

using science to create a better place

Conservation requirements of the Southern Damselfly in chalkstream and fen habitats

Science Report SC000017/SR

The Environment Agency is the leading public body protecting and improving the environment in England and Wales.

It's our job to make sure that air, land and water are looked after by everyone in today's society, so that tomorrow's generations inherit a cleaner, healthier world.

Our work includes tackling flooding and pollution incidents, reducing industry's impacts on the environment, cleaning up rivers, coastal waters and contaminated land, and improving wildlife habitats.

This report is the result of research commissioned and funded by the Environment Agency's Science Programme.

Published by:

Environment Agency, Rio House, Waterside Drive, Aztec West,
Almondsbury, Bristol, BS32 4UD
Tel: 01454 624400 Fax: 01454 624409
www.environment-agency.gov.uk

ISBN: 1 84432 431 1

© Environment Agency

May 2005

All rights reserved. This document may be reproduced with prior permission of the Environment Agency.

The views expressed in this document are not necessarily those of the Environment Agency.

This report is printed on Cyclus Print, a 100% recycled stock, which is 100% post consumer waste and is totally chlorine free. Water used is treated and in most cases returned to source in better condition than removed.

Further copies of this report are available from:
The Environment Agency's National Customer Contact Centre by emailing enquiries@environment-agency.gov.uk or by telephoning 08708 506506.

Author: J.R. Rouquette

Dissemination status: Publicly available

Keywords:

Southern Damselfly; *Coenagrion mercuriale*; Ecology; Conservation; Chalkstreams; Fens; UK Biodiversity Action Plan.

Research Contractor and Collaborator:

University of Liverpool
Liverpool
L69 3BX
Tel: 0151 794 2000

Environment Agency's Project Manager:

Tim Sykes, Winchester Office

Collaborators:

Countryside Council for Wales
Maes-y-Ffynnon
Penrhosgarnedd
Bangor
Gwynedd
LL57 2DW
Tel: 0845 1306229

English Nature
Northminster House
Peterborough
PE1 1UA
Tel: 01733 455000

Science Project reference: SC000017

Science at the Environment Agency

Science underpins the work of the Environment Agency, by providing an up to date understanding of the world about us, and helping us to develop monitoring tools and techniques to manage our environment as efficiently as possible.

The work of the Science Group is a key ingredient in the partnership between research, policy and operations that enables the Environment Agency to protect and restore our environment.

The Environment Agency's Science Group focuses on five main areas of activity:

- **Setting the agenda:** To identify the strategic science needs of the Environment Agency to inform its advisory and regulatory roles.
- **Sponsoring science:** To fund people and projects in response to the needs identified by the agenda setting.
- **Managing science:** To ensure that each project we fund is fit for purpose and that it is executed according to international scientific standards.
- **Carrying out science:** To undertake the research itself, by those best placed to do it – either by in-house Environment Agency scientists, or by contracting it out to universities, research institutes or consultancies.
- **Providing advice:** To ensure that the knowledge, tools and techniques generated by the science programme are taken up by relevant decision-makers, policy-makers and operational staff.

Professor Mike Depledge Head of Science

Contents

Executive summary.....	iv
1. Introduction.....	1
1.1 Conservation of insects and Odonata.....	2
1.2 The biology and ecology of the Southern Damselfly.....	3
1.2.1 Species description.....	3
Box 1.1 Southern Damselfly mercury marks.....	5
1.2.2 Habitat.....	6
1.2.3 Life history.....	6
1.3 Distribution and status.....	7
1.4 Conservation.....	10
1.5 Report overview.....	11
2. The Southern Damselfly in calcareous habitats.....	13
2.1 The Southern Damselfly in mainland Europe.....	14
2.1.1 Germany.....	14
2.1.2 France.....	18
2.1.3 Belgium.....	20
2.1.4 Spain.....	21
2.2 The Southern Damselfly in calcareous habitats in the UK.....	21
2.2.1 Introduction to the Test and Itchen Valleys and the historical context.....	21
2.2.2 The Itchen Valley.....	22
2.2.3 The Test Valley.....	30
2.2.4 Oxfordshire.....	31
2.2.5 Anglesey.....	33
3. Adult movement patterns.....	35
3.1 Introduction.....	35
3.2 Methods.....	37
3.2.1 Study sites.....	37
3.2.2 Mark-release-recapture (MRR) survey.....	38
3.2.3 Data analysis.....	38
3.3 Results.....	39
3.3.1 Numbers marked and recaptured.....	39
3.3.2 Movement patterns.....	41
3.3.3 Factors affecting movement.....	43
3.3.4 The effect of Southern Damselfly population density on distance moved.....	47
3.3.5 Investigation of the direction of each movement.....	49
3.3.6 Are motorway and railway bridges barriers to dispersal?.....	50
3.4 Discussion.....	51
3.4.1 Numbers recaptured and sex ratio.....	51
3.4.2 Movement patterns.....	52
3.4.3 Factors affecting movement and dispersal.....	53
3.4.4 The effect of Southern Damselfly population density on distance moved.....	55
3.4.5 Investigation of the direction of each movement.....	56
3.4.6 Are motorway and railway bridges barriers to dispersal?.....	57
3.4.7 Conservation implications.....	57
4. Adult habitat associations.....	59
4.1 Introduction.....	59
4.2 Methods.....	59

Box 4.1 Statistical analysis.....	61
4.3 Results.....	63
4.3.1 Southern Damselfly density.....	63
4.3.2 Habitat associations.....	63
4.3.3 Effects of local population density.....	65
4.3.4 Final model.....	65
4.3.5 Effect of habitat and density on movement.....	66
4.4 Discussion.....	67
4.4.1 Habitat associations.....	67
4.4.2 Local population size and habitat selection.....	68
4.4.3 Southern Damselfly movement.....	69
4.4.4 Methodological considerations.....	69
4.4.5 Conservation implications.....	70
5. Adult roosting site selection	71
5.1 Introduction.....	71
5.2 Methods.....	72
5.3 Results.....	74
5.4 Discussion.....	76
5.4.1 Method and recapture rate.....	76
5.4.2 Behaviour and habitat.....	77
5.4.3 Conservation implications.....	78
6. Macroinvertebrate communities associated with late instar Southern Damselfly larvae	80
6.1 Introduction.....	80
6.2 Methods.....	81
6.2.1 Study sites.....	81
6.2.2 Field and laboratory methods.....	82
Box 6.1 Statistical analysis.....	83
6.3 Results.....	83
6.3.1 Number of locations and abundance of Southern Damselfly.....	83
6.3.2 Are there differences in the invertebrate communities at sites in the Itchen and Test Valleys with and without Southern Damselfly?.....	89
6.3.3 What are the species that are the best indicators of Southern Damselfly?.....	91
6.3.4 Which species correlate with Southern Damselfly abundance?.....	94
6.3.5 Are the results broadly similar when run at a different taxonomic level?.....	95
6.3.6 How do other measures of the communities compare?.....	98
6.3.7 Seasonal variation.....	99
6.3.8 Oxfordshire.....	102
6.3.9 Anglesey.....	104
6.4 Discussion.....	106
6.4.1 Abundance of Southern Damselfly larvae and methodological issues.....	106
6.4.2 Associated species and community.....	106
6.4.3 Oxfordshire and Anglesey.....	108
6.4.4 Taxonomic level.....	109
6.4.5 Diet of Southern Damselfly larvae.....	109
6.4.6 Conservation implications.....	110
7. Habitat associations of late instar larvae.....	111
7.1 Introduction.....	111
7.2 Methods.....	111
Box 7.1 Statistical analysis.....	113
7.3 Results.....	114
7.3.1 Distribution as a function of habitat – occurrence of Southern Damselfly larvae.....	114
7.3.2 Distribution as a function of habitat – abundance of Southern Damselfly larvae.....	116
7.3.3 Multivariate ordination – vegetation.....	118
7.3.4 Multivariate ordination – habitat.....	121
7.3.5 Oxfordshire and Anglesey.....	124
7.3.6 Metals and pesticides.....	125

7.4 Discussion	125
7.4.1 <i>Habitat associations</i>	125
7.4.2 <i>Why are larvae associated with emergent dicots?</i>	127
7.4.3 <i>Oxfordshire and Anglesey</i>	128
7.4.3 <i>Methodological issues</i>	128
7.4.4 <i>Conservation implications</i>	129
8. Conclusion	130
8.1 The Southern Damselfly in the Itchen and Test Valleys	131
8.2 Ecology of the Southern Damselfly in chalkstream habitats	132
8.3 Status and ecology of the Southern Damselfly in fen habitats	135
8.4 Further work	136
8.5 Monitoring	137
8.5.1 <i>Monitoring of the Southern Damselfly directly</i>	137
8.5.2 <i>Monitoring of Southern Damselfly habitat</i>	137
8.6 Conservation and management	139
8.6.1 <i>The landscape component</i>	139
8.6.2 <i>Habitat creation/recreation</i>	139
8.6.3 <i>Ditch management</i>	140
8.6.4 <i>Bankside management</i>	140
8.6.5 <i>Adjacent land use and water quality</i>	141
References	143
Appendix 1	153
Appendix 2	158
Acknowledgements	160

Executive summary

Background

This report presents the findings of a PhD study investigating the ecology and conservation requirements of the Southern Damselfly, *Coenagrion mercuriale* in chalkstream and fen habitats in the UK.

The Southern Damselfly is a species of conservation concern. Its status in Europe is considered to be 'very vulnerable' and it is threatened over much of its range. It is listed on the EC Habitats and Species Directive and is the only species of dragonfly or damselfly currently given priority status in the UK Biodiversity Action Plan.

Further research into the damselfly's ecological requirements was identified as a key requirement in the Species Action Plan, published in 1995. Since that time, a number of studies have been undertaken, including a doctoral thesis on the ecology of the species in heathland streams (Purse 2001, and published as R&D Technical Report W1-021/TR). However, little work has been carried out on the Southern Damselfly in chalkstream and fen habitats in the UK and so important gaps remain in our knowledge of this species.

Main objectives

The primary aim of this study was to examine the ecology and habitat requirements of this species in its chalkstream and fen habitats. 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.

Fieldwork was performed primarily in the Itchen and Test Valleys in Hampshire (southern England), but also in fen habitat in Oxfordshire and Anglesey.

Results

A large multi-site mark-release-recapture study revealed that the Southern Damselfly was extremely sedentary, with dispersal only occurring between adjoining sites. The median net lifetime movement was 31.9 m and lifetime movements of greater than 500 m were rare. Factors affecting movement are examined and evidence of inverse density dependent movement is provided. It is argued that this latter finding, together with the short distances moved, has profound consequences for the population dynamics and conservation of this species.

Adult Southern Damselfly density and movement were analysed in relation to habitat variables and local population size. 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, 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.

