# The Ecology and Conservation Requirements of the Southern Damselfly, *Coenagrion mercuriale*, in Chalkstream Habitats

Thesis submitted in accordance with the requirements of the
University of Liverpool for the degree of Doctor in Philosophy

by James Robert Rouquette

December 2004

# The Ecology and Conservation Requirements of the Southern Damselfly, *Coenagrion mercuriale,* in Chalkstream Habitats

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## Abstract

This thesis presents the findings of a study investigating the ecology and conservation requirements of the Southern Damselfly, *Coenagrion mercuriale* (Odonata: Coenagrionidae) in chalkstream habitats in the UK. *Coenagrion mercuriale* (Charpentier) is threatened throughout Europe and is the only odonate currently given priority status in the UK Biodiversity Action Plan. The primary aim of this study was to examine the ecology and habitat requirements of this species in its chalkstream habitat, with a view to guiding conservation and management programmes. Fieldwork was performed in the Itchen and Test Valleys in Hampshire (southern England).

A large multi-site mark-release-recapture study revealed that *C. mercuriale* was extremely sedentary, with dispersal only occurring between adjoining sites. The median net lifetime movement was 31.9m and lifetime movements of greater than 500m were rare. Factors affecting movement are examined and evidence of inverse density dependent movement is provided.

Adult *C. mercuriale* density and movement were analysed in relation to habitat variables and local population size using Generalized Linear Models. Mean adjacent population density was the single most important factor determining density. However, the species was also shown to be associated with a number of habitat features, which are discussed.

*Coenagrion mercuriale* larvae were found to occur more often and in greater abundance at sites that contained abundant emergent dicots, particularly in smaller, more marginal channels with low flow. *Apium nodiflorum* and *Rorippa nasturtium-aquaticum* were found to be particularly important. Furthermore, they were associated with certain macroinvertebrate taxa that were indicative of well-vegetated, moderate to slow flowing waterbodies, with a predominantly silty substrate. Habitat requirements of adults and larvae have been found to be similar, although larvae were found in greatest abundance in habitats that were slightly further along the successional sequence than those favoured by adults.

The night-time roosting location of adult *C. mercuriale* has also been examined and it has been established that adults are strongly associated with two tussock-forming monocots. Differences in the abundance of these plants were shown to result in large differences in the numbers of *C. mercuriale* roosting in different parts of the study site.

It is concluded that loss of habitat, alterations to management on remaining sites, and fragmentation are the key threats facing this species. It is argued that successful conservation will involve active management of existing sites, together with the creation of a series of new sites to reconnect populations. Recommendations regarding the monitoring, conservation and management of *C. mercuriale* are presented.

# Acknowledgements

This study would not have been possible without the assistance of a very large number of individuals and organisations to whom I am extremely grateful. I must start by thanking my supervisor Dave Thompson for his invaluable support throughout this project. Tim Sykes, from the Environment Agency and the chairman of the Southern Damselfly National Steering Group was instrumental in providing funding, enthusiasm and an ongoing commitment to this project.

This PhD was funded by the University of Liverpool, the Environment Agency, English Nature and the Countryside Council for Wales. I am grateful to all these organisations for their continued support and in particular I would like to thank Martin Drake, Adrian Fowles and Jon Webb. I would also like to thank all the other past and present members of the Southern Damselfly National Steering Group for their encouragement and support.

This thesis has been greatly enhanced by the substantial amount of financial and practical support that it has received. Additional funding enabled the recruitment of a large number of fieldwork assistants for the mark-release-recapture study. I would like to thank Pearl Chung, Jason Farthers, Dave Giles, Nina Graham, Sam Jacobs, Sam Jones, Dave Lock, Ken Monro, Viv Owens, Lisa Parker, Jac Pearson, Rachel Remnant, Angie Squires, Gaya Sriskanthan, Debs Stickley, Pete Taylor, Jules Tipper, Carri Westgarth and Kerry Woodbine for all their hard work and enthusiasm. The additional funding was provided by the Itchen Sustainability Study Group, the Environment Agency, the Natural Environment Research Council (grant no. NER/A/S/2000/01322), Bovis Homes Ltd., Persimmon Homes Ltd. and Wimpey Homes Ltd.

In a separate initiative, much additional funding was also provided for a study of Southern Damselfly larval ecology. This was provided by the Environment Agency, English Nature (through the LIFE rivers project) and work in kind from Southern Water Services PLC. I would like to thank the Environment Agency Biology team at Colden Common, Hampshire, including Adam Fulton, Kevin Exley, Shirley Medgett, Emma McSwan, Will Phelps, Emily Hodgkinson, Stefan White and Tim Foster for expert field and laboratory assistance. I would like to thank Adam Fulton, in particular, for his continued assistance and enthusiasm for all aspects of this project, including even the statistical analysis. I would also like to thank Dave Leeming who performed the invertebrate species identification.

I would like to thank all the landowners for allowing us onto their land, particularly in June 2001, when the threat of foot and mouth disease had only just subsided. The Southern Damselfly is protected under Schedule 5 of the Wildlife and Countryside Act and all work was carried out under licence from English Nature.

At Liverpool University I would like to thank Ian Harvey, Rob Marrs, Sandra Telfer and David Carslake who gave invaluable advice on numerous aspects of the statistical analysis. Finally, I would like to thank my family for all their support over the years. I would especially like to thank Liz for standing by me through good and bad and for giving me the confidence to complete this project.

# Contents

# Preface

The bulk of this thesis has been written in the form of self-contained papers. It is therefore inevitable that there is some repetition of material, particularly regarding the species and study sites.

Chapter 4 has been published as:

Rouquette, J.R. & Thompson, D.J. (2005) Habitat associations of the endangered damselfly, *Coenagrion mercuriale*, in a water meadow ditch system in southern England. *Biological Conservation*, **123**, 225-235.

# Chapter 1: Introduction

This thesis presents the findings of a study investigating the ecology and conservation requirements of the Southern Damselfly, *Coenagrion mercuriale*, in chalkstream habitats in southern England. *Coenagrion mercuriale* is a species of conservation concern. Its status in Europe is considered to be "very vulnerable" (Grand, 1996) and it is threatened over much of its range. Its declining status has been recognised at both the national and international level and it has become the focus of Europe-wide conservation efforts. It has been listed in Annex II of the EC Habitats and Species Directive and Appendix II of the Bern Convention, and is the only species of Odonata currently given priority status in the UK Biodiversity Action Plan (HMSO, 1995; UKBG, 1999). It has thus taken on the role of a "flagship" species within the UK insect conservation movement.

Safeguarding species of conservation interest involves two parallel approaches. The first is site protection, normally achieved through designation and its accompanying legislation. The second is the encouragement of positive management practices at both the local (site) and regional scales. However, appropriate habitat management can only be applied once the precise ecological requirements of the species are understood, including population dynamics, patterns of movement and dispersal, and habitat requirements of all life stages. Indeed, the Species Action Plan for *C. mercuriale* (HMSO, 1995) states that the top priority for future research and monitoring is to:

> *"Encourage further research into the damselfly's ecological requirements throughout its range in England and Wales, especially to identify precise habitat requirements".*

Since that statement was written, a number of studies have been undertaken, including a doctoral thesis on the ecology of the species in its principal habitat in the UK, heathland streams (Purse, 2001), and an assessment of all known sites in the UK (Boyce, 2002). However, little work has been carried out on the species' calcareous habitats in this country and so important gaps remain in our knowledge of this species. Indeed, calcareous habitat is the more typical habitat in the remainder of its European range. Hence the findings presented here have wide application for the conservation of *C. mercuriale* throughout Europe.

In the remainder of this chapter I will briefly establish the context for a study of odonate conservation, before providing a short review of the biology and ecology of *C. mercuriale*, its life history, distribution and status. It is not my intention to provide a comprehensive review, as this is available elsewhere (see Thompson *et al.*, 2003a). This chapter will conclude with an overview of the chapters that make up the rest of this thesis.

## 1.1 Conservation of insects and Odonata

Insects are far and away the largest contributors to global biodiversity and play a fundamental role in ecosystem functioning. Until recently, however, they have received little in the way of conservation effort. Many insects have specific habitat requirements, are subject to rapid population dynamics, can occur in high abundance, and occupy small areas. This makes them ideal indicators of ecosystem health, and far more sensitive to change than vertebrate species.

Insects are declining more rapidly than vertebrates over much of Europe and throughout the World. Three reasons have been suggested to account for this disparity (Thomas, 1994): many insects occupy very narrow niches, often associated with a temporary successional phase; patches may remain suitable for only a short time period; and insects are often too sedentary to colonise new patches of suitable habitat that are not extremely close to old sites. Furthermore, it has become clear that landscape structure and connectivity play an important role. Metapopulation theory (e.g. Hanski, 1999) has shown that the presence of several interconnected populations in a fragmented landscape increases the probability of the long-term persistence of insect populations.

The UK has a relatively impoverished insect fauna due to its climate, history and isolation. Fortunately, however, its insects are probably the best studied in the world, largely thanks to the efforts of amateur naturalists over the last two or three centuries.

Larger, more charismatic insects, such as members of the Lepidoptera and Odonata have been particularly well studied. Furthermore, these groups of insects are becoming increasingly popular amongst the general public. Specialist societies, such as Butterfly Conservation and the British Dragonfly Society have been formed and have flourished in recent years, with a growing number of members actively involved in species monitoring and conservation activities. Butterflies and dragonflies are seen as flagships for the cause of conservation (Corbet, 1999).

Odonata are particularly threatened, because all are dependent upon aquatic habitats for larval development. These habitats, perhaps more than most, have been vulnerable to destruction or alteration over the last century. Drainage, pollution, canalisation of watercourses, and alteration of management practices, along with many other threats, have all impacted on the viability of aquatic biotopes. The resultant loss of habitat, together with the impoverishment and fragmentation of remaining areas, has had a critical impact on many species. Indeed, Van Tol and Verdonk (1988) evaluated the status of all 164 indigenous European odonate species and considered 61 to be endangered, vulnerable or rare. Their study indicated a steady decline in diversity almost everywhere in Europe during the 20th century, but the situation was worst in the most urbanised and industrialised regions, including England.

Six species of Odonata are included in the British Red Data Book (Shirt, 1987), indicating that they are rare or endangered in the British Isles. Only one of these species, however, is considered to be threatened across Europe, *Coenagrion mercuriale*.

## 1.2 The biology and ecology of *Coenagrion mercuriale*

### *1.2.1 Species description*

*Coenagrion mercuriale* (Charpentier, 1840) is one of five members of the genus *Coenagrion* currently found in the UK. Males in this genus are predominantly blue and black in colouration but vary in their pattern of marking. *Coenagrion mercuriale* characteristically possesses a “mercury” mark on the second abdominal segment, from which it derives its Latin name. However, there is remarkable variety in the extent of this mark both within and between sites, which was first reported by Mayo & Welstead (1983), and has been further investigated by Thompson & Rouquette (2004). Markings along abdominal segments 3-5 and the shape of the anal appendages are more reliable identification tools (Winsland, 1997; Smallshire & Swash, 2004). Furthermore, males are typically smaller and darker than the other blue damselflies occurring in the UK and have a weaker flight.

Females are usually dark with pale olive-green sides to the thorax and abdomen and can be distinguished by markings on the side of the thorax and on the head (Merritt *et al.*, 1996; Winsland, 1997). Small differences are also present in abdominal markings (Smallshire & Swash, 2004). In both sexes the pterostigma is shorter than in other members of the genus (Winsland, 1997). A second female form also occurs, where the light parts have the blue colouration of the male. This andromorph form accounts for 21% of females in the New Forest (McKee *et al.*, 2005), but is less frequent in the Itchen Valley (see Chapter 3). This type of female polymorphism is common within odonates (Sherratt, 2001), and its genetic basis has been determined in four species of Coenagrionidae (Wong *et al.*, 2003).

### *1.2.2 Habitat*

*Coenagrion mercuriale* breeds on two main habitat types within the UK; heathland bogs / valley mires; and calcareous streams / fens. The majority of sites occur on the former habitat type, with the latter restricted to sites in the Itchen and Test valleys in Hampshire, and small sites in Oxfordshire and Anglesey. However, on the continent the species is found predominantly on calcareous substrates; in limestone meadow streams, limestone marsh, and close to ground water springs (Buchwald, 1994; Sternberg *et al.*, 1999). Interestingly, most sites in the UK are influenced by alkaline flushes from deep-lying calcareous formations and typically have pH values greater than 6 (Winsland, 1985; Jenkins, 1998; Purse, 2001).

*Coenagrion mercuriale* requires a constant flow of water throughout the year and usually inhabits narrow, shallow runnels on flat or gently sloping ground (Evans, 1989;

Winsland, 1997; Jenkins *et al.*, 1998). It does not tolerate heavy shading by bankside vegetation, although it does use low shrubs for shelter, roosting and oviposition (Winsland, 1997). Slow flowing waters are preferred and it does not occur in streams that freeze during the winter. Indeed, in sites containing *C. mercuriale* water temperature rarely falls below 3-4 °C, and the annual range is moderate, no doubt influenced by ground water springs and seepages (Evans, 1989; Winsland, 1997; Jenkins *et al.*, 1998). Water quality at occupied sites is generally good, with high oxygen levels (Grand, 1996; Jenkins *et al.*, 1998).

### *1.2.3 Life history*

Eggs are laid directly into the stems of submerged and emergent plants. Females show a marked preference for plants with soft stems and thin cuticles, containing spongy parenchyma cells rather than thicker collenchyma cells (Purse, 2001). On heathland / mire sites *Potamogeton polygonifolius* (bog pondweed) and *Hypericum elodes* (marsh St John's-wort) are particularly favoured (Winsland, 1997; Purse, 2001). Species favoured for oviposition in calcareous sites in the UK include *Rorippa nasturtium-aquaticum* (water-cress), *Apium nodiflorum* (fool's water-cress), *Veronica beccabunga* (brooklime) and *Glyceria maxima* (reed sweet-grass) (Hold, 1998; Strange, 1999). In a study in the New Forest, females laid an average of 91 eggs, although there was wide variation and it is suggested that females do not lay their entire clutch of eggs in one visit to the breeding stream (Purse, 2001). Eggs took 3-4 weeks to hatch in an aquarium study by Corbet (1957).

Larval development usually takes two years in the UK, and the larvae develop through thirteen instars (Corbet, 1955). Growth is generally inhibited between November and March (Purse & Thompson, 2002). Little is known about larval habitat preferences, but it has been stated that first year larvae live in detritus among plant roots, whereas second year larvae move up onto the foliage of aquatic plants (Winsland, 1997). However, Purse (2001) found both age classes in the same habitat, living on aquatic plant foliage.

Adult emergence varies from year to year, and with locality, but usually starts in mid to late May and continues through to mid July. Adults generally emerge in the morning, using plants with rigid, upright stems. *Eleocharis palustris* (common spike-rush) and *Juncus articulatus* (jointed rush) were selected on a valley mire site in the New Forest (Purse, 2001). In Germany, a range of species is used including *Juncus* spp. (rushes), *Carex* spp. (sedges) *Berula erecta* (lesser water-parsnip), and *Rorippa nasturtium-aquaticum* (water-cress) (Buchwald, 1989; Sternberg *et al.*, 1999). It is believed that newly emerged adults do not fly far from their emergence site, and mature in 5-8 days (Sternberg *et al.*, 1999, Purse & Thompson, 2003a).

Adults are characterised by their slow and erratic flight, with frequent pauses to perch on low vegetation. They are considered to have the weakest flight of the British coenagrionids, but are able to fly earlier in the day than most other species and can remain active in overcast conditions (Winsland, 1997). General activity, as well as reproductive activity, peaks in the middle of the day (Jenkins, 1987; Purse, 2001).

Mean adult lifespan for both sexes is around 13 days (Purse, 2001). Males exceed females in the number of hours spent at breeding sites in their lifetime and in the number of individuals present on any one day. They are non-territorial and will scramble to seize females when they visit a breeding site. The number of hours on site, as well as the proportion of the lifespan affected by bad weather, influences the lifetime mating success of individuals (Purse & Thompson, 2005). At Aylesbeare, a heathland site in Devon, it was found that only 39% of males and 53% of females mated and made a genetic contribution to the next generation (Purse & Thompson, 2005). Copulation took an average of 24 minutes in a study in the New Forest (Purse & Thompson, 2003b), and is followed by egg-laying, with the pair usually still in tandem.

## 1.3 Distribution and status

*Coenagrion mercuriale* is mostly confined to the south and west of Europe (Figure 1.1), and is declining over much of its range (Table 1.1) (Grand, 1996). It is now extinct in Luxembourg, the Netherlands, Poland, Romania and Slovenia, and in danger of extinction in Austria, Belgium and Switzerland. In Germany and the UK it is local and declining. Fortunately, the species is still fairly widespread in France and Spain, where its status is vulnerable, while its distribution and status in Portugal is uncertain. Its status in Europe as a whole is considered to be "very vulnerable" (Grand, 1996).

Two subspecies of *C. mercuriale* also occur. The subspecies *C. m. castellanii* is endangered but fairly widespread in Italy, while the subspecies *C. m. hermeticum* is widespread in North Africa, particularly in Morocco, but its status is considered to be vulnerable.

**Table 1.1.** Summary of the status and frequency of occurrence of *Coenagrion mercuriale* throughout its range (Grand, 1996).

| Country | Status | Frequency of Occurrence |
|---|---|---|
| **Europe:** | | |
| Austria | in danger of extinction | extremely localised |
| Belgium | in danger of extinction | extremely localised |
| France | vulnerable | widespread |
| Germany | endangered | localised |
| Italy | endangered | mostly subspecies *C. m. castellanii* |
| Luxembourg | probably extinct | |
| Netherlands | extinct | |
| Poland | extinct | |
| Portugal | unknown | |
| Romania | extinct | |
| Slovenia | extinct | |
| Switzerland | in danger of extinction | extremely localised |
| Spain | vulnerable | widespread |
| United Kingdom | vulnerable | localised |
| **Outside Europe:** | | |
| Algeria | unknown | subspecies *C. m. hermeticum* |
| Morocco | vulnerable | subspecies *C. m. hermeticum* |
| Tunisia | unknown | subspecies *C. m. hermeticum* |

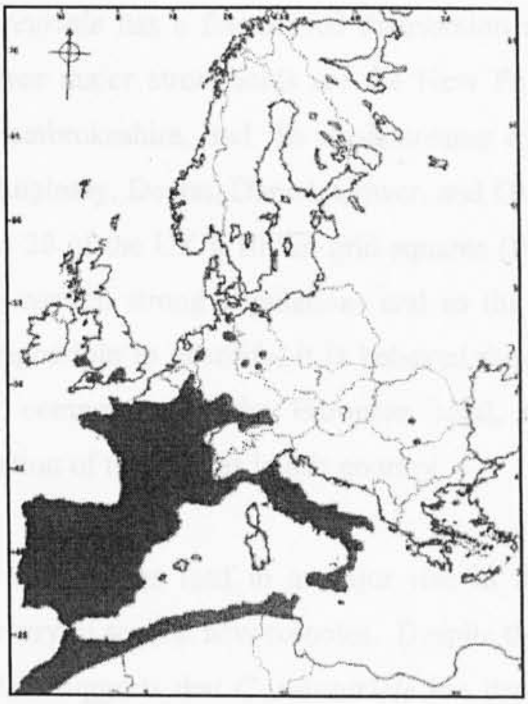

**Figure 1.1.** The worldwide distribution of *C. mercuriale* (from Askew, 1988).

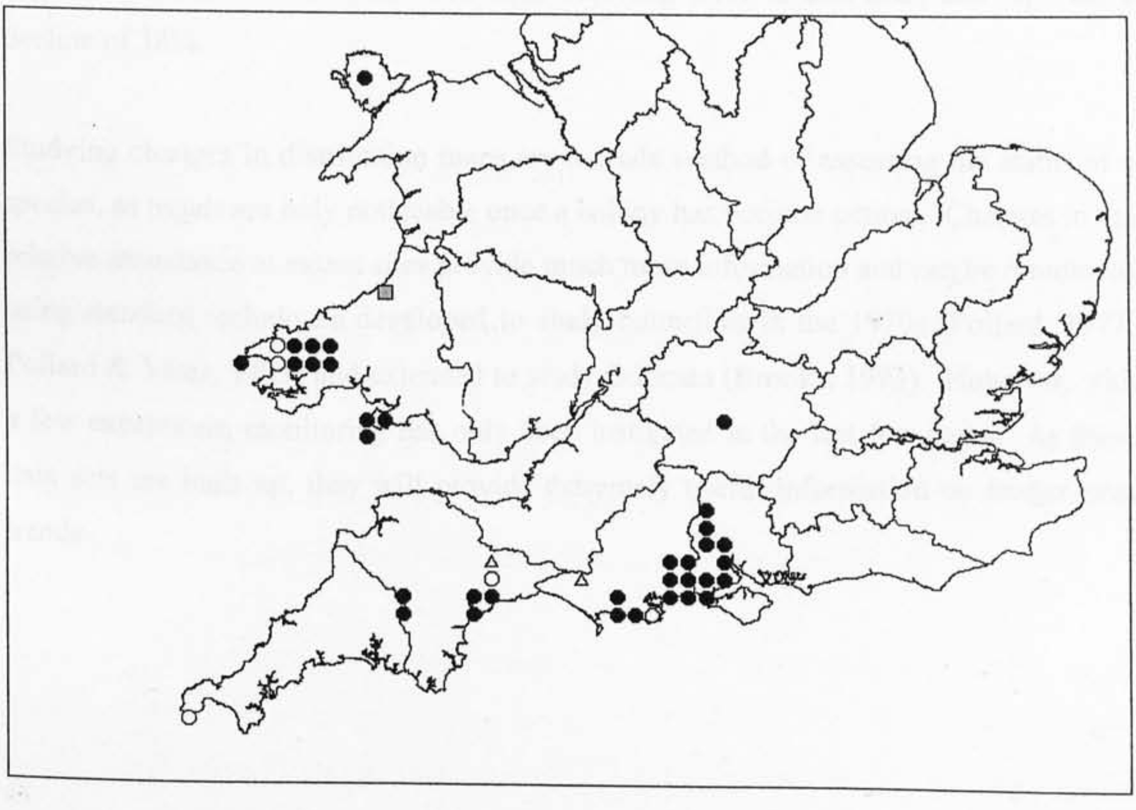

**Figure 1.2.** The distribution of *C. mercuriale* in the UK at a 10 km grid reference resolution. Symbols indicate the time period in which the species was last recorded at a particular grid reference and represent the years 1975-1999 (closed circles), 1950-1974 (open circles), 1925-1949 (grey squares), and 1900-1924 (open triangles).

Within the UK, *C. mercuriale* has a fragmented distribution and is restricted to the south and west. Its three major strongholds are the New Forest in Hampshire, the Preseli mountains in Pembrokeshire, and the chalkstreams of Hampshire. Smaller colonies also occur in Anglesey, Devon, Dorset, Gower, and Oxfordshire (Figure 1.2.). It is currently limited to 28 of the UK's 10 km grid squares (Purse, 2001). However, some of these colonies contain strong populations and so the species can be locally abundant. Although impossible to quantify, it is believed that the populations in the UK are an important component of the European total, thereby increasing the significance of conservation of the species in this country.

Recent interest in the species has lead to a major rise in the number of reported sightings, and the discovery of several new colonies. Despite this, however, analysis of the available historic data suggests that *C. mercuriale* has declined in distribution by 30% since 1960 (HMSO, 1995). To correct for biases in recording effort, Purse (2001) calculated the change in the number of occupied 1 km grid squares since 1985, using only data from those sites that had been recorded prior to that date, and reported a decline of 38%.

Studying changes in distribution maps are a crude method of assessing the status of a species, as trends are only noticeable once a colony has become extinct. Changes in the relative abundance at extant sites provide much more information and can be monitored using standard techniques developed to study butterflies in the 1970s (Pollard, 1977; Pollard & Yates, 1993) and extended to study Odonata (Brooks, 1993). However, with a few exceptions, monitoring has only been instigated in the last few years. As these data sets are built up, they will provide extremely useful information on longer-term trends.

## 1.4 Conservation

The decline of *C. mercuriale* in the UK is believed to be due to the following main factors (Evans, 1989; Jenkins *et al.*, 1998; Thompson *et al.*, 2003a):

- Cessation of traditional grazing – this results in small streams becoming overgrown and facilitates scrub encroachment which shades out aquatic vegetation.
- Clearance or burning of bankside or emergent vegetation – wholesale clearance removes larval habitat as well as shelter and roosting sites for adults.
- Drainage and abstraction of water – often results in the lowering of the water table, thus sites become prone to drying out over the summer.
- Dredging and canalisation of streams – this destroys habitat.
- Pollution or nutrient enrichment
- Fragmentation of suitable habitats – the damselfly appears to be a poor disperser and has difficulty colonizing new sites that are not close to extant sites.

The declining status of *C. mercuriale* has been recognised and the species is now protected by a number of UK and European laws and conventions. It is the only UK dragonfly species to be listed on Annex II of the 1992 EC Habitats and Species Directive. This requires the designation of Special Areas of Conservation (SACs) for habitats and species that are rare, endangered or vulnerable across the EC as a whole. Six areas have been notified as SACs in the UK specifically for *C. mercuriale*. The species is also listed on the Bonn Convention and Appendix II of the 1979 Bern Convention. This outlaws the collection or possession of listed species.

In the UK, *C. mercuriale* is listed as rare (category 3) in the British Red Data Book (Shirt, 1987). It is protected under Schedule 5 of the Wildlife and Countryside Act, 1981. This protects against the killing or selling of individuals, and damage or destruction of habitat. It is only the second British dragonfly species to be listed (the other is the Norfolk hawker - *Aeshna isosceles*). The Wildlife and Countryside Act also strengthened the law regarding Sites of Special Scientific Interest (SSSIs). This is the main national designation and is the principal statutory means of site safeguard.

In 1992 the UK government signed the Convention on Biological Diversity at the United Nations Conference on Environment and Development in Rio de Janeiro. One of the most important obligations that this entails is to develop, or adapt, existing national strategies, plans or programmes for the conservation and sustainable use of biological diversity. The UK government ratified the Convention in 1994 and published its response in *Biodiversity: the UK Action Plan* (HMSO, 1994). The plan lists objectives and targets in three broad areas; protected area management, wider countryside issues, and species conservation. The most ambitious part of the plan was to produce an action plan for all threatened species and habitats. Initially, 114 species and 14 habitats were selected as the top priority for conservation in the UK. The list was later expanded, and between 1995 and 1999 action plans were published for a total of 391 priority species and 45 priority habitats (UKBG, 1999). *Coenagrion mercuriale* was selected as a priority species in the initial phase, and a species action plan was published in 1995 (HMSO, 1995). A national steering group was set up to oversee conservation of *C. mercuriale* and implementation of the species action plan, comprising representatives from government agencies, NGOs and academia. This steering group played a key role in the commissioning of this thesis, with the aim of improving knowledge of the ecological requirements of the species in calcareous habitats.

## 1.5 Thesis overview

The aim of this thesis is to investigate aspects of the ecology of *C. mercuriale* in its chalkstream habitat. In particular, patterns of adult movement and dispersal, habitat requirements of mature adults, roosting site selection, and the ecology and habitat requirements of larvae are examined. It is hoped that the study will provide a basis for further conservation efforts by guiding habitat management plans, informing conservation strategies and suggesting targets for surveillance and monitoring programmes.

Following this introduction, the subsequent chapters will be organised in the order described below. Chapter 2 describes European studies of the species in calcareous habitats, before turning to chalk stream sites in the UK. In this I describe distribution patterns, provide information on habitat, management, and previous studies conducted, and introduce my study sites in the Itchen and Test Valleys.

Chapter 3 describes a large mark-release-recapture (MRR) experiment performed in the Itchen Valley in summer 2001. It outlines the numbers marked and recaptured and patterns of adult movement and dispersal. This includes net lifetime movement, movement between local populations, the effect of sex, site, age, time, season, order, mercury mark, and density on movement. It also looks at the effect of a road and railway barrier on movement, and the upstream or downstream direction of movements. It highlights the importance of landscape structure to *C. mercuriale* conservation.

In Chapter 4 I examine data collected regarding the physical habitat, management, bankside vegetation and in-channel vegetation in order to investigate the relationship between habitat and *C. mercuriale* density. I also examine the effect of local population size on density, as well as movement in relation to habitat variables. This chapter has important implications for management as it highlights the most suitable habitat conditions for adults as well as potential targets for habitat monitoring.

Chapter 5 reports on the results of a night-time study of adult roosting location. In it I describe the numbers of damselflies seen, patterns of aggregation, distance from daytime location, roosting height, plant species chosen in relation to available habitat, and orientation. This chapter highlights the need for appropriate habitat management in the areas surrounding watercourses, in addition to stream and bankside habitat management.

Chapters 6 and 7 present the results of a major study undertaken to investigate the ecology and habitat requirements of *C. mercuriale* larvae. The distribution and abundance of *C. mercuriale* larvae is described. In Chapter 6 the associated macroinvertebrate community is investigated, together with issues of taxonomic resolution and *C. mercuriale* diet. In Chapter 7 *C. mercuriale* occurrence and abundance are related to physical, chemical and vegetation attributes. Once again, these chapters have important conservation and management implications.

The final chapter (Chapter 8) draws together the findings from the previous chapters and provides a series of conservation and management recommendations. Fruitful areas for further research are highlighted and suggestions for monitoring are given.

This thesis has been greatly enhanced by the substantial amount of financial and practical support that it has received. Additional funding enabled the recruitment of 17 fieldwork assistants for the mark-release-recapture study presented in Chapter 3. Some of these also helped with the collection of habitat data used in Chapter 4 and night-time roosting information used in Chapter 5. In a separate initiative, much additional funding was also provided for the study of *C. mercuriale* larvae presented in Chapters 6 and 7. The scope of these studies is, therefore, far greater than would have been possible had I worked alone, and the findings are more comprehensive. It is, perhaps, a reflection of the importance with which *C. mercuriale* conservation is regarded, that so much additional input was provided.

# Chapter 2: *Coenagrion mercuriale* in calcareous habitats

In the UK, *Coenagrion mercuriale* occurs on two distinctive habitat types; base-enriched lowland heathland streams and calcareous streams and fens. Although the species is found less often on the latter habitat in the UK, this habitat is more typical in the remainder of its European range. To date, studies in the UK have focused largely on the former habitat and large gaps remain in our knowledge of the latter. However, studies have been performed on *C. mercuriale* in calcareous habitats in other parts of its European range and these provide important background to the present study.

The aim of this chapter is twofold; to review the literature concerning *C. mercuriale* in calcareous habitats and to introduce my study sites. The review will focus on studies performed outside of the UK, particularly from Germany, France and Belgium. I will briefly describe distribution and status of *C. mercuriale,* before providing details of habitat and conservation issues. I will then turn my attention to the Itchen and Test Valleys in the UK, the location of my study sites. I will provide some general information concerning this area, before providing a description of the distribution of *C. mercuriale*, its habitat, current management and an outline of previous studies. I will finish by providing a brief outline of the key characteristics of the study sites used in this investigation.

## 2.1 *Coenagrion mercuriale* in mainland Europe

### 2.1.1 Germany

*2.1.1.1 Distribution and Status*

*Coenagrion mercuriale* is more or less restricted to south-west Germany. It is found in 156 locations in Baden-Württemberg (Sternberg *et al.*, 1999) and in 102 locations in Bavaria (Kuhn, 1998), with few reports from other regions. However, despite the large number of occupied sites, abundance is low in the majority of them and hence a great number of the populations are at risk. In a survey in Baden-Württemberg in 1993, less than 10 individuals per 100 m was recorded at 80% of the sites, and no sites had more than 50 per 100 m (Röske, 1995). Buchwald *et al.* (1989) considered populations with a density of less than 10 per 100 m to be endangered, and those with between 10 and 20 to be threatened. According to these categories, 80% of the populations were endangered and a further 10% threatened in 1993 (Röske, 1995).

The populations in Baden-Württemberg, in particular, have been the subject of much research (e.g. Buchwald, 1983, 1989, 1994; Buchwald *et al.*, 1989; Röske, 1995; Hunger & Röske, 2001), which is summarised below.

### *2.1.1.2 Habitat – Abiotic factors*

*Coenagrion mercuriale* occupies three habitat types in south-west Germany (Buchwald, 1994; Sternberg *et al.*, 1999):

1) Meadow streams and ditches – which share the characteristics of being slow-flowing, sunny, calcareous, and are neutral to alkaline in pH. The majority of German sites occur in this habitat, which is comparable to the water meadow sites in Hampshire.
2) Rivulets in calcareous marshes – where the species establishes small populations in rivulets close to springs. This habitat type is rarely used in Germany, but appears to be comparable to the calcareous fen habitats of Oxfordshire and Anglesey.
3) The headwaters of major rivers – such as the upper Rhine, where it is usually found close to ground water springs.

Buchwald (1994) names four principal abiotic factors that are vital in the habitat choice of *C. mercuriale*:

1) Exposure to sunlight – in 117 sites investigated, 70% were completely unshaded, and no site was more than 20% shaded.

2) Current – a constant flow of water is required all year round. It is believed that this is linked to oxygen requirements, which must be at least 2.5-3.0 mg/l. In 64% of sites, the current flow was from 1-15 cm/sec, while the flow rate was up to 35 cm/sec at the remaining sites.
3) Permanent water flow – *C. mercuriale* is unable to survive the drying up of its habitat.
4) Proximity to springs and/or groundwater influence – this results in relatively warm ice-free winter temperatures, and encourages year-round growth of aquatic vegetation.

Streams are also usually shallow (1-20 cm), and this factor combined with the high exposure to sunlight results in rapid warming of larval habitats in the spring (Sternberg *et al.*, 1999). Streams are usually narrow (0.2 - 1.6 m wide) although *C. mercuriale* can sometimes be found on small rivers (1.6 – about 6 m) (Sternberg *et al.*, 1999). The pH measured at sites in Baden-Württemberg ranged from 6.6-8.5 (Buchwald, 1989; Sternberg *et al.*, 1999).

### *2.1.1.3 Habitat - Vegetation composition*

*Coenagrion mercuriale* is not linked to any specific species of plant, but is highly selective in its choice of breeding waters. In a study of 117 sites in Baden-Württemberg, Buchwald (1994) found that a range of species was present, but none was recorded at more than 40% of the sites (Table 2.1). However, when the vegetation was assigned to phytosociological communities the emergent vegetation could be categorised into one of only six associations out of a possible 35 that occur in flowing waters in south-west Germany. Several of the species and communities are indicators of groundwater influence and other abiotic factors. It appears, therefore, that the damselfly is selecting species that are indicators of a particular habitat type, rather than the species themselves.

A wide variety of plant species are used for oviposition, although plants with hard parts are avoided (Sternberg *et al.*, 1999). The same finding has been recorded in the UK

(Purse, 2001). *Berula erecta* is widely used in Germany, but other species chosen include *Callitriche* spp., *Eleocharis palustris, Elodea canadensis, Glyceria* spp., *Rorippa nasturtium-aquaticum,* and *Phalaris arundinacea* (Sternberg *et al.,* 1999). The use of these plant species was not significantly different from their abundance, indicating once more that *C. mercuriale* is selecting the habitat rather than individual species.

**Table 2.1.** Percentage occurrence of plant species at sites (n = 117) containing *C. mercuriale* in Baden-Württemberg (from Buchwald, 1994).

| | | |
|---|---|---|
| **Emergent plants:** | | |
| *Berula erecta* | lesser water-parsnip | 40 |
| *Mentha aquatica* | water mint | 32 |
| *Myosotis scorpioides* | water forget-me-not | 31 |
| *Veronica beccabunga* | brooklime | 31 |
| *Rorippa nasturtium-aquaticum* | water-cress | 28 |
| *Veronica anagallis-aquatica* | blue water-speedwell | 19 |
| *Glyceria fluitans* | floating sweet-grass | 18 |
| **Submerged and/or floating plants:** | | |
| *Callitriche stagnalis & platycarpa* | common & various-leaved water-starwort | 26 |
| *Callitriche obtusangula* | blue-fruited water-starwort | 21 |
| *Lemna minor* | common duckweed | 15 |
| *Callitriche (cf.) hamulata* | water-starwort | 7 |
| *Elodea Canadensis* | Canadian waterweed | 6 |
| *Ranunculus trichophyllos* | water-crowfoot | 3 |
| *Groenlandia densa* | opposite-leaved pondweed | 2 |

*Coenagrion mercuriale* occupies habitats in Germany with emergent vegetation cover ranging from 3-100%, and submerged vegetation of at least 1% (Buchwald, 1994). However, the species appears to prefer sections of water with 30-60% emergent vegetation. This has been suggested by observations, and was confirmed in an experiment involving selective cutting of the vegetation (Buchwald, 1994). It was shown that the species is able to differentiate and select between the vegetative structure of expanses of water as short as 1m in length. When five sections were cut to provide emergent vegetation ranging in cover from 5-85%, *C. mercuriale* abundance was highest where the coverage was 40% and 60%. It should be noted, however, that this was a small experiment with no replication. Other studies have indicated that the species prefers lower vegetation densities, and that there are regional differences.

Sternberg *at al.* (1999) reported a preferred density of 1-20% in the Upper Rhine Valley, but 10-40% in the Alpine region, and 50-90% in the calcareous marsh habitat.

In meadow streams in Baden-Württemberg the average vegetation height is less than 1 m, and the optimal height is 20-40 cm (Sternberg *et al.*, 1999).

### *2.1.1.4 Adjacent land*

Buchwald *et al.* (1989) investigated the use of adjacent land by *C. mercuriale*. During good weather they primarily used the stream and bankside vegetation, and abundance decreased with increasing distance from the water, up to about 8m. During bad weather and at dawn, few individuals were counted on aquatic plants, with most occurring on the adjacent land within a distance of about 10m. It is believed that individuals use these adjacent areas to survive periods of unfavourable weather, to spend the night, to look for food, and to mature. Hunger & Röske (2001) were the first people to study the location of night-time resting sites, by marking individuals with a UV-pen and then searching at night using a portable UV-lamp. They located marked individuals resting up to 100m from the nearest stream, although 70% were found within a strip 5m to either side of the streams, and 96% were resting within 25m of the streams.

Abundance was also influenced by the land use of the adjacent land (Buchwald *et al.*, 1989). Extensive grassland is the most favoured habitat, particularly rush-pasture, followed by fallow land and unmown improved grassland. Individuals were, however, never found in arable areas or meadows for a few weeks after they had been mown. Use of fallow land was dependent upon the vegetation present; reed communities were used, but *Rubus* spp. was not accepted. Furthermore, Buchwald (1994) revealed that almost all larger populations of *C. mercuriale* in Baden-Württemberg were either partially or wholly surrounded by meadow.

Following these results, a protection strip with a minimum width of 10m on both sides of the channel was recommended where populations occur on farmland (Buchwald *et al.*, 1989). This would have the benefit of protecting the stream from the direct influence of pesticides and nutrients from the agricultural land, as well as providing more suitable habitat for the adults. It was recommended that native grassland should be sown, with minimum nutrient input, and that the grassland should be cut twice a year, but in sections with a temporal shift. Röske (1995) attempted to implement this idea as part of a species protection programme in Baden-Württemberg, with compensation for lost earnings. Unfortunately, very few farmers agreed, as the compensation was considered to be too low, farmers did not wish to lose control of strips of their land, and the scheme was considered to conflict with the Common Agricultural Policy.

#### *2.1.1.5 Conservation and management*

The major threats to *C. mercuriale* in south-west Germany are considered to be (Buchwald, 1994):

- Lack of maintenance of the streams and banks, leading to the development of thick stands of vegetation, resulting in the channels becoming shaded and/or overgrown.
- Eutrophication of the channel as a result of fertilization of adjacent farmland.
- Intensive maintenance of streams and ditches by frequent clearing operations.

Other less frequent factors include organic pollution, rubble from construction work, hydraulic engineering works such as drainage, and drying out of the waters as a result of the lowering of the groundwater levels or changes in the water flow. These factors are almost identical to those believed to be responsible for the decline of the species in the UK (Section 1.4).

In 1993, 141 of the 156 known sites in Baden-Württemberg were assessed, and it was found that *C. mercuriale* was absent from 41% of these sites and had declined at a further 16% since the period from 1985-92 (Röske, 1995). Small and isolated colonies were particularly prone to extinction. The species had increased at only 5% of the sites and was unchanged at the remaining 38%. Density was also low, with 1-10 individuals per 100m recorded at 80% of the sites, and no sites had more than 50 per 100m.

*Coenagrion mercuriale* has been the subject of a species protection programme since 1991 (Röske, 1995). In the first three years of the programme (1991-3) conservation measures were undertaken at 35 sites. Populations increased at 31% of these sites, remained stable at 52%, and declined at 17%, a considerable improvement on the trends shown for the whole area (Röske, 1995).

More detailed studies of the effect of specific conservation measures were performed at a few sites. Two management practices were tested (Röske, 1995); the effect of a careful excavation of the channel bottom and clearance of aquatic vegetation, and the impact of cutting the river bank.

In the first test, the river bottom was cleared carefully using a scoop excavator. At one site the channel was divided into 5-10m sections and cleared on alternate sides so that a cleared section always lay opposite an uncleared section. At a second site the channel was divided into three 100m sections, 100m was cleared on one side in the first year, an additional 100m was cleared in the second year, and the final section remained uncleared. In both cases, abundance fell dramatically during the summer following initial clearance, but had largely recovered by the third summer. Unfortunately, data are not available beyond the third summer, and so it is difficult to ascertain longer-term trends. It was also not possible to determine which clearance method was more effective.

In the second set of tests, the river banks at two sites were cut with a manual motor scythe and the cuttings removed. The banks were divided into 10-40m sections and half were mown. At one site, *C. mercuriale* abundance was always greatest in the cut sections. At a second site, with more detailed observations, it was noted that the cut sections were avoided for a few weeks after mowing. As has previously been noted, habitat preference was determined by the weather. During fine weather most adults occurred over the water, but during sub-optimal weather they occurred more frequently on the bankside and the surrounding land.

### 2.1.2 France

#### *2.1.2.1 Distribution and status*

*Coenagrion mercuriale* is widespread in France, and was known to occur in 67 of the 95 national districts in the mid 1990s (Grand, 1996). According to that author the species was present in 17 of the 22 administrative regions of France, but this now stands at 20 (Anon., 2004a). It has been recorded from over 400 localities (Grand, 1996) and 129 sites are now protected as Natura 2000 sites (Anon., 2004a). Nevertheless, its status is considered to be vulnerable, as it is relatively widespread but in decline (Grand, 1996; Deliry & Grand, 1998). It is absent from the Parisian basin and the extreme north of the country, but occurs in low density across most of the rest of France. The Rhône-Alpes region contains perhaps the highest density of sites, with the greatest number of Natura 2000 sites (22).

Little appears to be known concerning the relative strengths of the populations. However, at Marais Vernier et Basse Vallée de la Risle in Haute-Normandie, which is considered to be an important site for *C. mercuriale* (Anon., 2004a), a daily maximum of approximately 80 has been recorded along a 600m stretch of ditch (C. Dodelin, *pers. comm.*).

Although it had been recorded in a few locations, little was known about the species in France until the 1980s and 1990s. Since that time, it has been discovered or rediscovered across a wide area and study has been focused in the Rhône Valley. It is anticipated that the species will be found in a significant number of additional sites following further investigations (Deliry and Grand, 1998). Although the distribution and status of *C. mercuriale* in France is generally understood, there have been few published reports on the ecology of the species.

#### *2.1.2.2 Habitat – Abiotic factors*

The habitat is described as "small running waters" (Deliry & Grand, 1998), and includes springs, rivulets and other flowing waters. Meadow streams and ditches are commonly used, for example in the alluvial plains of the Rhône. The species has been recorded in calcareous marshes, and in the headwaters of major rivers such as the Rhône and the Durance (Deliry & Grand, 1998). These are analogous to the habitat types described by Buchwald (1994) in south-west Germany.

The importance of a continuous flow of water throughout the year is stressed, and many of the sites are spring and/or groundwater influenced (Deliry & Grand, 1998). The substrate of most sites consists of calcareous alluvial deposits, usually of limestone origin.

The majority of sites are below 400 m in altitude, although this is clearly exceeded in certain areas. The highest known site in the Rhône-Alpes occurs at 1058 m in the Hautes-Alpes department (Deliry & Grand, 1998). There is a clear latitudinal gradient with respect to the maximum altitude at which the species can occur. In the UK the highest colonies have been found at 290 m at Waun Maes in the Preseli Hills (S. Coker, *pers. comm.*), and at Moortown Bottom in Dartmoor (D. Smallshire, *pers. comm.*). In Germany it is found up to 600 m (Sternberg *et al.*, 1999), in Spain up to 1500 m (Ancelin *et al.*, 1986, *cited in* Grand, 1996), and can colonise sites in Morocco over 1850 m (Jacquemin, 1994).

The site at Marais Vernier et Basse Vallée de la Risle is made up of a mosaic of different habitats, including both acid and alkaline marsh, semi-natural grassland, woodland and both stagnant and flowing waters (Anon, 2004b). The species occurs in small spring-fed ditches, with shallow water and very slow flow, flowing through unshaded open meadows (*pers. obs.*).

### *2.1.2.3 Habitat - Vegetation composition*

In the Durance, in southern France, optimal habitat is characterised by *Typha* spp., *Iris-Cladium* vegetation, and *Juncus* spp., but *C. mercuriale* also occurred in areas with willows (*Salix* spp.). Emergent vegetation typically consisted of *Berula erecta, Mentha aquatica, Rorippa nasturtium-aquaticum*, and *Veronica anagallis-aquatica*; while submerged and floating vegetation was dominated by *Lemna minor, Callitriche* *obtusangula, Enteromorpha intestinalis,* and *Lemna trisulca* (Hedderich *et al.*, 1985, *cited in* Sternberg *et al.*, 1999).

*Berula erecta, Sparganium* spp. and *Mentha* spp. were most frequent at sites in the Rhône Valley (Deliry & Grand, 1998). Meanwhile, the vegetation at a site in Brittany consisted of a rich mosaic of *Callitriche* spp., *Berula erecta, Mentha aquatica, Sparganium erectum, Typha latifolia, Solanum dulcamara, Lycopus europaeus, Rumex* spp. and *Iris pseudacorus* (Martens, 2000).

At Marais Vernier et Basse Vallée de la Risle ditches typically contain lots of bare silt and only pockets of emergent vegetation, such as *Apium nodiflorum* (*pers. obs.*). Banksides contain abundant *Phalaris arundinacea.* Signs of nutrient enrichment were present in some areas, including large quantities of *Cladophora* and *Lemna minor* (*pers. obs.*).

### 2.1.3 Belgium

#### *2.1.3.1 Distribution and Status*

*Coenagrion mercuriale* is extremely rare and in danger of extinction in Belgium, with most records dating back from before 1950 (Grand, 1996). Until recently, it was believed that only one population remained, in the plain of Focant close to Beauraing, in the province of Namur (Goffart, 1995). However, it has been recorded at three new locations since 1998 in the Gaume, in the province of Luxembourg (Ternaat, 1999; De Knijf & Demolder, 2000; Goffart *et al.*, 2001). The Gaume is in the southern most part of Belgium and it is believed that the species migrated from the adjacent northern part of France, perhaps related to climate change (Goffart *et al.*, 2001).

The new populations in the Gaume are extremely small (Ternaat, 1999; De Knijf & Demolder, 2000), but that from Focant is considerably larger. In 2001, 459 individuals were counted in one section of this site on a single visit, although counts from other sections were considerably weaker (Goffart *et al.*, 2001). The site has been monitored on an occasional basis since 1984 (Goffart, 1995; Goffart *et al.*, 2001), in which time there has been considerable changes in land use of the various sections, resulting in a shift in the precise location and abundance of *C. mercuriale* (see below).

### *2.1.3.2 Habitat*

The habitat in Focant is described as small drainage channels, with very slow flow, almost stagnant in places (Goffart, 1995). The channels are typically 1 to 1.5m wide, with a water depth ranging from 1 to 150cm. Vegetation typically consists of *Rorippa nasturtium-aquaticum, Berula erecta, Veronica beccabunga, Glyceria fluitans, Juncus inflexus and Myosotis scorpioides.* Typical bankside plants include *Iris pseudacorus, Sparganium erectum, Typha* sp., *Phalaris arundinacea* and *Equisetum* sp. Channels are relatively clear of vegetation when first cleared or dredged, but gradually become densely vegetated and eventually choked. The channels containing the highest population of *C. mercuriale* are unshaded and surrounded by meadows.

The habitat at one of the new locations in the Gaume is described as a small fast flowing stream with a sandy substrate (Ternaat, 1999).

### *2.1.3.3 Conservation and management*

The population of *C. mercuriale* at Focant has changed dramatically over the last 15 years (Goffart *et al.*, 2001). For example, the land surrounding the stream with the strongest population in the 1980s was planted with trees in 1989. The population subsequently fell from about 300 individuals in 1987, to 3 by 2001 (Goffart *et al.*, 2001). The species has also declined or disappeared from several other sections of ditch, but has colonised some new sections. Three major threats have been identified (Goffart, 1995; Goffart *et al.*, 2001):

- Eutrophication of the water, due to agricultural fertilization and sewage from nearby villages. This leads to a change in vegetation from that described above, to one dominated by algae in the channels and *Urtica dioica* on the banksides.

- Mismanagement of the ditches, usually caused by intensive maintenance and frequent clearing operations.
- Shading of sites by the planting of trees.

