveys at each site did not differ significantly between the river and backwater / floodplain sampling units. Mann-Whitney *U*-tests were used to test the null hypothesis that there was no difference in overall *H’* and relative abundance

Table 3.1 Details of sites surveyed for 0+ fishes in the Yorkshire Ouse river (R), backwaters (B) and floodplains (F), including substratum, key aquatic macrophytes and number of times sampled (*n*).

Site name	Habitat	Code	Dimensions	Substrate	Key aquatic macrophytes	*n*
Linton	Main river	R1	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	*Potamogeton pectinatus* L. (little)	31
Newton	Main river	R2	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	*P. pectinatus*	19
Beningbrough	Main river	R3	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	*P. pectinatus*	28
Clifton	Main river	R4	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Sand/clay	-	19
Fulford	Main river	R5	River width 50 m, max. depth 3-4 m, sampling depth 1.2 m	Mud/silt	*P. pectinatus*	30
Naburn	Main river	R6	River width 50 m, max. depth 3-4 m, sampling depth 1.5 m	Sand/clay	-	19
Acaster Malbis	Main river	R7	River width 50 m, max. depth 3-4 m, sampling depth 1.5 m	Concrete	-	31
Naburn weir	Main river	R8	River width 70 m, max. depth 3-4 m, sampling depth 1.5 m	Sand/clay	*P. pectinatus*	19
Clifton	Backwater	B1	River width 100 m, max. depth 9-10 m, sampling depth 2 m	Grass	-	8
Linton car park	Backwater	B2	River width 150 m, max. depth 10-12 m, sampling depth 1 m	Concrete	-	3
Newton	Backwater	B3	River width 100 m, max. depth 9-10 m, sampling depth 1 m	Grass	-	3
River Kyle	Backwater	B4	River width 30 m, max. depth 9-10 m, sampling depth up to 10 m	Grass	-	2
Naburn	Backwater	B5	River width 100 m, max. depth 9-10 m, sampling depth 1 m	Concrete	-	3
Naburn weir	Backwater	B6	River width 100 m, max. depth 10-12 m, sampling depth 2-4 m	Grass	-	2
Newton Ings	Floodplain	F1	Ings surface area 3 ha, drained down sampling area 2 ha, depth 0.5 m	Grass	-	6
Nun Ings	Floodplain	F2	Ings surface area 1 ha, drained down sampling area 0.4 ha, depth 0.5 m	Grass	-	5
Linton Ings	Floodplain	F3	Ings surface area 20 ha, drained down sampling area 0.1 ha, depth 0.5 m	Grass	-	2
Rawcliffe Ings	Floodplain	F4	Ings surface area 20 ha, drained down sampling area 0.3 ha, depth 0.5 m	Grass	-	4
South Ings	Floodplain	F5	Ings surface area 25 ha, drained down sampling area 0.5 ha, depth 0.5 m	Grass	-	1

of the main species (bleak (*Alburnus alburnus* (L.)), chub (*Leuciscus cephalus* (L.)), dace (*Leuciscus leuciscus* (L.)), gudgeon (*Gobio gobio* (L.)) and roach (*Rutilus rutilus* (L.))) in the river at the end of summer in 2005 (no floods during summer) and 2006 (elevated flow period during May (Figure 3.2)).

Mean SL (independent samples *t*-tests), median SL (Mann-Whitney *U*-tests, when variances were not equal (Levene statistic $P < 0.05$)) and length distributions (two-sample Kolmogorov-Smirnov tests) of each fish species in the river before floods were compared with fish in backwaters, on floodplains and in the river after floods. These comparisons tested the null hypotheses that there was no significant difference in 0+ fish size in surveys prior to floods compared to the size of fish in backwaters and stranded on floodplains, or fish size in the river after the floods, respectively. Comparisons were restricted to backwater and floodplain sites that had adjacent river sites (to avoid potential bias caused by spatial variations in fish size) and to samples when sufficient numbers (>30) of a given species were caught. All statistical analyses were carried out using SPSS (version 14.0) with a significance level $\alpha = 0.05$.

3.3 RESULTS

3.3.1 Species composition

More than 250 000 specimens of 19 fish species were captured during the study period (Table 3.2). Of these, all but rudd (*Scardinius erythrophthalmus* (L.)) were captured from the main river, 14 species (>25 000 individuals) were caught from backwaters and 12 species (>20 000 individuals) were captured on floodplains. Roach, gudgeon, chub and bleak occurred most frequently in main river and backwater catches. Roach, chub and bleak also occurred most frequently on floodplains, but gudgeon were captured less often on floodplains (Table 3.2). Median *H*', was significantly higher in the river surveys during normal flows than in backwaters during floods (Mann Whitney *U*-test: $Z = -2.160$, $n = 13$, $P = 0.031$), but not median richness (Mann Whitney *U*-test: $Z = -0.154$, $n = 13$, $P = 0.877$). Median *H*' and richness were significantly higher in the river surveys during normal flows than on floodplains after floods (Mann Whitney *U*-test: *H*': $Z = -2.623$, $n = 13$, $P = 0.009$; richness: $Z = -2.006$, $n = 13$, $P = 0.045$). Median *J*, did not differ significantly between river surveys during normal flows and in

Table 3.2 Frequency of occurrence and relative abundance of 0+ fish captured from the Yorkshire Ouse river (R), backwater (B) and floodplain (F).

Family Species	Vernacular name	Flow pref.[1]	Occurrence R	Occurrence B	Occurrence F	Abundance R	Abundance B	Abundance F
Balitoridae								
Barbatula barbatula (L.)	Stone loach	Rheo A	Infrequent	Infrequent	Not captured	Rare	Rare	Not captured
Cottidae								
Cottus gobio L.	Bullhead	Rheo A	Infrequent	Not captured	Not captured	Rare	Not captured	Not captured
Cyprinidae								
Barbus barbus (L.)	Barbel	Rheo A	Occasional	Infrequent	Not captured	Rare	Rare	Not captured
Alburnus alburnus (L.)	Bleak	Eury	Abundant	Dominant	Abundant	Occasional	Abundant	Frequent
Abramis brama (L.)	Bream	Eury	Occasional	Abundant	Occasional	Infrequent	Infrequent	Infrequent
Leuciscus cephalus (L.)	Chub	Rheo A	Abundant	Dominant	Abundant	Occasional	Occasional	Frequent
Leuciscus leuciscus (L.)	Dace	Rheo A	Frequent	Abundant	Occasional	Infrequent	Infrequent	Rare
Gobio gobio (L.)	Gudgeon	Rheo B	Abundant	Abundant	Occasional	Occasional	Infrequent	Rare
Phoxinus phoxinus (L.)	Minnow	Rheo A	Frequent	Abundant	Infrequent	Infrequent	Infrequent	Rare
Rutilus rutilus (L.)	Roach	Eury	Abundant	Dominant	Abundant	Frequent	Frequent	Frequent
Scardinius erythrophthalmus (L.)	Rudd	Limno	Not captured	Infrequent	Not captured	Not captured	Rare	Not captured
Abramis bjoerkna (L.)	Silver bream	Eury	Infrequent	Not captured	Not captured	Rare	Not captured	Not captured
Esocidae								
Esox lucius L.	Pike	Eury	Occasional	Occasional	Infrequent	Rare	Rare	Rare
Gasterosteidae								
Gasterosteus aculeatus L.	Three-spined stickleback	Eury	Occasional	Occasional	Frequent	Rare	Rare	Infrequent
Pungitius pungitius (L.)	Ten-spined stickleback	Limno	Infrequent	Not captured	Occasional	Rare	Not captured	Rare
Percidae								
Gymnocephalus cernuus (L.)	Ruffe	Eury	Occasional	Occasional	Infrequent	Infrequent	Rare	Rare
Perca fluviatilis L.	Perch	Eury	Occasional	Occasional	Occasional	Rare	Rare	Infrequent
Pleuronectidae								
Platichthys flesus (L.)	Flounder	Rheo C	Infrequent	Not captured	Not captured	Rare	Not captured	Not captured
Salmonidae								
Thymallus thymallus (L.)	Grayling	Rheo A	Infrequent	Not captured	Not captured	Rare	Not captured	Not captured

Notes: [1] flow preference classification according to Schiemer & Waidbacher (1992): Rheo A = rheophilic A, Rheo B = rheophilic B, Eury = eurytopic and Limno = limnophilic.

Key (percent frequency of occurrence and abundance)

Dominant (> 75 %)
Abundant (51-75 %
Frequent (26-50 %)
Occasional (6-25 %
Infrequent (1-5 %)
Rare (< 1 %)
Not captured

backwaters during floods (Mann Whitney U-test: $Z = -0.926$, $n = 13$, $P = 0.355$) or on floodplains (Mann Whitney U-test: $Z = -1.852$, $n = 13$, $P = 0.064$).

Roach (39%), gudgeon (20%), chub (16%) and bleak (14%) were the most abundant species in the river, while backwaters and floodplains were dominated by eurytopic species (bleak = 53 and 29%; roach = 25 and 41%, respectively) (Figure 3.3). Chub abundance in backwaters (10%) was similar to that in the river, but was higher on the floodplains (26%). Gudgeon were rarely found on floodplains (mean abundance = 0.1%), but accounted for up to 27% of the catches in backwaters (B1), along with some strictly rheophilic species (i.e. barbel (*Barbus barbus* (L.)) and stone loach (*Barbatula barbatula* (L.))) (Table 3.2).

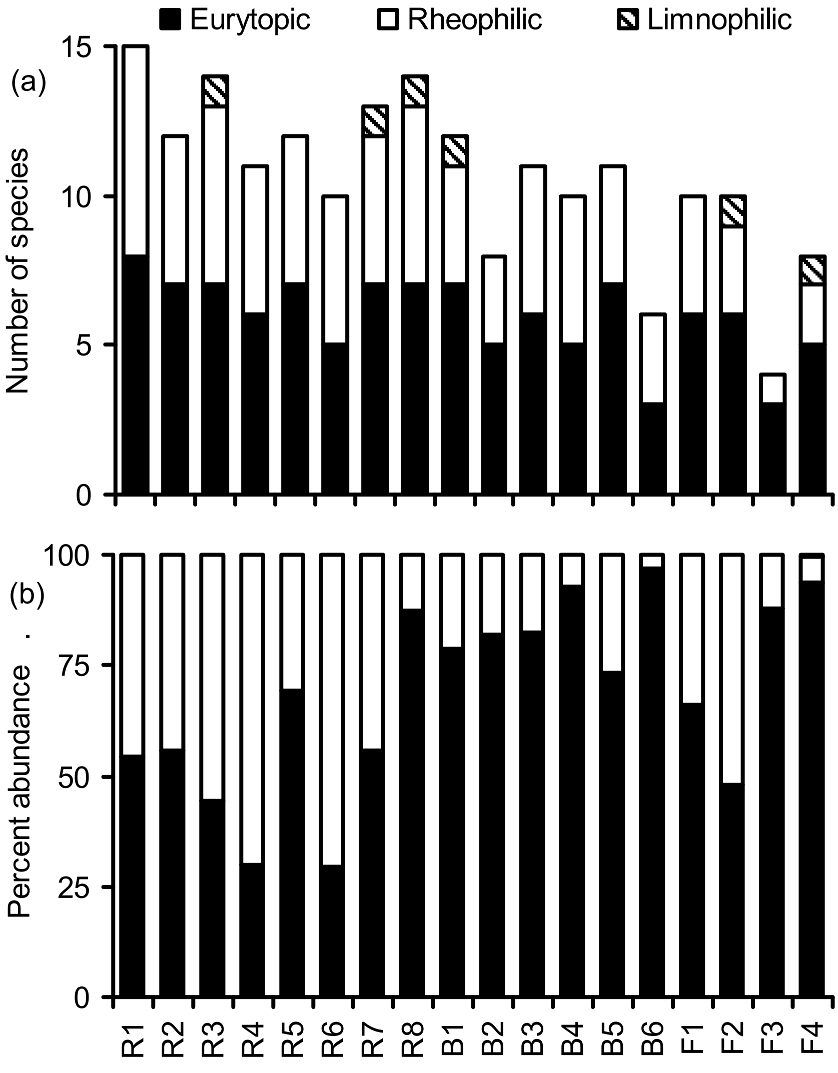


Figure 3.3 Number (a) and percent abundance (b) of rheophilic, eurytopic and limnophilic species captured from the Yorkshire Ouse river (R), backwater (B) and floodplain (F). Flow preference classification according to Schiemer & Waidbacher (1992). Site codes are as in Table 3.1.

During May 2006, a flood (Figure 3.2) coincided with the period immediately after fish hatching, and larvae of roach (L1-L3 (7.5 ± 0.7 mm)), dace (L3-L4 (11.6 ± 0.8 mm)), chub (L4 (12.8 mm)), perch (*Perca fluviatilis* L.) (L2-L6 (13.5 ± 1.5 mm)) and minnow (*Phoxinus phoxinus* (L.)) (L2-L3 (8.4 ± 0.4 mm)) were found in the river and backwaters. Unfortunately, an outbreak of VHS prevented post-flood sampling of floodplains and main river sites until August 2006, rendering immediate investigation of the impacts of the flood on the 0+ fish community impossible. Although there was a flood when the fish were in their larval period, it did not have a significant effect on H' (Mann Whitney U-test: $Z = -1.722$, $n = 18$, $P = 0.085$) and relative abundances of the main species (Mann Whitney U-tests: bleak: $Z = -0.574$, $n = 18$, $P = 0.566$; chub: $Z = -0.580$, $n = 18$, $P = 0.562$; dace: $Z = -1.820$, $n = 18$, $P = 0.069$; gudgeon: $Z = -0.397$, $n = 18$, $P = 0.691$; roach: $Z = -1.634$, $n = 18$, $P = 0.102$) in August 2006 were similar to those in August 2005, suggesting that the flood had no significant impact upon the species composition of the 0+ fish community.

3.3.2 Density

Overall, mean density of 0+ fishes during routine river sampling (all samples from R1-R8) was 11 ± 38 fish m^{-2}, but substantial spatial and temporal variations occurred (Figure 3.4). At the site level, the highest mean (37 fish m^{-2}) and maximum (455 fish m^{-2}) densities were found at R1, with the lowest mean density at R5 (2 fish m^{-2}). Densities of 0+ fishes were low in May, but increased in June and July and generally peaked in August, once the majority of species had hatched and had grown to a size when they could be effectively captured by the seine net (Figure 3.3). Thereafter, densities declined as the fish dispersed from the nursery areas and as density-dependent and -independent factors acted upon the 0+ fish populations. Densities of fish in main river sites before and after floods and at the end of each summer were not compared because temporal variations in density were so large (Figure 3.4).

During high flow and flood events, densities of 0+ fishes congregated in backwaters (B1-B6; mean = 30 ± 43 fish m^{-2})) were significantly higher than found in main river sites (R1-R8) during normal flows (Mann Whitney U-test: $Z = -3.602$, $n = 211$, $P < 0.000$). At the site level, maximum density of 0+ fishes in backwaters was 147 fish m^{-2} at B5, followed by 104 fish m^{-2} at B4 and 38 fish m^{-2} at B2.

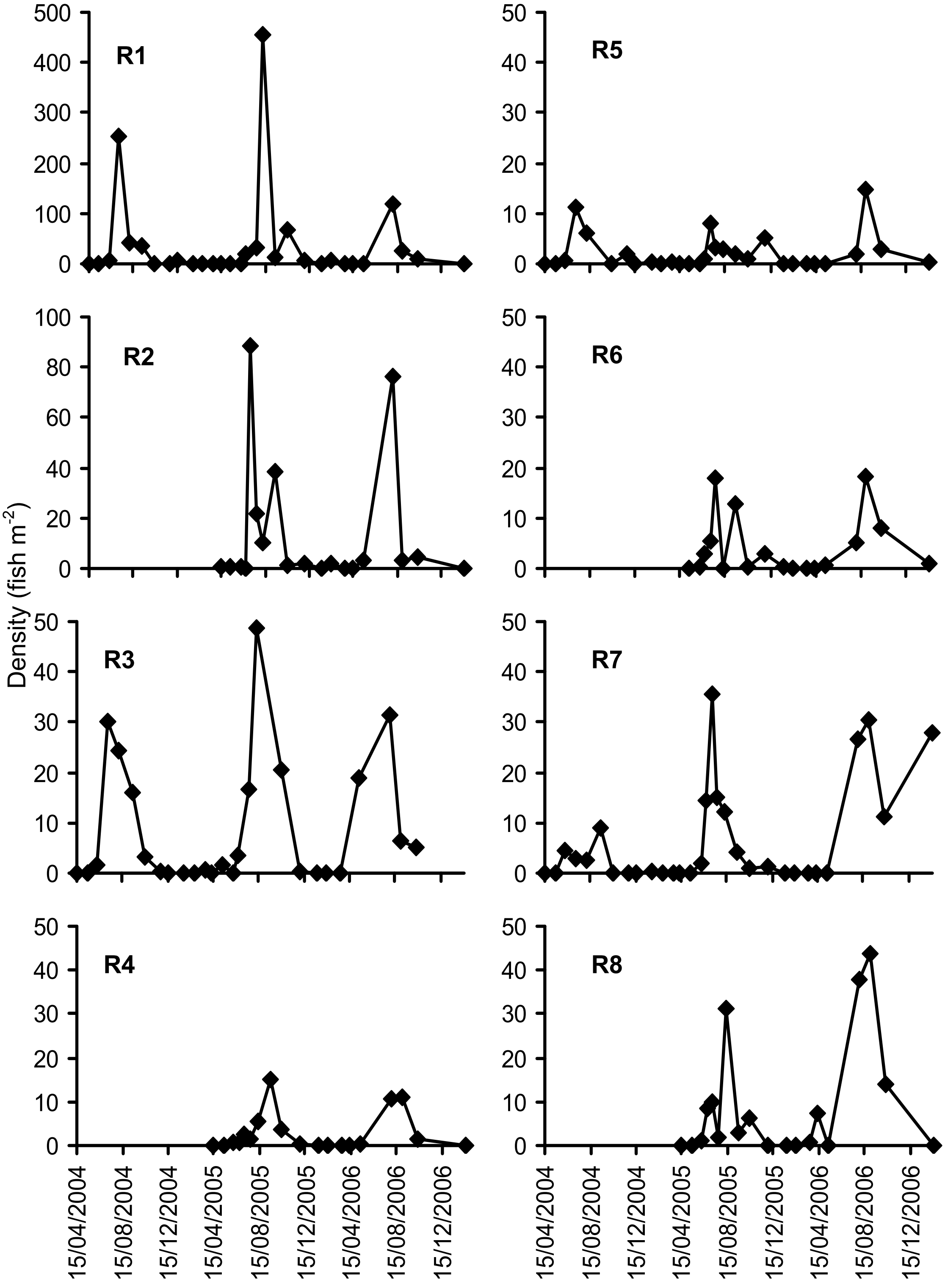


Figure 3.4 Temporal variations in the density (fish m^{-2}) of 0+ fishes (all species combined) at eight main river sites on the Yorkshire Ouse. Site codes are as in Table 3.1. Note the different y-axis scales for R1 and R2.

Substantial temporal variations in fish densities on the floodplains were observed. During the August 2004 flood, mean densities of 8 and 11 fish m^{-2} were recorded on F1 and F2, respectively. Extrapolating the densities found during sampling for the area of the water on floodplains at sampling (F1 = 2.0 hectares and F2 = 0.4 hectares), equates to approximantely 16 000 and 4400 stranded fish, respectively. Although there were floods of higher magnitude during winter months (October 2004, January 2005 and December 2006; Figure 3.2), densities of fishes recorded on floodplains were significantly lower than found during the August 2004 flood (Mann Whitney *U*-test: F1 (1 fish m^{-2}): $Z = -2.518$, $n = 12$, $P = 0.012$; F2 (<1 fish m^{-2}): $Z = -2.236$, $n = 8$, $P = 0.025$).

3.3.3 Fish size

Bleak, roach and chub in backwaters (Table 3.3) and stranded on floodplains (Table 3.4) were generally larger than those captured during main river sampling prior to a particular high flow or flood event, except for during the January 2007 flood when the first two species were larger in the river (Table 3.3). Significantly larger gudgeon (October 2005; independent samples *t*-test, $t = -8.877$, $P < 0.001$) and dace (December 2006; independent samples *t*-test, $t = -2.253$, $P = 0.025$) were found in backwaters than captured in the main river prior to each particular flood. These differences were caused by an increase in the relative abundance of larger 0+ fish in backwaters and on the floodplains compared with in the river, rather than an absence of smaller fish from the backwaters/floodplains (Figure 3.5). For example, bleak as small as 15 mm SL, and bream, chub and roach <20 mm SL were caught in backwaters during the January 2007 flood. In main river samples, mean lengths of bleak and roach at some sites were significantly larger after floods than before, (Table 3.5), suggesting that smaller fish had been displaced or had a reduced survival.

3.4 DISCUSSION

Floods and high flow events in the Yorkshire Ouse had various effects on habitat use and mortality of 0+ fishes, based on flood timing and magnitude. Backwaters and areas of slack water provided refuge for high densities of 0+ fishes, irrespective of flood timing. A flood in late spring, during the larval period (roach, dace, chub, perch and minnow) had negligible effects on relative abundance or community composition at the end of summer. Artificial levees initially prevented the occupation of floodplains during

Table 3.3 Comparison of bleak, chub and roach lengths (mean ± CI, mm) between main river sites pre-flood and backwater sites during particular flood events. (*, P <0.05; ** P < 0.01; *** P < 0.001 *t*-tests / Mann-Whitney *U*-test, backwater mean / median fish length significantly different to river) (†, P <0.05; †† P < 0.01; ††† P < 0.001 two-sample Kolmogorov-Smirnov test, backwater length frequency distribution significantly different to river).

Flood timing	Bleak		Chub		Roach	
	River	Backwater	River	Backwater	River	Backwater
Aug-04	-	-	20.5 ± 0.5	23.0 ± 0.9 *** †††	23.5 ± 0.7	22.3 ± 0.5 ** ††
Oct-04	-	-	27.4 ± 0.9	29.2 ± 1.0 **	29.5 ± 0.6	29.1 ± 0.6
Oct-05	25.6 ± 1.0	27.8 ± 0.8 ** ††	27.5 ± 1.3	27.5 ± 0.7	29.9 ± 0.8	29.6 ± 1.0
	25.0 ± 0.9	26.3 ± 0.8 * †	22.2 ± 1.1	26.9 ± 2.1 ** ††	30.4 ± 2.0	30.4 ± 1.0
			25.7 ± 1.0	29.3 ± 1.0 *** †††	-	-
Dec-06	27.4 ± 1.0	33.7 ± 2.1 *** †††	26.2 ± 1.2	29.7 ± 1.1 *** †††	34.5 ± 0.9	40.5 ± 1.1 *** †††
	27.4 ± 1.0	29.6 ± 0.8 *** †††	-	-	34.5 ± 0.9	35.3 ± 2.3
	27.2 ± 0.9	29.2 ± 1.4 * †	-	-	31.9 ± 1.1	30.9 ± 0.7
	-	-	-	-	29.4 ± 0.9	32.3 ± 1.6 ** †
Jan-07	27.4 ± 1.0	25.8 ± 0.9 * ††	26.2 ± 1.2	28.1 ± 1.5	31.9 ± 1.1	30.1 ± 0.7 * ††
	27.2 ± 0.9	26.1 ± 0.5	-	-	-	-

Table 3.4 Comparison of bleak, chub and roach lengths (mean ± CI, mm) between main river sites pre-flood and floodplain sites during particular August 2004 flood event. (*, P <0.05; ** P < 0.01; *** P < 0.001 *t*-tests / Mann-Whitney *U*-test, floodplain mean / median fish length significantly different to river) (†, P <0.05; †† P < 0.01; ††† P < 0.001 two-sample Kolmogorov-Smirnov test, floodplain length frequency distribution significantly different to river).

Site	Bleak		Chub		Roach	
	River	Floodplain	River	Floodplain	River	Floodplain
F1	-	-	20.5 ± 0.5	23.7 ± 0.5 *** †††	23.5 ± 0.7	23.9 ± 0.4
F2	20.8 ± 0.7	23.0 ± 0.4 *** †††	22.8 ± 0.5	22.2 ± 0.4 †	22.7 ± 0.6	22.5 ± 0.3 †
F3	18.8 ± 0.5	20.2 ± 0.9 ** †††	19.9 ± 0.7	23.0 ± 0.3 *** †††	20.9 ± 0.4	21.5 ± 0.4

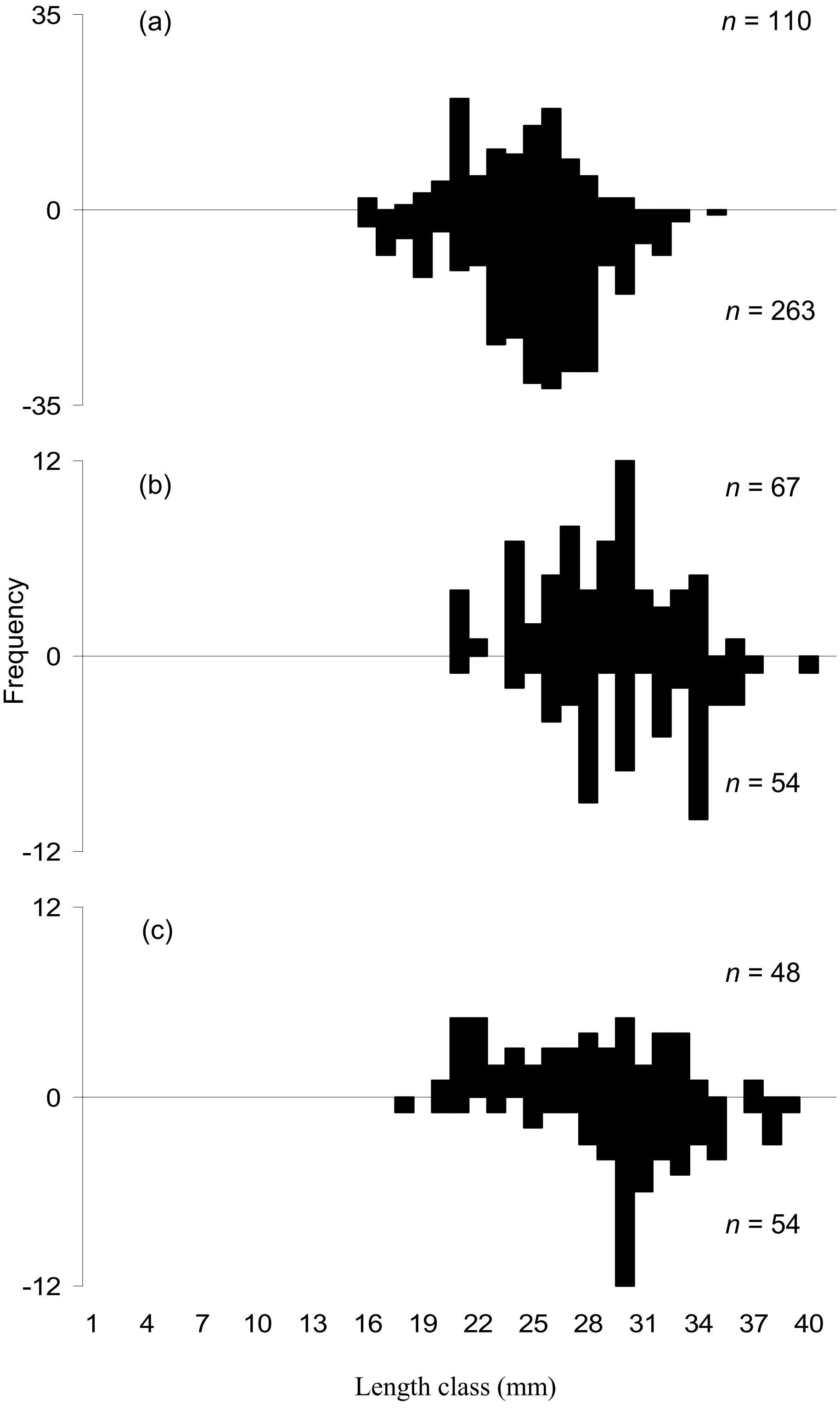


Figure 3.5 Comparative length-frequency distributions of chub catches from the river (top) and backwater / floodplain (bottom) when (a) similar median fish length but significantly different distribution (Aug 2004), (b) significantly different mean fish length but similar distribution (Oct 2004), and (c) significantly different mean fish length and distribution (Dec 2006).

Table 3.5 Comparison of fish lengths (mean ± CI, mm) before and after particular flood events. (*** $P < 0.001$ Mann-Whitney *U*-test, median fish length significantly different).

Flood date	Species	Sample site	Fish length (mean ± CI, mm)	
			Before	After
October 2004	Dace	R1	38.1 ± 0.9	39.0 ± 0.9
January 2005	Roach	R5	28.7 ± 0.4	29.6 ± 1.2
October 2005	Bleak	R1	25.7 ± 1.0	30.7 ± 0.9 ***
	Chub	R1	27.4 ± 1.3	28.9 ± 0.8
	Gudgeon	R1	33.7 ± 1.3	33.9 ± 1.1
	Minnow	R1	26.1 ± 0.8	25.6 ± 0.9
	Roach	R1	29.9 ± 0.8	32.7 ± 1.2 ***
	Roach	R5	26.8 ± 0.8	28.2 ± 1.1
Winter 2006	Bleak	R7	26.0 ± 0.7	29.8 ± 1.1 ***
	Chub	R7	28.2 ± 2.0	28.2 ± 0.8
	Dace	R6	46.3 ± 1.1	45.5 ± 1.9
	Gudgeon	R6	46.2 ± 1.1	44.3 ± 2.0
	Roach	R7	30.6 ± 1.0	31.3 ± 1.2

flood events, but over-topping resulted in the stranding of substantial numbers of 0+ fishes during summer floods. Backwaters and floodplains often supported larger fish than the main river, and fewer small fishes were caught after winter floods. The results are discussed below in relation to the resistance of 0+ fishes to flooding, based on the distribution of refuges, flood timing and, ultimately, the importance of lowland river rehabilitation.

Pearsons *et al.* (1992) reported that fish populations were more stable in physically complex habitats because of the increased availability of flow refugia. Such areas are believed to positively influence organism survival and recolonisation potential (Townsend, 1989). During all the high flow and flood events surveyed, high densities of 0+ fishes, including strictly rheophilic species, were found sheltering in backwaters and riparian vegetation, thus avoiding displacement, physical damage and/or mortality. Numerous studies document the importance of riparian shelters for juvenile fishes, including rheophilic species (Baras *et al.*, 1995; Grift *et al.*, 2003; Schiemer *et al.*, 2004; Humphries *et al.*, 2006). Also, the importance of marginal slack waters for benthic-dwelling fishes increases when floods mobilize bed sediments (Lojkásek *et al.*, 2005).

Fish species have evolved life-history strategies to survive floods based upon seasonal timing and predictability, i.e. the synchronization of a life-history stage to long-term flow regime dynamics (Poff & Allan, 1995). For example, spawning is timed so that hatching coincides with low flood probability (Seegrist & Gard, 1972; Erman *et al*., 1988), because of the poor swimming capabilities of 0+ fish (Harvey, 1987). Floods in the UK have been generally associated with heavy winter precipitation, i.e. summer floods are considered "atypical" and a disturbance (Sparks *et al*., 1990). During May 2006, elevated flows coincided with the larval period of roach, dace, chub, perch and minnow but impacts on diversity and species-specific relative abundance at the end of the summer appeared to be minimal, although the long-term effects of such floods may be realised subsequently in reduced abundance of adult fishes (Nunn *et al*., 2007b). Fish that survived the flood or hatched after the flood, experienced reduced intra- and interspecific competition (Elwood & Waters, 1969; Roghair *et al*., 2002). Although not significant, the relative abundance of roach was most reduced, perhaps due to the small size of the fish during the flood. Mann & Bass (1997) stated that the ability of 0+ roach and dace to hold station was positively related to fish length and water temperature, and negatively related to water velocity. Other studies have emphasised the importance of flood timing in relation to fish size and susceptibility to displacement and mortality (Harvey, 1987; Mion *et al*., 1998; Jensen & Johnsen, 1999; Nunn *et al*., 2007b).

Fish in backwaters and on floodplains during and after all the floods were larger than those caught in the river. However, this may reflect ontogenetic shifts in habitat use (Copp, 1992, 1997a; Garner, 1996), i.e. larger fish did not occupy marginal habitat at low flows and were thus under-represented in catches from the main river. Additionally, as fish increase in size through the summer they develop an escape response, i.e. differences are a result of investigator bias. Despite this, after floods during winter 2006, significantly larger roach and bleak were caught in the main river after the floods, again suggesting small fish were displaced or had lower survival.

During the flood in August 2004, large numbers of fish were stranded on three different 'over-topped' floodplains, but after the winter floods of greater magnitude, fewer fish were found stranded. King *et al*. (2003) similarly documented stranding of larval and juvenile cyprinids after a summer flood. Habitat use of fish prior to the flood event was probably of fundamental importance influencing lateral displacement and stranding. Juvenile cyprinid fish are known to select marginal habitat during summer months in relation to optimal temperature, feeding and predator avoidance (Garner, 1997a, b; Baras & Nindaba, 1999a, b), and are consequently more susceptible to lateral displacement. This is further supported by the lack of stranded gudgeon, which mainly occupy main channel benthic locations.

Fish were also found stranded in managed floodplains, i.e. 'over-topped' levees that drain through flap gates, and sluice-filled and -drained water storage areas that are pumped dry after floods recede. Although fish were found stranded in these areas, the majority of fish probably successfully returned to the main river through flap gates and sluices. Sommer *et al*. (2005) suggested that mortality of young chinook salmon in isolated ponds of engineered water-control structures were relatively small in relation to the overall area of floodplain. However, future floodplain rehabilitation or floodwater management structures should be designed so that all water is allowed to drain back into the river, thus removing the potential for fish mortality from stranding. Furthermore, water should be able to return to the river quickly, to reduce potential mortality from piscivorous birds, low dissolved oxygen and high levels of tannins (Lusk *et al*., 1998; Fontenot *et al*., 2001; Henning *et al*., 2007). As the flood waters receded, large numbers of black-headed gull (*Larus ridibundus* L.; flocks up to 200) and carrion crow (*Corvus corone* L.; up to 50) were observed on floodplains with isolated water, although it is believed they were feeding largely on slugs and worms, that drowned during the floods, and not on stranded fish.

Cowx & Gerdeaux (2004) emphasised the need to recreate functional habitats for spawning, feeding, nursery (growth) and resting (self protection) areas, and the connectivity between these habitats, i.e. improving the ecological functioning of the river system (Schiemer *et al*., 1999). This study provides empirical evidence for reinstating lowland river lateral connectivity and recreating habitat diversity and channel morphology (Cowx & Welcomme, 1998), thus improving the ecological status of rivers under the European Union, Water Framework Directive (2000/60/EEC). Importantly, these restoration strategies do not focus on a single taxonomic group or species (Sparks, 1995; Tockner *et al*., 2000). It is also important to recognize that floodplain rehabilitation increases system biodiversity, provides flood refuge and nursery areas for juvenile fish and benefits society from the natural functional attributes of river landscapes for flood protection (Poff, 2002; Tockner & Stanford, 2002; Brenner *et al*., 2003).

4 REHABILITATION OF LOWLAND RIVER-FLOODPLAIN ECOSYSTEMS: THE IMPORTANCE OF VARIABLE CONNECTIVITY BETWEEN MAN-MADE FLOODPLAIN WATERBODIES AND THE RIVER TRENT

4.1 INTRODUCTION

Unmodified alluvial floodplain rivers have a high spatio-temporal heterogeneity of habitats along a gradient of lateral connectivity (flow of energy, matter and organisms (Ward *et al.*, 2002c)) with the main channel (Amoros *et al.*, 1982). Consequently, there is a lotic-to-lentic succession of habitat moving from the main river channel into the floodplain, corresponding to a sequence of rheophilic-to-eurytopic-to-limnophilic fish species (Copp *et al.*, 1991; Schiemer & Waidbacher, 1992; Welcomme *et al.*, 2006). The mosaic of different waterbodies, which vary in connectivity across the floodplain, are potentially characterized by distinctive fish assemblages, that contribute to the overall high level of species diversity of riverine ecosystems (Copp, 1989). Flow regulation, channelisation and artificial levee construction (Ward, 1998a; Amoros & Bornette, 2002) invariably reduce rivers to single-thread channels and impede connectivity with their floodplains and lentic waters (Ward & Stanford, 1995a; Cowx & Welcomme, 1998). Such activities incur enormous losses in fish spawning, production and nursery areas, which may culminate in an increased number of endangered fish taxa (Schiemer & Waidbacher, 1992; Jungwirth *et al.*, 2002; Aarts & Nienhuis, 2003).