Southern Damselfly 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 slow flow. 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* (fool's water-cress) and *Rorippa nasturtium-aquaticum* (water-cress) 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 Southern Damselflies has also been examined and it has been established that adults are strongly associated with two tussock-forming monocots, *Juncus inflexus* (hard rush) and *Deschampsia cespitosa* (tufted hair grass). Differences in the abundance of these plants have been shown to result in large differences in the number of Southern Damselflies roosting in different parts of the study site.

Conclusions and recommendations

It is concluded that 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, and that these remain the greatest threats to its continued existence. It is argued that successful conservation of the Southern Damselfly will involve active management of existing sites, together with the creation (or recreation) of a series of new sites to reconnect populations. Recommendations regarding the monitoring, conservation and management of the Southern Damselfly are presented and include:

- New habitat should be created within 500 m to 1 km of existing sites, to create a series of 'stepping-stones' that would rejoin existing populations.
- Sluice gates should be installed at some sites to enable proper control over water flow. New ditches created should be shallow and slow flowing throughout, or have ample shallow margins. Bank profiles should be shallow or stepped.
- Ditch management operations should be carried out every few years on existing sites to prevent excessive siltation and vegetation choking the channels. Work should be performed on short sections of ditch on rotation or on one side of the channel only. In all deeper channels shallow berms should be created during dredging work.
- Banksides should be lightly grazed by cattle right to the water's edge. Extensive shading should be avoided.

1. Introduction

Chapter summary

A brief review of the ecology, distribution and conservation of the Southern Damselfly is provided. This reveals that the Southern Damselfly:

- **is a small blue and black damselfly;**
- **breeds on two main habitat types within the UK: small heathland streams and calcareous streams and fens;**
- **is mostly confined to the south and west of Europe and is declining over much of its range;**
- **is rare within the UK, has a fragmented distribution and is thought to have declined in the last century;**
- **is now protected by a number of UK and European laws and conventions, including the EC Habitats Directive and the UK Wildlife and Countryside Act.**

This report presents the findings of a PhD study investigating the ecology and conservation requirements of the Southern Damselfly, *Coenagrion mercuriale*, in chalkstream and fen habitats in the UK. The Southern Damselfly 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 dragonfly or damselfly 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 the Southern Damselfly (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 the UK 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 the Southern Damsfly throughout Europe.

In the remainder of this chapter I will briefly establish the context for a study of dragonfly and damselfly (odonate) conservation, before providing a short review of the biology and ecology of the Southern Damsfly, 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 report.



Figure 1.1. Male Southern Damsfly, *Coenagrion mercuriale*.

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 (butterflies and moths) and Odonata (dragonflies and damselflies) have been particularly well studied. Furthermore, these groups of insects are becoming increasingly popular among 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: the Southern Damselfly.

1.2 The biology and ecology of the Southern Damselfly

1.2.1 Species description

The Southern Damselfly, *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. The Southern Damselfly characteristically possesses a 'mercury' mark on the second abdominal segment, from which it derives its Latin name (Figure 1.1). However, there is remarkable variety in the extent of this mark both within and between sites (see Box 1.1),

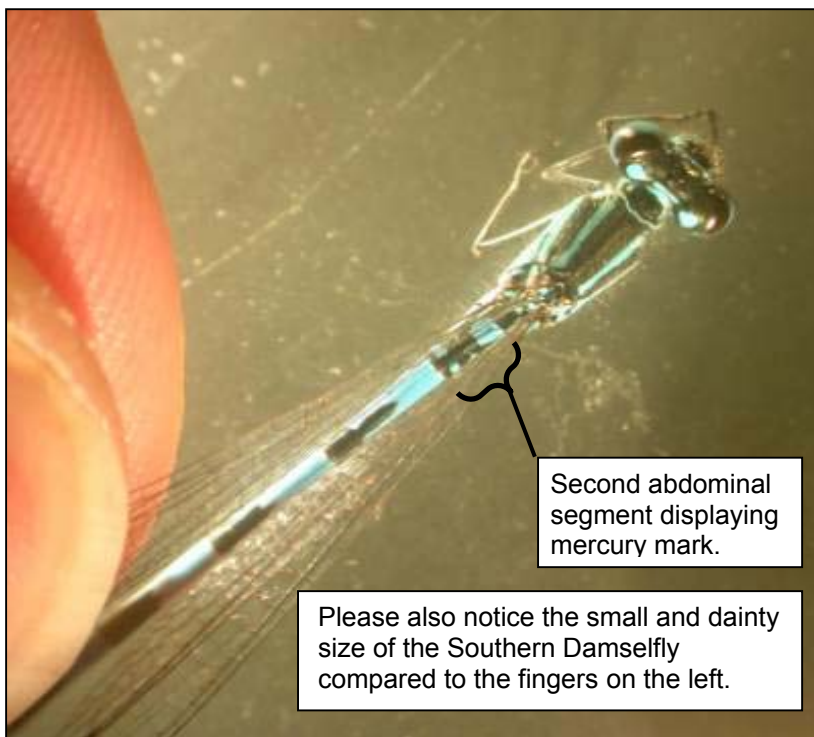
which was first reported by Mayo & Welstead (1983), and has been further investigated by Thompson & Rouquette (2004). Markings along abdominal segments 3–5 and the shape of the anal appendages are more reliable identification tools (Winsland, 1997; Smallshire & Swash, 2004). Furthermore, males are typically 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 (Figure 1.2) 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).



Figure 1.2. Southern Damselfly pair in tandem, showing male claspng the paler coloured female.

Box 1.1: Southern Damselfly mercury marks



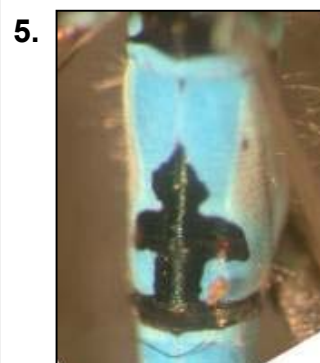
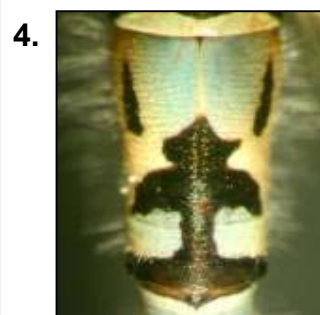
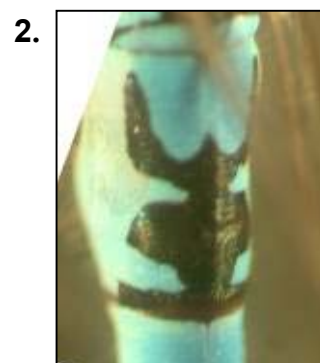
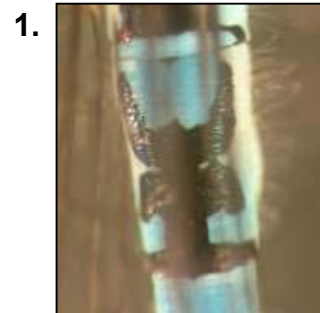
One of the key distinguishing features of male Southern Damselflies is the 'mercury' mark on the second abdominal segment. It resembles the traditional symbol of Mercury, the winged messenger of the Roman Gods, and is the origin of the scientific name (*Coenagrion mercuriale*).

The archetypal mercury mark is shown as number 1 (top right), and this is typical of Southern Damselflies from the New Forest. However, damselflies from the Itchen and Test Valleys show remarkable variety in their mercury marks (first reported by Mayo & Welstead, 1983). The typical range is shown in numbers 1 to 5 (right), which show a reduction in the upper part of the mark in particular. The mechanism determining the degree of mercury mark is unknown.

During this study, each male captured was given a score from 1 to 5 using a pre-determined chart. We have thus been able to investigate differences in the mercury mark, to see if it is indicative of differences in life history, survivorship or dispersal parameters.



The picture on the left shows an extreme form of the mercury mark found on one individual captured at Mariner's Meadow.



1.2.2 Habitat

The Southern Damselfly 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 groundwater 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).

The Southern Damselfly 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 Southern Damselfly 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 three to four weeks to hatch in an aquarium study by Corbet (1957).

Larval development usually takes two years in the UK, and the larvae develop through 13 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 five to eight 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

The Southern Damselfly is mostly confined to the south and west of Europe (Figure 1.3), 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 Southern Damselfly also occur. The subspecies *Coenagrion mercuriale 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 the Southern Damselfly 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 <i>C. m. castellanii</i>
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 <i>C. m. hermeticum</i>
Morocco	Vulnerable	Subspecies <i>C. m. hermeticum</i>
Tunisia	Unknown	Subspecies <i>C. m. hermeticum</i>



Figure 1.3. The worldwide distribution of the Southern Damselfly (from Askew, 1988).

Within the UK, the Southern Damselfly 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 1.4). 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. The populations in the UK are believed to make up a significant proportion of the European total, thereby increasing the significance of conservation of the species in this country.

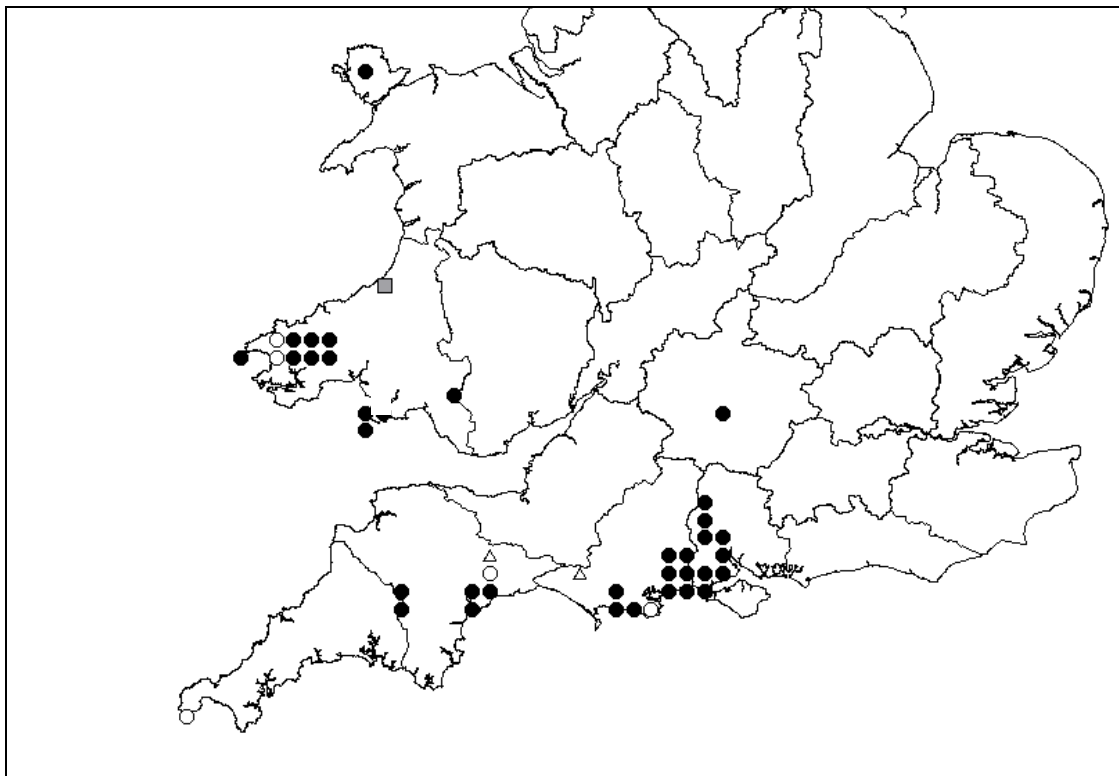


Figure 1.4. The distribution of the Southern Damselfly in the UK at a 10 km grid reference resolution. Symbols indicate the time period in which the species was last recorded at a particular grid reference and represent the years 1975–1999 (closed circles), 1950–1974 (open circles), 1925–1949 (grey squares), and 1900–1924 (open triangles).