## 2.2 *Coenagrion mercuriale* in calcareous habitats in the UK

*Coenagrion mercuriale* occurs in calcareous habitats in four areas in the UK. It occurs in calcareous fen in Oxfordshire, principally at Dry Sandford Pit, and at Cors Erddreiniog in Anglesey, and in chalk stream habitat in the floodplains of the River Itchen and River Test in Hampshire. The sites in Oxfordshire and Anglesey are isolated from other sites containing *C. mercuriale* and the populations are relatively small. The populations in the Itchen and Test Valley's, on the other hand, are large, with numerous colonies. These were the location of my study sites

### 2.2.1 Introduction to the Test and Itchen Valleys and the historical context

The River Itchen and the River Test are considered to be two of the finest examples of chalk streams in the country. All rivers reflect the nature of their catchments and many of the characteristics of the Test and Itchen can be attributed to their underlying chalk geology (Berrie, 1992). Chalk streams are predominantly fed from groundwater aquifers, and receive little surface runoff. This has the effect of smoothing the flow regime, as well as stabilizing the water temperature and chemical composition. Water is calcareous, typically with a pH of 7.4-8.0, contains low levels of suspended solids and a sufficient supply of plant nutrients (Berrie, 1992; Mainstone, 1999). These are conditions that support diverse and productive communities of plants and animals, including important game fisheries.

The importance of chalk streams extends beyond the boundary of the main river channel. Water meadows were constructed along most of the Itchen and Test flood plains in the period from about 1640 – 1730 (Bowie, 1987; Bettey, 1999). This involved the clearance of woodland and the construction of an extensive network of carriers and ditches to allow controlled flooding of the meadows. The objective was to maintain a steady flow of shallow water (25mm deep) flowing across the meadows on several occasions in winter and early spring (Cutting & Cummings, 1999). This protected the soils from frost and enabled early regrowth of grass in the spring, thereby increasing agricultural productivity. Indeed, they were a vital part of the agricultural economy of the region, with water meadows said to be worth three times as much as unwatered meadows (Bowie, 1987).

Water meadows were in operation until the end of the nineteenth century when they began to fall into disuse (Bettey, 1999). By the end of the Second World War they had been completely abandoned as agricultural tools. Before this time, however, fly fishing for trout and salmon had become established as a major income generator for the area. Although the network of small channels was abandoned, many of the larger carriers were maintained, often as fish hatcheries. These now provide a range of flow conditions and habitats, suitable for an array of plants and animals, thereby increasing the conservation value of the Test and Itchen floodplains.

### 2.2.2 Distribution and status of *C. mercuriale* in the Itchen and Test Valleys

#### *2.2.2.1 River Itchen*

The first recorded observation of *C. mercuriale* in the Itchen Valley dates from the 19th century, and was reported by Lucas (1900). Between 1900 and 1951 there are twelve records of the species (Stevens & Thurner, 1999), but the exact location of all these early sightings are difficult to ascertain. Names given are Winchester, Itchen, Eastleigh, Lower Itchen, Brambridge and Otterbourne. There are no records of the species between 1951 and 1982.

In 1983 an attempt was made to determine whether the species was still present, resulting in the discovery of two major breeding populations (Mayo & Welstead, 1983). These were at the Itchen Valley Country Park (IVCP), located between Eastleigh and Southampton, and at Otterbourne, approximately 7km to the north. Ten sites between Southampton and Winchester were assessed in 1998 as part of a survey commissioned to obtain baseline information on the status and distribution of *C. mercuriale* in Hampshire (Stevens & Thurner, 1999). The damselfly was present at eight of the sites investigated. Most recently, in 1999, a more comprehensive survey of the Itchen Valley was carried out between Bishopstoke and Winchester (Strange, 1999). The species was present at ten locations, and vegetation was recorded at each of these sites (see section 2.2.4.1).

The surveys in 1998 and 1999 also provided some information on the status of each population by categorizing them as weak (1 to 29 individuals), medium (30-99), or strong (100+). Only the populations in the IVCP were classified as strong. As the surveys progressed up the valley the populations became weaker, until finally petering out just downstream (south) of Compton Lock (NW of Twyford, see Figure 2.2) in spite of suitable habitat being available (Strange, 1999). A slight retraction in range is, therefore implied, as there are no extant records that correspond to the historical records from Winchester.

The IVCP has been the subject of more intensive survey and monitoring work. Following the initial survey in 1983 (Mayo & Welstead, 1983), *C. mercuriale* was recorded between 1988 and 1990 as part of a general invertebrate survey, with up to 50 seen on any one day (Oates, 1990, *cited in* EBC, 1995). In 1992 the park was visited by members of the British Dragonfly Society, who observed large numbers and concluded that the population was of equal importance to the largest colony in the UK (Crockford Stream in the New Forest) (Hold, 1998). However, it seems that 1992 was an exceptional year as numbers may have diminished since that time. The damselfly was recorded again in 1994, when over 100 were seen on a single visit (Hold, 1994).

In 1997, Hold (1998) carried out a more detailed investigation, examining larval habitat preference (see section 2.2.4.1) and adult distribution, and provided recommendations for the setting up of a monitoring scheme. A transect was the chosen method, and this was implemented the following year (Strange & Burt, 1998). Unfortunately, recording did not commence until the 19th July and so results cannot be compared with later years. However, the transect has been repeated over the complete flight period from 1999 onwards and the annual index of abundance is shown in Figure 2.1. There are numerous inaccuracies associated with transect recording, as numbers can vary enormously depending upon weather, time of day, recorder, missed weeks and so on. It is, therefore, unwise to draw conclusions from fluctuations in the data. However, the technique is extremely useful at highlighting longer-term trends in abundance. In this case, the population of *C. mercuriale* in the monitored part of IVCP appears to be stable (Figure 2.1.). It should be noted that the transect is situated in the upper section of the IVCP, where a strong population of *C. mercuriale* is present. The remainder of the site is not monitored on a regular basis. Indeed, no other sites in the Itchen Valley are routinely monitored.

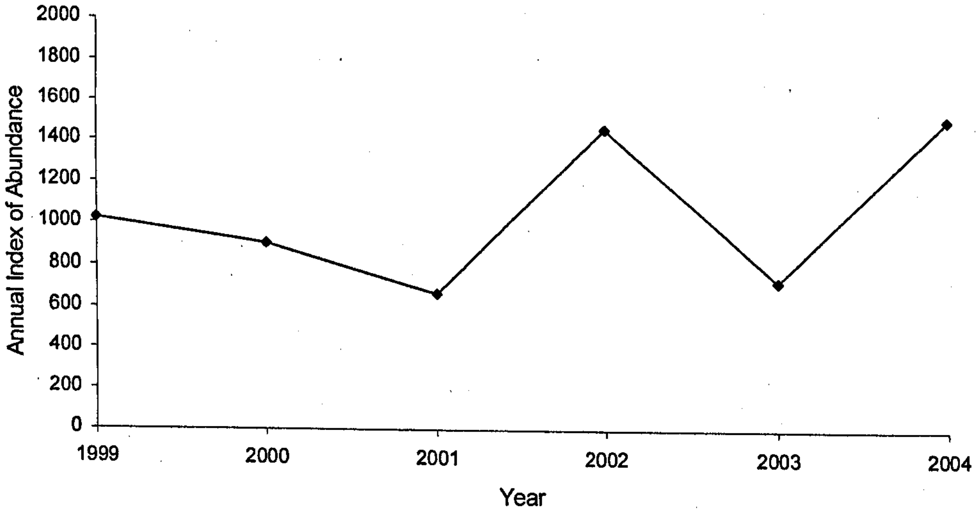

**Figure 2.1.** Annual Index of Abundance of male *C. mercuriale* recorded on weekly transects in the Itchen Valley Country Park (IVCP) (from K.Young, *unpublished*).

### *2.2.2.2 River Test*

The distribution and status of *C. mercuriale* in the Test Valley is far more uncertain. It was first recorded in the River Test Valley in 1927 (Merritt, 1983), at an imprecise location given as King's Somborne. There is also anecdotal evidence of the species occurring in the past at Chilbolton Common (8km further north). No other records are known until 1983, when a survey by Mayo and Welstead (1983) discovered the damselfly at a site close to King's Somborne.

Nine locations were surveyed during the 1998 county-wide survey (Stevens & Thurner, 1999). The damselfly was still present at the site of the 1983 record, and was recorded in large numbers at a site nearby. The status of the former colony was classified as medium, while the later was considered strong, with a maximum count of 350 recorded in one day, greater than any of the sites recorded on the River Itchen. However, it was not found at Chilbolton Common or any of the other locations searched. The authors noted that the survey was far from comprehensive and considered further unknown populations to be highly likely. Indeed, a new site was located nearby in 2000 (Strange, 2000) and a further small colony was found approximately 1 km further downstream (south) in 2002 (A. Hold, *pers. comm.*). However, much of the Test Valley remains unsurveyed and no sites are routinely monitored.

### 2.2.3 Habitat of *C. mercuriale* sites – abiotic factors

#### *2.2.3.1 River Itchen*

Most of the sites in the Itchen Valley, and all those supporting at least a medium population of *C. mercuriale,* were reported to share the following features in common (Stevens & Thurner, 1999; Strange, 1999):

- Occurred on old water meadow ditches.
- Ditches were maintained so that there was a year-round flow of water.
- Ditches were unshaded.
- Ditches had extensive shallow margins containing emergent vegetation.
- Sites were lightly grazed by cattle, or by cattle and horses.

The ditches most favoured by *C. mercuriale* appeared to be those with gently sloping banks showing natural transitions from terrestrial to aquatic plant communities. The vegetation type was indicative of unshaded water margins where there is some accumulation of medium to fine textured sediment. *Coenagrion mercuriale* occurred where there was marginal disturbance due to turbulence, cutting or moderate trampling (Strange, 1999).

Water velocity was measured at several nearby sub-habitats at Highbridge (Strange, 1999). *Coenagrion mercuriale* was found in channels where the velocity ranged from 7.5-20.5 cm/s, which can be classified as slow to moderate flows. The pH has been measured as 8.0 (Mayo & Welstead, 1983).

#### *2.2.3.2 River Test*

All known sites have been located on old water-meadow carriers and ditches on improved grassland, with a year-round supply of water from the main river (Mayo & Welstead, 1983; Stevens & Thurner, 1999). However, few details of the habitat at the *C. mercuriale* sites have been recorded.

### 2.2.4 Habitat of *C. mercuriale* sites - vegetation composition

#### *2.2.4.1 River Itchen*

The waterside plant community that appeared to be most preferred in the Itchen Valley was the NVC S23 *Glycerio-Sparganion* community (Strange, 1999). This is dominated by *Rorippa nasturtium-aquaticum* (water-cress), *Apium nodiflorum* (fool's water-cress) and *Veronica beccabunga* (brooklime). The vegetation communities on either side of the watercourses were extremely varied. However, a constant feature was the presence of grass tussocks, which were deemed to be important for *C. mercuriale* as shelter and roosting sites (Strange, 1999).

The ditches at the IVCP supporting *C. mercuriale* typically had an open central channel with a few submerged species, and a broad fringe of emergent and marginal species (EBC, 1995). Emergent vegetation was dominated by *Glyceria maxima* (reed sweet-grass) and *Phalaris arundinacea* (reed canary-grass), with *Rorippa nasturtium-aquaticum* (water-cress) and *Apium nodiflorum* (fool's water-cress) abundant in mid-channel (Mayo & Welstead, 1983; Strange & Burt, 1998). Other species commonly present included *Mentha aquatica* (water mint), *Rumex hydrolapathum* (water dock), *Carex acutiformis* (lesser pond-sedge), *Myosotis scorpioides* (water forget-me-not) and *Lycopus europaeus* (gipsywort) (Mayo & Welstead, 1983; EBC. 1995).

Species favoured for oviposition in the Itchen Valley included *Rorippa nasturtium-aquaticum*, *Apium nodiflorum* and *Veronica beccabunga* (Strange, 1999). Grasses were not favoured, although they were regularly used for perches. In the IVCP, a wide range of species was used, but *Glyceria maxima* and *Veronica* spp. were most commonly selected according to Hold (1998). *Coenagrion mercuriale* did not oviposit in sites that were overgrown with emergent vegetation (Hold, 1998).

Hold (1998) carried out the only investigation of larval habitat preference known to have taken place in the chalkstream habitat. Larvae were sampled over three dates in April 1997, using a sweep net and kitchen sieve. Four microhabitats were searched: the silt in the centre of the ditch, the silt bank / water interface, the main silt / vegetation bank, and the trampled area at the edge of the ditches.

Results indicate that *C. mercuriale* larvae were only found in those ditches with a year round water flow (Hold, 1998). No larvae were found in the centre of the ditches, and very few were collected from the trampled edge areas. Reasonable numbers were sampled in the remaining two microhabitats, with a preference for the silt bank / water interface. However, density of plant stems affected sampling effort and no attempt was made to sample the silt / detritus separately from the vegetation. Hold (1998) believed that larval microhabitat preference was areas of non-compacted silt at the base of plant stems, subject to a moderate water flow.

#### *2.2.4.2 River Test*

Detailed descriptions of vegetation composition at *C. mercuriale* sites in the Test Valley are lacking, once again. However, it is thought to be extremely similar to the sites in the Itchen Valley, with species such as *Glyceria maxima* (reed sweet-grass), *Phalaris arundinacea* (reed canary-grass), *Carex acutiformis* (lesser pond-sedge), *Rorippa nasturtium-aquaticum* (water-cress) and *Apium nodiflorum* (fool's water-cress) characteristic of the habitat (Mayo & Welstead, 1983; EN, 1996).

### 2.2.5 Conservation and management for *C. mercuriale*

#### *2.2.5.1 River Itchen*

*Coenagrion mercuriale* sites on the River Itchen are notified within the River Itchen SSSI and cSAC (candidate Special Area of Conservation), although full protection has only recently been achieved. The 1998 survey (Stevens & Thurner, 1999) revealed that many of the sites where the species was present were not included in the original notification. Fortunately, these areas were included in the SSSI following further notification in August 2000 (EN, 2000a), and an amendment was also made to the boundaries of the cSAC (EN, 2000b).

Most sites containing populations of *C. mercuriale* are on privately owned farmland. Until recently, conservation of *C. mercuriale* was not considered when managing these sites. The IVCP, however, is owned and managed by the local council as a public amenity, with recreation and conservation the principal management objectives. As such, conservation of *C. mercuriale* is considered to be a key priority (EBC, 1995) and this site is the only one in which the effects of management practices can be assessed.

In 1991, the IVCP was entered into the Countryside Stewardship Scheme, which led to an adjustment of management practices (EBC, 1995). The grazing regime was altered, so that 110-120 beef cattle grazed for six months between 1 April and 31 October at a stocking rate of 1 livestock unit per hectare. Prior to that time, the site had been grazed by a mixture of sheep and cattle all year round, at the discretion of the grazier. The use of artificial fertilisers was banned. New weirs were installed so that ditch levels could be maintained at a high level in the summer and shallow flooding created in winter. Finally, a programme of rotational clearance of short (20-50 m) sections of some ditches on a five-year cycle was begun in 1992. Work was carried out with a Hymac-type excavator, retaining a fringe of emergent vegetation on one or both sides of the ditch. The spoil was left on one side of the ditch.

Unfortunately there has been no monitoring of the effect of these management practices on *C. mercuriale* populations and little monitoring of the aquatic vegetation. Anecdotal evidence suggests that the species may have declined slightly following the raising of water levels in 1991. The damselfly responded positively when a previously dry ditch close to the centre of population was opened up. However, water flow was not maintained, the ditch quickly became choked with silt and vegetation and *C. mercuriale* disappeared. Management work on the key ditches is currently on hold, until more is known about the preferred conditions of the species at this site. From 2001 grazing was adjusted so that a stocking rate of 1.1 livestock units per hectare was maintained until the end of September each year (R. Mould-Ryan, *pers. comm.*).

#### *2.2.5.2 River Test*

The River Test was notified as a SSSI in 1996, but most of the known area occupied by the species is currently outside of the protected area (Stevens & Thurner, 1999). *Coenagrion mercuriale* sites on the River Test occur on privately owned farmland and fisheries and little is known of management practices or their effect on *C. mercuriale* populations.

### 2.2.6 Study sites

The investigations reported in this thesis were mostly performed in the Itchen Valley, between Winchester and Southampton. Study sites are shown on Figure 2.2 and included almost all locations where *C. mercuriale* had previously been recorded (Stevens & Thurner, 1999; Strange, 1999). Unfortunately, access to the Test Valley is extremely limited. As a consequence only one area close to King's Somborne was incorporated, although this did include both of the *C. mercuriale* sites identified by Stevens & Thurner (1999). Details of which sites were used for each investigation in this thesis are provided in the relevant chapters. Below I provide a brief outline of current management and general conditions at all of the study sites:

*Compton Lock* is publicly owned. It is cattle grazed and livestock have access to the water's edge. In one area of the site, management work has recently been undertaken to install a series of small channels to demonstrate the workings of the old water meadow system. There are no records of *C. mercuriale* from this site.

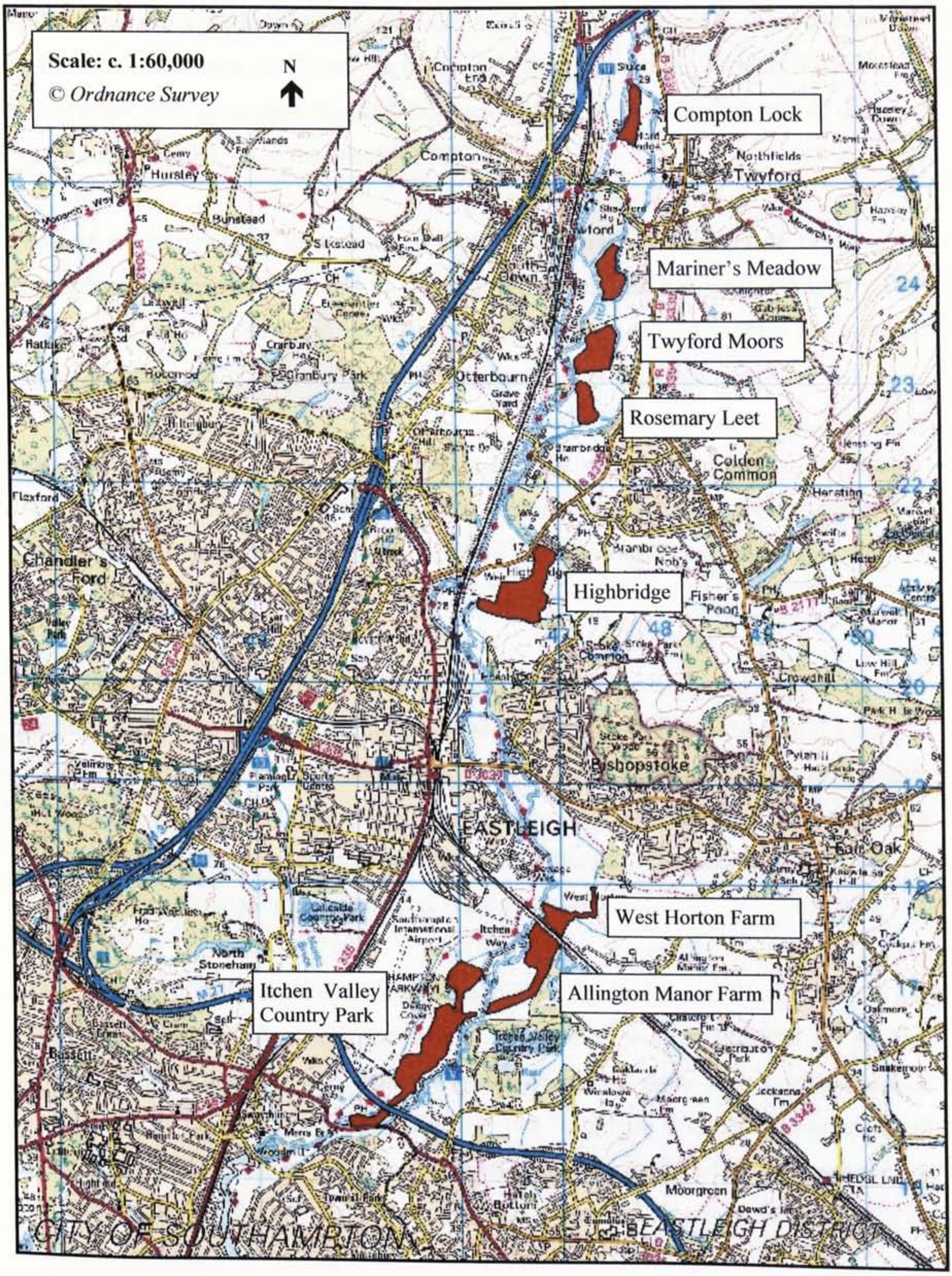

**Figure 2.2.** Location of study sites within the Itchen Valley

*Mariner's Meadow* is cattle grazed. Channels are open to grazing and are generally shallow and wide with abundant emergent and wetland vegetation. The owner has recently entered into a Countryside Stewardship Agreement, which includes a management plan to manage the ditches on a rotational basis. The first area of ditch in the plan was cleared out in the winter of 2001-2.

*Twyford moors* contains three ditches, each very different in terms of habitat and management. One ditch is open to grazing, unshaded, and has wide margins. The second is extremely small and is fenced and partially shaded. The third has a much larger discharge and is unfenced, but is heavily shaded by bankside trees.

*Rosemary Leet* is an important trout fishery and the channel is managed to promote fast-flowing gravel and *Ranunculus* habitats, ideal for spawning. The channels are steeply sided, the banks are low with a narrow fringe of emergent vegetation, and the bank tops are mown for use by fishermen.

*Highbridge* is mostly cattle grazed and the banksides are unfenced and so open to grazing. The water meadows at this site were only abandoned at the time of the Second World War (H. Russell, *pers. comm.*) and many of the original ditches are still visible. The owners are currently attempting to restore the original water meadows, including the construction of new sluices and the recreation of old ditches. This work is supported by a Countryside Stewardship Agreement.

No *C. mercuriale* sites had been identified between Highbridge and West Horton, a gap of about 3 km, when fieldwork was begun and no areas were included in my studies. However, small colonies have since been discovered in three places. This area is surrounded by urban areas and is divided in two by a road connecting Eastleigh and Bishopstoke. The northern part is mostly used as playing fields, while the southern part is under arable production. However, these areas were originally meadows and their land use has only been changed relatively recently. The playing fields were created in two stages in the late 1960s and 1970s, while the arable land was first ploughed in the mid 1990s (T. Sykes, *pers. comm.*).

*West Horton* is the only site that I studied that is sheep grazed. The ditches and banks are fenced and the banksides are vertical with little marginal vegetation. This site, together with Allington Manor and the Itchen Valley Country Park form a large area of near-continuous habitat that is referred to in the text as the Lower Itchen Complex (LIC).

*Allington Manor* is grazed by a combination of cattle and horses, which have access to the banksides. The channels tend to be deeper and faster flowing than in many of the other study sites. Grazing intensity is relatively high, although the site has just entered into a Countryside Stewardship Agreement, which will address this issue.

The *Itchen Valley Country Park* (IVCP) is owned and managed by Eastleigh Borough Council and extends over an area of 103 Ha. Due to its large size, I divided it into Upper, Middle and Lower sections during my investigations, corresponding to changes in management. The whole site is lightly cattle grazed at a stocking intensity of around 1.1 grazing units per hectare. The channels in the Upper section of the IVCP are open to grazing, but most of the Middle and Lower sections are fenced on one side to encourage habitat suitable for the water vole (*Arvicola terrestris*) and otter (*Lutra lutra*). A wide range of channel and bank profiles is present at this site. In several locations, underwater ledges or platforms were present at the edges of the main channel. These berms are formed either by dredging at two different levels during management works, or by the action of livestock trampling the soft banks, and provide ideal habitat for marginal aquatic vegetation.

The *River Test* was studied at a field site close to *King's Somborne*. This was a large site and included the two major *C. mercuriale* colonies previously identified by Stevens & Thurner (1999). Most channels at this site were relatively large, with variable depth and flow regimes, although two smaller channels were also present. One large channel was fished and so the bankside was mown and there was no access to livestock. Most of the site, however, consisted of open cattle grazed meadows, and channels were generally unfenced.

# Chapter 3: Adult movement patterns

## 3.1 Introduction

Movement and dispersal play a fundamental role in species ecology and evolution. These processes drive local and metapopulation dynamics, determine the spatial scale of evolutionary change, and dictate the response of organisms to fragmentation and climate change (Dieckmann *et al.*, 1999; Clobert *et al.*, 2001; Bullock *et al.*, 2002). Understanding movement and dispersal is becoming increasingly important as landscapes become ever more fragmented and species continue to decline.

Patterns of movement and dispersal are strongly influenced by the structure of the landscape. Increased habitat fragmentation will lead to an increased mortality rate associated with dispersal and this can eventually lead to the loss of genes coding for dispersal in isolated populations (Dieckmann *et al.*, 1999). If they become isolated, small populations will lose genetic variation through inbreeding and genetic drift and will become increasingly prone to extinction. Roads and railway lines can further increase fragmentation by acting as barriers to movement (Forman & Alexander, 1998; Keller & Largiadèr, 2003).

Most studies of dispersal in insects have concentrated on butterflies, and there have been relatively few studies of Odonata. However, odonates, and especially damselflies, are particularly good study organisms. They are large, conspicuous, easily handled and straightforward to mark. They live in inherently patchy environments, as they are restricted to aquatic habitats for larval development, and most of the mature adult life is spent at or near to the breeding sites.

In this chapter we use mark-release-recapture (MRR) methods to directly measure movement of the endangered damselfly *Coenagrion mercuriale* (Charpentier) (Odonata: Coenagrionidae). Previous studies of *C. mercuriale* have suggested that most individuals are extremely sedentary, although a few move distances of up to about 1km (Purse *et al.*, 2003; Hunger & Röske, 2001). Our study system is much larger in scale, includes several sites, and we are able to compare two areas of contrasting landscape structure. The study area is divided into two by a major urban area, with a large area of near–continuous habitat on one side and an area of smaller more isolated sites on the other. Sites are arranged in a linear series along a river valley; hence movement is constrained to one dimension at the landscape scale. Furthermore, the area is bisected by a motorway and a railway line, enabling us to investigate the potential of these structures as barriers to movement.

The aims of this study are to investigate patterns of movement and dispersal of *C. mercuriale* as part of an effort to understand the ecology and conservation requirements of this endangered species. Specifically, we examine the following issues:

- Patterns of movement, particularly with respect to landscape.
- Factors affecting movement such as season, age, time, and sex.
- Effect of density on movement.
- The direction of movements.
- The effect of a road and railway line on movement.

In a parallel study movement in these populations have been investigated indirectly, using DNA microsatellite markers (Watts *et al.*, 2004).

## 3.2 Methods

### *3.2.1 Study species*

*Coenagrion mercuriale* is highly specialised in its habitat requirements and is restricted to two fragmented biotopes in the British Isles (Thompson *et al.,* 2003a). These are small lowland heathland streams emanating from base-rich substrates, and calcareous streams and fens. Since 1985 it has declined by 38% and is currently limited to 28 of the UK's 10 km grid squares (Purse, 2001). It is classified as rare in the British Red Data Book (Shirt, 1987), is protected under the Wildlife and Countryside Act of 1981, and is the only odonate currently given priority status in the UK Biodiversity Action Plan (HMSO, 1994; 1995). It is also threatened in the rest of Europe, particularly at the northern and eastern boundaries of its distribution (Grand, 1996) and is protected under the Bern Convention and the EC Habitats Directive.

### *3.2.2 Study sites*

The study area is located between Winchester and Southampton in Hampshire (southern England). Here, *C. mercuriale* is found principally on old water meadow carriers and ditches along the flood plain of the River Itchen. The species occurs in three main areas (Stevens & Thurner, 1999; Strange, 1999), which from north to south are Mariner's Meadow, Highbridge, and the Lower Itchen Complex (Figure 3.1). The latter site is separated from the others by approximately 3km of largely sub-optimal habitat, made up of an urban area and sections of intensive agriculture. Mariner's Meadow and Highbridge are also separated by approximately 3km. An additional site does exist between these two, where *C. mercuriale* occurs in low numbers, but we were not able to perform the MRR study at that site.

The Lower Itchen Complex is a large area of near-continuous habitat, so to ensure comparable sampling intensity we divided this area into five sub-sites of approximately equal length. From north to south these are West Horton, Allington Manor, and three sub-sites (Upper, Middle and Lower) within the Itchen Valley Country Park (IVCP). In total, 7.65km of ditch was surveyed at the seven sites and sub-sites. A railway line on an embankment crosses between West Horton and Allington Manor and the Lower section of the IVCP is split in two by a motorway (Figure 3.1). We were therefore able to investigate their potential effects as barriers to movement.

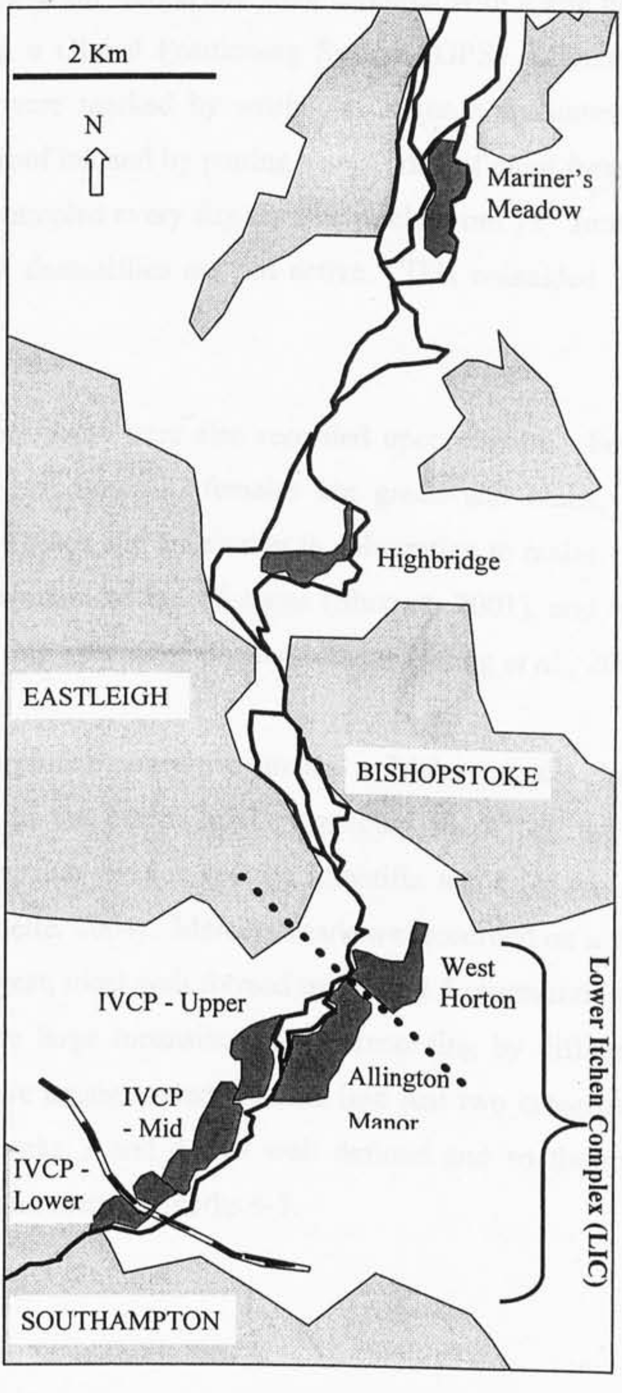

**Figure 3.1.** Location of the seven sites and sub-sites in the Itchen Valley, Hampshire. The main channels of the River Itchen are represented by the thick black line and urban areas are shown in grey. A railway line runs between West Horton and Allington Manor and is shown by the dotted line, and a motorway splits IVCP – Lower and is shown by the dashed line

### 3.2.3 MRR survey

The MRR survey was performed in all seven areas in the summer of 2001. At each site or sub-site a pair of research assistants walked slowly along the ditches and watercourses. *Coenagrion mercuriale* were captured with a kite net and their location was recorded using a Global Positioning System (GPS) calibrated to the Ordnance Survey. Animals were marked by writing a unique alphanumeric code on the left forewing in waterproof ink and by putting a small dab of paint from a paint marker pen on the thorax. We sampled every day for five weeks from 12th June, except during bad weather when adult damselflies are not active. This coincided with the peak flight period in this area.

Two visual polymorphisms were also recorded upon capture. Females occur in two forms, normal (or heteromorph) females are green and black, whilst andromorph females are blue and black and are similar in colouration to males. This type of female polymorphism is common within odonates (Sherratt, 2001), and its genetic basis has been determined in four species of Coenagrionidae (Wong *et al.*, 2003).

The other polymorphism concerned males. Males in the Itchen Valley show remarkable variety in the extent of the "mercury mark" on the second abdominal segment, from which the species gets its scientific name (Mayo & Welstead, 1983; Thompson & Rouquette, 2004). Mercury mark was recorded on a 5-point scale, with 1 representing the largest, most well formed mark, and 5 representing the slightest mark. However, there were large inconsistencies in recording by different observers, so to reduce error, we have amalgamated the data into just two categories. The difference between mercury marks 3 and 4 was well defined and so the groups chosen were mercury marks 1-3 and mercury marks 4-5.

### *3.2.4 Statistical analysis*

Distances moved were calculated as the straight-line distance between initial and subsequent captures. Multiple captures of the same individual on the same day were omitted. The following movement parameters were estimated (modified from Scott, 1973):

$d$ = distance between successive captures
$t$ = time in days between captures
$v$ = velocity = $d/t$
$D$ = cumulative distance moved = sum of $d$'s for each individual
$L$ = net lifetime movement = distance between first and last captures
$T$ = time between first and last capture
$V$ = net velocity = $L/T$

A multiple regression was performed to investigate the effects of site (coded as a series of dummy variables), sex, age (midpoint age during movement), season (midpoint day of season during movement), time ($t$) and order of movement (first movement, second movement and so on) on $d$. We used a combination of backwards elimination and stepwise procedures to select significant variables. All analyses were carried out on log transformed distances ($\log_{10}(d+1)$) as the data were highly skewed, and were performed using SPSS version 11.0.

To investigate whether movement patterns varied within each site, we divided each area into 50m x 50m sections and the damselflies marked or recaptured within each section were separated. We chose sections of this size as the majority of individuals moved less than 50m in their lifetime (see results). Thus the scale of each section reflects the approximate scale of lifetime movement for the majority of damselflies. We tested for differences between sections by running a 1-way ANOVA for each site. Density was then calculated as the average number of *C. mercuriale* seen in each section per day of recording. The effect of density on movement was investigated by running a regression of the $\log_{10}$ mean distance moved by damselflies starting in each section against $\log_{10}$ density, weighted by sample size. We also plotted cumulative distance dispersed for three density categories, low (<1 *C. mercuriale* per section per day), medium (1-10), and high (>10).

The direction of each movement was calculated using basic trigonometry. We were then able to examine patterns in the direction of movements within sites and sections and to search for ecological explanations. Finally, we extracted information on movements that crossed the railway line and the motorway and examined patterns of movement on either side.

## 3.3 Results

### *3.3.1 Numbers marked and recaptured*

In total 8708 *C. mercuriale* were marked, consisting of 7659 males and 1049 females. Out of these, 2523 individuals were recaptured (29.0%) at least once and there were 3727 recapture events. A breakdown of the numbers marked and recaptured at each site is provided in Table 3.1. The maximum number of times an individual was recaptured was eight for a male at Mariner's Meadow and the longest time between first and last capture was 29 days for a male at IVCP - Upper.

**Table 3.1.** Total numbers of adult *C. mercuriale* marked and recaptured at each site and movements between sites. Recapture figures refer to recaptures on days subsequent to marking or previous capture.

| **Site** | | **Marked** | **Recaptured** | | **Movement events** | |
|---|---|---|---|---|---|---|
| | | | **Individuals** | **Events** | **From** | **To** |
| Mariner's Meadow | Males | 959 | 433 | 793 | 0 | 0 |
| | Females | 185 | 47 | 59 | 0 | 0 |
| | Total | 1144 | 480 | 852 | 0 | 0 |
| Highbridge | Males | 716 | 285 | 450 | 0 | 0 |
| | Females | 63 | 11 | 11 | 0 | 0 |
| | Total | 779 | 296 | 461 | 0 | 0 |
| West Horton | Males | 251 | 71 | 104 | 13 | 8 |
| | Females | 14 | 0 | 0 | 0 | 0 |
| | Total | 265 | 71 | 104 | 13 | 8 |
| Allington Manor | Males | 637 | 226 | 373 | 10 | 22 |
| | Females | 57 | 3 | 3 | 0 | 0 |
| | Total | 694 | 229 | 376 | 10 | 22 |
| IVCP - Upper | Males | 2106 | 651 | 898 | 14 | 7 |
| | Females | 378 | 39 | 50 | 0 | 0 |
| | Total | 2484 | 690 | 948 | 14 | 7 |
| IVCP - Mid | Males | 2038 | 448 | 577 | 31 | 24 |
| | Females | 232 | 18 | 22 | 2 | 0 |
| | Total | 2270 | 466 | 599 | 33 | 24 |
| IVCP - Lower | Males | 952 | 278 | 374 | 17 | 24 |
| | Females | 120 | 13 | 13 | 0 | 2 |
| | Total | 1072 | 291 | 387 | 17 | 26 |
| **All sites** | Males | 7659 | 2392 | 3569 | 85 | 85 |
| | Females | 1049 | 131 | 158 | 2 | 2 |
| | Total | 8708 | 2523 | 3727 | 87 | 87 |

As each site contained similar lengths of stream the data presented in Table 3.1 reflect the strength of the *C. mercuriale* populations at each site. It is clear that the upper and middle sections of the Itchen Valley Country Park contained particularly strong populations, although the damselfly was present in reasonable numbers at all sites. The site with the lowest population was West Horton, where it was found in good numbers on one short stretch of stream, but was sparsely represented on the rest of the site.

The proportion of marked individuals recaptured varied at each site with the highest proportion occurring at Mariner's Meadow (42.0%) and the lowest at IVCP - Mid (20.5%). The differences were highly significant ($\chi^2 = 151.1$, d.f. = 6, $p < 0.001$) and were still apparent if the lower 5 sites were amalgamated before analysis ($\chi^2 = 112.8$, d.f. =2, $p < 0.001$). Males were significantly ($\chi^2 = 112.4$, d.f. =1, $p < 0.001$) more likely to be recaptured (31.2%) than females (12.5%) and this pattern was true at all sites (Figure 3.2).

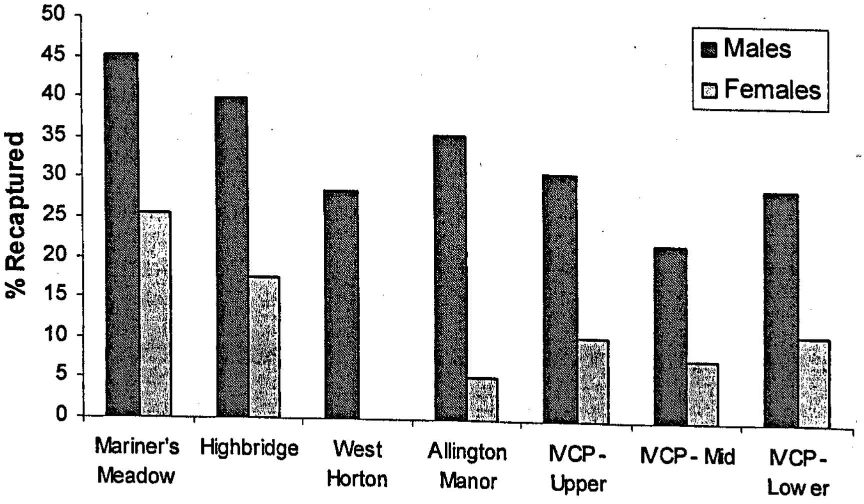

**Figure 3.2.** The percentage of marked individuals recaptured on at least one occasion at each site. Males and females are shown separately.

### *3.3.2 Movement Patterns*

85 individuals (3.4%) transferred between sites, with 2 individuals transferring twice to give a total of 87 movement events (see Table 3.1). There were no observed movements between Mariner's Meadow or Highbridge and any other site, but movement was recorded to and from the remaining five sites. These sites are adjacent to each other and although a small distance of unsuitable habitat separated some, these did not prove to be barriers to dispersal.

Net lifetime movement is defined as the distance from where the animal was first marked to the place where it was last recaptured. The pattern of movement is similar at each site, with the majority of individuals moving only a short distance in their lifetime, but a few travelling much further. The overall median net lifetime movement recorded in this study was 31.9m (geometric mean = 33.2m, n = 2523), and 65.7% of individuals moved less than 50m in their lifetime. However, differences between the sites are also apparent. Damselflies at Mariner's Meadow are the most sedentary with over 75% moving less than 50m in their lifetime, while only about 40% move that distance at Allington Manor. Furthermore, the maximum distance moved by any individual was 554m at Mariner's Meadow and 406m at Highbridge, but was 1374m at IVCP - Upper and 1790m at IVCP – Mid. This is illustrated in Figure 3.3, which shows the percentage of animals moving in 25m distance categories for Mariner's Meadow, Highbridge and LIC.

The mean net lifetime movement for each site is illustrated in Figure 3.4. This supports the patterns described above, as the mean is lowest at Mariner's Meadow (25.7m) and highest at Allington Manor (68.1m). The differences between the sites are highly significant (1-way ANOVA: F = 23.9, d.f. = 6,2516, $p < 0.001$). The same pattern of results was evident when we used cumulative distance moved (*D*) or net velocity (*V*). Indeed, both were highly correlated with *L* (*D*: $r_s = 0.863$, $p < 0.001$; *V*: $r_s = 0.697$, $p < 0.001$) and so have been omitted for the rest of this chapter.

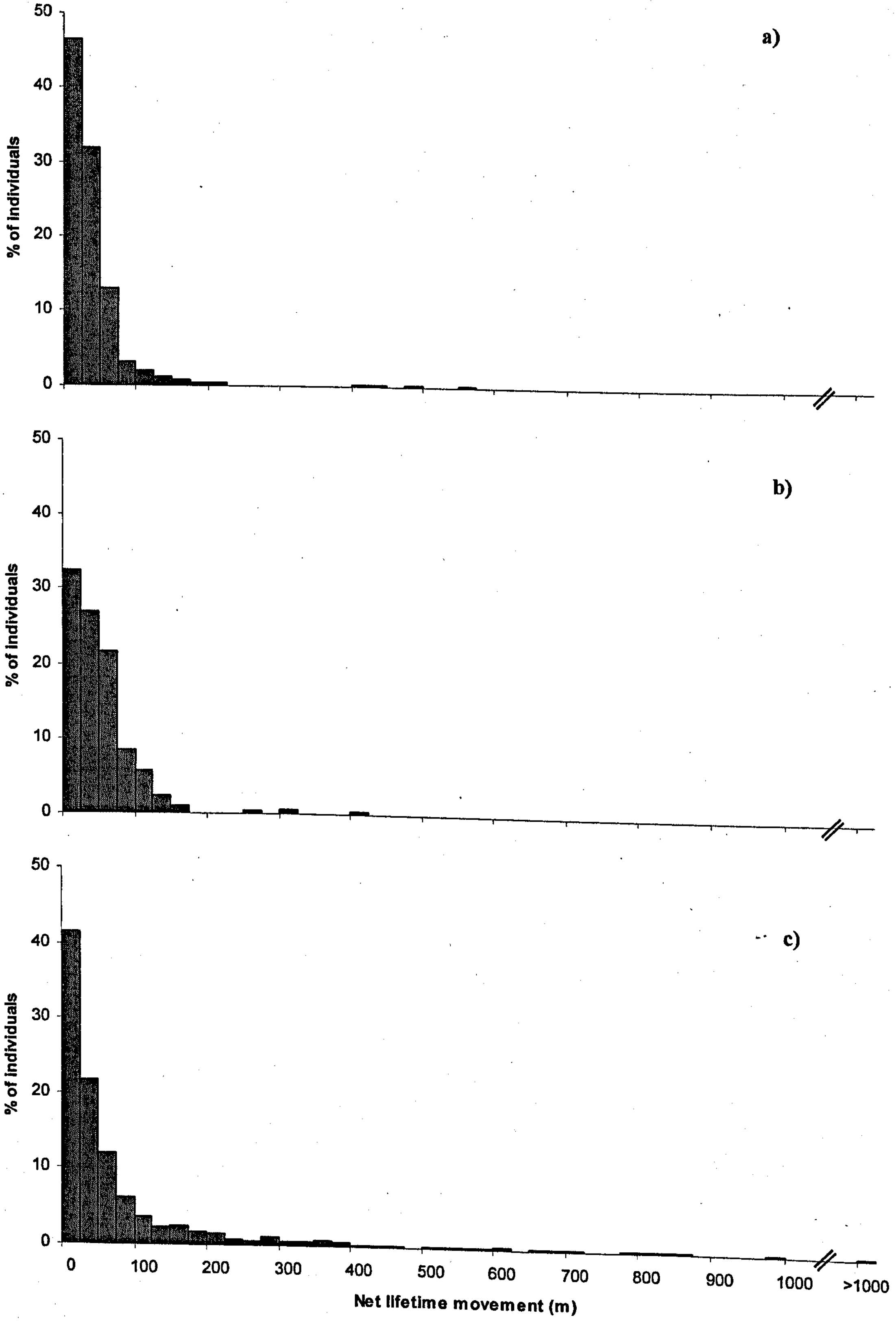

**Figure 3.3.** Percentage distribution of net lifetime movements (*L*) in 25m distance categories for (a) Mariner's Meadow, (b) Highbridge and (c) Lower Itchen Complex, all to the same scale. Sample sizes are 480, 296 and 1747 individuals respectively.

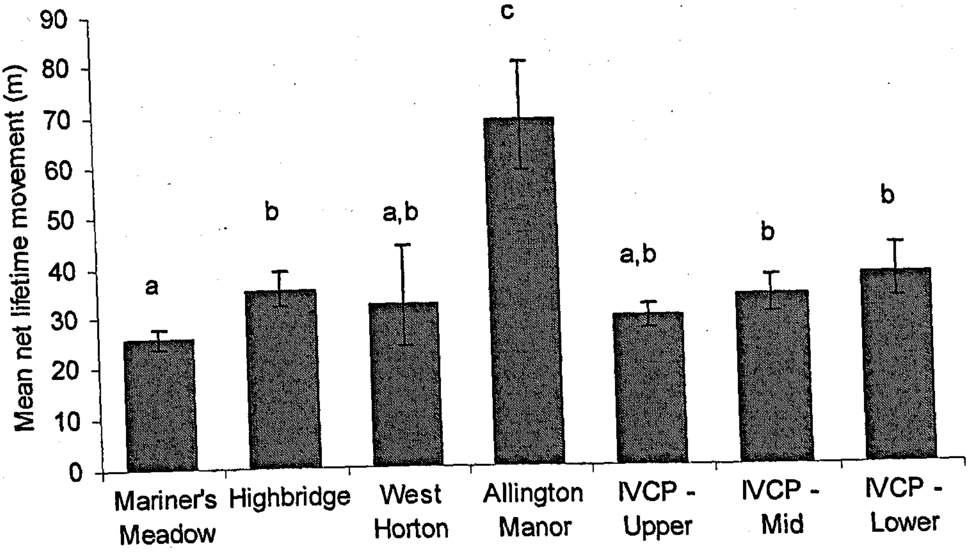

**Figure 3.4.** Net lifetime movement (*L*) at each site (bar shows mean and 95% confidence interval). Net lifetime movement is significantly different across the sites (1-way ANOVA: F = 23.9, d.f. = 6,2516, p < 0.001). *a,b,c* Means displaying the same letter are not significantly different at the 5% probability level (Tukey multiple comparison test).