The historic reductions in landscape connectivity, ecological functioning and ecosystem biodiversity described above, have driven initiatives to improve the ecological status of rivers, e.g. the European Union, Water Framework Directive (2000/60/EEC). Achieving good ecological status of degraded rivers, involves activities such as rehabilitation of the functional integrity (hydrological connectivity and habitat heterogeneity) and ecological processes of the river–floodplain complex, which are linked to high levels of biodiversity (Ward, 1998a; Schiemer *et al.*, 1999; Ward *et al.*, 1999). However, rehabilitation schemes rarely recognise the importance of variable floodplain connectivity, instead focus efforts on improving high levels of connectivity in an attempt to maintain riverine fish community structure. For example, most studies have documented the importance of permanently-connected man-made floodplain waterbodies as spawning, feeding, nursery (growth) and refuge areas for rheophilic species (Sabo & Kelso, 1991; Neumann *et al.*, 1994; Staas & Neumann, 1996; Pinder, 1997; Simons *et al.*, 2001; Grift *et al.*, 2003; Jurajda *et al.*, 2004). In these studies, isolated floodplain waterbodies were often reconnected to the main river channel, invariably at the expense of distinct communities dependent on the lotic environment within them. Consequently, riverine ecosystem rehabilitation needs to account for variable levels of floodplain waterbody connectivity. Moreover, many non-fish taxa attain different peak species richness along the lateral connectivity gradient (Tockner *et al.*, 1998).

The aim of this study was to evaluate the importance of variable connectivity between man-made floodplain waterbodies and the River Trent for rehabilitating the riverine-floodplain ecosystem. Specifically, the study compared age 0+ fish species richness, diversity and composition across a gradient of floodplain connectivity and the impact of man-made floodplain waterbodies on the overall community structure. The results are discussed with consideration of the ecological requirements of lowland river fishes and the overriding processes influencing fish presence and distribution, including floods and humans.

4.2 MATERIALS AND METHODS

4.2.1 Study site

The study was carried out on the lower River Trent, England (Figure 4.1). The River Trent is the third longest in the UK (274 km), and has a catchment area of 10 500 km^2 and a long-term mean discharge of 84 m^3 s^{-1}, but annual and seasonal variations occur, for example, the flood at the end of May 2006 (Figure 4.2). Historically, the Trent was geomorphically active and prone to meander, but its channel has remained relatively stable in recent times, particularly since regulation of the river began approximately 300 years ago (Large & Petts, 1996; Large & Prach, 1998). Currently, the lower Trent is channelized in many areas, and impounded by a number of large weirs and sluices. Overbank flooding occurs relatively infrequently because of the regulated nature of the river. In some areas, water depths are artificially maintained for the transport of freight and pleasure craft by periodic dredging, and much of the floodplain has been claimed

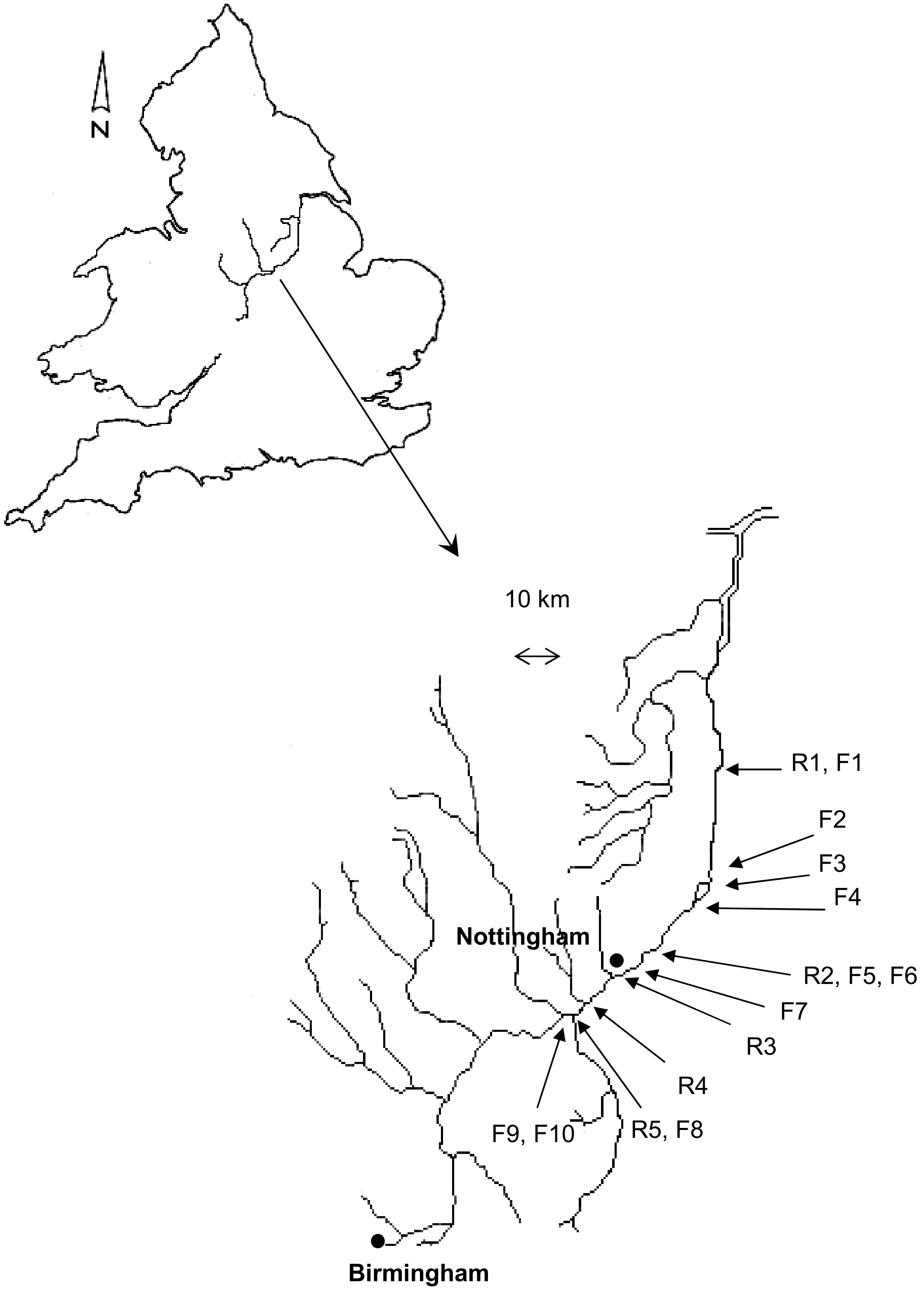


Figure 4.1 A map of England showing the location of the Trent catchment, and a more detailed catchment map showing sampling sites. Site codes are the same as in Table 4.1.

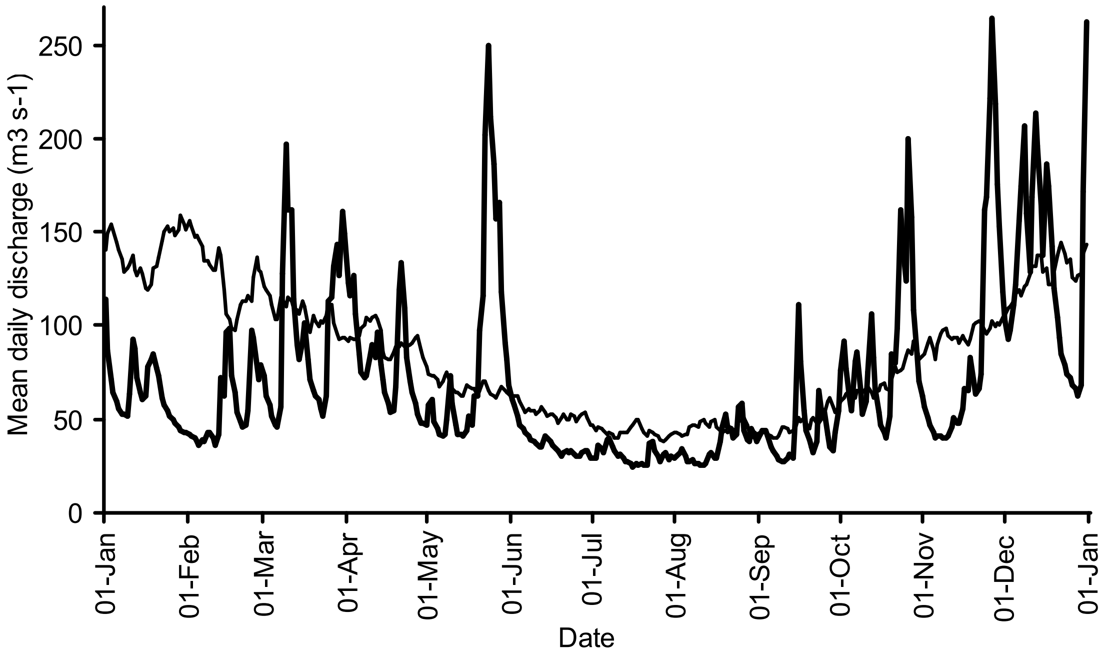


Figure 4.2 Mean daily discharge (m^3 s^{-1}) in the River Trent at Holme Pierrepont in 2006, compared with the long-term daily mean (thin line).

for urban development or agriculture. During the last decade, attempts have been made to re-establish the link between the lower reaches of the river and its floodplain by connecting a number of man-made waterbodies (e.g. flooded gravel quarries). The man-made floodplain waterbodies vary in their connection to the main river and can be separated into three categories: (1) permanently connected (parapotamon); (2) connected during annual periods of elevated flow (plesiopotamon); and (3) rarely connected by flood waters (paleopotamon). The main aim of the restoration project was to increase the availability and diversity (e.g. spawning and nursery habitat, refuge from floods) of habitat for fishes, particularly the early developmental stages, with a view to enhancing fish recruitment success within the lower reaches of the river. To date, approximately a dozen such waterbodies have been connected to the lower reaches of the river, with more planned for the future.

4.2.2 Surveys of 0+ fish

Populations of 0+ fish were surveyed at five river and ten floodplain waterbody sites approximately fortnightly from May to July and monthly from August to November 2006, in daylight hours (Table 4.1). Connectivity varied between floodplain waterbodies

Table 4.1 Details of sites surveyed for 0+ fishes in the River Trent (R) and floodplain waterbodies (F), including river width (W, m), floodplain waterbody area (A, ha), maximum depth (Max. D, m), dimensions of connectivity channel (W = width, D = depth and L = length, m) or river level rise required for connection (m), connectivity rank (see text for details), substratum and key aquatic macrophytes.

Site name	Habitat	Code	Dimensions		Connection channel		Substratum	Key aquatic macrophytes
			W (m) / A (ha)	Max. D (m)	L x W x D / river level rise (m)	Rank		
Dunham	Main river	R1	100	3–4	-	-	Gravel, mud	*Phalaris arundinacea* L.
Holme Pierrepont	Main river	R2	75	3–4	-	-	Sand, gravel	*Schoenoplectus lacustris* (L.), *Glyceria maxima* (Hartm.)
Trent Bridge	Main river	R3	75	3–4	-	-	Mud, silt	-
Attenborough	Main river	R4	100	3–4	-	-	Sand, gravel	*Acorus calamus* L., *G. maxima*, *Sparganium erectum* L.
Thrumpton	Main river	R5	75	3–4	-	-	Sand, gravel	*G. maxima*, *S. erectum*
Dunham Lake	Floodplain	F1	2	3	1.5	10	Mud, silt	*P. arundinacea*
Winthorpe Lake	Floodplain	F2	6	4	50 x 2 x 1	3	Sand, silt	*A. calamus*, *Butomus umbellatus* L., *G. maxima*, *S. erectum*
Binghams Pond	Floodplain	F3	2.5	3	40 x 2 x 1	2	Gravel, silt	*G. maxima*
Farndon Pond	Floodplain	F4	0.5	2	30 x 2 x 0.4	4	Sand, silt	*G. maxima*, *Phragmites australis* Trin.
Marina Pond	Floodplain	F5	3	3	0.1	7	Gravel, silt	*Potamogeton pectinatus* L.
Marina Pond	Floodplain	F6	3	3	0.1	6	Gravel, silt	*P. pectinatus*
Cowlick Marina	Floodplain	F7	1	3	30 x 20 x 3	5	Silt, concrete	*A. calamus*, *G. maxima*, *Lemna minor* L., *S. erectum*
Thrumpton Pond	Floodplain	F8	0.5	1.5	0.5	8	Mud, silt	*Elodea canadensis* Michx.
Ully Gully	Floodplain	F9	1	1.5	0 x 7 x 0.7	1	Mud, silt	*G. maxima*, *P. arundinacea*
Glazebrook Pond	Floodplain	F10	0.8	4	50 x 1.5 x 0.2	9	Sand, silt	*G. maxima*

(F), ranging from those permanently connected to the river (R) by deep, open channels to those connected only during 1.5 m rises in river level. Connectivity was ranked based on the width (m), depth (m) and length (m) of permanent connection or river level required for temporary connection; floodplain sites with the widest, deepest and shortest connecting channels were ranked higher than those with shallower, narrower and longer, or temporary, connecting channels (Table 4.1). Connectivity rankings for F7 and F10 were adjusted to account for the distance of the sampling locations from the river and because fish access to the pond was impeded by dense vegetation. In all cases, sampling was restricted to areas devoid of large woody debris, in water ≤1.5 m deep, where water velocity was slow and where 0+ fishes tend to aggregate. All samples were collected using a micromesh seine net (25 m long by 3-m deep, 3 mm hexagonal mesh) that was set in a rectangle parallel to the bank by wading. The seine net captured larvae as small as 5 mm, although its efficiency was reduced for fish smaller than ~15 mm (Cowx *et al*., 2001). Captured fish were identified to species (Pinder, 2001), separated into six larval (L1-L6) and one 0+ juvenile (J) developmental steps (Copp, 1990; Peňáz, 2001), and measured for standard length (SL, nearest mm).

4.2.3 Data analysis

For each site (all samples combined), the number of species caught (alpha diversity), the turnover of species between each floodplain waterbody and the nearest river site (beta diversity (Whittaker's measure)) and the overall number of species caught from all sites (gamma diversity) was calculated (Magurran, 1988). Whittaker's measure of beta diversity (βW) was calculated as:

$$\beta W = (S/\alpha) - 1 \qquad (4.1)$$

where S is the total number of species present along the gradient, and α is the average number of species caught (Magurran, 1988). The frequency of occurrence and relative abundance of each fish species (Hynes, 1950), the Shannon-Wiener diversity index (*H'*), species richness and Pielou's measure of evenness (*J*) (Washington, 1984) from all the surveys at each site and relative density (fish m^{-2}) of 0+ fishes (all species combined) were also calculated for each sampling occasion. Frequency of occurrence of a given species was defined as the number of surveys in which the species occurred, expressed as a frequency of the total number of surveys in which fish were captured. Relative abundance of a species was defined as the percentage of total catches (numbers) in all surveys contributed by the given species. Species-specific abundance was defined as the percentage contribution of a species of all fish in only those surveys where a particular species occurred. Species composition of 0+ fish catches was analysed for all sites using the graphical method of Costello (1990), as modified by Amundsen *et al*. (1996), by plotting species-specific abundance against frequency of occurrence at each site. Relative density of 0+ fishes was calculated by dividing the total numbers of 0+ fishes captured by the known area sampled by the net on each sampling occasion at each site (area calculated from direct *in situ* measurements of the study sites).

To investigate the similarity in 0+ fish species composition between sites, a Bray-Curtis similarity matrix of mean percentages of each 0+ fish species, was calculated and presented as a dendrogram using hierarchical agglomerative clustering (group average linkage) (PRIMER, version 6). The index ranges from 0 (no species in common) to 1 (identical samples), with a value of 0.6 (60% similarity) taken as a guide of when there was significant overlap between samples (e.g. Zaret & Rand, 1971; Garner, 1996).

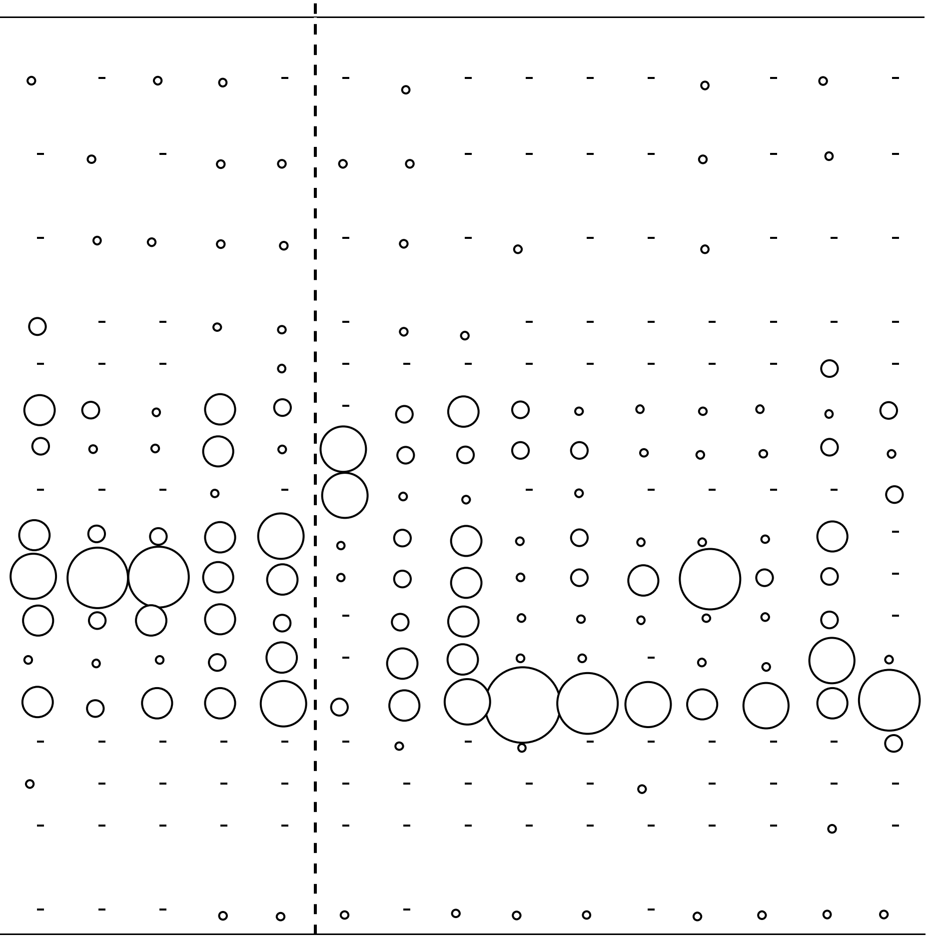
Mann-Whitney *U*-tests were used to test the null hypotheses that median *H'*, richness, *J* and density of 0+ fishes for all surveys at each site did not differ significantly between the river and floodplain sampling units. Spearman rank correlation tests were used to test the null hypotheses that floodplain waterbody connectivity was not significantly correlated with alpha diversity, beta diversity, *H'*, richness and *J*. Statistical analyses were carried out using SPSS (version 15.0) with a significance level $\alpha = 0.05$.

4.3 RESULTS

4.3.1 Species composition

More than 555 700 specimens of 25 fish species (gamma diversity) were captured during the study period (Table 4.2). Of these, 22 species (almost 220 000 individuals) were caught from the main river and 22 species (>336 000 individuals) were caught from floodplain waterbodies. Brown trout (*Salmo trutta* L.), flounder (*Platichthys flesus* (L.)) and common goby (*Pomatoschistus microps* (Krøyer)) were only captured from

Table 4.2 Relative abundance of 0+ fish captured from five main river sites (R1-R5) and ten floodplain waterbodies (F1-F10) on the River Trent.



Family *Species*	Ab.[1]	Vernacular name	Flow pref. [1]	R1	R2	R3	R4	R5	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
Cyprinidae																		
Barbatula barbatula (L.)	*Bt*	Stone loach	Rheo A	∘	-	∘	∘	-	-	∘	-	-	-	-	∘	-	∘	-
Cobitidae																		
Cobitis taenia L.	*Ct*	Spined loach	Rheo B	-	∘	-	∘	∘	∘	∘	-	-	-	-	∘	-	∘	-
Cottidae																		
Cottus gobio L.	*Cg*	Bullhead	Rheo A	-	∘	∘	∘	∘	-	∘	-	∘	-	-	∘	-	-	-
Cyprinidae																		
Barbus barbus (L.)	*Bb*	Barbel	Rheo A	○	-	-	∘	∘	-	∘	∘	-	-	-	-	-	-	-
Rhodeus sericeus (Pallas)	*Rs*	Bitterling	Limno	-	-	-		∘	-	-	-	-	-	-	-	-	○	-
Alburnus alburnus (L.)	*Aa*	Bleak	Eury	○	○	∘	○	○	-	○	○	○	∘	∘	∘	∘	∘	○
Abramis brama (L.)	*Ab*	Bream	Eury	○	∘	∘	○	∘	◯	○	○	○	○	∘	∘	∘	○	∘
Cyprinus carpio L.	*Cc*	Carp	Eury	-	-	-	∘	-	◯	∘	∘	-	∘	-	-	-	-	○
Leuciscus cephalus (L.)	*Lc*	Chub	Rheo A	○	○	○	○	◯	∘	○	○	∘	○	∘	∘	∘	○	-
Leuciscus leuciscus (L.)	*Ll*	Dace	Rheo A	◯	◯	◯	○	○	∘	○	○	∘	○	○	◯	○	○	-
Gobio gobio (L.)	*Gg*	Gudgeon	Rheo B	○	○	○	○	○	-	○	○	∘	∘	∘	∘	∘	○	-
Phoxinus phoxinus (L.)	*Pp*	Minnow	Rheo A	∘	∘	∘	○	○	-	○	○	∘	∘	-	∘	∘	◯	∘
Rutilus rutilus (L.)	*Rr*	Roach	Eury	○	○	○	○	◯	○	○	◯	◯	◯	◯	○	◯	○	◯
Scardinius erythrophthalmus (L.)	*Se*	Rudd	Limno	-	-	-	-	-	-	∘	-	∘	-	-	-	-	-	○
Abramis bjoerkna (L.)	*Aj*	Silver bream	Eury	∘	-	-	-	-	-	-	-	-	-	∘	-	-	-	-
Tinca tinca (L.)	*Tt*	Tench	Limno	-	-	-	-	-	-	-	-	-	-	-	-	-	∘	-
Esocidae																		
Esox lucius L.	*El*	Pike	Eury	-	-	-	∘	∘	∘	-	∘	∘	∘	-	∘	∘	∘	∘

Table 4.2 (cont.)

Family *Species*	Ab.[1]	Vernacular name	Flow pref. [2]	R1	R2	R3	R4	R5	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
Gasterosteidae																		
Gasterosteus aculeatus L.	*Ga*	Three-spined stickleback	Eury	◦	◦	◦	◦	◦	◯	◦	◦	◦	-	-	-	⭘	◦	-
Pungitius pungitius (L.)	*Pp*	Ten-spined stickleback	Limno	-	-	-	-	-	◦	◦	-	-	-	-	◦	◯	◦	-
Gobiidae																		
Pomatoschistus microps (Krøyer)	*Pm*	Common goby		◦	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Percidae																		
Gymnocephalus cernuus (L.)	*Gc*	Ruffe	Eury	-	-	◦	◦	-	-	◦	◦	◦	◦	◦	-	-	◦	-
Perca fluviatilis L.	*Pf*	Perch	Eury	◦	◯	○	○	◦	◦	⭘	◯	◯	❍	⭘	◯	○	○	❍
Sander lucioperca (L.)	*Sl*	Zander	Eury	-	◦	◦	◦	-	-	◦	-	◦	◦	◦	◦	-	-	-
Pleuronectidae																		
Platichthys flesus (L.)	*Pf*	Flounder	Rheo C	○	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae																		
Salmo trutta L.	*St*	Brown/sea trout	Rheo A	-	-	◦	-	-	-	-	-	-	-	-	-	-	-	-

[1] Ab. = Species abbreviation

[2] flow preference classification according to Schiemer & Waidbacher (1992): Rheo A = rheophilic A, Rheo B = rheophilic B, Eury = eurytopic and Limno = limnophilic.

N.B. Site codes are as in Table 4.1

Key (percent frequency of occurrence and abundance)

Dominant (> 75 %)	⚪
Abundant (51-75 %	⭘
Frequent (26-50 %)	❍
Occasional (6-25 %	◯
Infrequent (1-5 %)	○
Rare (< 1 %)	◦
Not captured	·

the main river, while three limnophilic species (ten-spined stickleback (*Pungitius pungitius* (L.)), rudd and tench (*Tinca tinca* (L.))) occurred exclusively in floodplain waterbodies. Dace (38%), roach (18%) and chub (17%) were most abundant in main river catches, with dace (92%), roach (85%), gudgeon (65%), perch (65%) and chub (65%) occurring most frequently (Table 4.2). Roach (37%), perch (22%) and dace (9%) were the most abundant species in floodplain waterbodies, and also occurred most frequently (roach = 72%, perch = 61% and dace = 58%; Table 4.2).

The number of species captured in individual floodplain waterbodies (alpha diversity) was positively correlated to connectivity (Spearman rank: $r = 0.829$, $n = 10$, $P = 0.003$), with a decline in the presence of rheophilic species with reduced connectivity (Table 4.2). Adult bream, perch, carp (*Cyprinus carpio* L.), roach and pike were captured in floodplain waterbodies in early summer (spawning period), and probably contributed to the dominance of 0+ eurytopic species in subsequent catches. Furthermore, >0+ rudd and tench were captured in floodplain waterbodies on numerous occasions, along with low numbers of 0+ limnophilic species (Figure 4.3). Beta diversity increased along the gradient of decreasing floodplain waterbody connectivity as the species composition became more dissimilar to the nearest river site, although the trend was not significant (Spearman rank: $r = -0.497$, $n = 10$, $P = 0.144$).

0+ fish community structure varied between sites, both in the river (Figure 4.4) and the floodplain waterbodies (Figure 4.5). For example, R1 was characterised by dace (species-specific abundance = 36%), roach (19%), chub (19%), bleak (15%) and gudgeon (7%), with perch captured in 78% of surveys but in smaller numbers, compared with R2 where dace, perch and roach accounted for 73%, 17% and 4% of catches, respectively. Using the Bray-Curtis similarity index based on the mean relative abundance (%) of each 0+ fish species at each site, eight main groups were identified with 0+ fish communities that were at least 60% similar (Figure 4.6a). One group contained R2, R3 and F7 (dominated by dace), one comprised R1, R4 and F3 (roach, dace and chub), another contained F4, F5 and F10 (roach), and the final group contained F2 and F6 (perch). There were also four dissimilar sites: R5 (chub and roach), F9 (minnow), F8 (three- (*Gasterosteus aculeatus* L.) and ten-spined sticklebacks) and F1 (carp and bream), respectively. The groups of sites identified correspond approximately to floodplain waterbody connectivity, with poorly connected waterbodies containing fish species compositions highly dissimilar to river sampling sites (Figure 4.6b). The

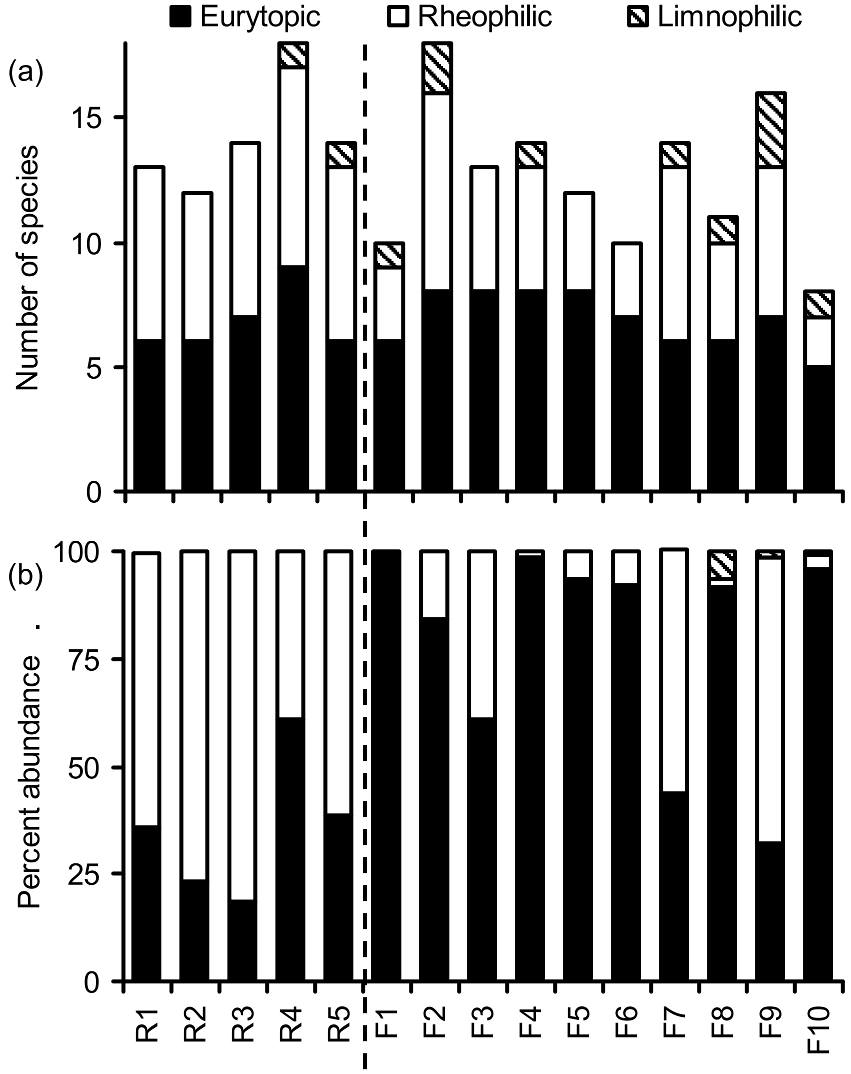


Figure 4.3 Number (a) and percent abundance (b) of rheophilic, eurytopic and limnophilic species captured from five main river sites (R1-R5) and ten floodplain waterbodies (F1-F10) on the River Trent. Flow preference classification according to Schiemer & Waidbacher (1992). Site codes are as in Table 4.1.

exceptions to the trend were F7 and F3, which were both permanently connected to the main river, but contained larger proportions of rheophilic fish than waterbodies with similar connectivity rankings.

H' (2.05), richness (1.81) and *J* (0.64) from all surveys in the Trent catchment (main river and floodplain sites) were high, but between-site variations occurred (Table 4.3). Median *H*' (Mann-Whitney *U*-test: Z = -0.1225, n = 15, P = 0.254), richness (Mann-Whitney *U*-test: Z = -0.1592, n = 15, P = 0.129) and *J* (Mann-Whitney *U*-test: Z = -

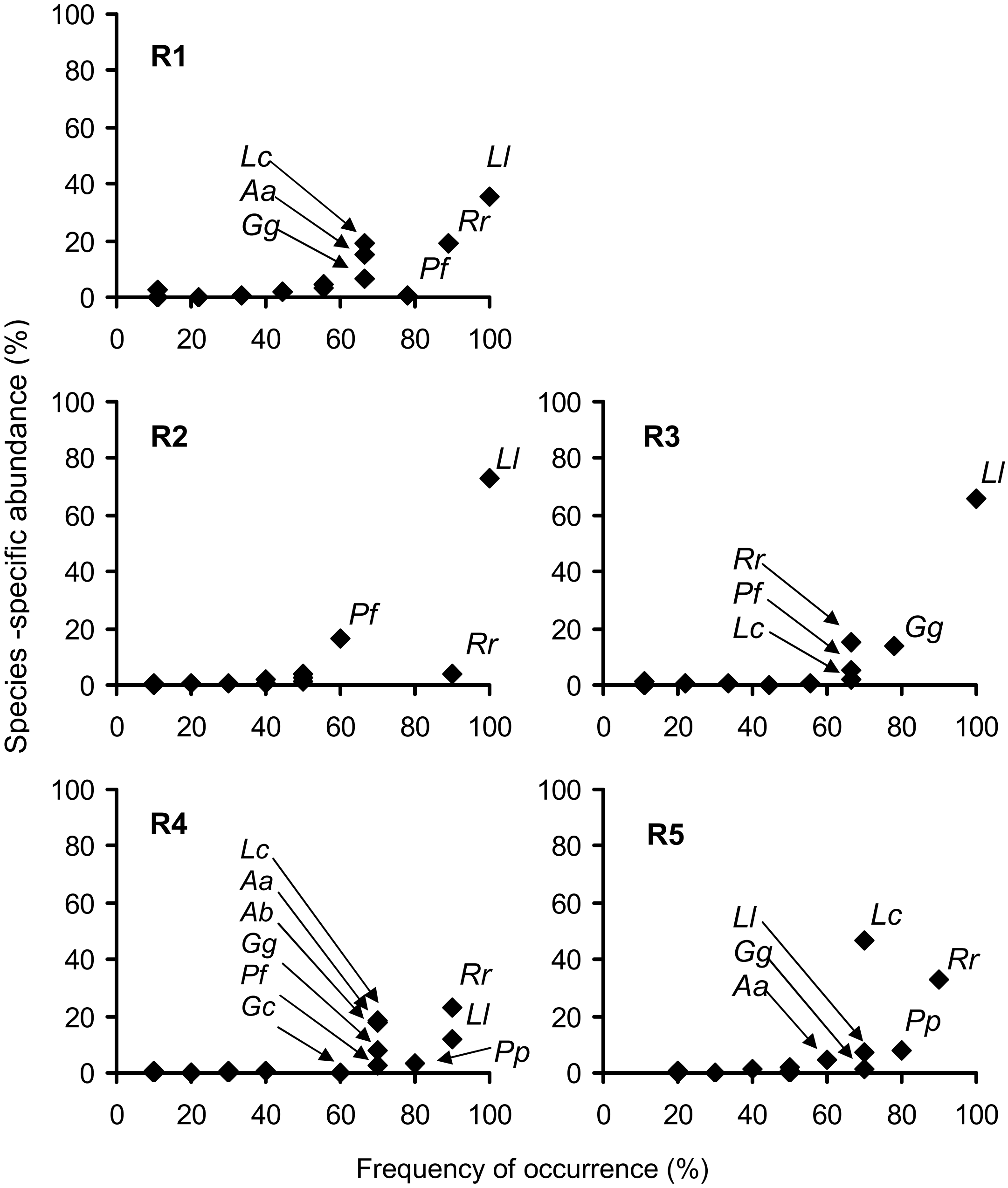


Figure 4.4 Costello plots demonstrating 0+ fish community structure at five main river sites on the River Trent. Site name abbreviations are as in Table 4.1, species name abbreviations are as in Table 4.2.

0.621, n = 15, P = 0.594) were not significantly different between main river and floodplain sites. Connectivity had a strong correlation with species richness within the floodplain (Spearman rank: r = 0.879, n = 10, P = 0.001). *H'* decreased with decreasing hydrological connectivity, but the trend was not significant (Spearman rank: r = 0.491, n = 10, P = 0.150).