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

Studying changes in distribution maps is 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 the Southern Damselfly 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 colonising new sites that are not close to extant sites.

The declining status of the Southern Damselfly 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 Southern Damselfly. 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, the Southern Damselfly 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 hawk – *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). The Southern Damselfly 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 the Southern Damselfly 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 study, with the aim of improving knowledge of the ecological requirements of the species in calcareous habitats.

1.5 Report overview

The aim of this study is to investigate aspects of the ecology of the Southern Damselfly 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 Southern Damselfly 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 adult Southern Damselfly 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 Southern Damselfly larvae. The distribution and abundance of Southern Damselfly larvae is described. In Chapter 6 the associated macroinvertebrate community is investigated, together with issues of taxonomic resolution and Southern Damselfly diet. In Chapter 7 Southern Damselfly 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.

2. The Southern Damselfly in calcareous habitats

Chapter summary

This chapter provides a review of the Southern Damselfly in mainland Europe and then describes the distribution, habitat, and current management of the Southern Damselfly in chalkstream and fen sites in the UK. This reveals that:

- **Southern Damselfly sites in mainland Europe share a number of common habitat features with UK sites.**
- **All sites had a constant year-round water flow, were generally unshaded, and were spring or groundwater influenced.**
- **The Southern Damselfly is highly selective in its choice of sites and vegetation communities at each site. The vegetation at European sites is similar to that at UK chalkstream and fen sites.**
- **UK sites have been the subject of much survey work in recent years, but only one site is monitored on a regular basis.**

In the UK, the Southern Damselfly 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 the Southern Damselfly 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 the Southern Damselfly in calcareous habitats and to introduce my study sites. The review will focus on studies performed outside the UK, particularly from Germany, France and Belgium. I will briefly describe distribution and status of the Southern Damselfly, before providing details of habitat and conservation issues. I will then turn my attention to the calcareous sites in the UK. For each of the main areas I will describe the distribution of the Southern Damselfly, 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 The Southern Damselfly in mainland Europe

2.1.1 Germany

2.1.1.1 *Distribution and status*

The Southern Damselfly 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 were 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*

The Southern Damselfly 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 groundwater springs.

Buchwald (1994) names four principal abiotic factors that are vital in the habitat choice of the Southern Damselfly:

- 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 to 15 cm/sec, while the flow rate was up to 35 cm/sec at the remaining sites.
- 3) Permanent water flow – the Southern Damselfly 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 Southern Damselfly can sometimes be found on small rivers (1.6 –c.6 m) (Sternberg *et al.*, 1999). The pH measured at sites in Baden-Württemberg ranged from 6.6 to 8.5 (Buchwald, 1989; Sternberg *et al.*, 1999).

2.1.1.3 Habitat – vegetation composition

The Southern Damselfly is not linked to any particular 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.

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

Emergent plants:		
<i>Berula erecta</i>	Lesser water-parsnip	40
<i>Mentha aquatica</i>	Water mint	32
<i>Myosotis scorpioides</i>	Water forget-me-not	31
<i>Veronica beccabunga</i>	Brooklime	31
<i>Rorippa nasturtium-aquaticum</i>	Water-cress	28
<i>Veronica anagallis-aquatica</i>	Blue water-speedwell	19
<i>Glyceria fluitans</i>	Floating sweet-grass	18
Submerged and/or floating plants:		
<i>Callitriche stagnalis</i> and <i>platycarpa</i>	Common and various-leaved water-starwort	26
<i>Callitriche obtusangula</i>	Blue-fruited water-starwort	21
<i>Lemna minor</i>	Common duckweed	15
<i>Callitriche (cf.) hamulata</i>	Water-starwort	7
<i>Elodea canadensis</i>	Canadian waterweed	6
<i>Ranunculus trichophyllos</i>	Water-crowfoot	3
<i>Groenlandia densa</i>	Opposite-leaved pondweed	2

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 Southern Damselflies are selecting the habitat rather than individual species.

The Southern Damselfly occupies habitats in Germany with emergent vegetation cover ranging from 3 to 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 1 m in length. When five sections were cut to provide emergent vegetation ranging in cover from 5 to 85%, Southern Damselfly abundance was highest where the coverage was between 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 *et 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 Southern Damselflies. During good weather they primarily used the stream and bankside vegetation, and abundance decreased with increasing distance from the water, up to about 8 m. 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 10 m. 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 100 m from the nearest stream, although 70% were found within a strip 5 m to either side of the streams, and 96% were resting within 25 m 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 Southern Damselfly in Baden-Württemberg were either partially or wholly surrounded by meadow.

Following these results, a protection strip with a minimum width of 10 m 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 the Southern Damselfly 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 fertilisation 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 the Southern Damselfly was absent from 41% of these sites and had declined at a further 16% since the period from 1985 to 1992 (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 100 m recorded at 80% of the sites, and no sites had more than 50 per 100 m.

The Southern Damselfly has been the subject of a species protection programme since 1991 (Röske, 1995). In the first three years of the programme (1991–1993) 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 5–10 m 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 100 m sections, 100 m was cleared on one side in the first year,

an additional 100 m 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 riverbanks at two sites were cut with a manual motor scythe and the cuttings removed. The banks were divided into 10–40 m sections and half were mown. At one site, Southern Damselfly 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 suboptimal weather they occurred more frequently on the bankside and the surrounding land.

2.1.2 France

2.1.2.1 Distribution and status

The Southern Damselfly 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 the Southern Damselfly (Anon., 2004a), a daily maximum of approximately 80 has been recorded along a 600 m 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 & Grand, 1998). Although the distribution and status of the Southern Damselfly 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 the species 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 in Morocco it can colonise sites 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, passing 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 Southern Damselflies 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

The Southern Damselfly 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 southernmost 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 have been considerable changes in land use of the various sections, resulting in a shift in the precise location and abundance of Southern Damselflies (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 1.5 m wide, with a water depth ranging from 1 to 150 cm. 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 Southern Damselflies 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 Southern Damselfly 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 fertilisation 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.

2.1.4 Spain

The species distribution is only partially known, but appears to be widespread across the country (Grand, 1996). It is present in many provinces, but is more common in the northern half of the country. Its status is considered to be vulnerable (Grand, 1996).

Few studies have been carried out into the ecology of the species. The habitat is described as 'small running waters, with sunny areas and a good cover of aquatic vegetation. When it appears in bigger rivers, this is in areas where small rivulets are present; it does not appear in fast waters. In NW Spain it also inhabits permanent eutrophic ponds, with sunny areas and dense aquatic vegetation' (Ochran, 1987, cited in Cordero-Rivera, pers. comm.).

2.2 The Southern Damselfly in calcareous habitats in the UK

The Southern Damselfly 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 chalkstream 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 Southern Damselfly and the populations are relatively small. The populations in the Itchen and Test Valleys, on the other hand, are large, with numerous colonies. My study sites were located in all four areas.

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 stabilising the water temperature and chemical composition. Water is calcareous, typically with a pH of 7.4–8.0, and 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 to 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 (25 mm 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 19th century when they began to fall into disuse (Betty, 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 The Itchen Valley

2.2.2.1 Distribution and status

The first recorded observation of the Southern Damselfly 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 7 km 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 the Southern Damselfly 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 2.2.2.3).

The surveys in 1998 and 1999 also provided some information on the status of each population by categorising 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 they finally petered out just downstream (south) of Compton Lock (north-west 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), the Southern Damselfly 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 2.2.2.3) 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 19 July and so results cannot be compared with later years. However, the transect was 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 the Southern Damselfly 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 Southern Damselflies 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.

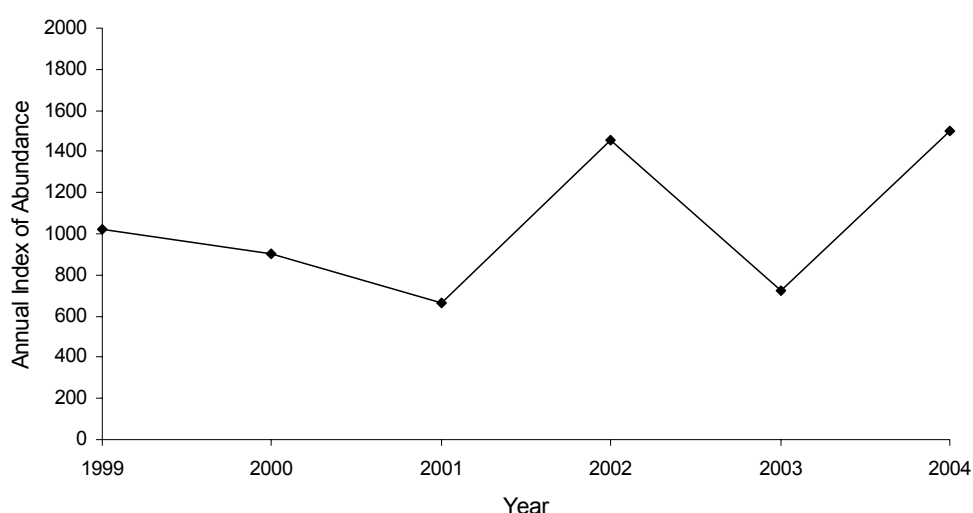


Figure 2.1. Annual Index of Abundance of male Southern Damselflies recorded on weekly transects in the Itchen Valley Country Park (IVCP) (from K.Young, unpublished).