### *3.3.3 Factors affecting movement*

A number of variables had a significant effect on *C. mercuriale* movement (Table 3.2). Time had a highly significant effect on distance moved (*d*) and other dispersal parameters and was the first variable selected in the multiple regression. The longer the time between consecutive captures, the further the damselfly had travelled (see Figure 3.5a). There was a quadratic effect of season, with slightly greater movement occurring in the middle of the season and a tail-off towards the end of the season (Figure 3.5b),

**Table 3.2.** Significant predictors of mean *C. mercuriale* movement ($\log_{10}$) derived from a multiple regression model. The *F*-value and the associated *p*-value, degrees of freedom, $R^2$, and adjusted $R^2$ are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). For each variable retained in the model, the *p*-value derived from *t*-tests, parameter estimates and standard errors are shown.

| **Model Summary** | **Variable** | **t** | ***p*** | **Parameter Estimates** | **Standard Error** |
|---|---|---|---|---|---|
| F = 73.04 | Time | 15.79 | *** | 0.0356 | 0.0023 |
| *P* = *** | Site - Allington Manor | 8.36 | *** | 0.210 | 0.025 |
| d.f. = 7,3719 | Site - Mariner's Meadow | -6.05 | *** | -0.115 | 0.019 |
| $R^2$ = 0.121 | Site - IVCP Upper | -4.33 | *** | -0.0770 | 0.0178 |
| Adj. $R^2$ = 0.119 | Order of movement | -3.34 | *** | -0.0299 | 0.0089 |
| | Season | 2.00 | * | 0.0062 | 0.0031 |
| | $\text{Season}^2$ | -2.79 | ** | -0.0002 | 0.0001 |
| | Constant | 43.18 | *** | 1.374 | 0.0318 |

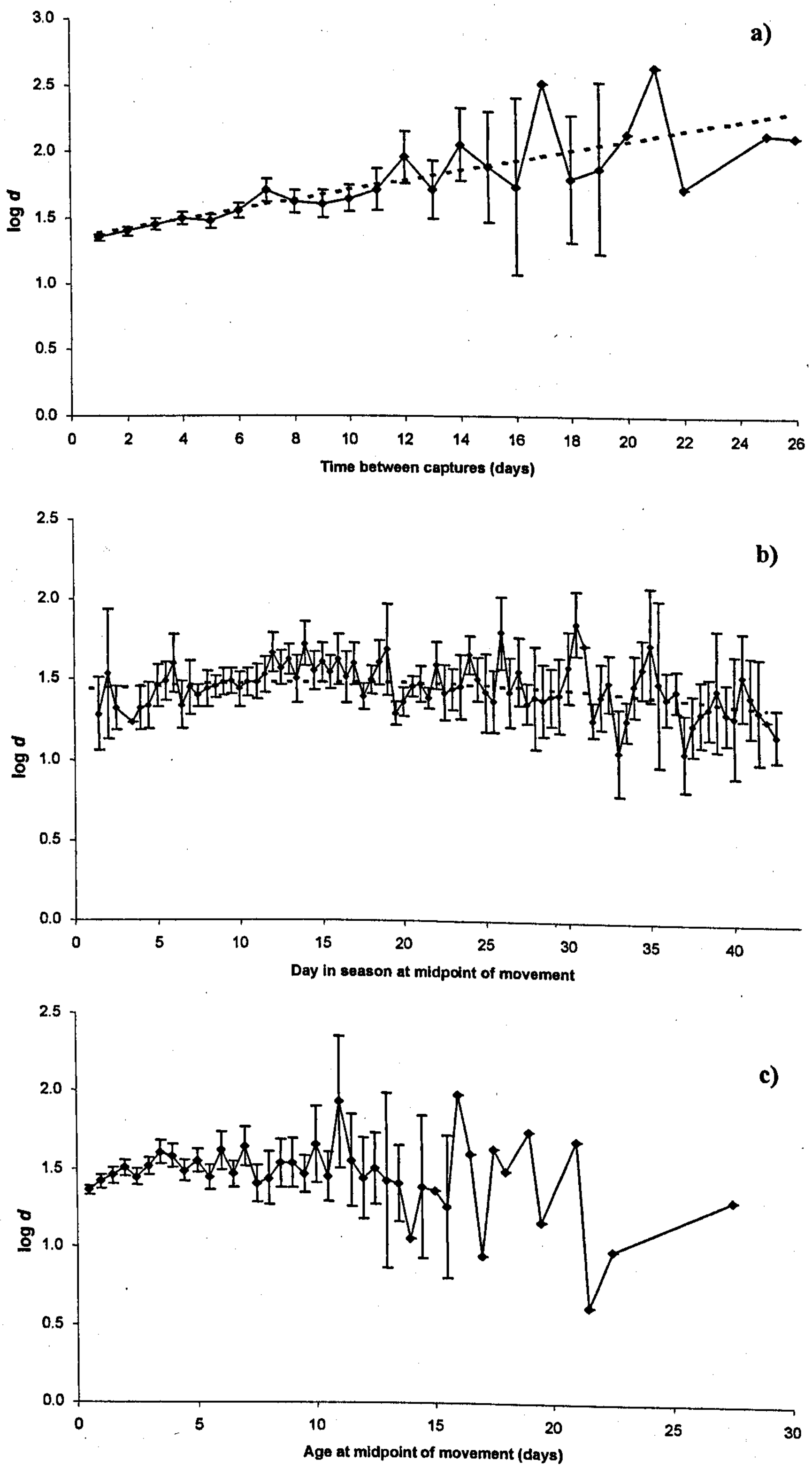

**Figure 3.5.** Effect of (a) time, (b) season and (c) age on mean distance moved (log *d*). Vertical lines show 95% confidence intervals, which are not included for samples with less than 5 individuals. Dotted lines on (a) and (b) are back-transformed regression lines derived from a multiple regression model (see text and Table 3.2 for more details). The effect of age (c) was not significant and so a regression line has not been added. Day in season is taken as the midpoint day between capture and recapture, where day 1 was the first day of marking (12th June 2001). Age is taken as the midpoint between first capture and each recapture.

although the effect was small. The effect of order of movement on distance moved was also significant and is shown in Figure 3.6a. Individuals travel further on their first move than subsequently and distance declines logarithmically the more moves that are made. Three sites were also included in the regression model; movement was significantly greater at Allington Manor, and significantly shorter at Mariner's Meadow and IVCP – Upper (Table 3.2, Figure 3.6b). This is consistent with the net lifetime movement patterns explained above. Overall these variables had a highly significant effect on distance moved, but the amount of variation explained was relatively small ($r^2 = 0.121$).

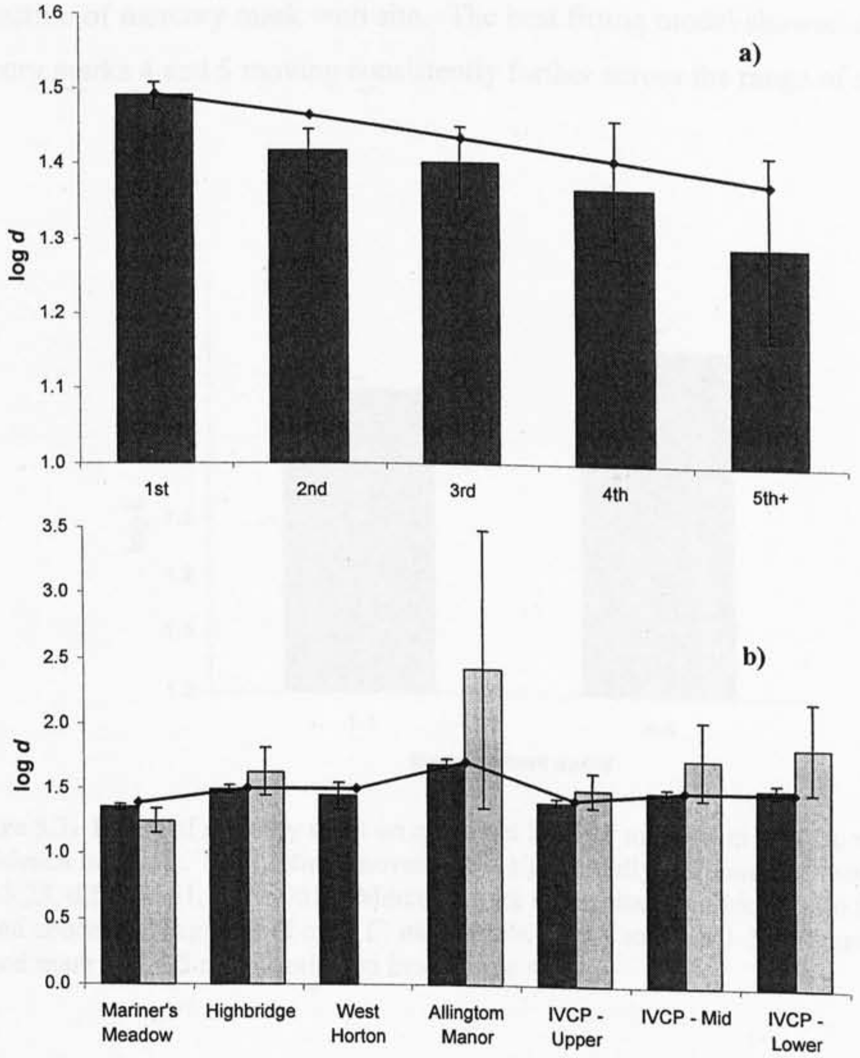

**Figure 3.6.** Effect of (a) order of movement (1st movement, 2nd movement etc.) and (b) site and sex on mean distance moved (log *d*). Males are shown with dark bars, females with light bars. Vertical lines show 95% confidence intervals. The solid lines are back-transformed regression lines derived from a multiple regression model (see text and Table 3.2 for more details). The effect of sex was not significant and so the regression line amalgamates the two sexes.

There was no effect of age on movement (Figure 3.5c). The effect of sex was not consistent across the sites (Figure 3.6b). Males moved further than females at Mariner's Meadow, but the reverse was true at all the other sites.

The effect of male mercury mark on net lifetime movement (*L*) was examined. There appears to be a trend for males with mercury marks 4 and 5 to move further than the others (t = -3.23, d.f. = 2361, p = 0.001) (Figure 3.7) and this effect remains significant when time is taken into account (mercury mark, ANCOVA F = 5.45, d.f. = 1,2354, p = 0.02; time, F = 181.97, d.f. = 1,2354, p < 0.001; site, F = 21.36, d.f. = 6,2354, p < 0.001). As previously, the effect of site was also significant, but there was no interaction of mercury mark with site. The best fitting model showed damselflies with mercury marks 4 and 5 moving consistently further across the range of sites.

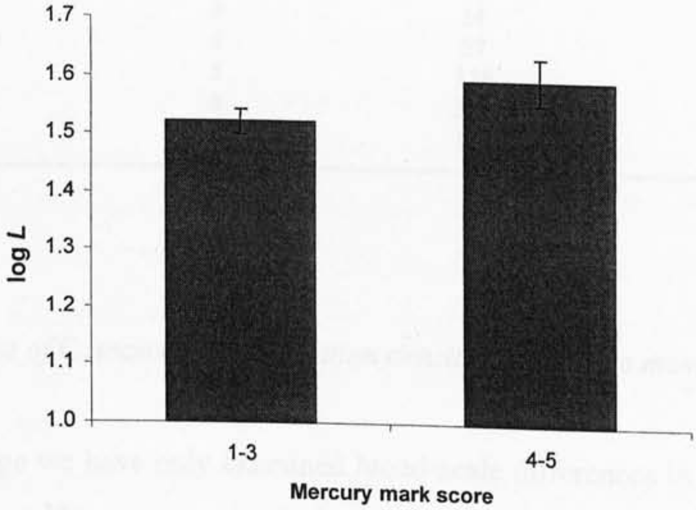

**Figure 3.7.** Effect of mercury mark on mean net lifetime movement (log *L*), with 95% confidence intervals. Net lifetime movement is significantly different between the two groups (t = -3.23, d.f. = 2361, p = 0.001). Mercury mark is the characteristic pattern found on the second abdominal segment of male *C. mercuriale*, with a score of 1-3 representing a well-formed mark and 4-5 representing an incomplete mark.

The effect of female polymorphism on movement could not be examined in detail, as very few andromorph females were present in the Itchen Valley. However, the pattern of andromorphs at each site is revealing (Table 3.3). None is present at the two northern sites of Mariner's Meadow and Highbridge. It is found throughout most of the LIC but is much more frequent in the Lower section and it is only in this section that its frequency of occurrence is close to that observed in the New Forest. The mean frequency at 8 sites in the New Forest recorded in a similar MMR study in 2002 was 21% (McKee *et al.*, 2005).

**Table 3.3.** Number of polymorphic female andromorphs marked, total female sample size and percentage of andromorphs in relation to sample size at each site.

| **Site** | **No of andromorphs marked** | **Female sample size** | **% Andromorphs** |
|---|---|---|---|
| Mariner's Meadow | 0 | 185 | 0.0 |
| Highbridge | 0 | 63 | 0.0 |
| West Horton | 0 | 14 | 0.0 |
| Allington Manor | 4 | 57 | 7.0 |
| IVCP - Upper | 5 | 378 | 1.3 |
| IVCP - Mid | 8 | 232 | 3.4 |
| IVCP - Lower | 20 | 120 | 16.7 |

### *3.3.4 The effect of* C. mercuriale *population density on distance moved*

Up to this stage we have only examined broad-scale differences in movement patterns between sites. However, an analysis of the 50m by 50m sections revealed that movement within each site was highly variable. There were highly significant differences in the distance moved in different sections in Mariner's Meadow and in all three sub-sites in the Itchen Valley Country Park, although movement was similar in all parts of Allington Manor (Table 3.4). There was no evidence for edge effects as the mean distance moved from sections at the edge of sites was little different from the average. The effect of barriers is examined in section 3.6. However, one obvious pattern did emerge; damselflies living in sections containing large numbers of individuals seemed to move less far than those living in less populated areas.

**Table 3.4.** Number of 50m by 50m sections at each site, the results of 1-way ANOVA's to test for differences in distance moved from different sections, and regressions of mean distance moved by damselflies marked in each section against density. 1-way ANOVA's were performed separately on movements that started and ended within each section. The regression analyses were performed on log-transformed data and were weighted by sample size. "Curve" indicates whether the best fitting model was linear (L) or quadratic (Q).

| Site | Number of sections | Statistical significance | | Regressions of mean distance against density | | | |
|---|---|---|---|---|---|---|---|
| | | Start | End | F | P | $R^2$ | Curve |
| Mariner's Meadow | 19 | < 0.001 | < 0.001 | 75.83 | < 0.001 | 0.817 | L |
| Highbridge | 7 | 0.229 | 0.006 | 0.91 | 0.385 | 0.154 | L |
| West Horton | 8 | 0.086 | 0.038 | 5.80 | 0.053 | 0.492 | L |
| Allington Manor | 32 | 0.288 | 0.345 | 10.00 | < 0.001 | 0.408 | Q |
| IVCP - Upper | 18 | < 0.001 | < 0.001 | 31.17 | < 0.001 | 0.806 | Q |
| IVCP - Mid | 29 | < 0.001 | < 0.001 | 22.89 | < 0.001 | 0.459 | L |
| IVCP - Lower | 27 | < 0.001 | 0.003 | 11.15 | 0.003 | 0.308 | L |
| **All sites** | 140 | < 0.001 | < 0.001 | 93.76 | < 0.001 | 0.578 | Q |

When the mean distance moved by damselflies starting in each section was plotted against density a clear relationship became apparent (Figure 3.8). A linear regression, weighted by sample size, provided a good fit to the data ($r^2 = 0.547$, $F = 166.41$, $p < 0.001$), but a slightly improved fit was achieved by adding a quadratic term ($r^2 = 0.578$, $F = 93.76$, $p < 0.001$). When the analysis was carried out on the seven original sites (Table 3.4), a significant effect of density was found at all sites except for Highbridge, and the effect was not quite significant at West Horton. These two sites are the smallest with only 7 and 8 sections respectively and so it was inevitably more difficult to discover trends there. At all the remaining sites a linear relationship was significant, but at two of the sites a quadratic relationship provided an improved fit. The strongest relationships were at Mariner's Meadow (linear $r^2 = 0.817$, $F = 75.83$, $p < 0.001$) and at IVCP – Upper (quadratic $r^2 = 0.806$, $F = 31.17$, $p < 0.001$), the two sites with the highest densities of *C. mercuriale.*

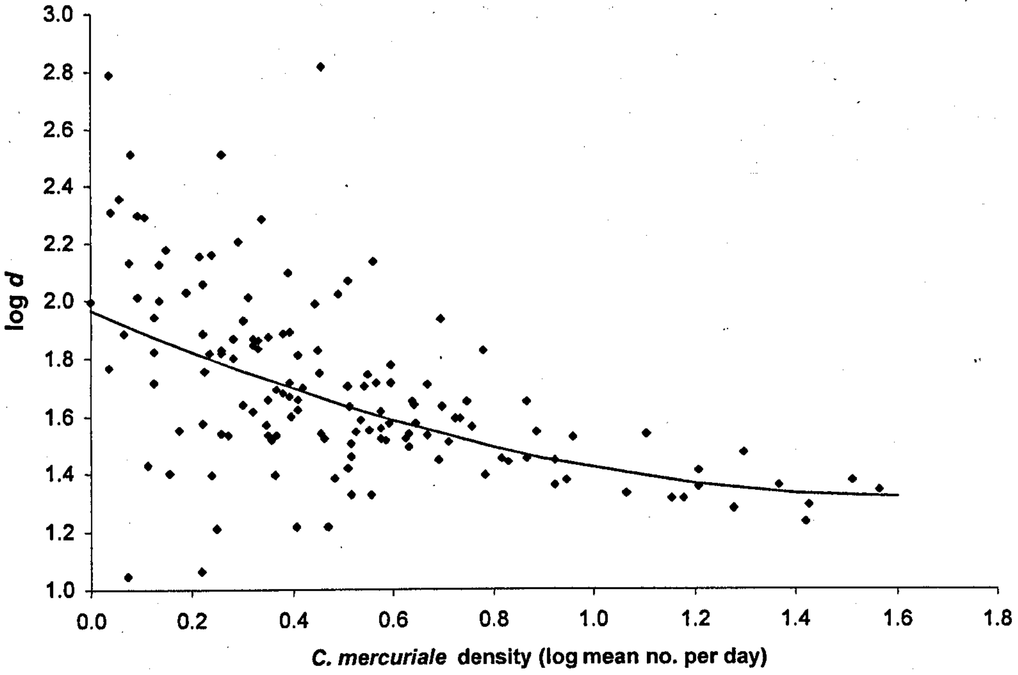

**Figure 3.8.** Regression of mean distance moved (log *d*) against density for each 50m by 50m section. Density is calculated as the average number of individuals (marks and recaptures) seen in each section per day. The solid line is the weighted regression line ($r^2 = 0.578$, $F = 93.76$, $p < 0.001$).

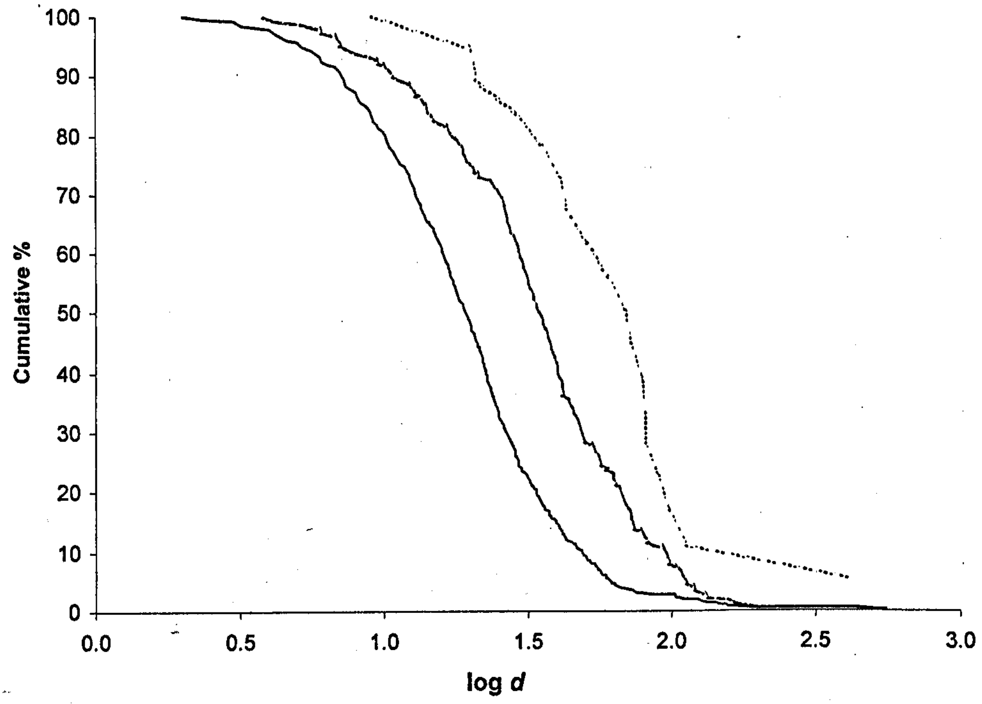

**Figure 3.9.** Cumulative distance moved by *C. mercuriale* in three density categories. The lightest line represents sections with a mean of less than 1 *C. mercuriale* per day, the medium-weight line 1-10 individuals and the thickest line represents sections with >10 individuals per day.

Our results indicate that the greater the density of *C. mercuriale*, the shorter the average movement and the quadratic term suggests that the effect levels off at higher densities. In other words, movement is inverse density dependent. This was confirmed when we plotted the cumulative distance moved by *C. mercuriale* for three density categories (Figure 3.9). There was a clear separation of each density category, with consistently shorter movements from damselflies in higher density areas. This effect was found at all sites and there was no difference in the response between males and females.

### *3.3.5 Investigation of the direction of each movement*

Figure 3.10 shows the direction of movements at Highbridge, and this pattern is typical across our study sites. There is a strong tendency for *C. mercuriale* to move along watercourses rather than across dry land, with the mean angle of movement along an axis equal to the angle of the stream.

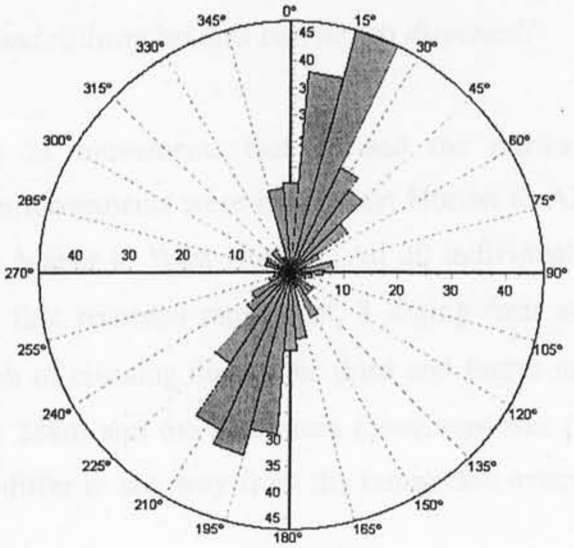

**Figure 3.10.** Rose diagram showing direction of movement of *C. mercuriale* at Highbridge. The mean angle of movement is along the 15°-195° axis. Each bar represents 10°.

To examine patterns of movement within each site in more detail, the direction of movement was examined for each section. We limited our analysis to sections where we had data from 20 or more individuals and where the watercourse did not change direction within the section. In total, chi-square analyses were performed on 42 sections. There were significantly ($p < 0.05$) more movements upstream in 9 sections and downstream in 5. However, in all 14 cases, movement was towards a higher density neighbouring area. If a Bonferroni correction was applied to the significance level, 7 sections remained significant ($p < 0.0012$), where movement was predominantly upstream in 4 cases and downstream in 3. There are 7 discrete patches within our study sites where density is high (>10 individuals per 50m per day). When 10 of the neighbouring sections were examined, damselflies moved significantly more frequently in the direction of the high density area in 7 of these sections and the trend was consistent although not significant in the remaining three.

There was no consistent effect of sex, mercury mark, or order of movement on the direction of movement. However, the longer the time interval between capture and recapture, the more uniform the direction of movement along the watercourses.

### *3.3.6 Are motorway and railway bridges barriers to dispersal?*

In total there were 21 movements that crossed the railway line, involving 20 individuals. Thirteen movements were from West Horton to Allington Manor, and 8 were from Allington Manor to West Horton. All 20 individuals were male. Sixteen crossed during their first recorded movement, 3 during their second movement, and there was 1 case each of crossing during the third and fourth movements. The mean distance moved was 288m and the maximum movement was 674m. The individuals that crossed did not differ in any way from the remainder, except in terms of distance travelled.

There was no suggestion that mean distance moved was reduced at the sections closest to the railway line (Figure 3.11), although sample sizes were quite small. The direction of movements was also examined. On the north (West Horton) side, there were more upstream movements, away from the railway, than downstream, whereas on the south (Allington Manor) side, there were more downstream movements, also away from the railway, than upstream. However differences between the sections were not quite statistically significant ($\chi^2 = 6.8$, d.f. = 3, $p = 0.08$), but sample size was small.

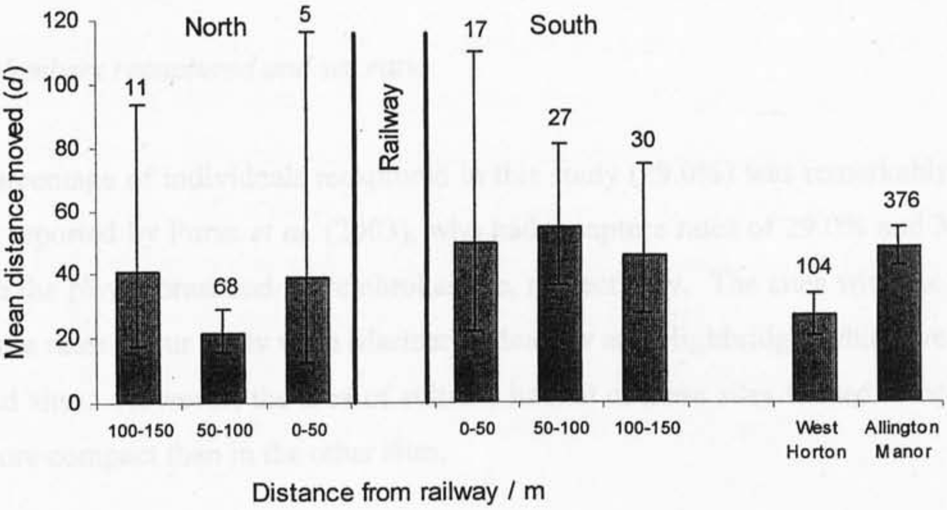

**Figure 3.11.** Diagrammatic representation of the railway crossing, showing the effect of distance from railway on mean distance moved (*d*) for *C. mercuriale*. The mean distance moved in West Horton (north of the railway line) and Allington Manor (south of the railway line) is shown for comparison. 95% confidence intervals are displayed and sample sizes are given above the bars.

A similar picture was recorded for the motorway bridge. In total there were 18 movements that crossed the motorway, 9 in each direction. This involved 16 individuals, 14 of which were male and 2 female; 2 individuals crossed twice. The individuals that crossed the motorway did not differ from the remainder in any way, except in terms of distance moved. The mean distance moved was 602m and the maximum movement was 1374m. This individual was first marked and recaptured in IVCP – Upper and was then recaptured south of the motorway 17 days later having travelled most of the length of the Country Park.

There was no reduction in the mean movement of damselflies captured close to the motorway. However, there were very few damselflies present within 100m of the motorway, on either side, which meant that it was difficult to perform a rigorous statistical analysis. The small sample size also made it impossible to compare direction of movement on the opposite sides of the road. It appeared that habitat to either side of the motorway had been adversely affected by the construction of the motorway and bridge.

## 3.4 Discussion

### *3.4.1 Numbers recaptured and sex ratio*

The percentage of individuals recaptured in this study (29.0%) was remarkably similar to that reported by Purse *et al.* (2003), who had recapture rates of 29.0% and 30.9% in sites in the New Forest and in Pembrokeshire, respectively. The sites with the greatest recapture rates in our study were Mariner's Meadow and Highbridge, which are the two isolated sites. However, the area of suitable habitat at these sites tended to be smaller and more compact than in the other sites.

The sex ratio at the breeding sites is strongly male biased in all populations. This is a pattern found in most odonate species (e.g. Cordoba-Aguilar, 1994; Stettmer, 1996; Stoks, 2001a) and is probably brought about through a combination of developmental, survival and behavioural differences between the sexes. There is no difference in the pattern of emergence of the two sexes in *C. mercuriale* (Purse & Thompson, 2003a). However, it is believed that as female odonates take longer to mature, survivorship during this period is lower (Banks & Thompson, 1985; Bennett & Mill, 1995; Stoks, 2001b) and their pattern of behaviour once mature is also different. Females will only visit oviposition sites when ready to mate and will then egg-lay whilst still in tandem. They will subsequently leave the area and will not return until a new batch of eggs has matured. Males, on the other hand, will remain at breeding sites for much longer periods once they have matured. This means that males will tend to arrive at the breeding sites first and will almost always outnumber females. It should also be noted that females are less conspicuous than the brightly coloured males, which may have led to a slight recording bias towards the males.

### *3.4.2 Movement Patterns*

There were no direct movements of marked damselflies between the two fragmented northern sites and the remainder, but several movements between the sites in the area of continuous habitat. Movements over 500m were rare (1.3% of individuals) and there were only 3 movements greater than 1000m (0.1%). This would suggest that the northern sites are ecologically isolated, but that the southern sites could be considered to be one large population. These findings are encouraging as they are remarkably well supported by our analysis of DNA microsatellite markers (Watts *et al.*, 2004). Watts *et al.* (2004) found that damselflies from the five areas of continuous habitat were genetically similar, but that samples from Highbridge and Mariner's Meadow showed significant genetic differentiation. Indeed there was a significant correlation between genetic differentiation and geographic distance and evidence for isolation by distance even over the short distances present in our study area. Within the area of continuous habitat genetic samples show a pattern of positive autocorrelation over short distances, but showed isolation by distance over a distance of about 1000m.

One of the limitations of our study is that we were not granted access to the River Itchen itself as it is almost all privately owned and access was restricted. Although no strong populations occur on the river itself, *C. mercuriale* is known to be present in some localities. It may also be using the river as a corridor by which movement could occur between different populations. It is inevitable, therefore, that we would have failed to catch some individuals.

Net lifetime movement measured in this study was similar to that reported by Purse *et al.* (2003) and slightly greater than that reported by Hunger and Röske (2001) for the same species in Germany. This is perhaps not surprising given that the latter study used a relatively small sample size, was of a shorter duration and involved a smaller study area. Distance moved has been related to time in this study and in Purse *et al.* (2003), and a linear relationship has been found between mean movement distances and the size of the study area for a number of butterfly studies (Schneider, 2003).

The maximum net lifetime movement recorded in this study (1790m) is longer than that recorded previously. Purse *et al.* (2003) recorded a maximum movement of 1060m, as did Thompson and Purse (1999) in a separate study. However, the maximum distance between patches was 1560m and the maximum within patch distance was c. 600m (Purse *et al.*, 2003). In our study system the maximum between patch dispersal distance was approximately 9km, and the LIC provided a near continuous patch 3.5km in length. The scale of our study system was clearly much greater than the scale over which *C. mercuriale* moves, providing us with increased confidence in the accuracy of our results.

*Coenagrion mercuriale* is considered to be a weak flier and a poor disperser compared to other odonates (Winsland, 1997; Smallshire & Swash, 2004) and this assumption appears to be borne out when movement is compared to other species. It is the smallest of the blue damselflies found in the UK and distance moved and dispersal probability have been reported to increase with increasing species size for a range of odonates (Conrad *et al.*, 1999; Angelibert & Giani, 2003). *Calopteryx splendens*, which occurs in similar habitat to *C. mercuriale,* was reported to have a median movement of 90m for males and 45m for females (Schutte *et al.*, 1997), and Stettmer (1996) found that the median movement was about 50m for both this species and *Calopteryx virgo*. The longest recorded movements were 1725m (Schutte *et al.*, 1997) and 4km (Stettmer, 1996). Within the Coenagrionidae, 73% of *Enallagma cyathigerum* were reported to move less than 100m (Garrison, 1978). This compares to 85% for *C. mercuriale* in the present study. Bennett and Mill (1995) reported that approximately 83% of male *Pyrrhosoma nymphula* and 63% of females moved less than 50m per day. In our study the equivalent figure is 92% and 91% for males and females respectively.

All movement parameters measured were lowest at Mariner's Meadow. It is interesting to speculate whether this was due to isolation, landscape, *C. mercuriale* density, or habitat quality. As sites become more isolated, dispersing individuals become less likely to find suitable habitat. Thus the mortality rate associated with dispersal increases and this can eventually lead to the loss of genes coding for dispersal in these populations (Dieckmann *et al.*, 1999). Thus theory predicts that movement will be lower at Mariner's Meadow and at Highbridge. There is further support for this in the genetic analysis, as Mariner's Meadow has low genetic variability, a relatively high inbreeding coefficient and quite different allele frequencies from other sites in the Itchen Valley (Watts *et al.*, 2004). However, Mariner's Meadow and Highbridge also contained the smallest lengths of suitable habitat, and so long-distance within patch movements are inevitably missing. Mariner's Meadow also contained some of the highest density sections of *C. mercuriale*, along with IVCP Upper, and movement was lowest from these two sites. This could provide further evidence of inverse density dependent movement (see section 3.4.4). Finally, habitat quality was good at Mariner's

Meadow and IVCP – Upper, and correspondingly bad at Allington Manor. *Coenagrion mercuriale* may simply be moving away from areas of less suitable habitat and staying put in the best areas.

### *3.4.3 Factors affecting movement and dispersal*

Length of time between captures had the greatest effect on distance moved and this is consistent with a previous study of *C. mercuriale* (Purse *et al.*, 2003). It has also been reported for *Calopteryx splendens* (Schutte *et al.*, 1997), and *E. cyathigerum* (Garrison, 1978).

As far as we are aware, this is the first study of mature adult odonates to observe an effect of season on local movement patterns, although the effect was small. The two most likely causes are weather or phenotype. Weather is known to affect odonate activity; damselflies are more likely to be on the wing in good weather (Angelibert & Giani, 2003), but could be dispersed over long distances in windy weather (Corbet, 1999). During our study period the weather was fine and settled for much of the early and middle periods but unsettled towards the end, in a pattern that would appear to mirror the trend in movement distances (Figure 3.5b). Damselfly phenotype also varies with season. For example, body size at emergence declines over the course of the season in *C. mercuriale* (Purse & Thompson, 2003a). If movement were correlated with body size then this would explain the pattern in our data. However, Purse (2001) found no evidence for this in her study sites in the New Forest and Pembrokeshire.

*Coenagrion mercuriale* moves further on its first movement than subsequently, and movement declines with each subsequent move. Order of movement is highly correlated with age ($r_s = 0.642$, $p < 0.001$) but provides a better fit to the data. Indeed, if order of movement is removed from the multiple regression, age is added in its place. This pattern is different to that seen in *Sympetrum danae* (Michiels & Dhondt, 1991) and in many butterflies, where it is common for females in particular to move increasing distances with age or number of moves (e.g. Warren, 1987; Bergman & Landin, 2002).

This study has only examined movement patterns in mature adults. Movement during other life stages has been reported in some species. For example newly matured males of the territorial damselfly *Calopteryx haemorrhoidalis* moved considerably further than all other life stages in search of suitable territories (Beukema, 2002). Most damselflies mature away from the breeding sites and dispersal by tenerals (newly emerged immature adults), usually by means of a maiden flight, has been suggested to be the most important dispersive phase for some odonates (Anholt, 1990; Corbet, 1999). However, Conrad *et al.* (1999) found no difference in dispersal between immature and mature adults in 7 species of pond-dwelling odonates, and the same result was reported by Angelibert & Giani (2003) for 3 pond-dwelling species. Maiden flight behaviour has not been observed in *C. mercuriale* (*pers. obs.*) but has been observed in *Coenagrion puella* (Anholt, 1990; D.J. Thompson, *pers. comm.*). Tenerals were not marked in our study due to the risk of damaging this protected species, and retaining individuals until their wings harden may alter behaviour upon release. It is also possible that movement occurs through the process of larval drift, which is common in many groups of riverine invertebrates (Bilton *et al.*, 2001; Elliott, 2003; but see section 3.4.5). However, the genetic structure of the Itchen Valley populations and the ecology of the species would suggest that larval or teneral dispersal does not play a significant role in this species.

No consistent differences between the sexes were found in this study and this is consistent with previous work on *C. mercuriale* (Purse, 2001). Sex differences in movement patterns in other damselflies is equivocal, although where present it is usually females that move further. Conrad *et al.* (2002) reported that dispersing females of *Ischnura elegans* moved significantly further than dispersing males, but that there was no sex differences in *C. puella*. However Angelibert & Giani (2003) found that *C. puella* females were more likely to move than males. *P. nymphula* females were significantly more mobile than males (Bennett & Mill, 1995), as were *Hetaerina cruentata* females (Cordoba-Aguilar, 1994), but net lifetime movement did not differ between sexes in *Calopteryx aequabilis* (Conrad & Herman, 1990).

Males with reduced mercury marks travelled further than those with more normal patterning, but the mechanism driving this is unclear at present. There appears to be no genetic basis to the difference in mercury marks (P.C. Watts, *pers. comm.*). Female polymorphism, on the other hand, almost certainly does have a genetic basis, as this has been deduced for other members of the Coenagrionidae (Wong *et al.,* 2003). No andromorph females were present at Mariner's Meadow and Highbridge, suggesting that the genes coding for this feature are absent from these isolated sites. They are present throughout most of the LIC but with increasing frequency to the south of the area. This suggests that these sites are interconnected, but that the scale of the LIC is considerably larger than the scale of movements, thereby creating distinct genetic clusters in different parts of the site. This pattern closely matches the findings of our analysis of movement and our genetic analysis (Watts *et al.*, 2004). Nevertheless, it is surprising that there is such a big difference between IVCP - lower and IVCP – mid, considering that these sites adjoined each other and the division was not based on any physical boundary. We do not, however, know the relationship between our microsatellite loci, on which we presume there is no selection, and the andromorph gene, on which we presume there is. It is difficult to comment further as our study was not designed to answer this type of question.

### *3.4.4 The effect of* C. mercuriale *population density on distance moved*

One of the most interesting findings of this study is that *C. mercuriale* movement is inverse density dependent. This makes some biological sense, as the damselflies are staying in areas that are clearly suitable, but is a different strategy to that adopted by many other species. Species that are territorial will tend to spread themselves out fairly evenly across all suitable habitat (Stettmer, 1996; Beukema, 2002). Many other species will stay in the same place in low densities but will readily disperse as density increases – classic density dependent dispersal (e.g. Denno & Peterson, 1995; Sutherland *et al.*, 2002).

As habitat quality and *C. mercuriale* density are correlated, it is difficult to determine which factor is driving the process. It is likely that the two are interlinked, with the presence of conspecifics used as indicators of good habitat quality. Martens (2000) showed that tandem pairs of *C. mercuriale* landed preferentially on leaves where a single motionless male in the typical vertical position of a tandem male had been placed. When a range of habitat features were included in our analysis (Chapter 4), density remained a highly significant predictor of *C. mercuriale* movement. Two habitat features were also added to the model and the species was found to be disassociated with these features. Damselflies were more mobile as density decreased, and as the two habitat features increased.

Inverse density dependent dispersal has not, to our knowledge, been observed previously in natural populations of odonates, but two manipulation experiments have hinted at this behaviour. Conrad & Herman (1990) experimentally increased the density of *Calopteryx aequabilis* in a natural riverine population. They found that when females were increased, more females emigrated, more males immigrated, and male movements were shorter. On the other hand, when males were added, most emigrated quickly. Michiels & Dhondt (1991) used a large outdoor field cage to study the non-territorial dragonfly *Sympetrum danae*. They found that males showed increased escape behaviour at lower density, which they believed was probably related to female density, but that females showed increased escape behaviour at higher female density. Both these studies have shown that male movement is inverse density dependent, using female density as the cue, but that females showed the reverse behaviour.

Inverse density dependent movement has been reported in some butterfly studies (Gilbert & Singer, 1973; Brown & Ehrlich, 1980; Kuussaari *et al.*, 1996; Roland *et al.*, 2000; Menendez *et al.*, 2002) and in a study of bush crickets (Kindvall *et al.*, 1998). All of these studies have shown a tendency for individuals to move further in low density areas and/or to have a greater propensity to emigrate from these areas. Conversely, immigration is more likely to high density patches. This attraction to conspecifics and emigration from small populations could be due to the need to find mates, avoid inbreeding or to find high quality habitat. It could also be a side effect of mate finding behaviour; the tendency of males to chase all conspecifics can lead to the incidental formation of aggregations (Odendaal *et al.*, 1988). Matter and Roland (2002) reported that the immigration of male butterflies was related positively to aspects of habitat quality and to female density in a manipulation experiment where they were able to tease apart these two factors.

Reduced individual fitness or population growth rate at low population size or density is generally referred to as an Allee effect (Stephens *et al.*, 1999; Courchanp *et al.*, 1999; Stephens & Sutherland, 1999) and has been reported in some studies (Kuussaari *et al.*, 1998; Menendez *et al.*, 2002). We do not know if mating success is reduced in our lower density areas, but by increasing movement in these areas, individuals may be enhancing the chances of securing a successful mating, thereby increasing fitness and reducing the chance of an Allee effect (Kindvall *et al.*, 1998). Such behaviour is likely to have profound consequences for the population dynamics of the region. In areas of continuous habitat, this behaviour will lead to aggregation and increased competition for mates. In areas of patchy habitat, small populations in relatively isolated areas are more likely to go extinct due to higher emigration rates. Increased emigration would also make surviving populations more susceptible to other causes of extinction such as inbreeding depression, genetic drift, Allee effects and stochastic environmental processes.

### *3.4.5 Investigation of the direction of each movement*

*Coenagrion mercuriale* moved towards areas of higher density, thus providing further evidence for inverse density dependent processes. There was little evidence to suggest that damselflies move upstream. Upstream movement by adults is seen in a number of aquatic insects, such as Ephemeroptera, Plecoptera, and Trichoptera, as it is used to counteract the affect of drifting downstream during the aquatic stage of the lifecycle (Bilton *et al.*, 2001; Briers *et al.*, 2002). However, it has only rarely been observed in the Odonata (Corbet, 1999) and there appear to be no records from the Coenagrionidae. Beukema (2002) reported that maturing males of *Calopteryx haemorrhoidalis* showed a strong tendency to move upstream and that mature males were a little more likely to move upstream. However, this was on a mountain stream in the Pyrenees where larvae were washed downstream in times of spate. Higashi & Ueda (1982) have also reported upstream movement in tenerals of *Calopteryx cornelia*. In the same family, Cordoba-Aguilar (1994) reported that no age class of *Hetaerina cruentata* showed any tendency to move upstream or downstream. Within the Coenagrionidae, Garrison (1978) discovered no direction to the movements of *Enallagma cyathigerum.*

Odonates are not significant components of the larval drift fauna and it appears that any drift that does occur is due to accidental dislodgement rather than an active process. Furthermore, *C. mercuriale* prefers slow flowing marginal habitats (Thompson *et al.*, 2003a; Chapters 4 & 7) and so is unlikely to drift far. It is unlikely, therefore, that upstream movement is necessary as a compensatory mechanism. It should also be noted that over most of our study area upstream movement was correlated with the direction of the prevailing wind.

### *3.4.6 Are motorway and railway bridges barriers to dispersal?*

Roads, railways and their associated bridges can impact on biodiversity in a number of ways. They can cause direct mortality, can alter behaviour through disturbance and avoidance, can cause barrier effects and habitat fragmentation, adversely affect adjacent habitat, and can increase runoff, sediment loads and pollution (Mader, 1984; Forman & Alexander, 1998). The barrier affect is considered to be the least studied and perhaps most important impact, particularly for invertebrates (Forman & Alexander, 1998; Keller & Largiadèr, 2003). Indeed, roads have been shown to act as strong barriers to movement in snails (Baur & Baur, 1990) and in ground beetles (Mader, 1984; Keller & Largiadèr, 2003) leading to significant genetic differences in populations separated by roads (Keller & Largiadèr, 2003). Even in bumblebees, which are capable of strong flight, a road and a railway were shown to restrict movement (Bhattacharya, 2003) and certain types of field boundary acted as barriers to movement in hover-flies (Wratten, 2003).

During our study there were 21 movements across the railway and 18 across the motorway. It is clear, therefore, that these obstacles are not complete barriers to movement. This is confirmed by our genetic analysis, as samples from either side of these obstacles were not genetically different from each other (Watts *et al.*, 2004). However, this does not preclude an ecological effect altogether. Construction of the motorway has impacted on the channel for approximately 100m to either side. The channel is deeper and has less emergent vegetation than anywhere else in the IVCP and as a result very few *C. mercuriale* were recorded. Unfortunately, the low abundance precluded a rigorous statistical analysis of movement patterns in these areas.

Schutte *et al.* (1997) recorded the impact of bridges on the behaviour of *Calopteryx splendens*. They reported that of 235 individuals approaching three bridges, 37.5% crossed under the bridge with no noticeable reaction, 2.1% flew over the bridge, but 58.7% turned around and flew away in another direction. Furthermore, there was a significant difference between bridges, with 71.8% of individuals turning back from the longest and darkest bridge. They also reported that damselflies were less likely to approach one of the bridges where the banks were paved and nearly free of vegetation for 50m to one side.

Perhaps a similar effect is occurring in *C. mercuriale*, with many individuals turning back in front of the bridges, although this is purely speculative. In an area where populations were smaller than in the LIC, or if bridges occurred further away from the populations, any reduction in movement could have important consequences. Populations that would have been connected by only occasional movements could become completely isolated. We are carrying out further studies on this topic in other sites in the UK.

### *3.4.7 Conservation implications*

The limited dispersal capability shown by *C. mercuriale* has implications for its conservation and management. The species requires slow to medium flowing channels, with shallow margins and abundant emergent vegetation (Chapters 4 & 7). In most of the areas that *C. mercuriale* occupies in the UK, this represents a successional phase that will not last without active management. Indeed, *C. mercuriale* has been lost from sites that have become choked with vegetation or shaded (Purse, 2001). It is therefore imperative that management works are carried out and that they are tailored to the scale of movements observed. In other words, only small sections of stream should be managed in any one year and new areas should be created close to existing populations.

It has been suggested that insects living in successional habitats should show dispersal ability related to the lifespan of the habitat (Southwood, 1962). This does not seen to be the case with *C. mercuriale* and its limited dispersal is likely to be one of the factors causing its decline. However, this may be a reflection of past landscape stability created through years of traditional land management, rather than the situation that currently prevails.

It is encouraging that the direct measurements of dispersal described here fit well with the pattern shown by indirect genetic analysis (Watts *et al.,* 2004). It is clear from both studies that the two populations in the north of the study area are isolated from each other and from the southern population even though the distance between Mariner's Meadow and Highbridge is about the same as the distance between IVCP – Lower and West Horton. This also illustrates that suitable habitat management between sites that are beyond the dispersal distance of individuals can be used to connect or reconnect populations. Another important finding of this study is that movement is inverse density dependent. One effect of this is that small isolated sites will be more likely to go extinct, as a larger proportion of individuals will emigrate. Thus landscape connectivity becomes even more important. The long-term persistence of *C. mercuriale* in the Itchen Valley and elsewhere requires a landscape approach. New habitat should be created between the existing sites to reconnect the extant populations and connectivity should be a key component of all management planning.

# Chapter 4: Adult habitat associations

## 4.1 Introduction

Many dragonfly and damselfly species have shown a significant decline in Europe during the last century (Van Tol & Verdonk, 1988). These authors evaluated the status of 164 indigenous European odonate species and considered 61 to be endangered, vulnerable or rare. A steady decline in diversity was reported from almost everywhere in Europe, but the situation was worst in the most urbanised and industrialised regions, including England.

The Odonata are one of the most well-known and well documented invertebrate groups and, along with Lepidoptera, have been used as indicators of a more widespread reduction in insect abundance and diversity. Insects are declining more rapidly than vertebrates over much of Europe and three reasons have been suggested to account for this disparity (Thomas, 1994): many insects occupy very narrow niches, often associated with a temporary successional phase; patches may remain suitable for only a short time period; and insects are often too sedentary to colonise new patches of suitable habitat that are not extremely close to old sites.

All odonates are dependent upon aquatic habitats for larval development. These habitats, perhaps more than most, have been vulnerable to destruction or alteration over the last century. Drainage, pollution, canalisation of watercourses, and alteration of management practices, along with many other threats, have all impacted on the viability of aquatic biotopes. The resultant loss of habitat, together with impoverishment and fragmentation of remaining areas, has had a critical impact on many species. This chapter is concerned with one such declining species, the damselfly *Coenagrion mercuriale* (Charpentier).

*Coenagrion mercuriale* (the southern damselfly) is principally confined to the south and west of Europe and is threatened over much of its range. The main centres of population are in France, Spain and Italy, where its status is considered to be widespread but vulnerable (Grand, 1996). Elsewhere, it is declining (Germany and the UK), in danger of extinction (Austria, Belgium and Switzerland), or extinct (Luxembourg, the Netherlands, Poland, Romania and Slovenia) (Grand, 1996). In the UK it is currently limited to 28 of the UK's 10 km grid squares and has declined by 38% since 1985 (Purse, 2001). Its declining status has been recognised both at the national and international level and it has become the focus of European-wide conservation efforts. It is protected under the Bern Convention and the EC Habitats and Species Directive. In the UK it is protected under the Wildlife and Countryside Act of 1981 and is the only odonate currently given priority status in the UK Biodiversity Action Plan (HMSO, 1994; 1995).

*Coenagrion mercuriale* is restricted to two fragmented biotopes in the British Isles. These are small lowland heathland streams emanating from base-rich substrates, and calcareous streams and fens. Although the species is found less often on the latter habitat type in the UK, this is the more typical habitat in the remainder of its European range (Buchwald, 1994; Sternberg *et al*., 1999). Within these biotopes, *C. mercuriale* is believed to require unshaded, permanently flowing small channels with groundwater influence and abundant marginal aquatic vegetation. Thus the species is highly specialised in its habitat requirements and probably needs active management if it is to persist in the long term. It also means that it will tend to be patchily distributed and will shift its occupancy of areas as habitat management progresses.

The development of an effective conservation strategy for *C. mercuriale* is dependent upon a detailed knowledge of the species ecological requirements, including its population dynamics, patterns of movement and dispersal, and habitat requirements of all life stages (Thompson *et al.*, 2003a). Appropriate management can then be applied at both the local and the regional scale. The work described in this chapter investigates variation in the density of mature adult *C. mercuriale* in relation to habitat variables and local population size in its calcareous stream habitat. The aim is to provide management guidelines on the habitat preferences of C. *mercuriale* so that sites can be managed to conform to these preferences. Our findings are applicable throughout the European range of this species.

## 4.2 Study sites

The distribution of *C. mercuriale* in the Itchen Valley was taken from survey work carried out in 1998 (Stevens & Thurner, 1999) and 1999 (Strange, 1999). The species occurs principally on old water meadow carriers and ditches in three main areas along the Itchen flood plain between Southampton and Winchester (see Figure 3.1 in Chapter 3). From north to south these are, Mariner's Meadow, Highbridge, and the Lower Itchen Complex, with the three areas separated by two gaps of approximately 3km of largely sub-optimal habitat. The Lower Itchen Complex is a large area of near-continuous habitat, so to ensure comparable sampling intensity we divided this area into five sub-sites of approximately equal length. These divisions also corresponded to changes in management practices and hence potential differences in habitat. From north to south these are West Horton, Allington Manor, and three sub-sites (Upper, Middle and Lower) within the Itchen Valley Country Park (IVCP). In total, 7.65km of ditch was surveyed at the seven sites and sub-sites.