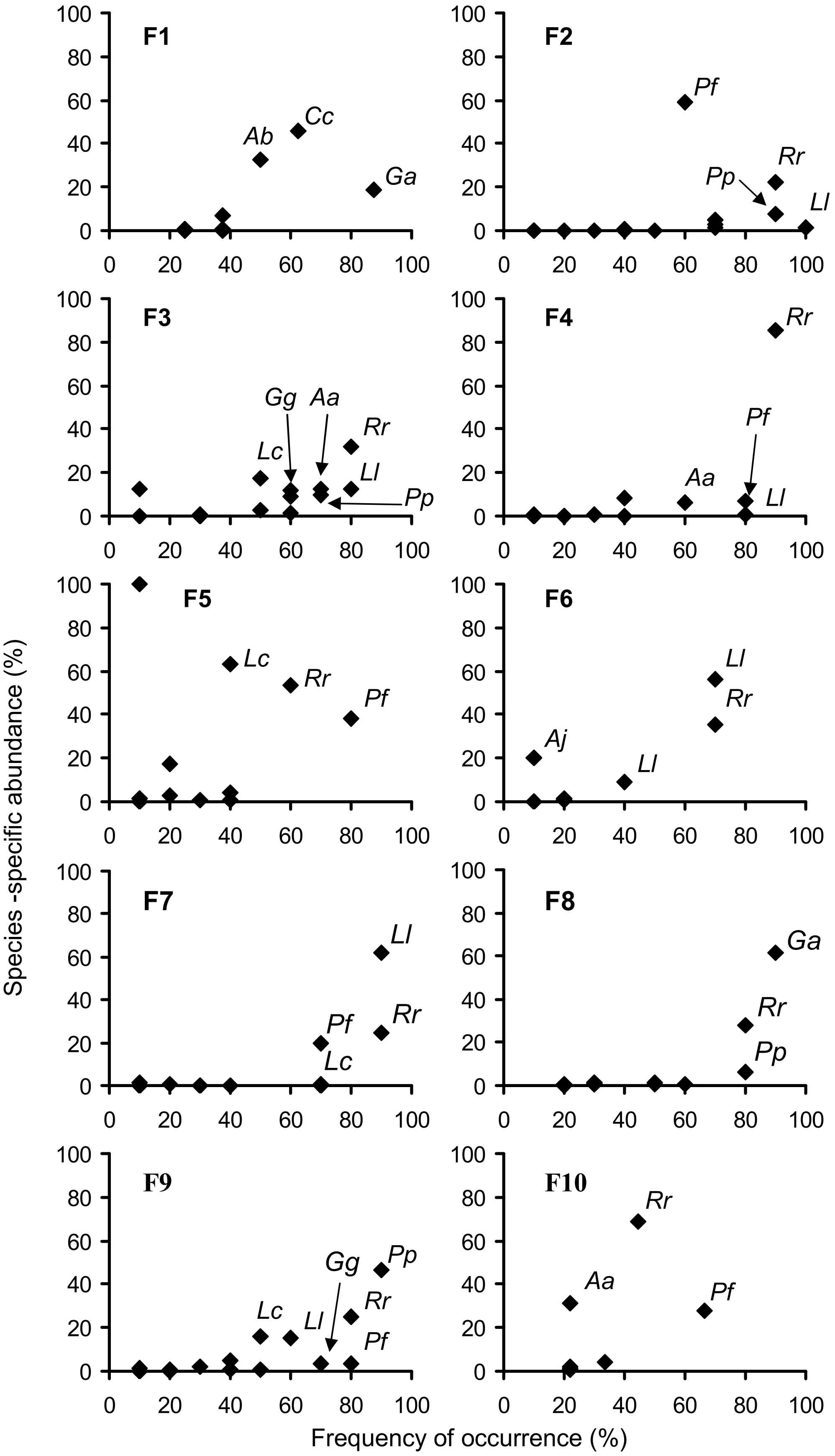


Figure 4.5 Costello plots demonstrating 0+ fish community structure at ten floodplain waterbodies on the River Trent. Site name abbreviations are as in Table 4.1, species name abbreviations are as in Table 4.2

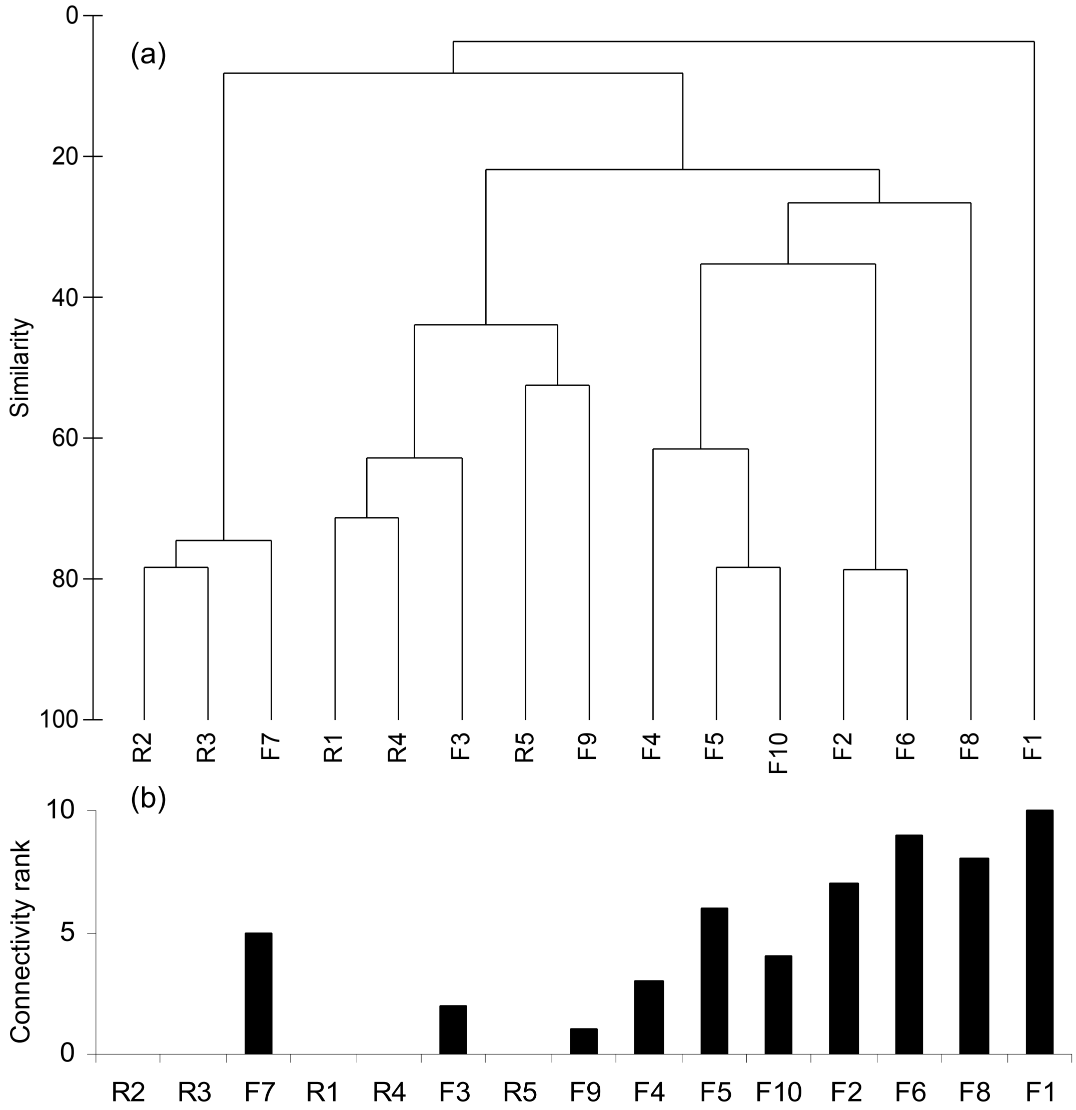


Figure 4.6 Similarity (a) of 0+ fish species composition between five main River Trent (R) and ten floodplain waterbodies (F) of variable connectivity (b). Note low connectivity rank = highly connected. Site codes are as in Table 4.1.

4.3.2 Density

Overall, the mean (± SD) density of 0+ fishes (all river and floodplain sites combined) was 60 ± 143 fish m^{-2}, with the highest mean (260 ± 258 fish m^{-2}) and maximum (921 fish m^{-2}) densities found at R4 and F2, respectively, and the lowest mean density at F10 (3 ± 5 fish m^{-2}). The mean density of 0+ fishes in the main river (71 ± 155 fish m^{-2}) was not significantly different to those in permanently- (73 ± 166 fish m^{-2}; Mann-Whitney *U*-test: Z = -0.365, n = 11, P = 0.792) and occasionally-connected (28 ± 63 fish m^{-2}; Mann-Whitney *U*-test: Z = -0.490, n = 9, P = 0.730) floodplain waterbodies, but substantial spatial (between sites) and temporal (within a site) variations occurred

Table 4.3 Shannon-Wiener diversity index (*H'*), species richness and Pielou's measure of evenness (*J*) for all samples from five main river sites (R1-R5) and ten floodplain waterbodies (F1-F10), and beta diversity (βW) between floodplain waterbodies and local river sampling sites on the River Trent.

	Site code														
	R1	R2	R3	R4	R5	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
H'	1.76	0.94	1.10	1.92	1.43	1.19	1.41	1.96	0.63	1.10	0.93	1.08	1.03	1.52	0.89
Richness	1.52	1.14	1.35	1.41	1.45	1.00	1.48	1.34	1.20	1.25	1.03	1.14	0.93	1.52	0.92
J	0.67	0.38	0.42	0.66	0.54	0.52	0.49	0.77	0.24	0.44	0.40	0.41	0.43	0.55	0.43
βW	-	-	-	-	-	0.50	0.20	0.28	0.15	0.25	0.27	0.19	0.20	0.20	0.36

Site codes are the same as in Table 4.1.

(Figures 4.7-4.8). Densities of 0+ fishes were low in May and early June (immediately after the flood; Figure 4.2), but increased and generally peaked in June and July, once the majority of species had hatched and grown to a size that could be efficiently captured by the seine net. Densities of 0+ fishes declined at most sites during August and September as biotic (predation, disease, starvation) and abiotic (light, temperature, flow, nutrients) factors acted upon the populations, and 0+ fishes dispersed from the margins.

4.4 DISCUSSION

Effective management and restoration of riverine floodplains requires an understanding of how species distributions are produced, by consideration of how natural and man-made floodplain waterbodies function in other catchments. In the River Trent, local (alpha) and overall (gamma) species diversity, richness, turnover (beta diversity) and guild composition of fish communities in ten man-made floodplain waterbodies were influenced by variable hydrological connectivity to the river.

Hydrological connectivity is the transfer of water between the river channel and the floodplain, and thus refers to the ease with which organisms, matter or energy traverse the ecotones between the main river and the floodplain waterbody (Ward *et al*., 1999). During the study on the River Trent, man-made habitats ranged from waterbodies with permanent connection (parapotamon), those temporarily connected during elevated river levels (plesiopotamon) and those with no connection to the main river (paleopotamon). This broad spectrum of connectivity represented habitats similar to a natural riverscape. Consequently, species richness and diversity (alpha and beta) compared favourably with studies on unmodified river reaches. For example, Tockner *et al*. (1998) found that fish species richness in floodplain waterbodies declined with increasing distance from the main channel of the River Danube, and Ward *et al*. (1999) reported that alpha diversity of fish community composition decreased while beta diversity increased with increasing isolation of Danubian floodplain waterbodies.

Species compositions of the waterbodies in this study were similar to natural riverscapes (Copp, 1989), reflecting the ecological requirements and life-history strategies of the lowland river fish species present. In the River Trent, fish communities in highly-connected floodplain waterbodies were composed of a large proportion of

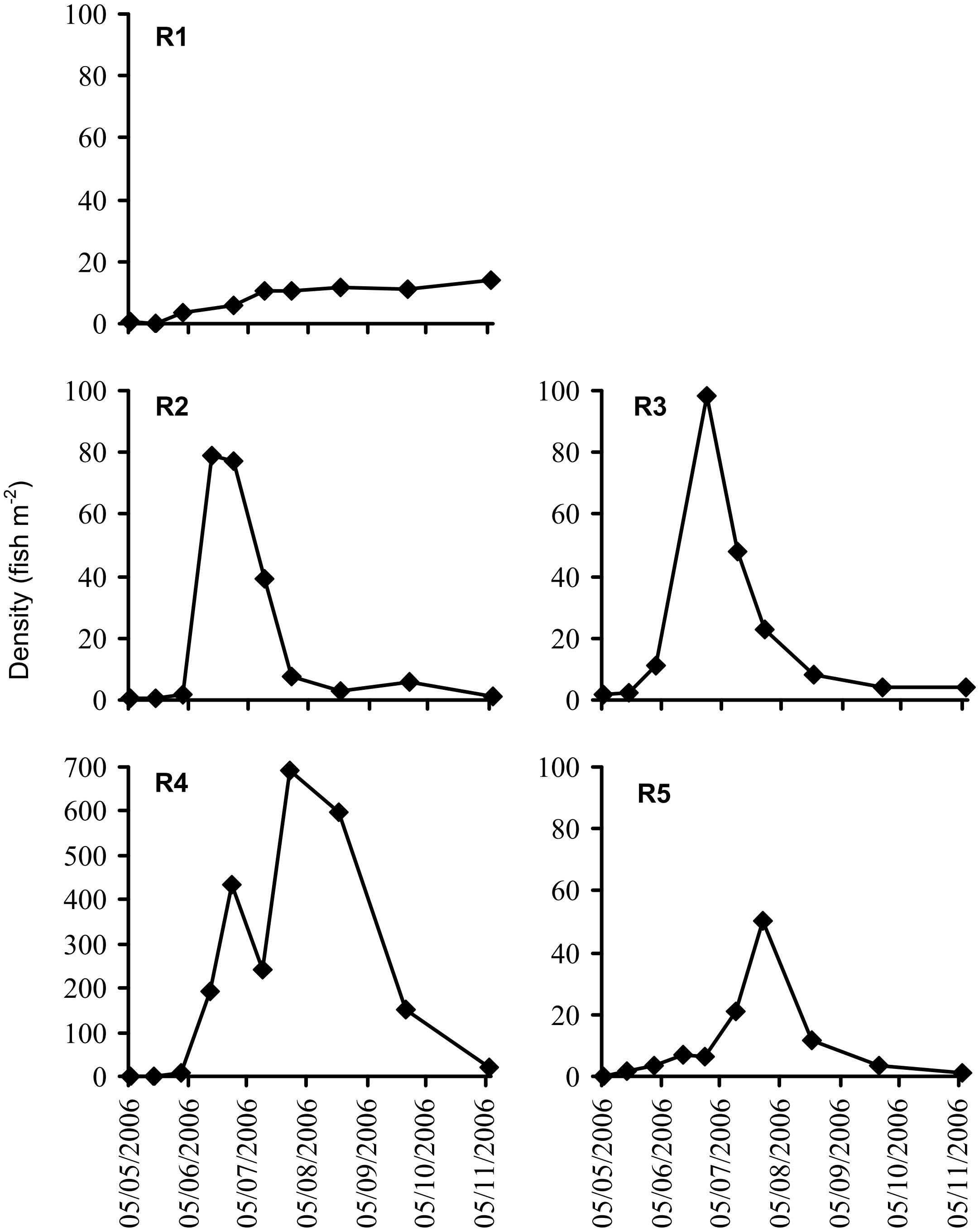


Figure 4.7 Temporal variations in the density (fish m^{-2}) of 0+ fishes (all species combined) at five main river sites on the River Trent. Site codes are as in Table 4.1. Note the different y-axis scale for R4.

eurytopic fishes and moderate numbers of rheophilic species (especially dace). In natural floodplains, eurytopic adults perform spawning migrations from the main river into connected waterbodies, and 0+ fish spawned in the main river (eurytopic and rheophilic) disperse into connected floodplain waterbodies (Hohausova, 2000; Borcherding *et al.*, 2002; Hohausova *et al.*, 2003). Such movements enable young progeny to take advantage of abundant food resources and refuge from velocity (i.e. the

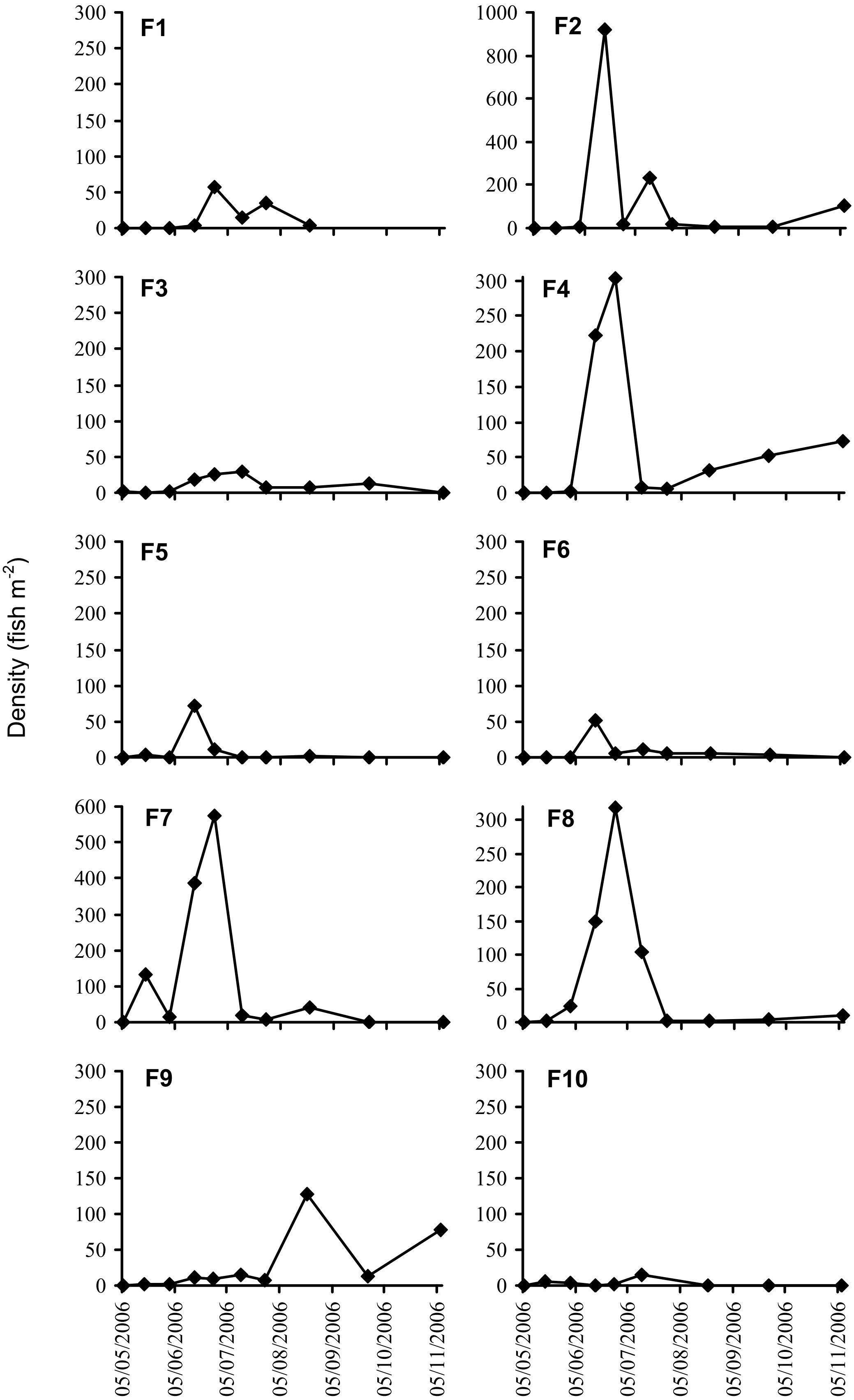


Figure 4.8 Temporal variations in the density (fish m^{-2}) of 0+ fishes (all species combined) at ten floodplain sites on the River Trent. Site codes are as in Table 4.1. Note the different y-axis scales for F2 and F7.

Inshore Retention Concept; Schiemer *et al*., 2001). The findings of this study support numerous investigations that documented the importance of permanently-connected man-made floodplain waterbodies to provide essential spawning, nursery and feeding habitat (e.g. Sabo & Kelso, 1991; Neumann *et al*., 1996; Staas & Neumann, 1996; Copp, 1997b; Pinder, 1997; Pinder *et al*., 1997; Grift *et al*. 2003; Nunn *et al*., 2007a).

Along the gradient of reducing floodplain waterbody connectivity, the number of species present declined in relation to the inability of rheophilic species to disperse from their lotic spawning habitat in the main river (Schiemer & Waidbacher, 1992). Large proportions of eurytopic species were present in the main river and all levels of floodplain waterbody connectivity, reflecting their plasticity towards spawning and other habitat prerequisites. The largest relative abundance of bream was found in Dunham Lake (F1), which remained permanently disconnected during the study period. Molls (1999) found that adult bream develop permanent stocks in oxbow lakes on the River Rhine because of the irregularity of connection, thus giving bream a reproductive advantage in years with low flows, because species that require seasonal timing of connectivity are unable to perform lateral spawning migrations. Limnophilic species were found in seven of the floodplain waterbodies, probably because the areas provided dense vegetation and the low-flow environment necessary for larvae and juveniles (Copp, 1993; Copp & Mann, 1993; Aarts *et al*., 2004). Bitterling (*Rhodeus sericeus* (Pallas)) was the only limnophilic species caught in the main river, but the presence of unionid mussels for spawning has an overriding influence on its distribution (Smith *et al*., 2004), although they could have been washed-out or dispersed from local floodplain waterbodies.

0+ fish species distribution may have been affected by the flood in May 2006 (Chapter 3). In the UK, summer floods are considered “atypical” and a disturbance (Sparks *et al*., 1990) because of the poor swimming capabilities of 0+ fishes (Harvey, 1987). Dace, roach and perch all hatched at least two weeks prior to the May flood, but were among the most abundant species in 2006. This finding suggests that these species had reached a sufficient size to hold station (Harvey, 1987; Mann & Bass, 1997; Nunn *et al*., 2007b) or find suitable flow refuge during the flood (Chapter 3; Baras *et al*., 1995; Grift *et al*., 2003; Schiemer *et al*., 2004; Humphries *et al*., 2006). The presence of 0+ rheophilic species in previously unconnected floodplain waterbodies during summer 2006, suggests that river fishes were displaced laterally and could take advantage of different floodplain habitats for refuge (Sedell *et al.*, 1990; Molls & Neumann, 1994; Copp, 1997b; Pinder *et al.*, 1997). Despite this, densities of fishes in all floodplain waterbodies immediately after the flood were low, suggesting that most fish had moved back into the river as floodwaters receded or they were dispersed from the usual sampling locations by the flood

Floodplain waterbody connectivity appeared to influence 0+ fish species composition, but numerous abiotic (pH, water temperature, nutrient content, suspended solids/turbidity, dissolved oxygen, lake morphology) and biotic (predation and competition) variables could have influenced assemblage structure (Amoros & Bornette, 2002). Furthermore, it is necessary to recognise that man-made floodplain waterbodies undergo the process of succession, i.e. newly-created waterbodies will consist of opportunistic, highly-tolerant generalists (Lake *et al.*, 2007), thus the species compositions observed during the study may not persist. For example, the dominance of three-spined stickleback in the relatively recently-created (2003) Thrumpton Pond (F8) may not persist. Similarly, the emphasis of this study was restoration of habitat diversity based on the assumption that biotic composition and function will self-assemble – if you build it, they will come (‘The Field of Dreams approach’ *sensu* Hilderbrand *et al.*, 2005). However, particular species may not have the ability to colonise poorly-connected habitats or the regional species pool may not be sufficient to return to an historical natural state (Lake *et al.*, 2007). In the River Trent, relatively rare limnophilic fishes were present in numerous floodplain waterbodies of variable connectivity, thus alleviating the concerns proposed by Lake *et al.* (2007).

Guidelines for holistic riverine ecosystem management state implicitly the necessity for restoring the spatio-temporal diversity and functional integrity of the river-floodplain complex responsible for high levels of biodiversity (Ward 1998a; Schiemer *et al.*, 1999; Ward *et al.*, 1999). This study provides the evidence of the importance of variable connectivity between the main river and man-made floodplain waterbodies for rehabilitating the lowland river fish community. Fish assemblages (ecological guilds, species and developmental stages) with different environmental requirements contributed to a high overall level of species diversity, resembling natural floodplain ecosystems. This knowledge has crucial implications for potentially improving the ecological status of rivers under the European Union, Water Framework Directive (2000/60/EEC). Furthermore, overall biodiversity is highest at intermediate levels of floodplain connectivity (Tockner *et al*., 1998), thus restoration of variable connectivity should not focus on a single species or taxonomic group (Sparks, 1995; Tockner *et al*., 2000a). Therefore, this study supports the incorporation of man-made floodplain waterbodies of variable, not just high, levels of hydrological connectivity into holistic riverine ecosystem management plans.

5 IMAGING FISH ACTIVITY AT A LOWLAND RIVER-BACKWATER CONNECTION DURING ELEVATED FLOW

5.1 INTRODUCTION

Lateral connectivity between rivers and their floodplain habitats is essential for the functioning and integrity of floodplain ecosystems (Amoros & Bornette, 2002). Several studies have investigated lateral fish movements, especially into floodplain waterbodies and off-channel areas during elevated flows (Sedell *et al*., 1990; Molls & Neumann, 1994; Allouche *et al*., 1999), and the importance of backwaters for juvenile (Copp, 1997b; Nunn *et al*., 2007a) and adult fish (Hohausová *et al*., 2003). However, little is known about the daily lateral movements of adult and sub-adult fish between such water bodies and the river channel, especially during winter and under the influence of elevated flow. This is, in part, because present sampling techniques have inherent problems, especially in large rivers. For example, Hohausová *et al*. (2003) captured only 170 fish moving between a backwater and the River Morava, Czech Republic, using traps which sampled half the channel width. They stated "avoidance behaviour could have biased the results"; yet the movements were considered representative of the population and ecological conclusions were drawn. Split-beam hydroacoustic surveys are limited by low signal to noise ratio and beam-fit relative to the bed profile and water surface, and conventional underwater cameras are limited by low light levels and high turbidity. DIDSON (Dual-Frequency Identification Sonar; Sound Metrics Corporation, Washington, USA), a high-definition imaging sonar, overcomes some of these limitations because it provides high definition imaging of fish movements when in a fixed location (Moursund *et al*., 2003). Consequently, it may be suitable for *in situ* observation of fish movements and activity in the murky waters of the relatively narrow but deep connection channels between lowland rivers and floodplain waterbodies.

The aim of this study was to determine, using DIDSON, whether movements of fish between the main channel and a backwater in a temperate floodplain river during winter-time vary with time of day and water level. This was achieved by examining movements of fish about the entrance of a marina on the lowland Yorkshire Ouse.

5.2 MATERIALS AND METHODS

5.2.1 Study site

The Yorkshire Ouse (Figure 5.1), described in Chapter 3, is isolated from its floodplain through channelisation and levee construction, except for artificial floodplain features such as marinas. Precipitation run-off from the Pennines often results in elevated river levels, as observed during the sampling period (Figure 5.2), and regular overbank floods. Hydrological responses of the catchment are perhaps the most important factors stimulating changes in fish distribution (Lucas, 2000).

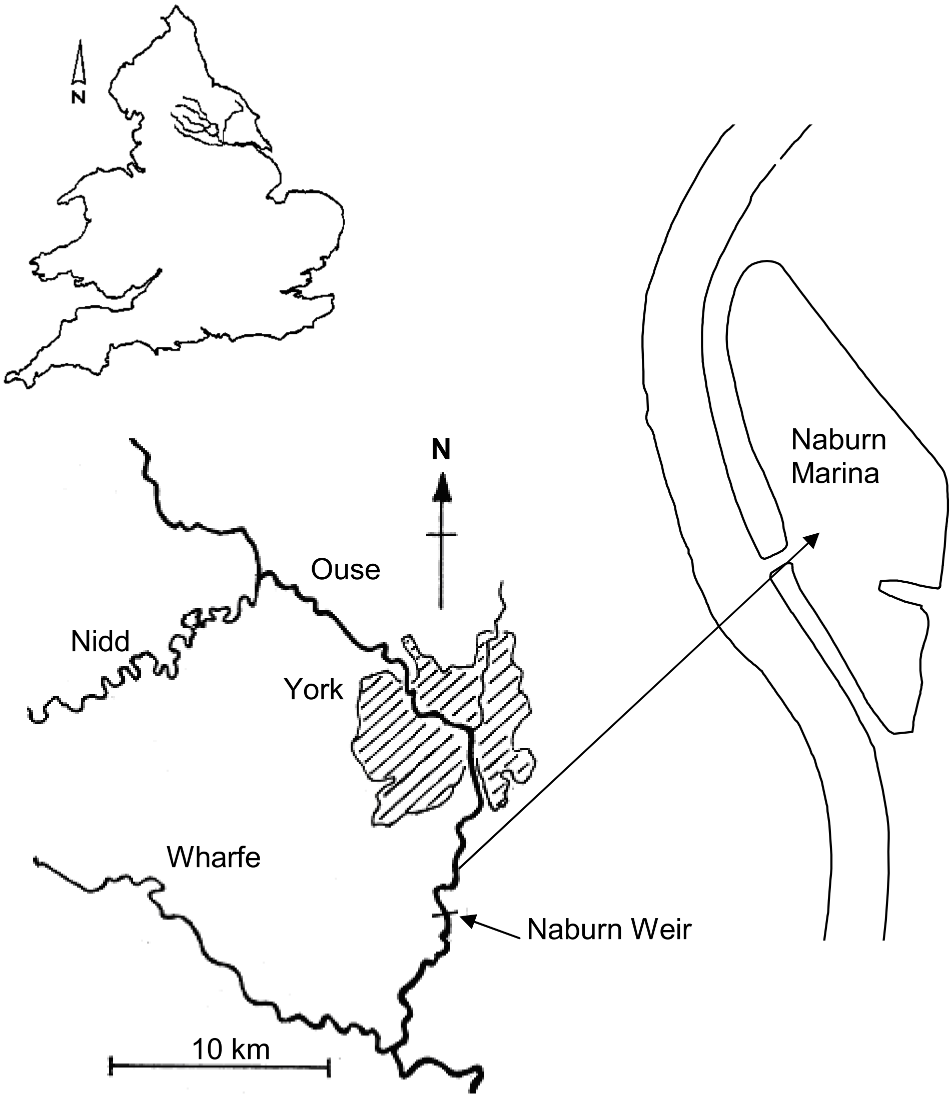


Figure 5.1 Yorkshire Ouse catchment map and Naburn Marina sampling location.

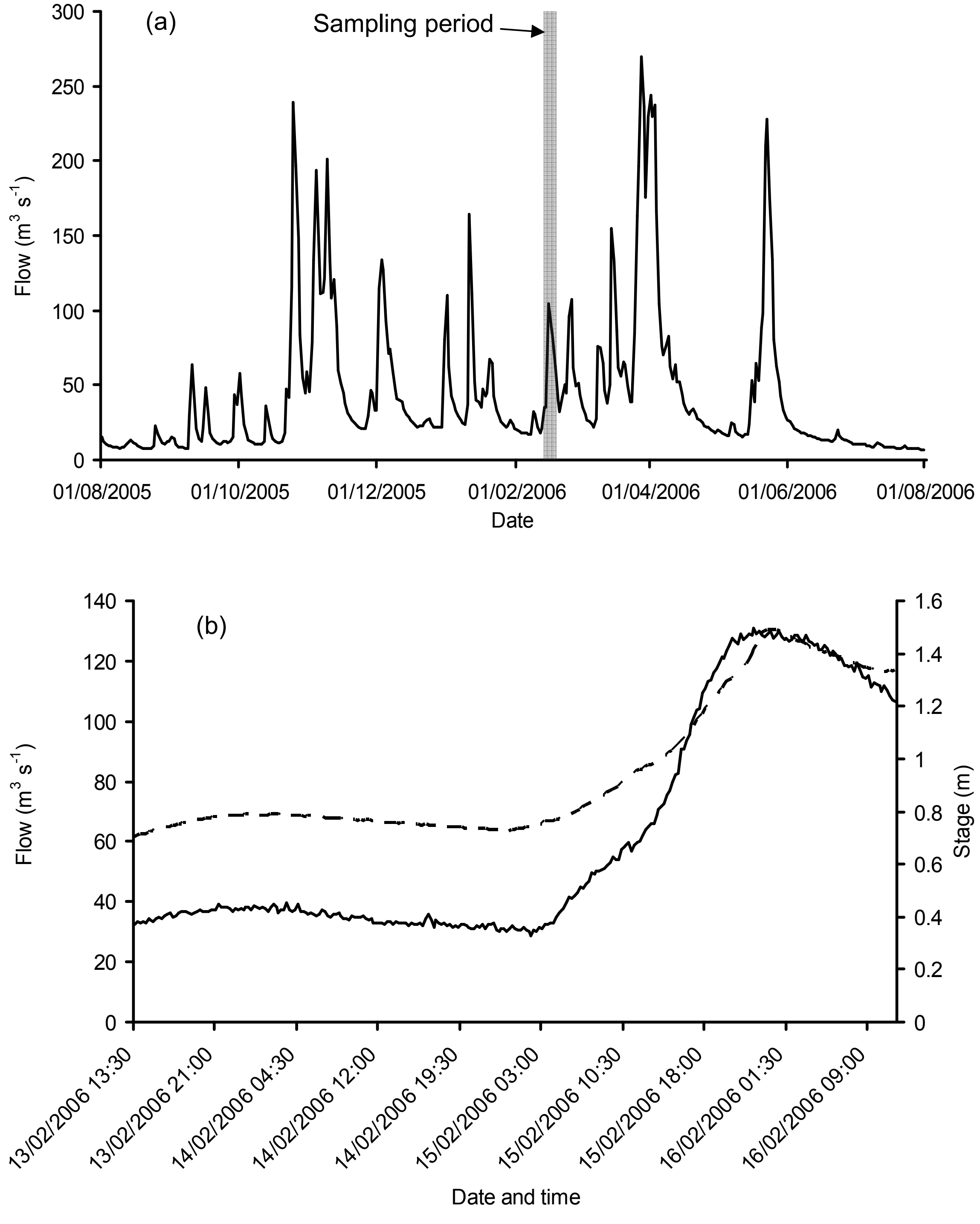


Figure 5.2 Mean daily discharge (m^3 s^{-1}, complete line) in the Yorkshire Ouse at Skelton (a) August 2005 to August 2006, and (b) during sampling period (13-16 February 2006) and river level (m, dashed line) at Skelton.

The deep, slow flowing waters of the lower Ouse are dominated by eurytopic cyprinids and percids, such as roach, bream, bleak, perch and ruffe (*Gymnocephalus cernuus* (L.)), as well smaller numbers of chub (Whitton & Lucas, 1997; Lucas *et al.*, 1998).

The study was carried out at Naburn Marina; a backwater feature with an area of 5 ha, an average depth of 2 m and moorings for about 100 boats during the winter months. It is located approximately 2 km upstream of Naburn weir, the tidal limit of the Yorkshire Ouse. The study was carried out in the connection channel (20 m long, 15 m wide and 1.75 m deep (under normal flow)) between the river and the marina.

5.2.2 Sampling procedure

A twin-hulled boat was moored on the downstream side of the connection channel inside Naburn Marina between 13 and 16 February 2006, inclusive. The DIDSON was secured to a "pan-and-tilt" mechanism mounted on a vertical shaft attached to the front of the boat with the beam directed across the channel entrance. The equipment was mechanically adjusted until the beam produced bottom shadows, enabling a sampling reference point during elevated flows, and was subsequently tilted up or down as the water level changed. The boat was able to rise and fall with the increasing and decreasing water level. River discharge (≈32 $m^3 s^{-1}$) and level (≈0.75 m) remained stable, near to base level (long term mean discharge ≈50 $m^3 s^{-1}$), for the first 37.5 hr of the study, but at 03:00 on 15 February the river began to rise (Figure 5.2). By 18:00 on 15 February the river level was sufficiently high to sample the upper and lower sections of the water column alternately every 15 minutes. The river reached a maximum flow (130 $m^3 s^{-1}$) and level (1.49 m) at 01:00 on 16 February, equating to a four times increase in discharge and an increase in depth of ≈0.75 m. By the end of sampling period the flow (110 $m^3 s^{-1}$) and level (1.34 m) had dropped slightly.

The equipment was operated at high frequency (1.8 MHz: 96 beams oriented 0.3° apart, creating a field of view that is 12° vertically and 29° horizontally), with a 5-m field of view, which began 4.5 m from the DIDSON transponder. Directing fences could not be installed to force fish through the DIDSON beam because these interfere with boat traffic; sampling at low frequency mode (1.1 MHz) was not employed, despite range benefits, because of reduced ability to identify small fish. Thus, sampling the full channel width was compromised for a more detailed resolution and higher quality data. Continuous observations over a 70-hr period, at a rate of seven frames per second, were recorded onto external hard-drives in 15-min, date- and time-stamped files.