2.2.2.2 Habitat – abiotic factors

Most of the sites in the Itchen Valley, and all those supporting at least a medium population of the Southern Damselfly, 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 the Southern Damselfly 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. The Southern Damselfly 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). Southern Damselflies were found in channels where the velocity ranged from 7.5 to 20.5 cm/s, which can be classified as slow to moderate flows. The pH has been measured as 8.0 (Mayo & Welstead, 1983).

2.2.2.3 Habitat – vegetation composition

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 the Southern Damselfly as shelter and roosting sites (Strange, 1999).

The ditches at the IVCP supporting the Southern Damselfly 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). The Southern Damselfly 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 Southern Damselfly 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.

2.2.2.4 Conservation and management

Southern Damselfly sites on the River Itchen are notified within the River Itchen SSSI and candidate SAC (cSAC), 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 the Southern Damselfly are on privately owned farmland. Until recently, conservation of Southern Damselflies 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 the Southern Damselfly 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 Southern Damselfly 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 the Southern Damselfly 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.).

2.2.2.5 Study sites

The investigations described in this report 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 the Southern Damselfly had previously been recorded (Stevens & Thurner, 1999; Strange, 1999). A selection of sites is illustrated in Figure 2.3. Details of which sites were used for each investigation in this report 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 the Southern Damselfly from this site.

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 2001/02.

Twyford Moors contains three ditches, each very different in terms of habitat and management. One ditch is open to grazing, is 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 steep sided, the banks are low with a narrow fringe of emergent vegetation, and the banktops are mown for use by fishermen (see Figure 2.3).

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. The Southern Damselfly is known to occupy the main river channel here, as well as the ditch network.

No Southern Damselfly 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 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 (see Figure 2.3). 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 Mid 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 (see Figure 2.3).

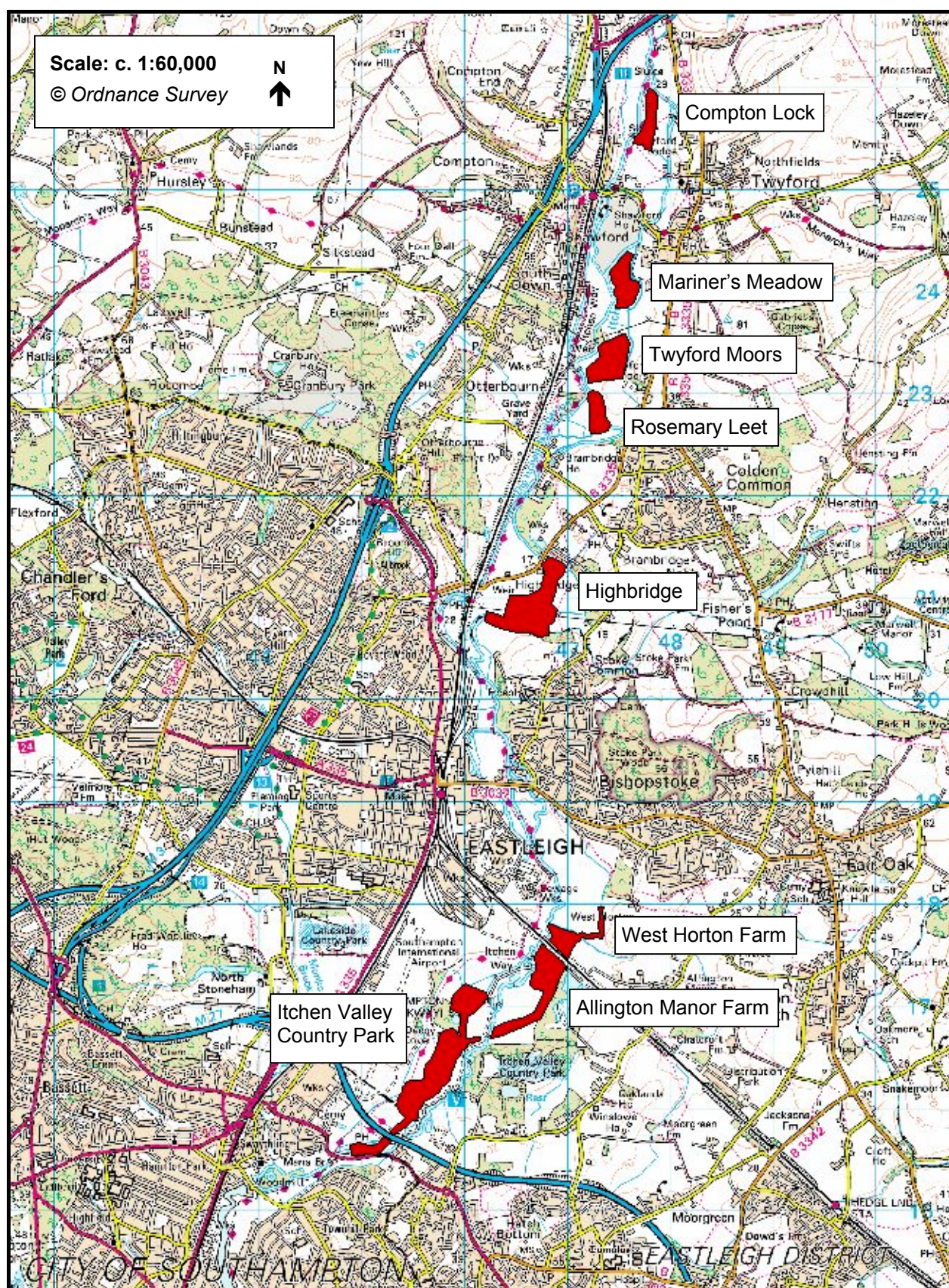


Figure 2.2. Location of study sites within the Itchen Valley



Figure 2.3. A selection of the study sites in the Itchen Valley, showing the range of channel types sampled. Clockwise from top left, these are IVCP – Upper, Allington Manor, Highbridge main river, Rosemary Leet and Highbridge water meadows.

2.2.3 The Test Valley

2.2.3.1 *Distribution and status*

The distribution and status of the Southern Damselfly 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 (8 km 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 latter 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.

2.2.3.2 *Habitat*

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 Southern Damselfly sites have been recorded.

Detailed descriptions of vegetation composition at Southern Damselfly sites in the Test Valley are also lacking. 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).

2.2.3.3 *Conservation and management*

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

2.2.3.4 Study site

Unfortunately, access to the Test Valley is extremely limited. As a consequence, only one area close to King's Somborne was studied, although this was a large site and included the two major Southern Damselfly 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.

2.2.4 Oxfordshire

2.2.4.1 Distribution and status

The Southern Damselfly was first recorded in Oxfordshire as recently as 1991, when a single specimen was caught at Cothill Fen National Nature Reserve (Paul, 1998). It is unlikely that the species had been previously overlooked as the author had made numerous visits to this site between 1986 and 1991, and the area is well visited by entomologists. Four possible explanations were suggested:

- accidental or deliberate introduction;
- a vagrant from Hampshire;
- there is a resident population but at a very low density;
- it was a stray from an undiscovered colony somewhere in the vicinity.

Despite numerous searches, the Southern Damselfly has only been recorded twice again at Cothill Fen since 1991, both in July 1997 (Thurner, 2000). However, the species was recorded at nearby Dry Sandford Pit SSSI in 1996 and has been recorded there each year since. Abundance was initially low, with less than 10 individuals recorded on each visit from 1996 to 1999, but had increased greatly by 2000, with over 20 recorded on separate visits in June and July (Thurner, 2000).

It is probable that the species is not breeding at Cothill Fen, with those seen in 1997 being vagrants from Dry Sandford Pit. However, speculation remains regarding the origin of Southern Damselfly in the area. Dry Sandford Pit was well visited by entomologists prior to the first sightings, and so it is unlikely that a relict population occurred unnoticed. It therefore seems likely that the species first arrived in the area in 1991, or a few years previously, and has since become established. The nearest extant colonies are in the Itchen and Test Valleys in Hampshire but the species is known for its poor flight and limited dispersal abilities. It therefore remains unknown as to whether it naturally colonised the area, perhaps wind blown during a storm, or whether it was introduced by humans.

2.2.4.2 Habitat

Dry Sandford Pit is an abandoned sand quarry, with outcrops of limestone, supporting fen, grassland, scrub and lichen-rich heath. The area occupied by the Southern

Damselfly comprises a complex of spring-fed shallow pools with clear, calcareous water overlying hard calcareous rock on the quarry floor. This supports a rich calcareous fen unique to this part of Oxfordshire. Aquatic vegetation includes *Rorippa nasturtium-aquaticum* (water-cress) and *Apium nodiflorum* (fool's water-cress), surrounded by reedbeds and invading willow, ash and birch scrub. The site is particularly noted for its fine displays of orchids, including *Epipactis palustris* (marsh helleborine) and for its entomological value (EN, 1986; Thurner, 2000).

Cothill Fen supports outstanding examples of nationally rare calcareous fen and moss-rich mire communities together with associated wetland habitats (EN, 1993). The site exhibits succession from open water to fen, scrub and carr, together with an adjacent area of ancient woodland. The Sandford Brook flows through the site, but is fast flowing and is considered to be an unlikely habitat for the Southern Damselfly (Thurner, 2000). However, several springs drain into the brook, and an extensive system of slow flowing ditches traverses the site, probably created during 18th century peat cutting.

Several fen habitats are present within the site: the *Juncus subnodulosus* – *Schoenus nigricans* mire community, *Molinia caerulea* – *Cirsium dissectum* fen meadow, and *Phragmites australis* – *Eupatorium cannabinum* fen. The flora is rich and in turn supports a rich invertebrate fauna including over 25 species listed in the *Red Data Book of Invertebrates* (EN, 1993).

2.2.4.3 Conservation and management

Dry Sandford Pit (8 ha) is owned by the Berkshire, Buckinghamshire and Oxfordshire Wildlife Trust (BBOWT), and the fen area (4 ha) is notified as an SSSI for both its geological and biological interest. Habitat management has included tree thinning/removal around the shallow pools, which has opened up the area to the apparent benefit of dragonflies (Thurner, 2000) and light grazing has recently been introduced onto part of the site.

Cothill Fen is a complex of three separate reserves and their adjoining areas. The whole area (44 ha) is a SSSI and cSAC (Southern Damselfly has not been listed on the citation), and one part of the site is also a National Nature Reserve. The site is owned by a number of different landowners, including English Nature, BBOWT, the National Trust and private landowners. As a result, management work has been undertaken on an *ad hoc* basis, and it has been noted that the habitat has become much more rank and the stream more overgrown by rushes (particularly *Juncus subnodulosus*) in recent years (Thurner, 2000). However, direct management control of the main fen areas by English Nature and BBOWT has recently been obtained. Management work now being undertaken includes reed cutting by hand, and peat cutting in certain areas to re-start the process of fen development. Part of the fen was fenced in 2002 with the intention of instigating a programme of light grazing.