The IVCP is owned and managed by the local council as a public amenity, with recreation and conservation the principal management objectives. The other sites are all privately owned farmland. All of the areas investigated in this study are managed as grazing pastures, although practices vary between sites. The IVCP, Mariner's Meadow and Highbridge are cattle grazed, West Horton is sheep grazed, whilst Allington Manor is grazed by a combination of cattle and horses. Stocking intensity is lowest at the IVCP, at around 1.1 grazing units per hectare, and is highest at Allington Manor. The ditches and their banks are fenced in West Horton, but are open to grazing in Mariner's Meadow, Highbridge and Allington Manor. The Upper section of the IVCP is also open to grazing, but most of the Middle and Lower sections are fenced on one side to encourage habitat suitable for the water vole (*Arvicola terrestris*) and otter (*Lutra lutra*). Finally, the channel and bank profiles varied both within and between sites. The channels at West Horton, for example, were u-shaped with almost vertical banks and little marginal vegetation, the channels at Mariner's Meadow were generally shallow and wide, whilst a wide range was present at the IVCP. In several locations, underwater ledges or platforms were present at the edges of the main channel. These berms are formed either by dredging at two different levels during management works, or by the action of livestock trampling the soft banks, and provide ideal habitat for marginal aquatic vegetation. Thus we were able to investigate the association of *C. mercuriale* with a variety of different habitats and management regimes during the course of this study.

## 4.3 Methods

### *4.3.1* Coenagrion mercuriale *survey*

Density of *C. mercuriale* was derived from a large mark-release-recapture (MRR) experiment that we performed in all seven areas in the summer of 2001. At each site or sub-site a pair of research assistants captured damselflies with a kite net and recorded the location using a Global Positioning System (GPS) calibrated to the Ordnance Survey. Animals were marked by writing a unique alphanumeric code on the left forewing in waterproof ink and by putting a small dab of paint from a paint marker pen on the thorax. We sampled every day for five weeks from 12th June, except during bad weather when adult damselflies are not active. This coincided with the peak flight period in this area.

We divided each site into 50m x 50m sections and the damselflies marked or recaptured within each section were tabulated. We chose sections of this size as the median net lifetime movement recorded in this study was 31.9m, and 65.7% of individuals moved less than 50m in their lifetime (see Chapter 3). Thus the scale of each section reflects the approximate scale of lifetime movement for the majority of damselflies. Density was then calculated as the average number of *C. mercuriale* seen in that section per day of recording.

### *4.3.2 Habitat survey*

Immediately following the end of the MRR work, we recorded a suite of environmental variables (Table 4.1). We measured eight variables describing the physical characteristics of the channel and banksides, including one that recorded the management regime. The width of berms was recorded where present. We collected information on whether a section was fenced on one or both sides, but this variable was dropped from the analysis as it was highly correlated with our grazing variable.

We recorded the percentage cover of vegetation in two 1m$^2$ quadrats, one on each bank, and averaged the results. The percentage cover of in-channel vegetation in a strip between the two bankside quadrats was also assessed. Due to the enormous number of potential variables, vegetation was recorded in terms of functional groups rather than individual species (Table 4.1). Bankside vegetation height was measured on both sides at 0, 0.25, 0.5, 1, 2, 5 and 10m from the water's edge. This was converted into two variables, the mean vegetation height from 0-1m and the mean vegetation height from 2-10m from the water's edge.

Only channels with flowing water were surveyed, as it is known that year-round flow is a pre-requisite for this species (Buchwald, 1994; Winsland, 1997; Jenkins *et al.*, 1998; Thompson *et al.*, 2003a). We collected habitat data from 82 sections, which represented 54% of the ditch network.

**Table 4.1.** Habitat variables measured in each section and used as potential predictors of *C. mercuriale* density.

| Variable | Description |
|---|---|
| **Physical variables** | |
| Water depth | Mean of 3 measurements (cm) taken at ¼, ½ & ¾ across channel |
| Water width | Width of channel (cm) |
| Bank height | Height of bank (cm) from water's edge to bankfull level |
| Bank width | Width of bank (cm) from water's edge to bankfull level |
| Bank gradient | Gradient of bank ($\theta$) where $\tan \theta$ = width / height |
| Substrate | Composition of bed substrate. Scale: 1 – predominantly silt; 2 – silt & gravel; 3 – predominantly gravel. |
| Berm width | Width of underwater ledge / platform (see text). Scale: 0 – no berm; 1 – 1st quartile of widths; 2 – 2nd quartile; 3 – 3rd quartile; 4 – 4th quartile |
| Grazing | Grazing animals have access to bankside. Scale: 0 – no grazing on either bank; 1 – grazing on one bank only; 2 – grazing on both banks. |
| **In-channel vegetation** | |
| Emergent dicots | % cover of emergent dicots, principally *Apium nodiflorum, Rorippa nasturtium-aquaticum, Veronica* spp., *Myosotis scorpioides*, and *Mentha aquatica* |
| Emergent monocots | % cover of emergent monocots, principally *Glyceria maxima, Phalaris arundinacea, Sparganium erectum, Iris pseudacorus* and *Carex* spp. |
| Submerged | % cover of submerged plants, *Ranunculus* spp., *Callitriche* spp. and others |
| Floating | % cover of floating plants, principally *Lemna minor* |
| Open water | % open water |
| **Bankside vegetation** | |
| Helophyte dicots | % cover of dicots typically associated with water's edge habitat, principally *Apium nodiflorum, Rorippa nasturtium-aquaticum, Veronica* spp., *Myosotis scorpioides, Mentha aquatica, Rumex hydrolapathum*, and *Epilobium* spp. |
| Helophyte monocots | % cover of monocots typically associated with water's edge habitat, principally *Glyceria maxima, Phalaris arundinacea, Sparganium erectum, Iris pseudacorus, Carex* spp., and *Juncus* spp. |
| Forbs | % cover of terrestrial dicots, including *Urtica dioica, Montia sibirica, Solanum dulcamara, Rumex acetosa, Cirsium* spp. and others |
| Terrestrial monocots | % cover of terrestrial monocots, including terrestrial Gramineae, Juncaceae and Cyperaceae |
| Bare ground | % cover of bare ground |
| Trees | Presence (1) or absence (0) of trees rooted in-channel or on the bankside. |
| Vegetation height 0-1m | Direct measurement of vegetation height. Mean of 4 readings taken at water's edge, 0.25, 0.5 & 1m from edge on both banks. |
| Vegetation height 2-10m | Direct measurement of vegetation height. Mean of 3 readings taken at 2, 5 & 10m from water's edge on both banks. |

### *4.3.3 Statistical analysis*

We used generalized linear models (GLM; McCullagh & Nelder, 1983; Dobson, 2002) to assess which variables explained a significant proportion of variation in *C. mercuriale* density. GLMs are able to handle distributions other than the normal, including the binomial distribution, which can be used to model presence / absence data, and the Poisson distribution, which is used to model count data. These distributions have proved particularly useful in modelling species distributions with respect to habitat variables and have been used in a large number of studies in recent years (Guisan & Zimmermann, 2000; Pearce & Ferrier, 2001; Guisan *et al.*, 2002 and references therein; Rushton *et al.*, 2004).

In our study, mean density of *C. mercuriale* was used as the dependent variable. As this is based on count data, a Poisson error structure was the most appropriate, and it was related to the set of predictors using a logarithmic link function (Crawley, 1993; Dobson, 2002). However, the distribution of *C. mercuriale* was aggregated and so a quasi-likelihood function was used (SAS Institute Inc., 1999; Crawley, 2002). In effect this adjusts the scale parameter of the model (using Pearson's $\chi^2$ / d.f.) so that the variance in *C. mercuriale* density is proportional to, rather than equal to, the mean. Poisson regression has been used widely on a variety of different taxa, including birds (Chamberlain *et al.*, 1999; Bradbury *et al.*, 2000; Robinson *et al.*, 2001; Henderson *et al*, 2004), mammals (Laurance, 1997; Jaberg & Guisan, 2001), insects (Maggini *et al.*, 2002, Mac Nally *et al.*, 2003; Meggs *et al.*, 2004), and the species richness of plants (Heikkinen & Neuvonen, 1997).

A backwards selection procedure was used starting from the maximal model with all variables included (Crawley, 2002). The least significant variables were removed sequentially until all remaining variables were significant at $P \leq 0.05$. All removed variables were then refitted to check whether they explained additional variance. Where categorical variables remained in the minimal adequate model, simplified categories were also tested (Crawley, 1993). $D^2$ and adjusted $D^2$ (the equivalents of $R^2$ and adjusted $R^2$) were calculated according to standard formulae (Guisan & Zimmermann, 2000).

All variables that were not normally distributed were subjected to an appropriate transformation before model building. Water width, bank gradient and both vegetation height variables were $\log_{10}$ transformed, bank height was square root transformed, and all plant percentage cover variables were arcsine transformed. Quadratic terms were included to test for possible non-linear effects of the continuous variables. Due to the large number of potential explanatory variables, model building followed a two-stage process. In the first stage, the 8 physical variables and their quadratic terms, where appropriate, were fitted. In the second stage the in-channel and bankside vegetation variables and their quadratic terms were added to the minimal adequate model from the first stage.

One potential problem with our study design was that sections were not spatially independent because they were clustered within sites. It is possible that sections within one site or sub-site are more similar than those from a different site, particularly if unmeasured variables acting at the site / sub-site level were present. This potential problem was dealt with by adding a series of dummy variables representing each site or sub-site into the best model from stage two. Two factors were tested; a "sites" factor with three levels, corresponding to the three principal areas (Mariner's Meadow, Highbridge, and the Lower Itchen Complex), and a "sub-sites" factor, corresponding to the seven sub-sites. This is the "raw data approach" suggested by Legendre (1993) to deal with broadscale spatial autocorrelation.

We also examined whether patterns of *C. mercuriale* density were related to local population size. This could result as sections were not spatially independent from their neighbours and damselflies may aggregate in areas where large populations are already present. To investigate this possibility we calculated variables representing the mean density and the maximum density of *C. mercuriale* in all adjacent sections. These variables were added to the minimum adequate habitat model. All analyses were performed in SAS release 8 (SAS Institute Inc., 1999).

### *4.3.4 Movement in relation to habitat features and density*

If habitat is sub-optimal, individuals may move further in search of more suitable areas. There may, therefore, be a link between movement and certain habitat features. We investigated this possibility by calculating the mean net lifetime movement for all damselflies first marked in each section. This was then used as the dependent variable in a new GLM, with the habitat variables and density as predictors. This time the response variable was normally distributed, so a normal error structure was assumed and was related to the predictors using an identity link function (Crawley, 1993). This is analogous to least-squares linear regression. Model building followed the same procedure as above.

## 4.4 Results

### *4.4.1* Coenagrion mercuriale *density*

During the five weeks of the MRR experiment, 7816 *C. mercuriale* were marked, and there were 3325 recapture events. A breakdown of the numbers at each site and sub-site is given in Table 4.2. As each site contained roughly equal lengths of potential ditch habitat, these figures give a crude indication of the strength of the colonies. The damselfly was present in reasonable numbers at all sites, but the Upper and Middle sections of IVCP contained particularly strong populations. The site with the lowest population was West Horton, where it was found in good numbers on one short stretch of stream, but was almost absent from the rest of the site.

**Table 4.2.** Total numbers of *C. mercuriale* marked and recaptured at each site or sub-site in the Itchen valley, Hampshire, over a 5 week period in June and July 2001.

| Site or Sub-site | Individuals Marked | Recapture Events | Total Number |
|---|---|---|---|
| Mariner's Meadow | 1071 | 773 | 1844 |
| Highbridge | 779 | 460 | 1239 |
| West Horton | 351 | 182 | 533 |
| Allington Manor | 558 | 324 | 882 |
| IVCP - Upper | 2152 | 764 | 2916 |
| IVCP - Mid | 1874 | 427 | 2301 |
| IVCP - Lower | 1031 | 395 | 1426 |

Figure 4.1 shows the frequency distribution of mean *C. mercuriale* densities for each of the 82 sections for which we collected habitat data. *C. mercuriale* was recorded in 77 of these sections and the modal density was less than 1 damselfly per section per day. However, the data deviated from a Poisson distribution as there were more high density sections than expected, indicating that *C. mercuriale* was from an aggregated or under-dispersed distribution. The highest recorded was an average of 35.7 damselflies per day, from a section in IVCP – Upper.

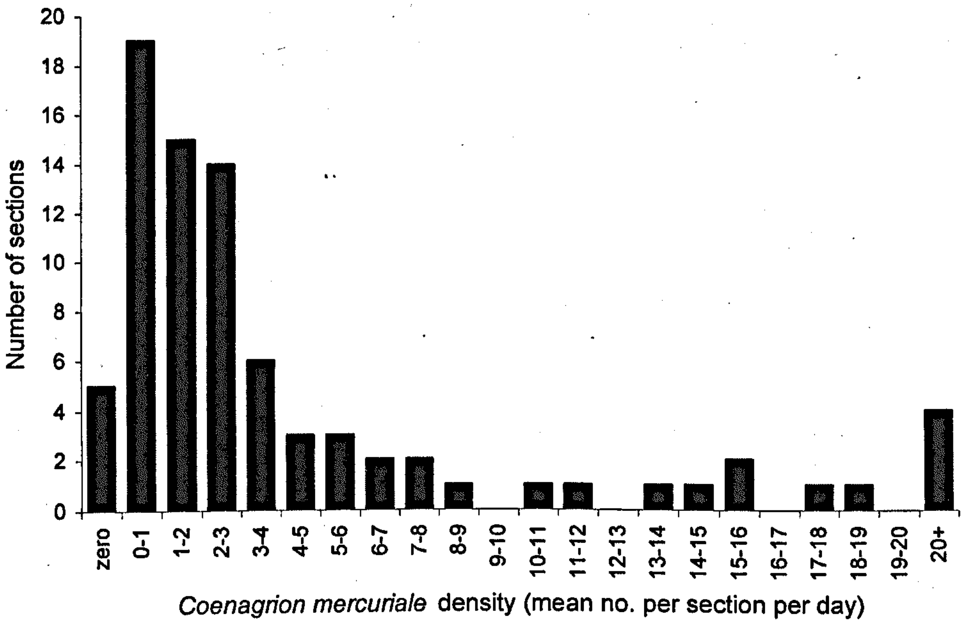

**Figure 4.1.** Frequency distribution of mean *C. mercuriale* densities in 82 sections in the Itchen Valley, Hampshire.

*4.4.2 Habitat associations*

The single best predictor of high *C. mercuriale* density was the presence of wide berms (Table 4.3 – Habitat model), and this factor alone explained 31.2% of the total variance. Initially, both the 3rd and 4th width quartiles were fitted to the model, but this was replaced by a single variable describing the wider half of berm widths (Berm width B) without a significant fall in deviance and leading to a slightly improved fit.

Moderately wide banks were also favoured, which together with berms underneath the water, provide habitat for bankside and in-channel vegetation. Channel substrates consisting primarily of silt were also preferred. *C. mercuriale* was significantly associated with three of the four types of in-channel vegetation - emergent dicots, submerged, and floating vegetation. However, it was also associated with open water and was not found in large numbers where the channel was substantially choked. On the bankside, both helophyte and terrestrial monocots were favoured but there was no preference for other groups. Taller vegetation was preferred in the first metre, but shorter vegetation from 2-10m from the water's edge. Finally, an element of bare ground, usually caused by grazing livestock, was associated with higher densities.

**Table 4.3.** Significant predictors of *C. mercuriale* density derived from two Poisson regression models. Deviance, degrees of freedom, deviance/d.f., $D^2$, and adjusted $D^2$ are shown for both models. For each variable retained in the model, the $p$-value derived from $\chi^2$ tests, parameter estimates and standard errors are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). "Habitat model" is derived using habitat variables only; "Final model" incorporates a variable for the density of *C. mercuriale* in adjacent sections and a "sub-sites" variable. For a fuller explanation of variables see Table 4.1 and text.

| **Model** | **Variable** | $\chi^2$ | $p$ | **Parameter Estimates** | **Standard Error** |
|---|---|---|---|---|---|
| **Habitat model** | Berm width B | 44.73 | *** | 1.336 | 0.200 |
| Deviance = 158.49 | Vegetation height 2-10m | 15.91 | *** | -1.310 | 0.329 |
| d.f. = 68 | Emergent dicots | 12.12 | *** | 0.0344 | 0.0099 |
| Dev./d.f. = 2.33 | Bank width | 11.97 | *** | 0.0332 | 0.0096 |
| $D^2 = 0.725$ | Vegetation height 0-1m | 11.82 | *** | 1.420 | 0.413 |
| Adj. $D^2 = 0.672$ | Helophyte monocots | 11.00 | *** | 0.0349 | 0.0105 |
| | Bank width$^2$ | 10.18 | ** | -0.0001 | 0.0000 |
| | Bare ground | 8.61 | ** | 0.0266 | 0.0091 |
| | Open water | 8.11 | ** | 0.0253 | 0.0089 |
| | Submerged | 8.00 | ** | 0.0235 | 0.0083 |
| | Floating | 7.53 | ** | 0.0529 | 0.0193 |
| | Substrate 1 | 5.32 | * | 0.436 | 0.189 |
| | Terrestrial monocots | 4.64 | * | 0.0250 | 0.0116 |
| | Intercept | 30.78 | *** | -6.510 | 1.174 |
| **Final model** | Adjacent mean density ($\log_{10}$) | 63.27 | *** | 1.827 | 0.230 |
| Deviance = 98.58 | Terrestrial monocots | 27.85 | *** | 0.0377 | 0.0071 |
| d.f. = 71 | Substrate 1 | 16.67 | *** | 0.562 | 0.138 |
| Dev./d.f. = 1.39 | Helophyte monocots | 13.84 | *** | 0.0188 | 0.0050 |
| $D^2 = 0.829$ | Berm width B | 5.84 | * | 0.406 | 0.168 |
| Adj. $D^2 = 0.805$ | Emergent dicots | 5.54 | * | 0.0212 | 0.0090 |
| | Trees | 5.05 | * | -0.820 | 0.365 |
| | Site IVCP-Lower | 4.78 | * | -0.564 | 0.258 |
| | Helophyte dicots | 4.69 | * | 0.0467 | 0.0216 |
| | Helophyte dicots$^2$ | 4.00 | * | -0.0009 | 0.0004 |
| | Intercept | 27.99 | *** | -2.524 | 0.477 |

There was a significant improvement to the habitat model on fitting a "sites" factor with 3 levels, but a much greater improvement on fitting a "sub-sites" factor (Table 4.4). However, only one level was significant and this corresponded to the IVCP – Lower sub-site. This implies that there was some factor acting on this sub-site that was unmeasured but could explain additional variance. The factor was negative, indicating that there were lower than expected densities throughout the sub-site. This factor level was retained in the final model.

**Table 4.4.** The fit of Poisson regression models to explain *C. mercuriale* density, incorporating (a) habitat variables only; (b) habitat variables and variables representing each site or sub-site; (c) habitat variables, sub-sites variables and variables describing local population size; (d) removal of non-significant variables and addition of significant ones to derive the final model described in Table 4.3. The habitat model from Table 4.3 is used as the base habitat model. The best model from (b) is used as the base model for (c) and the best model from (c) is used as the base model in (d). The deviance, degrees of freedom, deviance/d.f., $D^2$, and adjusted $D^2$ are shown for each model.

| | **Deviance** | **d.f.** | **Dev. / d.f.** | $D^2$ | **Adj.** $D^2$ |
|---|---|---|---|---|---|
| (a) Habitat model | 158.49 | 68 | 2.33 | 0.725 | 0.672 |
| (b) + sites | 147.14 | 66 | 2.23 | 0.744 | 0.686 |
| + sub-sites | 123.24 | 62 | 1.99 | 0.786 | 0.720 |
| (c) + maximum adjacent density | 116.04 | 61 | 1.90 | 0.798 | 0.732 |
| + mean adjacent density | 111.27 | 61 | 1.82 | 0.807 | 0.743 |
| + $\text{Log}_{10}$(mean adj. density) | 100.49 | 61 | 1.65 | 0.825 | 0.768 |
| (d) non-significant variables removed | 113.47 | 74 | 1.53 | 0.803 | 0.784 |
| significant variables added - Final model | 98.58 | 71 | 1.39 | 0.829 | 0.805 |

### *4.4.3 Effects of local population density*

Density of *C. mercuriale* could be better explained by incorporating information on local population size. Indeed, mean adjacent population density was the single most important factor determining density in the final model, and could explain 56.0% of the total variance. To investigate whether the relationship was exponential, linear or asymptotic, three different versions of this factor were fitted (Telfer *et al.*, 2001). These were the maximum density in adjacent sections, the mean density, and $\text{Log}_{10}$ transformed mean density respectively. $\text{Log}_{10}$ mean density provided the best fit to the data, with the worst fit provided by the maximum density (Table 4.4). An asymptotic response was, therefore, implied.

### *4.4.4 Final model*

$\text{Log}_{10}$ mean density was the single best predictor in the final model (Table 4.3). However, even accounting for this spatial autocorrelation and including the "sub-sites" factor relating to IVCP – Lower, five of the habitat variables from the best habitat model continued to significantly improve the fit of the model. These were; a channel substrate consisting primarily of silt, wide berms, in-channel emergent dicots, and bankside monocots, both those associated with water's edge habitat (helophyte monocots) and those of a more terrestrial nature (terrestrial monocots). All were positively associated with *C. mercuriale* density. In addition, three further variables significantly improved the fit of the model when refitted in the final step of the model building process. The presence of trees was negatively associated with damselfly density, whilst bankside helophyte dicots showed a quadratic response, with greatest damselfly densities at intermediate percentage cover of this vegetation type.

### *4.4.5 Effect of habitat and density on movement*

We were able to calculate movement data for 68 of the 82 sections for which we had collected habitat data. This represents a subset of the movement data. The mean net lifetime movement for damselflies first marked in these 68 sections ranged from 10.1m to 144.2m with a median of 33.8m.

Three habitat variables had a significant effect on *C. mercuriale* movement (Table 4.5 – Habitat model). Movement was increased from sections with smaller than average berms (Berm width A), and from sections with deeper water. There was a quadratic effect of bank height, with greatest movement occurring from sections with either low or high banks.

There was no improvement to the model on fitting a "site" or "sub-site" factor. However, the addition of *C. mercuriale* density did significantly improve the model, with greatest movement occurring in sections with low densities of damselflies. $\text{Log}_{10}$ mean density provided a slightly better fit than the untransformed variable. Narrow berm width and water depth remained significant, although bank height was no longer significant and was deleted from the final model. Density in neighbouring sections did not improve the fit of the model.

**Table 4.5.** Significant predictors of mean *C. mercuriale* movement derived from two GLM regression models. The *F*-value and the associated *p*-value, degrees of freedom, $R^2$, and adjusted $R^2$ are shown for both models (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). For each variable retained in the model, the *p*-value derived from *t*-tests, parameter estimates and standard errors are shown. "Habitat model" is derived using habitat variables only; "Final model" incorporates a variable for the density of *C. mercuriale*. For a fuller explanation of variables see Table 4.1 and text.

| **Model** | **Variable** | **t** | ***p*** | **Parameter Estimates** | **Standard Error** |
|---|---|---|---|---|---|
| **Habitat Model** | Berm width A | 4.04 | *** | 0.235 | 0.058 |
| F = 6.81 *** | Water depth | 2.82 | ** | 0.0028 | 0.0010 |
| d.f. = 4,63 | Bank height | -2.01 | * | -0.238 | 0.119 |
| $R^2 = 0.302$ | Bank height$^2$ | 2.01 | * | 0.0150 | 0.0074 |
| Adj. $R^2 = 0.258$ | Intercept | 4.80 | *** | 2.264 | 0.472 |
| **Final Model** | Berm width A | 3.50 | *** | 0.201 | 0.057 |
| F = 11.23 *** | *C. mercuriale* density ($\log_{10}$) | -2.93 | ** | -0.220 | 0.075 |
| d.f. = 3,64 | Water depth | 2.39 | * | 0.0022 | 0.0009 |
| $R^2 = 0.345$ | Intercept | 17.17 | *** | 1.529 | 0.089 |
| Adj. $R^2 = 0.314$ | | | | | |

## 4.5 Discussion

### *4.5.1 Habitat associations*

Mature adult *C. mercuriale* are strongly associated with certain physical and vegetation characteristics of the water meadows ditches in the Itchen Valley. The most important physical features were the presence of wide underwater berms and a substrate consisting primarily of silt. Wide berms provide suitable habitat for emergent vegetation and warm shallow areas with slow flow for larvae. Indeed, the percentage cover of emergent dicots was positively correlated with wide berms (Spearman's correlation with Berm width B, $r_s = 0.319, p < 0.01$). Similarly, silt deposits occur in areas of slow flow and around the roots of aquatic vegetation. *C. mercuriale* larvae are most often found in shallow, slow-flowing channels or in the silty margins of larger channels, on or around the roots of emergent vegetation (Hold, 1998; Purse, 2001; see also Chapter 7). Thus, adults are likely to be associated with channels that provide such habitats.

The plant groups that were associated with the highest densities of *C. mercuriale* were in-channel emergent dicots, bankside monocots, and bankside helophyte dicots. Trees were actively avoided. The roots of in-channel emergent dicots form the preferred habitat for developing larvae. Adults also preferentially choose such plants for oviposition, as eggs are laid directly into the stems of submerged and emergent plants. In a study in the New Forest, Purse (2001) found that females showed a marked preference for plants with soft stems and thin cuticles, containing spongy parenchyma cells rather than thicker collenchyma cells. Strange (1999) reported that species favoured for oviposition in the Itchen Valley included *Apium nodiflorum*, *Rorippa nasturtium-aquaticum* and *Veronica beccabunga*, and that grasses were not favoured. Similarly, Sternberg *et al.* (1999) reported that a wide variety of plant species are used for oviposition in Baden-Württemberg, Germany, but plants with hard parts are avoided.

Bankside monocots are used by adult *C. mercuriale* for a variety of purposes. They provide suitable perching sites close to the water's edge for basking, foraging, for males waiting for females, and for copulating pairs. They provide shelter during periods of inclement weather and to escape from predators. They may also increase the availability of prey items, although greatest prey abundance is likely to occur in areas with a diverse and heterogeneous vegetation structure (Drake, 1995). Finally, they could provide suitable night-time roosting sites, although adults will usually roost away from the water's-edge in the Itchen Valley (Chapter 5).

Bankside helophyte dicots are also able to provide shelter and potential perching sites. However, the species in this group are largely the same as the species in the in-channel dicots group (Table 4.1), differing only in whether the plants are rooted in the channel or on the bankside. They are probably, therefore, assessed in the same way by *C. mercuriale* and could be used as a cue to indicate suitable oviposition and larval habitat.

Trees are avoided in the Itchen Valley, probably because they cast shade onto the watercourse, reducing temperature and hence flight manoeuvrability. In 117 sites investigated in Germany, 70% were completely unshaded, and no site was more than 20% shaded (Buchwald, 1994). The vast majority of sites in the UK are also unshaded (Winsland, 1997; Purse, 2001). The tree variable that we measured during this study only included trees that were rooted in the channel or bankside quadrats, and so will have underestimated the effect of shading. Unfortunately, we did not include a direct measurement of shade, although it has been collected for a related research project (Chapter 7). Most sections were completely unshaded, or at most shaded for a small part of the day. However, larger areas of the IVCP – Lower sub-site were overgrown by bankside trees and shrubs. It is likely that this unmeasured factor resulted in the lower than expected densities throughout this sub-site that was evident in the final model.

It is worth noting that although the density of *Coenagrion mercuriale* was higher in areas with ample emergent dicots, high percentage cover of vegetation *per se* was not favoured, and open water was positively associated with density in the earlier habitat model. In this study emergent vegetation cover ranged from 0-100% with a mean of 32%. Typically this was made up of 14% emergent dicots and 18% emergent monocots. Other authors have previously noted that *C. mercuriale* did not occur on sites that were overgrown with emergent vegetation in the Itchen Valley (Hold, 1998;

Strange, 1999) and in other parts of the UK (Evans, 1989; Winsland, 1997; Stevens & Thurner, 1999). In Germany, *C. mercuriale* occupied habitats with emergent vegetation cover ranging from 3-100%, and submerged vegetation of at least 1%, but appears to prefer sections of water with 30-60% emergent vegetation (Buchwald, 1994). Other studies have indicated that the species preferred lower vegetation densities, and that there are regional differences. Sternberg *at al.* (1999) reported a preferred density of 1-20% in the Upper Rhine Valley, but 10-40% in the Alpine region, and 50-90% in calcareous marsh habitat.

### *4.5.2 Local population size and habitat selection*

Local population size has a major effect on *C. mercuriale* density, implying a degree of spatial autocorrelation. That is to say, individuals are attracted to areas that already contain high densities of conspecifics. There are a number of reasons that could explain this pattern. Firstly, there is strong selection pressure for females to choose oviposition sites with habitat features that maximise the growth and survival of offspring. Secondly, individuals may be using the presence of conspecifics as a cue for habitat quality. For example, in a small experiment in Brittany, France, Martens (2000) showed that tandem pairs of *C. mercuriale* landed preferentially on leaves where a single motionless male in the typical vertical position of a tandem male was present. Finally, this pattern may be driven by the need to find mates and avoid inbreeding in this non-territorial species.

It is believed that odonates select habitat in a hierarchical manner (Corbet, 1999). Selection follows a sequence of decreasing scale from biotope to larval habitat to oviposition site, using different selection cues at each stage. At the larger scales it is likely that odonates use mostly visual cues and are, for example, attracted by light reflecting from water bodies. Given a range of artificial materials, *Aeshna juncea* was most attracted to black plastic foil, which gave a coarse pattern of reflection on a dark background (Wildermuth, 1993). This may go some way to explain why *C. mercuriale* is not common in sites that are overgrown with emergent vegetation. At finer scales it is likely that they use a combination of visual, tactile and thermosensory cues (Corbet, 1999). At all stages, damselflies may be assessing habitat directly or using presence of conspecifics as a cue, or a combination of these factors.

### *4.5.3* Coenagrion mercuriale *movement*

As further confirmation of the tendency of this species to aggregate, we found that movement was inverse density dependent. In other words, the greater the density of *C. mercuriale*, the shorter the average distance moved. This is the opposite effect to that found in most other species. It is beyond the scope of this chapter to discuss this feature in detail; the factors affecting movement and dispersal are described elsewhere (see Chapter 3). However, the most plausible explanations are likely to be once again, access to high quality habitat and to conspecifics in a species utilizing scramble competition (Thompson *et al.*, 2003a).

The only habitat features that significantly affected movement in the final model were the presence of narrow berms and deep water, both of which resulted in greater movements. It would seem that *C. mercuriale* is moving away from areas where these two features are present. This ties in well with the habitat model, where larger than average berms were favoured. If damselflies are associated with wide berms, which provide large areas of suitable habitat then it seems reasonable that they should move away from areas providing less suitable habitat, particularly if better is available nearby. The response to water depth is probably similar. Channels that are deep provide less of the preferred shallow margins with abundant emergent vegetation and so damselflies are likely to move away.

### *4.5.4 Methodological considerations*

Although our regression models uncovered statistically significant relationships between the predictor variables and *C. mercuriale* density that appear to fit with the known ecology of the species (Thompson *et al.*, 2003a), the results are subject to a number of assumptions and limitations. Ideally, we would have validated our findings using an independently collected data set. However, this was not logistically feasible and our data set was too small to be able to divide it into a training subset and a validation subset. This makes it harder to ascertain the general usefulness and application of our models. Indeed, lack of field validation has been identified as a serious issue limiting the validity of this type of study (e.g. Guisan *et al.*, 2002). Linked with this, models developed for one part of a species range often have only limited success when applied to a separate area. It would be interesting to test our model in the neighbouring Test Valley, where the species occurs in a similar habitat to the Itchen Valley, or to other parts of the UK where *C. mercuriale* occurs on different habitats.

There is always the potential problem of overfitting when performing a regression with a large number of predictor variables. Crawley (1993) suggests that there should be no more than about *n*/3 parameters in the initial model and we achieved this by fitting the model in stages. Again, however, field validation would have improved our confidence in the final model.

We chose to amalgamate plant species into functional groups, which we felt was justified on both statistical and ecological grounds. This radically reduced the number of potential predictor variables, thereby reducing the chance of overfitting and of spurious correlations. Many of the plant species were sparsely distributed and could not have been normalized before analysis. Although *C. mercuriale* has been associated with particular plant communities and functional types, it has never been associated with individual species. For example, Purse (2001) found that *C. mercuriale* selected a variety of soft-stemmed emergent dicots for oviposition but used a variety of hard stemmed emergent monocots for emergence. Therefore, we did not think that there would be any loss of information by grouping plant species into these structural and functional groups.

### *4.5.5 Conservation implications*

The results of this study have revealed a number of habitat features with which *C. mercuriale* is associated. It is encouraging that these results have confirmed notions of habitat preferences that have until now been based on a combination of survey work and anecdotal evidence (e.g. Winsland, 1997; Hold, 1998; Jenkins *et. al*, 1998; Stevens & Thurner, 1999; Strange, 1999). Management, therefore, should be undertaken that encourages the key habitat attributes identified. Channels with wide shallow margins and abundant emergent herbaceous vegetation are the primary goal and can best be achieved by a combination of mechanical re-profiling and light grazing. Periodic dredging is required to stop the channels from silting up completely and to remove excess vegetation. During dredging operations, berms should be created. Cattle can also help to create a complex bank profile by poaching the channel edges. Cattle are also extremely important for maintaining the correct vegetation structure on both the banksides and in the margins of the channels. Water level management is an important prerequisite in some areas and could be achieved by the installation and maintenance of sluice gates and other control features. Year-round flowing water is essential for the survival of the species, but reasonably constant water levels would further enhance stability.

Movement patterns and the population structure of *C. mercuriale* should have an important bearing on the spatial scale of any planned management works. The majority of individuals move considerably less than 50m in their lifetimes. It is therefore essential that habitat enhancement is carried out on short sections at a time and that these are close to strong centres of population. On a landscape scale, movements over 500m are rare and the longest recorded lifetime movement is less than 2km (Chapter 3). This ecological distance corresponds very closely with genetic distance and we have discovered that the populations at Mariner's Meadow and Highbridge are genetically isolated from those in the Lower Itchen Complex (Watts *et al.*, 2004). Long-term persistence of the species in the Itchen Valley and elsewhere will depend upon creation of new sites between existing locations, to re-connect populations and enable gene flow over large distances.

# Chapter 5: Adult roosting site selection

## 5.1 Introduction

Habitat is one of the most fundamental concepts in ecology. In its most basic form, it describes the place where a species lives, but is actually comprised of a suite of resources and environmental conditions (Dennis *et al.*, 2003 and references therein). For the Odonata, a habitat must meet the ecological needs of all stages in the life cycle and for all activities at each stage. In the adult stage, for example, it must include provision for several distinct activities such as foraging, mate-seeking, pairing, oviposition and nocturnal roosting (Corbet, 1999). However, habitat is often defined too narrowly. It has been argued that structural elements of habitat providing shelter, roosting and mate location sites for butterflies have often been ignored (Dover *et al.*, 1997; Dennis, 2004). Similarly, odonate habitat is usually defined by the larval habitat or by adult breeding habitat (Corbet, 1999). Habitat used by roosting adults is often overlooked.

Different species of Odonata vary widely in their roosting habits (see review in Corbet, 1999). Many roost solitarily (O'Farrell, 1971; Askew, 1982), but some roost in large aggregations (Switzer & Grether, 2000). Smaller damselflies, generally roost close to the ground among grasses and rushes while larger damselflies often roost on trees and bushes (Corbet, 1999). This chapter describes the roosting habitat and behaviour of the endangered damselfly, *Coenagrion mercuriale* (Charpentier) (Odonata: Coenagrionidae). This damselfly has declined in the UK (Purse, 2001) and across other parts of its European range (Grand, 1996). It is protected under the Bern Convention and the EC Habitats directive, and in the UK it is protected under the Wildlife and Countryside Act of 1981, and is the only odonate currently given priority status in the UK Biodiversity Action Plan (HMSO, 1994; 1995). In the UK its habitat is defined as small lowland heathland streams emanating from base-rich substrates, and calcareous streams and fens (Thompson *et al.*, 2003a). It is believed that individuals use the land adjacent to watercourses to survive periods of unfavourable weather, to spend the night, to look for food, and to mature (Buchwald *et al.*, 1989; Strange, 1999). Indeed, *C.*

*mercuriale* abundance in Germany has been shown to be influenced by the land use of the adjacent area (Buchwald *et al.*, 1989). Adjacent land does, therefore, have an important influence on this species, but detailed knowledge is lacking.

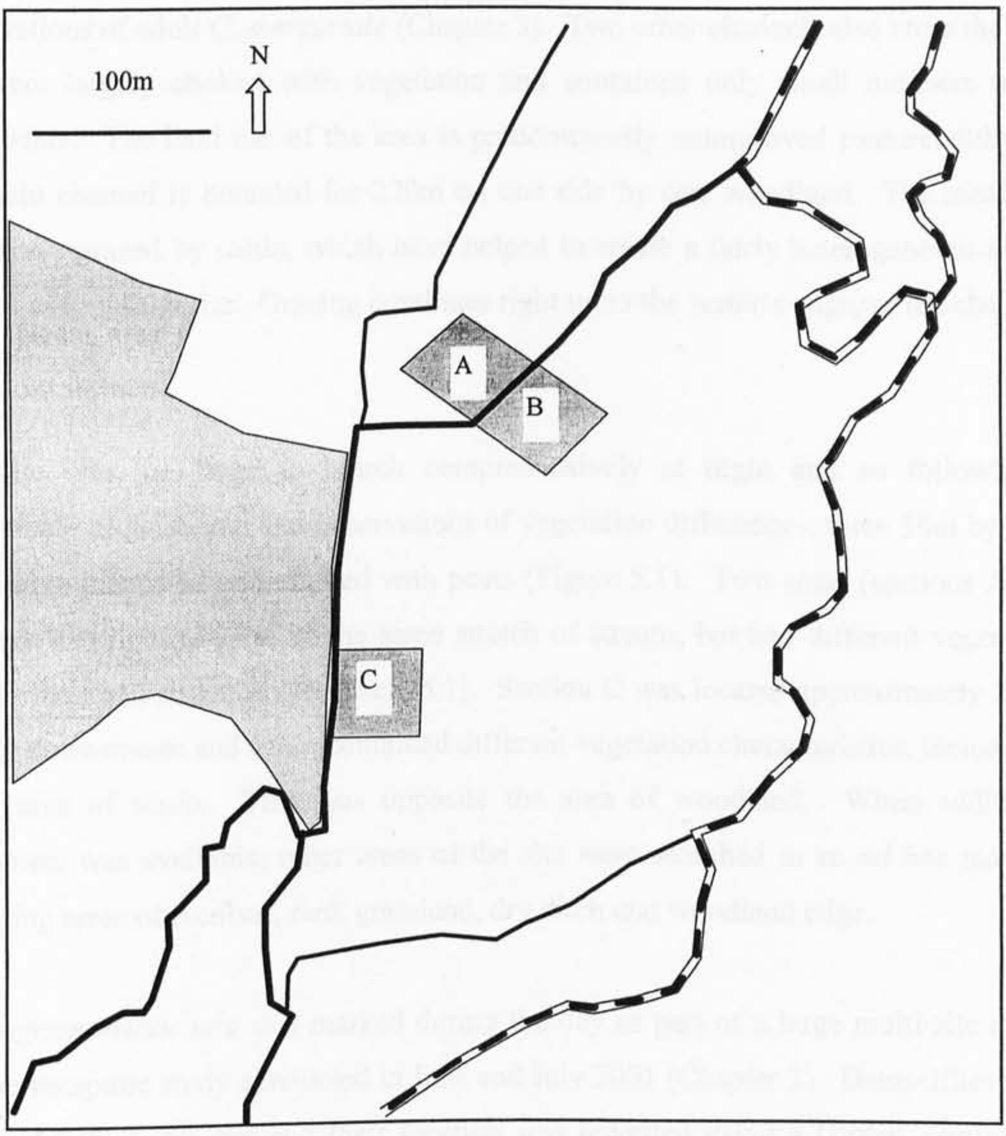

**Figure 5.1.** Study area in the Itchen Valley, Hampshire. The main channel where *C. mercuriale* was marked is represented by the thick black line, smaller channels are shown by the thinner black lines and the main River Itchen by the thick dashed line. Woodland is shown in grey, meadow in white. The location of the three 50m by 50m night-time study sections are shown by the stippled areas and are marked A, B and C. *Ad hoc* night-time observations were performed in the whole of the area to the west of the main river channel.

## 5.2 Methods

The study site is situated on the flood plain of the River Itchen, close to the city of Southampton in Hampshire (southern England). A channel drains water from the nearby river and passes through the site before eventually rejoining the river 1.6 km below the main sampling area (Figure 5.1). This was one of the best areas for daytime observations of adult *C. mercuriale* (Chapter 3). Two other channels also cross the site, but were largely choked with vegetation and contained only small numbers of *C. mercuriale*. The land use of the area is predominantly unimproved pasture, although the main channel is bounded for 220m on one side by carr woodland. The meadows are lightly grazed by cattle, which have helped to create a fairly heterogeneous sward structure across the site. Grazing continues right up to the water's edge, as the channels are unfenced.

The site was too large to search comprehensively at night and so following a preliminary night search and observations of vegetation differences, three 50m by 50m areas were identified and marked with posts (Figure 5.1). Two areas (sections A and B) were on opposite sides of the same stretch of stream, but had different vegetation composition and structure (see Table 5.1). Section C was located approximately 200m further downstream and again contained different vegetation characteristics, including a small area of scrub. This was opposite the area of woodland. When additional manpower was available, other areas of the site were searched in an *ad hoc* manner, including areas of reedbed, rank grassland, dry ditch and woodland edge.

*Coenagrion mercuriale* was marked during the day as part of a large multi-site mark-release-recapture study conducted in June and July 2001 (Chapter 3). Damselflies were captured with a kite net and their location was recorded using a Global Positioning System (GPS) calibrated to the Ordnance Survey. Animals were marked by writing a unique alphanumeric code on the left forewing in waterproof ink and by putting a small dab of UV fluorescent yellow paint (Rosco) on the thorax. This provides a visible yellow mark in the daytime and fluoresces brightly under UV light. Fluorescent dusts have been used to mark insects for many years (Hagler & Jackson, 2001). More recently, Neubauer and Rehfeldt (1995) marked *Calopteryx haemorrhoidalis* with selfglowing fabric paint and Hunger and Röske (2001) successfully marked *C. mercuriale* with UV fluorescent ink and relocated them with a UV lamp.

Nightly observations were carried out from 3rd July, beginning approximately one hour after sunset, and lasting for about two hours. Damselflies were located using a portable UV torch run on a 12V battery. Each of the three 50m by 50m areas were searched systematically each night by two field workers and the starting section was varied. Upon locating a damselfly we recorded its position using a GPS, the time, identification code (if a recapture), sex, the head height, the height of the plant stem upon which the damselfly was roosting, the species of plant and the direction of orientation of the body. We also searched carefully within tussocks so that we did not miss more hidden individuals. In total, nightly observations were performed on 16 nights over a 20-day period.

**Table 5.1.** Total numbers of *C. mercuriale* recorded over 16 nights in each 50m by 50m location, a description of the vegetation at each location and the % of *C. mercuriale* roosting on three plant species.

| **Location** | **Total number** | **Description of vegetation** | **% of individuals roosting on plant species** | | |
|---|---|---|---|---|---|
| | | | ***Juncus inflexus*** | ***Carex acutiformis*** | ***Deschampsia cespitosa*** |
| A | 121 | Tall vegetation with dominant tussocks of *J. inflexus*, *C. acutiformis* and *D. cespitosa* interspersed with mixed short sward and poached ground. | 43.0 | 7.4 | 37.2 |
| B | 27 | Mixed short sward with tall thistles (*Cirsium* spp.) and occasional tussocks. | 34.6 | 3.7 | 26.9 |
| C | 53 | Tall vegetation consisting primarily of *J. inflexus* tussocks interspersed with *C. acutiformis*. Small area of hawthorn (*Crataegus monogyna*). | 86.8 | 1.9 | 1.9 |

## 5.3 Results

A total of 276 damselfly observations were made at night during the study period, of which 201 were in the three 50 m by 50 m areas. Overall there were 192 recapture events of marked animals and 84 observations of unmarked individuals. The recaptures of marked animals comprised 165 individuals, of which 145 were recorded just once, 15 were recorded twice, 3 were recorded three times, and 2 four times. It is difficult to compare recapture rate at night with recapture rate in the daytime as daytime observations occurred over a larger area, but of individuals marked in the whole study site from the date of the start of the night observations, 13.0% were recaptured at night. The recapture rates for the two sexes were similar, 13.4% for males and 12.0% for females. The daytime recapture rate for the equivalent period was 27.4%, with a recapture rate of 30.8% for males and 11.1% for females.

*Coenagrion mercuriale* roosted more or less vertically, with its head uppermost. Individuals did not roost together, although occasionally a male and female were found roosting on the same stem. Although there was no evidence for aggregation on a nightly basis, individuals were not distributed at random within the study plots, probably because suitable roosting habitat was patchily distributed. Individuals that were recorded at night on more than one occasion did not return to the same spot to roost, moving on average 24.9 m (S.E. = 3.37 m, n = 27) from their previous roosting location. There is no apparent preference for roosting close to the watercourses, with an even spread of individuals across the 50 m by 50 m study plots. Movements between roosting site and daytime capture site tended to be greater than day-to-day movements or night-to-night movements (1-way ANOVA on $\log_{10}$ distance moved: F = 4.21, d.f. = 2,298, p = 0.016) and this effect remains significant when time is taken into account (ANCOVA: movement type, F = 3.85, d.f. = 2,297, p = 0.022; time, F = 20.34, d.f. = 1,297, $p < 0.001$).

The mean height of *C. mercuriale* above ground level was 46.5 cm (S.E. = 1.1 cm, n = 276) with a range from 4.0 to 116.0 cm. There was no difference between males and females in roosting height (t-test: t = -0.63, d.f. = 275, $p > 0.05$). The mean height of the stems on which individuals roosted was 53.3 cm (S.E. = 1.2 cm, n = 276). In other words, they were found towards the top of the vegetation and this vegetation was considerably taller than the mean height of the vegetation in the study area. There was a tendency for damselflies to roost at a lower height on days with stronger wind, although this effect was not significant (regression of roosting height against mean wind speed: $r^2 = 0.161$, $F = 2.69$, $p = 0.123$). Mean roosting height was lowest (31.6 cm) when we collected data during rain, but the number of days with rain was insufficient to test this more thoroughly.

The plant species used for roosting is shown on Figure 5.2 and it was found that 75% of individuals roosted on either *Juncus inflexus* (hard rush) or *Deschampsia cespitosa* (tufted hair grass). These species are tussock forming and did not occur evenly across the area of investigation. For example, section A contained the greatest amount of these two species and was the location of 121 night-time roosting sites, whereas section B, which was on the opposite side of the same stretch of stream, contained only small amounts of these species and only 28 individuals were found roosting (Table 5.1). Furthermore, other species, particularly *Carex acutiformis* (lesser pond sedge), *Cirsium* spp. (thistles) and fine grasses, were avoided even though they were present in high abundance in some areas. No damselflies were found roosting on scrub and none was found on the banksides amongst emergent vegetation or on bankside monocots. Furthermore, no individuals were found roosting on trees, in reedbed or in any other habitat types during *ad hoc* searching.

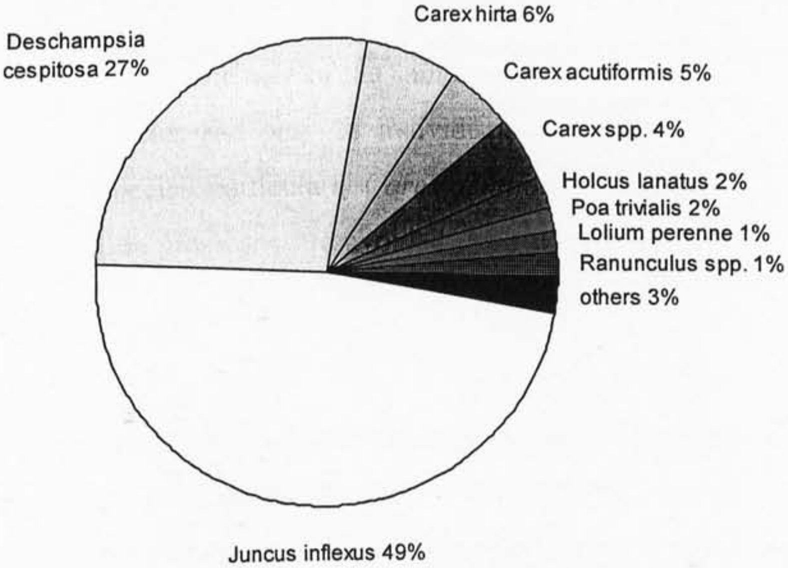

**Figure 5.2.** Plant species chosen for roosting by *C. mercuriale*, with percentage shown (n = 273).

The orientation of each individual is displayed in Figure 5.3, which shows clearly that there was no preference for any particular direction ($\chi^2 = 4.63$, d.f. = 7, $p > 0.05$). However, we did notice that after shining a light onto the damselflies for a few seconds, many would move around their perch so that they were orientated with the direction of the light source. It is quite likely that they show this sort of behaviour at dawn, in order to raise their body temperature as quickly as possible.