5.2.3 Output processing

Post-sampling, image files (Figure 5.3) produced by the DIDSON were reviewed to estimate fish density in the marina entrance and the direction of fish movements. Data were reduced to a manageable level for analysis by processing the first minute in every five. Files were replayed in image mode and fish were manually counted. Playback speeds and direction were adjusted to enhance elimination of non-fish targets and so enable the best quality counts of fish targets. A grid and a measuring tool built into the DIDSON software viewing program allowed simple processing of fish numbers and length. Fish size data were assigned to the following size categories (cm): <15, 15-19, 20–24, 25–29, 30–34, 35-39, 40-44, 45-49, 50-54, 55-59 and >59, but fish lengths were not validated in the field. In high-frequency mode, images were formed enabling outline and fin definition of larger fish. Under certain scenarios, it was possible to identify larger fish based on differences in morphology (often aided by the acoustic shadow), i.e. large pike (*Esox lucius* L.) and bream. However, a reliable identification protocol was not available for these species, so fish were not identified to species for this study.

5.2.4 Data analysis

Fish density (fish m^{-2}) was calculated from the number of fish in the grid either side of the centre line (4° either side, area = 4.9 m^2) at the start of every fifth minute. Fish were considered to be moving either towards or away from the marina when they crossed the centre line of the viewing window, although some “milling” behaviour occurred. Analysis of Variance (ANOVA) was used to test the null hypothesis that density, movements and size composition of imaged fish did not differ significantly between day and night, river level (i.e. between days 2 and 3 and night 3 compared with nights 1 and 2) or the section of the water column sampled (during elevated flow) (river level (i.e. between days 2 and 3). In addition, daytime (dawn till dusk) was separated into five, two-hour periods, for comparisons both within the same day (e.g. dawn to all other sampling periods on day 2) and between days/river level (e.g. dawn between days 2 and 3). The Least Significance Difference (LSD) *post hoc* test was used, except when variance was not equal (Levene statistic < 0.05), then the Games-Howell test was applied. A Mann-Whitney *U*-test was used when two sample groups were compared and variance was not equal. Comparisons between day sampling periods excluded the first

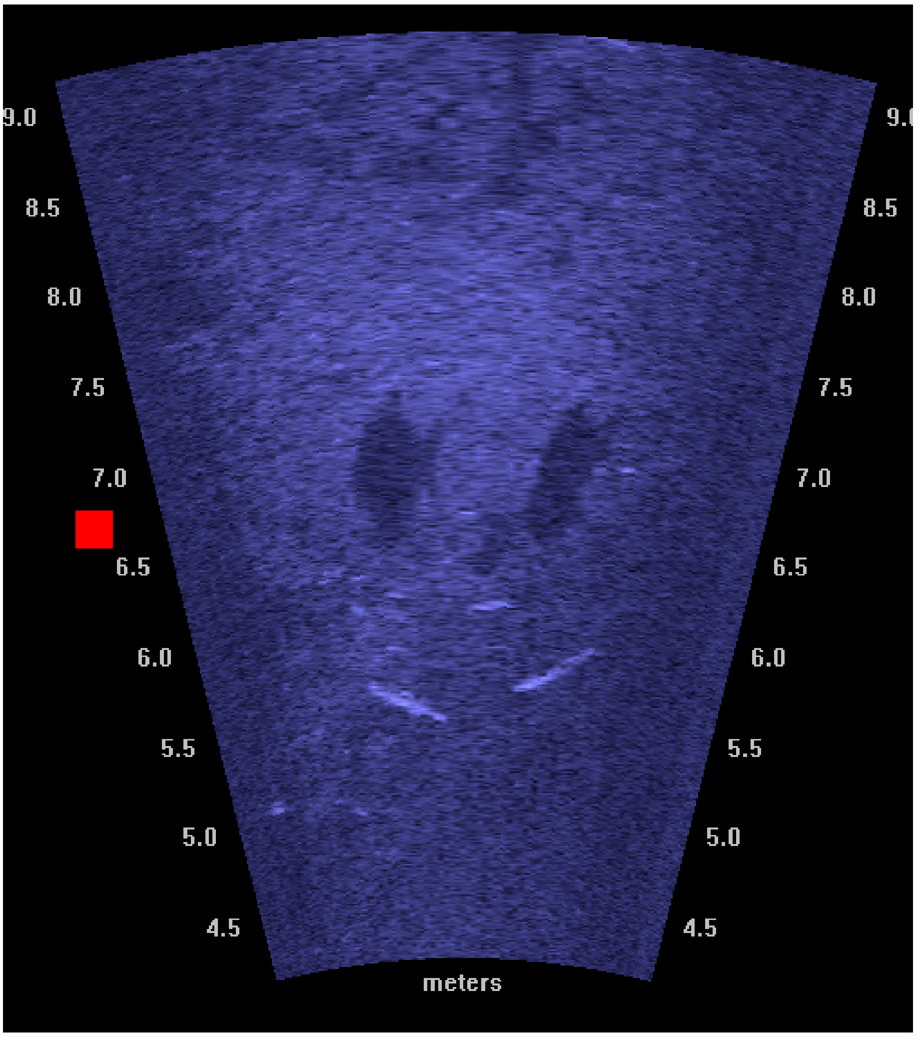


Figure 5.3 Example of a DIDSON image, showing three fish (approximately 20, 45 and 50 cm long) between 5.5 and 6.5 m from the DIDSON transponder.

and last days of sampling because of incomplete data sets. All statistical analysis was carried out using SPSS (version 14.0) with a significance level α = 0.05.

5.3 RESULTS

Totals of 11 013 fish were counted moving towards and 5671 moving away from Naburn Marina. Extrapolating counts to include unprocessed minutes (4 in every 5) equated to over 60 000 and 30 000 directional fish movements, during the three day study period. Large variations in fish movements and fish presence in the marina entrance occurred, influenced by time of day, river discharge and position in the water column (Figure 5.4).

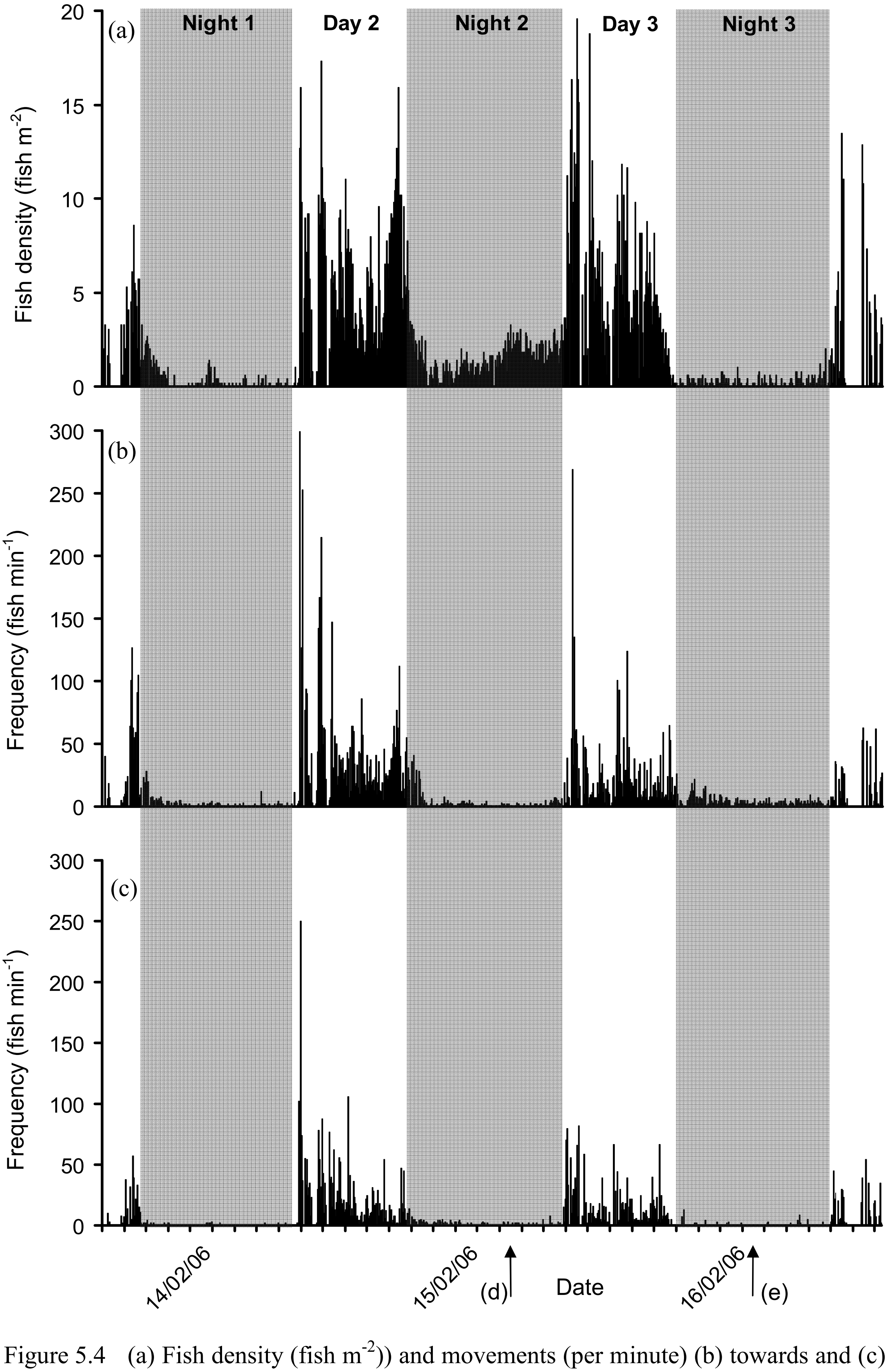


Figure 5.4 (a) Fish density (fish m^{-2})) and movements (per minute) (b) towards and (c) away from the marina throughout the study period. Shaded area represents night and (d) and (e) correspond to start and peak of elevated flow.

The largest and most consistent variations between fish density and movements in the marina entrance were between day and night samples, although other differences were identified (Tables 5.1-5.3; Figure 5.5). Under normal flow conditions (day 2), density and movements into the marina were similar throughout the day (Games-Howell: all $P > 0.05$), but significantly less fish were imaged leaving the marina at dusk than in the morning ($F_{4,122} = 6.166$, $P < 0.001$). River levels and flows increased substantially during day 3 and night 3, but no large influx of fish into the marina for refuge was observed. Instead, movements of fish into the marina on day 3 were less than the previous day (Table 5.2). In contrast with day 1 (dusk period only) and day 2, three periods of reduced movements into the marina on day 3 were identified: mid morning (Mann Whitney U-test: $Z = -4.179$, $n = 49$, $P < 0.001$), late afternoon ($F_{1,51} = 16.764$, $P = 0.015$) and dusk ($F_{2,70} = 6.778$, $P = 0.002$). Density ($F_{2,70} = 26.719$, $P < 0.001$) and movements of fish away from the marina ($F_{2,70} = 4.134$, $P = 0.020$), were also significantly less during the period just prior to darkness on day 3 compared with day 1 and day 2.

Significantly fewer fish occupied the upper section of the water column during raised river levels on night 3 (Mann Whitney U-test: $Z = -5.742$, $n = 155$, $P < 0.001$) and day 3 (Mann Whitney U-test: $Z = -3.818$, $n = 37$, $P < 0.001$) than in the low flows experienced on days 1 and 2. Significantly more fish moved towards the marina close to the surface during the night (Mann Whitney *U*-test: $Z = -1.976$, $n = 156$, $P = 0.048$), but the opposite was found for fish moving towards the river (ANOVA: $F_{1,155} = 6.032$, $P = 0.015$). During the day, the number of fish moving in both directions was significantly greater near the bottom (Mann Whitney *U*-test: towards - $Z = -4.013$, $n = 37$, $P < 0.001$; ANOVA: away from - $F_{1,36} = 13.036$, $P = 0.001$).

Size composition of imaged fish was highly variable throughout the sampling period (Table 5.1) because of the mixed species and size groups of mainly cyprinid fishes prevalent in the river; this limited analysis of size class results. However, on the last night, during elevated river levels, significantly greater density ($F_{4,635} = 21.137$, $P < 0.001$) and movements of >30 cm fish were observed than during all other sampling periods (towards: $F_{4,635} = 15.198$, $P < 0.001$; away from: $F_{4,635} = 17.622$, $P < 0.001$) (Tables 5.1-5.3). Although no species identification protocol has been produced, the fish were considered to be bream because of body shape characteristics evident on the DIDSON images.

Table 5.1 Mean density (fish m^{-2} ± SD (%)) at start of each minute processed (*n*, no. of fish (%)), during day and night sampling periods for all length classes (cm). Sampling periods (from night 1 to night 3, bottom) sharing the common subscript (a) are not significantly different, whereas the other comparisons differ at *P* < 0.001, except where *P* <0.05, denoted by * for both sampling periods.

Size class (cm)	Day 1	Night 1	Day 2	Night 2	Day 3	Night 3, bottom	Night 3, surface	Day 4, bottom	Day 4, surface
<15	2.66 ± 1.94 (93.1)	0.21 ± 0.37 (89.1)	4.99 ± 3.25 (88.5)	1.27 ± 0.63 (87.4)	4.69 ± 3.84 (92.3)	0.10 ± 0.18 (24.8)	0.07 ± 0.14 (53.1)	4.86 ± 3.34 (88.1)	1.77 ± 3.33 (94.6)
15-19	0.15 ± 0.27 (5.2)	0.01 ± 0.06 (4.9)	0.61 ± 1.08 (10.9)	0.17 ± 0.26 (11.9)	0.36 ± 0.38 (7.1)	0.10 ± 0.15 (26.9)	0.04 ± 0.09 (32.7)	0.49 ± 0.40 (8.9)	0.06 ± 0.16 (3.5)
20–24	0.03 ± 0.09 (1.2)	0.01 ± 0.04 (2.2)	0.02 ± 0.08 (0.4)	0	0.02 ± 0.06 (0.3)	0.10 ± 0.13 (24.8)	0.01 ± 0.05 (8.2)	0.08 ± 0.13 (1.5)	0.02 ± 0.06 (1.0)
25–29	0.01 ± 0.30 (0.2)		0.00 ± 0.02 (0.0)		0.00 ± 0.03 (0.1)	0.01 ± 0.03 (1.4)	0.00 ± 0.02 (2.0)		
30–34	0	0.00 ± 0.02 (0.6)	0	0.00 ± 0.02 (0.1)	0.00 ± 0.02 (0.0)	0	0	0.01 ± 0.05 (0.3)	0.01 ± 0.04 (0.5)
35-39	0	0.00 ± 0.02 (0.6)	0	0	0	0.01 ± 0.05 (2.76)	0	0.01 ± 0.05 (0.3)	0
40-44	0	0.00 ± 0.03 (1.64)	0.00 ± 0.04 (0.1)	0.00 ± 0.02 (0.2)	0.00 ± 0.02 (0.0)	0.01 ± 0.05 (2.8)	0	0.03 ± 0.07 (0.5)	0
45-49	0.01 ± 0.03 (0.2)	0	0.00 ± 0.02 (0.0)	0.00 ± 0.02 (0.2)	0.00 ± 0.03 (0.1)	0.04 ± 0.08 (9.7)	0	0.03 ± 0.07 (0.5)	0
50-54	0	0.00 ± 0.02 (0.6)	0.00 ± 0.03 (0.1)	0.00 ± 0.02 (0.2)	0.00 ± 0.03 (0.1)	0.01 ± 0.05 (2.76)	0.01 ± 0.03 (4.1)	0	0.01 ± 0.04 (0.5)
55-59	0	0.00 ± 0.02 (0.6)	0	0	0	0.00 ± 0.02 (0.7)	0	0	0
>59	0.01 ± 0.03 (0.2)	0	0	0.00 ± 0.02 (0.1)	0.00 ± 0.03 (0.1)	0.01 ± 0.05 (3.5)	0	0	0
All	2.86 ± 2.03	0.23 ± 0.39*	5.64 ± 3.50^{a}	1.46 ± 0.77	5.09 ± 4.08^{a}	0.39 ± 0.35*	0.13 ± 0.19	5.51 ± 3.51	1.87 ± 3.45

Table 5.2 Mean (± SD, (%)) number of fish moving towards the marina per minute, during day and night sampling periods for all length classes (cm). Sampling periods (from night 1 to night 3, bottom) sharing the common subscript (a, b) are not significantly different, whereas the other comparisons differ at $P < 0.001$, except where $P < 0.05$, denoted by * for both sampling periods.

Size class (cm)	Day 1	Night 1	Day 2	Night 2	Day 3	Night 3, bottom	Night 3, surface	Day 4, bottom	Day 4, surface
<15	25.9 ± 31.4 (90.3)	1.2 ± 1.9 (74.7)	30.8 ± 30.2 (74.3)	1.6 ± 2.3 (78.0)	20.2 ± 28.8 (84.3)	0.9 ± 1.3 (31.8)	2.6 ± 3.4 (55.2)	25.2 ± 18.1 (82.0)	5.7 ± 7.5 (73.9)
15-19	2.5 ± 3.4 (8.7)	0.3 ± 0.5 (16.3)	9.9 ± 19.8 (23.9)	0.3 ± 1.1 (15.2)	3.5 ± 4.8 (14.5)	1.2 ± 1.1 (40.7)	1.8 ± 1.7 (37.7)	4.4 ± 2.9 (14.1)	1.8 ± 2.8 (22.9)
20–24	0.1 ± 0.3 (0.3)	0.1 ± 0.2 (3.3)	0.7 ± 1.3 (1.6)	0.0 ± 0.2 (1.2)	0.2 ± 0.7 (0.9)	0.3 ± 0.5 (11.7)	0.2 ± 0.5 (4.3)	0.4 ± 0.6 (1.3)	0.2 ± 0.4 (2.0)
25–29	0.1 ± 0.3 (0.3)	0.0 ± 0.1 (0.8)	0	0.0 ± 0.1 (0.3)	0.0 ± 0.1 (0.0)	0.0 ± 0.1 (0.5)	0.0 ± 0.2 (0.8)	0.4 ± 0.7 (1.3)	0
30–34	0	0	0.0 ± 0.2 (0.1)	0	0	0.0 ± 0.2 (1.4)	0.0 ± 0.2 (0.8)	0	0
35-39	0.0 ± 0.2 (0.1)	0.0 ± 0.2 (1.6)	0.0 ± 0.1 (0.0)	0.0 ± 0.1 (0.3)	0	0.1 ± 0.3 (2.3)	0	0.1 ± 0.2 (0.2)	0
40-44	0	0.0 ± 0.1 (0.8)	0.0 ± 0.1 (0.0)	0.0 ± 0.1 (0.3)	0.0 ± 0.2 (0.1)	0.1 ± 0.3 (3.7)	0.0 ± 0.2 (0.5)	0.1 ± 0.2 (0.2)	0.1 ± 0.2 (0.7)
45-49	0.1 ± 0.3 (0.3)	0	0.0 ± 0.1 (0.0)	0.1 ± 0.3 (3.1)	0.0 ± 0.2 (0.2)	0.2 ± 0.4 (5.6)	0.0 ± 0.2 (0.5)	0.1 ± 0.2 (0.2)	0
50-54	0	0.0 ± 0.2 (2.0)	0.0 ± 0.1 (0.0)	0.0 ± 0.2 (1.2)	0.0 ± 0.1 (0.0)	0.0 ± 0.2 (1.4)	0	0.1 ± 0.3 (0.4)	0.1 ± 0.2 (0.7)
55-59	0	0	0	0	0.0 ± 0.1 (0.0)	0.0 ± 0.2 (0.9)	0	0.1 ± 0.2 (0.2)	0
>59	0	0.0 ± 0.1 (0.4)	0.0 ± 0.1 (0.0)	0.0 ± 0.1 (0.3)	0.0 ± 0.1 (0.0)	0	0.0 ± 0.1 (0.3)	0	0
All	28.6 ± 33.3	1.5 ± 2.0 ^{a}	41.4 ± 45.3*	2.1 ± 3.2 ^{ab}	23.9 ± 31.9*	3.0 ± 2.0^{b}	4.8 ± 4.3	30.8 ± 18.9	7.7 ± 9.9

Table 5.3 Mean (± SD, (%)) number of fish moving away from the marina per minute, during day and night sampling periods for all length classes (cm). Sampling periods (from night 1 to night 3, bottom) sharing the common subscript (a, b) are not significantly different, whereas the other comparisons differ at P <0.001, except where P <0.05, denoted by * for both sampling periods.

Size class (cm)	Day 1	Night 1	Day 2	Night 2	Day 3	Night 3, bottom	Night 3, surface	Day 4, bottom	Day 4, surface
<15	8.4 ± 12.2 (85.2)	0.3 ± 0.5 (64.2)	16.7 ± 23.9 (76.4)	1.0 ± 1.2 (78.6)	11.2 ± 14.1 (79.9)	0.2 ± 0.5 (21.0)	0.2 ± 0.6 (41.7)	18.1 ± 12.6 (84.1)	5.6 ± 11.1 (91.1)
15-19	1.3 ± 2.2 (12.9)	0.0 ± 0.2 (10.4)	4.8 ± 8.8 (22.1)	0.2 ± 0.4 (13.5)	2.6 ± 4.6 (18.5)	0.1 ± 0.3 (9.7)	0.1 ± 0.5 (27.8)	1.6 ± 1.7 (7.7)	0.6 ± 1.3 (8.9)
20–24	0.2 ± 0.4 (1.7)	0.0 ± 0.2 (6.0)	0.3 ± 0.7 (1.2)	0	0.1 ± 0.5 (0.9)	0.1 ± 0.3 (8.1)	0.0 ± 0.2 (5.6)	0.4 ± 0.6 (1.9)	0
25–29	0.0 ± 0.2 (0.3)	0	0	0.0 ± 0.1 (0.5)	0.0 ± 0.1 (0.1)	10.0 ± 0.1 (1.6)	0.0 ± 0.2 (8.3)	0.4 ± 0.6 (1.6)	0
30–34	0	0.0 ± 0.1 (1.5)	0.0 ± 0.1 (0.1)	0	0.0 ± 0.1 (0.1)	0	0	0.2 ± 0.5 (0.8)	0
35-39	0	0	0	0	0.0 ± 0.1 (0.1)	0.0 ± 0.1 (1.6)	0	0.1 ± 0.2 (0.3)	0
40-44	0	0.0 ± 0.1 (4.5)	0.0 ± 0.1 (0.1)	0.0 ± 0.1 (1.6)	0.0 ± 0.1 (0.1)	0.1 ± 0.4 (12.9)	0.0 ± 0.2 (5.6)	0.1 ± 0.3 (0.5)	0
45-49	0	0.0 ± 0.1 (4.5)	0	0.0 ± 0.2 (3.6)	0.0 ± 0.1 (0.1)	0.2 ± 0.5 (27.4)	0	0.3 ± 0.5 (1.4)	0
50-54	0	0.0 ± 0.2 (6.0)	0	0.0 ± 0.2 (2.1)	0	0.1 ± 0.3 (9.7)	0.0 ± 0.2 (5.6)	0.3 ± 0.6 (1.4)	0
55-59	0	0.0 ± 0.1 (1.5)	0	0	0.0 ± 0.1 (0.1)	0.0 ± 0.2 (4.8)	0.0 ± 0.2 (5.6)	0.1 ± 0.2 (0.3)	0
>59	0	0.0 ± 0.1 (1.5)	0.0 ± 0.2 (0.1)	0	0.0 ± 0.1 (0.1)	0.0 ± 0.2 (3.2)	0	0	0
Total	9.9 ± 13.8	0.4 ± 0.7*	21.8 ± 29.9^{a}	1.2 ± 1.3^{b}	14.0 ± 17.5^{a}	$0.9 \pm 1.1*^{b}$	0.4 ± 1.1	21.5 ± 13.8	6.2 ± 12.0

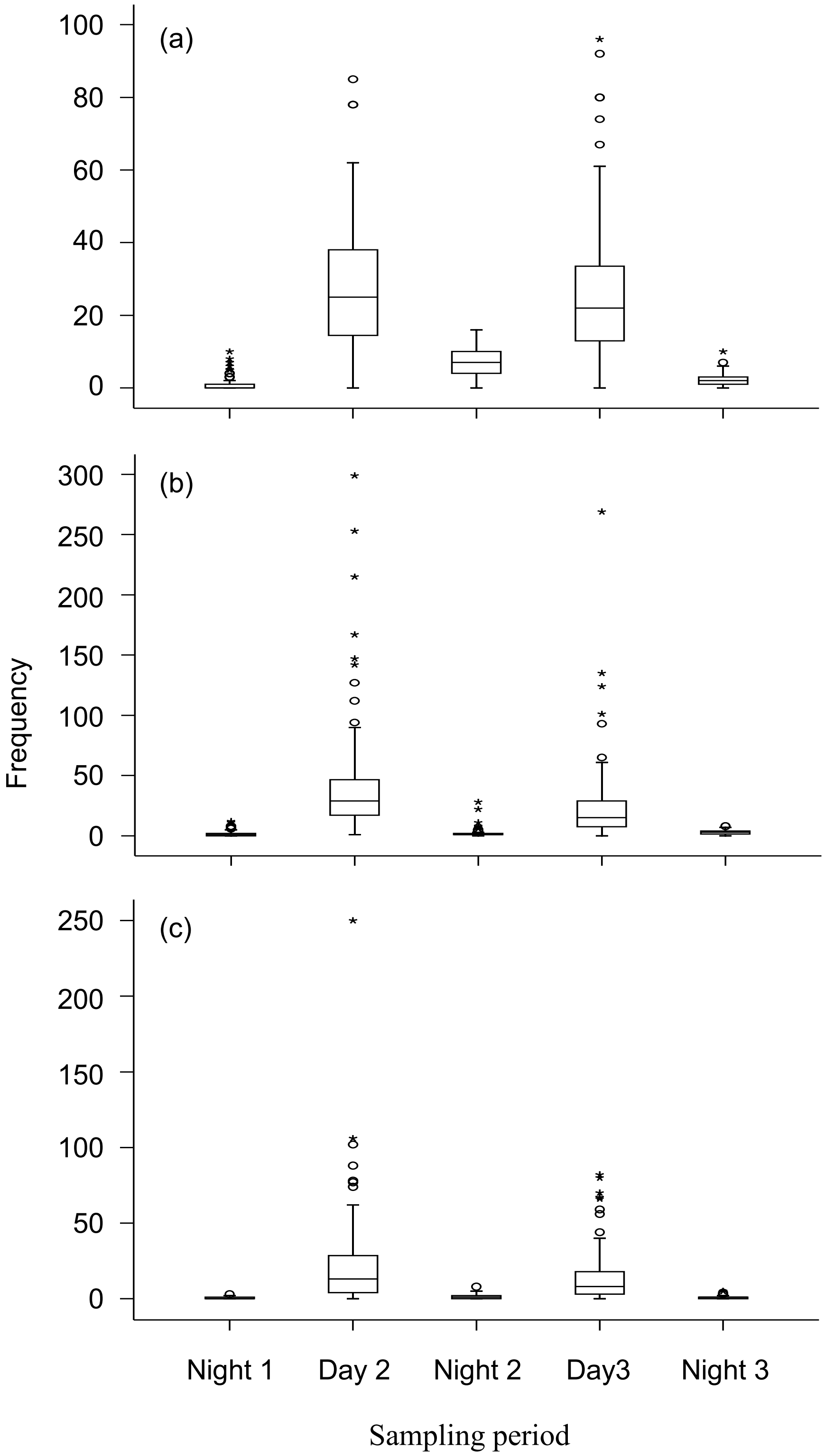


Figure 5.5 Box plots (10th, 25th, 50th, 75th and 90th percentiles and symbols = outliers) for (a) fish density (fish in sampled area (4.9 m^2)) and movements (per minute) (b) towards and (c) away from the marina throughout the study period.

5.4 DISCUSSION

DIDSON offers a valuable, non-intrusive, high-resolution tool to study patterns of individual fish movements between river channels and backwaters. Fish movements were generally towards the marina during the study period, but large scale diel variations in fish density and movements were found between the river and the marina backwater, within which flow and size-based influences exist. Processes that influence fish distribution are rarely random (Huntingford, 1993). It is hence necessary to consider the sources of variation found in movement and activity of cyprinids and percids in relation to foraging, predator avoidance trade-offs and the influence of flow on energy expenditure.

Despite the potential mosaic of movements by different species, the use of DIDSON in the marina entrance identified diurnal (principally around dawn) peaks in fish density and activity, with lowest presence and movement levels at night. Alabaster & Robertson (1961) found roach, bream and perch activity increased at dusk and dawn, and perch and bream shoals broke up at night. For most fishes, diel behaviour is often separated into active periods of foraging and passive periods of resting, linked to predator avoidance (Werner *et al.*, 1983; Helfman, 1993). However, during winter, food supplies are scarce and feeding rates are low (van Dijk *et al.*, 2005), thus fish may use backwaters to minimise energetic costs, with diel movements in relation to predation risk from birds (Gliwicz & Jachner, 1992; Jepsen & Berg, 2002; Heermann & Borcherding, 2006). Numerous piscivorous birds, including cormorant, *Phalacrocorax carbo* L., overwinter on the lower Ouse local to the study location (Whitton & Lucas, 1997) and have been observed feeding in the river adjacent to the marina, but human activity in the marina may make it a safer environment for fish. Even low numbers of birds feeding on the river could pose sufficient threat to induce habitat shifts because of the cumulative probability of an encounter (Gliwicz *et al.*, 2006) alongside the daily food requirements of warm-blooded predators during winter months (Gremillet *et al.*, 2003).

During the night, habitat usage altered as shown by the significantly fewer fish that were observed in the marina entrance, and their behaviour changed, since significantly fewer fish were imaged moving between the river and the marina. Bi-directional movements of fish at dusk suggest they moved both into the marina and the river.

Ultimately, fish dispersed to areas outside of the area visualised by the DIDSON, thus interpretation of activity and habitat use is somewhat limited.

During river level rises, fish may be attracted to low flow areas because they are energetically less demanding than maintaining a position in the potentially faster flowing water of the main channel (Gillette *et al*., 2006). However, significantly fewer fish moved towards Naburn Marina during the elevated flow event prevalent during the present study, contrary to reported fish movements into floodplain waterbodies (Sedell *et al*., 1990; Molls & Neumann, 1994) and off-channel areas (Allouche *et al*., 1999) for refuge during floods. Among the possible explanations are: First, that habitat complexity within the river or inundated terrestrial vegetation provided sufficient localised refuge from elevated flows (Pearsons *et al*., 1992; Schwartz & Herricks, 2005). Lucas *et al*. (1998) reported echo-counted fish densities were three times lower during high flows, suggesting fish remained on the bottom or in the margins, thus avoiding higher velocities in the water column. Second, conditions in the river were not sufficiently severe to cause such movements. During winter, the Yorkshire Ouse regularly reaches flows observed during the study, thus fish in the river are probably capable of living in the regularly fluctuating environment. Third, fish were moving into the marina as monitoring started in response to weather patterns in anticipation of high flows, but continued to make localised feeding forays except during the period of highest flows. However, the likelihood of the latter was slim, because rainfall fell on the upper part of the catchment, not local to the sampling location.

During the elevated flow, fish believed to be large bream were imaged in the marina channel, but only at night. Rakowitz & Zweimuller (2001) found fish > 400 mm total length tended to move upstream during increasing discharge levels. Lyons & Lucas (2002), Borcherding *et al*. (2002) and Schulz & Berg (1987) documented diel feeding migrations by bream, suggesting foraging requirements provide the stimulus for the observed diel behaviour.

Although, the study was of limited duration, did not sample the full width of the channel and the extent of "milling" behaviour could not be ascertained, the experimental design was comparable to similar studies employing split beam hydroacoustic technology (Rakowitz & Zweimuller, 2001; Lilja *et al*., 2003). Additionally, these limitations were considered necessary to obtain the detailed, high resolution information desired, but such experimental decisions possibly generated unexpected results. For example, the net movement of fish into the marina during the study period could be attributed to lunar cycles (Gaudreau & Boisclair, 2000), temperature (Lilja *et al.*, 2003) or turbidity (Jepsen & Berg, 2002) variations beyond the timescale of the study.

The study demonstrated the usefulness of the DIDSON to provide a fine-resolution insight into the movements of fish between a lowland river and connected floodplain waterbody during winter months. In particular, temporal changes in density, activity and size distributions of fish suggest connected floodplain waterbodies serve as essential winter habitat and are important for river ecosystem functioning. The findings of this study and other investigations involving backwater use in winter months should be explicitly incorporated into plans for lowland river rehabilitation and floodplain restoration (Cowx & Welcomme, 1998), including actions to improve the ecological status of rivers under the European Union, Water Framework Directive (2000/60/EEC). From a conservation perspective, it is important to note that these patterns may be applicable on an assemblage-wide, and not just a species specific level. Future investigations should attempt to verify numbers, species and size composition of imaged fish, and analyse stomach contents over multiple 24-hour periods. Further studies should be over an extended period and area, and measuring detailed water quality variables (suspended solids, ammonia and the distribution of food items) in the marina and the river. There is also a need to gather data throughout the year to describe seasonal patterns in marina use.

6 EVALUATION OF VISIBLE IMPLANT ELASTOMER MARKING AND PASSIVE INTEGRATED TRANSPONDER TAGGING PROTOCOLS FOR JUVENILE CYPRINID FISHES

6.1 INTRODUCTION

Stocking is one of the primary actions taken in response to poor performance of fisheries or to compensate for loss of stock caused by fish kills or environmental degradation (Cowx, 1994). The efficacy of these stocking events is usually unknown (Cowx, 1999). To improve the effectiveness of stock enhancement measures, there is a need to understand the fate of stocked fish and this generally requires some form of marking to identify individual fish or batches of fish stocked. Marking of animals to enable their identification, either individually or as part of a group, is also of fundamental importance in assessing population size, movement, growth, age or fecundity (Wydoski & Emery, 1983).

In general, marking techniques should: (1) identify individual fish or batches; (2) not affect growth, survival, behaviour or capture probability of marked individuals; (3) be retained for the duration of the study; (4) be easily applied and identified; and (5) be inexpensive (Kelly, 1967; Wydoski & Emery, 1983; McFarlane *et al.*, 1990). Studies that require such characteristics limit the type of mark that can be used (Lucas & Baras, 2000), and the choice of mark is further limited when considering juveniles (Thedinga *et al.*, 1997).

Visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, USA) compound is a biologically inert, brightly coloured, fluorescent polymer that is externally visible after being injected subcutaneously under transparent or semi-opaque tissue. VIE marks are commonly used as a batch mark in mark–recapture fisheries studies using multiple combinations of locations and VIE colours (Bonneau *et al.*, 1995; Olsen & Vollestad, 2001; Walsh & Winkelman, 2004). A disadvantage of VIE marking is its applicability for group marking rather than individual identification (Woods & James, 2003), although small ecological studies have uniquely marked all individuals (e.g. Dewey & Zigler, 1996; Brennan *et al.*, 2005). The only study in which cyprinid fishes have been VIE marked was on barbel, where high retention rates were found after 57 days when marked in the head and fins (Farooqi

& Morgan, 1996). However, other studies implanting VIE in the head and fins found variable retention (Dewey & Zigler, 1996; Brennan *et al*., 2005), emphasising the need to validate VIE marking for the species under study.

Passive integrated transponder (PIT) tags are biocompatible, sealed, electronic modules that return a unique identification number when energised from an external antenna (Gibbons & Andrews, 2004). PIT tags theoretically have an indefinite life span and allow repeated, non-destructive sampling or direct telemetric data transmission. They have proven useful for monitoring individual fish movements, migrations and habitat use (Prentice *et al*., 1990a, b; Castro-Santos *et al*., 1996; Armstrong *et al*., 1996; Ombredane *et al*., 1998; Lucas *et al*., 1999; Roussel *et al*., 2000; Zydlewski *et al*., 2001; Riley *et al*., 2003). Many PIT systems use 12-mm tags, which, despite their small detection range (< 0.4 m), can be used to tag fish as small as 6 cm and are ideal for mark-recapture and some telemetry applications (Lucas & Baras, 2000). Larger (e.g. 23-mm) PIT tags have greater range and this enhances their utility for certain telemetry applications, but there is a trade-off with the potential impacts on the health of smaller fishes (Roussel *et al*., 2000; Lucas & Baras, 2000). Many telemetry studies have recommended that tag weight should not exceed 2 % of the fish body mass (e.g. Winter, 1996; Adams *et al*., 1998), because of the adjustment capacity of the swimbladder in teleost fish (Alexander, 1966). Ultimately, proportionally smaller tags are likely to have lesser effects on fish released into the wild.