2.2.4.4 Study sites

Three sites were studied in Oxfordshire: Dry Sandford Pit, Parsonage Moor (which is in the central part of the Cothill Fen complex) and Lashford Lane Fen (at the northern end

of this area). None of these areas were grazed at the time of the studies reported here, but grazing has since been introduced onto parts of the former two locations.

2.2.5 Anglesey

2.2.5.1 *Distribution and status*

The Southern Damselfly was first discovered at Cors Erddreiniog in August 1983, the first record of the species from North Wales (Colley, 1983). Since that time, adults have been recorded more or less annually, with numbers peaking at 60+ in July 1993 (Colley, 1993) and 75 in July 1999 (Fowles & Colley, 1999). An annual transect was established in 1996 to monitor changes in the abundance and location of the population (Howe, 1997), although this has not been completed in recent years following a dispute with the landowners. These counts indicate that the population is larger in odd rather than even years (Fowles & Colley, 1999). Cors Erddreiniog remains the only confirmed breeding location for the species in North Wales, but the population has shifted within the site.

Occasional Southern Damselflies have also been recorded at Cors Goch, approximately 2 km to the south-west. However, the habitat at this site is largely unsuitable and there is no evidence of breeding.

2.2.5.2 *Habitat*

Cors Erddreiniog is a large calcareous fen system with three main peat-filled basins extending across two watersheds. The damselfly is found within the Nant Isaf section of the reserve, an area of extensive springs and flushes arising from the underlying Carboniferous Limestone. The water flow at Nant Isaf is continuous throughout the year, slow flowing, and flows over a marl and gravel bed (Colley, 1983). Initially, the damselfly was recorded solely from the main spring fed ditch flowing through Nant Isaf, but shifted in the early to mid 1990s to the main area of springs and flushes approximately 180 m to the south (Colley, 1993; Colley & Howe, 1999). Small populations have also been found in Cors Nant Isaf, approximately 300 m further west (Fowles & Colley, 1999). It is believed that this occurred due to the vegetation along the ditch becoming increasingly rank (Colley & Howe, 1998, 1999). More recently, however, the best area for Southern Damselfly appears to have shifted back to the main spring-fed ditch, following a change in management practices (see below).

The vegetation in Nant Isaf is dominated by *Schoenus nigricans* – *Juncus subnodulosus* mire (NVC group M13b) (Howe, 1997), the same vegetation type found at Cothill Fen (EN, 1993). Furthermore, there is considerable overlap with plant species found at calcareous marsh sites in Germany (Section 2.1.1), and Evans (1989) reported that some plant species occurring in Nant Isaf are common to other areas with Southern Damselfly in the UK.

2.2.5.3 Conservation and management

Cors Erddreiniog is a SSSI and cSAC, although the Southern Damselfly is not a qualifying feature. Much of the site is owned and managed by the Countryside Council for Wales (CCW) as a National Nature Reserve, although Nant Isaf (7 ha) is owned by a syndicate and subject to a management agreement with CCW (CCW, 1988). Nant Isaf is grazed by a mixture of cattle, ponies and sheep throughout the year, although grazing intensity is variable.

At the end of the 1990s, the conservation status of the site was judged to be unfavourable and declining (Fowles & Colley, 1999) as the flushes were becoming increasingly rank and overgrown. To rectify this, grazing was increased during winter 1998/99, with 8 ponies on site until April and 32 cattle grazing from July until the middle of September (Fowles & Colley, 1999). In addition, dense stands of *Juncus subnodulosus* and *Schoenus nigricans* were trimmed and raked off during winter 1997/98 and 1998/99 (Colley & Howe, 1999; Fowles & Colley, 1999). It is believed that this management was successful at creating and maintaining a more open sward, although large stands of rank vegetation remained and the central ditch was in need of dredging (Colley & Howe, 1999; Fowles & Colley, 1999). Clearly, management efforts will need to be maintained for some time.

2.2.5.4 Study sites

Access to Nant Isaf is limited due to an ongoing dispute between the statutory agency and the landowners, regarding management of the site. I was therefore only able to visit this site on an occasional basis. During visits, the whole of the Nant Isaf area was investigated, together with the nearby area of Cors Nant Isaf. Cors Goch, where Southern Damselflies have occasionally been recorded, was also visited, but was deemed to be largely unsuitable.

3. Adult movement patterns

Chapter summary

This chapter examines patterns of movement in mature adult Southern Damselflies, following a large multi-site mark-release-recapture study performed in the Itchen Valley. Key findings were:

- **In total 8708 Southern Damselfly were marked and 2523 individuals were recaptured at least once. 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 species was found to be extremely sedentary, with dispersal only occurring between adjoining sites. The median net lifetime movement was 31.9 m and 65.7% of individuals moved less than 50 m in their lifetime. Movements of greater than 500 m were rare and only 0.1% of individuals moved over 1000 m.**
- **Time between capture and recapture, season and order of movement all had an effect on movement, but sex and age did not.**
- **Evidence of inverse density dependent movement is provided. Damselflies first captured at high density sub-sites (optimal habitat) move less far than those captured at low density sub-sites (suboptimal habitat). This finding, together with the short distances moved, has profound consequences for the population dynamics and conservation of this species.**
- **A motorway and railway did not prove to be barriers to movement, but habitat close to the motorway bridge appears to have been damaged.**

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 mark-release-recapture (MRR) methods are used to directly measure movement of mature adult Southern Damselflies. Previous studies of Southern Damselfly have suggested that most individuals are extremely sedentary, although a few move distances of up to about 1 km (Hunger & Röske, 2001; Purse *et al.*, 2003). The study system used here is, however, much larger in scale, includes several sites, and enables a comparison of two areas of contrasting landscape structure. As explained in the previous chapter, 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 an investigation into the potential of these structures as barriers to movement.

The aims of this study were to 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 sites

This study was conducted in the Itchen Valley at Mariner's Meadow, Highbridge, West Horton, Allington Manor, and three sub-sites within the Itchen Valley Country Park (IVCP). Site descriptions are provided in Section 2.2.2.5. In total, 7.65 km of ditch was surveyed at the seven sites and sub-sites. A railway line on an embankment crosses between West Horton and Allington Manor, passing over two stream channels and the main river on high arched bridges. The lower section of the IVCP is split in two by a motorway, crossing a large stream channel as well as the main river channel on 50 m wide, low concrete bridges. We were therefore able to investigate their potential effects as barriers to movement. These bridges are shown in Figure 3.1.

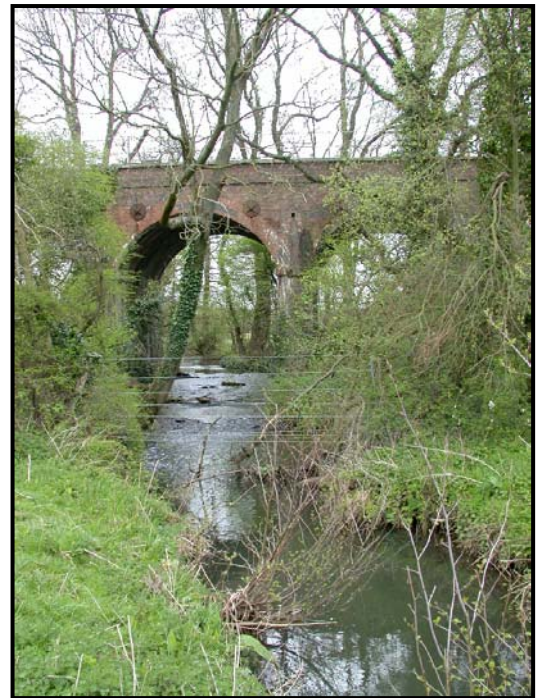


Figure 3.1. The bridges that bisected the study sites in the Itchen Valley. Clockwise from top left these are: the railway bridge crossing the west stream and river between Allington Manor and West Horton, the railway bridge over the east channel at the same location, and the motorway bridge that bisected IVCP – Lower.

3.2.2 Mark-release-recapture (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. Southern 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 paint from a paint marker pen on the thorax. We sampled every day for five weeks from 12 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. We noted whether females were normal or andromorph in colouration (see Section 1.2.1). Secondly, the mercury mark of the males was recorded on a 5-point scale (see Box 1.1). 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.

3.2.3 Data 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 50 m x 50 m 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 50 m 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 Southern Damselfly 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 Southern Damselfly 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 Southern Damselfly 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 and maps showing the location of all marked Southern Damselflies are shown in Appendices 1.1–1.7. 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.

As each site contained similar lengths of stream the data presented in Table 3.1 and Appendices 1.1–1.7 reflect the strength of the Southern Damselfly 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 the damselfly 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 five 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).

Table 3.1. Total numbers of adult Southern Damselfly 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

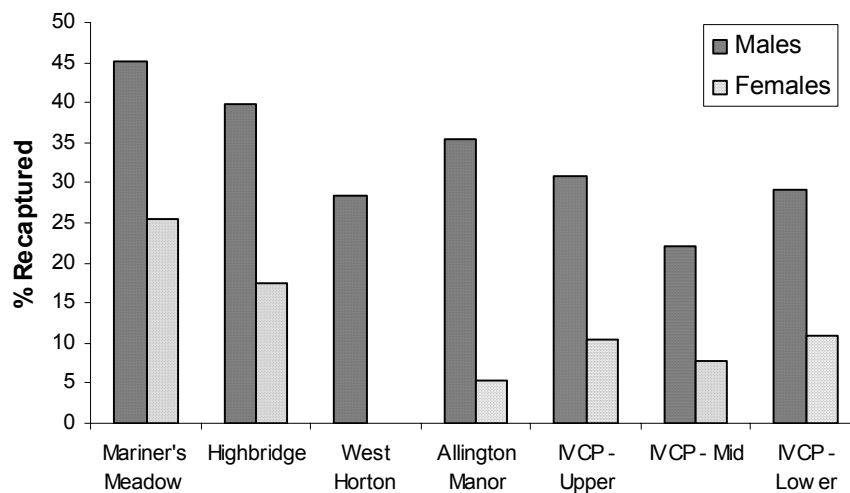


Figure 3.2. The percentage of marked individuals recaptured on at least one occasion at each site. Males and females are shown separately.

3.3.2 Movement patterns

A total of 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 31.9 m (geometric mean = 33.2 m, $n = 2523$), and 65.7% of individuals moved less than 50 m 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 50 m in their lifetime, while only about 40% move that distance at Allington Manor. Furthermore, the maximum distance moved by any individual was 554 m at Mariner's Meadow and 406 m at Highbridge, but was 1374 m at IVCP – Upper and 1790 m at IVCP – Mid. This is illustrated in Figure 3.3, which shows the percentage of animals moving in 25 m distance categories for Mariner's Meadow, Highbridge and the Lower Itchen Complex.