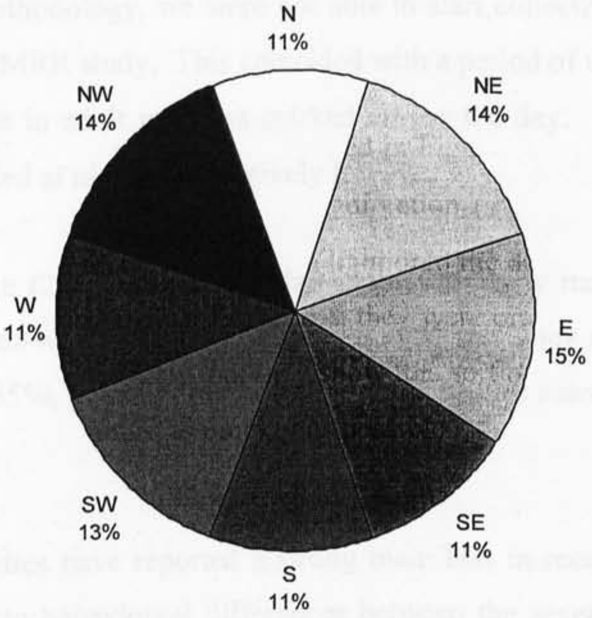

**Figure 5.3.** Orientation of the body during roosting, with percentage shown (n = 262).

## 5.4 Discussion

### *5.4.1 Method and recapture rate*

The method of marking damselflies with UV fluorescent paint and relocating them with a UV torch has proved useful for studying night-time roosting patterns. Marked individuals were easy to spot at a distance of several metres and were much easier to locate than unmarked animals. Unfortunately however, due to problems with equipment and methodology, we were not able to start collecting data until the fourth week of our main MRR study. This coincided with a period of unsettled weather, and a subsequent decline in adult numbers marked during the day. Hence, the numbers of damselflies recorded at night was relatively low.

Hunger and Röske (2001) used a similar method to study movement patterns of *C. mercuriale* in south-west Germany, with great success. They reported a much higher recapture rate of 35%, probably because they were able to search their entire site each night.

Most odonate studies have reported a strong male bias in recapture rates at breeding sites, due in part to behavioural differences between the sexes. Once mature, males will spend most of their adult lives close to the breeding sites, whereas females will only remain there for copulation and oviposition. They will subsequently leave the area and will not return until a new batch of eggs has matured. By searching away from the streams at night, we achieved the same recapture rate for the two sexes. Hunger and Röske (2001) also reported similar recapture rates for both sexes.

### *5.4.2 Behaviour and habitat*

*Coenagrion mercuriale* is similar to the majority of damselflies in that it rests vertically when roosting, with its head up (Corbet, 1999). There was no evidence that *C. mercuriale* forms roosting aggregations. Individuals were not distributed at random within the study plots, but this was almost certainly because suitable roosting habitat was patchily distributed. Neubauer and Rehfeldt (1995) reported a similar finding for

*Calopteryx haemorrhoidalis*; there was no preference for aggregation but roosting locations were not at random as leaves (the roosting site) were not at random. Three species of Coenagrionidae studied by Askew (1982) in the UK were also reported to be non-aggregating. On the other hand, large aggregations have been reported for some species such as *Hetaerina americana* (Switzer and Grether, 2000). This species roosted in small groups with a mean of 5.6 individuals per roost and 13.7 individuals per $m^2$. However, it showed no preference for particular plant species and was found roosting 0.2-2m above ground on most vegetation types.

*Coenagrion mercuriale* was usually found towards the top of the vegetation at a mean height of 46.5cm. Hunger and Röske (2001) reported that *C. mercuriale* was usually found at a height of about 20cm, while roosting height of *Ischnura elegans*, *C. puella* and *Enallagma cyathigerum* was similar for all species at 75-83cm (Askew, 1982). It is likely that height *per se* is not important, but rather height relative to the plant stem used and to the surrounding vegetation. Height was similar for both sexes, as was the case for *I. elegans* (Askew, 1982). There was a suggestion from our study that *C. mercuriale* may roost at a lower height during inclement weather, although sample sizes were too small to test this thoroughly. *Calopteryx haemorrhoidalis* was reported to roost at a mean height of 1.46m during good weather conditions in southern France, but reduced roosting height to 0.79m during strong winds (Neubauer & Rehfeldt, 1995). Similarly, *Platycnemis pennipes* roosted on taller stems after a sunny day than after a rainy day (Martens, 1996, *cited in* Corbet, 1999).

In our study, *C. mercuriale* was found throughout the 50m by 50m study blocks, showing no preference for roosting sites closest to the water's edge. Although the species is generally sedentary in nature (Chapter 3), this distance is well within its flight capabilities and it would appear that locating a suitable roosting site is more important than minimising flight distance. This is in marked contrast to the study by Hunger and Röske (2001) who found 69.8% of *C. mercuriale* within 5m of water, and 96.4% within 25m. However, almost all of their study streams were bordered on at least one side by arable land or forest and the vegetation of the remaining meadowland is unknown. On their site, *C. mercuriale* may have been forced to roost close to the water's edge if little suitable habitat had been available elsewhere.

*Coenagrion mercuriale* showed clear preferences for certain types of vegetation, choosing *Juncus inflexus* or *Deschampsia cespitosa* on 75% of occasions. Wide-stemmed herbs, shrubs and trees were avoided. Similarly, Hunger and Röske (2001) reported that most *C. mercuriale* were found on blades or stalks of grass, with occasional observations on young corn plants. None was found along forest edges or other linear features. Similarly, *Ischnura heterostica, Austrolestes annulosus* and *A. leda* roosted in clumps of *Juncus* in Australia (O'Farrell, 1971). *Ischnura elegans* roosted on *Carex* in Belgium (Dumont, 1971, *cited in* Corbet, 1999).

One of the few detailed studies of the roosting habitats of damselflies was carried out by Askew (1982). He reported that 50% of *I. elegans* roosted on grass stems (mainly *Arrhenatherum elatius* with some *Dactylis glomerata*), 12% on *Juncus* stems and 18% on *Equisetum* stems. *Coenagrion puella* roosted on grass stems 18% of the time and on grass leaves 46% of the time, while 56% of *E. cyathigerum* roosted on grass stems and 24% on grass leaves. All avoided wide-stemmed herbs. The mean diameter of these stems was 1.86, 1.89 and 2.17mm for the three species respectively. In a supplementary cage experiment where sticks of three different sizes were provided, all three sizes were used by all species but *I. elegans* and *C. puella* preferred small diameter sticks (2.1mm) while *E. cyathigerum* preferred small and medium (3.1mm) sticks. The author notes that the stem diameter chosen ranked in the same order as the size of the damselfly and suggested that the optimum width of a roosting site was wider than the damselfly's body but narrower than its eye width. This would provide ready concealment of the body, but would allow surveillance. Indeed, the mean minimum separation of the eyes for males of *I. elegans, C. puella* and *E. cyathigerum* was 1.90, 1.91 & 2.13mm respectively. Our results would seem to lend support to this hypothesis as *C. mercuriale* appears to be selecting plants with stems of a particular diameter, whilst avoiding fine grasses and wide-stemmed plants. It is slightly smaller than the three species studied by Askew (1982).

The two plant species favoured as roosting sites in our study are both tussock forming. Tussocks may provide additional protection from inclement weather, from predators and may provide a warmer microclimate than isolated plant stems. Interestingly, *I. elegans, C. puella* and *E. cyathigerum* showed a preference for *Arrhenatherum elatius*, which is loosely tufted (Askew, 1982), and *I. heterostica, Austrolestes annulosus* and

*A. leda* roosted in clumps of *Juncus* (O'Farrell, 1971). It is interesting to speculate whether *C. mercuriale* is choosing *J. inflexus* and *D. cespitosa* because the stems are the most suitable diameter, because they are tussock forming, or for some other reason. Some simple experiments could be performed to tease these factors apart.

### *5.4.3 Conservation implications*

In the daytime, adult *C. mercuriale* at our study site are significantly associated with emergent dicots such as *Apium nodiflorum, Rorippa nasturtium-aquaticum, Veronica* spp., *Myosotis scorpioides*, and *Mentha aquatica* (Chapter 4). These are used for oviposition, as perching sites and the roots provide the main larval habitat. Adults are also associated with bankside monocots such as *Glyceria maxima, Phalaris arundinacea, Sparganium erectum,* and *Iris pseudacorus*, which are used as perching sites for foraging, mate-seeking, and pairing, as well as for shelter and escape from predators (Chapter 4). However, no individuals were observed to roost on any of these thick-stemmed plant species during our night-time study.

Buchwald *et al.* (1989) investigated the use of adjacent land by *C. mercuriale* in south-west Germany. During good weather they primarily used the stream and bankside vegetation, and abundance decreased with increasing distance from the water. During bad weather and at dawn, few individuals were counted on aquatic plants, with most occurring on the adjacent land. Abundance was influenced by the land use of the adjacent area. Extensive grassland was the most favoured habitat, particularly rush-pasture, followed by fallow land and unmown improved grassland. Individuals were, however, never found in arable areas or meadows for a few weeks after they had been mown. Use of fallow land was dependent upon the vegetation present; reed communities were used, but *Rubus* spp. was not accepted. Furthermore, Buchwald (1994) revealed that almost all larger populations of *C. mercuriale* in that part of Germany were either partially or wholly surrounded by meadow. Similarly, following a survey of sites in the Itchen Valley, Strange (1999) noted that the vegetation communities on either side of the watercourses were extremely varied but the presence of tussocky grass clumps seemed to be important.

Our findings have confirmed and expanded upon these ideas. It is clearly preferable if water-courses are surrounded by meadow, but meadows can have very different vegetation structure, even when grazed by the same animals. In our study, the whole area was open to grazing by the same group of cattle and yet there were considerable differences in vegetation. Section A was most suitable and was used 4.5 times as frequently as section B, directly opposite. Other sites in the Itchen Valley are more heavily grazed and have a lower abundance of *C. mercuriale*. Although it is difficult to prove without experimentation, it is quite feasible that lack of suitable areas for night-time roosting (as well as providing daytime shelter during inclement weather) is a significant factor in the lower abundance at these sites.

This study has shown the importance of the roosting habitat for this species, and is an area that has been largely overlooked in the past. *C. mercuriale* shows a preference for tussock forming monocots, a habitat that is not always abundant at all sites. Clearly it is important to consider the habitat requirements of all life stages and the requirements of all activities performed by those life stages when designing conservation management plans for this and other species of odonate.

# Chapter 6: Macroinvertebrate communities associated with late-instar *Coenagrion mercuriale* larvae

## 6.1 Introduction

Chalk streams support diverse and productive communities of plants and animals and have been recognised as a priority habitat in the UK Biodiversity Action Plan (HMSO, 1995). They are fed from groundwater aquifers, producing clear waters and a generally stable flow and temperature regime (Berrie, 1992; HMSO, 1995). These are conditions which support a rich diversity of invertebrate life and important game fisheries. However, the importance of chalk streams extends beyond the boundary of the main river channel. Between the 17th and 19th centuries, water meadows were constructed along the flood plains of most chalk streams, to improve the quality and quantity of grassland for agricultural purposes (Bowie, 1987; Cutting & Cummings, 1999). This involved the clearance of woodland and the construction of an extensive network of carriers and ditches to allow controlled flooding of the meadows. Although much of this network of channels has been abandoned, some of the larger carriers have been maintained. These now provide a range of flow conditions and habitats, suitable for an array of macrophytes and invertebrates, that may not normally be associated with chalk streams.

A number of ecological studies have been carried out on the invertebrate fauna of chalk streams, including the use of different in-stream habitats (Harrod, 1964; Wright *et al.*, 1983, Wright, 1992; Pardo & Armitage, 1997), the ecology of aquatic margins (Harrison, 2000) and the effect of management (Harrison & Harris, 2002; Wright *et al.*, 2003). Additionally, studies have been carried out into the ecology of slow-flowing ditch communities (Caspers & Heckman, 1981; Clare & Edwards, 1983; Scheffer *et al.*, 1984, Foster *et al.*, 1990; Painter, 1999; Armitage *et al.*, 2003; Watson & Ormerod, 2004). However, few studies have been conducted on the network of ditches and carriers present on the floodplain of chalk streams and their associated invertebrates.

One species of invertebrate that appears to prefer the conditions provided by these carriers is *Coenagrion mercuriale* (Charpentier). This is a rare and declining species of damselfly. It is confined to the south and west of Europe and is threatened over most of its range (Grand, 1996). It is listed on the EC Habitats Directive, is protected under the Wildlife and Countryside Act and is the only odonate currently given priority status in the UK Biodiversity Action Plan (HMSO, 1995).

*Coenagrion mercuriale* occurs principally in two habitat types in the UK; small lowland heathland streams emanating from base-rich substrates and the water meadow ditches of chalk streams (Thompson *et al.*, 2003a). Until recently, however, knowledge of the ecology and habitat requirements of the species in its chalkstream habitat was scant and based primarily on anecdotal evidence. Even less was known about the ecology of the larvae and most conservation efforts have been based on observations of the adults.

This chapter and the next present the findings of a study undertaken to investigate the ecology and habitat requirements of *C. mercuriale* larvae. The primary aim is to investigate the biological, physical and chemical attributes of all chalkstream sites where *C. mercuriale* is present and nearby sites where it is not, to determine the habitat requirements of the larvae. In addition, this investigation provides the first detailed ecological study of a water meadow ditch network. The information acquired can then be used to guide habitat management programmes and to devise a monitoring programme for the species. In this chapter the macroinvertebrate community associated with *C. mercuriale* is investigated. I also address issues of taxonomic resolution, seasonal variation and *C. mercuriale* diet. In the following chapter (Chapter 7) *C. mercuriale* occurrence and abundance is related to physical, chemical and vegetation attributes.

## 6.2 Methods

### *6.2.1 Study sites*

This study was performed in the Itchen and Test Valleys in Hampshire (southern England), which are amongst the most famous and important chalk streams in the country. Both are designated as SSSIs and the River Itchen is a candidate SAC. The River Itchen is a major stronghold for *C. mercuriale* and the species has been declared a cSAC interest feature. The distribution of *C. mercuriale* was taken from survey work carried out in 1998 (Stevens & Thurner, 1999) and 1999 (Strange, 1999). These surveys were not comprehensive, particularly that of the River Test, and further sites have been discovered since the beginning of this study. However, this is not deemed to be detrimental to this investigation as the aim was to compare a range of sites where *C. mercuriale* occurs with sites where it does not. Thus additional sites were also investigated where the species was thought not to occur. We were able to gain access to much of the Itchen Valley between Winchester and Southampton and the major sampling areas are shown on Figure 2.2 (Chapter 2). Unfortunately, we were only allowed access to the River Test at one site close to King's Somborne, although we were still able to sample a range of habitats at this site.

At each site, sampling locations were identified at approximately 150m intervals, using a stratified random approach. A range of habitats was sampled, representing the full range of ditch succession, from recently dredged open channels to ones with little flow, which were completely choked with vegetation. We also sampled the main river at two sites. In total we took samples at 83 locations in the Itchen Valley and 17 in the Test Valley.

### *6.2.2 Field and laboratory methods*

Fieldwork was carried out four times over the course of one year, beginning in mid October 2001, and repeated in January, April and July 2002. At each location physical, chemical and vegetation characteristics were recorded. More detail and analysis of these factors is provided in Chapter 7. A sample of the macroinvertebrate community was collected using standard Environment Agency methodology (Environment Agency, 1999). This involves collecting a kick / sweep sample over 3-minutes with a 1.0 mm mesh pond net, with sampling effort allocated proportionally between the different habitat types present.

As *C. mercuriale* is a protected species, all samples were live-sorted for two man-hours on return to the laboratory. All damselfly (Zygoptera) larvae were separated for identification to species level and counted. *Coenagrion mercuriale* larvae were then returned to their original sampling locations. All other macroinvertebrates were removed and preserved in 70% alcohol, except for extremely numerous species, whose abundance was estimated. Invertebrates were then identified to the lowest taxonomic level possible and counted. This level of identification is subsequently referred to as "species-level", although some taxa could not be identified this precisely. Each season was analysed separately and in addition a combined analysis was performed where the sum of each taxon over the four seasons was calculated. Analyses were initially performed at species-level but were repeated at family-level to investigate the effect of taxonomic resolution. Thus 10 data-sets were available for analysis.

### *6.2.3 Statistical analysis*

A range of multivariate statistics was used to compare the community composition of sites where *C. mercuriale* was present with those where it was not. Bray-Curtis dissimilarities based on log ($\log_{10} x + 1$) transformed abundances were calculated using all taxa except for *C. mercuriale* abundance, which was excluded prior to the analysis. Patterns were then assessed by ordination, using Principal Co-ordinate Analysis (PCoA, also known as metric multi-dimensional scaling). This highlights major differences in the data structure.

Differences between the two groups were assessed in two ways; using ANalysis Of SIMilarities (ANOSIM) in the PRIMER statistical package (Clarke & Warwick, 1994), and Canonical Discriminant Analysis (CDA) of the principal co-ordinates in the CAP computer program (Anderson & Willis, 2003). ANOSIM is an unconstrained test that compares the within-group differences in similarity with the between group differences using ranks and is similar to a Mantel statistic (Clarke & Warwick, 1994; Legendre & Legendre, 1998). Group differences will only be highlighted if they are a major source of variation within the data structure. CDA of the principal co-ordinates, on the other hand, is a new constrained method in which ordination axes are drawn so as to maximize differences among groups (Anderson & Willis, 2003). The significance of both results was tested by permutation (10,000 times).

To identify the macroinvertebrates that were the best indicators of the presence or absence of *C. mercuriale*, we used the Indicator Value method (IndVal) (Dufrêne & Legendre, 1997). This method combines a measure of a species relative abundance with its relative frequency of occurrence in the two groups, to produce an index that varies from 0 to 100. The score for each species is independent of the occurrence of other species. IndVal is considered superior to more traditional methods of identifying indicators, such as TWINSPAN (Dufrêne & Legendre, 1997; McGeoch & Chown, 1998). The significance of each invertebrate taxon was tested using 10,000 permutations.

To identify macroinvertebrates that were correlated with *C. mercuriale* abundance, we used a Canonical Correlation Analysis (CCorA) of the principal co-ordinates, in the program CAP (Anderson & Willis, 2003). In this method, a PCoA analysis is first performed (as above). A CCorA is then performed, in which ordination axes are drawn so as to maximise their correlation with a quantitative predictor variable, in this case *C. mercuriale* abundance. Once, again, the significance of the relationship was tested by permutation.

Finally, a range of diversity and biological indices were calculated for each site. Sites where *C. mercuriale* was present were compared to sites where it was absent using Mann-Whitney U-tests and correlations were performed against *C. mercuriale* abundance using Spearman's rank correlation. The number of taxa and number of families in each sample were used as measures of richness. Hill's diversity numbers N1 and N2 were calculated as measures of diversity. Hill's numbers measure the effective number of species in a sample and are related to Shannon's Index H' and Simpson's Index $\lambda$ respectively, but are generally preferred on theoretical and practical grounds (Ludwig & Reynolds, 1988). Evenness was measured using Hill's modified ratio, which varies from 0 to 1, approaching zero as a single species becomes more and more dominant in the community. In addition, BMWP (Biological Monitoring Working Party) score and ASPT (Average Score Per Taxa) were calculated, which are measures of the extent to which invertebrate communities are influenced by organic pollution. Finally, LIFE (Lotic-invertebrate Index for Flow Evaluation) scores, which indicate flow requirements of the invertebrate community, were compared (Extence *et al.*, 1999).

## 6.3 Results

### *6.3.1 Number of sites and abundance of* C. mercuriale

Larval *C. mercuriale* were captured at 53 out of the 100 sampling locations on at least one occasion during the study. The breakdown for each season is given in Table 6.1. Larvae were captured across all four seasons at 11 of these locations, in three out of the four seasons at 11 further locations, in two seasons at 15 locations, and were captured on just one occasion at 16 of the remaining sampling locations. Figures 6.1-6.4 show the position of all sampling locations and indicate the number of seasons in which *C. mercuriale* was captured. These figures also give a crude indication of the relative strength of the populations across the range of sites. It is clear that the strongest populations occur in the Itchen Valley Country Park (Figure 6.1). Frequency of capture was reasonably high at Highbridge (Figure 6.2) and some locations within the Mariner's Meadow / Twyford Moors area (Figure 6.3). However, no larvae were captured at any of the sampling locations at Rosemary Leet or Compton Lock (Figure 6.3).

**Table 6.1.** Number of sites at which larval *C. mercuriale* were captured and abundance for each season (n = 100).

| | **Autumn** | **Winter** | **Spring** | **Summer** | **Total** |
|---|---|---|---|---|---|
| No of sites | 38 | 33 | 40 | 12 | 53 |
| No of individuals | 499 | 191 | 191 | 43 | 924 |

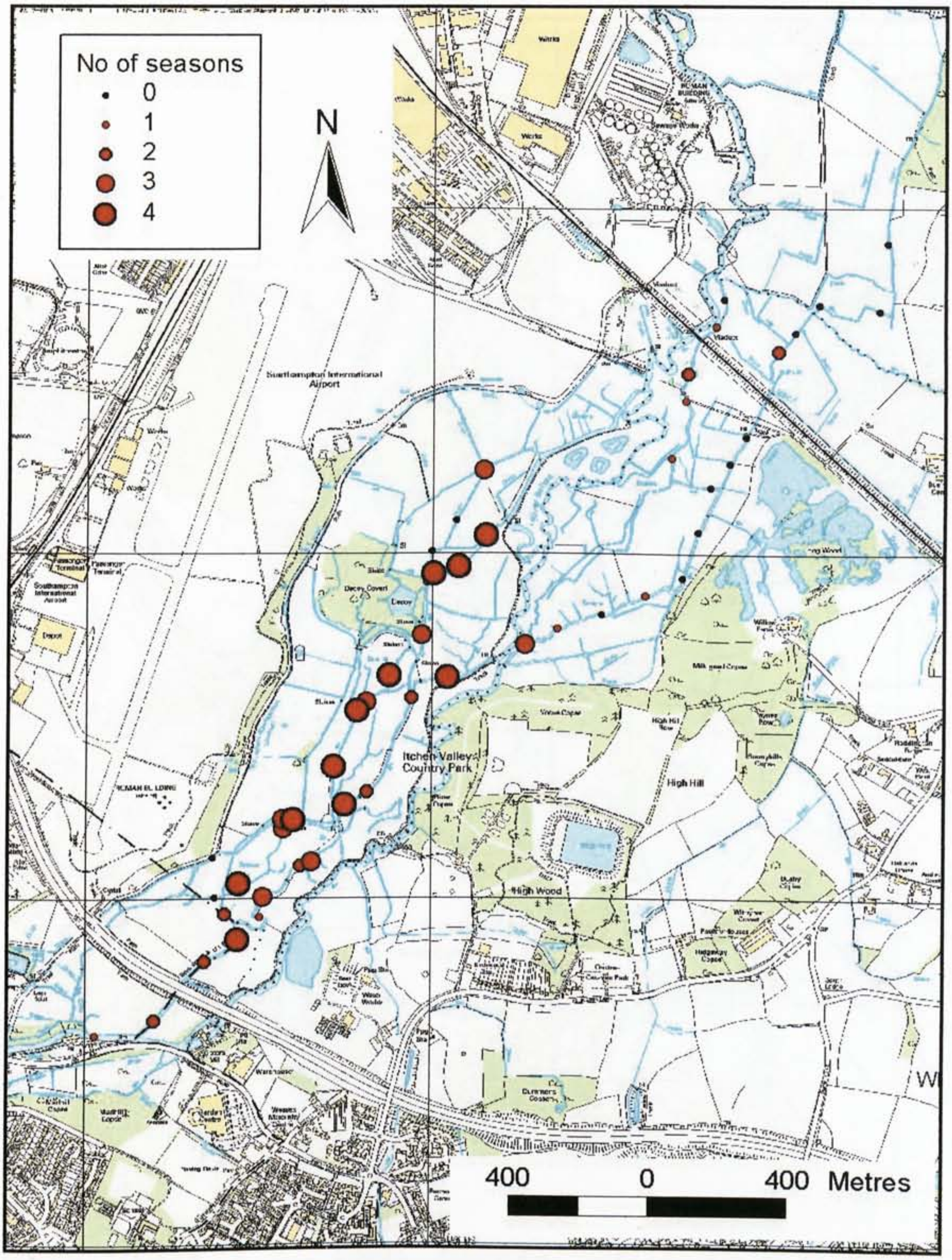

**Figure 6.1.** Itchen Valley from the Itchen Valley Country Park to West Horton Farm showing frequency of capture of *C. mercuriale* larvae at each sampling location.

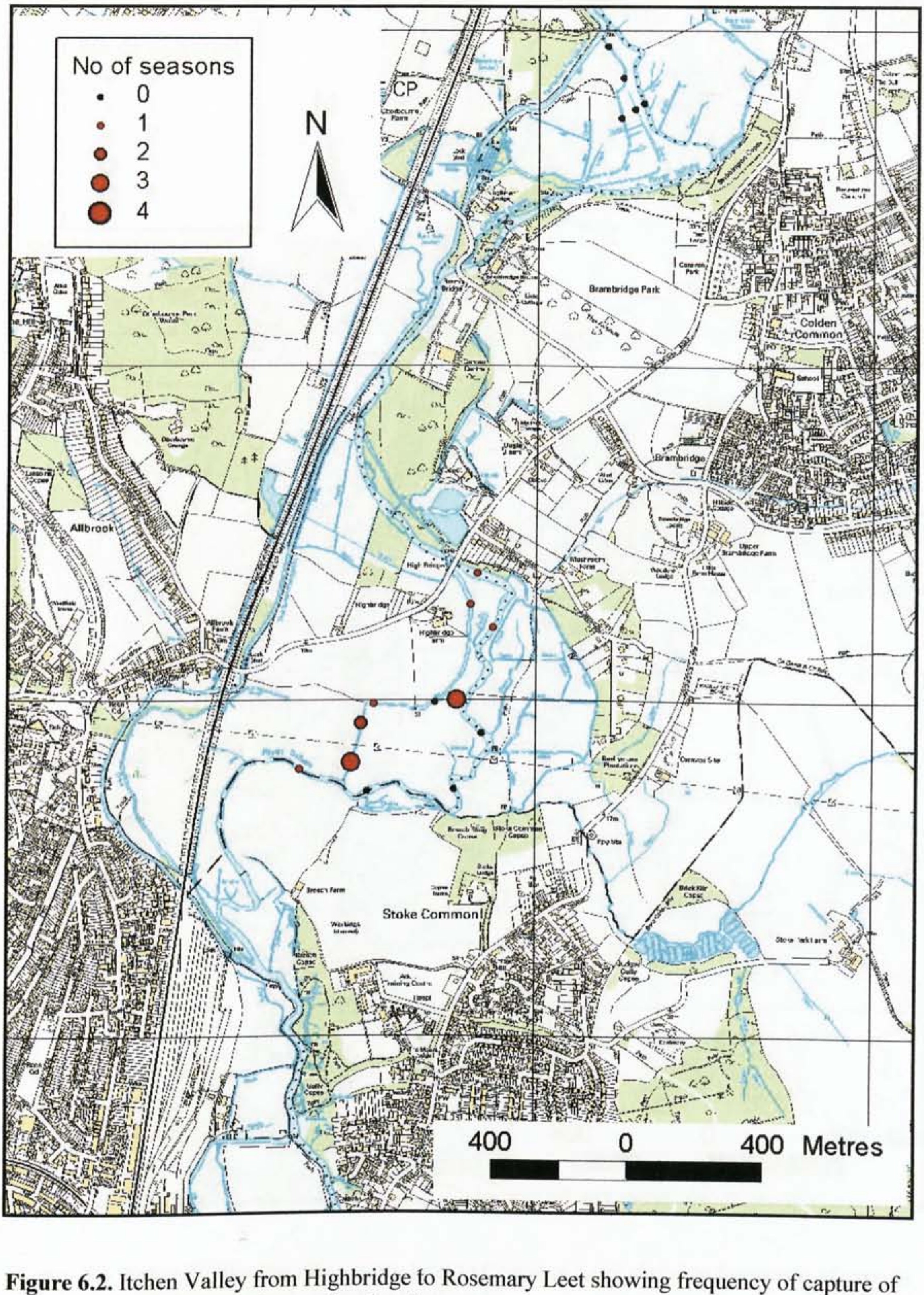

**Figure 6.2.** Itchen Valley from Highbridge to Rosemary Leet showing frequency of capture of *C. mercuriale* larvae at each sampling location.

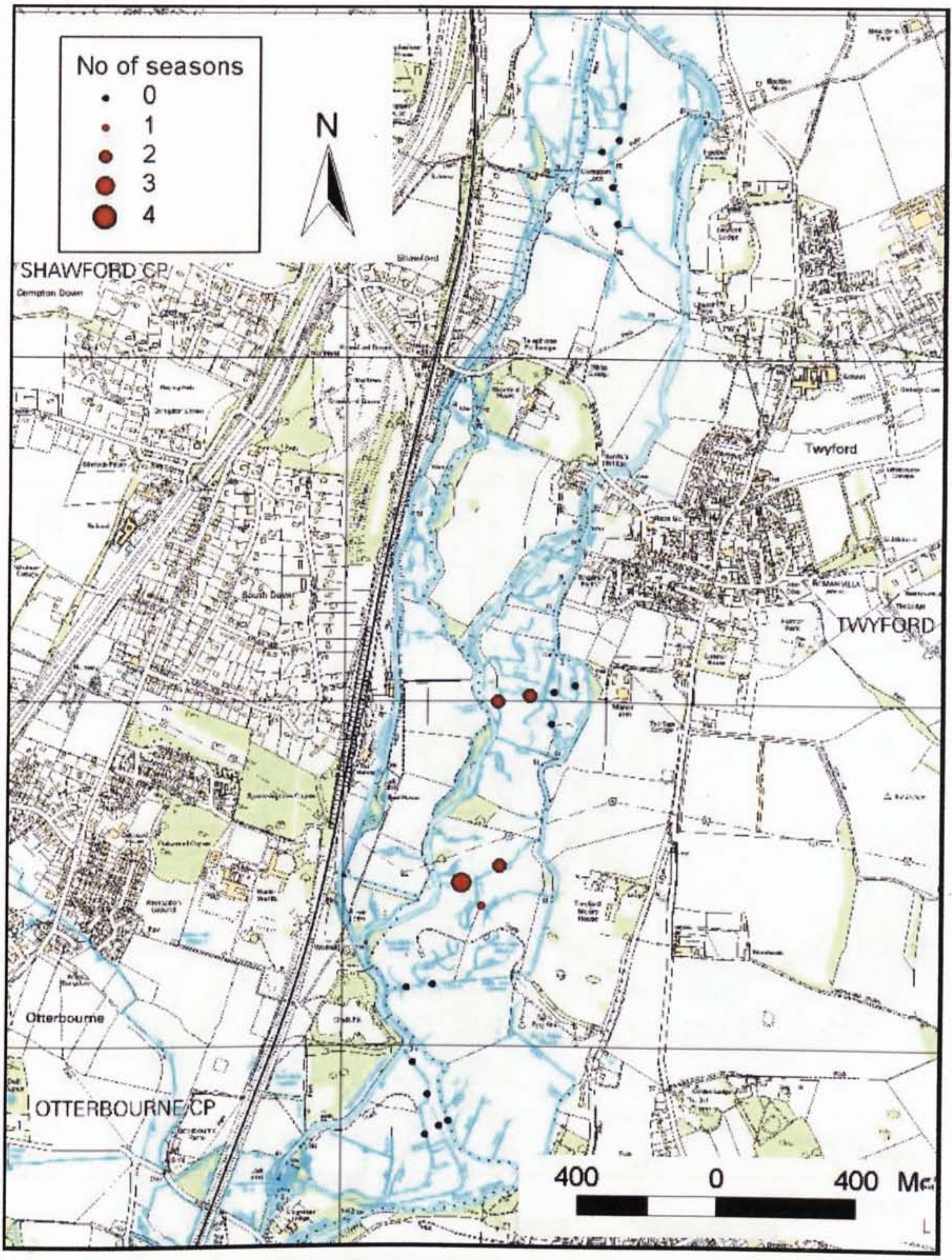

**Figure 6.3**. Itchen Valley from Rosemary Leet to Compton Lock showing frequency of capture of *C. mercuriale* larvae at each sampling location.

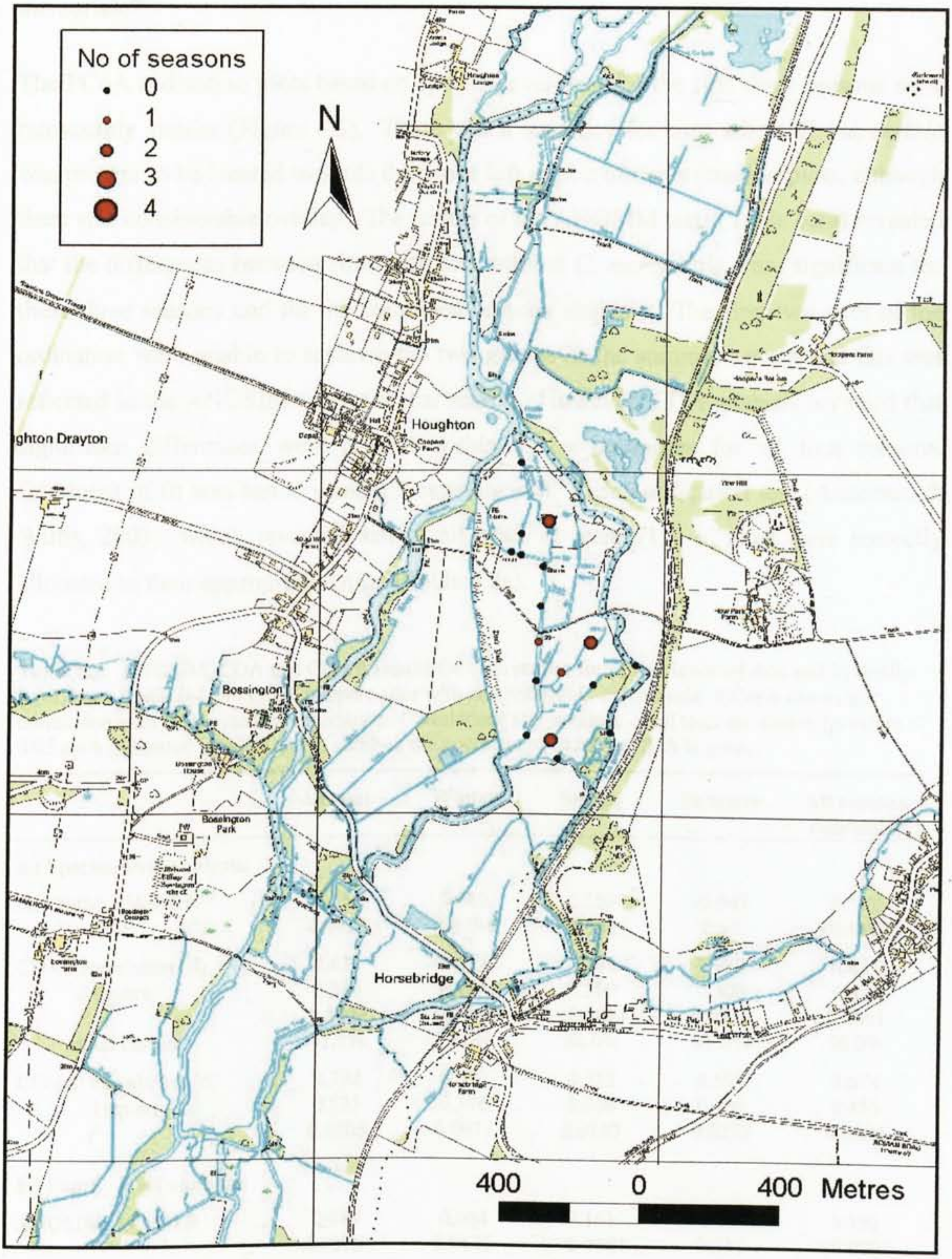

**Figure 6.4.** Test Valley from Horsebridge to Houghton showing frequency of capture of *C. mercuriale* larvae at each sampling location.

### *6.3.2 Are there differences in the invertebrate communities at sites with and without* C. mercuriale?

The PCoA ordination plots based on species-level data for the first three seasons were remarkably similar (Figure 6.5). There was a tendency for sites where *C. mercuriale* was present to be located towards the lower left region of the ordination plots, although there was considerable overlap. The results of the ANOSIM tests (Table 6.2a) revealed that the differences between sites with and without *C. mercuriale* were significant for these three seasons and for the combined seasons analysis. The first two axes of the ordination were unable to separate the two groups in the summer season and this was reflected in the ANOSIM result for that season. However, CDA analysis revealed that significant differences were present within the communities for all four seasons. Goodness of fit was tested using a "leave-one-out" misclassification test (Anderson & Willis, 2003), which revealed that in all cases at least 71% of sites were correctly allocated to their appropriate group (Table 6.2a).

**Table 6.2.** ANOSIM, CDA and CCorA results for each season for a) species-level data and b) family-level data. ANOSIM and CDA compare sites with and without *C. mercuriale*. CCorA shows the correlation with *C. mercuriale* abundance. Correlations and *p*-values of all tests are shown (*p*-values < 0.05 are highlighted in bold) and in addition the goodness of fit of the CDA is given.

| | **Autumn** | **Winter** | **Spring** | **Summer** | **All seasons combined** |
|---|---|---|---|---|---|
| **a.) Species-level analysis:** | | | | | |
| ANOSIM: Global R | 0.106 | 0.082 | 0.159 | -0.041 | 0.182 |
| *P* | **0.0017** | **0.0284** | **<0.0001** | 0.67 | **<0.0001** |
| CDA: correlation (d) | 0.621 | 0.533 | 0.762 | 0.632 | 0.831 |
| d square | 0.386 | 0.284 | 0.580 | 0.400 | 0.691 |
| *P* | **0.0005** | **0.0018** | **<0.0001** | **0.0048** | **0.0001** |
| total correct | 71.7% | 72.0% | 84.0% | 91.0% | 80.0% |
| CCorA: correlation (d) | 0.732 | 0.630 | 0.713 | 0.592 | 0.674 |
| d square | 0.535 | 0.396 | 0.508 | 0.350 | 0.455 |
| *P* | **0.0003** | 0.0617 | **0.0137** | **0.0293** | **0.0283** |
| **b.) Family-level analysis:** | | | | | |
| ANOSIM: Global R | 0.087 | 0.064 | 0.161 | -0.008 | 0.193 |
| *P* | **0.0078** | 0.0608 | **<0.0001** | 0.511 | **<0.0001** |
| CDA: correlation (d) | 0.553 | 0.475 | 0.792 | 0.614 | 0.678 |
| d square | 0.305 | 0.226 | 0.627 | 0.377 | 0.460 |
| *P* | **<0.0001** | **0.0011** | **<0.0001** | **0.0035** | **0.0001** |
| total correct | 74.8% | 71.0% | 81.0% | 85.0% | 78.0% |
| CCorA: correlation (d) | 0.765 | 0.583 | 0.645 | 0.535 | 0.761 |
| d square | 0.585 | 0.340 | 0.416 | 0.287 | 0.579 |
| *P* | **<0.0001** | 0.0556 | **0.0057** | 0.0591 | **0.0031** |

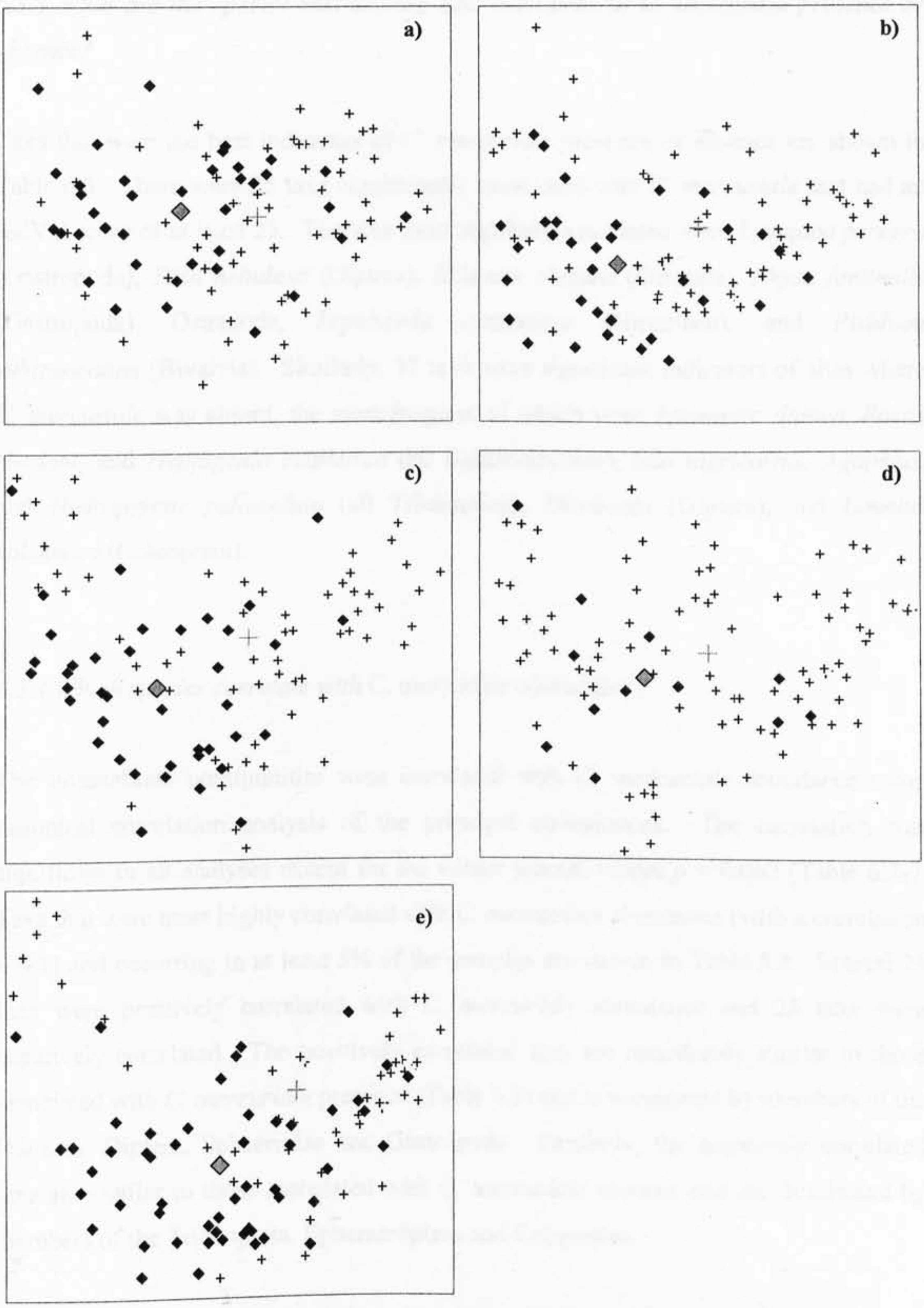

**Figure 6.5.** Ordination plots showing the first two axes of Principal Co-ordinate Analyses (PCoA) for a) autumn season, b) winter, c) spring, d) summer and e) all seasons combined. Samples are log-transformed abundances of species-level data and show sites where *C. mercuriale* was present (◆) and sites where it was absent (+). Larger symbols in grey show mean values for the two groups. Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

### *6.3.3 What are the species that are the best indicators of* C. mercuriale *presence or absence?*

Taxa that were the best indicators of *C. mercuriale* presence or absence are shown in Table 6.3. There were 25 taxa significantly associated with *C. mercuriale* that had an IndVal score of at least 25. The taxa most regularly associated were *Lymnaea peregra* (Gastropoda), *Dixa nebulosa* (Diptera), *Ischnura elegans* (Odonata), *Physa fontinalis* (Gastropoda), Ostracoda, *Erpobdella octoculata* (Hirudinea), and *Pisidium subtruncatum* (Bivalvia). Similarly, 37 taxa were significant indicators of sites where *C. mercuriale* was absent, the most frequent of which were *Ephemera danica, Baetis rhodani*, and *Heptagenia sulphurea* (all Ephemeroptera), *Silo nigricornis, Agapetus,* and *Hydropsyche pellucidula* (all Trichoptera), *Dicranota* (Diptera), and *Limnius volckmari* (Coleoptera).

### *6.3.4 Which species correlate with* C. mercuriale *abundance?*

The invertebrate communities were correlated with *C. mercuriale* abundance using canonical correlation analysis of the principal co-ordinates. The correlation was significant in all analyses except for the winter season, where $p = 0.062$ (Table 6.2a). Taxa that were most highly correlated with *C. mercuriale* abundance (with a correlation $> 0.2$) and occurring in at least 5% of the samples are shown in Table 6.4. In total 25 taxa were positively correlated with *C. mercuriale* abundance and 26 taxa were negatively correlated. The positively correlated taxa are remarkably similar to those associated with *C. mercuriale* presence (Table 6.3) and is dominated by members of the Odonata, Diptera, Sphaeriidae and Gastropoda. Similarly, the negatively correlated taxa are similar to those associated with *C. mercuriale* absence and are dominated by members of the Trichoptera, Ephemeroptera and Coleoptera.