All methods of marking fish (of which tags are a subset), with the exception of certain natural marks (e.g. genetic marks) have the potential to influence fish survival, performance (e.g. growth) and behaviour (Lucas & Baras, 2000). As a result, feasibility studies on mark suitability are strongly encouraged, for both ethical considerations and validation of results (Baras *et al*., 2000), i.e. for ecological experiments to be meaningful, marked fish should be representative of unmarked populations (Malone *et al*., 1999). Therefore, before incorporating marking techniques into field research, mark retention, survival and growth rate of marked fish, along with ease of application and detectability should be evaluated for each marking technique, fish species, attachment location and size of fish marked (Guy *et al*., 1996). Although there have been numerous studies conducted on mark retention, mortality and growth rates of fishes, especially salmonids, marked with VIE or PIT tags, few have considered their suitability for cyprinids (Farooqi & Morgan, 1996; Skov *et al*., 2005). This study tested the performance of VIE marks and PIT tags and their effects on juvenile chub, dace and roach. The overall objective was to determine the most reliable and appropriate long-term marking technique for potential application in field studies assessing dispersal of juvenile cyprinids.

6.2 MATERIALS AND METHODS

6.2.1 Fish origin and experimental setup

All fish were artificially reared in the hatchery and pond facility of the Environment Agency's Calverton Fish Farm, Nottinghamshire, England. This was also the site of the experimental work. Fish marked in this experiment covered the range of ages and sizes usually stocked into UK rivers, to ensure the results were applicable to future field studies on marked stock fish. In April 2004, approximately 400 fish of each of the following species groups were brought into indoor tanks (2.02 m^3) supplied (in parallel) with filtered ground water (60 L^{-1} min^{-1} $tank^{-1}$): chub (87-167 mm fork length, Lt), dace (77-152 mm Lt) and roach (103-150 mm Lt) and larger chub (114-210 mm Lt). Fish were acclimated to the experimental environment for one month prior to marking. Water temperature (range 17–21 °C) and dissolved oxygen (> 90 % saturation throughout) were monitored, and photoperiod was controlled to simulate the daily cycle. Fish were fed a ration of approximately 3 % body mass per day using automatic feeders, supplemented by natural frozen gamma-radiated feed. Treatments (Table 6.1) were tested on groups of 100 fish per tank for large chub and 240 small fish per tank (comprising 80 each of small chub, dace and roach). Limited availability of tanks (nine) required the small fish to be held as mixed species rather than separately, and prevented treatment replication, although they were on exactly the same water delivery system, in the same building, with the same feed delivery system, to minimise any possible variation.

6.2.2 Marking procedure

Fish were lightly anaesthetised using buffered tricaine methane-sulphonate (MS-222, 0.1 g L^{-1}) before handling and marking. Initial body mass (Wt, g) and fork length (mm) were recorded (Table 6.1). Fish were placed ventral side up in a clean V-shaped foam support soaked in water deep enough to submerge the gills of the fish.

Table 6.1 Summary of treatment, species of fish, initial sizes (mm, g) and ratio (%) of PIT tag weight to initial fish mass for each treatment.

Treatment applied	Species group	Fish length (mean (range), mm)	Fish mass (mean (range), g)	Tag / body wt ratio (mean (range), %)
Control	Large chub	164.9 (114 - 210)	56.6 (18.3 - 113.9)	-
VIE (head + fin)	Large chub	140.4 (123 - 164)	35.3 (23.7 - 55.4)	-
23 mm PIT, no closure	Large chub	167.3 (136 - 192)	58.1 (29.4 - 89.0)	1.03 (0.67 - 2.04)
23 mm PIT, with closure	Large chub	169.4 (141 - 210)	60.7 (37.3 - 112.7)	0.99 (0.53 - 1.61)
Control	Small chub	122.2 (88 - 158)	22.8 (8.4 - 48.7)	-
	Dace	116.5 (99 - 143)	16.4 (10.6 - 30.4)	-
	Roach	118.1 (103 - 136)	22.8 (15.1 - 33.9)	-
VIE (head + fin)	Small chub	120.8 (100 - 157)	20.9 (11.1 - 46.6)	-
	Dace	116.6 (101 - 152)	16.0 (10.7 - 39.0)	-
	Roach	120.4 (104 - 140)	34.1 (15.6 - 42.0)	-
Sham 12 mm PIT	Small chub	117.7 (91 - 167)	19.1 (8.3 - 32.2)	-
	Dace	115.7 (101 - 129)	15.6 (9.7 - 25.3)	-
	Roach	117.7 (104 - 134)	21.9 (15.1 - 34.3)	-
12 mm PIT, no closure	Small chub	113.2 (87 - 126)	16.8 (7.0 - 24.1)	0.59 (0.41 - 1.43)
	Dace	114.7 (101 - 121)	15.3 (10.9 - 21.2)	0.64 (0.47 - 0.92)
	Roach	116.3 (104 - 133)	21.2 (14.6 - 34.8)	0.47 (0.29 - 0.68)
23 mm PIT, with closure	Small chub	124.7 (110 - 153)	22.9 (14.6 - 43.3)	2.62 (1.39 - 4.11)
	Dace	120.5 (108 - 140)	17.5 (11.1 - 30.1)	3.42 (1.99 - 5.41)
	Roach	122.6 (109 - 150)	24.7 (16.2 - 45.9)	2.43 (1.31 - 3.70)

VIE treatment procedures for both size classes involved marking the head (subcutaneously, over the cranium) and a fin (between fin rays) with a single ≈2 mm fluorescent orange, elastomer mark (Northwest Marine Technology, Shaw Island, Washington), using a 1-mL syringe and a 27-gauge x 12-mm long needle. VIE was applied to one of the paired fins, normally a pectoral fin but, when difficulty was experienced in application to the pectoral fin, especially in small fish, a pelvic fin was used. Elastomer was injected as the needle was withdrawn, stopping before the needle bevel reached the entry point, and a thumb was then gently wiped over the wound to remove any excess elastomer (Olsen & Vollestad, 2001).

Tagging of fish with a 12-mm PIT tag used an alcohol-sterilised and distilled water-rinsed UKID transponder (model 122GL, 12.0-mm long x 2.1-mm diameter, 0.1 g weight in air, 125 kHz, full-duplex, E. Collinson and Co Ltd, Preston, UK) inserted into the body cavity through an approximately 3-mm long ventro-lateral incision made with a scalpel, 2-3 mm anterior to the muscle bed of the pelvic fins. No closure was required because of the small size of the incision. The sham incision treatment involved the same experimental and surgical procedure but no transponder was inserted into the fish.

The 23-mm PIT tag treatment was tested on the small chub, dace and roach (with adhesive closure) and the large chub (with and without adhesive closure). The 23-mm tags used were half-duplex transponders (Texas Instruments model RI-TRP-RRHP, 23.0-mm long x 3.4-mm diameter, 0.6 g weight in air, 134.2 kHz, RFID components Ltd, Bedford, UK). Each tag was sterilised in alcohol and rinsed with distilled water before being inserted into the body cavity through an approximately 5-mm long ventro-lateral incision made with a scalpel, 4-6 mm anterior to the muscle bed of the pelvic fins. In one group of large chub tagged with 23-mm PITs, the incision was not closed. In the other large chub treatment group and for all small chub, dace and roach tagged with 23-mm PITs, clinical grade cyanoacrylate adhesive (Vetbond, 3M) was applied to the periphery of the incision and gentle pressure applied for five seconds to close the wound. A large range of PIT tag weight / body mass ratios was achieved by using different-sized PIT tags and fish (Table 6.1).

Control fish were weighed, measured and handled to the same protocol as the fish in the other treatments but no surgery was performed or tag implanted. After treatment, fish were allowed to recover from the anaesthetic in a well-aerated observation tank until they regained balance and were actively swimming, before returning them to the experimental tanks.

All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986. Home Office licence number PPL 60/3260.

6.2.3 Monitoring procedure

Tanks were inspected daily for mortalities (removed, frozen and the tank number of origin recorded) and signs of disease throughout the experiment. All fish were examined after 29 days (1 month), 89 days (3months) and 182 days (6 months) to determine mark retention, wound healing and growth over short and longer timescales. On each occasion fish were anaesthetised with MS-222, and fork length (mm) and mass (g) were recorded to assess growth. Fish (and the tank bottom) were screened for PIT tag presence and function using a Trovan LID 500 hand detector (Trovan Ltd, Douglas, UK) for 12-mm tags and an Allflex compact reader P/N 930009-001 (Allflex, Hawick, UK) for 23-mm tags. Identification of fluorescent VIE marks was carried out using a Northwest Marine Technology, 7-LED 'blue' flashlight and amber lens spectacles. Despite fragmentation and partial losses of VIE in both mark locations, marks were still considered to be retained if any fragment was visible, since this is the useful field assessment condition. Marking site condition was examined and assessed in four classes: 0 = fully healed (no scar visible), 1 = visible wound but no reddening, 2 = slight inflammation (slight reddening around the incision sight) and 3 = strong inflammation (marked reddening around the incision site). For consistency the same person performed the visual inspection throughout the entire experiment. After inspection, fish were allowed to recover from the anaesthetic in a well-aerated observation tank until they recovered balance and were actively swimming, before being returned to the experimental tanks.

6.2.4 Data analysis

Mark retention was expressed as a percentage of the total number of marks implanted. A chi-squared test with continuity correction was used to test the null hypothesis that mark retention did not differ significantly between marking technique and locations. Mortality rate was calculated as a cumulative percentage of dead fish per treatment for each species during the experiment. A chi-squared test was used to test the null hypothesis that survival did not differ significantly between marking techniques, followed by a Mann-Whitney *U*-test, as a *post hoc* test, to determine mortality rates in treatment groups that were significantly different from control fish. A *t*-test was performed on initial fish length and mass of surviving and dead PIT tagged fish to test the null hypothesis that there was no influence of size on mortality.

VIE-marked fish could not be individually identified through the course of the experiment, thus all data analyses for growth were conducted on tank mean values for species. The specific growth rate (SGR_{w}) by mass (%d^{-1}) was calculated according to:

$$SGR_{\mathrm{wt}} = 100(\ln W_2 - \ln W_1) / t, \qquad (3.1)$$

where Wt_1 and Wt_2 are mass in grams at the start and the end of the study period and t is that period in days. The mass of all tagged fish was corrected for PIT tag weight (by subtracting 0.1 g for 12-mm PIT tags and 0.6 g for 23-mm PIT tags). The specific growth rate for length (SGR_L) was calculated using the same formula analysed for mass. Analysis of variance showed that initial fish length between the treatments was significantly different for small chub ($F_{4,396} = 16.86$, $P < 0.001$), dace ($F_{4,395} = 11.14$, $P < 0.001$), roach ($F_{4,400} = 11.77$, $P < 0.001$) and large chub ($F_{2,298} = 3.56$, $P = 0.03$). As a result, SGR values were standardised against means of the previous sampling occasion to allow comparison using one-way ANOVA (*post hoc* test= LSD test or Dunnett T3 test if a Levene test revealed significantly unequal variance). All statistical analysis was carried out using SPSS (version 14.0) with a significance level $\alpha = 0.05$. Growth comparisons of large chub to small chub VIE treatments were not drawn because initial size and tank density were not controlled.

6.3 RESULTS

In total, 1606 hatchery-reared chub, dace and roach were subjected to nine different mark treatments for six months. Large variations in retention, survival and growth rate occurred at various stages of the experiment, influenced by mark type, fish size and mark location.

6.3.1 Mark retention

Considerable differences in retention rates were found between marks. PIT tag retention was highest over the six-months of the experiment, with 100 % retention for 12-mm PIT tags in all three species and for 23-mm PIT tags in both small and large chub. Two dace and one roach expelled 23-mm PIT tags, resulting in 96.6 % and 98.7 % retention, respectively. Throughout the experiment all PIT tags remained operational.

Mark location influenced VIE retention (Figure 6.1). Short-term (1 month) VIE retention was significantly better in the head than fins of dace (97.5 % compared with 78.8 %; χ^2 with continuity correction = 12.857, d.f. = 1, $P < 0.001$), and small chub (98.8 % and 85.0 %; χ^2 with continuity correction = 8.373, d.f. = 1, $P = 0.004$), but not roach (96.3 % and 87.5 %; χ^2 with continuity correction = 3.014, d.f. = 1, $P = 0.083$). After 6 months, VIE mark retention in the head fell markedly (small chub 57.5 %, dace 21.5 %, roach 42.9 %, large chub 29.6 %) and was significantly higher in the fins (small chub 87.5 %, dace 77.2 %, roach 80.8 %, large chub 88.8 %) (χ^2 with continuity

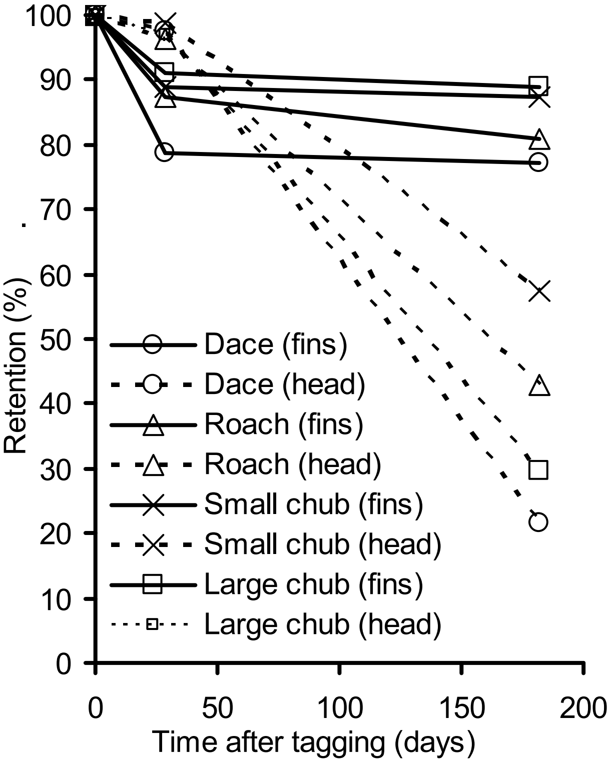


Figure 6.1 VIE retention (%) in head and fins of chub, roach and dace with time (days).

correction: small chub = 16.583, d.f. = 1, $P < 0.001$; large chub = 68.621, d.f. = 1, $P < 0.001$; dace = 46.225, d.f. = 1, $P < 0.001$; roach = 21.541, d.f. = 1, $P < 0.001$).

6.3.2 Survival

Only two roach (survival = 97.5 %), two dace (97.5 %) and one large chub (99 %) marked with VIE died over the course of the experiment (Table 6.2). Survival was also high for small chub tagged with 23-mm PITs; i.e. 96.3 % survival compared with 100 % for the control fish (Table 6.2). Two large chub tagged with 23-mm PITs (no closure) died after 12 and 127 days respectively (Table 6.3). Chub survival was not significantly different between marked and control groups ($\chi^2 = 5.229$, d.f. = 4, $P = 0.265$). Similar trends were observed for roach (($\chi^2 = 4.998$, d.f. = 4, $P = 0.287$; Table 6.4).

Survival of dace tagged with 23-mm PITs and 12-mm PIT sham tagged dace and was poor compared with small chub and roach (Table 6.5). Survival of these groups, but not VIE and 12 mm PIT tagged dace, was significantly lower than controls, on all sampling

Table 6.2 Survival (%. *n*, no. of fish), length (mean ± SD, mm), mass (mean ± SD, g), SGR (*, $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ significantly lower than control) and mark site condition for small chub treatments and control at 29, 89 and 182 days post marking.

Treatment	Control	VIE	12-mm sham	12-mm PIT	23-mm PIT
Survival (%. (*n*, no. of fish)), after n days					
Initial *n*	80	80	81	80	80
29 d	100 (80)	100 (80)	98.8 (80)	100 (80)	100 (80)
89 d	100 (80)	100 (80)	98.8 (80)	100 (80)	97.5 (78)
182 d	100 (80)	100 (80)	97.5 (79)	97.5 (78)	96.3 (77)
Length (mean ± SD, mm), after n days					
0 d	122.2 ± 12.4	120.8 ± 9.5	117.7 ± 10.7	113.2 ± 6.4	124.7 ± 7.6
29 d	128.9 ± 12.0	126.7 ± 9.9	122.2 ± 10.0	118.4 ± 6.6	128.9 ± 8.1
89 d	143.6 ± 12.4	145.6 ± 10.1	146.4 ± 10.3	136.6 ± 7.2	139.4 ± 8.3
182 d	164.6 ± 12.1	173.2 ± 12.2	171.5 ± 11.3	163.7 ± 8.4	159.6 ± 8.2
Mean specific growth rate (% Ln day^{-1})					
dd 0-29	0.184	0.164	0.128	0.153	0.113
dd 29-89	0.181	0.231	0.301	0.238	0.131
dd 89-182	0.147	0.187	0.170	0.195	0.145
dd 0-182	0.164	0.198	0.207	0.203	0.135***
Mass (mean ± SD, g), after n days					
0 d	22.8 ± 7.7	20.9 ± 5.5	19.1 ± 4.9	16.8 ± 3.0	22.9 ± 4.9
29 d	26.3 ± 8.4	23.9 ± 6.2	19.1 ± 5.2	19.2 ± 3.4	27.3 ± 17.5
89 d	39.4 ± 10.3	41.8 ± 9.0	45.1 ± 10.1	32.1 ± 5.3	32.6 ± 6.1
182 d	58.0 ± 13.4	69.0 ± 15.2	65.3 ± 14.1	54.9 ± 9.3	52.4 ± 8.7
Mean specific growth rate (% Wt day^{-1})					
dd 0-29	0.486	0.466	0.005*	0.459	0.602
dd 29-89	0.677	0.935	1.432	0.851	0.297***
dd 89-182	0.415	0.537	0.399	0.578	0.509
dd 0-182	0.513	0.657	0.677	0.649	0.454*
Mean mark site condition, after n days					
29 d	-	0.00	0.14	0.06	0.48
89 d	-	0.00	0.00	0.00	0.00
182 d	-	0.00	0.00	0.00	0.00

Table 6.3 Survival (%. *n*, no. of fish), length (mean ± SD, mm), mass (mean ± SD, g), SGR (*, *P* <0.05; ** *P* < 0.01; *** *P* < 0.001 significantly lower than control, † = *P* <0.05; †† *P* < 0.01; ††† *P* < 0.001 closure significantly lower than no closure)) and mark site condition for large chub treatments and control at 29, 89 and 182 days post marking.

Treatment	Control	VIE (head + fin)	23-mm PIT, no closure	23-mm PIT, closure
Survival (%. (*n*, no. of fish)), after n days				
Initial *n*	100	99	101	100
29 d	100.0 (100)	100 (99)	99.0 (100)	100.0 (100)
89 d	100.0 (100)	99 (98)	99.0 (100)	100.0 (100)
182 d	100.0 (100)	99 (98)	98.0 (99)	100.0 (100)
Length (mean ± SD, mm), after n days				
0 d	164.9 ± 14.7	140.4 ± 6.8	167.3 ± 9.5	169.4 ± 10.9
29 d	171.3 ± 14.0	146.3 ± 7.2	171.1 ± 9.5	173.6 ± 10.8
89 d	180.3 ± 14.2	165.9 ± 8.8	178.8 ± 10.1	175.3 ± 10.9
182 d	195.8 ± 13.4	190.1 ± 9.8	190.4 ± 10.4	185.9 ± 10.8
Mean specific growth rate (% Ln day^{-1})				
dd 0-29	0.131	0.141	0.077	0.084
dd 29-89	0.084	0.209	0.073	0.016*** †††
dd 89-182	0.089	0.147	0.068*	0.063**
dd 0-182	0.094	0.166	0.071***	0.051*** †††
Mass (mean ± SD, g), after n days				
0 d	56.6 ± 15.1	35.3 ± 5.4	58.0 ± 10.1	60.7 ± 12.5
29 d	56.5 ± 14.3	34.0 ± 5.4	61.6 ± 11.0	66.6 ± 13.5
89 d	82.3 ± 18.7	68.9 ± 11.1	73.1 ± 14.3	63.8 ± 13.1
182 d	101.9 ± 21.2	96.6 ± 15.0	89.5 ± 15.9	82.2 ± 15.8
Mean specific growth rate (% Wt day^{-1})				
dd 0-29	-0.004	-0.035	0.197	0.318
dd 29-89	0.626	1.131	0.285***	-0.071*** †††
dd 89-182	0.230	0.363	0.219	0.272
dd 0-182	0.323	0.553	0.237***	0.166*** †††
Mean mark site condition, after n days				
29 d	-	0.00	0.59	0.61
89 d	-	0.00	0	0
182 d	-	0.00	0	0.01

Table 6.4 Survival (%. *n*, no. of fish), length (mean ± SD, mm), mass (mean ± SD, g), SGR (*, P <0.05; ** P < 0.01; *** P < 0.001 significantly lower than control) and mark site condition for roach treatments and control at 29, 89 and 182 days post marking.

Treatment	Control	VIE	12-mm sham	12-mm PIT	23-mm PIT
Survival (%. (*n*, no. of fish)), after n days					
Initial *n*	80	80	85	80	80
29 d	100.0 (80)	100.0 (80)	97.6 (83)	100.0 (80)	98.8 (79)
89 d	100.0 (80)	100.0 (80)	97.6 (83)	100.0 (80)	98.8 (79)
182 d	100.0 (80)	97.5 (78)	96.5 (82)	100.0 (80)	97.5 (78)
Length (mean ± SD, mm), after n days					
0 d	118.1 ± 6.3	120.4 ± 7.1	117.7 ± 6.4	116.3 ± 5.3	122.6 ± 6.8
29 d	120.1 ± 6.3	122.6 ± 7.2	120.5 ± 6.5	118.9 ± 5.4	124.9 ± 7.2
89 d	128.4 ± 6.8	129.9 ± 7.5	131.6 ± 7.4	127.5 ± 5.8	128.0 ± 7.6
182 d	135.4 ± 6.7	141.3 ± 8.3	141.0 ± 8.6	138.1 ±6.5	134.2 ± 8.3
Mean specific growth rate (% Ln day^{-1})					
dd 0-29	0.058	0.063	0.079	0.077	0.065
dd 29-89	0.111	0.096	0.147	0.117	0.041***
dd 89-182	0.057	0.091	0.074	0.086	0.051
dd 0-182	0.075	0.088	0.099	0.095	0.050***
Mass (mean ± SD, g), after n days					
0 d	22.8 ± 4.2	24.1 ± 5.3	21.9 ± 4.2	21.2 ± 3.4	24.7 ± 5.5
29 d	23.1 ± 4.0	24.6 ± 5.2	20.6 ± 4.1	22.4 ± 3.4	25.3 ± 5.3
89 d	32.3 ± 4.9	34.9 ± 7.4	37.2 ± 7.2	32.0 ± 4.6	28.7 ± 5.3
182 d	38.0 ± 7.7	42.7 ± 9.2	41.3 ± 8.7	38.4 ± 6.1	35.0 ± 7.2
Mean specific growth rate (% Wt day^{-1})					
dd 0-29	0.043	0.072	-0.214*	0.196	0.086
dd 29-89	0.561	0.580	0.988	0.592	0.207***
dd 89-182	0.174	0.217	0.112	0.198	0.215
dd 0-182	0.281	0.313	0.349	0.328	0.192***
Mean mark site condition, after n days					
29 d	-	0	0.78	0.58	1.01
89 d	-	0	0.00	0.00	0.08
182 d	-	0	0.00	0.00	0.00

Table 6.5 Survival (%. *n*, no. of fish) (†, *P* <0.05; †† *P* < 0.01; ††† *P* < 0.001 Mann Whitney *U*-test, significantly lower than control), length (mean ± SD, mm), mass (mean ± SD, g), SGR (*, *P* <0.05; ** *P* < 0.01; *** *P* < 0.001 significantly lower than control) and mark site condition for dace treatments and control at 29, 89 and 182 days post marking.

Treatment	Control	VIE	12-mm sham	12-mm PIT	23-mm PIT
Survival (%. (*n*, no. of fish)), after n days					
Initial *n*	80	81	80	80	80
29 d	97.5 (78)	98.8 (80)	83.8 (67) ††	100 (80)	78.8 (63) †††
89 d	93.8 (75)	98.8 (80)	83.8 (67) †	97.5 (78)	76.3 (61) ††
182 d	92.5 (74)	97.5 (79)	80.0 (64) †	96.3 (77)	72.5 (58) ††
Length (mean ± SD, mm), after n days					
0 d	116.5 ± 6.3	116.6 ± 6.9	115.7 ± 6.0	114.7 ± 3.7	120.5 ± 7.4
29 d	117.5 ± 6.4	118.4 ± 6.9	117.5 ± 6.5	117.4 ± 3.6	122.6 ± 5.9
89 d	125.3 ± 6.1	125.2 ± 7.9	127.7 ± 7.2	124.1 ± 4.2	124.1 ± 6.2
182 d	132.5 ± 5.7	138.7 ± 8.4	139.2 ± 7.6	136.7 ± 5.3	131.7 ± 6.3
Mean specific growth rate (% Ln day^{-1})					
dd 0-29	0.030	0.052	0.053	0.079	0.059
dd 29-89	0.107	0.093	0.140	0.093	0.021***
dd 89-182	0.060	0.110	0.092	0.104	0.064
dd 0-182	0.071	0.095	0.102	0.096	0.049***
Mass (mean ± SD, g), after n days					
0 d	16.4 ± 3.1	16.0 ± 3.7	15.6 ± 3.0	15.3 ± 1.8	17.5 ± 4.7
29 d	16.3 ± 3.2	16.8 ± 4.6	13.9 ± 3.0	17.7 ± 16.2	18.0 ± 3.4
89 d	23.0 ± 3.6	25.2 ± 5.8	28.6 ± 5.5	23.1 ± 3.7	20.2 ± 3.7
182 d	28.9 ± 4.3	34.0 ± 6.5	33.9 ± 5.3	31.5 ± 4.1	27.6 ± 4.9
Mean specific growth rate (% Wt day^{-1})					
dd 0-29	-0.003	0.162	-0.400	0.495	0.094
dd 29-89	0.570	0.678	1.203	0.446*	0.193***
dd 89-182	0.247	0.320	0.185	0.333	0.334
dd 0-182	0.313	0.413	0.428	0.396	0.249*
Mean mark site condition, after n days					
29 d	-	0.00	0.90	0.59	0.98
89 d	-	0.01	0.03	0.00	0.11
182 d	-	0.00	0.00	0.00	0.00

occasions because of high early mortality, for 23-mm PIT (Mann Whitney *U*-test: month 1: $Z = -3.365$, $n = 160$, $P < 0.001$; month 3: $Z = -3.090$, $n = 160$, $P = 0.002$; month 6: $Z = -3.319$, $n = 160$, $P = 0.001$) and 12-mm PIT tag sham treatments (Mann Whitney *U*-test: month 1: $Z = -2.974$, $n = 160$, $P = 0.003$; month 3: $Z = -1.995$, $n = 160$, $P = 0.046$; month 6: $Z = -2.288$, $n = 160$, $P = 0.022$). Mass at tagging influenced survival of 23-mm PIT tagged dace ($t = -2.170$, $P = 0.033$) (Figure 6.2).

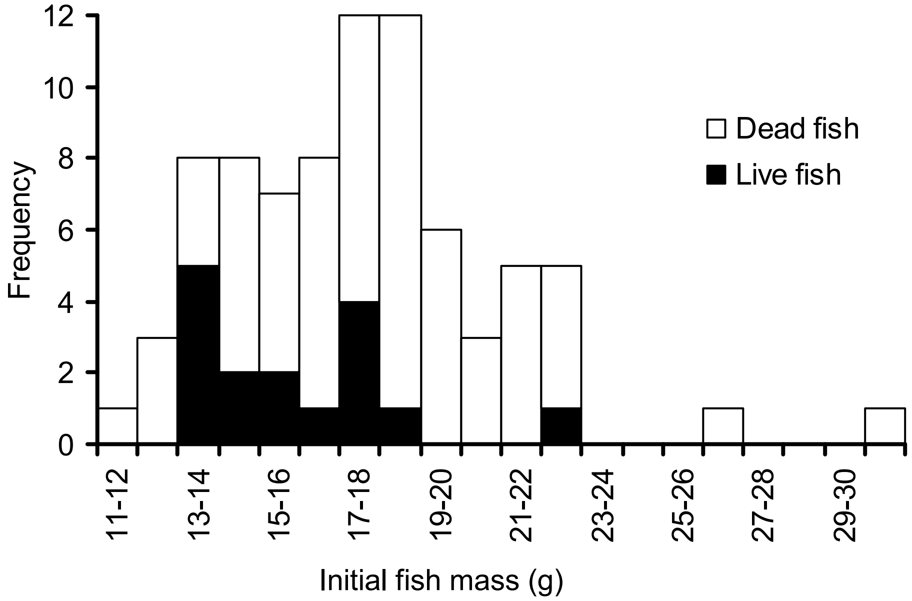


Figure 6.2 Mass frequency of initial size (g) at tagging for 23-mm PIT tagged dace, highlighting fish that died.

6.3.3 Growth rate

Although restrictions on space and tanks prevented treatment replication, patterns of growth were similar in all trials, i.e. growth rates of both control and marked fish were generally lowest in the first month following marking, possibly indicating a handling effect (Tables 6.2-6.5). Over the 6-month period of the experiment, significant differences were found in SGRs among treatments for both length (ANOVA: small chub: $F_{4,390} = 57.522$, $P < 0.001$; dace: $F_{4,347} = 40.591$, $P < 0.001$; roach: $F_{4,399} = 31.639$, $P < 0.001$ and large chub: $F_{2,298} = 41.801$, $P < 0.001$) and mass (ANOVA: small chub: $F_{4,390} = 53.116$, $P < 0.001$; dace: $F_{4,347} = 38.316$, $P < 0.001$; roach: $F_{4,399} = 20.282$, $P < 0.001$ and large chub: $F_{2,298} = 50.874$, $P < 0.001$). The main period of reduced growth in 23-mm PIT tagged fish compared with controls was between months

1-3 (Figure 6.3). Similar SGRs between control and treatments for months 3-6 suggest long term growth effects of 23-mm PIT tagged fish were small.

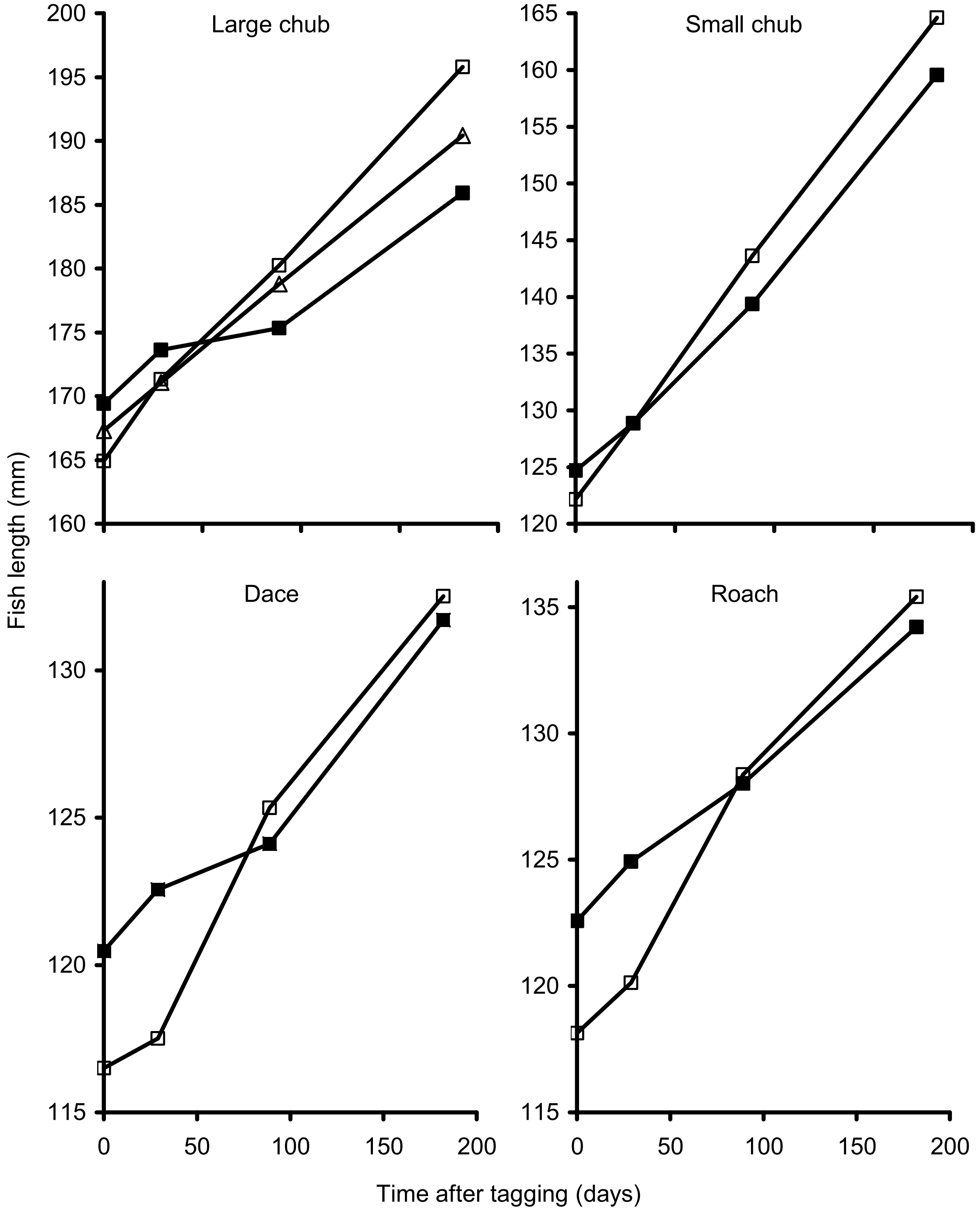


Figure 6.3 Mean length (mm) of chub, dace and roach at time (days) after tagging (control (□), 23-mm PIT with adhesive closure (■) and 23-mm PIT without closure (Δ)).

6.3.4 Mark site condition

VIE mark site condition was nearly always excellent (Table 6.3). Incision trauma scores for the tag site remained elevated for longer for 23-mm PIT mark sites than for 12-mm PIT tag sites, indicating that the larger incision was associated with greater inflammation and took longer to heal completely (Tables 6.2, 6.4 and 6.5). Adhesive closure in 23-mm PIT tagged large chub had no influence on rate of wound healing or chronic wound inflammation (Table 6.3).

6.4 DISCUSSION

Mark retention in chub, roach and dace varied markedly in relation to mark type, body location and fish species and size. Mark type and application in relation to the size and fish species also had a substantial effect on the survival and growth of these cyprinids. The 12-mm PIT tagging had several benefits over VIE for marking juvenile cyprinids, including high tag retention and functionality, negligible tagging mortality and no apparent long-term effects on growth. Growth retardation, mostly in the short term, was recorded for fish implanted with 23-mm PIT tags, and small dace suffered elevated mortality with the larger PIT tags.

6.4.1 Effects of mark type, location and size of fish on retention

VIE mark retention was higher in the head than fins over the short term (one month) but declined thereafter, unlike in the fins where retention was constant in the long term. Similar findings were reported by Dewey & Zigler (1996) and Brennan *et al*. (2005). By contrast, Bonneau *et al*. (1995) and Farooqi & Morgan (1996) found high levels of retention in both the head and fins of bull trout (*Salvelinus confluentus* (Suckley)) (4 months) and barbel (2 months), respectively. Increasing VIE mark loss with time after good initial retention was also found for other marking locations (Bailey *et al*., 1998; Close & Jones, 2002; Fitzgerald *et al*., 2004; Goldsmith *et al*., 2003; Hale & Gray, 1998). The long term retention rates in fins (>80 %) compare favourably with other studies: 97 % in brown trout (Summers *et al*., 2006), 96 % in rainbow trout (*Oncorhynchus mykiss* (Walbaum); Walsh & Winkelman, 2004), and 70 % in adult black bream (*Acanthopagrus butcheri* (Munro)) (Doupe *et al*., 2003). Although application of VIE into the fins of smaller cyprinids was more difficult than application under the dermal tissue overlying the cranium because of the thinness of the tissue, long-term retention was much better in the former and shows the importance of adopting an adequate experimental trial period.