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 (25.7 m) and highest at Allington Manor (68.1 m). 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.

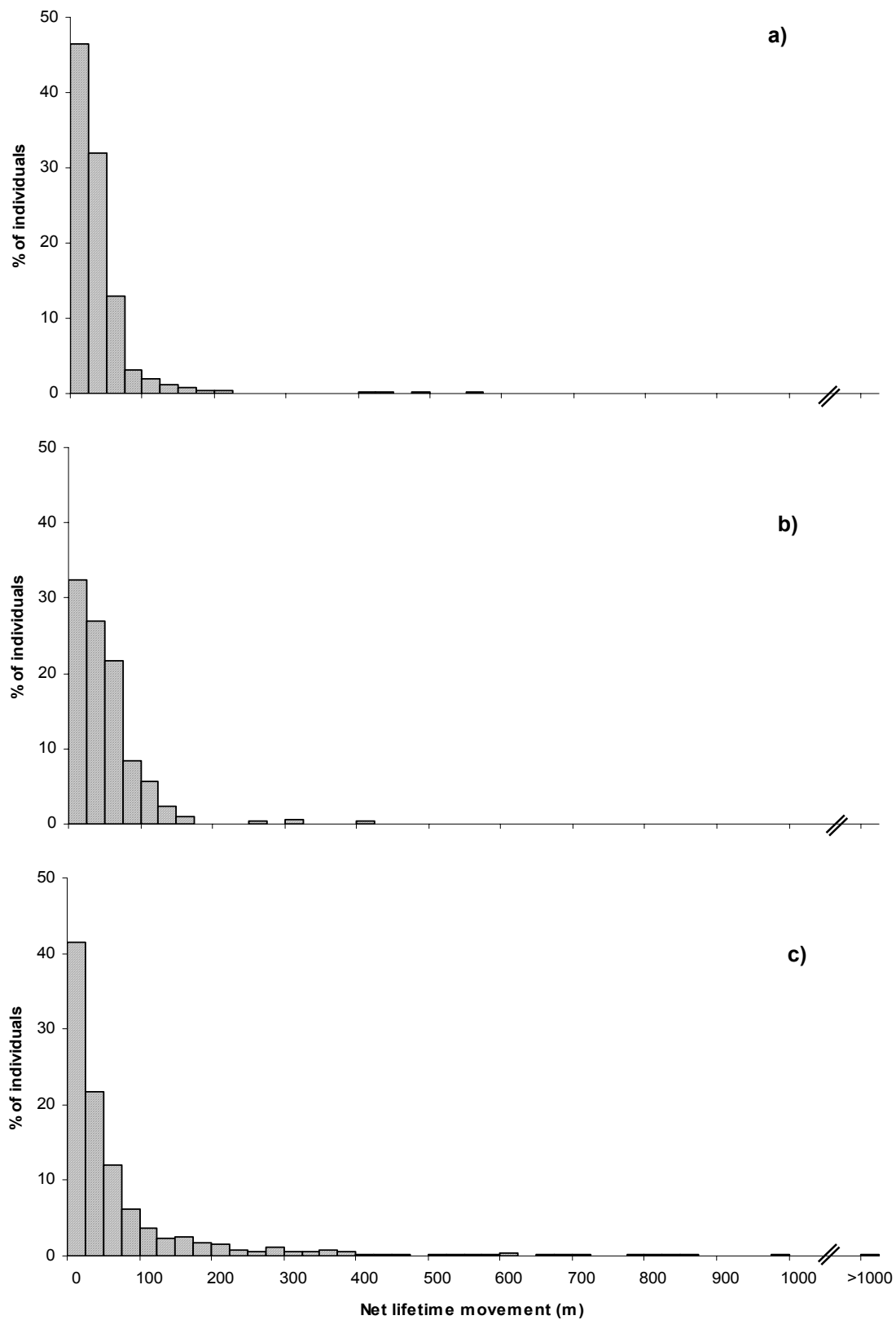


Figure 3.3. Percentage distribution of net lifetime movements (L) in 25 m distance categories for (a) Mariner's Meadow, (b) Highbridge and (c) Lower Itchen Complex, all to the same scale. Sample sizes are 480, 296 and 1747 individuals respectively.

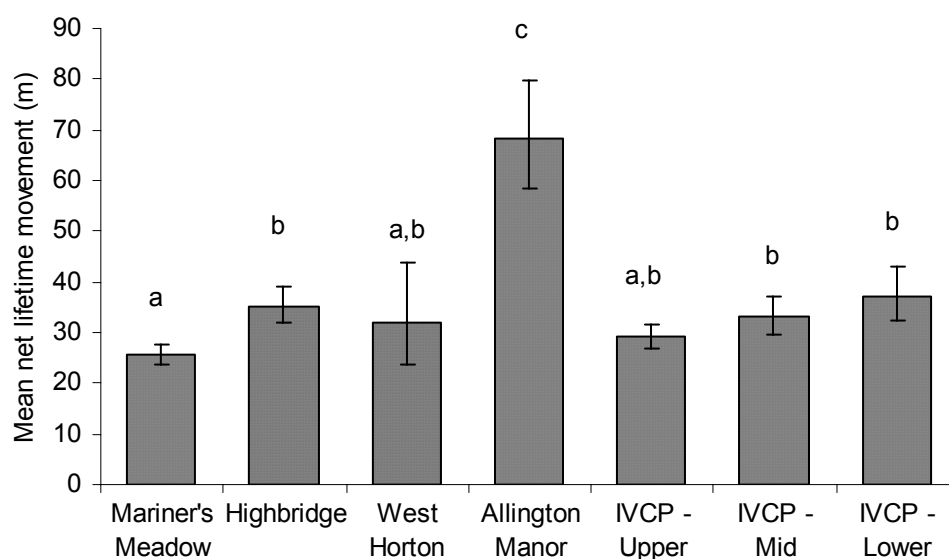


Figure 3.4. Net lifetime movement (L) at each site (bar shows mean and 95% confidence interval). Net lifetime movement is significantly different across the sites (1-way ANOVA: $F = 23.9$, d.f. = 6,2516, $p < 0.001$). *a,b,c* Means displaying the same letter are not significantly different at the 5%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

3.3.3 Factors affecting movement

A number of variables had a significant effect on Southern Damselfly 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), 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.

Table 3.2. Significant predictors of mean Southern Damselfly movement (\log_{10}) derived from a multiple regression model.

Model summary	Variable	<i>t</i>	<i>p</i>	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
	Season ²	-2.79	**	-0.0002	0.0001
	Constant	43.18	***	1.374	0.0318

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.

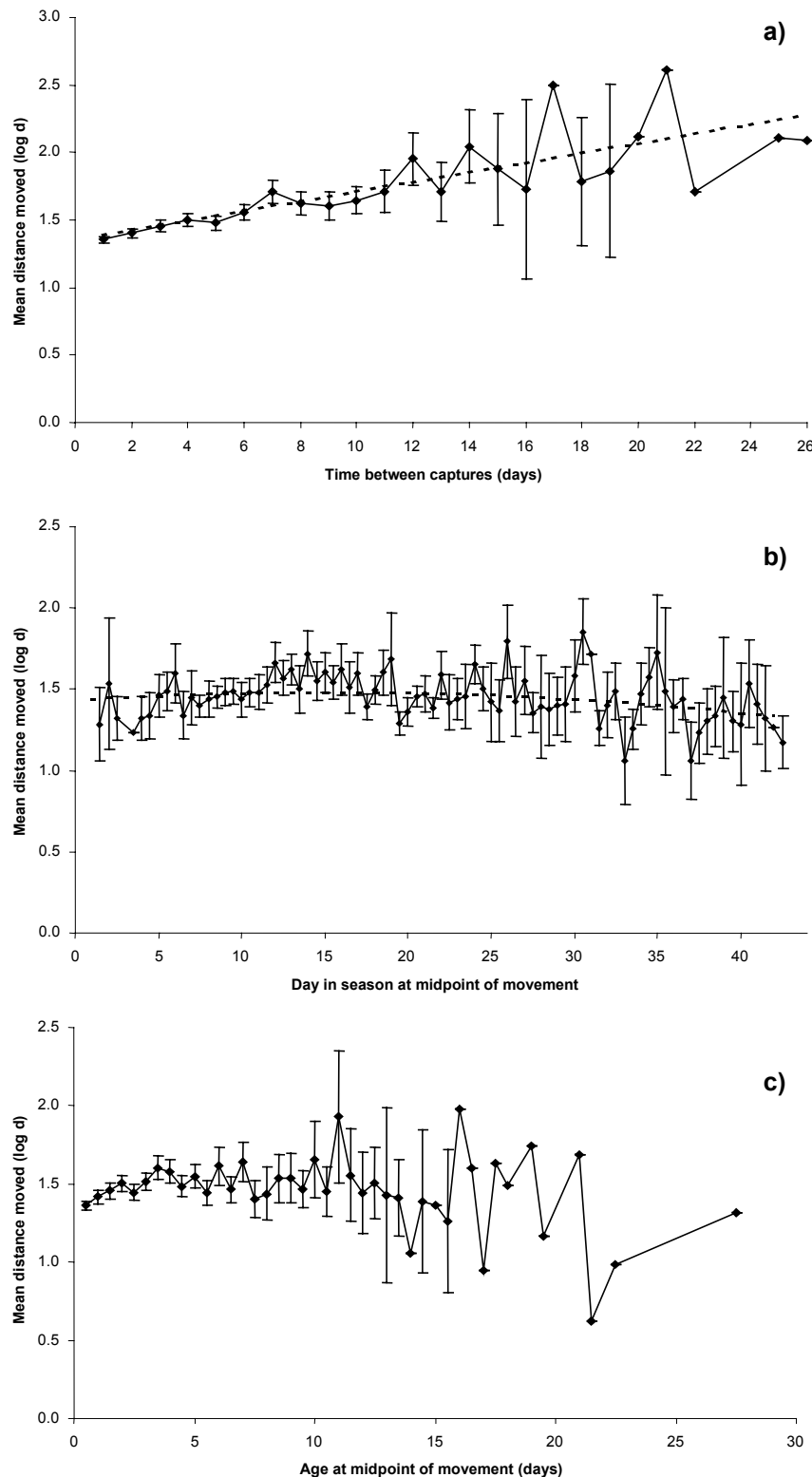


Figure 3.5. Effect of (a) time, (b) season and (c) age on mean distance moved (log d). Vertical lines show 95% confidence intervals, which are not included for samples with less than five individuals. Dotted lines on (a) and (b) are back-transformed regression lines derived from a multiple regression 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 (12 June 2001). Age is taken as the midpoint between first capture and each recapture.

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 ($r^2 = 0.121$).