**Table 6.3.** Taxa that are indicators of locations where *C. mercuriale* is present (Group 1) or absent (Group 2) for each season, based on **species-level** data. For each taxon, indicator value (IndVal) and the *p*-value based on 10,000 permutations are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Only taxa with an IndVal of at least 25 and a *p*-value < 0.05 are included.

| Group | Taxa | Family | Autumn | | Winter | | Spring | | Summer | | Combined | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | IndVal | p | IndVal | p | IndVal | p | IndVal | p | IndVal | p |
| 1 | *Dixa nebulosa* | Dixidae | 69.5 | *** | 45.5 | *** | | | 67.0 | *** | 71.3 | *** |
| | *Calopteryx splendens* | Calopterygidae | 61.1 | ** | | | | | 60.7 | *** | | |
| | *Lymnaea peregra* | Lymnaeidae | 33.5 | ** | 31.8 | *** | 35.1 | *** | 41.4 | ** | 53.2 | *** |
| | *Ischnura elegans* | Coenagrionidae | 30.7 | *** | 35.1 | *** | 41.7 | *** | | | 39.4 | *** |
| | *Pericoma trivialis* group | Pscyodidae | 26.3 | * | 28.0 | ** | | | | | | |
| | *Cloeon dipterum* | Baetidae | 25.1 | *** | | | | | | | 27.9 | * |
| | *Asellus aquaticus* | Asellidae | | | 70.4 | *** | | | | | 60.4 | ** |
| | *Gammarus / Crangonyx* | | | | 59.9 | * | | | 68.4 | ** | | |
| | *Physa fontinalis* | Physidae | | | 49.0 | ** | 35.8 | * | | | 61.1 | ** |
| | *Limnephilus marmoratus* | Limnephilidae | | | 44.3 | *** | | | | | 39.3 | *** |
| | Ostracoda | | | | 38.0 | * | 37.0 | ** | | | 57.4 | *** |
| | *Limnephilus rhombicus* | Limnephilidae | | | 35.0 | * | | | | | | |
| | *Pisidium milium* | Pisidiidae | | | 25.2 | *** | 34.1 | *** | | | | |
| | *Pisidium subtruncatum* | Pisidiidae | | | | | 56.7 | *** | 53.7 | * | 59.2 | * |
| | *Erpobdella octoculata* | Erpobdellidae | | | | | 55.9 | *** | 62.8 | ** | 63.7 | * |
| | *Glossiphonia complanata* | Glossiphoniidae | | | | | | | 48.9 | * | | |
| | Succineidae | | | | | | | | 48.6 | *** | | |
| | *Halesus radiatus* | Limnephilidae | | | | | | | 31.2 | *** | | |
| | *Gerris* | Gerridae | | | | | | | 30.8 | *** | | |
| | *Nepa cinerea* | Nepidae | | | | | | | 30.4 | *** | | |
| | *Molanna angustata* | Molannidae | | | | | | | 29.7 | ** | 31.2 | *** |
| | *Bithynia tentaculata* | Hydrobiidae | | | | | | | | | 54.9 | * |
| | *Valvata piscinalis* | Valvatidae | | | | | | | | | 33.2 | *** |
| | *Pisidium casertanum* | Pisidiidae | | | | | | | | | 27.1 | * |
| | *Ilybius fuliginosus* | Dytiscidae | | | | | | | | | 26.8 | ** |
| 2 | *Ephemera danica* | Ephemeridae | 70.5 | *** | 61.6 | ** | 71.2 | *** | 67.8 | ** | 66.1 | *** |
| | *Baetis rhodani* | Baetidae | 62.6 | ** | 58.6 | ** | 47.3 | * | | | | |
| | *Potamophylax* group | Limnephilidae | 53.9 | ** | | | | | | | | |

**Table 6.3 cont.**

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Heptagenia sulphurea* | Heptageniidae | 40.7 | * | | | 49.2 | *** | | | 61.6 | *** |
| *Silo nigricornis* | Goeridae | 32.8 | * | 34.2 | ** | 28.4 | ** | | | 50.2 | *** |
| *Ithytrichia* | Hydroptilidae | 29.8 | *** | | | | | | | 41.0 | *** |
| *Agapetus* | Glossosomatidae | 29.0 | *** | 29.9 | * | | | | | 45.6 | *** |
| *Baetis vernus* | Baetidae | 28.7 | * | | | | | | | | |
| *Dicranota* | Tipulidae | 25.6 | * | 38.8 | * | | | | | 49.5 | ** |
| *Odontocerum albicorne* | Odontoceridae | 25.3 | ** | | | | | | | 44.1 | *** |
| Hydracarina | | | | 53.7 | ** | | | | | | |
| *Limnius volckmari* | Elmidae | | | 53.4 | *** | 48.1 | ** | | | 60.7 | *** |
| *Simulium* | Simuliidae | | | 46.6 | * | | | | | 53.4 | * |
| *Hydropsyche pellucidula* | Hydropsychidae | | | 39.3 | * | 41.8 | *** | | | 56.7 | *** |
| *Rhyacophila* | Rhyacophilidae | | | 36.9 | ** | | | | | 47.2 | ** |
| *Sericostoma personatum* | Sericostomatidae | | | | | 60.2 | *** | | | | |
| *Hydropsyche siltalai* | Hydropsychidae | | | | | 45.4 | *** | | | 50.7 | *** |
| *Baetis muticus* | Baetidae | | | | | 43.1 | *** | | | 47.6 | *** |
| *Lepidostoma hirtum* | Lepidostomatidae | | | | | 36.5 | ** | | | 44.8 | *** |
| *Ephemerella ignita* | Ephemerellidae | | | | | 34.6 | ** | | | | |
| *Isoperla grammatica* | Perlodidae | | | | | 33.9 | *** | | | 37.4 | *** |
| *Rhithrogena semicolorata* | Heptageniidae | | | | | 29.4 | ** | | | 36.9 | *** |
| *Ancylus fluviatilis* | Ancylidae | | | | | 27.4 | * | | | 43.2 | ** |
| *Caenis rivulorum* | Caenidae | | | | | 26.4 | ** | | | 33.7 | *** |
| *Paraleptophlebia submarginata* | Leptophlebidae | | | | | | | | | 57.2 | * |
| *Polycelis nigra* group | Planariidae | | | | | | | | | 55.8 | * |
| *Baetis scambus/fuscatus* | Baetidae | | | | | | | | | 41.2 | ** |
| *Orectochilus villosus* | Gyrinidae | | | | | | | | | 38.7 | * |
| *Leuctra geniculata* | Leuctridae | | | | | | | | | 38.6 | *** |
| *Polycentropus flavomaculatus* | Polycentropidae | | | | | | | | | 38.4 | *** |
| *Rhyacophila dorsalis* | Rhyacophilidae | | | | | | | | | 37.0 | ** |
| *Adicella reducta* | Leptoceridae | | | | | | | | | 34.9 | *** |
| *Leuctra fusca* | Leuctridae | | | | | | | | | 33.2 | *** |
| *Antocha vitripennis* | Tipulidae | | | | | | | | | 29.5 | ** |
| *Baetis atrebatinus* | Baetidae | | | | | | | | | 28.9 | *** |
| *Oecetis testacea* | Leptoceridae | | | | | | | | | 26.5 | * |
| *Theodoxus fluviatilis* | Neritidae | | | | | | | | | 25.3 | * |

**Table 6.4.** Taxa that are positively (Group 1) or negatively (Group 2) correlated with *C. mercuriale* abundance for each season, based on species-level data. For each taxon, the correlation with canonical axes from the CCorA is shown (see text for details). Only taxa with a correlation >0.2 and occurring in at least 5% of the sampling locations for that season are included.

| Group | Taxa | Family | Autumn | Winter | Spring | Summer | Combined |
|---|---|---|---|---|---|---|---|
| 1 | *Calopteryx splendens* | Calopterygidae | 0.446 | 0.205 | | 0.245 | 0.281 |
| | *Pyrrhosoma nymphula* | Coenagrionidae | 0.356 | 0.345 | | | 0.374 |
| | *Gammarus / Crangonyx* | | 0.334 | 0.207 | | 0.279 | 0.321 |
| | *Ischnura elegans* | Coenagrionidae | 0.289 | 0.270 | 0.367 | | 0.316 |
| | *Nepa cinerea* | Nepidae | 0.248 | | | 0.410 | 0.305 |
| | Ostracoda | | 0.227 | 0.296 | 0.41 | | 0.291 |
| | *Dixa nebulosa* | Dixidae | | 0.563 | | | 0.380 |
| | *Pisidium pulchellum* | Pisidiidae | | 0.555 | | | 0.240 |
| | *Pisidium amnicum* | Pisidiidae | | 0.416 | | | |
| | *Asellus aquaticus* | Asellidae | | 0.365 | | | |
| | *Physa fontinalis* | Physidae | | 0.352 | 0.347 | | 0.245 |
| | *Pisidium subtruncatum* | Pisidiidae | | 0.341 | 0.438 | 0.250 | 0.402 |
| | *Pisidium nitidum* | Pisidiidae | | 0.293 | 0.250 | | |
| | *Pisidium casertanum* | Pisidiidae | | 0.287 | 0.455 | | 0.310 |
| | *Pisidium milium* | Pisidiidae | | 0.275 | 0.466 | | 0.337 |
| | *Bithynia tentaculata* | Hydrobiidae | | 0.259 | 0.232 | | |
| | *Lymnaea stagnalis* | Lymnaeidae | | 0.231 | 0.250 | | |
| | *Erpobdella octoculata* | Erpobdellidae | | 0.210 | 0.393 | 0.304 | 0.295 |
| | *Lymnaea peregra* | Lymnaeidae | | | 0.392 | 0.387 | 0.232 |
| | *Hydroporus palustris* | Dytiscidae | | | 0.323 | | |
| | *Phryganea* | Phryganeidae | | | | 0.408 | |
| | *Halesus radiatus* | Limnephilidae | | | | 0.393 | |
| | *Hesperocorixa sahlbergi* | Corixidae | | | | 0.369 | |
| | *Notonecta glauca* | Notonectidae | | | | | 0.358 |
| | *Notonecta* | Notonectidae | | | | | 0.245 |
| 2 | *Ephemera danica* | Ephemeridae | -0.590 | -0.255 | -0.379 | -0.235 | -0.525 |
| | *Elmis aenea* | Elmidae | -0.388 | | -0.276 | | -0.360 |
| | Limnephilidae | | -0.342 | | | | -0.234 |
| | *Potamophylax* group | Limnephilidae | -0.321 | | | | -0.274 |
| | *Sericostoma personatum* | Sericostomatidae | -0.319 | -0.228 | -0.341 | | -0.429 |
| | *Limnius volckmari* | Elmidae | -0.316 | -0.241 | -0.315 | | -0.368 |
| | *Baetis scambus/fuscatus* | Baetidae | -0.302 | | -0.227 | -0.207 | -0.249 |
| | Hydracarina | | -0.300 | -0.243 | | -0.258 | -0.383 |
| | *Heptagenia sulphurea* | Heptageniidae | -0.268 | -0.283 | -0.295 | | -0.458 |
| | Oligochaeta | | -0.249 | -0.270 | | | |
| | *Paraleptophlebia submarginata* | Leptophlebidae | -0.25 | | -0.221 | | -0.465 |
| | *Rhyacophila* | Rhyacophilidae | -0.233 | -0.202 | -0.225 | | -0.375 |
| | *Silo nigricornis* | Goeridae | -0.217 | | -0.286 | -0.213 | -0.341 |
| | *Orectochilus villosus* | Gyrinidae | | -0.270 | -0.227 | | -0.357 |
| | *Hydropsyche siltalai* | Hydropsychidae | | | -0.347 | | -0.422 |
| | *Hydropsyche pellucidula* | Hydropsychidae | | | | | -0.383 |
| | *Rhyacophila dorsalis* | Rhyacophilidae | | | | | -0.35 |
| | *Agapetus* | Glossosomatidae | | | | | -0.353 |
| | *Ithytrichia* | Hydroptilidae | | | | | -0.346 |
| | *Baetis rhodani* | Baetidae | | | | | -0.343 |
| | *Centroptilum luteolum* | Baetidae | | | | | -0.327 |
| | *Leuctra* | Leuctridae | | | | | -0.326 |

**Table 6.4 cont.**

| | | |
|---|---|---|
| *Simulium* | Simuliidae | -0.324 |
| *Polycentropus flavomaculatus* | Polycentropidae | -0.318 |
| *Dicranota* | Tipulidae | -0.315 |
| *Isoperla grammatica* | Perlodidae | -0.306 |

### *6.3.5 Are the results broadly similar when run at a different taxonomic level?*

In total 96 families were represented in the family-level analyses, as well as 8 groupings from higher taxonomic levels, such as Oligochaeta, Hydracarina, Ostracoda and Tricladida. Community structure revealed by the first two axes of the PCoA ordination was almost identical despite the coarser taxonomic resolution. The PCoA ordination plot for the autumn season at both taxonomic levels is shown in Figure 6.6 and results for the other seasons were similar. Differences in the community structure between sites where *C. mercuriale* was present or absent were significant in autumn, spring and all seasons combined (ANOSIM results, Table 6.2b). However, as before, CDA analysis revealed that significant differences were present within the communities for all four seasons. Goodness of fit was similar when compared to the species level analysis, but was slightly reduced in four out of the five analyses (Table 6.2).

The best indicators of *C. mercuriale* presence or absence are shown in Table 6.5 and are extremely similar to the species-level indicators shown in Table 6.3. In most cases the indicator species was dominant within its family (such as *Dixa nebulosa* within the Dixidae family), or other members of the same family occurred in similar habitats (such as many of the Ephemeroptera and Trichoptera families).

Canonical correlation with abundance of *C. mercuriale* was significant in the autumn, spring and combined analysis, and the remaining two seasons were almost significant at the 0.05 level (Table 6.2b). As before, the families correlated with *C. mercuriale* abundance (Table 6.6) strongly reflect the species that were correlated (Table 6.4).

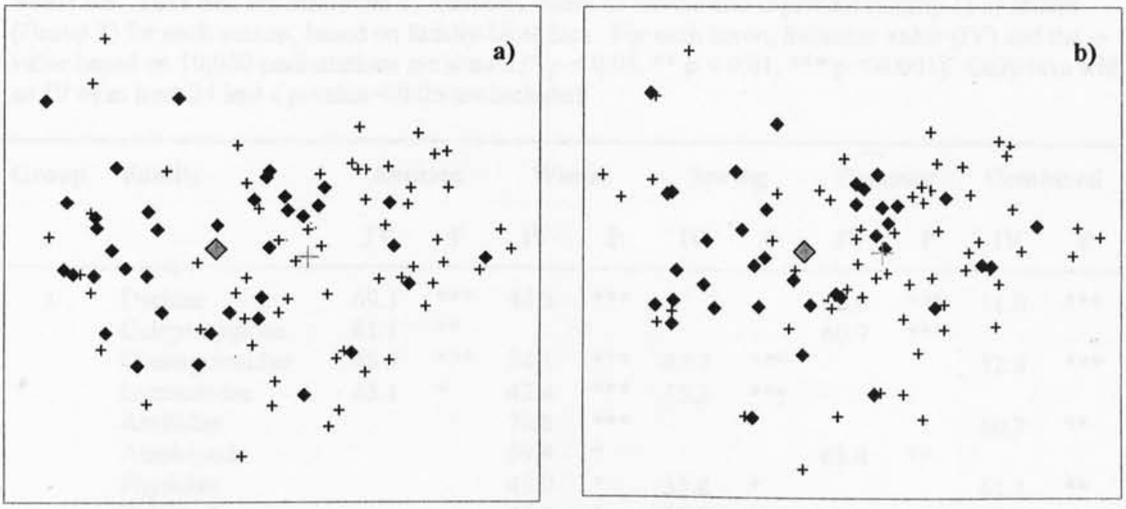

**Figure 6.6.** Ordination plots showing the first two axes of Principal Co-ordinate Analyses (PCoA) for the autumn season. Samples are log-transformed abundances of a) species-level data and b) family-level data, and show sites where *C. mercuriale* was present (◆) and sites where it was absent (+). Larger symbols in grey show mean values for the two groups. Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

**Table 6.5.** Taxa that are indicators of locations where *C. mercuriale* is present (Group 1) or absent (Group 2) for each season, based on family-level data. For each taxon, indicator value (IV) and the *p*-value based on 10,000 permutations are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Only taxa with an IV of at least 25 and a *p*-value < 0.05 are included.

| Group | Family | Autumn | | Winter | | Spring | | Summer | | Combined | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | IV | P | IV | P | IV | P | IV | P | IV | P |
| 1 | Dixidae | 69.3 | *** | 44.5 | *** | | | 66.9 | *** | 71.0 | *** |
| | Calopterygidae | 61.1 | ** | | | | | 60.7 | *** | | |
| | Coenagrionidae | 48.5 | *** | 34.1 | *** | 42.7 | *** | | | 52.8 | *** |
| | Lymnaeidae | 45.1 | * | 42.4 | *** | 45.2 | *** | | | | |
| | Asellidae | | | 70.8 | *** | | | | | 60.7 | ** |
| | Amphipoda | | | 59.9 | * | | | 68.4 | ** | | |
| | Physidae | | | 49.0 | * | 35.8 | * | | | 61.1 | ** |
| | Ostracoda | | | 38.0 | * | 37.0 | ** | | | 57.4 | *** |
| | Pscyodidae | | | 38.0 | ** | | | | | | |
| | Pisidiidae | | | | | 57.4 | * | | | | |
| | Erpobdellidae | | | | | 57.0 | ** | 61.8 | ** | 62.8 | * |
| | Glossiphoniidae | | | | | | | 53.2 | * | | |
| | Succineidae | | | | | | | 48.6 | *** | | |
| | Phryganeidae | | | | | | | 33.3 | *** | | |
| | Gerridae | | | | | | | 30.9 | *** | | |
| | Nepidae | | | | | | | 30.4 | *** | | |
| | Molannidae | | | | | | | 29.7 | ** | 31.2 | *** |
| | Notonectidae | | | | | | | 25.1 | ** | 34.7 | *** |
| | Corixidae | | | | | | | | | 52.7 | * |
| | Valvatidae | | | | | | | | | 32.1 | * |
| 2 | Ephemeridae | 70.5 | *** | 61.6 | ** | 71.2 | *** | 67.8 | ** | 66.1 | *** |
| | Baetidae | 66.7 | * | 61.7 | * | 57.7 | ** | | | 62.9 | * |
| | Heptageniidae | 40.7 | * | | | 53.3 | *** | | | 64.0 | *** |
| | Hydroptilidae | 32.3 | *** | | | | | | | | |
| | Glossosomatidae | 29.0 | *** | 29.9 | * | 29.4 | ** | | | 45.6 | *** |
| | Polycentropidae | 27.9 | *** | | | | | | | 43.9 | *** |
| | Odontoceridae | 25.3 | ** | | | | | | | 44.1 | *** |
| | Simuliidae | | | 61.1 | * | | | | | 62.5 | * |
| | Elmidae | | | 57.9 | ** | 57.3 | ** | | | 61.8 | * |
| | Hydracarina | | | 53.7 | ** | | | | | | |
| | Rhyacophilidae | | | 40.6 | ** | 25.5 | * | | | 51.3 | *** |
| | Sericostomatidae | | | | | 60.0 | *** | | | 54.5 | * |
| | Hydropsychidae | | | | | 55.5 | *** | | | 59.4 | *** |
| | Lepidostomatidae | | | | | 41.5 | ** | | | 52.5 | *** |
| | Ephemerellidae | | | | | 34.6 | ** | | | | |
| | Perlodidae | | | | | 33.9 | *** | | | 37.6 | *** |
| | Leuctridae | | | | | 32.6 | *** | | | 54.2 | *** |
| | Caenidae | | | | | 32.5 | * | | | 48.9 | *** |
| | Tipulidae | | | | | | | | | 63.5 | *** |
| | Leptophlebidae | | | | | | | | | 57.3 | * |
| | Planariidae | | | | | | | | | 55.4 | * |
| | Goeridae | | | | | | | | | 54.1 | ** |
| | Ancylidae | | | | | | | | | 48.7 | ** |
| | Neritidae | | | | | | | | | 25.3 | * |

**Table 6.6.** Taxa that are positively (Group 1) or negatively (Group 2) correlated with *C. mercuriale* abundance for each season, based on **family-level** data. For each taxon, the correlation with canonical axes from the CCorA is shown (see text for details). Only taxa with a correlation >0.2 and occurring in at least 5% of the sampling locations for that season are included.

| Group | Family | Autumn | Winter | Spring | Summer | Combined |
|---|---|---|---|---|---|---|
| 1 | Calopterygidae | 0.452 | 0.292 | 0.250 | 0.230 | 0.330 |
| | Amphipoda | 0.373 | | | 0.257 | 0.307 |
| | Coenagrionidae | 0.345 | 0.466 | 0.389 | 0.269 | 0.374 |
| | Hydrophilidae | 0.247 | 0.195 | | | 0.224 |
| | Ostracoda | 0.234 | 0.326 | 0.418 | | 0.270 |
| | Nepidae | 0.232 | | | 0.403 | 0.278 |
| | Notonectidae | 0.198 | | 0.322 | | 0.399 |
| | Dixidae | | 0.601 | | | 0.413 |
| | Asellidae | | 0.453 | | | |
| | Physidae | | 0.382 | 0.313 | | 0.242 |
| | Pisidiidae | | 0.376 | 0.334 | 0.263 | 0.210 |
| | Lymnaeidae | | 0.340 | 0.329 | 0.290 | 0.254 |
| | Glossiphoniidae | | 0.331 | | | |
| | Erpobdellidae | | 0.274 | 0.412 | 0.388 | 0.329 |
| | Molannidae | | 0.269 | | 0.288 | |
| | Gerridae | | | 0.230 | 0.347 | 0.299 |
| | Phryganeidae | | | | 0.466 | |
| 2 | Ephemeridae | -0.544 | -0.265 | -0.410 | | -0.468 |
| | Elmidae | -0.421 | | -0.319 | | -0.357 |
| | Limnephilidae | -0.374 | | | | |
| | Tipulidae | -0.328 | -0.209 | -0.289 | | -0.346 |
| | Hydracarina | -0.321 | -0.303 | -0.303 | -0.249 | -0.402 |
| | Sericostomatidae | -0.314 | -0.272 | -0.370 | | -0.373 |
| | Goeridae | -0.263 | | -0.199 | | -0.207 |
| | Baetidae | -0.258 | -0.235 | -0.274 | | -0.331 |
| | Rhyacophilidae | -0.240 | -0.263 | -0.250 | | -0.377 |
| | Hydropsychidae | -0.239 | | -0.293 | -0.210 | -0.374 |
| | Simuliidae | -0.231 | -0.258 | | | -0.245 |
| | Heptageniidae | -0.223 | -0.325 | -0.327 | | -0.442 |
| | Odontoceridae | -0.194 | -0.231 | | -0.225 | -0.269 |
| | Oligochaeta | | -0.320 | | | |
| | Ephemerellidae | | -0.291 | -0.264 | | -0.199 |
| | Perlodidae | | -0.280 | -0.258 | | -0.272 |
| | Glossosomatidae | | -0.264 | -0.233 | -0.251 | -0.313 |
| | Leptophlebidae | | -0.224 | -0.286 | | -0.371 |
| | Leuctridae | | | -0.399 | | -0.370 |
| | Lepidostomatidae | | | -0.366 | | -0.319 |
| | Ceratopogonidae | | | | -0.362 | |
| | Caenidae | | | | | -0.343 |

### *6.3.6 How do other measures of the communities compare?*

We went on to investigate differences between communities with and without *C. mercuriale* using a range of diversity and biological indices (Table 6.7). The number of individuals recorded, taxonomic richness and family richness were no different between the two groups of sites. Evenness, which was measured using Hill's modified ratio, was significantly lower in sites containing *C. mercuriale* only in the summer season and the combined seasons analysis. Diversity (measured using Hill's diversity numbers N1 and N2) was significantly lower in occupied sites in the winter, summer and combined seasons. LIFE (Lotic Invertebrate Flow Evaluation) score was highly significantly different in the first three seasons at both species and family level, indicating that sites where *C. mercuriale* occurred had lower flow velocities than sites from which it was absent. BMWP was lower in the winter and spring seasons at locations with *C. mercuriale*, while ASPT was lower in the autumn, winter and spring seasons.

When the diversity and biotic indices were correlated against *C. mercuriale* abundance (Table 6.3d), the results were almost identical to those revealed by the presence / absence analysis.

### *6.3.7 Seasonal variation*

Patterns within the communities were broadly similar across the four seasons, as indicated by the similarity of the ordination plots (Figure 6.5). Indeed, if all samples were considered to be independent and analysed at the same time (Figure 6.7, n = 399), axis 1 of the resulting ordination plot revealed almost the same community differences evident in axis 1 of the individual season's plots. Axis 2 was effective at separating the seasonal effect, with mostly low axis scores for samples from the autumn and winter and high axis scores for samples from the spring and summer seasons.

**Table 6.7.** Diversity and biological indices for each season, showing a) the mean value for sampling locations where *C. mercuriale* was present, b) the mean value where it was absent c) the $p$-value of Mann-Whitney U-tests to compare these sites and d) the $p$-value of Spearman's Correlation with *C. mercuriale* abundance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

| Index | Autumn | Winter | Spring | Summer | All seasons combined |
|---|---|---|---|---|---|
| **a.) Group 1** | | | | | |
| Total individuals | 507 | 562 | 205 | 433 | 1639 |
| Total taxa | 38.2 | 38.6 | 36.4 | 32.0 | 74.2 |
| Total families | 29.2 | 27.3 | 26.7 | 26.5 | 45.2 |
| Hill's diversity number N1 | 12.0 | 11.0 | 17.8 | 7.87 | 16.0 |
| Hill's diversity number N2 | 6.85 | 6.41 | 11.3 | 4.16 | 7.89 |
| Hill's modified ratio (evenness) | 0.49 | 0.51 | 0.59 | 0.44 | 0.43 |
| LIFE (species level) | 6.80 | 6.86 | 6.83 | 6.84 | N.A. |
| LIFE (family level) | 6.70 | 6.71 | 6.65 | 6.66 | N.A. |
| BMWP | 129.7 | 122.2 | 124.1 | 123.8 | N.A. |
| ASPT | 5.20 | 5.22 | 5.30 | 5.17 | N.A. |
| **b.) Group 2** | | | | | |
| Total individuals | 594 | 613 | 244 | 351 | 1855 |
| Total taxa | 37.9 | 37.8 | 37.7 | 30.9 | 74.4 |
| Total families | 28.7 | 27.9 | 28.1 | 24.3 | 44.5 |
| Hill's diversity number N1 | 13.2 | 12.6 | 17.8 | 10.9 | 19.1 |
| Hill's diversity number N2 | 7.87 | 7.65 | 11.0 | 6.64 | 10.2 |
| Hill's modified ratio (evenness) | 0.54 | 0.56 | 0.58 | 0.55 | 0.49 |
| LIFE (species level) | 7.15 | 7.28 | 7.25 | 7.09 | N.A. |
| LIFE (family level) | 6.96 | 7.10 | 7.05 | 6.90 | N.A. |
| BMWP | 141.5 | 140.9 | 147.7 | 116.6 | N.A. |
| ASPT | 5.56 | 5.69 | 5.84 | 5.31 | N.A. |
| **c.) Presence / absence** | | | | | |
| Total individuals | n.s. | n.s. | n.s. | n.s. | n.s. |
| Total taxa | n.s. | n.s. | n.s. | n.s. | n.s. |
| Total families | n.s. | n.s. | n.s. | n.s. | n.s. |
| Hill's diversity number N1 | n.s. | * | n.s. | * | ** |
| Hill's diversity number N2 | n.s. | * | n.s. | ** | ** |
| Hill's modified ratio (evenness) | n.s. | n.s. | n.s. | *** | ** |
| LIFE (species level) | *** | *** | *** | n.s. | - |
| LIFE (family level) | ** | *** | *** | n.s. | - |
| BMWP | n.s. | * | ** | n.s. | - |
| ASPT | *** | *** | *** | n.s. | - |
| **d.) Abundance** | | | | | |
| Total individuals | n.s. | n.s. | n.s. | n.s. | n.s. |
| Total taxa | n.s. | n.s. | n.s. | n.s. | n.s. |
| Total families | n.s. | n.s. | n.s. | n.s. | n.s. |
| Hill's diversity number N1 | * | * | n.s. | * | *** |
| Hill's diversity number N2 | * | * | n.s. | ** | *** |
| Hill's modified ratio (evenness) | n.s. | * | n.s. | *** | *** |
| LIFE (species level) | *** | *** | *** | n.s. | - |
| LIFE (family level) | *** | *** | *** | n.s. | - |
| BMWP | * | n.s. | ** | n.s. | - |
| ASPT | *** | *** | *** | n.s. | - |

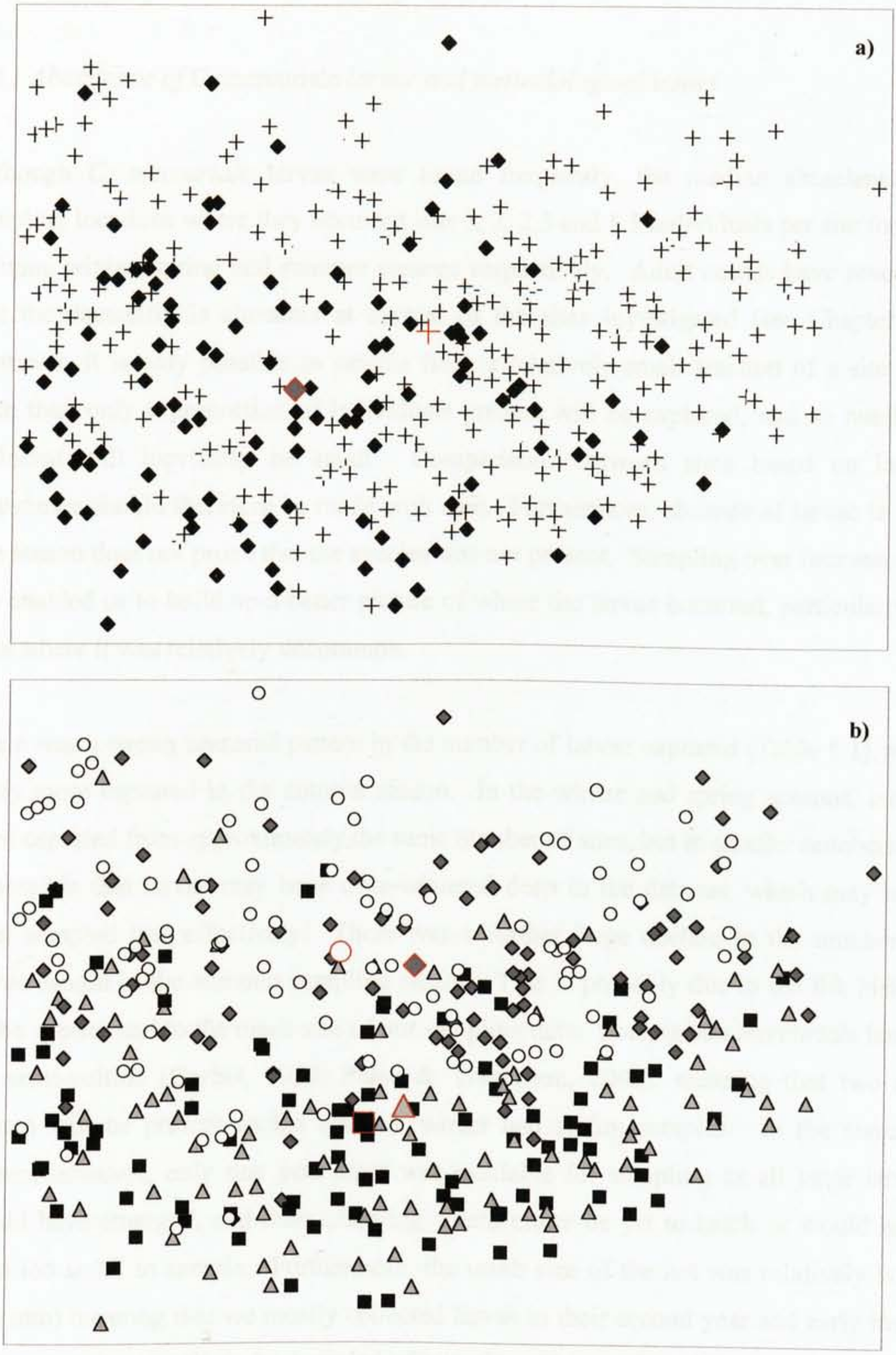

**Figure 6.7.** PCoA ordination plot of all samples from all four seasons showing a) sampling locations where *C. mercuriale* was present (◆) or absent (+) and b) the same plot highlighting the location of autumn (■), winter (△), spring (◆) and summer (○) samples. Larger symbols outlined in red show mean values for the respective groups. Samples are log-transformed abundances of species-level data.

## 6.4 Discussion

### 6.4.1 *Abundance of* C. mercuriale *larvae and methodological issues*

Although *C. mercuriale* larvae were found frequently, the median abundance in sampling locations where they occurred was 5, 2, 2.5 and 1.5 individuals per site for the autumn, winter, spring and summer seasons respectively. Adult counts have revealed that the damselfly is abundant at several of the sites investigated (see Chapter 3). However, it is only possible to sample from a relatively small fraction of a site and even then only a proportion of individuals present will be captured, and so numbers collected will inevitably be small. Comparisons between sites based on larval abundance should therefore be made with care. Furthermore, absence of larvae in any one season does not prove that the species was not present. Sampling over four seasons has enabled us to build up a better picture of where the larvae occurred, particularly in sites where it was relatively uncommon.

There was a strong seasonal pattern in the number of larvae captured (Table 6.1), with many more captured in the autumn season. In the winter and spring seasons, larvae were captured from approximately the same number of sites, but in smaller numbers. It is possible that larvae may have over-wintered deep in the detritus, which may have been sampled less effectively. There was a further large decline in the number of larvae caught in the summer sampling season. This is probably due to the life history of the species and to the mesh size of our sampling nets. *Coenagrion mercuriale* larvae are semi-voltine (Corbet, 1957; Purse & Thompson, 2002), meaning that two age classes will be present in the autumn, winter and spring samples. In the summer season, however, only one year class was available for sampling as all large larvae would have emerged, and their offspring would either be yet to hatch or would have been too small to sample. Furthermore, the mesh size of the net was relatively large (1.0 mm) meaning that we mostly collected larvae in their second year and early instar larvae were too small to be sampled efficiently. The results of the summer season should therefore be treated with caution. We experimented using nets with smaller mesh sizes, but these quickly became clogged up with silt, which was the dominant substrate at most of the sampling locations. Sampling would have been extremely inefficient and live sorting impossible had we used this approach. Furthermore, it would have been difficult to distinguish early-instar *C. mercuriale* from other members of the Coenagrionidae.

### *6.4.2 Associated species and community*

This study has shown that *Coenagrion mercuriale* is clearly associated with particular species or groups of species and disassociated with others. This enables us to build up a picture of the habitat preferences of the species and to suggest suitable indicator species for future survey and monitoring.

The taxa with which *C. mercuriale* is most closely associated predominantly live in moderate to slow flowing habitats, with plenty of aquatic vegetation. For example, *Dixa nebulosa* is found in the margins of rivers and small streams and is often associated with emergent grasses and rushes and with watercress beds (Smith, 1989; Disney, 1999). Harrison (2000) reported that it was associated with marginal habitats in all seasons. *Physa fontinalis* is found in running water containing dense vegetation (Macan, 1977; Kerney, 1999). In mesohabitat studies, Pardo and Armitage (1997) reported that it was an indicator of emergent macrophytes, while Harrison (2000) found that it significantly avoided gravel habitats. *Lymnaea peregra*, *Ischnura elegans* and Ostracoda are fairly ubiquitous in their habitat choices but are more common in slow-flowing waters with abundant aquatic vegetation (Macan, 1977; Brooks, 1997; Kerney, 1999; Olsen *et al.*, 2001; Smallshire & Swash, 2004). Pardo and Armitage (1997) reported that Ostracoda were an indicator of silted substrates, while Harrison (2000) found that they were most abundant in marginal habitats. The leech *Glossiphonia complanata* is a widespread carnivore that feeds mostly on molluscs, including *Physa, Lymnaea* and *Pisidium* (Elliott & Mann, 1979). It occurs in all types of freshwater, but is most abundant in waters containing large populations of its prey.

The taxa with which *C. mercuriale* is rarely found typically occur in faster flowing water with gravel or stony substrates. *Ephemera danica* prefers gravel or sandy-bottomed channels where it typically burrows into the substrate (Elliott *et al.*, 1988; Pardo & Armitage, 1997; Harrison, 2000). *Baetis rhodani* and *Heptagenia sulphurea* are usually associated with riffles (Elliott *et al.*, 1988). *Silo nigricornis* and *Agapetus* spp. are found in stony streams and rivers and *Hydropsyche pellucidula* is generally not found in small streams (Wallace, 1991). All three Trichoptera taxa were more common in gravel habitats in mesohabitat studies (Harrison, 2000). *Limnius volckmari* is a riffle beetle, associated with that habitat, while *Simulium* require a relatively fast flow with a clean substratum on which to secure an attachment for their habit of filter feeding (Bass, 1998). They are usually associated with mid-channel *Ranunculus* habitats (Wright *et al.*, 1983; Pardo & Armitage, 1997; Harrison, 2000).

There is a large degree of overlap between the species that indicate the presence or absence of *C. mercuriale* with those that are most highly correlated with its abundance. Additional taxa that are correlated with *C. mercuriale* abundance in several seasons include *Calopteryx splendens, Pyrrhosoma nymphula, Nepa cinerea* and several species of *Pisidium*. *Calopteryx splendens* prefers slow-flowing, silty channels where the larvae live on the roots of aquatic vegetation (Brooks, 1997; Smallshire & Swash, 2004). It was recorded in almost every sample during our study, but was more abundant at sites where *C. mercuriale* was abundant. It would seem that its optimum habitat requirements are similar to *C. mercuriale*, but it is able to cope with a much wider range of conditions. *Pyrrhosoma nymphula* is a bottom-dweller, living amongst vegetation in silty channels, but also in still-water (Lawton, 1970; Brooks, 1997; Smallshire & Swash, 2004). Similarly, *Nepa cinerea* is usually found in ponds and requires medium levels of plant cover and organic matter (Savage, 1989). The Pisidiidae are a family that generally prefer low energy environments, with a stable substrate in which to bury, typically fine sand, silt or mud (Kerney, 1999; Killeen *et al.*, 2004).

Additional taxa that are negatively correlated with *C. mercuriale* abundance in several seasons include *Baetis scambus/fuscatus,* which are typically associated with sand or gravel substrates (Elliott *et al.*, 1988), *Rhyacophila*, which requires at least some stony substrate (Wallace, 1991), and *Elmis aenea* and *Orectochilus villosus*, which are both associated with riffles (Friday, 1988).

Taxonomic and family richness was similar in sites with and without *C. mercuriale*. However, in some seasons there was a tendency for evenness and hence diversity measures to be lower in sites containing *C. mercuriale*, indicating that *C. mercuriale* may have existed in structurally simpler communities. Much more striking, however, was the difference in BMWP, and especially ASPT and LIFE scores. Lower BMWP and ASPT are indicative of lower levels of dissolved oxygen. This suggests that *C. mercuriale* is not associated with the most oxygen-enriched chalkstream sites such as faster flowing riffles and runs, but rather the slower flowing ditch sites. LIFE score was also lower in the first three seasons, indicating that sites at which *C. mercuriale* was present contained taxa indicative of significantly slower flow conditions. This is consistent with the ecology of the individual species discussed above. Furthermore, Extence *et al.* (1999) classify most species into flow groups, ranging from 1 (rapid flow) to 6 (drought impacted). If these scores are applied to our list of indicator taxa (Table 6.3), the group associated with *C. mercuriale* have a mean score of 3.76, while the group that are indicative of *C. mercuriale* absence have a mean score of 1.94. Similarly, taxa positively correlated with abundance (Table 6.4) produce a score of 3.68 and those negatively correlated have a mean score of 1.92.

### *6.4.3 Taxonomic level*

We have repeated all our analyses at family level, which has enabled us to investigate the effect of taxonomic resolution on our findings. It has become clear that in this investigation family level analysis is almost as informative as species level work. In most cases one particular species is dominant within its family, or else all members of a family have similar habitat requirements. There are of course exceptions. For example, the Baetidae generally prefer moderate to fast-flowing conditions with a gravel or stony substrate (Elliott *et al.*, 1988), and several species are frequent on sites where *C. mercuriale* is absent. However, *Cloeon dipterum* prefers slower-flowing or still waters, is associated with macrophytes in the margins of channels (Elliott *et al.*, 1988), and was an indicator of *C. mercuriale* presence in the autumn season and in the combined seasons analysis. However, identification of samples to species level requires considerably more resources, both in terms of time and expertise, and would appear to provide only minor benefits in this study.

### *6.4.4 Diet of* C. mercuriale

Bousfield (2003) examined the faecal pellets of approximately 40 of the *C. mercuriale* larvae collected in the spring and summer seasons of this study. Although small in scope, this study provides a good qualitative indication of the main components of the larval diet at our sample sites. She found that in the spring season the percentage contribution of prey types to the diet consisted of 20% Chironomidae, 7% *Gammarus*, 27% Copepoda, with the remaining 46% unknown. In the summer season the faecal pellets contained 48% Chironomidae, 8% *Gammarus*, 8% Copepoda, 4% Ephemeroptera, while the remaining 32% was unknown. This alteration in the proportion of different prey types in the diet in the two seasons may be caused by shifting diet preferences of the different sized larval instars, or by seasonal patterns in prey abundance, or may simply be a consequence of the small sample sizes involved.

Bousfield (2003) suggests that *C. mercuriale* is an opportunistic feeder with a similar dietary prey composition to that available in its habitat. Indeed, Chironomidae, *Gammarus*, and Ephemeroptera are extremely numerous at all our sampling locations, comprising cumulatively 39% and 53% of the total invertebrate abundance in the spring and summer seasons respectively. Copepoda were rare in our samples, but this is a reflection of our sampling methodology, as the net mesh was not fine enough to collect organisms of this size. It would be interesting to re-sample a selection of our sites for micro-invertebrates and to see if there was any correlation with *C. mercuriale* presence or abundance.

Faecal analysis of other species of Odonata has revealed a similar pattern of opportunistic feeding, although the Chironomidae always feature strongly. This family comprised 60-75% of the dietary dry weight of *Pyrrhosoma nymphula* larvae (Lawton, 1970) and were an important component in the diet of *Ischnura elegans* (Thompson, 1978).

Unfortunately, soft-bodied prey items are overlooked when conducting faecal analysis. These include the Oligochaeta, the Hirudinea, and the Gastropoda and Bivalvia if removed from their shells before consumption, all of which were numerous in our samples. The technique can therefore only give us an indication of feeding preferences.

Furthermore, Bousfield (2003) only examined the diet of medium and large instar larvae. It is likely that Copepoda and other micro-invertebrates would be especially important in the diet of early instar larvae. Indeed, microcrustacea, particularly Cladocera and Copepoda, were found to be an important component of the diet of early instar *P. nymphula* (Lawton, 1970). Despite these limitations, it seems unlikely that dietary requirements are limiting the success of middle to late instar larvae. Further work is required to clarify the position for early instar larvae.

### *6.4.5 Conservation implications*

This study has shown that *C. mercuriale* larvae are clearly associated with particular species or groups of species and disassociated with others. It is associated with taxa that require well-vegetated, moderate to slow flowing waterbodies, with a predominantly silty substrate. Management should therefore be undertaken to achieve these attributes. In particular, this requires the maintenance of the old water meadow ditches still present in much of the Itchen and Test valleys. It also suggests the importance of margins on the edges of larger channels. If left unmanaged, water meadow ditches follow a succession from vegetation-free, relatively fast flowing channels to choked, slow flowing and ultimately stagnant conditions. It is apparent from this study that *C. mercuriale* larvae will favour ditches in mid-succession, with plenty of emergent vegetation, but still with flowing water. Therefore, ditches will need to be dredged from time to time on rotation. It is recommended that dredging operations are performed either on relatively short sections at a time or on one side only.

Our study has also provided a list of associated species and families that could be used to monitor the suitability of a site for *C. mercuriale* or the response of the community to new management practices.

This study, together with a study of the diet of *C. mercuriale* (Bousfield, 2003), has shown that larvae in their second year are unlikely to be food limited. It is more likely that a lack of suitable habitat or alterations to management, together with its limited dispersal ability (see Chapter 3), were the driving forces behind the decline of this species. However, it would be interesting to conduct further investigations into the habitat and diet of early instar larvae and the abundance of micro-invertebrates across a range of sites.

# Chapter 7: Habitat associations of late-instar larvae

## 7.1 Introduction

Understanding the links between a species abundance and habitat is one of the primary goals of ecology and conservation biology. It helps us understand species' distributions, enables us to predict the effects of habitat and climate change, and drives conservation management programmes. Approaches to measure these associations generally fall into two classes: regression methods and multivariate ordination (although see Guisan & Zimmermann, 2000, for a range of other methods). Regression techniques have been used in numerous studies and include simple linear regression, generalized linear models (GLM) and generalized additive models (GAM). GLMs are mathematical extensions of linear regression that are able to handle distributions other than the normal (McCullagh & Nelder, 1983; Crawley, 2002). This family of techniques includes Poisson regression which is used to model count data, and binary logistic regression which is used to model presence / absence data. Multivariate ordination techniques are particularly useful when dealing with large multivariate data sets and include canonical correspondence analysis (CCA), canonical correlation analysis (CCorA), canonical discriminant analysis (CDA) and redundancy analysis (RDA).

Regression and ordination have been used on numerous occasions to predict the distribution of a wide variety of taxa (see Guisan & Zimmermann, 2000; Guisan *et al.*, 2002; Rushton *et al.*, 2004 for recent reviews). Regression techniques are frequently used when describing the distribution of a target species and have been used extensively to study birds and mammals. Within freshwater ecology, patterns across the community are often the focus of study, with multivariate ordination the technique of choice. Regression techniques have been used less frequently, although they have been used to study the distribution of the white-clawed crayfish (Naura & Robinson, 1998), invertebrate abundance (Manel *et al.*, 2000), the freshwater pearl mussel (Hastie *et al.*, 2003) and three rare species of gastropod (Watson & Ormerod, 2004). In this study, both techniques are used to study the occurrence and abundance of an aquatic invertebrate of conservation concern in relation to the vegetation community and abiotic environment.

*Coenagrion mercuriale* (the southern damselfly) has been identified as a priority species in the UK Biodiversity Action Plan (HMSO, 1995) and is listed as rare in the UK Red Data Book (Shirt, 1987). Its status in Europe is considered to be "very vulnerable" (Grand, 1996) and it has been listed on Annex II of the EC Habitats and Species Directive and Appendix II of the Bern Convention. In the UK it occurs primarily on small base-enriched lowland heathland streams and on the old water-meadow carriers and ditches associated with lowland chalk rivers (Thompson *et al.*, 2003a). However, little is known about the habitat requirements of the species, particularly those of the larval phase.

In order to quantify the habitat preferences of *C. mercuriale* larvae we have investigated the biological, physical and chemical attributes of all chalkstream sites where *C. mercuriale* is present and nearby sites where it is not. The associated macroinvertebrates have been described in the previous chapter (Chapter 6). In this chapter *C. mercuriale* occurrence and abundance are related to physical, chemical and vegetation attributes. It is hoped that the study will provide a basis for further conservation efforts, by guiding habitat management plans, informing conservation strategies and suggesting targets for surveillance and monitoring programmes.

## 7.2 Methods

### *7.2.1 Study sites*

*Coenagrion mercuriale* is known to occur on the floodplain of two chalk streams in the UK, the River Itchen and the River Test in Hampshire. A range of sites where *C. mercuriale* was known to occur (Stevens & Thurner, 1999; Strange, 1999), as well as additional sites where the species was thought not to occur, were investigated. Details of the study sites have been described previously (see Chapters 2 & 6) and are shown on Figure 2.2. Samples were taken from a total of 83 locations in the Itchen Valley and 17 in the Test Valley.

### *7.2.2* Coenagrion mercuriale *and habitat surveys*

Sampling locations were surveyed four times over the course of one year, beginning in mid October 2001, and repeated in January, April and July 2002. At each location a sample of the macroinvertebrate community was collected using standard Environment Agency methodology (Environment Agency, 1999). On return to the laboratory, samples were live-sorted and larval *C. mercuriale* were identified and counted. More detail of macroinvertebrate field and laboratory techniques, as well as an analysis of the associated macroinvertebrate community, is provided in Chapter 6.

Habitat variables were collected from each sampling location immediately prior to collecting the macroinvertebrate samples. These were assigned into four broad categories: channel variables, bankside variables, chemical variables and in-channel vegetation. A complete list of these variables is given in Appendix 2.1. Bankside variables were collected on both sides of the channel but were amalgamated prior to analysis. A limited suite of chemical parameters, including alkalinity, conductivity and pH, were recorded with handheld equipment on site, and a water sample was collected for further analysis at Southern Water Services PLC. The species and percentage cover of submerged and emergent vegetation was recorded over the complete sampling area. All variables that were not normally distributed were subjected to an appropriate transformation prior to analysis.

To investigate whether pesticides or metals were having a deleterious impact on *C. mercuriale*, we collected additional water samples from a sub-sample of 15 locations during the summer sampling season. Samples were tested for 6 metals and 42 different types of pesticide (see Appendix 2.2 for complete list).

### *7.2.3 Statistical analysis*

We used regression techniques and multivariate ordination to investigate the factors associated with *C. mercuriale* occurrence and abundance.

#### *7.2.3.1 Generalized Linear Models*

Two types of generalized linear models were fit to the data (GLM; McCullagh & Nelder, 1983). Firstly, *C. mercuriale* occurrence was modelled, which has a binomial error structure and was related to the set of predictors using a logit link function (Crawley, 1993; Dobson, 2002). In the second set of models, *C. mercuriale* abundance was modelled using a Poisson error structure and a logarithmic link function (Crawley, 1993; Dobson, 2002). In this case, however, the distribution of *C. mercuriale* was aggregated, and the resulting models displayed marked overdispersion, particularly in the autumn season. Therefore, a quasi-likelihood function was used (SAS Institute Inc., 1999; Crawley, 2002), which adjusts the scale parameter of the model (using Pearson's $\chi^2$ / d.f.) so that the variance in *C. mercuriale* abundance is proportional to, rather than equal to, the mean.

A large number of potential predictor variables were available for entry into the GLMs, many of which were inter-correlated. It was therefore decided to first run a series of principal components analyses (PCA) to reduce the variables to a smaller number of uncorrelated principal factors. This procedure has been used in a number of other studies (e.g. Manel *et al.*, 2000; Ecke *et al.*, 2002; Rundle *et al.*, 2002, Hall *et al.*, 2003). Three separate PCAs were run, one for the channel, bankside and chemical variables respectively and only principal components with eigenvalues of greater than 1 were included in subsequent analyses. Vegetation variables were amalgamated to produce four new variables based on structural and functional characteristics. These were emergent dicots, emergent monocots, submerged and floating vegetation groups.

One potential problem with our study design was that sampling locations were not spatially independent because they were clustered within sites. It is possible that locations within one site or sub-site are more similar than those from a different site, particularly if unmeasured variables acting at the site / sub-site level were present. This potential problem was dealt with by adding a series of dummy variables representing each sub-site. This is the "raw data approach" suggested by Legendre (1993) to deal with broadscale spatial autocorrelation.

Thus the maximal model for each GLM contained variables representing four vegetation groups, principal components relating to channel, bankside and chemical parameters, and dummy variables relating to each site and sub-site. A backwards selection procedure was used starting from this maximal model with all variables included (Crawley, 2002). The least significant variables were removed sequentially until all remaining variables were significant at $P \leq 0.05$. All removed variables were then refitted to check whether they explained additional variance. $D^2$ and adjusted $D^2$ (the equivalents of $R^2$ and adjusted $R^2$) were calculated according to standard formulae (Guisan & Zimmermann, 2000). A different GLM was run for each season. Thus four models were produced that related habitat variables to the occurrence of *C. mercuriale* and four more related habitat to the abundance of *C. mercuriale*.

#### *7.2.3.2 Multivariate Ordination*

Factors associated with *C. mercuriale* occurrence and abundance were also investigated using a range of multivariate statistics. Two sets of analyses were completed, a "vegetation" analysis and a "habitat" analysis. In the former, the percentage cover of all in-channel vegetation species was used and in the latter, the channel, bankside and chemical variables (see Appendix 2.1) were analysed.

Initially, similarity matrices were calculated and patterns within the data sets were assessed using Principal Co-ordinate Analysis (PCoA). The vegetation analysis was based on Bray-Curtis dissimilarities of arcsine transformed percentage cover data, whereas habitat analysis was based on Euclidean distance of standardised variables. Differences between sites where *C. mercuriale* was present or absent were assessed using ANalysis Of SIMilarities (ANOSIM) in the PRIMER statistical package (Clarke & Warwick, 1994), and Canonical Discriminant Analysis (CDA) of the principal co-ordinates in the CAP computer program (Anderson & Willis, 2003). The significance of both results was tested by permutation (10,000 times).

To identify the plants that were the best indicators of the presence or absence of *C. mercuriale*, we used the Indicator Value method (IndVal) (Dufrêne & Legendre, 1997). This method combines a measure of a species relative abundance with its relative frequency of occurrence in the two groups, to produce an index that varies from 0 to 100. The score for each species is independent of the occurrence of other species. The significance of each plant species was tested using 10,000 permutations. However, it was not appropriate to use the Indicator Value method on the habitat data set. Instead, the correlation of habitat variables with the constrained ordination axis of the CDA was calculated.

To identify variables that were correlated with *C. mercuriale* abundance, we used a Canonical Correlation Analysis (CCorA) of the principal co-ordinates, in the program CAP (Anderson & Willis, 2003). In this method, a PCoA analysis is first performed (as above). A CCorA is then performed, in which ordination axes are drawn so as to maximise their correlation with a quantitative predictor variable, in this case *C. mercuriale* abundance. Once, again, the significance of the relationship was tested by permutation.

## 7.3 Results

### *7.3.1 Number of sites and abundance of* Coenagrion mercuriale

Larval *C. mercuriale* were captured at 53 out of the 100 sampling locations on at least one occasion during the study. The breakdown for each season is given in Table 7.1 and is described in more detail in the previous chapter (Chapter 6). During live sorting, larvae were often found clinging to aquatic vegetation.

**Table 7.1.** Number of sites at which larval *C. mercuriale* were captured and abundance for each season (n = 100).

| | **Autumn** | **Winter** | **Spring** | **Summer** | **Total** |
|---|---|---|---|---|---|
| No of sites | 38 | 33 | 40 | 12 | 53 |
| No of individuals | 499 | 191 | 191 | 43 | 924 |

### *7.3.2 Distribution as a function of habitat - occurrence of* C. mercuriale *larvae*

Four different models were developed using logistic regression to model the presence or absence of *C. mercuriale* larvae in each season (Table 7.2). Each model was highly significant and was able to correctly classify a minimum of 79.8% of the sites.