Variable VIE retention for different implantation sites has been attributed to inexperience of the people marking the fish, damage to the marking site during injection, handling related losses, loss or fragmentation during fish growth and swimming activity, the elastomer not solidifying and/or the implantation wound not healing quickly (Farooqi & Morgan, 1996; Frederick, 1997; Hale & Gray, 1998; Willis & Babcock, 1998; Bailey *et al.*, 1998; Astorga *et al.*, 2005; Thompson *et al.*, 2005). Elastomer loss from the head may have increased with time because it was forced out as the fish grew (Goldsmith *et al.*, 2003). The differing VIE retention in fin and head tissues in this study may relate to the degree of porosity in the target tissue causing migration of elastomer (Brennan *et al.*, 2005). In this study, VIE retention was similar for both large and small chub, although others suggest elastomer loss occurs in small fish because the target site was too fragile or the smaller target site requires more precise application (Bailey *et al.*, 1998; Hale & Gray, 1998; Olsen & Vollestad, 2001; Close, 2000). To reduce the impact of initial losses on field experiments, an 18-day laboratory wound healing / elastomer hardening period has been recommended (Thompson *et al.*, 2005; Brennan *et al.*, 2005). Additionally, less than 100 % retention is acceptable if the detection rate over time is known, therefore, a sub-sample of fish could be monitored in a laboratory environment during a field study (Close, 2000) since Brennan *et al.* (2005) reported no differences in VIE retention between field and laboratory trials.

Tags surgically implanted into the peritoneal cavity can be expelled through the body wall (Lucas, 1989; Moore *et al.*, 1990), via transintestinal expulsion (Summerfelt & Mosier, 1984; Chisholm & Hubert, 1985; Marty & Summerfelt, 1986; Baras & Westerloppe, 1999) or during spawning in females (Prentice *et al.*, 1990a). In this study, 100 % retention rates of 12-mm tags were observed, similar to those reported for Atlantic salmon parr (Juanes *et al.*, 2000; Gries & Letcher, 2002; Riley *et al.*, 2003) and bullhead (*Cottus gobio* L.) (Bruyndoncx *et al.*, 2002). Retention of 23-mm PIT tags was also high (> 96.6 %) in this study, and was not significantly affected by size, species or wound closure. These results are comparable with Zydlewski *et al.* (2001) for surgically implanted 23-mm PIT tags in salmon parr > 9 cm (99 %). Roussel *et al.* (2000) reported high retention of 23-mm PITs in Atlantic salmon parr > 8.4 cm, but sutures increased tag retention in fish of 6.4-8.4 cm. Gries & Letcher (2002) stated the need to make the incision small enough so the tag cannot easily work its way out. Buzby & Deegan (1999) found instantaneous tag losses were often linked to poor tag placement, and suggested PIT tags may be retained for the life of the fish if they are not rejected soon after implantation.

6.4.2 Effects of marking on survival

Survival of all marked cyprinids in the present study was high, and similar to the unmarked control fish, except for the 23-mm PIT-tagged dace. This is consistent with previous studies observing negligible mortality when using VIE marks on fish (Farooqi & Morgan, 1996; Dewey & Zigler, 1996; Olsen & Vollestad, 2001; Bruyndoncx *et al.*, 2002; Astorga *et al.*, 2005). Similarly. high survival rates were found up to nine months after tagging following surgical implantation of 12-mm and 23-mm PIT tags into the peritoneal cavity of salmonids (Zydlewski *et al.*, 2001; Gries & Letcher, 2002; Riley *et al.*, 2003), Nile tilapia (*Oreochromis niloticus* (L.)) (Baras *et al.*, 1999), juvenile perch (Baras *et al.*, 2000) and bullhead (Bruyndoncx *et al.*, 2002).

The high dace mortality rate observed in this study appears to be related to the fish mass at tagging, with smaller fish more prone to death. However, the condition of dace at the start of the experiment was poor, with fin erosion and scale loss on a number of individuals. Higher mortalities were also found in smaller sized Atlantic salmon parr surgically implanted with 23-mm PITs (Roussel *et al.*, 2000).

With the exception of the dace, mortality rates of marked fish are unlikely to have an impact on experimental studies relying on recaptures by lowering the probability of recapture and potentially over-estimating population size when using mark-recapture calculations (Woods & Martin-Smith, 2004). The initial small mortality observed was probably the result of stress from either handling and/or anaesthesia (Ombredane *et al.*, 1998; Brennan *et al.*, 2005; Willis & Babcock, 1998; Gries & Letcher, 2002; Dussault & Rodriguez, 1997), whilst any later mortality was more likely to have resulted from other factors, such as the holding facilities, fish density (Malone *et al.*, 1999) and length of study (Gries & Letcher, 2002).

6.4.3 Effects of marking on fish growth

Growth is a more sensitive indicator of chronic physiological stress or trauma caused by marking than is survival (Malone *et al.*, 1999). Growth is an important consideration when selecting the type of mark to use, particularly in animals that are to be released into the wild to serve as indicators of various biological parameters in the natural population (Woods & James, 2003), i.e. reduced fitness of the study animal may reduce the validity of the data collected (Cote *et al.*, 1999). However, detection of marginal growth depression in marked fish is often difficult because of high levels of variation between individuals and/or experimental units (Woods & Martin-Smith, 2004).

No significant effect of VIE marking or implanting 12-mm PITs on growth was found during this study. Similarly, no growth depression was found in other studies using elastomer marked fish (Bailey *et al.*, 1998; Olsen & Vollestad, 2001; Dewey & Zigler, 1996; Thompson *et al.*, 2005; Astorga *et al.*, 2005) or 12-mm PITs (Peterson *et al.*, 1994; Ombredane *et al.*, 1998; Juanes *et al.*, 2000; Das Mahapatra *et al.*, 2001). It was hypothesised that the greatest effects of marking on growth would be for 23-mm PIT tagged small cyprinids, because of the larger incision relative to body size (Baras *et al.*, 2000) as well as the larger tag relative to fish size. It is generally accepted that the internal transmitter weight should not exceed 2 % of the fish body mass (Winter, 1996; Swanberg & Geist, 1997; Walsh *et al.*, 2000), although there is increasing recognition that smaller fishes can often cope with a higher loading without ill effect (Claireaux & Lefrançois, 1998; Martinelli *et al.*, 1998; Brown *et al.*, 1999; Cote *et al.*, 1999; Jepsen *et al.*, 2001, 2002). In this study, tag weight exceeded 2 % body mass for all of the small 23-mm PIT tagged fish (Table 6.1), with the highest tag to body mass ratios in dace. Although restrictions on space and tanks prevented treatment replication for groups of the same-sized fish, small, but significant, reductions in growth rate were recorded for all groups of cyprinids tagged with 23-mm PIT tags (3 tanks) over the 6-month period.

Typically the growth response of 23-mm PIT tagged cyprinids was suppression of growth over the first three months after tagging, followed by similar growth to controls in the period 3-6 months after tagging. This change in response may have occurred because physiological stress response to surgery reduces with time (Jepsen *et al.*, 2001), and growth reduces the tag/body mass ratio (Adams *et al.*, 1998) and buoyancy effects

(Perry *et al*., 2001). Additionally, larger fish can accommodate the tag better, reducing pressure in the stomach allowing unimpeded food consumption (Lacroix *et al*., 2004). In the large chub treatments, fish without tissue adhesive closure of the incision grew significantly faster than those with tissue adhesive closure. While growth of chub to which tissue adhesive had been applied was lower over the 6 months, it was markedly higher in the first month after tagging and longer term effects would not be expected to be directly attributable to the adhesive. Skov *et al*. (2005) noted no effect of 23-mm PIT tags, applied without tissue adhesive on roach and rudd survival and growth and there may be little or no benefit to its application for this purpose.

6.5 CONCLUSIONS AND FIELD STUDY RECOMMENDATIONS

In summary, PIT tags are effective, reliable and the most suitable method for marking individual juvenile chub, dace and roach at modest cost, potentially providing high spatial and temporal resolution of data. VIE implantation in fins could provide a cheap, batch marking alternative, as long as retention rates are monitored. The size distribution of fish marked in this experiment covered the range of sizes typically stocked into river fisheries, so that the results are applicable to marking studies on stocked fish. Small cyprinids (> 9 cm fork length) can be tagged with 12-mm PIT tags, and slightly larger fish (> 12 cm fork length) tagged with 23-mm tags, with minimal concerns over retention, mortality or long-term growth. However, hatchery fish are not exposed to the same stresses encountered in a natural environment (predation, density, and feeding), thus survival and growth may be artificially elevated in a controlled setting (Gries & Letcher, 2002). This perspective is perhaps most relevant for dace which, out of the three species studied, is most sensitive to capture and handling, with higher incidence of scale loss and fin damage. Although the use of 12-mm PIT tags would be preferred for mark-recapture purposes, given their negligible recorded effects on fish health, the range advantages of 23-mm PIT tags for telemetry applications (Lucas & Baras, 2000; Zydlewski *et al*., 2001) probably outweigh the minor effects on growth identified.

7 DISPERSAL OF STOCKED CYPRINIDS IN A SMALL ENGLISH RIVER: COMPARISON TO WILD FISH USING A MULTI-METHOD APPROACH

7.1 INTRODUCTION

Movement of animals, a process which is rarely random (Kramer *et al.*, 1997), affects individual fitness by changing growth and survival, but also influences their distribution and abundance, with genetic and evolutionary consequences. Thus, with respect to fish in stream and river environments, a sound understanding of their movements and factors affecting them is crucial for managing and conserving populations, especially in relation to habitat fragmentation (Lucas & Baras, 2001). Historically, field studies have documented the pattern of distribution and extent of movement of stream fishes using mark-recapture; concluding populations are composed of both sedentary and highly mobile individuals (Gerking, 1953; Gowan *et al.*, 1994; Rodriguez, 2002). However, although mark-recapture studies offer value in providing measures of movement and survival, they are biased by the location and timing of the recapture efforts, potentially leading to erroneous conclusions (Lucas & Baras, 2000). Recently, greater attention has been paid to the mechanisms triggering movement in stream fishes, but the influence of environmental variation (flow and temperature) is poorly understood, especially during non-breeding periods (but see Albanese *et al.*, 2004).

Stocking with hatchery-reared fish is one of the primary actions taken in response to poor fishery performance, to compensate for loss of stock due to fish kills or environmental degradation, or as part of a rehabilitation programme (Cowx, 1994). Post-stocking evaluations have mainly involved salmonids, and indicated limited benefits (Huntingford, 2004). For example, studies suggest stocked fish may disperse rapidly from their initial stocking location (Arctic grayling, *Thymallus arcticus* (Pallas); Thorfve, 2002), particularly during high flow events (rainbow trout; Bettinger & Bettoli, 2002). The persistence of cyprinids stocked into rivers has also been suggested to be low (Aprahamian *et al.*, 2004), but the behaviour of stocked cyprinids has been little investigated. Behavioural deficits and naivety to predation have been identified in hatchery-reared salmonids (Huntingford, 2004), but knowledge and understanding of spatial behaviour and the influence of environmental variables is lacking, especially for stocked non-salmonid river fishes. Of particular interest is the response of stocked fish to elevated flows, since these fish may have lower capability to resist high flows than resident, wild fish (MacDonald *et al*., 1998; Cowx *et al*., 1986). Rearing fish for stocking incurs substantial costs (Barnard *et al*., 2002) and significant ecological and/or fisheries benefits may not be achieved if the survival and persistence of stocked fishes is low. Ultimately, *in situ* comparisons of movement, site fidelity and survival between hatchery-reared fish and wild populations are crucial to improve the effectiveness of stock enhancement measures.

Although little is known regarding movements of stocked cyprinids, several radio telemetry studies have examined space use by wild chub (e.g. Fredrich *et al*., 2003), dace (e.g. Clough & Ladle, 1997; Clough & Beaumont, 1998) and roach (Baade & Fredrich, 1998), but these are limited by small samples of large fish. Hence, information is needed to improve the understanding of the spatial behaviour of wild juvenile cyprinids in lowland rivers during non-breeding periods. This study used radio-telemetry to compare the short-term movements and habitat selection of these stocked fish with those of wild juvenile chub, under both normal and elevated flows. In addition, passive integrated transponder (PIT) tags (Prentice *et al*., 1990a, b), provided unique identities and were suitable for tagging relatively large samples of small fish, thus were used for mark-recapture and fixed station telemetry (Zydlewski *et al*., 2001) to determine the space use and survival of wild and stocked cyprinids. It was hypothesised that stocked fish would move more than wild fish because the former were released into an unfamiliar environment about which they had no opportunity for spatial mapping of their surroundings, unlike wild fish. Specifically, the objectives were to 1) compare the movements of wild cyprinids between two consecutive winters, 2) compare the movements of wild and stocked chub and roach during the second winter, and 3) evaluate the timing and direction of fish movements and how they are influenced by temperature and flow (including flood scenarios). The results are discussed with consideration to the proximate mechanisms influencing individual movement, under the assumption that animals make movement decisions at least in part to increase their fitness (Kramer *et al*., 1997).

7.2 METHODS

7.2.1 Study site

The study was carried out on the River Roding, south-east England, between October and March in both 2005-6 and 2006-7. The River Roding rises at an altitude of 110 m above sea level (51°53’59”N 0°16’19”E), and flows south for approximately 80 km to join the tidal River Thames at Barking Creek (52°24’47”N 0°16’19”E). It drains a predominately clay agricultural catchment (340 km^2). The study site was a 10-km section of river, approximately 20 km from the source, mostly 5-8 m wide with alternating riffle / glide (20 - 40 cm depth) and pool (< 150 cm depth) topography, although there are some wider and deeper areas. Wheypules Mill (51°77’05”N 0°30’59”E) at the upstream end of the study section acts as a barrier to upstream fish movement. Fyfield Mill (51°44’13”N 0°16’26”E), approximately 6 km from the top of the study reach also act as a barrier to upstream fish movements, but downstream movements are possible, especially under elevated flow when a sluice gate is opened manually. There is no obstruction to downstream movement for at least 10 km, but a flat-v flow-gauging weir (51°42’47”N 0°15’29”E) was present 4 km downstream of the second mill, and represents the downstream limit of the study reach. Throughout the study reach were extensive areas of instream macrophytes and overhanging / submerged terrestrial vegetation.

The River Roding exhibits a typical flow regime of a small temperate lowland river, with low summer flows and highly variable winter flows. Flow rises rapidly in response to substantial rainfall in the catchment. Mean daily flow (m^3 s^{-1}) was measured at 15-min intervals at the gauging weir and water temperature was recorded at 15-min intervals using a logger (Tinytalk, Orion Instruments, Chichester). Mean daily flow in each of the two years (2005 = 0.129 m^3 s^{-1}, and 2006 = 0.613 m^3 s^{-1}) was used to calculate the magnitude of flow peaks observed during the study periods. During the 2006-7 study period, six periods of elevated flow (greater than 6.9 times normal flow) were observed, with the largest peak reaching ≈ 14.4 times normal flow (14 February 2007), but no such events occurred in 2005-6.

In June 2003, a polluting input to the River Roding 12 km upstream of the study site resulted in an oxygen sag that killed several thousand fish up to 20 km downstream. The pollution did not markedly affect invertebrate communities, which recovered within the same year of the pollution (Environment Agency, unpublished data). In December 2003, approximately 1000 hatchery-reared, unmarked chub (age 1+ and 2+), dace (1+) and roach (1+) were stocked to aid recovery of the river. Subsequent electric fishing surveys in summer and autumn 2005 found a wide range of species through the study reach, many of which were not stocked, including bullhead, stone loach, minnow, eel (*Anguilla Anguilla* (L.)), gudgeon, perch, rudd, tench, and pike, as well as chub, dace and roach. Thus, a substantial proportion of the fish community in the study reach survived or recolonised following the pollution event, potentially augmented by the stocked fish. Despite this, the fish stocks in the area remained below recent historical levels (EA, unpublished data) and therefore presumably below carrying capacity. It was therefore felt that additional stocking was appropriate to aid further recovery of the fishery and study the behaviour of stocked fish. It should be noted that 'wild' fish were either progeny of adults that spawned in the Roding or fish stocked in December 2003; it was not possible to distinguish wild fish from those that had been stocked into the river and naturalised.

7.2.2 Sampling and tagging procedure

Wild fish were obtained from the study reach in both 2005 and 2006 using pulsed DC (50 Hz) electric fishing equipment, by wading or from a boat (Electracatch control box, 1.5 V single anode with Honda 1 kVA generator, or Electracatch control box, 6 V twin anode with Honda 7.5 kVA generator) (Table 7.1). Representative sampling sites (approximately 200 m long) were selected comprising riffle, glide and pool habitats. Natural morphological limiters of fish escape (riffles or channel bottlenecks) were used to delimit each section. Once selected, site locations were consistent throughout future sampling occasions. Wild chub for radio tracking (n = 20 in 2005 and n = 12 in 2006) were obtained from the 1-km section of the study reach around the most downstream stocking location.

Chub, roach and dace were tagged with 12 or 23 mm PIT tags. Small (e.g. 12-mm) PIT tags can be used to tag fish as small as 6 cm (Lucas & Baras, 2000) and are ideal for mark-recapture, while larger (e.g. 23-mm) PIT tags have greater range and offer advantages for fixed-station telemetry of somewhat larger fish (Lucas & Baras, 2000; Zydlewski *et al.*, 2001). Previous studies of cyprinids (Skov *et al.*, 2005; Chapter 6)

Table 7.1 Summary of electric fishing surveys to tag wild fish, including the date sampled, number of sites fished, total length of river fished (m), mean site length (m ± SD) and the number of fish (all species) tagged.

Sampling date	Number of sites	Total length of river sampled (m)	Mean site length (m ± SD)	Number tagged (all species)
19/10 - 1/11/2005	29	5890	203.1 ± 78.7	546
2/12 - 8/12/2005	19	3160	166.3 ± 49.0	210
11/03 - 17/03/2006	33	6330	191.8 ± 74.8	206
28/10 - 2/11/2006	19	3650	192.1 ± 74.8	328

have shown high long-term survival for fish larger than 12 cm, tagged with 23-mm PIT tags. Radio transmitters were implanted in samples of chub larger than 15 cm to provide detailed short-term movement and habitat selection information. By implanting PIT tags, large numbers of individual fish movements (including direction) were monitored continuously using fixed location stations, while survival and distribution after each winter was assessed using mark-recapture.

Prior to tagging in the field, fish were anaesthetised using buffered tricaine methane-sulphonate (MS-222, 0.1 g L^{-1}). Body mass (g) and fork length (mm) were recorded (Tables 7.2-7.4). Fish were placed ventral side up in a clean V-shaped foam support with the gills submerged in fresh, oxygenated water. Tags were sterilised with alcohol and rinsed with distilled water prior to use. 12-mm tags, (UKID model 122GL, 12.0-mm long x 2.1-mm diameter, 0.1 g weight in air, 125 kHz, full-duplex, E. Collinson and Co Ltd, Preston, UK) were inserted into the body cavity through a 3-mm long ventro-lateral incision made with a scalpel, 2-3 mm anterior to the muscle bed of the pelvic fins. 23-mm tags, (half-duplex,Texas Instruments model RI-TRP-RRHP, 23.0-mm long x 3.4-mm diameter, 0.6 g weight in air, 134.2 kHz, RFID components Ltd, Bedford, UK) were inserted in a similar way, in to the body cavity through a 5-mm long ventro-lateral incision. Due to the small size of the incisions, they were not closed (Skov *et al.*, 2005). Additionally, a small Panjet (Wright Dental Group, Dundee, UK) was used to apply an Alcian blue mark anterior to the pelvic fins, to enable field estimation of tag loss. PIT tag weight / body mass ratios are given in Tables 7.2-7.4. Fish were held in a well-aerated observation tank until they regained balance and were actively swimming, before returning them to the river, at the approximate site of capture.

Table 7.2 Number (n), length (mean ± SD (range), mm), mass (mean ± SD (range), g) and ratio (%) of tag weight of wild and stocked chub.

Treatment / release date	*n*	Fish length (mean ± SD (range), mm)	Fish mass (mean ± SD (range), g)	Tag / body wt ratio (mean (range), %)
Wild 12-mm PIT				
Oct-05	13	216.2 ± 96.1 (112 - 373)	209.7 ± 245.3 (14 - 633)	0.05 (0.02 - 0.71)
Dec-05	20	250.3 ± 85.1 (132 - 470)	301.9 ± 361.2 (25 - 1500)	0.03 (0.01 - 0.40)
Mar-06	23	212.5 ± 56.7 (119 - 348)	163.9 ± 157.2 (18 - 686)	0.06 (0.01 - 0.56)
Oct-06	11	234.1 ± 119.1 (113 - 446)	236.1 ± 306.9 (16 - 894)	0.04 (0.01 - 0.63)
Wild 23-mm PIT				
Oct-05	81	256.7 ± 75.3 (135 - 472)	323.0 ± 320.9 (29 - 1474)	0.19 (0.04 - 2.07)
Dec-05	56	248.6 ± 36.4 (168 - 383)	215.1 ± 124.6 (54 - 872)	0.28 (0.07 - 1.11)
Mar-06	56	242.0 ± 67.0 (139 - 490)	241.5 ± 242.9 (39 - 1132)	0.28 (0.05 - 1.54)
Oct-06	36	253.5 ± 73.7 (132 - 435)	287.3 ± 273.2 (28 - 1274)	0.21 (0.05 - 2.14)
Wild radio tagged				
Oct-05	20	199.7 ± 31.3 (153 - 243)	106.5 ± 49.8 (44 - 198)	0.02 (0.01 – 0.04)
Oct-06	12	188.3 ± 24.1 (158 - 239)	96.9 ± 40.5 (48 - 172)	0.02 (0.01 – 0.04)
Stocked 23-mm PIT				
Nov-06 S1	175	143.9 ± 8.1 (109 - 171)	38.5 ± 6.9 (16 - 66)	1.56 (0.91 - 3.87)
Nov-06 S2	175	143.3 ± 8.1 (115 - 176)	38.3 ± 6.9 (17 - 68)	1.57 (0.88 - 3.47)
Nov-06 S3	200	147.6 ± 11.5 (128 - 183)	42.7 ± 11.4 (27 - 80)	1.41 (0.75 - 2.24)
Stocked radio tagged				
Nov-06 S3	12	168.0 ± 6.7 (158 - 178)	65.0 ± 7.2 (54 – 77)	0.03 (0.02 – 0.03)
Stocked Alcian blue control				
Nov-06	225	144.7 ± 8.9 (111 - 169)	38.7 ± 7.6 (16 - 61)	-

Table 7.3 Number (n), length (mean ± SD (range), mm), mass (mean ± SD (range), g) and ratio (%) of PIT tag weight of wild and stocked dace.

Treatment / release date	*n*	Fish length (mean ± SD (range), mm)	Fish mass (mean ± SD (range), g)	Tag / body wt ratio (mean (range), %)
Wild 12-mm PIT				
Oct-05	28	124.3 ± 16.3 (100 - 177)	22.5 ± 15.8 (10 - 92)	0.44 (0.11 – 1.00)
Dec-05	10	142.5 ± 24.8 (110 - 178)	38.0 ± 19.1 (15 - 63)	0.26 (0.16 - 0.67)
Mar-06	19	142.2 ± 28.2 (110 - 192)	40.4 ± 29.2 (12 - 100)	0.25 (0.10 - 0.83)
Oct-06	10	178.5 ± 33.7 (122 - 224)	84.4 ± 48.1 (20 - 171)	0.12 (0.06 - 0.50)
Wild 23-mm PIT				
Oct-05	118	256.7 ± 75.3 (135 - 472)	323.0 ± 320.9 (29 - 1474)	0.19 (0.04 - 2.07)
Dec-05	23	248.6 ± 36.4 (168 - 383)	215.1 ± 124.6 (54 - 872)	0.28 (0.07 - 1.11)
Mar-06	42	242.0 ± 67.0 (139 - 490)	241.5 ± 242.9 (39 - 1132)	0.28 (0.05 - 1.54)
Oct-06	72	253.5 ± 73.7 (132 - 435)	287.3 ± 273.2 (28 - 1274)	0.21 (0.05 - 2.14)

Table 7.4 Number (n), length (mean ± SD (range), mm), mass (mean ± SD (range), g) and ratio (%) of PIT tag weight of wild and stocked roach.

Treatment / release date	*n*	Fish length (mean ± SD (range), mm)	Fish mass (mean ± SD (range), g)	Tag / body wt ratio (mean (range), %)
Wild 12-mm PIT				
Oct-05	91	119.4 ± 27.2 (87 - 233)	25.8 ± 28.7 (11 - 216)	0.39 (0.05 - 0.91)
Dec-05	52	136.9 ± 20.9 (93 - 180)	40.8 ± 19.3 (13 - 93)	0.25 (0.11 - 0.77)
Mar-06	18	134.4 ± 21.6 (107 - 198)	41.2 ± 26.1 (16 - 135)	0.24 (0.07 - 0.63)
Oct-06	69	128.2 ± 22.9 (103 - 220)	36.8 ± 29.9 (12 - 214)	0.27 (0.05 - 0.83)
Wild 23-mm PIT				
Oct-05	215	167.9 ± 36.9 (113 - 307)	88.2 ± 80.4 (20 - 547)	0.68 (0.11 – 3.00)
Dec-05	49	156.3 ± 25.4 (117 - 245)	66.0 ± 46.9 (22 - 272)	0.91 (0.22 – 2.73)
Mar-06	48	151.2 ± 23.7 (113 - 209)	60.2 ± 35.4 (21 - 166)	1.00 (0.36 – 2.86)
Oct-06	130	167.3 ± 29.1 (117 - 239)	82.0 ± 47.3 (22 - 234)	0.73 (0.26 - 2.73)
Stocked 23-mm PIT				
Nov-06 S1	174	126.2 ± 6.7 (106 - 153)	34.1 ± 6.1 (20 - 76)	1.76 (0.79 - 3.00)
Nov-06 S2	174	126.8 ± 6.8 (112 - 152)	35.0 ± 6.1 (21 - 60)	1.71 (1.00 – 2.86)
Nov-06 S3	175	126.2 ± 7.3 (108 - 165)	33.4 ± 6.5 (19 - 71)	1.80 (0.85 – 3.16)
Stocked Alcian blue control				
Nov-06	225	125.4 ± 6.9 (88 - 157)	32.8 ± 6.2 (10 - 70)	-

To insert radio transmitters (type PIP, 19 x 9 x 6 mm, ~ 12 cm long, 0.1 mm diameter whip antenna, potted in medical grade silicone, 1.2 g weight in air, expected life of 45 days; Biotrack, Wareham, U.K.) chub were placed ventral side up in a surgical trough and the gills irrigated with a diluted dose of anaesthetic, until the final minute of the procedure when only fresh water was supplied. Prior to surgery, fork length (mm) and body mass (g) were recorded, and the unique frequency (between 173.200 and 173.970 MHz, with a nominal spacing of 10 kHz) of each tag was verified using a hand-operated receiver. An 8-10-mm-long, ventro-lateral incision was made anterior to the muscle bed of the pelvic fins and the whip antenna was run via the incision in the body cavity to the exterior, posterior to the pelvic fins using a shielded needle. The transmitter was then inserted into the body cavity. A 23-mm, half-duplex PIT tag was also inserted into the fish, providing verification of fish location by remote monitoring stations and, in some cases, evidence of radio-tag failure. The incision was closed with 2-3 separate absorbable sutures. The procedure lasted approximately 6 min.

All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986 Home Office licence number PPL 60/3260.

Stocked fish were the progeny of broodstock taken from the River Bain, eastern England (chub) and a lake in north eastern England (roach), and reared in the hatchery and pond facilities of the Environment Agency's Calverton Fish Farm, Nottingham UK. Fish were exposed to flow in all rearing environments. The age (1+) and size distributions (Tables 7.2 and 7.4) of fish tagged in this experiment were representative of sizes usually stocked into UK rivers, so that the results would be applicable to future fish stocking programmes. Stocked fish were tagged with 23-mm PIT tags at the fish farm 2 weeks prior to release (due to the large number needing to be tagged), using the same procedure described above but were allowed to recover in indoor tanks (2.02 m^3) supplied with filtered groundwater (60 L^{-1} min^{-1} $tank^{-1}$). In addition, 225 fish of each species, were not implanted with a PIT tag but were Alcian blue dye-marked posterior to the pelvic fins, to act as a tagging control (Tables 7.2 and 7.4). Until the day prior to release, fish were fed at approximately 3 % body mass per day using automatic feeders, supplemented by natural frozen gamma-radiated feed. Fish were transported in large aerated containers and released into the river on 3 November 2006. Stocking locations (S1 to S3) were 1450 m, 4150 m and 7160 m, from the upstream limit of the study section. A total of 550, 1+ hatchery-reared chub and 525, 1+ hatchery-reared roach, PIT tagged (23-mm) and marked with Alcian blue dye, were stocked in equal numbers at the three locations along the study river (Tables 7.2 and 7.4). In addition, 25 radio tagged chub were stocked at the downstream site only. A further 75 fish of each species, marked only with Alcian blue dye were also stocked at each location.

7.2.3 Monitoring

Radio tagged chub were located daily (between 07.00 and 16.00) from the bank using a hand-operated receiver (Sika model, Biotrack, Wareham, UK) and a three-element Yagi antenna, over a 4-week period (20 October - 21 November 2005 and 28 October - 1 December 2006). During both study periods, two separate, intensive, 24-hour surveys found both wild and stocked fish to be inactive at night, thus daytime locations were considered representative of overall movement patterns. Tagged fish could be recorded at a distance of up to 200 m with the antenna held at head height. The location of individual fish was determined from the bank (avoiding disturbing the fish) to within 1 m by triangulation, or more usually by reducing the gain on the receiver to localise the fish from either bank. When fish were located, their position was recorded with reference to riverside features and the type of habitat occupied was noted. Fish locations were subsequently plotted in ArcGIS (ESRI ArcMAP version 9.1) and the distance fish moved (to the nearest metre) between successive tracking trips was calculated along the river midline. Habitat use was categorised into open water and within complex habitat (instream macrophytes and overhanging / submerged terrestrial vegetation). During the 26-27 November 2006 flood event, specific habitat (e.g. reed bed) could not be determined because the river was too deep and turbid, but location within the stream was recorded (e.g. deep pool, slack water or backwater).

At the end of the study period in both years, if fish had not moved for several days they were disturbed to ensure they were alive (upstream movement had to be observed) or had not shed their tags or been eaten, especially because pike are abundant in the Roding. Jepsen *et al*. (1998) found radio tags from salmon smolts on the river bed 3-6 days after being eaten by pike, thus a similar response was assumed to be applicable I this study. Large fish-eating birds were not observed along the study reach in more than 150 hours of observation. Ten radio-tagged wild fish were recaptured using electric fishing in December 2005, but elevated flow during most of the winter in 2006 prevented post tracking sampling.

Mark-recapture sampling (single run, pulsed DC electric fishing (Bateman *et al*., 2005)) was performed on 11-17 March 2006 (Table 7.1) and 19-28 March 2007. All fish were measured (fork length), hand-scanned for PIT tags and examined for Alcian marks. During March 2006, random stratified sampling was performed, ensuring at least 600 m within every 1 km of the study river (10 km) were sampled, thus minimising sampling bias (Gowan *et al*., 1994). During March 2007, the whole study reach (except a few short, inaccessible sections) was sampled (50 sites, mean length (m ± SD) = 187.7 ± 63.5), plus 0.5 km upstream of the upstream limit and 1.4 km downstream of the study reach. Further to this, three sites were enclosed using stop nets and fished three times to test sampling efficiency, derived from absolute abundance estimates determined from the Maximum Likelihood Methods (Carle & Strub, 1978) (Table 7.5).

The PIT antenna stations were cross-channel swim-through loop antennae, half duplex systems with 23-mm tags (Texas Instruments RFID, 134 kHz; see Zydlewski *et al*., 2001 for further information). Two loops, ca. 2 m apart, were used at a single site, enabling direction of movement to be recorded. Five dual-loop stations (A1-A5) were installed during the first study period, and an extra station (A6) was added before the

Table 7.5 Total population (n ± SE) and probability of capture (P ± SE) for chub, dace and roach as determined by the Maximum Likelihood Methods (Carle & Strub 1978) for the three sites sampled quantitatively.

Site	Total population (n ± SE)			Probability of capture (P ± SE)		
	Chub	Dace	Roach	Chub	Dace	Roach
24	-	29 ± 1	7 ± 0	-	0.76 ± 0.14	0.78 ± 0.24
42	5 ± 0	-	24 ± 3	0.83 ± 0.25	-	0.61 ± 0.22
47	-	-	62 ± 3	-	-	0.71 ± 0.12

second study year. PIT stations (A1 to A6) were located 1050 m, 3450 m, 4550 m, 6700 m, 8050 m and 9150 m, from the upstream limit of the study section; site selection was influenced by the river width (< 8.0 m), depth (< 0.7 m) and bankside access to change batteries. Each PIT detector interrogated the two loops synchronously at a rate of 3 times per second with a maximum horizontal range (perpendicular to river cross-section) of 0.6 m. PIT detectors were powered by two 110 Ah deep cycle lead-acid batteries connected in parallel, giving at least 14 days life. Preliminary studies (M. Lucas unpublished) showed that this frequency of interrogation, while relatively slow (thus conserving power), detected more than 99.5% of tagged cyprinids passing a single loop, as their swimming and water velocities were normally well under 1 m s^{-1}. Tag detection data (identity, date, time) for each antenna were stored on a flash memory card housed in the logger unit (Flinka Fiskar, Sweden) and were downloaded onto a portable laptop computer at every battery change. Throughout the study, the effectiveness of each antenna was periodically tested using a tag mounted on the tip of a wooden pole. Efficiency of detection for actual fish was determined from direction of movement from a known location (tagging location or previous loop record) or recaptured fish that passed a loop without producing a record. During the first year of study, average field detection efficiency was 99.0 % (Table 7.6). During the second year, loops were unable to sample the full depth of the water column during several elevated flow events and were not operational 100 % of the time (to avoid flooding), but 92.8 % of fish movements were recorded (Table 7.7).

7.2.4 Output processing and data analysis

Radio tracking

Analysis of spatial behaviour of radio-tracked chub was based on two descriptors of the pattern and extent of movements: range per day tracked and daily distance. Range per day tracked was calculated by dividing the linear range (the difference between the

Table 7.6 PIT antenna operational details, downstream, upstream and milling fish movements recorded and missed, and the proportion of movements missed during 2005-06 sampling.

	A1	A2	A3	A4	A5
Date installed	14/11/05	06/11/05	05/11/05	05/11/05	05/11/05
Date removed	09/06/06	09/06/06	09/06/06	09/06/06	09/06/06
Days installed	206.8	215.0	215.3	215.7	215.7
% of time operational	100.0	100.0	100.0	100.0	100.0
Downstream					
Recorded	227	148	118	111	37
Not detected (%)	0 (0.0)	2 (1.3)	1 (0.8)	1 (0.9)	1 (2.6)
Upstream					
Recorded	247	151	138	131	69
Not detected (%)	2 (0.8)	4 (2.6)	1 (0.7)	2 (1.5)	1 (1.4)
Milling fish	150	6	23	118	33
Total fish records	624	305	279	360	139
Missed fish (%)	2 (0.3)	6 (1.9)	2 (0.7)	3 (0.8)	2 (1.4)

maximum distance upstream and downstream recorded throughout the tracked period) by the number of days the fish was tracked. This describes the extent of river used, standardised for the period of tracking. Daily distance for each fish was calculated by dividing the total distance moved (calculated from the position recorded every day) by the period over which the fish was tracked, and reflects the overall level of movement. Differences in mean range per day tracked and mean daily distance between years for wild fish and between wild and stocked fish in 2006 were compared using the Mann Whitney *U*-test. Spearman rank correlation was used to investigate the influence of temperature and flow on the movements of wild and stocked chub. Habitat use was calculated for each fish as the percentage of tracking events located in either open water or in complex habitat. A chi-squared test was used to test the null hypothesis that habitat use did not differ significantly between wild and stocked fish in 2006. In addition, mean daily distance and habitat use comparisons between wild and stocked fish were made before and after the initial elevated flow period (18-19 November) in 2006 sampling. During 2006, three tags in wild fish failed in the period 15-22 November and five tags in stocked fish failed in the period 13-18 November, thus these fish were only included in analysis of movements prior to the first elevated flow period.

Table 7.7 PIT antenna operational details, downstream, upstream and milling fish movements recorded and missed, and the proportion of movements missed during 2006-07 sampling.