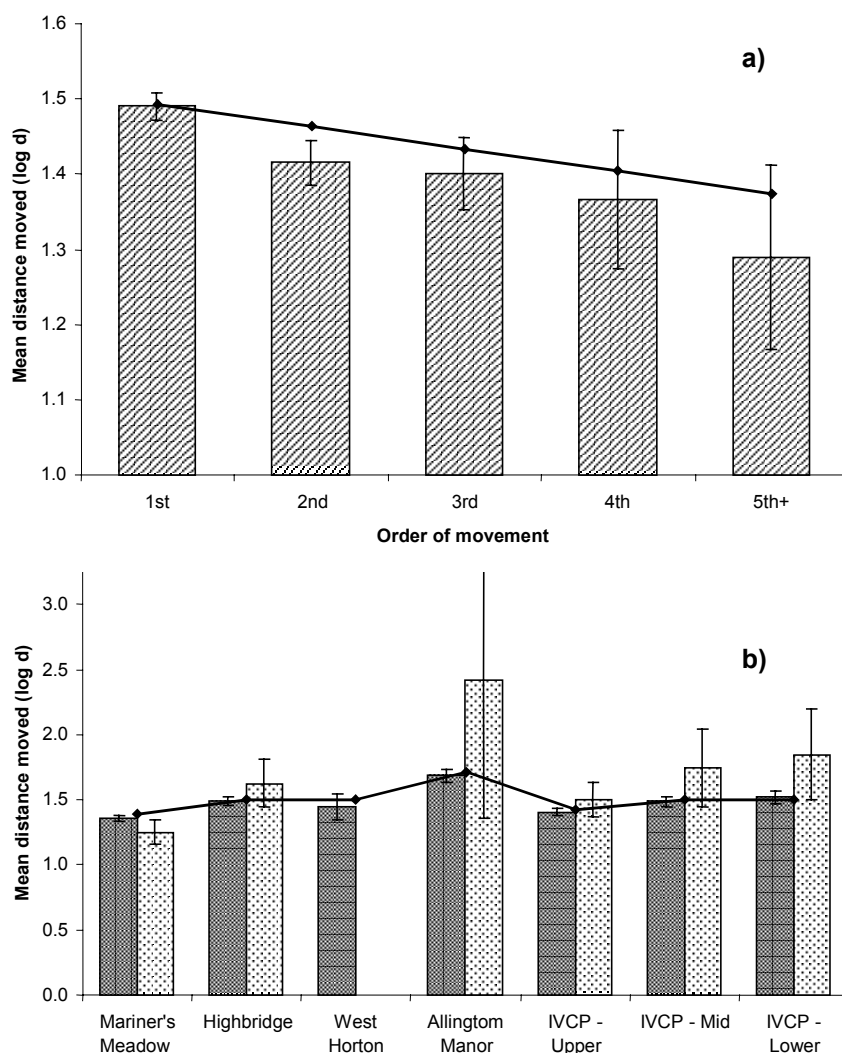


Figure 3.6. Effect of (a) order of movement (1st movement, 2nd movement etc.) and (b) site and sex on mean distance moved (log *d*). Males are shown with dark bars, females with light bars. Vertical lines show 95% confidence intervals. The solid lines are back-transformed regression lines derived from 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.

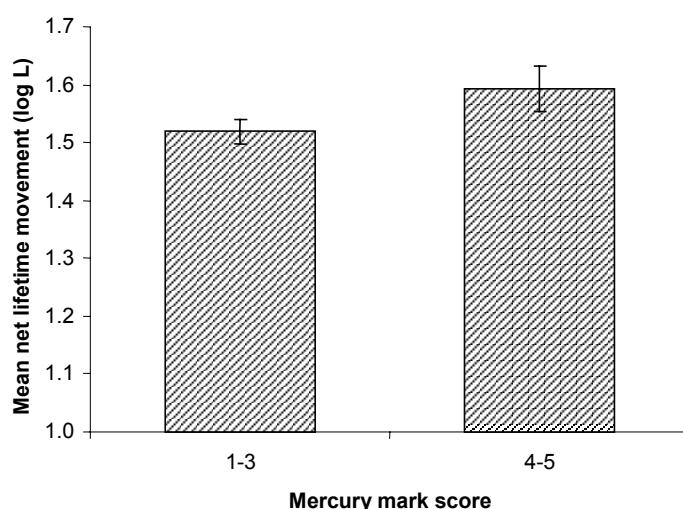


Figure 3.7. Effect of mercury mark on mean net lifetime movement (log L), with 95% confidence intervals. Net lifetime movement is significantly different between the two groups ($t = -3.23$, d.f. = 2361, $p = 0.001$). Mercury mark is the characteristic pattern found on the second abdominal segment of male Southern Damselflies, 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 are present at the two northern sites of Mariner's Meadow and Highbridge. Andromorph females are found throughout most of the Lower Itchen Complex but are much more frequent in the IVCP – Lower section and it is only in this section that their frequency of occurrence is close to that observed in the New Forest. The mean frequency at eight 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 Southern Damselfly 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 50 m by 50 m 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 50 m by 50 m sections at each site, the results of 1-way ANOVAs to test for differences in distance moved from different sections, and regressions of mean distance moved by damselflies marked in each section against density.

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

1-way ANOVAs 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).

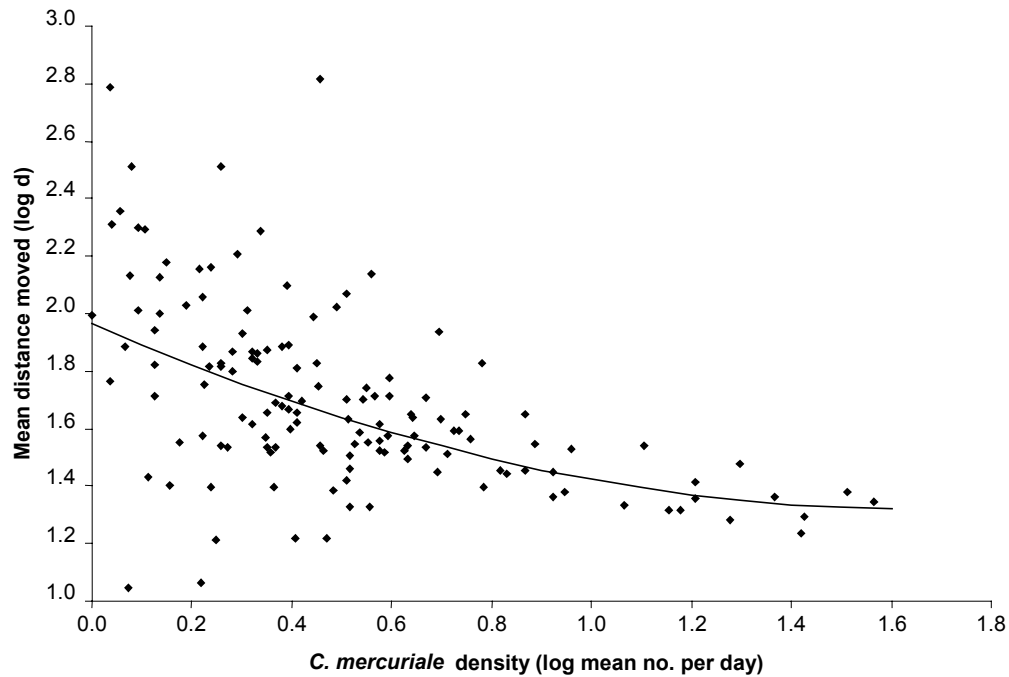


Figure 3.8. Regression of mean distance moved (log d) against density for each 50 m by 50 m section. Density is calculated as the average number of individuals (marks and recaptures) seen in each section per day. The solid line is the weighted regression line ($r^2 = 0.578$, $F = 93.76$, $p < 0.001$).

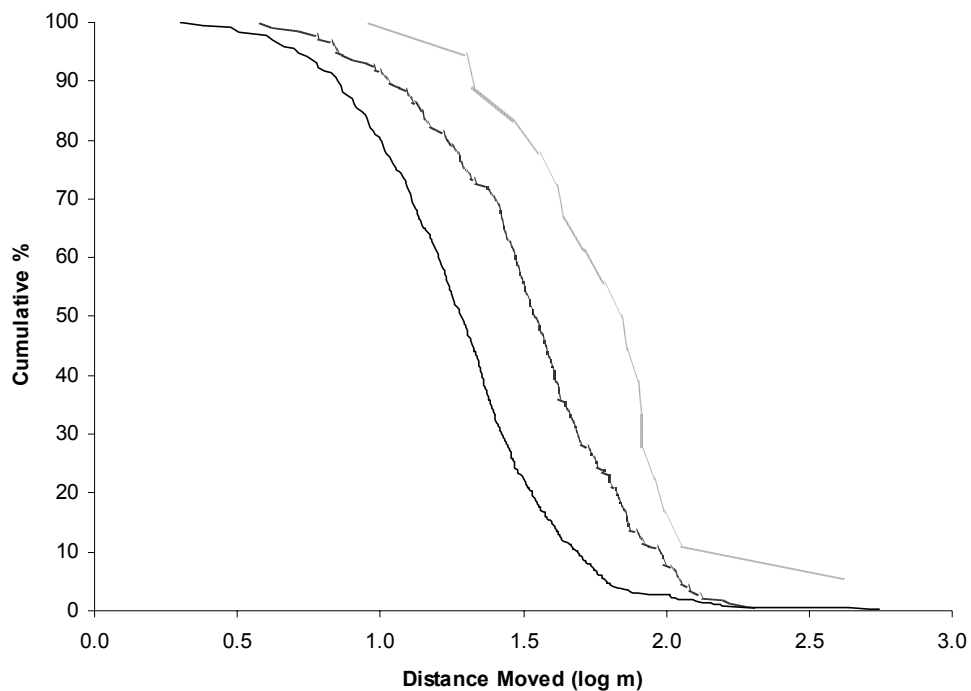


Figure 3.9. Cumulative distance moved by Southern Damselflies in three density categories. The lightest line represents sections with a mean of less than 1 Southern Damselfly per day, the medium-weight line 1–10 individuals and the thickest line represents sections with more than 10 individuals per day.

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 seven and eight 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 Southern Damselfly.

Our results indicate that the greater the density of Southern Damselflies, 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 Southern Damselflies 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 Southern Damselflies 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.