In the autumn season the abundance of emergent dicots was the single best predictor of *C. mercuriale* presence, while the abundance of submerged macrophytes was a significant predictor of sites where the species did not occur. Occurrence of *C. mercuriale* was negatively related to bankside principal component 5, which indicated that larvae were associated with locations with scrub on the adjacent land, and was positively related to chemistry PC2, which was positively correlated with chloride, nitrite and phosphate levels in the water.

**Table 7.2.** Significant predictors of *C. mercuriale* occurrence derived from four logistic regression models. Deviance, $D^2$, adjusted $D^2$ and the percentage of samples assigned to the correct group are shown for all models. For each variable retained in the model, the *p*-value derived from $\chi^2$ tests, parameter estimates and standard errors are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

| Model | Variable | $\chi^2$ | $p$ | Parameter Estimates | Standard Error |
|---|---|---|---|---|---|
| **Autumn** | Intercept | 4.94 | * | -1.225 | 0.551 |
| Deviance = 79.75 | Submerged | 7.02 | ** | -0.0424 | 0.0160 |
| $D^2 = 0.395$ | Emergent dicots | 11.49 | *** | 0.0752 | 0.0220 |
| Adj. $D^2 = 0.369$ | Bankside PC5 | 7.05 | ** | -0.664 | 0.250 |
| % correct = 79.8 | Chemistry PC2 | 10.00 | ** | 0.603 | 0.191 |
| **Winter** | Intercept | 19.27 | *** | -1.946 | 0.443 |
| Deviance = 74.59 | Channel PC1 | 9.13 | ** | -0.409 | 0.135 |
| $D^2 = 0.412$ | Bankside PC1 | 4.39 | * | -0.417 | 0.199 |
| Adj. $D^2 = 0.367$ | Chemistry PC1 | 8.04 | ** | -0.728 | 0.257 |
| % correct = 87.0 | Chemistry PC2 | 10.02 | ** | 0.595 | 0.188 |
| | Chemistry PC4 | 4.61 | * | -0.732 | 0.341 |
| | Site Highbridge | 8.82 | ** | 3.044 | 1.025 |
| | Site IVCP-Upper | 8.70 | ** | 4.394 | 1.490 |
| **Spring** | Intercept | 11.14 | *** | -7.161 | 2.145 |
| Deviance = 41.93 | Emergent dicots | 10.10 | ** | 0.438 | 0.138 |
| $D^2 = 0.689$ | Channel PC1 | 4.34 | * | 0.586 | 0.281 |
| Adj. $D^2 = 0.654$ | Channel PC2 | 7.74 | ** | -1.040 | 0.374 |
| % correct = 90.0 | Channel PC6 | 8.26 | ** | -1.972 | 0.686 |
| | Bankside PC1 | 6.31 | * | 0.693 | 0.276 |
| | Bankside PC2 | 10.74 | ** | -1.037 | 0.317 |
| | Bankside PC4 | 7.93 | ** | -1.598 | 0.568 |
| | Bankside PC7 | 8.00 | ** | -1.803 | 0.637 |
| | Chemistry PC1 | 12.62 | *** | 1.275 | 0.359 |
| | Chemistry PC2 | 12.32 | *** | 2.558 | 0.729 |
| **Summer** | Intercept | 23.08 | *** | -3.479 | 0.724 |
| Deviance = 45.83 | Channel PC1 | 5.30 | * | -0.548 | 0.238 |
| $D^2 = 0.373$ | Chemistry PC2 | 12.05 | *** | 1.012 | 0.292 |
| Adj. $D^2 = 0.353$ | Site IVCP-Upper | 5.15 | ** | 2.033 | 0.896 |
| % correct = 91.9 | | | | | |

In the winter season, seven variables were selected for inclusion in the final model. Channel PC1 and bankside PC1, were both negatively associated with *C. mercuriale* occurrence. Channel PC1 represented a range of inter-correlated variables corresponding to substrate and flow, with negative values representing sites with high levels of silt, low levels of all other substrate types, low flow, low discharge, a low proportion of flow types "riffle" and "run" and a high proportion of "marginal deadwater". Bankside PC1 represented variables connected with shade and trees, with negative values representing low levels of these factors. Water chemistry variables generated four principal components, three of which were significantly associated with

*C. mercuriale* occurrence in this season. *Coenagrion mercuriale* was associated with negative values of chemistry PC1, representing low levels of BOD, COD, suspended solids, turbidity and salinity, positive values of chemistry PC2, representing high levels of ammonia, nitrite, phosphate and conductivity, and negative values of chemistry PC4, representing low pH. Finally, the sites Highbridge and IVCP Upper were both included in the final model, suggesting that *C. mercuriale* occurred at these sites more often than expected by the habitat variables alone.

The model created from the spring data set was the best fitting model, with a $D^2$ of 0.689, and was able to classify 90% of sites correctly. However, 10 habitat parameters were included in this final model. *Coenagrion mercuriale* occurrence was associated with emergent dicots, with high flows and large substrate sizes (channel PC1), deep water (channel PC2), deep silt (channel PC6), shade and low levels of short herbs and grasses (bankside PC1), low levels of scrub and trees on the bankface, but high levels of tall herbs and grasses (bankside PC2), low levels of trees and bare ground on the adjacent land (bankside PC4), low banks (bankside PC7), high levels of alkalinity, COD, suspended solids, turbidity, conductivity and salinity (chemistry PC1) and high levels of ammonia, chloride, nitrite and phosphate (chemistry PC2).

The summer model was simpler, with two habitat components and one sites factor included in the final model. *Coenagrion mercuriale* was associated with low flows and small substrate sizes (channel PC 1), with high levels of chloride, nitrate and nitrite, but low levels of suspended solids (chemistry PC2), and occurred at IVCP Upper more frequently than expected.

### *7.3.3 Distribution as a function of habitat - abundance of* C. mercuriale *larvae*

A further four models were developed to relate habitat to *C. mercuriale* abundance, using Poisson regression (Table 7.3). In the autumn season, *C. mercuriale* was more abundant at locations containing greater amounts of emergent dicots, and with channel features comprising of deep water and a "glide" flow type (channel PC2), narrow channels (channel PC4), a small depth of silt (channel PC5), and was not abundant at sites with very deep silt or with boulders (channel PC6). *Coenagrion mercuriale* abundance was strongly negatively associated with bankside fencing (bankside PC4), but was weakly associated with trees on the bankface. It was positively associated with levels of chloride, nitrite and phosphate (chemistry PC2). Finally, the site IVCP Upper was retained in the final model, suggesting that abundance was higher at this sub-site than could be explained by the habitat variables alone.

In the winter season, emergent dicots was a significant predictor of *C. mercuriale* abundance, along with low flow and substrate conditions (channel PC1), low quantities of exposed silt (channel PC5), low shade and tree cover (bankside PC1), and was positively associated with grazing, short vegetation on the bank face and the adjacent land, but low levels of tall vegetation (bankside PC2). It was most abundant at locations with low levels of BOD, COD, suspended solids, turbidity, and salinity (chemistry PC1) and high levels of ammonia, nitrite, phosphate and conductivity (chemistry PC2). It was less abundant than expected at Allington Manor, but was more abundant at IVCP – Upper.

*Coenagrion mercuriale* was associated with three vegetation groups in spring. It was negatively associated with submerged macrophytes and emergent monocots, but was positively associated with emergent dicots. It was not associated with medium (channel PC5) or deep (channel PC6) levels of silt, with trees and scrub on the bankface (bankside PC2) or adjacent land (bankside PC4), but was associated with bare ground on the bankface (bankside PC6) and with high levels of ammonia, chloride, nitrite and phosphate (chemistry PC2). Three sites were included in the final model, indicating that *C. mercuriale* was more abundant than expected at Highbridge, IVCP - Upper, and IVCP- Mid.

The summer model contained only three factors. Locations with a high abundance of *C. mercuriale* tended to have higher levels of scrub on the adjacent land (bankside PC1), high levels of chloride, nitrate and nitrite, but low levels of suspended solids (chemistry PC2), and occurred at IVCP Upper more frequently than expected.

**Table 7.3.** Significant predictors of *C. mercuriale* abundance derived from four Poisson regression models. Deviance, degrees of freedom, deviance/d.f., $D^2$, and adjusted $D^2$ are shown for all models. For each variable retained in the model, the $p$-value derived from $\chi^2$ tests, parameter estimates and standard errors are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

| **Model** | **Variable** | $\chi^2$ | $p$ | **Parameter Estimates** | **Standard Error** |
|---|---|---|---|---|---|
| **Autumn** | Intercept | 12.52 | *** | -1.438 | 0.406 |
| Deviance = 277.67 | Emergent dicots | 36.73 | *** | 0.0412 | 0.0068 |
| d.f. = 89 | Channel PC2 | 7.33 | ** | -0.290 | 0.107 |
| Dev./d.f. = 3.12 | Channel PC4 | 5.60 | * | -0.329 | 0.139 |
| $D^2 = 0.844$ | Channel PC5 | 9.31 | ** | 0.462 | 0.151 |
| Adj. $D^2 = 0.828$ | Channel PC6 | 8.41 | ** | -0.546 | 0.188 |
| | Bankside PC4 | 49.78 | *** | -0.799 | 0.113 |
| | Bankside PC7 | 5.40 | * | 0.247 | 0.106 |
| | Chemistry PC2 | 15.35 | *** | 0.497 | 0.127 |
| | Site IVCP-Upper | 6.57 | * | 0.837 | 0.327 |
| **Winter** | Intercept | 33.49 | *** | -1.394 | 0.241 |
| Deviance = 100.66 | Emergent dicots | 37.61 | *** | 0.0532 | 0.0087 |
| d.f. = 90 | Channel PC1 | 6.45 | * | -0.171 | 0.067 |
| Dev./d.f. = 1.12 | Channel PC5 | 4.34 | * | -0.258 | 0.124 |
| $D^2 = 0.875$ | Bankside PC1 | 9.58 | ** | -0.272 | 0.088 |
| Adj. $D^2 = 0.863$ | Bankside PC2 | 8.16 | ** | 0.227 | 0.080 |
| | Chemistry PC1 | 32.02 | *** | -0.477 | 0.084 |
| | Chemistry PC2 | 24.15 | *** | 0.352 | 0.072 |
| | Site Allington Manor | 11.35 | *** | -2.506 | 0.744 |
| | Site IVCP-Upper | 46.55 | *** | 2.214 | 0.325 |
| **Spring** | Intercept | 0.92 | n.s. | -0.460 | 0.479 |
| Deviance = 96.33 | Submerged | 32.53 | *** | -0.100 | 0.018 |
| d.f. = 87 | Emergent dicots | 17.47 | *** | 0.100 | 0.024 |
| Dev./d.f. = 1.11 | Emergent monocots | 8.20 | ** | -0.035 | 0.012 |
| $D^2 = 0.822$ | Channel PC5 | 6.78 | ** | 0.386 | 0.148 |
| Adj. $D^2 = 0.797$ | Channel PC6 | 8.14 | **3 | -0.450 | 0.158 |
| | Bankside PC2 | 47.59 | *** | -0.507 | 0.073 |
| | Bankside PC4 | 8.85 | ** | -0.300 | 0.101 |
| | Bankside PC6 | 6.74 | ** | 0.343 | 0.132 |
| | Chemistry PC2 | 56.58 | *** | 0.786 | 0.105 |
| | Site Highbridge | 7.74 | ** | 1.167 | 0.419 |
| | Site IVCP-Upper | 31.09 | *** | 1.764 | 0.316 |
| | Site IVCP-Mid | 4.14 | * | 0.634 | 0.312 |
| **Summer** | Intercept | 12.68 | *** | -3.681 | 1.034 |
| Deviance = 55.27 | Bankside PC6 | 4.46 | * | -0.917 | 0.434 |
| d.f. = 95 | Chemistry PC2 | 10.80 | ** | 1.122 | 0.341 |
| Dev./d.f. = 0.582 | Site IVCP-Upper | 19.15 | *** | 4.362 | 0.997 |
| $D^2 = 0.759$ | | | | | |
| Adj. $D^2 = 0.751$ | | | | | |

### *7.3.4 Multivariate ordination – vegetation*

The PCoA ordination plots for each season are shown in Figure 7.1. There was a tendency for sites where *C. mercuriale* was present to be located towards one side of the ordination plots, although there was considerable overlap. Unconstrained ANOSIM tests (Table 7.4a) revealed that the differences between sites with and without *C. mercuriale* were significant for the autumn and spring seasons. Differences were not significant in the winter or summer data sets, but could be extracted using constrained ordination (CDA). Goodness of fit of the CDA analysis revealed that in all cases at least 69% of sites were correctly allocated to their appropriate group (Table 7.4a).

**Table 7.4.** ANOSIM, CDA and CCorA results for each season for a) vegetation data and b) habitat data. ANOSIM and CDA compare sites with and without *C. mercuriale.* CCorA shows the correlation with *C. mercuriale* abundance. Correlations and *p*-values of all tests are shown (*p*-values < 0.05 are highlighted in bold) and in addition the goodness of fit of the CDA is given.

| | **Autumn** | **Winter** | **Spring** | **Summer** |
|---|---|---|---|---|
| **a.) Vegetation analysis:** | | | | |
| ANOSIM: Global R | 0.129 | 0.037 | 0.081 | -0.026 |
| *p* | **<0.0001** | 0.108 | **0.0017** | 0.631 |
| CDA: correlation (d) | 0.612 | 0.443 | 0.586 | 0.463 |
| d square | 0.375 | 0.196 | 0.343 | 0.214 |
| *p* | **<0.0001** | **0.0052** | **<0.0001** | **0.0167** |
| total correct | 73.7% | 69.0% | 78.0% | 77.0% |
| CCorA: correlation (d) | 0.501 | 0.390 | 0.465 | 0.305 |
| d square | 0.251 | 0.152 | 0.216 | 0.093 |
| *p* | **<0.0001** | 0.2053 | **0.0038** | 0.4086 |
| **b.) Habitat analysis:** | | | | |
| ANOSIM: Global R | 0.037 | -0.014 | 0.013 | 0.169 |
| *p* | 0.125 | 0.605 | 0.310 | 0.0626 |
| CDA: correlation (d) | 0.856 | 0.581 | 0.910 | 0.720 |
| d square | 0.733 | 0.338 | 0.829 | 0.519 |
| *p* | **0.0006** | **0.0005** | **<0.0001** | **0.0017** |
| total correct | 77.8% | 73.0% | 82.0% | 85.9% |
| CCorA: correlation (d) | 0.549 | 0.463 | 0.561 | 0.903 |
| d square | 0.302 | 0.215 | 0.315 | 0.815 |
| *p* | **0.0053** | 0.0777 | **0.0273** | **0.0297** |

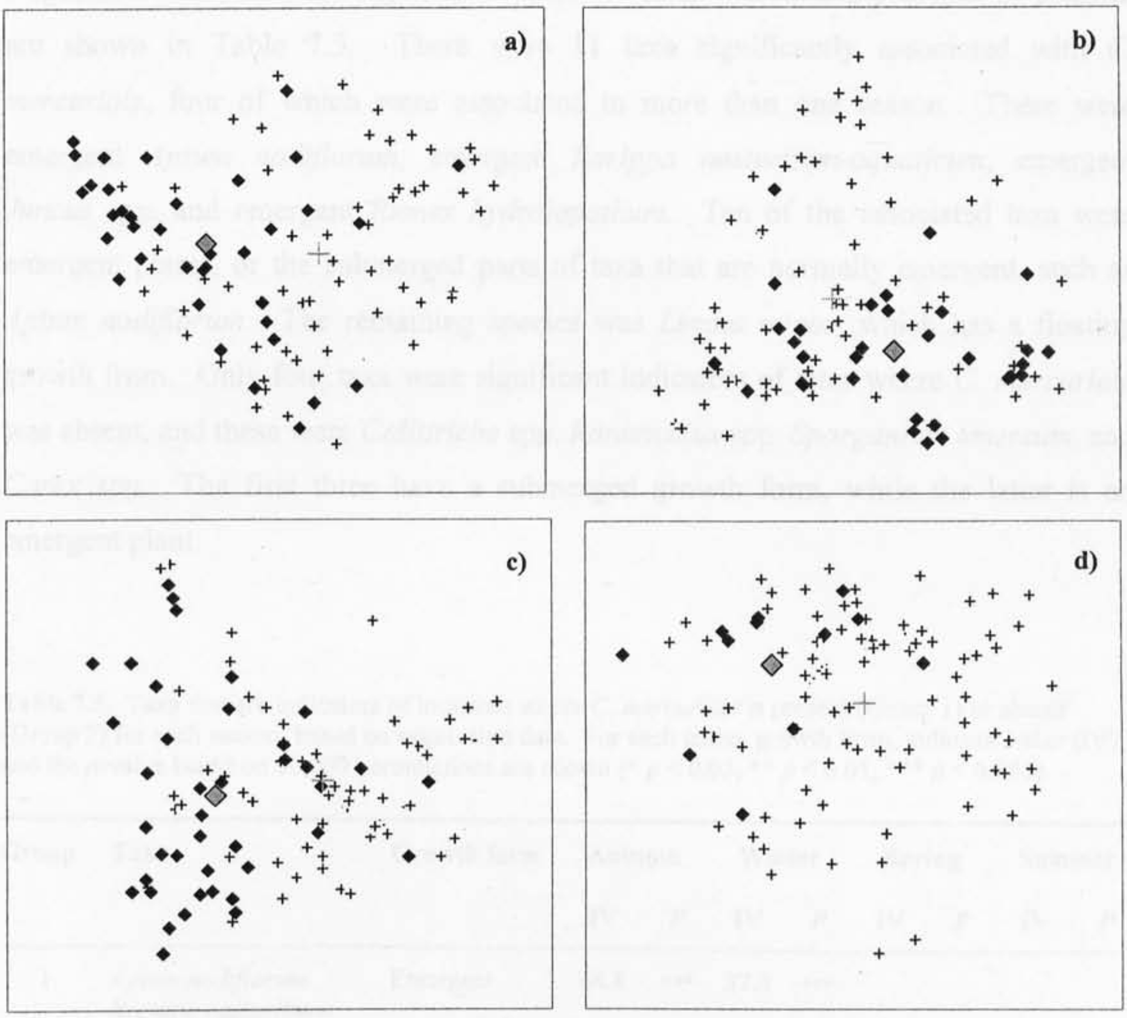

**Figure 7.1.** Ordination plots showing the first two axes of Principal Co-ordinate Analyses (PCoA) of **vegetation** data for a) autumn season, b) winter, c) spring, and d) summer. Samples are arcsine-transformed percentage cover data and show sites where *C. mercuriale* was present (◆) and sites where it was absent (+). Larger symbols in grey show mean values for the two groups. Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

Vegetation taxa that were significant indicators of *C. mercuriale* presence or absence are shown in Table 7.5. There were 11 taxa significantly associated with *C. mercuriale*, four of which were associated in more than one season. These were emergent *Apium nodiflorum*, emergent *Rorippa nasturtium-aquaticum*, emergent *Juncus* spp. and emergent *Rumex hydrolapathum.* Ten of the associated taxa were emergent plants, or the submerged parts of taxa that are normally emergent, such as *Apium nodiflorum.* The remaining species was *Lemna minor*, which has a floating growth from. Only four taxa were significant indicators of sites where *C. mercuriale* was absent, and these were *Callitriche* spp. *Ranunculus* spp. *Sparganium emersum*, and *Carex* spp. The first three have a submerged growth form, while the latter is an emergent plant.

**Table 7.5.** Taxa that are indicators of locations where *C. mercuriale* is present (Group 1) or absent (Group 2) for each season, based on **vegetation** data. For each taxon, growth form, indicator value (IV) and the $p$-value based on 10,000 permutations are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

| **Group** | **Taxa** | **Growth form** | **Autumn** | | **Winter** | | **Spring** | | **Summer** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | **IV** | ***P*** | **IV** | ***P*** | **IV** | ***P*** | **IV** | ***P*** |
| 1 | *Apium nodiflorum* | Emergent | 64.8 | *** | 37.3 | *** | | | | |
| | *Rorippa nasturtium-aquaticum* | Emergent | 25.9 | * | 13.6 | ** | | | | |
| | *Lemna minor* group | Floating | | | 32.5 | * | | | | |
| | *Glyceria maxima* | Emergent | | | 30.4 | * | | | | |
| | *Apium nodiflorum* | Submerged | | | 24.0 | * | | | | |
| | *Juncus* spp. | Emergent | | | 13.3 | ** | 12.5 | *** | 32.5 | *** |
| | *Glyceria maxima* | Submerged | | | 9.0 | * | | | | |
| | *Sparganium erectum* | Emergent | | | | | 49.1 | ** | | |
| | *Rumex hydrolapathum* | Emergent | | | | | 39.3 | *** | 24.2 | *** |
| | *Sparganium erectum* | Submerged | | | | | 13.9 | * | | |
| | *Phalaris arundinacea* | Emergent | | | | | | | 59.5 | ** |
| 2 | *Callitriche* spp. | Submerged | 43.2 | *** | | | | | | |
| | *Ranunculus* spp. | Submerged | 40.1 | *** | | | 32.9 | *** | | |
| | *Sparganium emersum* | Submerged | 16.4 | ** | | | | | | |
| | *Carex* spp. | Emergent | | | | | 37.6 | * | | |

The plant communities were correlated with *C. mercuriale* abundance using canonical correlation analysis of the principal co-ordinates. The correlation was significant in the autumn and spring seasons (at $p < 0.05$), but not in the winter and summer seasons (Table 7.4a). Taxa that were most highly correlated with *C. mercuriale* abundance and occurring in at least 10% of the samples are shown in Table 7.6. The positively correlated taxa are similar to those associated with *C. mercuriale* presence (Table 7.5) and included the emergents *Apium nodiflorum*, *Rorippa nasturtium-aquaticum*, *Sparganium erectum*, and *Phalaris arundinacea*. Similarly, the negatively correlated taxa included all those associated with *C. mercuriale* absence and mostly have a submerged growth form.

**Table 7.6.** Taxa that are positively (Group 1) or negatively (Group 2) correlated with *C. mercuriale* abundance for each season, based on **vegetation** data. For each taxon, the correlation with canonical axes from the CCorA is shown (see text for details). Only taxa with a correlation >0.2 and occurring in at least 10% of the sampling locations for that season are included.

| Group | Taxa | Growth form | Autumn | Winter | Spring | Summer |
|---|---|---|---|---|---|---|
| 1 | *Apium nodiflorum* | Emergent | 0.866 | 0.891 | 0.217 | 0.275 |
| | *Sparganium erectum* | Emergent | 0.356 | | 0.417 | 0.379 |
| | *Lemna minor group* | Floating | 0.257 | | | |
| | *Veronica anagallis-aquatica* | Submerged | 0.212 | | | |
| | *Juncus spp.* | Emergent | | | 0.299 | |
| | *Phalaris arundinacea* | Emergent | | | 0.696 | 0.441 |
| | *Rumex hydrolapathum* | Emergent | | | 0.318 | |
| | *Rorippa nasturtium-aquaticum* | Emergent | | | 0.241 | 0.221 |
| | *Ranunculus spp.* | Submerged | | | | 0.324 |
| 2 | *Ranunculus spp.* | Submerged | -0.309 | | -0.349 | |
| | *Callitriche spp.* | Submerged | -0.270 | | -0.265 | |
| | *Cladophora* | Submerged | -0.246 | | | |
| | *Carex spp.* | Emergent | -0.238 | | -0.314 | -0.320 |
| | *Sparganium emersum* | Submerged | -0.210 | | | -0.370 |
| | *Berula erecta* | Submerged | -0.209 | | -0.384 | -0.245 |
| | *Rorippa nasturtium-aquaticum* | Emergent | | -0.236 | | |

### *7.3.5 Multivariate ordination - habitat*

The PCoA ordination plots of habitat data for each season are shown in Figure 7.2. The separation of sites where *C. mercuriale* was present or absent was less distinct than in the vegetation analysis, and this is reflected in the results of the ANOSIM tests (Table 7.4b). Differences between sites with and without *C. mercuriale* were not significant for any season, although differences did become apparent when CDA was performed. Goodness of fit of the CDA analysis revealed that it was still possible to correctly allocate at least 73% of sampling locations to their appropriate group in all seasons (Table 7.4b).

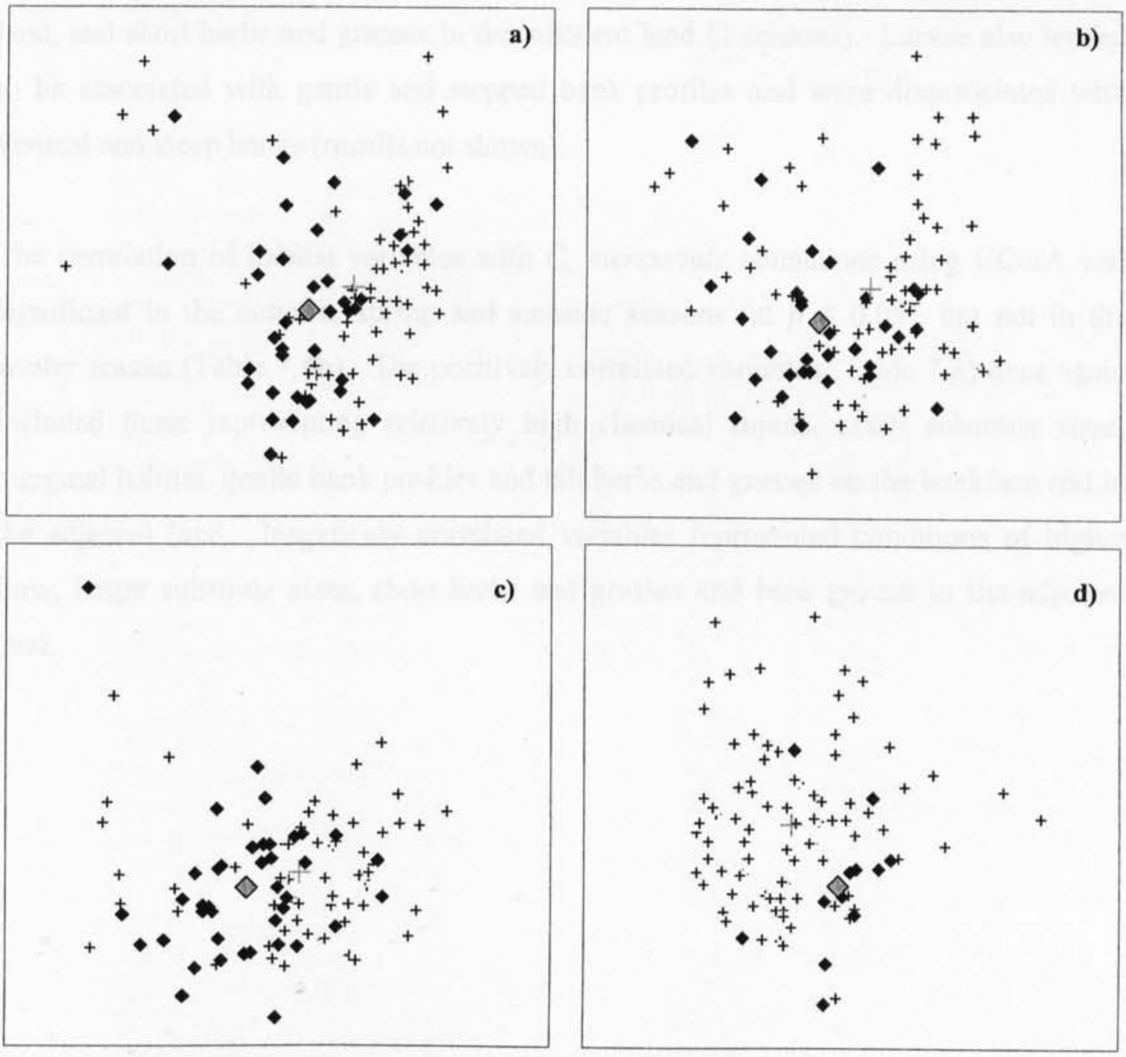

**Figure 7.2.** Ordination plots showing the first two axes of PCoAs of **habitat** data for a) autumn season, b) winter, c) spring, and d) summer. Samples show sites where *C. mercuriale* was present (◆) and sites where it was absent (+). Larger symbols in grey show mean values for the two groups. Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

It was not appropriate to use the Indicator Value method on the habitat data set, but the correlation of habitat variables with the constrained ordination axis of the CDA analysis was appropriate. The most highly correlated variables are shown in Table 7.7, which includes 24 variables positively correlated with *C. mercuriale* occurrence and 22 negatively correlated. Phosphate and MSUB (mean substrate size) were positively correlated in all four seasons. Silt, nitrite, ammonia and chloride were positively associated in three seasons, while COD, conductivity, salinity, short herbs and grasses on the bankface, and tall herbs and grasses in the adjacent land were correlated in two seasons. Habitat variables that were negatively associated with *C. mercuriale* occurrence included pebbles (4 seasons), boulders, gravel, sand, "run" (3 seasons), flow, discharge, width, bankfull height, bare ground on the bank face or in the adjacent land, and short herbs and grasses in the adjacent land (2 seasons). Larvae also tended to be associated with gentle and stepped bank profiles and were disassociated with vertical and steep banks (results not shown).

The correlation of habitat variables with *C. mercuriale* abundance using CCorA was significant in the autumn, spring and summer seasons (at $p < 0.05$), but not in the winter season (Table 7.4b). The positively correlated variables (Table 7.8) once again included those representing relatively high chemical inputs, small substrate sizes, marginal habitat, gentle bank profiles and tall herbs and grasses on the bankface and in the adjacent land. Negatively correlated variables represented conditions of higher flow, larger substrate sizes, short herbs and grasses and bare ground in the adjacent land.

**Table 7.7.** Variables that are positively (Group 1) or negatively (Group 2) correlated with *C. mercuriale* occurrence for each season, based on **habitat** data. For each variable, the correlation with canonical axes from the CDA is shown (see text for details). Only variables with a correlation >0.2 are included.

| Group | Variable | Autumn | Winter | Spring | Summer |
|---|---|---|---|---|---|
| 1 | Suspended solids | 0.562 | | | |
| | Marginal deadwater | 0.445 | | | |
| | COD | 0.393 | | | 0.551 |
| | Phosphate | 0.387 | 0.543 | 0.454 | 0.532 |
| | Shade - none | 0.375 | | | |
| | MSUB | 0.334 | 0.586 | 0.292 | 0.295 |
| | Poaching | 0.234 | | | |
| | Fenced | 0.233 | | | |
| | Silt | | 0.606 | 0.268 | 0.271 |
| | Nitrite | | 0.523 | 0.537 | 0.436 |
| | Ammonia | | 0.402 | 0.299 | 0.268 |
| | Bankface - short herbs and grasses | | 0.402 | 0.223 | |
| | Silt & detritus depth >30cm | | 0.363 | | |
| | Chloride | | 0.329 | 0.472 | 0.462 |
| | Conductivity | | 0.283 | 0.409 | |
| | Water depth 0-5cm | | 0.233 | | |
| | Salinity | | | 0.417 | 0.241 |
| | 5-50m - tall herbs and grasses | | | 0.282 | 0.330 |
| | 5-50m - scrub | | | 0.248 | |
| | Mean water depth | | | 0.228 | |
| | 0-5m - tall herbs and grasses | | | 0.205 | |
| | Glide | | | 0.201 | |
| | BOD | | | | 0.405 |
| | Nitrate | | | | 0.387 |
| 2 | Glide | -0.504 | | | |
| | Mean water depth | -0.470 | | | |
| | Exposed silt | -0.386 | | | |
| | Gravel | -0.313 | -0.463 | -0.248 | |
| | Bankfull height | -0.27 | -0.249 | | |
| | Sand | -0.270 | -0.531 | | -0.269 |
| | Pebbles | -0.264 | -0.429 | -0.204 | -0.331 |
| | 0-5m - short herbs and grasses | -0.256 | | -0.201 | |
| | Silt | -0.203 | | | |
| | Mean flow | | -0.514 | | -0.254 |
| | Discharge | | -0.484 | | -0.246 |
| | 0-5m – bare ground | | -0.368 | -0.237 | |
| | Run | | -0.355 | -0.240 | -0.247 |
| | Suspended solids | | -0.354 | | |
| | Turbidity | | -0.331 | | |
| | Boulders | | -0.313 | -0.349 | -0.224 |
| | 5-50m – bare ground | | -0.298 | -0.236 | |
| | Bankface - bare ground | | -0.286 | -0.288 | |
| | Silt & detritus depth - 0-5cm | | -0.285 | | |
| | Mean water width | | -0.259 | | -0.202 |
| | 5-50m - scrub | | -0.204 | | |
| | Water depth - 5-30cm | | | -0.263 | |

**Table 7.8.** Variables that are positively (Group 1) or negatively (Group 2) correlated with *C. mercuriale* abundance for each season, based on **habitat** data. For each variable, the correlation with canonical axes from the CCorA is shown (see text for details). Only variables with a correlation >0.2 are included.

| Group | Variable | Autumn | Winter | Spring | Summer |
|---|---|---|---|---|---|
| 1 | Suspended solids | 0.771 | | | |
| | Phosphate | 0.703 | 0.610 | 0.518 | 0.323 |
| | COD | 0.667 | | | 0.734 |
| | Shade - none | 0.572 | | | |
| | MSUB | 0.543 | 0.345 | 0.459 | |
| | Marginal deadwater | 0.483 | 0.204 | | |
| | Boulders | 0.418 | | | |
| | Fenced | 0.346 | | | |
| | Turbidity | 0.311 | | | |
| | 5-50m - bare ground | 0.276 | | | |
| | Bankface - tall herbs and grasses | 0.272 | | 0.273 | |
| | 5-50m - scrub | 0.247 | | | |
| | 5m – bare ground | 0.245 | | | |
| | Salinity | 0.227 | | 0.311 | |
| | 5m - scrub | 0.224 | | | |
| | Nitrite | | 0.601 | 0.620 | |
| | 5m - tall herbs and grasses | | 0.445 | 0.581 | |
| | Conductivity | | 0.394 | 0.296 | |
| | Silt | | 0.374 | 0.444 | |
| | Ammonia | | 0.330 | 0.265 | |
| | 5-50m - tall herbs and grasses | | 0.303 | 0.520 | |
| | Silt & detritus depth >30cm | | 0.302 | 0.287 | |
| | Chloride | | 0.302 | 0.367 | 0.443 |
| | Water depth - 0-5cm | | 0.289 | | |
| | Alkalinity | | 0.249 | | |
| | Water depth - 5-30cm | | 0.203 | | |
| | Nitrate | | | 0.218 | |
| | BOD | | | | 0.278 |
| | Bankface - short herbs and grasses | | | | 0.233 |
| | Poaching | | | | 0.206 |
| 2 | Mean water depth | -0.542 | | | |
| | Glide | -0.512 | | | |
| | Exposed silt | -0.463 | | | |
| | Gravel | -0.438 | -0.320 | -0.368 | |
| | Sand | -0.415 | -0.345 | -0.287 | |
| | Silt | -0.401 | | | |
| | Pebbles | -0.294 | | | |
| | 5m - tall herbs and grasses | -0.253 | | | |
| | 5-50m - short herbs and grasses | -0.243 | | -0.341 | |
| | Run | -0.234 | -0.239 | | |
| | Bankface - scrub | -0.231 | | | |
| | Silt & detritus depth - 5-30cm | -0.210 | | | |
| | Bankface - short herbs and grasses | -0.209 | | | |
| | Discharge | | -0.513 | | |
| | Mean flow | | -0.456 | -0.206 | |
| | Mean water width | | -0.415 | | |
| | 5-50m - bare ground | | -0.381 | | |
| | 5m – bare ground | | -0.333 | -0.229 | |
| | Suspended solids | | -0.290 | | |
| | Bankface - bare ground | | -0.278 | | |
| | Turbidity | | -0.277 | | |
| | 5m - short herbs and grasses | | -0.250 | -0.506 | |

**Table 7.8 cont.**

| | | |
|---|---|---|
| Pebbles | -0.224 | -0.338 |
| Silt & detritus depth - 0-5cm | -0.207 | -0.218 |
| Water depth >30cm | -0.204 | |
| 5-50m - scrub | -0.204 | |
| Boulders | | -0.421 |
| Bankfull height | | -0.277 |

### *7.3.6 Metals and pesticides*

In total, samples were tested for 42 different types of pesticide (see Appendix 2.2), but only two were found at detectable levels. These were atrazine and simazine. However, even these were found at extremely low concentrations and there was no link between concentration and occurrence or abundance of *C. mercuriale*. We also tested samples for calcium, copper, iron, magnesium, sodium and zinc. All were within the expected values for a chalk stream and none had any effect on *C. mercuriale* presence or abundance.

## 7.4 Discussion

### *7.4.1 Habitat associations*

*Coenagrion mercuriale* larvae were associated with certain physical, chemical and vegetation characteristics of their habitat in the Itchen and Test Valleys. Generalized linear modelling and multivariate ordination have revealed similar variables with which *C. mercuriale* is associated, although details vary from season to season and on which method is used. The most consistent variables associated with the occurrence of *C. mercuriale* using GLM logistic regression are the abundance of emergent dicots, relatively high levels of chloride, nitrite and phosphate, and the lack of trees. In two seasons the species was associated with low flow conditions and small substrate sizes, although a small but significant negative relationship with these features was apparent in the spring season. When GLM Poisson regression was used to model the variables associated with *C. mercuriale* abundance, the most consistent variables were once again the abundance of emergent dicots, high levels of chloride, nitrite and phosphate, a lack of trees, and the species was not associated with deep silt banks (> 30cm deep). There was also a suggestion in two seasons that larvae were more abundant in sites that were grazed to the water's edge. In both types of modelling, the species occurred more often and in greater abundance at IVCP – Upper than expected.

Multivariate ordination of the habitat variables revealed a fairly similar picture, although *C. mercuriale* presence and abundance was correlated with all aspects relating to low flow, small substrate sizes and laminar or marginal stream types, as well as many of the chemical variables. It was associated with tall herbs and grasses but not with short herbs and grasses or bare ground. Larvae were also associated with gentle and stepped bank profiles and were disassociated with vertical and steep banks.

Multivariate analysis of the plant data provided greater detail of the species with which *C. mercuriale* is associated. Both statistical techniques have shown that *C. mercuriale* is associated with emergent vegetation and tends to be disassociated with submerged vegetation. However, analysis of individual plant species and their indicator values has shown that *Apium nodiflorum* is particularly important, along with the ecologically similar species *Rorippa nasturtium-aquaticum*. *Apium nodiflorum* was extremely highly correlated with *C. mercuriale* abundance in the autumn and winter seasons, but was less important in the spring and summer seasons. This is a reflection of its growth pattern, as it is at its most abundant in the autumn, is one of the last species to die back in the winter, and is slow to re-establish itself in the spring.

The most consistent factor with which *C. mercuriale* was associated was relatively high chemical inputs, particularly chloride, nitrite and phosphate. By using principal components of the chemical variables in the GLMs, we were able to distinguish between sites with high levels of chloride, nitrite and phosphate, from those with high salinity, conductivity, COD, BOD, suspended solids and turbidity. The latter group were highly inter-correlated, were dependent partly on flow (e.g. season 1 correlation of chemistry PC1 with flow: $R = -0.411$, $p < 0.001$), and were highest in stagnant locations. Some associations with *C. mercuriale* were apparent using multivariate ordination, as these chemicals were higher in the slow-flowing, silt-impacted, vegetation rich locations favoured by *C. mercuriale*. However, *C. mercuriale* did not occur in locations with no flow and consequently did not occur in locations with the highest inputs of this group of chemicals. On the other hand, chloride, nitrite and phosphate were not governed by flow. The strong association between *C. mercuriale* and these chemicals may, however, be an artefact, as all of the sites at the lower end of the Itchen (IVCP, Allington Manor and West Horton) had significantly higher inputs of these chemicals than the remaining sites. These sites are located downstream of a large urban area with its associated sewage works and industry, and are also downstream of an arable area. IVCP is the strongest site for *C. mercuriale* in its chalkstream habitat and so it is perhaps inevitable that high chemical inputs would be selected in the models. We tried to remove this spatial autocorrelation effect by entering the sites as factors into the GLM and by applying trend surface analysis (not shown), but these were not able to fully factor out this effect.

Trees were generally associated with locations where *C. mercuriale* did not occur or was in low abundance, although the effect of shade was equivocal. This is almost certainly a reflection of adult behaviour. Adults are almost never found in deeply shaded areas and most sites in the UK and the rest of Europe are largely unshaded (Buchwald, 1994; Purse, 2001). Although larvae were more abundant in unshaded sites, they did occur in some heavily shaded locations, suggesting that the larvae are probably not restricted by this factor. Limited larval movement would result in occupied habitat reflecting oviposition history as well as habitat choice.

In two seasons *C. mercuriale* was associated with a range of variables representing low flow and fine substrates. These conditions are ideal for the growth of emergent dicots such as *Apium nodiflorum*. Indeed, emergent dicots were negatively correlated with flow and substrate (e.g. season 1 correlation of channel PC1 with emergent dicots: $R = -0.382$, $p < 0.001$) and one of these two factors was included in all of the logistic models.

*Coenagrion mercuriale* occurred more frequently and was more abundant than expected at IVCP- Upper, which was the only sites factor consistently selected in the models. This suggests either that an unmeasured factor was operating throughout this sub-site resulting in higher than expected densities, or that larvae were aggregated. IVCP- Upper contained the highest densities of adults during mark-release-recapture studies and individuals exhibited behaviour such as inverse density dependent movement that resulted in marked aggregations (Chapter 3). The species also exhibits group oviposition. Martens (2000) showed that tandem pairs of *C. mercuriale* landed preferentially on leaves where a conspecific was present. These behaviours will result in high densities of eggs and then larvae in particular patches of habitat.

### *7.4.2 Why are larvae associated with emergent dicots?*

Perhaps the key habitat feature with which *C. mercuriale* larvae are associated is emergent dicots. In a variety of mesohabitat studies carried out in chalk streams, macrophytes have been found to support a richer invertebrate community than silt or gravel habitats alone (e.g. Wright *et al.*, 1983; Wright, 1992, Pardo & Armitage, 1997; Harrison, 2000). Each habitat is characterised by a suite of invertebrates reflecting the physical and biological differences between the habitats, but marginal habitats have proved to be particularly important for invertebrates in chalk streams (Pardo & Armitage, 1997; Harrison, 2000). Furthermore, the dicot *Rorippa nasturtium-aquaticum* was found to support a more diverse and abundant fauna than the monocot *Phragmites australis*, owing to its greater structural complexity (Pardo & Armitage, 1997). Emergent dicots therefore provide particular physical and biological conditions that are favourable to species such as *C. mercuriale*. Larvae may be associated with these species because these plants offer a refuge from predation, or their prey is more abundant, or simply that they provide the most suitable physical conditions. In still waters, oxygen concentration was always found to be higher in the root zone of vegetation than in plant free sediment (Sagova-Mareckova, 2002), and this could be an additional factor in slow flowing, marginal habitats.

Coenagrionidae larvae observed during this study displayed a wide range of colour forms, from dark brown to bright green, but *C. mercuriale* was most commonly a fairly pale green-brown colour. This colour would appear to offer some camouflage from predators and prey for a species associated with aquatic vegetation.

The association of *C. mercuriale* with plant communities was generally consistent across broad functional groupings. Amalgamating species into these groupings in the GLMs was statistically valid as it radically reduced the number of potential predictor variables, reduced the chance of overfitting and removed the problems of non-normal and sparse variables. *Coenagrion mercuriale* was associated with emergent dicots in several models and was disassociated with submerged macrophytes in two models. By investigating the plant community in more detail using multivariate ordination, we have been able to confirm the generality of these results and have highlighted species of particular importance. Associations amongst emergent dicots and submerged species were consistent with the above generalizations. However, the pattern for emergent monocots was less clear, as several species were associated with *C. mercuriale* (e.g. *Sparganium erectum, Phalaris arundinacea* and *Juncus* spp.) but *Carex* spp. was not. This may explain why emergent monocots rarely featured in the regression models. Ordination has also revealed the importance of *Apium nodiflorum* and *Rorippa nasturtium-aquaticum* within the emergent dicots. It would be interesting to repeat the regression modelling using a few key plant species highlighted by the ordination and Indicator Value methods, instead of the broad vegetation groups used here.

### *7.4.3 Methodological issues*

Using habitat variables to predict the occurrence or abundance of a species has been practised on numerous occasions. Although extremely useful tools in applied ecology and conservation planning, a number of general assumptions associated with the use of regression techniques remain. Firstly, they are dependent upon there being an equilibrium between the study organism and the environment (Guisan *et al.*, 2002). If a species occurrence and abundance shifts dynamically over the course of time, such as is predicted by metapopulation models, or if a species range is rapidly expanding or contracting, then this can bias results of regression modelling. Furthermore, a positive relationship between species abundance and habitat quality is assumed, but has been called into question (Van Horne, 1983; Pearce & Ferrier, 2001). For example, species are often able to persist for a number of years as habitat becomes gradually more unsuitable.

Colonization history can mask habitat choice in relatively sedentary organisms. For example, Fonseca & Hart (2001) demonstrated that dispersal constraints limited the ability of larval black flies (*Simulium vittatum*) to reach preferred habitats. In our study, oviposition choice by adults could be of more importance than larval habitat choice. Dispersal ability of *C. mercuriale* larvae has never been quantified, but odonates are not significant components of the larval drift fauna and it is likely that they are fairly sedentary. Habitat associations of larvae, therefore, almost certainly reflect both adult oviposition choices and larval habitat preferences.

A further problem relates to spatial autocorrelation, whereby species abundances at nearby points tend to be more similar than would be expected by random chance. This pattern can be driven by environment processes, such as an autocorrelated environment, or disturbance, or may relate to the biology and behaviour of the species, such as conspecific attraction, dispersal limitation and demography (Legendre, 1993; Lichstein *et al.*, 2002). Using GLMs reduces the problem, and a Poisson error structure with a quasi-likelihood function is particularly robust to deviations from the expected distribution (Crawley, 2002). Furthermore, we have tried to account for broad-scale spatial autocorrelation by incorporating a sites factor into the regression models (Legendre, 1993). Nevertheless, problems remain and so our results should be interpreted with caution. New techniques to deal with spatial autocorrelation, such as auto-regressive models, are becoming available (Keitt *et al.*, 2002; Lichstein *et al.*, 2002) and it would be interesting to analyse *C. mercuriale* occurrence using auto-logistic models. However, these techniques are not able to deal with a Poisson error structure (Lichstein *et al.*, 2002).

### *7.4.4 Conservation implications*

In rivers and streams the distribution of macro-invertebrates is driven largely by substrate size, the nature and amount of organic detritus and flow conditions. The spatial distribution of macroinvertebrates in ditches appears to be determined by vegetation pattern and particularly by the seral stage (Caspers & Heckman, 1981; Clare & Edwards, 1983; Scheffer *et al.*, 1984, Foster *et al.*, 1990; Painter, 1999). In the Itchen and Test Valleys, *C. mercuriale* distribution seems to be determined chiefly by vegetation pattern, which is in turn governed by flow and substrate conditions.

The previous chapter showed that *C. mercuriale* is associated with macroinvertebrates that require well-vegetated, moderate to slow flowing waterbodies, with a predominantly silty substrate. By analysing habitat variables directly, this chapter has confirmed and enhanced many of those findings. Late-instar larvae occur more often and in greater abundance at sites that contain abundant emergent dicots, particularly in smaller, more marginal channels with low flow. The abundance of *Apium nodiflorum* and *Rorippa nasturtium-aquaticum* are particularly important. Bankside variables are more equivocal, but larvae are rarely found in areas with much tree cover and are more abundant in locations with a gentle or stepped bank profile and at locations that are grazed to the water's edge.

It is clear, therefore, that ditches should be managed in such a way as to encourage the growth of emergent dicots, particularly *Apium nodiflorum* and *Rorippa nasturtium-aquaticum*. These require shallow, slow-flowing margins in which to take root. Flow is a prerequisite for *C. mercuriale* and so ditches should be periodically dredged on rotation to halt succession. Banksides should be gently sloping, lightly grazed and should contain little in the way of tree cover. Light grazing will also help to create suitable bankside and channel conditions and will help to maintain channels in mid-successional phase.

# Chapter 8: Conclusion

The purpose of this final chapter is to review the key findings of the study and to discuss themes that reach across several chapters. I will summarise the current distribution and status of *C. mercuriale* in the Itchen and Test Valleys and then review the findings of this thesis regarding the ecology of *C. mercuriale* in its chalkstream habitat before proposing some avenues for further research. I will end by providing recommendations regarding the monitoring, conservation and management of *C. mercuriale*.

## 8.1 *Coenagrion mercuriale* in the Itchen and Test Valleys

Knowledge of the distribution and status of *C. mercuriale* in the Itchen Valley has increased vastly in the last six years, due in part to the work presented in this thesis and in part to the increasing number of surveys performed. The stronghold is the Itchen Valley Country Park (IVCP), where a population numbering into the tens of thousands is present. This suggests that it is one of the most important sites for *C. mercuriale* in the UK. The site also appears to be of great importance in the European context. Although knowledge of population sizes in its strongholds of France and Spain remains scant, 80% of sites in Germany had small populations of *C. mercuriale*, with less than 10 individuals recorded per 100m of ditch (Röske, 1995) and no sites had more than 50 per 100m. In comparison, considerably more than 50 individuals per 100m are regularly recorded on sections of the transect in IVCP – Upper (K.Young, *unpublished*). Other areas of the IVCP, as well as sections in West Horton, Highbridge and Mariner's Meadow all contained dense populations of *C. mercuriale* as my study has shown (Chapter 3).