	A1	A2	A3	A4	A5	A6
Date installed	03/10/06	04/10/06	03/10/06	03/10/06	03/10/06	26/10/06
Date removed	08/05/07	08/05/07	06/05/07	08/05/07	05/05/07	08/05/07
Days installed	216.6	215.9	214.3	216.6	213.9	193.7
Days operational (%)	214.6	211.6	198.0	195.4	208.9	169.0
% of time operational	99.1	98.0	92.4	90.2	97.6	87.3
Downstream						
Recorded	659	559	351	771	378	380
Not detected (%)	54 (7.6)	35 (5.9)	71 (16.8)	123 (13.8)	76 (16.7)	27 (6.6)
Upstream						
Recorded	851	710	308	943	301	301
Not detected (%)	52 (5.8)	36 (4.8)	36 (10.5)	57 (5.7)	34 (10.1)	33 (9.9)
Milling fish	446	279	252	627	249	436
Total fish records	1956	1539	906	2334	928	1097
Missed fish (%)	106 (5.1)	71 (4.4)	107 (10.6)	180 (7.2)	111 (10.6)	60 (5.2)

Mark recapture

A chi-squared test was used to test the null hypothesis that proportion of PIT tagged wild fish recaptured did not differ significantly between tagging occasion, followed by Mann-Whitney *U*-test, as a *post hoc* test. Mann-Whitney *U*-tests were also used to test the hypothesis that the proportion recaptured did not differ significantly between species, fish origin (wild / stocked) and stocking location. A *t*-test was performed on initial fish mass of recaptured and non-recaptured fish, for all species and tag sizes, to test the null hypothesis that there was no influence of size on mortality.

Sampling sites were plotted in ArcGIS (ESRI ArcMAP version 9.1) and the mark-recapture movement distance (to the nearest metre) was calculated from the midpoint of the capture / release site to the midpoint the recapture site. For each individual recaptured, positive values were assigned to upstream movers and negative values to downstream movers. Movement distance distributions for each species were plotted using 200 m classes. Daily distance moved for each fish was calculated by dividing the total distance moved by the time since last capture. A Mann Whitney U-test was used to compare differences in mean daily distance between years for wild fish and between fish species and origin within each year. A chi-squared test was used to test the null hypothesis that there was no directional bias in fish movements.

Fixed station PIT telemetry

The proportion of active individuals for each species throughout the study period was expressed as a proportion of the tagged fish recorded on a PIT antenna. Daily distance moved for each remotely PIT detected fish was calculated based on PIT antenna locations, and a Mann Whitney U-test was used to compare movement distances between sampling techniques, sampling years, species and origin. All statistical analyses described above were carried out using SPSS (version 14.0) with a significance level $\alpha = 0.05$.

Generalised Linear Models (GLM) with logratio link function and a negative binomial error function were constructed to examine the influence of environmental factors on fish activity (Genstat, version 10.0, VSN International Ltd, U.K.). Activity (percentage of known alive fish recorded on antennae per day) was used as the response, and flow, temperature and flow and temperature as predictors into the model. Full factorial models were initially constructed then least significant factors removed.

7.3 RESULTS

Between October 2005 and May 2007, a total of 2814 wild and hatchery reared fish were tagged (Table 7.1), released and monitored using radio telemetry, mark recapture and fixed location PIT telemetry equipment. Large variations in the numbers recaptured and movements were identified between species, fish origin and monitoring technique.

7.3.1 Radio tracking

Thirty two wild juvenile chub (n = 20 in year 2005 and n = 12 in 2006) and 12 stocked chub (2006) were tracked for up to 30 days each year, equating to 1181 daily fish records. During 2005, one tag malfunctioned after 13 days, but in 2006, despite the same tag design being used, 10 tags applied to stocked chub failed prior to release. A further three tags in stocked fish and three in wild fish failed within a week of release, thus limiting any further analysis of these fish. All fish recaptured in December 2005 were in good condition and wounds had begun to heal (not completely healed in some cases because of low temperatures and slight variations in the day tagged), suggesting any variability in movements and behaviour were not the result of the tagging. Elevated flow during most of the winter in 2006 prevented post-tracking capture of chub but there was no reason to suspect any fish died, i.e. all fish with operational tags were still mobile at the end of the study. Additionally, towards the end of the study period, all but two stocked fish suspected of tag malfunction were recorded moving upstream through remote PIT antenna (A4) 460 m upstream of the stocking location. The antenna was 400 m downstream of Fyfield Mill. The 400-m section between the antenna and the mill was searched extensively but no signal could be detected, thus validating suspicions of tag malfunction whilst removing concerns of poor signal searching technique by the tracker and / or unrecorded long-range movements from the study reach. In addition, no mortality of wild and stocked cyprinids was observed during the first month after release.

During both study years, the mean ranges per day tracked (2005 = 6.5 m day^{-1}, 2006 = 7.3 m day^{-1}: Mann Whitney U-test: $Z = -1.479$, $n = 32$, $P = 0.146$) and mean daily distances (2005 = 12.1 m day^{-1}, 2006 = 14.7 m day^{-1}: Mann Whitney U-test: $Z = -0.272$, $n = 32$, $P = 0.803$) of radio tagged wild chub were similar (Figure 7.1). During 2006, radio tagged stocked chub exhibited significantly larger mean range per day tracked (43.2 m day^{-1}: Mann Whitney U-test: $Z = -3.550$, $n = 19$, $P < 0.001$) and mean daily movement (96.7 m day^{-1}: Mann Whitney U-test: $Z = -3.467$, $n = 19$, $P < 0.001$) than wild fish (Figure 7.1). When examined in more detail, daily movements of radio tagged stocked chub were similar to radio tagged wild chub at low flows, i.e. for the first 15 days after release (Mann Whitney U-test: $Z = -1.914$, $n = 24$, $P = 0.060$), but were significantly larger than radio tagged wild chub during periods of elevated flow (Mann Whitney U-test: $Z = -3.228$, $n = 16$, $P < 0.001$). For example, during the first elevated flow event of 19 November 2006, five of the seven radio tagged stocked chub moved at least 725 m upstream. During the second elevated flow period of 26-27 November 2006, two radio tagged stocked chub moved long distances downstream (at least 1990 m) but returned to the area of stocking two days later. At the end of the radio tracking period (1 month) all radio tagged stocked chub were upstream of the stocking location.

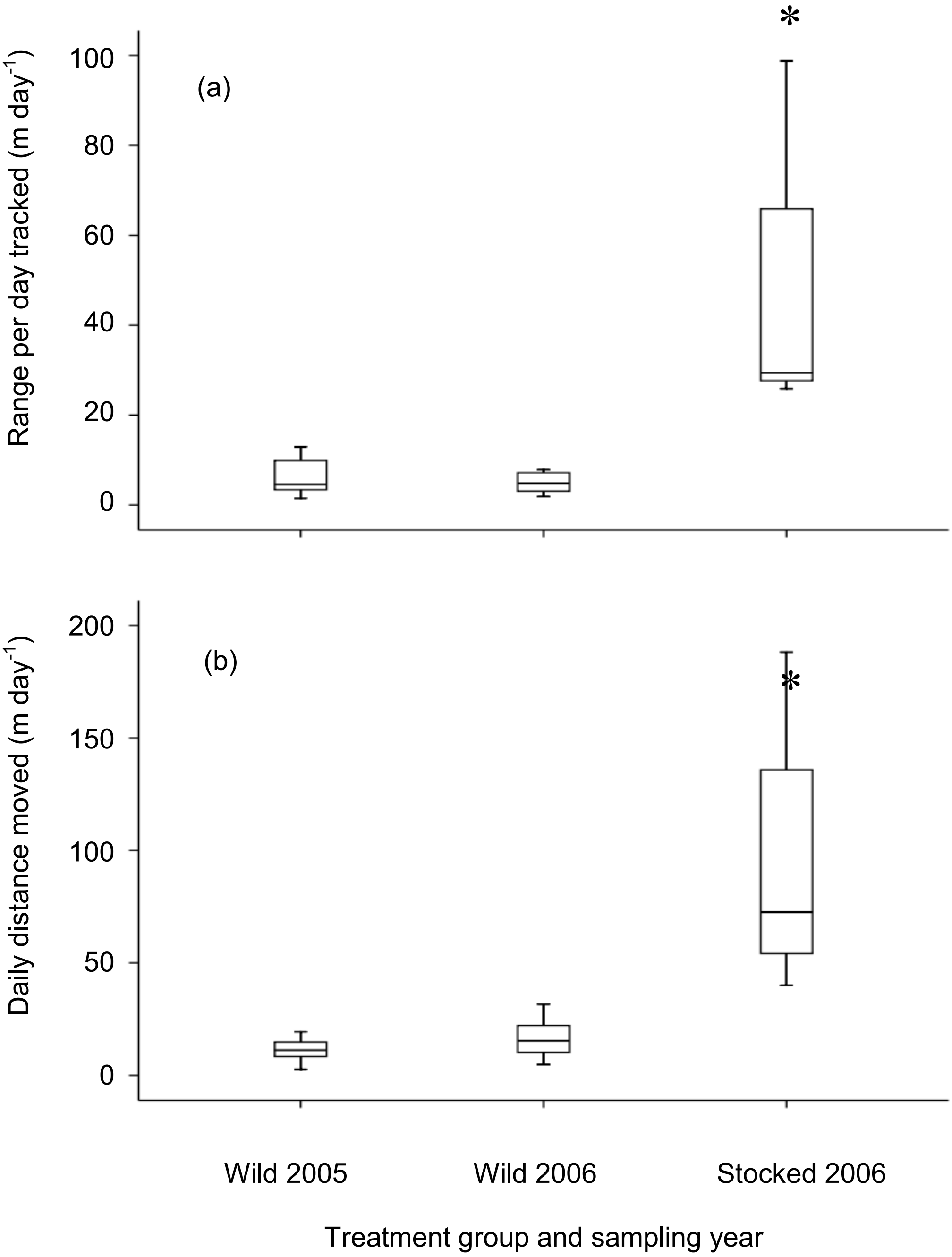


Figure 7.1 (a) Range per day tracked and (b) distance moved per day tracked of chub in the different treatment groups (wild 2005, wild 2006 and stocked 2006). Box plots represent the 10th, 25th, 50th, 75th and 90th percentiles (* denotes $P < 0.001$ stocked fish movements significantly larger than wild fish).

During 2005, radio tagged wild chub spent 30.9 % of the time swimming in open water. Comparison of habitat use during the 2006 tracking found radio tagged stocked chub spent significantly more time in open water than wild chub (68.2 % versus 27.1 %; χ^2 with continuity correction = 249.712, d.f. = 1, $P < 0.001$), although differences were less significant under elevated flow later in the tracking period (37.1 % versus 17.7 %; χ^2 with continuity correction = 5.112, d.f. = 1, P = 0.024). During the 26-27 November 2006 flood, both stocked and wild radio tagged chub occupied deep and wide pools with reduced flow (40 % versus 11 %) and areas of slack water (created by trees, terrestrial vegetation or macrophytes; 60 % and 70 %), but only wild chub were located in an off-channel backwater (19 %).

7.3.2 Mark recapture

During the March 2007 sampling 137 wild chub, 116 dace and 140 wild roach were recaptured. Wild fish were tagged on four occasions during the study (Table 7.1), but this had no influence on the subsequent recapture of chub (χ^2: 12-mm PIT = 1.540, d.f. = 3, P = 0.673; 23-mm PIT = 4.641, d.f. = 3, P = 0.200) and roach (χ^2: 12-mm PIT = 1.484, d.f. = 3, P = 0.686; 23-mm PIT = 0.834, d.f. = 3, P = 0.841) (Table 7.8). Significantly less dace tagged with 12-mm PIT in October 2005 were recaptured (Mann Whitney U-test: March 2006: Z = -2.468, n = 47, P = 0.014; October 2006: Z = -2.581, n = 38, P = 0.010), and significantly more dace tagged with 23-mm PIT in October 2006 were recaptured (Mann Whitney U-test: October 2005: Z = -2.007, n = 190, P = 0.045; December 2005: Z = -2.636, n = 95, P = 0.008) (Table 7.8).

The proportion of wild chub (12-mm PIT = 40.3 %, 23-mm PIT = 48.0 %) recaptured in March 2007 was significantly more than wild roach (12-mm PIT = 18.3 %, 23-mm PIT = 22.2 %) (Mann Whitney U-test: 12-mm PIT: Z = -3.846, n = 297, P <0.001; 23-mm PIT: Z = -6.863, n = 671, P <0.001) and dace with 23-mm PIT (38.0 %) (Mann Whitney U-test: Z = -2.305, n = 484, P = 0.021), but dace were captured significantly more than 23-mm PIT roach (Mann Whitney U-test: Z = -4.388, n = 697, P <0.001). Fish mass at tagging had no influence on subsequent recapture of chub (12-mm PIT: t = 0.126, P = 0.900; 23-mm PIT: t = -0.619, P = 0.536), dace (12-mm PIT: t = -1.706, P = 0.093; 23-mm PIT: t = -1.523, P = 0.129) or roach (12-mm PIT: t = -1.612, P = 0.113; 23-mm PIT: t = -0.395, P = 0.693).

Proportionally, fewer stocked chub (28.0 %) were recaptured in comparison to wild chub (55.6 %) (Mann Whitney U-test: Z = -3.561, n = 586, P <0.001), but the opposite was observed for roach (stocked 50.5 %, wild 22.3 %) (Mann Whitney U-test: Z = -5.606, n = 652, P <0.001) (Table 7.8). Fish mass at tagging had no influence over

Table 7.8 Number of chub, dace and roach tagged (n) during each sampling occasion and the proportion recaptured (% (n)) in March 2007.

Treatment / Release date	Chub Tagged (n)	Recap. % (n)	Dace Tagged (n)	Recap. % (n)	Roach Tagged (n)	Recap. % (n)
Wild 12-mm PIT						
Oct-05	13	38.5 (5)	28	10.7 (3)	91	18.7 (17)
Dec-05	20	30.0 (6)	10	30.0 (3)	52	15.4 (8)
Mar-06	23	47.8 (11)	19	42.1 (8)	18	11.1 (2)
Oct-06	11	45.5 (5)	10	50.0 (5)	69	21.7 (15)
Wild 23-mm PIT						
Oct-05	81	40.7 (33)	118	34.7 (41)	215	21.4 (46)
Dec-05	56	57.1 (32)	23	17.4 (4)	49	20.4 (10)
Mar-06	56	44.6 (25)	42	40.5 (17)	48	27.1 (13)
Oct-06	36	55.6 (20)	72	48.6 (35)	130	22.3 (29)
Stocked 23-mm PIT						
Nov-06 S1	175	33.7 (59)	-	-	174	57.5 (100)
Nov-06 S2	175	35.4 (62)	-	-	174	58.6 (102)
Nov-06 S3	200	16.0 (32)	-	-	175	36.0 (63)
Stocked Alcian blue control						
Nov-06	225	32.0 (72)	-	-	224	53.6 (120)

subsequent recapture of stocked chub (Mann Whitney U-test: $Z = -0.436$, $n = 550$, $P = 0.663$) or roach ($t = -1.864$, $P = 0.063$). A similar proportion of Alcian control stocked fish and 23-mm PIT tagged stocked fish were caught (Mann Whitney U-test: chub: $Z = -1.216$, $n = 775$, $P = 0.224$; roach: $Z = -0.990$, $n = 746$, $P = 0.322$), i.e. PIT tagging had no influence on stocked fish recapture rate. In addition, all recaptured fish (including wild) were in good condition and tagging sites had healed, suggesting variability in movements and behaviour were not the result of tagging. The number of recaptured fish was significantly fewer for stocking at site S3 (chub 16.0 %, roach 36.0 %), the most downstream stocking location, compared with S1 (chub 33.7 %, roach 57.5 %) (Mann Whitney U-test: chub : $Z = -4.115$, $n = 375$, $P <0.001$; roach: $Z = -4.406$, $n = 348$, $P <0.001$) and S2 (chub 35.4 %, roach 58.6 %) (Mann Whitney U-test: chub: $Z = -4.452$, $n = 375$, $P = <0.001$; roach: $Z = -4.406$, $n = 348$, $P <0.001$) (Table 7.8), possibly a result of sampling difficulties in the deeper and wider section of river downstream of Fyfield Mill.

Wild fish were exposed to marked differences in temperature and flow between sampling years, but the mark-recapture mean daily distances (total distance moved divided by the time since last capture) moved by chub were similar (2005-6 = 1.0 m day^{-1}, 2006-7 = 4.3 m day^{-1}; Mann Whitney *U*-test: $Z = -1.096$, $n = 65$, $P = 0.273$) (Figure 7.2). Dace (2005-6 = 2.2 m day^{-1}, 2006-7 = 6.8 m day^{-1}; Mann Whitney *U*-test: $Z = -3.379$, $n = 89$, $P = 0.001$) and roach (2005-6 = 2.1 m day^{-1}, 2006-7 = 3.1 m day^{-1}; Mann Whitney *U*-test: $Z = -2.028$, $n = 79$, $P = 0.043$) moved significantly more in 2006-7, but the movements were mainly upstream (χ^2: dace = 13.520, d.f. = 1, $P < 0.001$; roach = 4.568, d.f. = 1, $P = 0.033$) (Figure 7.3), but no PIT tagged fish were caught upstream of the upper reach limit. In 2005-6, movements were similar between species ($\chi^2 = 1.139$, d.f. = 2, $P = 0.566$), but in 2006-7 dace moved significantly more than chub (Mann Whitney *U*-test: $Z = -3.389$, $n = 112$, $P = 0.001$) and roach (Mann Whitney *U*-test: $Z = -2.659$, $n = 115$, $P = 0.008$) (Figure 7.2).

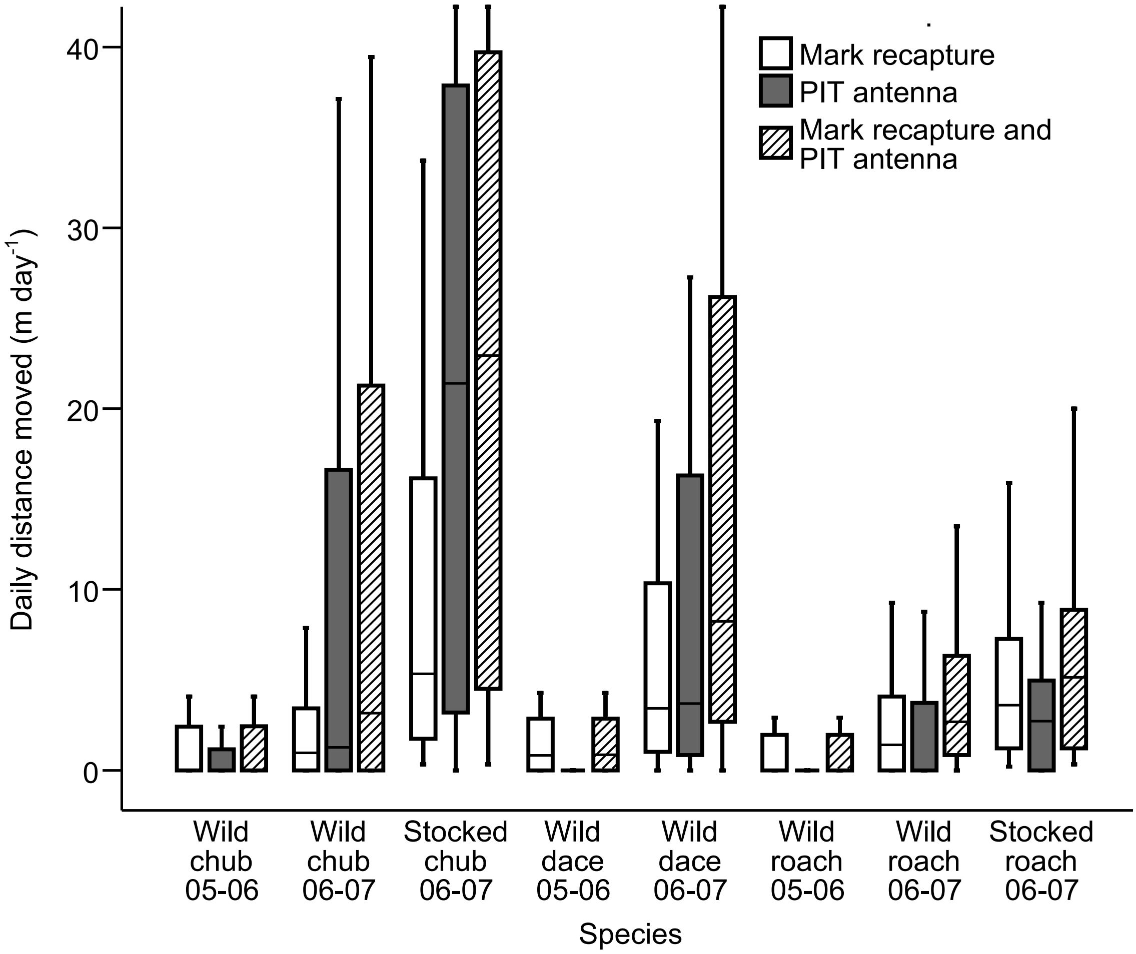


Figure 7.2 Daily distance moved found from mark-recapture, PIT antenna records and a combination of both techniques, for wild chub, dace and roach (05-06 and 06-07) and stocked chub and roach (06-07). Box plots represent the 10th, 25th, 50th, 75th and 90th percentiles. See text for the explanation.

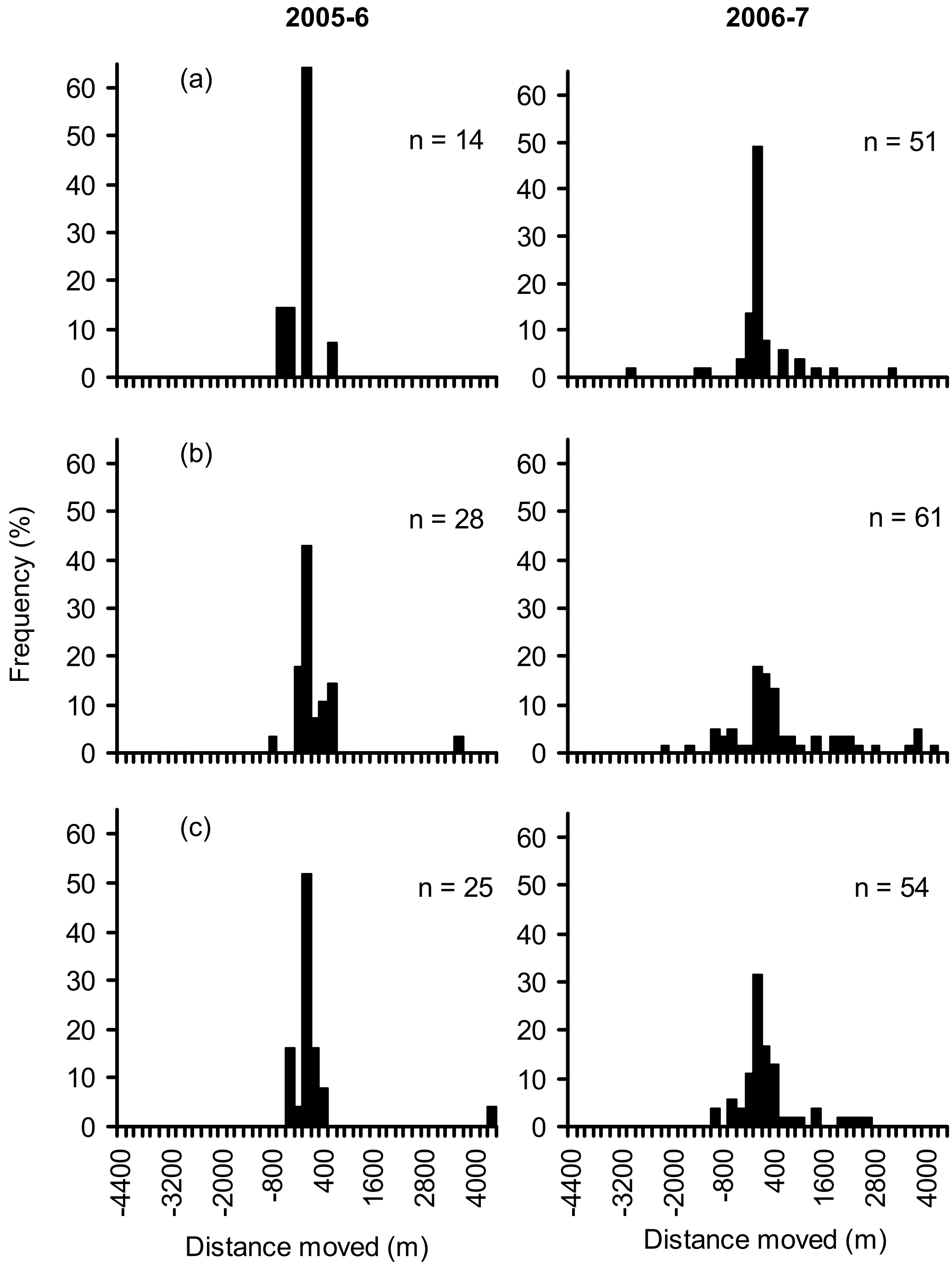


Figure 7.3 Range of dispersal (mark-recapture) (m) of PIT tagged wild (a) chub, (b) dace and (c) roach between October 2005 - March 2006 and October 2006 - March 2007.

During 2006-7, mean daily distance moved calculated using mark-recapture was significantly larger for stocked fish than wild fish (Mann Whitney *U*-test: chub (9.2 m day^{-1}): $Z = -5.667$, $n = 203$, $P < 0.001$; roach (5.3 m day^{-1}): $Z = -3.751$, $n = 314$, $P < 0.001$) (Figure 7.2). No differences were found in distance moved for wild fish of both species, but stocked chub moved significantly further than stocked roach (Mann

Whitney *U*-test: $Z = -3.423$, $n = 412$, $P = 0.001$). At the end of the study period, proportionally more stocked chub (χ^2: S2 = 20.903, d.f. = 1, $P < 0.001$) and roach (χ^2: S1 = 43.560, d.f. = 1, $P < 0.001$; S2 = 49.991, d.f. = 1, $P < 0.001$) were upstream of the stocking location (Figure 7.4), despite experiencing flows reaching up to 14.4 times normal flow (14 February 2007). However, significantly more chub stocked at S3 were recaptured downstream ($\chi^2 = 23.516$, d.f. = 1, $P < 0.001$).

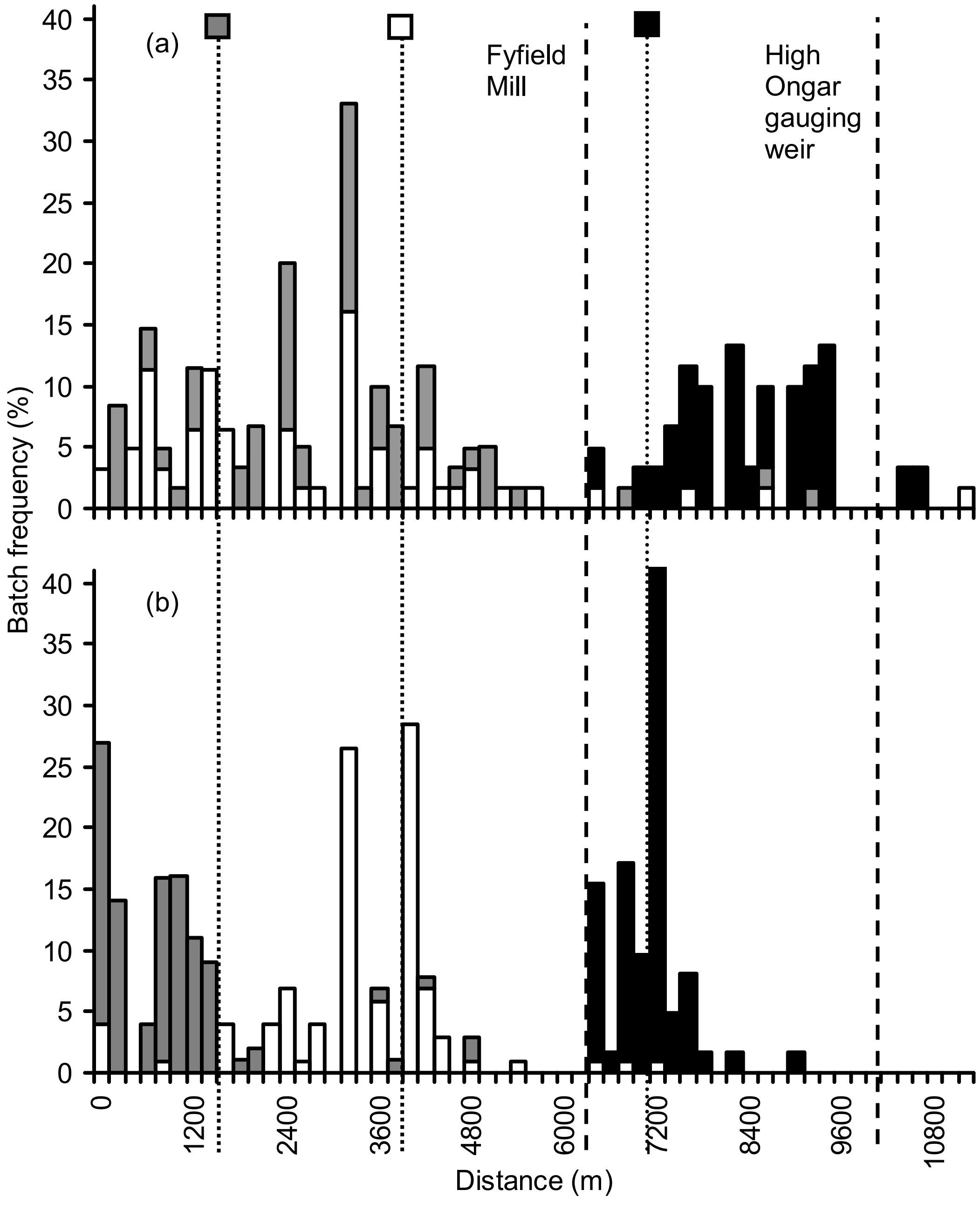


Figure 7.4 Stocking locations (fine dashed line: S1, ■; S2, □; and S3, ■) and recapture distribution (batch frequency (%)) of (a) chub and (b) roach. Thick dashed lines represent the location of Fyfield Mill and High Ongar gauging weir.

7.3.3 Fix station PIT telemetry

The trends found from the mark-recapture were only partially supported by fixed station PIT antenna records. For example, in 2005-6 distances moved using mark-recaptue were similar between species (see above), but the proportion of each species recorded on antennae differed (chub = 21.2 %, dace = 5.0 % and roach = 1.9 %). In addition, daily distance moved by wild chub and their locations after each winter were similar between years using mark-recapture, but proportionally more fish were found to move through PIT antennae during 2006-7 (Chub = 21.2 % and 48.8 %), suggesting more wild chub moved during 2006-7 but subsequently returned to the area local to tagging. Similarly, proportionally more dace (5.0 % and 57.3 %) and roach (1.9 % and 29.0 %) moved during 2006-07. However, the proportions of wild fish moving through PIT loops were small (chub 48.8 %, roach 29.0 %) compared with stocked chub (91.6 %) and roach (58.1 %).

Large differences in distances moved by fish were also found between mark-recapture and PIT antenna records for individual species within years (Figure 7.2). During 2005-6, fish moved relatively short distances and hence rarely moved through PIT antennae and average daily movements (chub = 0.9 m day^{-1}, dace = 0.7 m day^{-1}, roach = 0.4 m day^{-1}) based on mark-recapture were significantly higher (Mann Whitney *U*-test: chub: $Z = -0.848$, $n = 129$, $P = 0.396$; dace: $Z = -4.372$, $n = 89$, $P < 0.001$; roach: $Z = -4.940$, $n = 117$, $P < 0.001$). However, the maximum distance moved by an individual PIT tagged chub, dace and roach were 3080 m, 3380 m and 4450 m based on PIT antenna records. During 2006-7, wild fish moved greater distances and passed more antennae, thus the daily distances moved based on PIT antenna records (chub = 10.9 m day^{-1}, dace = 10.8 m day^{-1}, roach = 2.9 m day^{-1}), were significantly greater than the previous winter for all wild fish (Mann Whitney *U*-test: chub: $Z = -4.086$, $n = 135$, $P < 0.001$; dace: $Z = -7.810$, $n = 119$, $P < 0.001$; roach: $Z = -5.776$, $n = 124$, $P < 0.001$). Maximum distance moved by individual wild chub (11 350 m) and dace (9630 m) were considerable but the largest distance moved by an individual wild roach was 2050 m based on PIT antenna records. Thus, during 2006-7 PIT antennae recorded more wild fish on loops and greater daily distance moved than found during 2005-6, but the distributions of wild fish were similar between years (Figure 7.3), i.e. PIT antennae often recorded widespread back and forth movements during periods between marking and recapture, but fish were often recaptured not far from the last capture. Consequently, for those fish that were recaptured, calculation of distance moved between the release and the recapture locations, combined with PIT antenna records provides a better estimate of movement during the study, for both relatively sedentary (roach) and mobile (chub and dace) species (Figure 7.2).

Daily distances moved by PIT tagged stocked chub (21.3 m day^{-1}) recorded on PIT antennae were significantly larger than those found using mark-recapture (Mann Whitney U-test: $Z = -4.180$, $n = 304$, $P < 0.001$), and were significantly larger than daily movements of PIT tagged wild chub recorded on PIT antennae (Mann Whitney U-test: $Z = -3.748$, $n = 195$, $P < 0.001$). Movements of individual PIT tagged stocked chub were also far larger than for wild chub, but tended to remain in the study area. One individual moved a maximum gross distance of 25 535 m (measured at the resolution of PIT detector separation). Unlike stocked chub, PIT tagged stocked roach (3.0 m day^{-1}) moved relatively little, thus distances calculated from PIT antenna records were significantly smaller than those from mark-recapture (Mann Whitney U-test: $Z = -6.920$, $n = 520$, $P = < 0.001$), but were similar to movements of wild roach calculated from PIT antenna records (Mann Whitney U-test: $Z = -0.976$, $n = 293$, $P = 0.329$).

Large variations in the number of PIT tagged fish detected on antennae per day were found for all species of wild fish, in both years (Figure 7.5). During 2005-6, movements of wild chub were significantly influenced by river flow (GLM: deviance = 8.28, d.f. = 111, residual deviance = 28.86, P (χ^2) = 0.004), whereas dace and roach activity was influenced by river temperature (GLM: dace: deviance = 14.26, d.f. = 111, residual deviance = 20.56, P (χ^2) < 0.001; roach: deviance = 4.14, d.f. = 111, residual deviance = 20.62, P (χ^2) = 0.042). Wild fish activity in 2006-7 was driven by a combination of flow and temperature for all species of wild fish (GLM: chub: deviance = 5.38, d.f. = 145, residual deviance = 34.89, P (χ^2) = 0.020; GLM: dace: deviance = 4.56, d.f. = 145, residual deviance = 37.67, P (χ^2) = 0.033; roach: deviance = 5.54, d.f. = 145, residual deviance = 37.70, P (χ^2) = 0.019).

Despite large variations in flow, the daily directions of fish movements were never significantly different for chub ($P > 0.05$), i.e. on each day the numbers of fish moving in an upstream direction were similar to the numbers moving downstream. Only on day 48 (0.8 m^3/s) were numbers of fish moving downstream significantly greater for dace

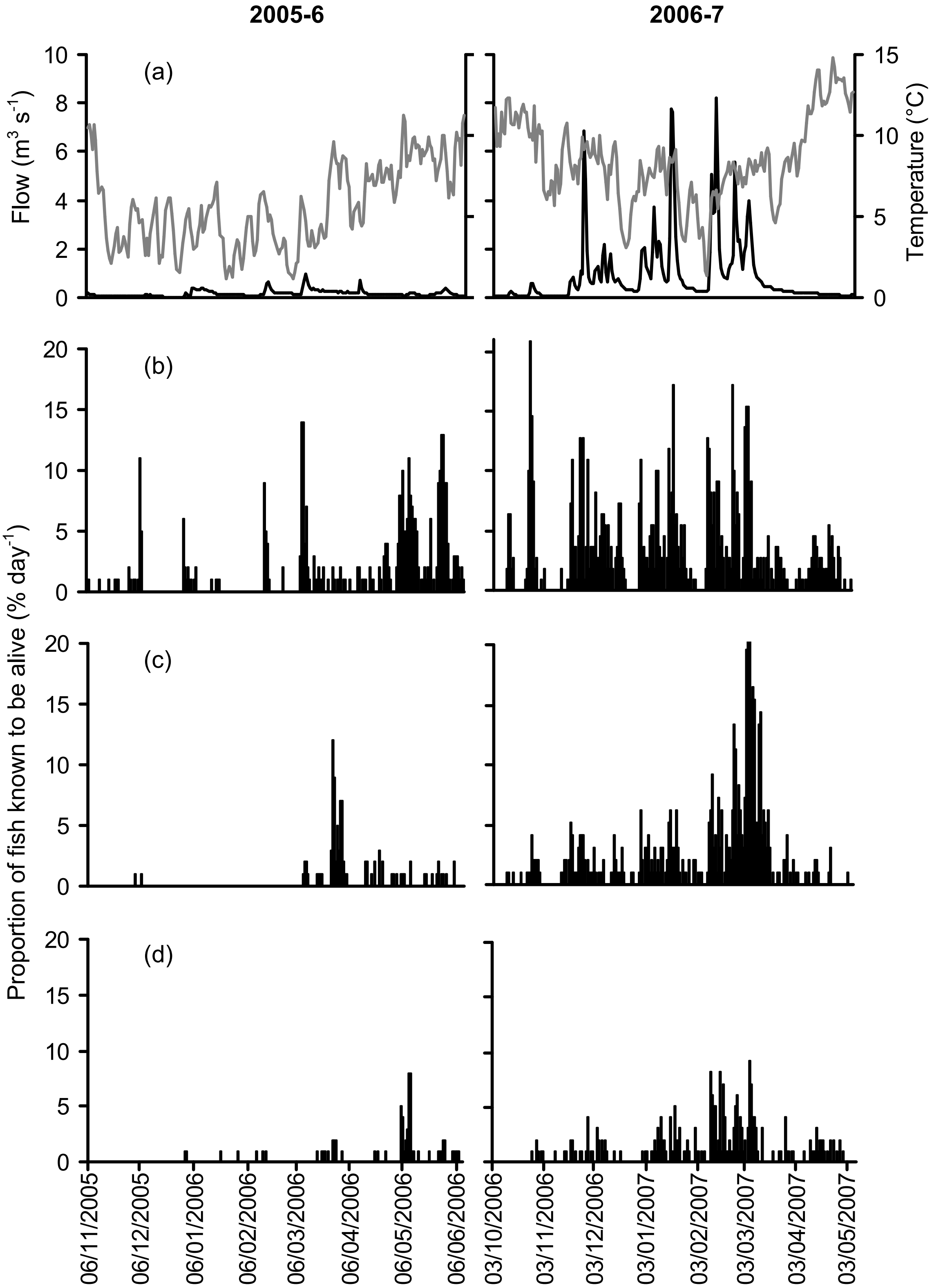


Figure 7.5 (a) Flow (m^3 s^{-1}, black line) and temperature (°C, grey line), in comparison to the daily detections (proportion of fish known to be alive (% day^{-1})) of (b) wild chub, (c) wild dace, and (d) wild roach during 2005-6 and 2006-7 sampling periods.

(χ^2 = 4.455, d.f. = 1, *P* = 0.035), and days 63 (1.3 m^3/s: χ^2 = 6.400, d.f. = 1, *P* = 0.011) and 137 (2.0 m^3/s: χ^2 = 4.571, d.f. = 1, *P* = 0.033) for roach, but not under the influence of elevated flow, i.e. fish were not washed downstream while PIT antenna were operational. On day 161 (12/03/2006) significantly more PIT tagged dace moved upstream through antennae (χ^2 = 6.545, d.f. = 1, *P* = 0.011).

Stocked chub and roach daily activity was not significantly influenced by any combination of factors (GLM: *P* > 0.05), although variations in activity were observed through the sampling period (Figure 7.6). A large proportion of stocked chub, but not wild chub or stocked roach, were recorded on PIT antennae during the first two days after release. During the first two periods of elevated flow (18-19 November and 26-27 November 2006; up to 14.2 times normal flow), stocked chub and roach moved extensively (Figure 7.6). Although daily directions of stocked fish movements were not significantly different during this period (*P* > 0.05), large numbers of stocked chub (56) moved downstream through A6, but 40 % subsequently returned to the area upstream of A6. Proportionally more stocked fish moved during the first 6 weeks after release (chub = 64.0 % and roach = 53.5 % of all movements detected), thus recorded movements of stocked fish were far less during subsequent elevated flows periods. The movements of stocked PIT tagged chub after the first thirty days after release were significantly influenced by river flow (GLM: deviance = 4.06, d.f. = 118, residual deviance = 22.47, *P* (χ^2) = 0.044), but no combination of factors significantly influenced stocked PIT tagged roach with up to the first six weeks after release removed for analysis (GLM: *P* > 0.05).

7.4 DISCUSSION

The combination of sampling techniques employed in this study enabled identification of the spatial distributions, temporal patterns of movements and habitat use of wild and stocked cyprinids. Wild fish distribution (mark-recapture) after each winter was similar between years, but radio telemetry and fixed location PIT telemetry revealed significantly more wild fish moving in the second winter, correlated with environmental influences (temperature and flow). During the second year of study, PIT tagged stocked fish moved extensively during the period soon after release (radio telemetry and PIT antennae) and the final distributions (mark-recapture) were more dispersed than observed for wild fish. To maximise the success of river improvement schemes and

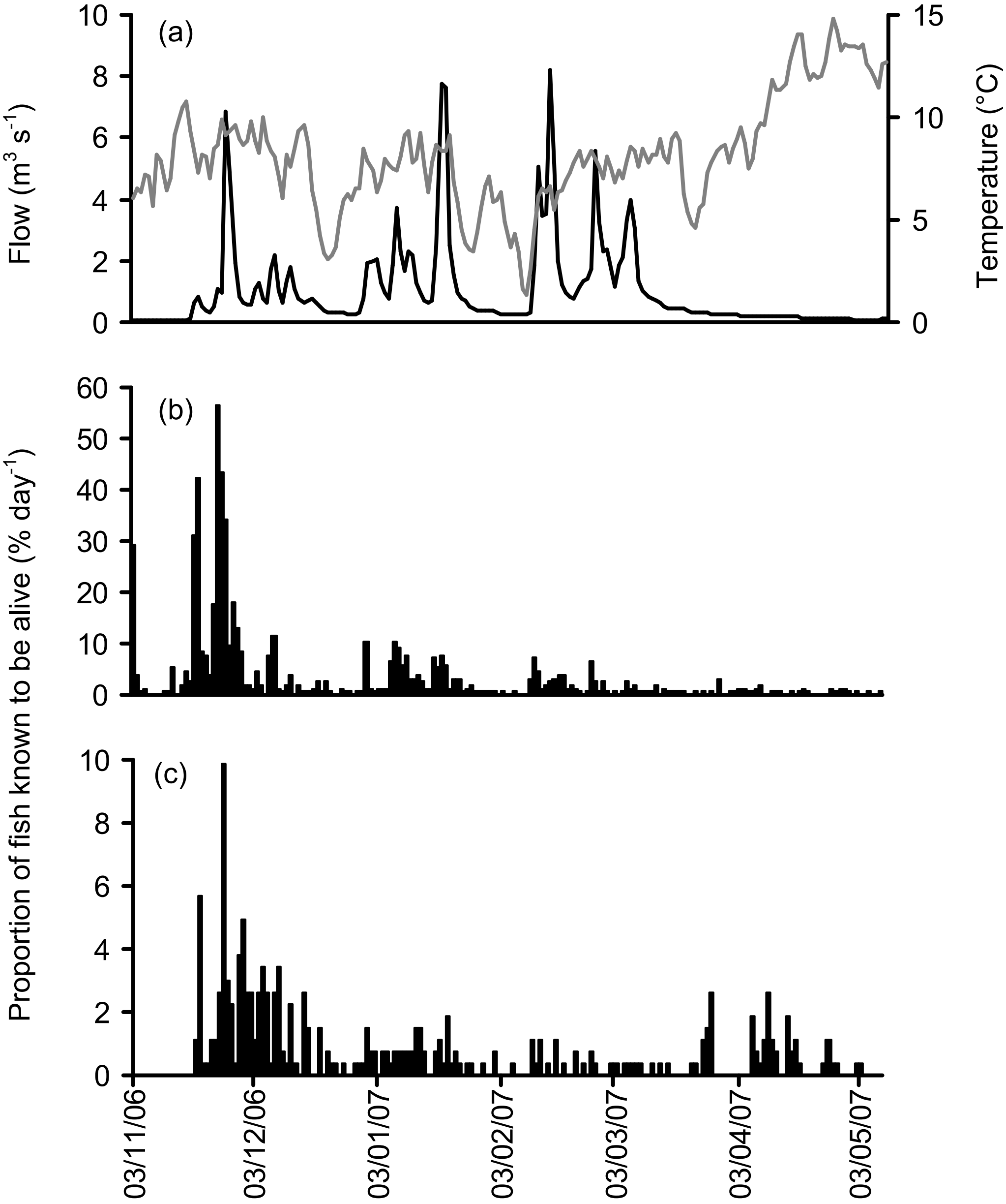


Figure 7.6 (a) Flow (m^3/s, black line) and temperature (°C, grey line), in comparison to the daily detections (proportion of fish known to be alive (% day^{-1})) of (b) stocked chub, and (c) stocked roach, during 2006-7 sampling period.

future stocking activities, these variations are considered in relation to existing knowledge of wild and stocked fish movement.

7.4.1 Wild fish movements

At the end of both winters, recaptured marked wild cyprinids had high levels of 'site fidelity' (Spencer *et al.*, 1990) and only a few fish moved large distances (leptokurtically distributed), These findings support previous mark-recapture studies documenting restricted movements of stream fish during non-migratory periods, but the population contains a small proportion of ‘mobile’ fish that perform long range movements (e.g. Stott, 1967; Gowan *et al.*, 1994; Hilderbrand & Kershner, 2000; Skalski & Gilliam, 2000; Nakamura *et al.*, 2002; Rodriguez, 2002). Other studies have similarly described strong site fidelity of chub (Allouche *et al.*, 1999; Penczak, 2006), dace (Clough & Beaumont, 1998) and roach (Stott, 1967; Williams, 1965; Baade & Fredrich, 1998). Even Linfield (1985), who stated that cyprinids lack a home range in large lowland rivers, concluded they did overwinter in specific habitats. Consequently, the high site fidelity displayed by the species studied in the River Roding may be to an overwintering home range.

Radio tracking and PIT telemetry permitted analysis of movement over finer temporal scales than was possible with mark–recapture studies and provided an insight into the behavioural mechanisms associated with movements. Wild fish activity and movements were influenced by temperature and flow, an observation regularly reported for migratory movements of temperate river fishes (Lucas & Baras, 2001). During the first year of study, cold winter temperatures and low flows persisted throughout the winter. As a result, movements were restricted because cold temperatures reduced metabolism, feeding and swimming ability, whilst increasing the need to conserve energy. Furthermore, wild fish tended to occupy areas of habitat complexity, possibly to avoid predation from pike, which were abundant in the Roding study reach (fish-eating birds were quite rare). Predation threat during low flows may cause fish to shelter and reduce movement, thus reducing the probability of encounter (Allouche & Gaudin, 2001; Fraser *et al.*, 2006), i.e. the benefits of moving (improved feeding or shelter) are weighed against the cost of movement. Although, it should be noted that Gilliam & Fraser (2001) found that movement rates increased with exposure to predation threat. Additionally, sections of river may be less hospitable or more resistant to movement, i.e. longer riffles (Lonzarich *et al.*, 2000; Schaefer, 2001) or shallower depth (Aparicio & Sostoa, 1999). However, fish in the Roding were capable of moving past such potential barriers. Crook (2004) considered fish occasionally moved long distances because of predator interactions, reduced habitat quality through winter or for exploratory purposes.

During the second study year, greater ranges of flow and temperature occurred. Radio tagged stocked chub movements were small in both years, even during elevated flow

(26-27 November 2006) as fish occupied areas of complex habitat, slack waters, wider and deeper pools with reduced flow, and off channel areas. Other studies reported similar habitat use during elevated flows (Pearsons *et al*., 1992; Allouche *et al*., 1999). Limited movements of radio tagged fish are probably a reflection of small sample size, because interpretation of data from PIT antenna found that proportionally more wild fish moved and individual wild fish moved significantly greater distances during the second study year, i.e. individual cyprinid behaviour appears to be temporally variable and characterized by 'switching' (Harcup *et al*., 1984). Numerous studies support the theory that fish are capable of switching between sedentary and long-range movement behaviours (Smithson & Johnston, 1999; Hilderbrand & Kershner, 2000; Knaepkens *et al*., 2004; Crook, 2004). Fish moved during elevated flows (both up and down stream), perhaps because increased depth and turbidity reduced the potential exposure to predation, i.e. dispersal success may be higher if the animal chooses to disperse under safer conditions (Zollner & Lima, 2005). We do not know the definitive reasons for such movements, but fish may have been performing exploratory movements for feeding (Gowan *et al*., 1994; Smithson & Johnston, 1999; Albanese *et al*., 2004), habitat for refuge (Brown *et al*., 2001) or simply searching to gain knowledge (Gowan & Fausch, 2002), i.e. stream fish explore and exploit at great distances.

Mark–recapture fish distributions were comparable at the end of each winter but fish moved extensively during the second study winter, suggesting fish exhibited strong site fidelity by homing to the initial tagging location. Site fidelity and homing has been reported in cyprinids for diel feeding (Clough & Ladle, 1997), spawning (Fredrich *et al*., 2003), after displacement by high flows (Lucas, 2000), and following translocation experiments (Stott, 1967; Crook, 2004). Kramer & Chapman (1999) suggested fish home to original home ranges after displacement because of the costs associated with learning a new home range. Homing of fish to a site could be based on a combination of several learnt aspects of specific locations, including odours and landmarks (Odling-Smee & Braithwaite, 2003). Some fish that did not show fidelity to the initial tagging location (home range shift), possibly because of individual differences in ability (sensory or physiological) and/or motivation to return to the initial home range, physical alteration to initial home range during elevated flow, and/or the availability of suitable or even superior habitat elsewhere in the river (Crook, 2004). Alternatively, fish may have been outside their home range at the time of tagging.

7.4.2 Stocked fish movements

In the Roding, large numbers of PIT tagged stocked chub moved considerable distances in the first two days immediately after release and radio tagged stocked chub largely occupied open water. Evidence from wild fish suggests it is preferable to restrict movements and occupy areas of habitat complexity during low flows. Such variations in movement and behaviour between wild and stocked fish are considered a consequence of genetic differences (local adaptation of stocks), domestication (rearing environments influencing development and learning) and / or acclimation to the new environment (reviewed by Weber & Fausch, 2003). Notwithstanding this, stocked fish movements were not within or between habitat patches, i.e. fish moved long distances past numerous areas of available and suitable habitat. Thus, stocked fish probably moved to assess the suitability of potential residence areas prior to settling into home ranges, i.e. habitat exploration (Crook, 2004). Exploratory behaviour for stocked chub (rheophilic species) was more extensive than for stocked roach (eurytopic species), probably because of more specific habitat requirements of the former. Armstrong *et al*., (1997) reported that most transplanted Atlantic salmon settled in to new home ranges after a short period (<2.5 days) of exploratory behaviour in an experimental stream channel. Following exploratory movements and settlement, movements of stocked fish in the Roding were minimal under the influence of low flow.

During the initial elevated flow periods (18-19 November and 26-27 November 2006; up to 14.2 times normal flow) radio tagged stocked chub were found occupying local areas of habitat complexity or marginal vegetation (Pearsons *et al*., 1992; Schwartz & Herricks, 2005) but large numbers of stocked fish (radio and PIT telemetry) moved (both up and downstream). As suggested for wild fish, stocked fish probably moved for exploratory purposes, using areas of low flow associated with marginal vegetation to minimise energy expenditure. Although a large number of stocked chub moved downstream during the first elevated flow period, a finding reported for salmonids (Bettinger & Bettoli, 2002), a large proportion (40%) of fish quickly returned to the area local to stocking, possibly suggesting a homing ability in stocked fish. This conclusion is further supported by limited movement of stocked fish during subsequent elevated flow periods, suggesting development of site fidelity in stocked fish. However, validation of this was not possible, because the location of the home range after initial exploratory movements was not established. More importantly from a stocking perspective, was that stocked cyprinids have the behavioural and physiological ability to cope with elevated flows, a concern previously raised for salmonids (MacDonald *et al.*, 1998) and cyprinids (Cowx *et al.*, 1986), and nearly all recaptured stocked fish remained in the reach depleted by the pollution event.

Despite the majority of recaptured fish remaining in the target section of river, timing and extent of stocked chub movement had possible consequences for survival. Aprahamian *et al.* (2004) reported substantially higher loss rates for stocked cyprinids than for wild populations. Although, there was no evidence of reduced survival of stocked radio tagged chub, increased activity and long range movements of PIT tagged stocked chub probably exposed fish to increased predation (Sparrevohn *et al.*, 2002; Henderson & Letcher, 2003; Aarestrup *et al.*, 2005) and ultimately resulted in greater energy expenditure which may have reduced long-term survival (Hurst, 2007). Thus, based on the lower recapture rate of stocked chub, high rates of exploration and movement may not be advantageous traits for stocked cyprinids establishing in new locations. In addition, stocked roach were largely recaptured in shoals with wild fish (authors' personal observations), thus diluting individual predation threat (Pitcher & Parrish, 1993) and predator-naïve fish could learn anti-predator responses from experienced wild fish (Brown & Smith, 1998; Kelley & Magurran, 2003). Similarly, predator exposure and experience after release could have induced predator recognition and avoidance behaviour (Kelley & Magurran, 2003), thus explaining why stocked fish reduced movements during the study.

7.4.3 Experimental considerations

Although variable rates of stocked fish recapture were found, directly influenced by movement, recapture rates of wild roach were low, despite limited movements. Low recapture rates of fish could result from several causes, such as low tag retention, mortality, sampling escapement or fish moving out of the study area (Gowan *et al.*, 1994). Laboratory trials prior to the field study, reported 100 % tag retention and no negative effects of tagging on survival or growth on roach of the size tagged during the field study (Chapter 6). Electric fishing is known to cause stress (Bracewell *et al.*, 2004) and injuries (Synder, 2003) to fish. However, Skov *et al.* (2005) reported electric fishing and tagging (23-mm PIT without sutures, as in this study) had no effects on condition or survival of similar-sized roach in both laboratory and field investigations. Furthermore, wild chub and dace were subjected to the same experimental procedure and displayed better recapture rates than wild roach. It is therefore considered most likely that wild roach were perhaps more difficult to catch, because of greater electric fishing avoidance or that their preferred habitat was more difficult to sample (deep pools or dense vegetation). Ultimately, the recapture rates are comparable to other studies describing movements of stream fishes (e.g., 26%, Hill & Grossman, 1987; 8% and 20% Freeman, 1995), suggesting that mortality or low sampling efficiency have not biased the conclusions (Roberts & Angermeier, 2007).

Gowan *et al*. (1994) suggested that the findings of many historic studies of fish movements were undermined by insufficient sampling of long-range movements out of study sections. In the study on the Roding, 14 km of river were sampled, thus suggesting that most tagged fish that were not recaptured either died or were missed by the electric fishing. This is further supported by PIT antennas, which documented the medium-term movements of large samples of individual small fish past certain locations within the study reach. Without PIT antenna technology the movement of fish from the study section could have been interpreted as mortality and returning fish would have been interpreted as not moving. For example, Jonssonn *et al*. (1999) concluded that mark-recaptured stocked brown trout caught in the area of stocking did not actively search for new habitats after introduction, but the low temporal resolution of this technique cannot confirm it. Furthermore, had a combination of full-reach resampling and continuous telemetry not been carried out, it could have been easy to suggest that stocked cyprinid fish persistence was low (*cf*. Aprahamian *et al*., 2004).

7.5 CONCLUSIONS

By employing three different techniques (radio tracking, mark-recapture and fixed station PIT telemetry) over two years, detailed and precise spatial and temporal information on fish distribution and movements in relation to environmental factors were obtained. Specifically, evidence from mark-recapture revealed similar distributions of wild fish between years, suggesting restricted movement of fish, although the populations comprised both residents and mobile fish. However, data from fixed location PIT telemetry during the second study year found that wild fish were far more active, performing extensive movements (exploratory, exploitation or refuge) when exposed to more variable environmental influences (flow and temperature). By considering individual movements at suitable spatial and temporal scales and using a combination of techniques, a more complete understanding of wild cyprinid ecology and general stream fish movement is provided. The results provide evidence of variations in behaviour in response to relatively natural flow regimes (Poff *et al.*, 1997), and the importance of aquatic habitat diversity and the necessity for protecting and restoring longitudinal connectivity.

After the second study winter, stocked fish were more widely distributed than wild fish, movements were larger than found for wild fish and movements of stocked chub were not correlated to abiotic factors. Specifically, PIT telemetry identified exploratory movements immediately after stocking, large numbers of fish moving during the first flood, the return of displaced fish, reduced movements of stocked fish with time and the large total distances stocked fish moved during the 5 months after release. Genetic and phenotypic factors (review in Weber & Fausch, 2003) are regularly cited as explanations for stocked fish behaviours, but we believe our understanding of stocked fish behaviour has been enhanced by considering their movements in relation to simultaneous studies of wild fish. In this study, although most of the stocked fish remained in the stream section local to stocking, extensive movements of stocked chub appear to have had direct consequences for survival, a vital measure of stocking success. Future efforts to improve post-release behavioural performance of chub and other stocked cyprinids could include environmental enrichment (Braithwaite & Salvanes, 2005) and life skills training (Brown & Laland, 2001).

8 GENERAL DISCUSSION

8.1 INTRODUCTION

Movements and dispersal of cyprinid fish, in both lateral and longitudinal directions, are strongly influenced by flow. In lowland reaches, floods are characterized by lateral expansion onto floodplains resulting in high levels of aquatic habitat heterogeneity, essential for fish refuge, spawning, nursery and feeding (Chapter 2). However, in rivers subjected to anthropogenic disturbance to floodplain connectivity, floods have detrimental effects on 0+ fish populations (Chapter 3). Thus, there is a need to restore and rehabilitate lowland rivers in an attempt to recover natural features or functionality. In rivers where man-made floodplain waterbodies have created functional habitats, lateral connectivity is important for both juvenile (Chapter 4) and adult fish (Chapter 5). Marking and tracking of individual cyprinids (Chapter 6) improved understanding of the influence of temperature and flow on the longitudinal movements of both wild and stocked sub adult cyprinids (Chapter 7). The overall aim of the study was to examine the factors influencing the lateral and longitudinal dispersal of juvenile and adult (wild and stocked) cyprinid fish in lowland rivers, and to ascertain the influence of elevated flows on these respective communities. To this end, the study was divided into key topics that are addressed in Chapters 2 to 7. This chapter integrates and discusses the knowledge gained from the previous six chapters; key conclusions are drawn and it provides recommendations for further study.

8.1.1 Lateral dispersal of fish

Chapter 2 provided a review of how natural floodplains in lowland rivers have high structural diversity, which is not only maintained but is often increased by erosional and depositional processes during floods. Freshwater fish species have evolved different life history strategies, classified according to where particular species spawn along the lotic-to-lentic succession of habitat that occurs along downstream and lateral directions of rivers. Even the larvae and juveniles of strictly rheophilic species such as dace and gudgeon disperse from river spawning grounds and use floodplain habitats as nurseries. Floodplain habitats are also essential for young progeny to take refuge during floods, primarily because of their poor swimming capabilities.

Anthropogenic disconnection of floodplains from the river can have adverse consequences for fishes, during both elevated and normal flow conditions. Isolation of rivers from their floodplains is of particular importance during floods, because of the increased severity of conditions in the main river channel, prevention of fish seeking refuge in floodplain habitats, and stranding of fish when artificial levees are 'over-topped'. During elevated flow events of varying timing and magnitude in the River Yorkshire Ouse, backwaters provided refuge for high densities of 0+ eurytopic fishes, with gudgeon and other strictly rheophilic species also captured on a regular basis. However, rheophilic fishes were rarely stranded on the floodplain (Chapter 3). Peak fish densities on the floodplain occurred in the summer (August), despite there being floods of higher magnitude during the winter. Thus, floods can be directly detrimental to recruitment if they occur immediately after spawning. Furthermore, samples of fish from rivers immediately after floods contained significantly larger bleak and roach than pre-flood samples, suggesting small fish were more susceptible to displacement and / or mortality.

Rehabilitation efforts should reinstate lateral and longitudinal connectivity by restoring a more natural hydrologic regime and recreating functional habitats, i.e. recovery towards a "normative" condition. In the river Trent, local and overall species diversity, richness, turnover and guild composition of fish communities in ten man-made floodplain waterbodies were influenced by variable hydrological connectivity to the river. The broad spectrum of connectivity represented habitats similar to a natural riverscape and fish assemblages compared favourably with studies on unmodified river reaches i.e. the lotic-to-lentic succession of habitat moving from the main river channel into the floodplain, corresponding to a sequence of rheophilic-to-eurytopic-to-limnophilic fish species. This study supports the incorporation of man-made floodplain waterbodies of variable, not just high, levels of hydrological connectivity into holistic riverine ecosystem management plans.

DIDSON was used to provide fine-resolution, non-interventional insight into adult fish movements between the Yorkshire Ouse and a permanently connected man-made floodplain waterbody (a marina), under normal and elevated flow (Chapter 5). The largest and most consistent variations in movements in the connecting channel were between day and night samples, with fish being present at higher densities and being much more active by day. The diurnal variations were considered most likely to be a trade-off between foraging and avoidance of piscivorous birds in the main river, particularly cormorants. Increased river flow resulted in significantly reduced fish movements, both in and out of the marina, and fish presence in the entrance. This result is contrary to the findings from other studies, possibly because fish found localised refuge (bottom / margins) from elevated flows within the main river, but lateral movements may occur during higher flow events, i.e. when conditions are more severe in the main channel.

8.1.2 Longitudinal movements of fish

Longitudinal movements of small cyprinids (both wild and stocked) have been little studied, partly because of monitoring limitations. Although there have been numerous studies on the suitability of VIE or PIT tags for fishes, especially salmonids, few have determined the most reliable and appropriate long-term marking techniques for cyprinids. It is shown in Chapter 6 that VIE implantation could provide a cheap, batch marking technique, as long as retention rates are monitored. However, based on high retention, survival and minimal growth effects PIT tags are recommended as the most suitable method for tagging individual juvenile chub, dace and roach. Specifically, small cyprinids (> 9 cm fork length) can be tagged with 12-mm PIT tags, and slightly larger fish (> 12 cm fork length) tagged with 23-mm tags. Although the use of 12-mm PIT tags would be preferred for mark-recapture purposes, given their negligible recorded effects on fish health, the range advantages of 23-mm PIT tags for telemetry applications (Lucas & Baras, 2000; Zydlewski *et al*., 2001) probably outweigh the minor effects on growth identified.

The combination of PIT and radio telemetry employed in the River Roding enabled identification of the habitat use, spatial distribution and temporal movements of individual wild and stocked cyprinids (Chapter 7). The mark-recapture distribution of wild cyprinids at the end of both winters suggested wild cyprinids largely had high levels of ‘site fidelity’ but highly mobile individuals were present within the population. Radio-tracking revealed that wild chub tended to occupy areas of habitat complexity, whilst PIT telemetry identified that wild cyprinid behaviour was temporally variable, correlated with temperature and flow. Habitat use and movements are probably related to energy expenditure, metabolic capacity, feeding and predation threat. During elevated winter flows, wild fish occupied areas of reduced flow, and since feeding and metabolic capacity are low at this time of the year, we interpret this as a response to reduce energy expenditure. However, some fish performed exploratory movements under the influence of increased depth and turbidity (reduced predation), possibly because of reduced habitat quality through winter or to find flow refuge. Despite extensive movements, some fish returned to their initial tagging site.

Passive Integrated Transponder telemetry and radio-tracking identified that movements of stocked fish were more frequent and larger than for wild fish, particularly in the period soon after release, possibly for exploratory purposes. Subsequently, movements of stocked fish were minimal, did not correlate with flow or temperature and the final distributions were more dispersed than observed for wild fish. Importantly from a stocking perspective, stocked cyprinids had the behavioural and physiological ability to cope with elevated flows and mostly remained in the section of river affected by the pollution event. However, had a combination of full-reach scale re-sampling and continuous telemetry not been carried out it could have been easy to suggest that stocked cyprinid fish persistence was low (*cf.* Aprahamian *et al*., 2004). Differences in habitat use between wild and stocked chub were observed, and the timing and extent of stocked chub movement probably had consequences for survival.

8.2 CONCLUSIONS AND RECOMMENDATIONS

8.2.1 Lateral movements

Backwaters (areas of slack water in the main channel) provide refuge for high densities of 0+ fishes, including eurytopic and strictly rheophilic species during high flow and flood events. **It is recommended that backwater areas are constructed on channelized rivers for fish refuge during elevated flows, especially in sections of river where it is not possible to reconnect floodplains.** Specifically, altering channel morphology and encouraging riparian vegetation (trees) will increase habitat diversity and create areas of slack water at high flows, with inevitable benefits for a large proportion of the 0+ fish population.

Large numbers of 0+ fish were stranded and died on floodplains behind ‘over-topped’ levees, especially after summer floods. **It is recommended that such areas have levees set back and be designed so that ditches/channels enable all water to drain**

back into the river. Furthermore, water should be able to return to the river quickly (as flood waters recede), to reduce potential mortality from piscivorous birds, low dissolved oxygen and high levels of tannins. In areas where flood levees must remain, but are still liable to 'over-topping', water drainage structures such as flap-gates are encouraged, whilst sluices and pumps should be avoided because they are likely to cause physical damage or even mortality of fish during operation. By following these guidelines, such managed floodplain areas will provide refuge for fish during floods and safe egress back to the river as flood waters recede. It is also important to recognize the benefits to society from the natural functional attributes of river landscapes for flood protection.

Both adult and juvenile fish used man-made floodplain waterbodies. The findings of this study should be explicitly incorporated into plans for lowland river rehabilitation and floodplain restoration. **It is recommended that man-made floodplain waterbodies, with variable connectivity, should be excavated where anthropogenic activities have reduced floodplain habitats.** Such waterbodies recreate functional habitats for spawning, feeding, nursery (growth) and resting (self protection) areas, i.e. improving the status of fish populations in degraded rivers. Such efforts are integral to the UK's obligations under the European Union, Water Framework Directive (2000/60/EEC) to improve the ecological status of rivers. Importantly, these restoration strategies do not focus on a single taxonomic group or species.

DIDSON provided a fine-resolution insight into the lateral movements of fish in a connection channel between a lowland river and connected floodplain waterbody, an environment where current sampling techniques have inherent problems. **It is recommended that future investigations of lateral movements specifically incorporate DIDSON technology, whilst attempting to verify numbers, species, and size composition of imaged fish.** By doing so, a far greater of understanding of the importance of floodplain waterbodies for adult fish will be gleaned.

Movements of juvenile and adult fish between the main river channel and floodplain waterbodies are complex, within which spawning, foraging, predator avoidance and flow refuge behaviours exist. Furthermore, lunar cycles (Gaudreau & Boisclair, 2000), temperature (Lilja *et al.*, 2003) and turbidity (Jepsen & Berg, 2002) could potentially influence the movements, activity patterns and habitat use of fish. **It is recommended**

that future investigations should monitor lateral movements over both finer (e.g. diel) and longer time scales (e.g. seasonal), in an attempt to elucidate species-specific timings and environmental influences on such movements, including analysis of stomach contents over 24-hour periods. Such efforts could employ DIDSON, as well as traps for juvenile fish and tags for adult fish, whilst measuring detailed water quality variables (suspended solids, ammonia and the distribution of food items) in both the main river channel and the floodplain waterbody. These studies need to be replicated at the same site under similar conditions, but where possible the methodology should also be applied across multiple sites and rivers to determine the degree to which observed patterns are generic to lowland river systems.

8.2.2 Tag retention trials

Variations in survival, mark retention and growth rates between species over the duration of the laboratory experiment emphasised the importance of long-term mark feasibility trials for the species under study. **It is recommended that future tagging investigations are species specific and of sufficient duration to determine the most reliable and appropriate long-term marking technique.** Such efforts will provide validation of field results, i.e. recaptures of marked fish are representative of unmarked populations and recapture rates are not reduced by low survival of marked fish or poor retention of marks.

During the laboratory tagging investigation, fish were not exposed to the same stresses as encountered in a natural environment (predation, density, and feeding), thus survival and growth may have been artificially elevated in the controlled setting. This perspective is perhaps most relevant for dace which, out of the three species studied, is most sensitive to capture and handling, with higher incidence of scale loss and fin damage. **It is recommended that future tagging trials incorporate predation and growth experiments under field conditions but in a "controlled" environment, e.g. in managed outdoor ponds.** Specifically, experiments should test the effects of anaesthesia, tagging and transportation on growth and survival. Such trials would reduce concerns over large amounts of field variability and remove issues of variable sampling efficiency in the field.

Differences in recapture rates between wild fish were considered to be a consequence of electric fishing avoidance and / or habitat use variations between species, but these could also be attributed to capture and tagging procedures. Furthermore, hatchery-reared fish were not exposed to electric fishing and were tagged two weeks prior to stocking, due to the large numbers being handled, thus were allowed to recover from immediate tagging effects. **It is recommended that future field studies should attempt to quantify the individual and combined effect of electric fishing, handling, anaesthesia and tagging on wild fish.** Although, we belive the affacts of these factors to be negligible, such trials would further validate the ecological conclusions drawn from field studies.

8.2.3 Longitudinal movements

By employing different monitoring techniques (mark-recapture, PIT telemetry and radio-tracking) this study obtained detailed and precise spatial and temporal information of fish movements, in relation to environmental variables. Without careful spatial and temporal stratification of post-release monitoring of stocked freshwater fish, there is great potential for erroneous interpretation of their fate. **It is recommended that future studies on individual movements need to be considered at an appropriate spatial and temporal resolution, using the correct combination of techniques.** By doing so, such studies will provide a more complete understanding of stream fish movement, general fish ecology, and possibly a greater insight into the species specific variations observed in this study.

Radio-tagged wild (and stocked) chub occupied areas of habitat complexity (instream macrophytes and overhanging / submerged terrestrial vegetation) at all river levels, possibly to avoid predation and reduce energy expenditure. Additionally, PIT telemetry identified extensive longitudinal movements (upstream and downstream) during elevated flow, which were presumed to occur in areas of low flow (marginal vegetation) to minimise energy expenditure. **It is recommended that lowland river rehabilitation efforts include recognition of the importance of habitat diversity for juvenile cyprinids in winter conditions.** Such efforts will help conserve stream fish populations, especially in relation to increases in flood frequency and magnitude in relation to climate change.

The findings of this study address concerns over the susceptibility of both stocked and wild juvenile cyprinids to displacement during high flows. Furthermore, all species of wild fish surveyed occasionally performed long range movements correlated with temperature and flow. **It is recommended that natural flow regimes and longitudinal connectivity are protected and restored.** It is important to recognize the importance of long-range movements for individual fish, but also the influence on the distribution and abundance of a population, with genetic and evolutionary consequences.

Although most of the stocked fish remained in the stream section local to stocking, behavioural differences (movements and habitat use) between wild and stocked chub were prevalent throughout the study, and probably had consequences for survival. These differences may be the result of genetic differences (local adaptation of stocks), domestication (rearing environments influencing development and learning), acclimation to the new environment (reviewed by Weber & Fausch, 2003) and / or issues relating to home range. **It is recommended that future studies should determine the factors affecting stocked cyprinid behaviour post-release and quantify such differences in relation to survival.** Specifically, efforts should reduce the effects of domestication, through environmental enrichment (Braithwaite & Salvanes, 2005) and life skills training (Brown & Laland, 2001). Such efforts will inevitably improve the success of future riverine fish stock enhancement measures.

The findings of this study provide a preliminary insight into the movements of stocked fish during winter months immediately after release. **It is recommended that further study on non-salmonid stocked fish should continue to compare their behaviour to wild fish, of which there is a paucity of information.** Specifically, studies should be over longer durations (including spawning periods), include comparisons between rivers with different habitat complexity, hydrology and morphology, including both longitudinal and lateral connectivity.

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