Despite the strong position of *C. mercuriale* in the IVCP, its long-term future in the Itchen Valley is not guaranteed without conservation action. To the north of this site, the area is largely sub-optimal, with only short areas of good habitat. This has led to the isolation of the northern populations, putting them at increased risk of extinction in the medium to long term. Anecdotal evidence suggests that *C. mercuriale* may once have been found throughout the Itchen Valley as far north as Winchester. Although far from conclusive, there is therefore a suggestion of a retraction in range as well as fragmentation of the remaining areas. Development and agricultural pressures on the landscape still remain, particularly in the built up areas around Eastleigh and Bishopstoke, where much potential habitat has been lost in the last few decades.

The status and distribution of *C. mercuriale* in the Test Valley is far less clear. The species is present in a fairly extensive area close to King's Somborne. Outside of this area, however, very little is known. It has not been found in any other locations during survey work, but these have been extremely limited in their overall coverage. It is likely that *C. mercuriale* will be discovered in several other locations, but a more comprehensive survey remains a key priority. The status of the species also remains largely unknown. Stevens and Thurner (1999) recorded a peak of 58 and 350 individuals in one day to the north and south of the Clarendon Way respectively, suggesting a strong population in the survey year (1998). However, only 17 and 36 were recoded in these same locations on a visit in 2002 and similarly low numbers were observed in 2003 (*pers. obs.*). Furthermore, the entire stretch of stream containing the greatest abundance of *C. mercuriale* was dredged in the winter of 2003/4, with no areas left as refuge. Although harmful in the short term, this may actually result in an increase in population over time, if individuals are able to recolonize from nearby. This whole area would benefit from regular monitoring.

## 8.2 Ecology of *C. mercuriale* in chalkstream habitats

*Coenagrion mercuriale* occurs in two habitat types in the UK; small lowland heathland streams and calcareous streams / fens. Although the species is found more often on the former biotope in the UK, a review of *C. mercuriale* sites in mainland Europe (Chapter 2) has revealed that outside of the UK the species is almost always found in calcareous habitats. Research carried out in these countries, particularly the detailed studies available from Germany, can be used to inform and guide conservation efforts in the chalkstream sites in the UK.

The habitat of *C. mercuriale* sites in mainland Europe is similar to that in the Test and Itchen valleys. All sites containing good populations of *C. mercuriale* share a number of biotic and abiotic features, which will be summarised in due course. Where they do differ, perhaps, is in physical dimensions. Occupied channels in mainland Europe are often narrow, with lower flow and discharge compared to many occupied ditches in UK chalkstreams. This is because many of these channels are directly and solely fed by springs, or else are small drainage channels. The chalkstreams of England are different, because of their landscape history. Almost all suitable areas on the floodplains of chalkstreams were used as water meadows until relatively recently, which required the creation and maintenance of an extensive network of carriers and ditches. It is the remains of this network that provides the primary habitat for *C. mercuriale* in the Itchen and Test valleys. These ditches tend to be larger, with a much larger discharge, as they are fed from the main river channel. One advantage of our historic system is that we are better able to influence the physical properties of these ditches, including flow and discharge, than would be possible in spring-fed systems. This has important and useful conservation implications. It also suggests that the perennial springs and headwaters of the Test and Itchen and their tributaries may harbour suitable habitat for the Southern Damselfly and would be worthy of a thorough survey.

Chapter 3 revealed important information regarding movement patterns in *C. mercuriale*. *Coenagrion mercuriale* is extremely sedentary; lifetime movements of greater than 500 m were shown to be rare and only 3 individuals moved further than 1 km. This is less than any other odonate so far studied. Damselflies readily moved between the adjacent sites at the southern end of the Itchen Valley, but there were no movements between the isolated northern colonies. This finding has been confirmed by genetic studies (Watts *et al.*, 2004), which suggest that the northern sites, particularly Mariner's Meadow, are genetically isolated.

In contrast with many species of Lepidoptera, *C. mercuriale* movement declined with age. In Lepidoptera, females, in particular, readily disperse following one or more oviposition bouts close to their natal site. Dispersive behaviour was also seen to increase with age in the odonate *Sympetrum danae* (Michiels & Dhondt, 1991). An equivalent behavioural mechanism does not appear to be present in *C. mercuriale*, limiting its dispersal capabilities still further.

One of the most intriguing findings presented in this thesis is that *C. mercuriale* movement is inverse density dependent, something that has not been reported before in natural odonate populations. This finding, together with the short distances moved, has profound consequences for the population dynamics and conservation of this species. *Coenagrion mercuriale* will not readily colonize new areas unless they are close to existing sites; sub-optimal sites are more likely to be abandoned; and small, isolated sites are at increased risk of extinction.

Inverse density dependent movement of adult *C. mercuriale* was confirmed when density and movement was analysed in relation to habitat variables and local population size (Chapter 4). Mean adjacent population density was the single most important factor determining density, and movement was greatest from sections with low density. However, the species was also associated with a number of habitat features, the most important of which were: a channel substrate consisting primarily of silt, wide underwater ledges (berms), in-channel emergent dicots, and bankside monocots. The presence of trees was negatively associated with damselfly density.

*Coenagrion mercuriale* larvae were found to occur more often and in greater abundance at sites that contained abundant emergent dicots, particularly in smaller, more marginal channels with low flow (Chapter 7). They were rarely found in areas with much tree cover and were more abundant in locations where the banksides were open to grazing and with gentle or stepped bank profiles. *Apium nodiflorum* and *Rorippa nasturtium-aquaticum* were found to be particularly important. Furthermore, they were associated with certain macroinvertebrate species or groups of species that were indicative of well-vegetated, moderate to slow flowing waterbodies, with a predominantly silty substrate (Chapter 6). Clearly, both direct habitat associations and indirect preferences suggested through associations with other macroinvertebrates, have revealed extremely similar habitat requirements for these mid to late-instar larvae.

What then, are the similarities and differences between the habitat requirements of the adults and larvae of this species? Broadly speaking, *C. mercuriale* adults were found in high density in areas where larvae occurred in high density. As previously stated, this was in areas with ample in-channel emergent dicots, in silty channels that were largely unshaded. There were some differences, however. Adults were not found in channels that were highly choked with vegetation but were associated to some extent with open water. Larvae, however, were more abundant in locations with greater quantities of in-channel vegetation and occurred in sites that were almost completely choked. Furthermore, larvae were abundant in some extremely slow flowing locations and were associated with some species that were indicative of extremely marginal habitats. There was no link between flow and adult density and adults were often present in quite fast flowing areas. It seems, therefore, that larvae are found in greatest abundance in habitats that are slightly further along the successional sequence than that favoured by adults. For example, the very best location for larvae during this project, with 193 individuals sampled over four seasons, was almost completely choked with emergent vegetation, and contained extremely slow flowing, shallow water. Few adults were captured here during the MRR study in the previous summer.

The most likely cause for this difference is that adults require open water as a visual cue during site selection. Following emergence, adults move away from their natal site to mature. After a few days, they are ready to return, but probably use the reflection of light from the water surface as a cue that water and hence a potential breeding site is present. Ultimately, this also enables adults to select habitats that are less likely to dry up completely or become stagnant over the two-year lifecycle of their offspring. It is probable that the most favoured location for larvae, described above, contained more open water during the summer of 2000 and hence oviposition occurred on this stretch of ditch. It is also possible that larval survival is much greater in this type of habitat. Unfortunately, there are no records available to test these hypotheses. Interestingly however, although many larvae were captured here in the first three seasons, there were few larvae captured in the summer 2002 sampling season. This would correspond with a drop in use by ovipositing adults in summer 2001.

There is anecdotal evidence that the *C. mercuriale* population in the Itchen Valley Country Park may have declined slightly following a raising of water levels in 1991 and that recently, strong populations have developed in slower flowing channels downstream of the traditional stronghold in IVCP – Upper. In the larval habitat study reported in Chapter 7, *C. mercuriale* larvae were disassociated with deep silt banks, usually found in the larger, deeper channels. Furthermore, evidence from other calcareous sites in Europe and from the heathland sites in the UK suggests that the species is more commonly found on shallow, slower flowing watercourses. In the Itchen Valley, this discrepancy is partly alleviated by the presence of berms along several of the channels in the IVCP. These underwater ledges provide shallower, slower-flowing areas along the edges of channels that are ideal for the growth of emergent vegetation.

Another key finding of this study is the association between *C. mercuriale* and particular species of emergent vegetation, especially *Apium nodiflorum* and *Rorippa nasturtium-aquaticum.* In other calcareous sites in Europe a similar, albeit weaker, association has been reported. *Rorippa nasturtium-aquaticum* is the most frequently reported plant species at *C. mercuriale* sites, along with *Berula erecta*, which is ecologically similar. *Apium nodiflorum* appears to be less common in mainland Europe.

An investigation into the diet of *C. mercuriale* (Bousfield, 2003) performed in conjunction with this study, has suggested that mid to late-instar larvae are generalist predators feeding in particular on Chironomidae, Copepoda and *Gammarus*. It is unlikely that they are food limited.

This thesis has also examined night-time roosting location of adult *C. mercuriale* (Chapter 5), a habitat that has often been overlooked in the past. It has been established that adults are strongly associated with two tussock-forming monocots, *Juncus inflexus* and *Deschampsia cespitosa*. Differences in the abundance of these plants have been shown to result in large differences in the numbers of *C. mercuriale* roosting in different parts of the site. It is possible that lack of suitable areas for night-time roosting and daytime shelter could limit the abundance of the species at some sites and is an important factor to consider when managing sites for *C. mercuriale*.

Loss of habitat, alterations to management on remaining sites, and fragmentation of a once continuous network of sites, are likely to have been the driving forces behind the decline of this species in the Itchen and Test Valleys, and remain the greatest threats to its continued existence. Successful conservation of *C. mercuriale* will involve active management of existing sites, together with the creation (or recreation) of a series of new sites to reconnect populations.

## 8.3 Further work

Some suggestions for further study have been presented in each chapter. The aim here is to provide a brief summary of the principal outstanding areas where further research is required.

*Movement and dispersal by tenerals* – Although movement patterns of mature adults have been well studied, movement by tenerals remains a matter of conjecture. In the congener *Coenagrion puella*, dispersal during the maiden flight following emergence has been observed (Anholt, 1990; D.J.Thompson, *pers. comm.*) and is believed to be the major dispersive phase for some odonates (Anholt, 1990; Corbet, 1999). *Coenagrion mercuriale* does not appear to display the same behaviour (*pers. obs.)* and genetic evidence supports this assertion (Watts *et al.*, 2004), but this has never been tested. Teneral damselflies are not robust enough to mark using the methods employed in this study and retaining individuals until this is possible is thought to affect behaviour (Purse, 2001). Other marking techniques, such as stable isotope enrichment, used, for example, to mark Plecoptera in headwater streams in Wales (Briers *et al.*, 2004), are not possible on a protected species such as *C. mercuriale.* A successful non-destructive marking technique remains to be found.

*Survival and lifetime reproductive success* – Inverse density dependent movement results in large aggregations of this species in favourable areas. It would be interesting to ascertain whether adult survival varies between low density and high density locations and the effect of density on lifetime reproductive success for both sexes.

*Night-time roosting locations* – Does *C. mercuriale* select *Juncus inflexus* and *Deschampsia cespitosa* because they are tufted or because they have the most suitable stem diameter? Simple cage experiments could be used to tease these two factors apart. The night-time study reported in this thesis (Chapter 5) was relatively small in scale and the results somewhat preliminary. There is much to be gained by repeating the study, particularly at a range of sites, with different vegetation conditions. It would also be interesting to try to create some suitable night-time roosting conditions in sites where this is lacking (such as Allington Manor), to determine whether this is a limiting factor.

*Habitat and diet of early-instar larvae* – This study has mostly examined mid to late-instar larvae and gaps remain in our knowledge of the early-instars. However, field studies would be difficult to perform, as it is extremely difficult to distinguish early instar *C. mercuriale* larvae from other members of the Coenagrionidae. It would also be difficult to carry out using live sampling, as nets with a small mesh diameter would be required, which inevitably capture lots of silt and detritus. It is likely, however, that early instar larvae feed predominantly on microcrustaceans and small chironomids and it would be useful and interesting to assess the abundance of these taxa across a range of sites.

*Habitat management for* C. mercuriale – It had originally been my intention to study the effect of management operations on both larval and adult abundance. This was not possible, however, due to factors beyond my control, but remains an area of prime importance. The habitat preferences of this species have been largely determined by observational evidence rather than experimental manipulation. Experiments with follow-up monitoring, particularly within the IVCP, which is managed sympathetically, would greatly enhance the validity of the findings of this thesis. Furthermore, monitoring of other sites where ditch or bankside management is taking place would provide valuable information, and should be prescribed as part of Agri-Environment agreements. Due to the two-year life cycle of this species, monitoring should be carried out for several years, and in some sites at least, should involve monitoring of both larvae and adults as well as the habitat itself.

*Status and distribution of* C. mercuriale *on the River Test* – It is clear that large gaps remain in our knowledge of *C. mercuriale* in the Test Valley. More comprehensive surveys should be conducted as a matter of urgency to address this issue.

## 8.4 Monitoring

Site condition assessment is an important part of conservation management and can be performed either on the species of interest directly, or indirectly by assessing habitat. A separate monitoring strategy document has been produced in conjunction with this thesis (Thompson *et al.*, 2003b), detailing background and proposed methodology. Hence only a summary of the key points is provided here.

### *8.4.1 Monitoring of* C. mercuriale *directly*

It would be possible to monitor *C. mercuriale* at any one of the stages of its life history. However, work reported here has shown that larvae are difficult to sample quantitatively, particularly in small populations, time-consuming to identify, and only relatively small sections of stream can be monitored. Counting exuviae, although perhaps the most accurate method of measuring abundance at a particular site, is labour-intensive and costly. Counting mature adults is therefore the recommended approach for routine monitoring. It is best carried out using a modified "Pollard walk" as has been developed and used extensively with butterflies (Pollard, 1977; Pollard & Yates, 1993) and some other odonates (Brooks, 1993). This type of monitoring is now being used at the IVCP and at many other *C. mercuriale* sites across the country. Its value increases as a time-series for a particular site is built up over a number of years. Methodological details are provided in Thompson *et al.* (2003b).

### *8.4.2 Monitoring of* C. mercuriale *habitat*

Although monitoring of adults is being carried out more frequently, habitat monitoring is often ignored. This thesis has, however, revealed a number of key habitat attributes with which *C. mercuriale* is associated in its chalkstream sites, which can form the basis of a monitoring strategy. Table 8.1 lists eight key habitat attributes identified by this study. It is recommended that these attributes are measured once a year at as many sites as possible. A 10m strip of stream could be assessed per 50m at larger sites. A monitoring regime of this nature would be relatively easy, quick and cost-effective.

Tables 6.3 and 6.4 have provided a list of macroinvertebrate taxa that are associated or disassociated with *C. mercuriale* occurrence and abundance. This list could be used to assess the suitability of new sites or the change in macroinvertebrate communities following management.

**Table 8.1.** Key habitat attributes, with suggested upper and lower limits, that indicate favourable condition for *C. mercuriale* on chalkstream sites in the Itchen and Test Valleys (modified from Purse, 2001).

| Key habitat attributes | Definition of upper and lower limits for favourable condition |
|---|---|
| 1. Ditch with year-round flowing water. Flow velocity either slow or with moderate flow in central channel and shallow slow-flowing areas at ditch edges. | *Lower and upper limit of extent on site*: 100% of site must have year round flow. 50-100% of ditch/stream with suitable flow velocities. |
| 2. Ditch edges with broad fringe of herbaceous emergent dicots, especially *Apium nodiflorum* and *Rorippa nasturtium-aquaticum*. May also include *Mentha aquatica, Veronica* spp. and *Myosotis scorpioides.* | *Lower and upper limit of cover*: 10-50% in summer. Could be higher in the autumn and likely to be lower in winter and spring. |
| 3. Some open water present: i.e. ditch not completely choked with vegetation. | *Lower and upper limit of cover*: 20-80% in summer, but with seasonal variations. |
| 4. Bankside vegetation with heterogeneous sward of helophyte monocots, typically including *Glyceria maxima, Phalaris arundinacea, Sparganium erectum, Iris pseudacorus, Carex* spp., and *Juncus spp* | *Lower and upper limit of extent on site*: 30-100% of bankside. |
| 5. Ditch largely unshaded by bankside shrubs and trees | *Lower and upper limit of scrub or trees shading ditch*: 0-40% cover. |
| 6. Channel substrate consisting primarily of silt and detritus. | *Lower and upper limit of extent on site*: 50-100% of ditch/stream |
| 7. Unpolluted conditions indicated by a lack of areas of watercourse with encroachment of algae (except brown flocculent algae) or bacterial film. | *Lower and upper limit of extent on site*: 0-10% of watercourse |
| 8. Ditch surrounded by lightly grazed meadow, containing tussocks of *Juncus inflexus* or *Deschampsia cespitosa.* | *Lower and upper limit of extent on site*: 50-100% meadow in surrounding area, containing 20-80% tussocks. |

## 8.5 Conservation and management

### *8.5.1 The landscape component*

The effect of landscape structure and connectivity on the persistence of populations has become apparent over the last few decades. The developments of metapopulation theory (e.g. Hanski, 1998, 1999) and landscape ecology have highlighted the importance of spatial structure and the effects of fragmentation. As populations and species have become ever more fragmented, these aspects have taken on a primary role in conservation efforts. It is no longer enough to manage populations of rare species in isolation in a nature reserve; landscape structure and connectivity must be taken into account.

In the Itchen and Test Valleys, *C. mercuriale* lives essentially in a linear habitat, defined by the floodplain of these rivers. Its distribution, however, is far from continuous. In the Itchen Valley, large gaps of sub-optimal habitat separate areas of good habitat. Due to the limited dispersal capacity of the species, it shows evidence of genetic isolation by distance even within the continuous habitat of the Lower Itchen Complex, and the sites to the north show evidence of genetic isolation. It is therefore essential that conservation actions are applied at the landscape level, and that management works are tailored to the scale of the movements observed. In essence, this requires the reconnection of the existing populations through habitat creation, or recreation, at a scale in keeping with *C. mercuriale* movement parameters. In all studies of *C. mercuriale*, movements of up to 500m have been readily observed, even across largely unsuitable habitat. Longer distances have only been achieved along continuous areas of habitat, and even then distances over 1km are extremely rare. It is recommended, therefore, that new habitat is created within 500 m to 1 km of existing sites, to create a series of "stepping-stones" that would rejoin existing populations. This would encourage gene flow and maintain the genetic diversity in the population that is essential for securing its long-term future.

Two additional points of interest are worth noting. Firstly, the recent landuse changes in the Itchen Valley, particularly in the area between West Horton and Highbridge suggest that any isolation in the Itchen Valley populations is probably of recent origin.

Prompt action to recreate habitat here would be particularly beneficial. Secondly, during the course of this study, it has become increasingly apparent that *C. mercuriale* is present on the main channel of the River Itchen at several locations. Although it does not generally occur in large numbers, it is clearly able to persist in suitable margins and may well be using the river as a corridor. This will make conservation efforts somewhat easier as the species is likely to travel further along this habitat than it would across completely unsuitable land. The creation of suitable habitat along the main river channels would greatly enhance efforts to reconnect *C. mercuriale* populations and can be achieved by creating shallow, silty margins with abundant broad-leaved emergent vegetation.

### *8.5.2 Habitat creation / recreation*

One of the most important ways in which *C. mercuriale* populations in the Itchen and Test Valleys can be enhanced is through habitat creation or recreation at suitable locations. The floodplains contain numerous dry ditches that were once part of the old water meadow systems, which provide ideal locations for this type of work. Furthermore, the recent trend to reinstall old water meadow systems to recreate a more historic landscape setting has enormous potential benefit for *C. mercuriale*.

All sites chosen for habitat recreation should be located within easy dispersal of existing colonies. An important pre-requisite in many locations is control over water flow. The installation of sluice gates and other control features at some sites is essential to allow this to happen. The ditches created should have slow flow throughout, or medium flow in the central part of the channel, but with ample shallow margins, that will provide suitable habitat for colonization by emergent macrophytes. It is recommended that new channels are either shallow across their profile, or else berms are created on both sides of a deeper central section. Bank profiles should be shallow or stepped, to provide ample habitat for marginal vegetation and to give access to livestock.

### *8.5.3 Ditch management*

Key habitat attributes have been identified in Table 8.1 and management of existing ditches should be tailored to meet these requirements. Maintenance of ditches in these conditions will require periodical dredging and clearing of the vegetation to stop them becoming completely choked and eventually drying up. Ideally, *C. mercuriale* populations should be monitored and management performed before numbers decline by much. Where healthy populations already exist, management operations should be performed on short sections of ditch on rotation (perhaps 100m stretches) or on one side of the channel only. However, exact prescriptions will vary from site to site dependent upon local conditions, hydrology, and the condition of the *C. mercuriale* population. Dredging will also allow for some reprofiling of the channel. In all deeper channels (>50cm deep) it is recommended that shallow berms are created on both sides to provide the shallow slow flowing conditions that are the optimum for both emergent dicots and for *C. mercuriale.*

### *8.5.4 Bankside management*

Bankside and adjacent land management has an important influence on *C. mercuriale* abundance, particularly that of the adults. Light grazing by cattle right to the water's edge appears to be the optimum management technique. This will create a heterogeneous sward structure on the bankside and in-channel, will create shallow poached margins at the edges of the channel, and will lead to the formation of lightly grazed meadows with ample tussocks that are used by adult *C. mercuriale* for roosting and resting. Grazing should not be too heavy, as this will result in the loss of suitable resting and roosting locations, and heavy poaching will damage banks and destroy vegetation. In a study of the effect of fencing versus light grazing on Diptera, Trichoptera and Odonata in the Itchen Valley, Drake (1995) reported slightly greater species diversity, particularly of species typical of the water's edge and of species of conservation interest, on banksides open to light grazing. He suggested that this was because light grazing had created a more diverse physical structure. In apparent contrast however, Harrison and Harris (2002) reported that in-channel and marginal macroinvertebrate diversity and abundance was greater in ungrazed stretches than in grazed stretches of chalkstreams in Dorset. However, the grazing intensity at sites in this study was much greater, resulting in a lower structural diversity of bankside vegetation in these grazed sections. It is clear, therefore, that creating a heterogeneous sward structure is of most benefit to invertebrates. This will benefit *C. mercuriale* directly, due to the reasons described above, and indirectly, by providing increased abundance of invertebrate prey.

Shading of the watercourse by bankside trees and shrubs is a problem in some areas. Some shading is acceptable, particularly if it is only on one side of the channel, but extensive shading is detrimental. Tree and scrub clearance is, therefore, required on some sites.

### *8.5.5 Adjacent land use and water quality*

All of the sites containing good populations of *C. mercuriale* on chalkstream sites are surrounded by grazed meadows and this is also the optimum land use at German sites (Buchwald *et al.*, 1989; Buchwald, 1994). Where ditches flow through arable land, such as to the south of Bishopstoke, it is recommended that a strip of land is left fallow to either side of the channel, as has been suggested in Germany (Buchwald *et al.*, 1989). This should be 10m wide on each side of the channel, although the wider the strip, the more effective it would be. This protection strip would provide some more suitable habitat close to the water's edge and would protect the stream to some extent from agricultural chemicals.

Eutrophication is considered to be a major threat to *C. mercuriale* in several parts of Europe (e.g. Buchwald, 1994; Goffart, 1995). Although *C. mercuriale* was associated with higher chemical inputs in this study than occurs in "classic" chalkstreams (Chapter 7), these inputs were still relatively low. Evidence from other areas suggests that the species would be sensitive to gross changes in water quality, probably through changes in the vegetation composition of the ditches. Although water quality in the Test and Itchen is currently high, a change would be detrimental to all of the sites. Runoff from arable land remains a cause of concern in some parts of the Itchen.

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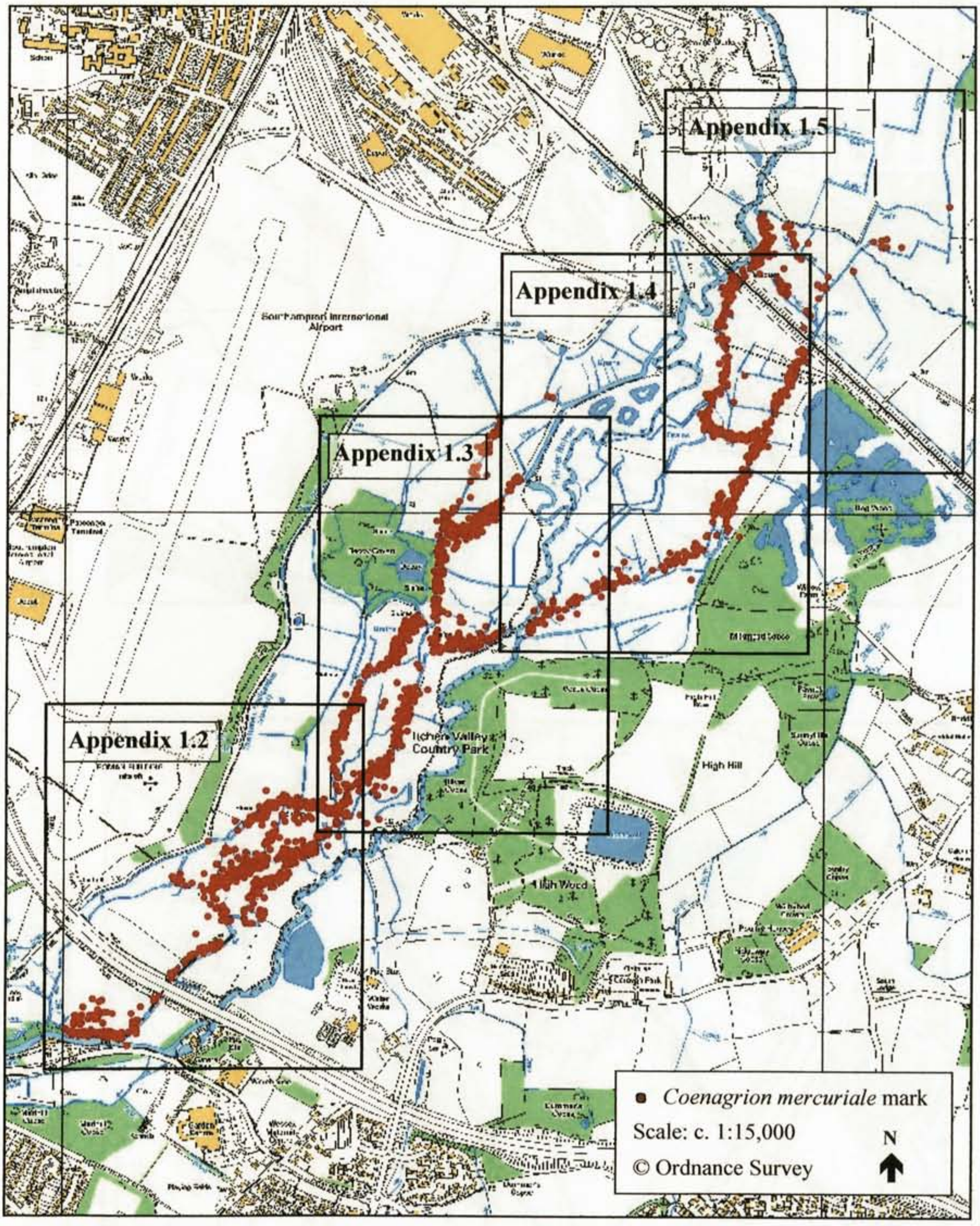
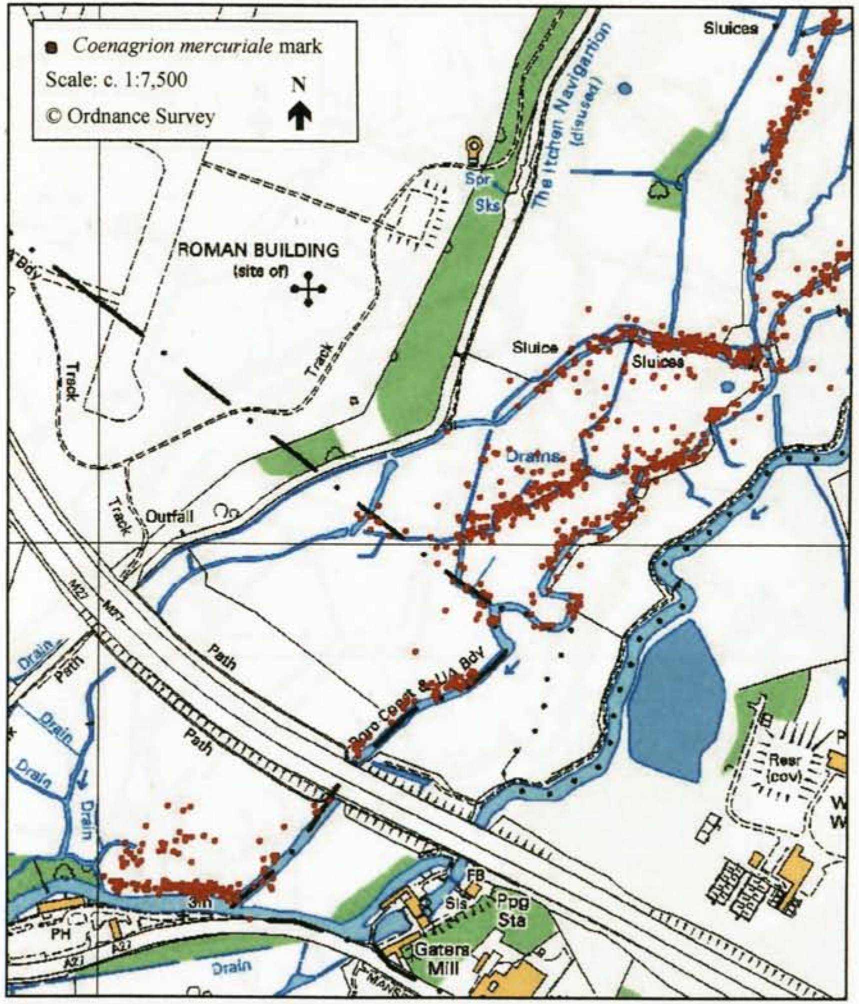
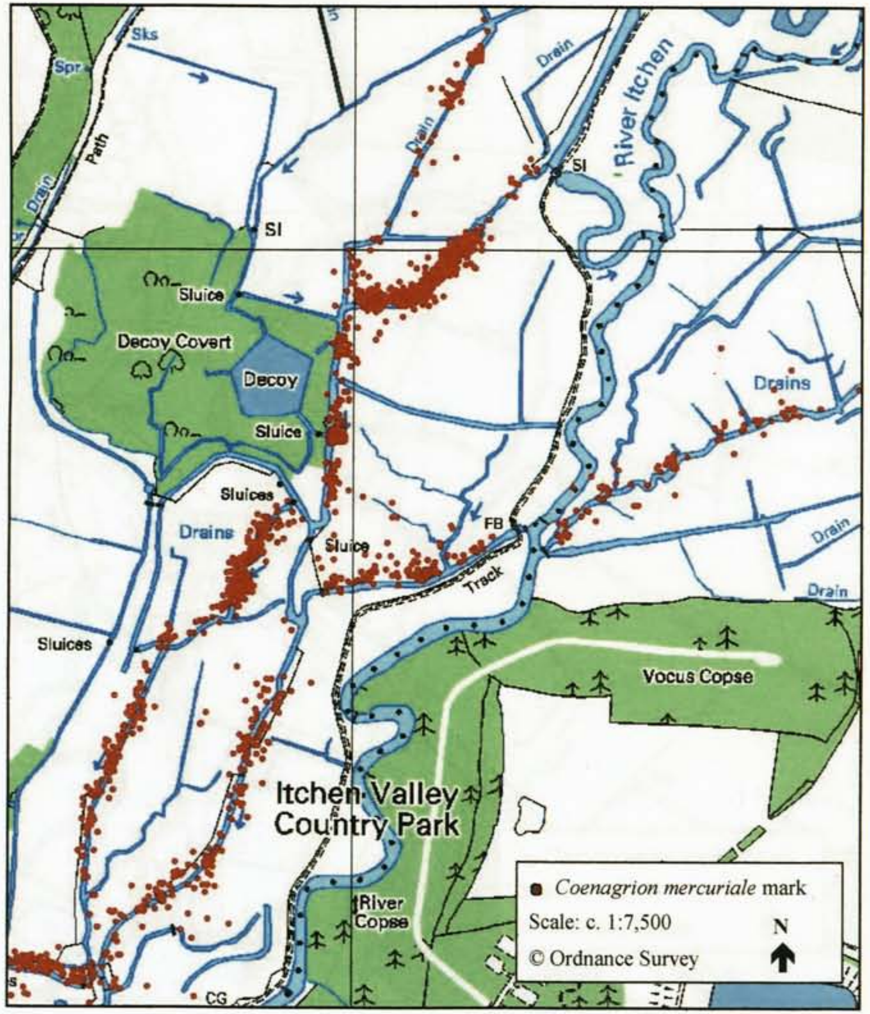
**Appendix 1.1.** Map of Lower Itchen Complex, showing site location and position of all *C. mercuriale* marked during mark-release-recapture survey (Chapter 3).



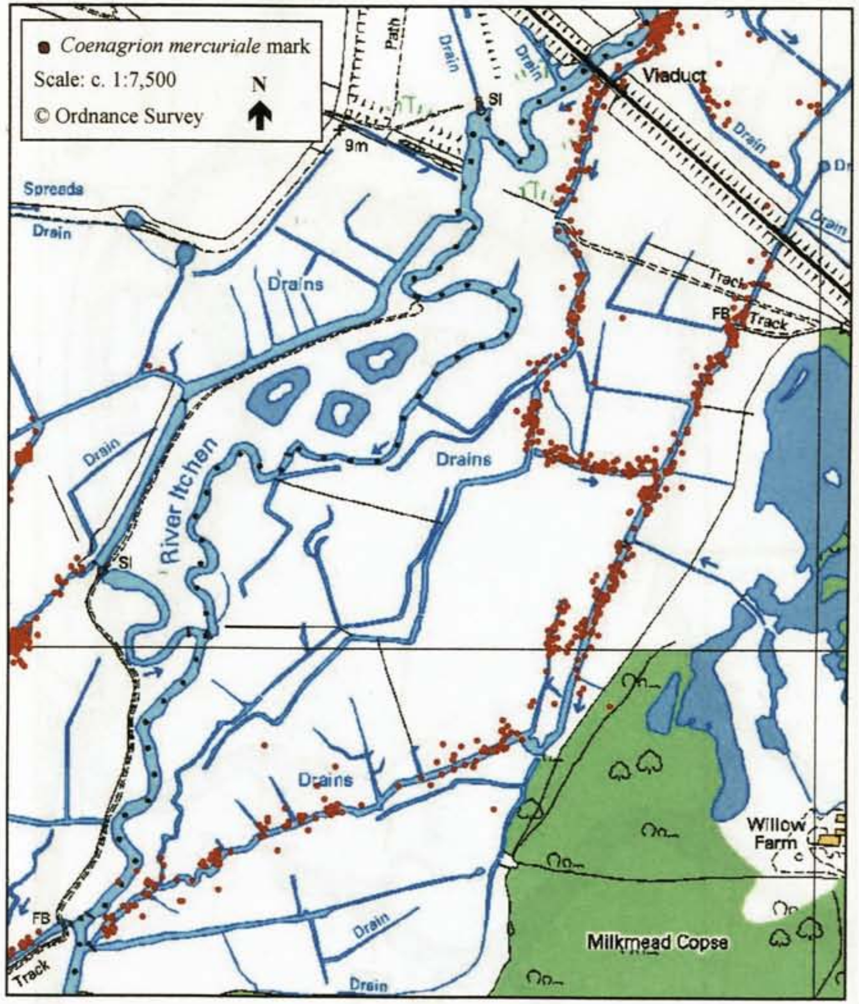
**Appendix 1.2.** Map of Itchen Valley Country Park (south), showing location of all marked *C. mercuriale*. Note location of M27 motorway.



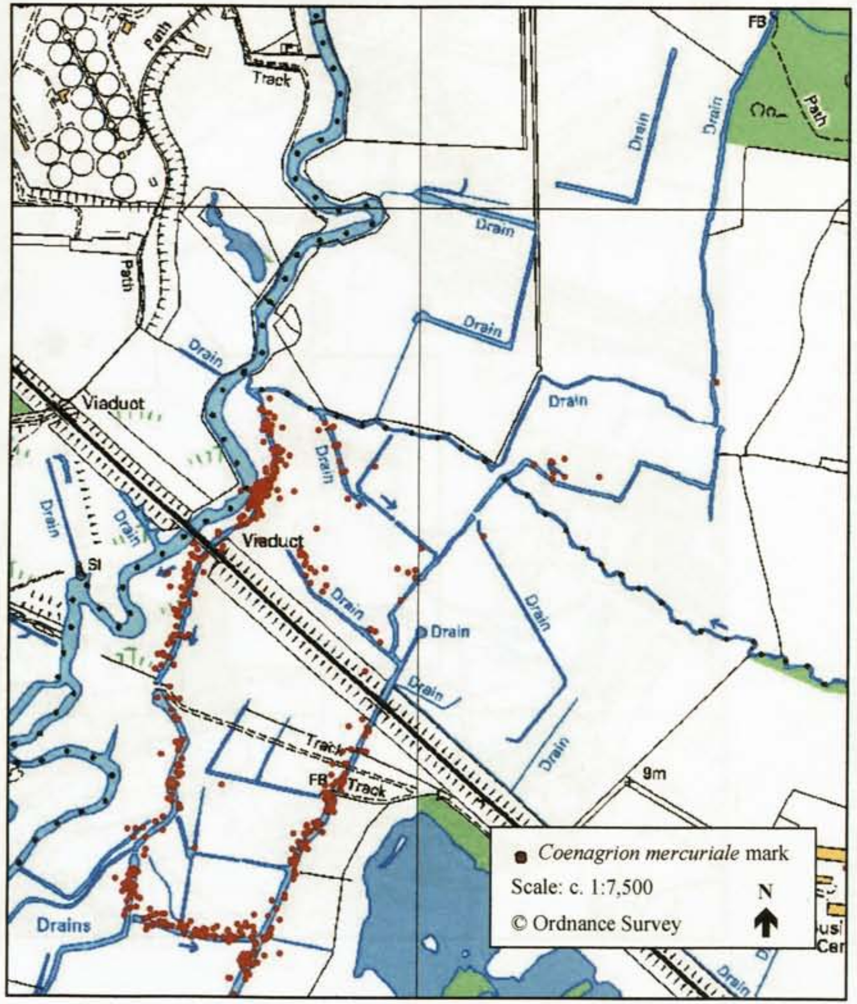
**Appendix 1.3.** Map of Itchen Valley Country Park (north), showing location of all marked *C. mercuriale*.



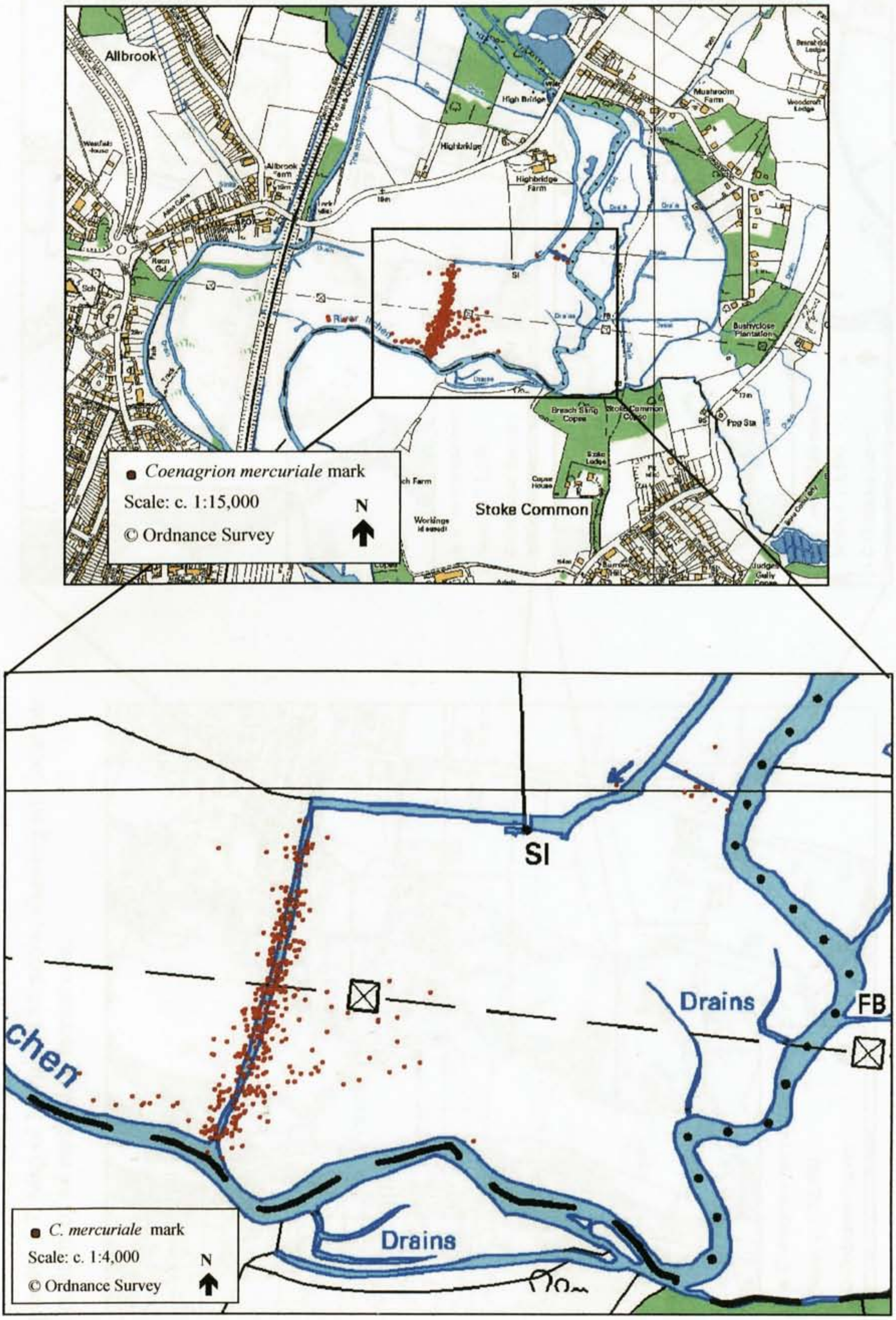
**Appendix 1.4.** Map of Allington Manor Farm showing location of all marked *C. mercuriale*. Note location of railway embankment.



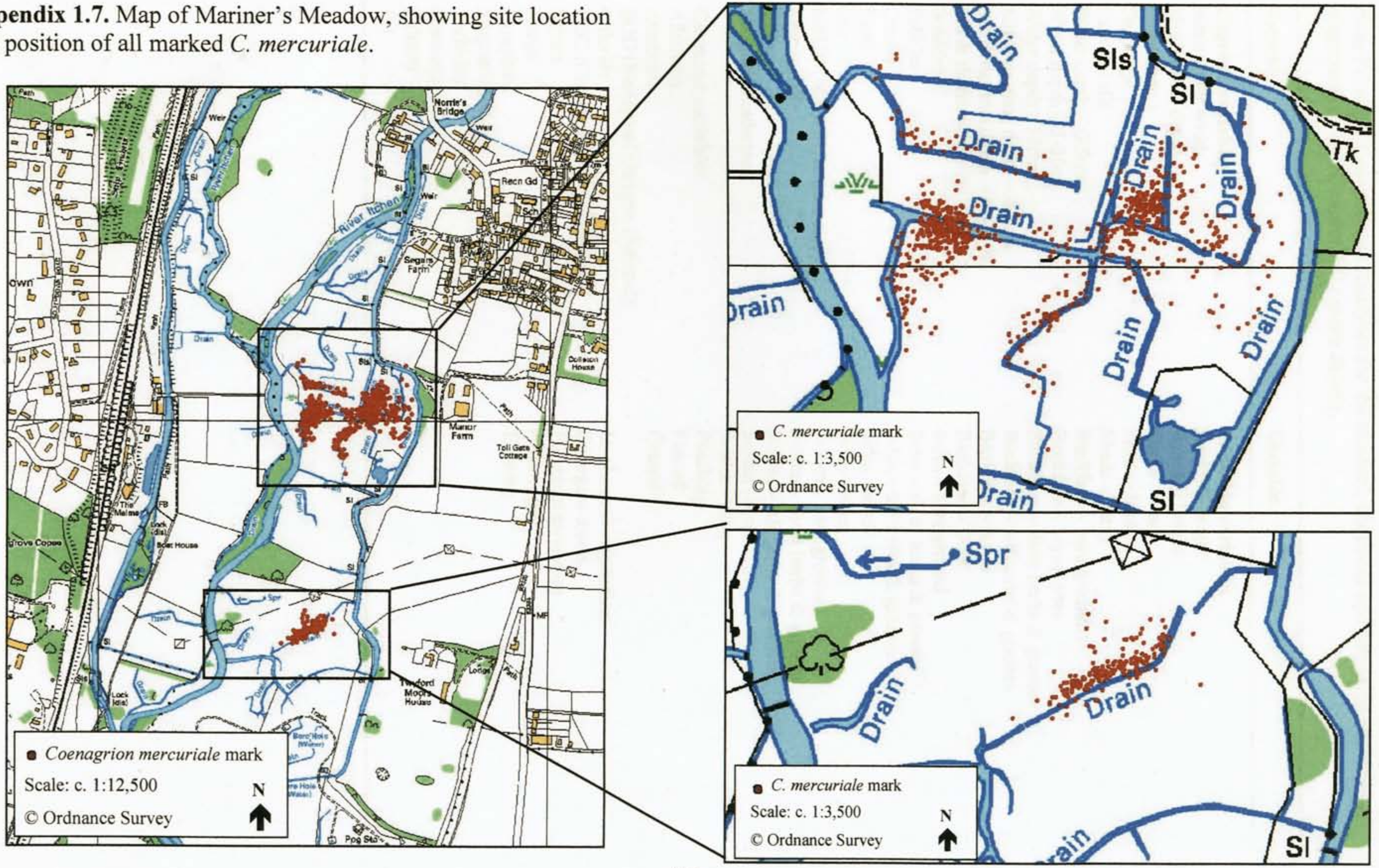
**Appendix 1.5.** Map of West Horton Farm showing location of all marked *C. mercuriale*. Note location of railway embankment.



**Appendix 1.6.** Map of Highbridge showing site location and position of all marked *C. mercuriale*.



**Appendix 1.7.** Map of Mariner's Meadow, showing site location and position of all marked *C. mercuriale*.



**Appendix 2.1.** Habitat variables measured at each location and used as potential predictors of larval *C. mercuriale* occurrence and abundance. Before use in GLMs, variables were input into three Principal Components Analyses for the channel, chemical and bankside variables respectively. See Chapter 7 for more details.

**Variable**

**Channel variables**
Mean water width
Mean water depth
Mean flow
Discharge
Exposed silt
Water depth – 0-5cm
Water depth – 5-30cm
Water depth >30cm
Silt & detritus depth – 0-5cm
Silt & detritus depth – 5-30cm
Silt & detritus depth – >30cm
Boulders
Pebbles
Gravel
Sand
Silt
MSUB (Mean SUBstrate size)
Run or riffle
Glide
Marginal deadwater

**Chemical variables**
Alkalinity
Ammonia
BOD (Biological Oxygen Demand)
Chloride
COD (Chemical Oxygen Demand)
Nitrate
Nitrite
Phosphate
Suspended solids
Turbidity
Conductivity
Salinity
PH

**Variable**

**Bankside variables**
Bankfull height
Banktop height
Shade - none
Shade - broken
Shade - heavy
Bankface – bare ground
Bankface – bryophytes
Bankface – short herbs & grasses
Bankface – tall herbs & grasses
Bankface – scrub
Bankface – trees
0-5m – bare ground
0-5m – short herbs & grasses
0-5m – tall herbs & grasses
0-5m - scrub
0-5m - trees
5-50m – bare ground
5-50m – short herbs & grasses
5-50m – tall herbs & grassses
5-50m - scrub
5-50m - trees
Poaching
Fenced
Grazed

**In-channel vegetation**
Emergent dicots
Emergent monocots
Submerged
Floating

**Appendix 2.2.** Metal and pesticide variables measured at 15 locations in the summer sampling season of the larval field study. See Chapter 7 for more details.

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**Variable**

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**Metals**
Calcium
Copper
Iron
Magnesium
Sodium
Zinc

**Organo-chloride pesticides**
Aldrin
Dieldrin
Endrin
Isodrin
Hexachlorobenzene (HCB)
Hexachlorobutadiene (HCBD)
Hexachlorocyclohexane (alpha)
Hexachlorocyclohexane (beta)
Hexachlorocyclohexane (delta)
Hexachlorocyclohexane (gamma)
PCB 28
PCB 52
PCB 101
PCB 118
PCB 138
PCB 153
PCB 180
DDT (o-p)
DDT (p-p)
Endosulphan (alpha)
Endosulphan (beta)
Heptachlor
Trifluralin

**Variable**

**Organo-phosphorus pesticides**
Carbophenothion
Dichlorvos
Fenitrothion
Malathion
Parathion (Parathion-ethyl)
Demeton (Demeton-S-Methyl)

**Phenoxyalkanoic herbicides**
Dichlorprop
MCPA
MCPB
Mecoprop
Trichlorophenoxyacetic Acid (2,4,5)
24D

**Triazine & conazole herbicides**
Atrazine
Simazine
Propazine

**Redlist Aromatic solvents**
Benzene (1,2,3 Trichlorobenzene)
Benzene (1,2,4 Trichlorobenzene)
Benzene (1,3,5 Trichlorobenzene)

**Extended ECD**
Triallate

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