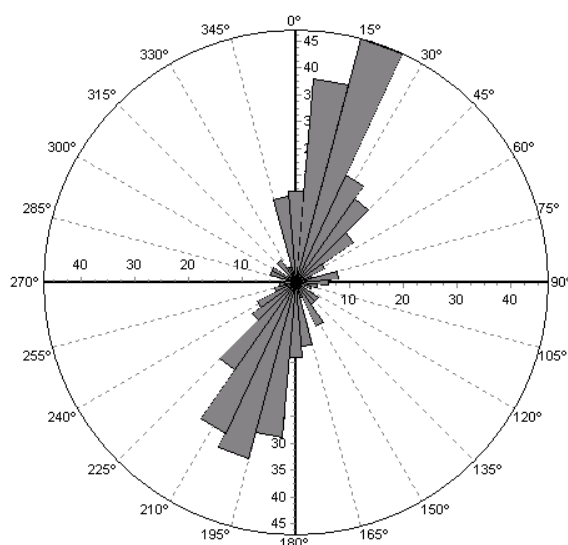


Figure 3.10. Rose diagram showing direction of movement of Southern Damselflies at Highbridge. The mean angle of movement is along the 15°–195° axis. Each bar represents 10°.

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 nine sections and downstream in five. However, in all 14 cases, movement was towards a higher density neighbouring area. If a Bonferroni correction was applied to the significance level, seven sections remained significant ($p < 0.0012$), where movement was predominantly upstream in four cases and downstream in three. There are seven discrete patches within our study sites where density is high (> 10 individuals per 50 m per day). When ten of the neighbouring sections were examined, damselflies moved significantly more frequently in the direction of the high density area in seven 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 eight were from Allington Manor to West Horton. All 20 individuals were male. Sixteen crossed during their first recorded movement, three during their second movement, and there was one case each of crossing during the third and fourth movements. The mean distance moved was 288 m and the maximum movement was 674 m. The individuals that crossed did not differ in any way from the remainder, except in terms of distance travelled.

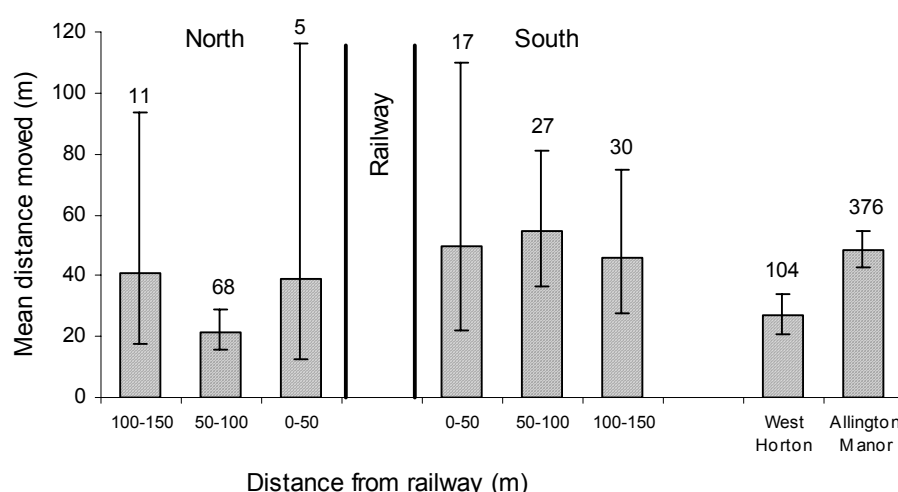


Figure 3.11. Diagrammatic representation of the railway crossing, showing the effect of distance from railway on mean distance moved by Southern Damselflies. The mean distance moved in West Horton (north of the railway line) and Allington Manor (south of the railway line) is shown for comparison. 95%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

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.

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 602 m and the maximum movement was 1374 m. 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 100 m 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 the Southern Damselfly (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 while 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 500 m were rare (1.3% of individuals) and there were only three movements greater than 1000 m (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 1000 m.

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

The Southern Damselfly 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* (the Banded Demoiselle), which occurs in similar habitat to the Southern Damselfly, was reported to have a median movement of 90 m for males and 45 m for females (Schutte *et al.*, 1997), and Stettmer (1996) found that the median movement was about 50 m for both this species and *Calopteryx virgo* (Beautiful Demoiselle). The longest recorded movements were 1725 m (Schutte *et al.*, 1997) and 4 km (Stettmer, 1996). Within the Coenagrionidae, 73% of *Enallagma cyathigerum* (Common Blue Damselfly) were reported to move less than 100 m (Garrison, 1978). This compares to 85% for Southern Damselflies in the present study. Bennett & Mill (1995) reported that approximately 83% of male *Pyrrosoma nymphula* (Large Red Damselfly) and 63% of females moved less than 50 m 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, Southern Damselfly 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 Southern Damselfly, along with IVCP – Upper, and movement was lowest from these two sites. This could provide further evidence of inverse density dependent movement (see Section 4.4). Finally, habitat quality was good at Mariner's Meadow and IVCP – Upper, and correspondingly bad at Allington Manor. Southern Damselflies 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 the Southern Damselfly (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 the Southern Damselfly (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.

The Southern Damselfly 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*, the Black Darter (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 teneral (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 seven species of pond-dwelling odonates, and the same result was reported by Angelibert & Giani (2003) for three pond-dwelling species. Maiden flight behaviour has not been observed in the Southern Damselfly (pers. obs.) but has been observed in *Coenagrion puella*, the Azure Damselfly (Anholt, 1990; D.J. Thompson, pers. comm.). Teneral were not marked in our study because of 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 the Southern Damselfly (Purse, 2001). Sex difference 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* (Blue-tailed Damselfly) 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 aquabilis* (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 Lower Itchen Complex (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).

3.4.4 The effect of Southern Damselfly population density on distance moved

One of the most interesting findings of this study is that Southern Damselfly 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 Southern Damselfly 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 Southern Damselflies 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 was included in our analysis (Chapter 4), density remained a highly significant predictor of Southern Damselfly 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, to 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 (Courchamp *et al.*, 1999; Stephens & Sutherland, 1999; Stephens *et al.*, 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

The Southern Damselfly 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 (mayflies), Plecoptera (stoneflies), and Trichoptera (caddis flies), as it is used to counteract the affect of drifting downstream during the aquatic stage of the life cycle (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 teneral 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, the Southern Damselfly prefers slow flowing marginal habitats (Thompson *et al.*, 2003a; Chapters 4 and 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, alter behaviour through disturbance and avoidance, cause barrier effects and habitat fragmentation, adversely affect adjacent habitat, and increase runoff, sediment loads and pollution (Mader, 1984; Forman & Alexander, 1998). The barrier effect 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 *et al.*, 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. Unfortunately, we were not able to determine which route the Southern Damselflies used to cross the railway and motorway, and whether they flew underneath or over the top of the bridges. It is clear, however, 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 100 m to either side. The channel is deeper and has less emergent vegetation than anywhere else in the IVCP and as a result very few Southern Damselflies 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 50 m to one side.

Perhaps a similar effect is occurring in the Southern Damselfly, 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 Lower Itchen Complex, 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 the Southern Damselfly has implications for its conservation and management. The species requires slow to medium flowing channels,

with shallow margins and abundant emergent vegetation (Chapters 4 and 7). In most of the areas that the Southern Damselfly occupies in the UK, this represents a successional phase that will not last without active management. Indeed, the Southern Damselfly 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 seem to be the case with the Southern Damselfly 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 the Southern Damselfly 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.

4. Adult habitat associations

Chapter summary

In this chapter the association between Southern Damselfly density and movement was analysed in relation to habitat variables and local population size. Key findings were:

- **Mean adjacent population density was the single most important factor determining density.**
- **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.**
- **Mean net lifetime movement was greatest from sections with low density, with smaller than average berms, and with deeper water.**

4.1 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. It becomes even more vital for endangered species, where habitat loss or alteration is often one of the driving forces behind a decline. Habitat creation and management are vital tools in conservation programmes, but will only be successful once detailed knowledge of the precise habitat requirements of the different life stages of a species have been recognised.

The work described in this chapter investigates variation in the density of mature adult Southern Damselflies in relation to habitat variables and local population size in its chalkstream habitat. The aim is to provide management guidelines on the habitat preferences of Southern Damselfly so that sites can be managed to conform to these preferences. This chapter deals with daytime habitat use by mature adult Southern Damselflies, while Chapter 5 examines habitat used by mature adults for night-time roosting. In Chapter 7, the relationship between larval Southern Damselfly and their habitat is studied.

4.2 Methods

This study was conducted in the same locations as the mark-release-recapture (MRR) study described in the previous chapter. Thus it took place in the Itchen Valley at Mariner's Meadow, Highbridge, West Horton, Allington Manor, and three sub-sites within

the Itchen Valley Country Park (IVCP). Site descriptions are provided in Section 2.2.2.5. Habitat and management practices vary considerably between these sites, which enabled us to investigate a wide range of potentially influential factors.

Density of Southern Damselflies was derived from the MRR experiment that was performed in all seven areas in the summer of 2001 (described in the previous chapter). We divided each site into 50 m x 50 m sections and the damselflies marked or recaptured within each section were tabulated. Density was then calculated as the average number of Southern Damselfly seen in that section per day of recording.

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 1 m² 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 10 m from the water's edge. This was converted into two variables, the mean vegetation height from 0 to 1 m and the mean vegetation height from 2 to 10 m from the water's edge.

Only channels with flowing water were surveyed, as it is known that year-round flow is a prerequisite 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.

We used generalised linear models, which are mathematical extensions of linear regression, to assess which habitat variables explained a significant proportion of variation in Southern Damselfly density. We also used this technique to investigate the link between Southern Damselfly movement and these habitat features. Further details of the statistical analyses are provided in Box 4.1.

Box 4.1: Statistical analysis

We used generalised linear models (GLMs; McCullagh & Nelder, 1983; Dobson, 2002) to assess which variables explained a significant proportion of variation in Southern Damselfly density. GLMs are mathematical extensions of linear regression that are able to handle distributions other than the normal. 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. These techniques 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; Rushton *et al.*, 2004).

In our study, mean density of Southern Damselflies 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 Southern Damselflies was aggregated, showing marked under-dispersion 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 $\chi^2/\text{d.f.}$) so that the variance in Southern Damselfly 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; MacNally *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 eight 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 broad-scale spatial autocorrelation.

We also examined whether patterns of Southern Damselfly 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 Southern Damselflies in all adjacent sections. These variables were added to the minimum adequate habitat model.

If habitat is suboptimal, 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. All analyses were performed in SAS release 8.

Table 4.1. Habitat variables measured in each section and used as potential predictors of Southern Damselfly density.

Variable	Description
Physical variables	
Water depth	Mean of three measurements (cm) taken at $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ 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 (θ) where $\tan \theta = \text{width/height}$
Substrate	Composition of bed substrate. Scale: 1 – predominantly silt; 2 – silt and 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. Also used berm width A – narrower half of berms; B – wider half.
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 <i>Apium nodiflorum</i> , <i>Rorippa nasturtium-aquaticum</i> , <i>Veronica</i> spp., <i>Myosotis scorpioides</i> and <i>Mentha aquatica</i>
Emergent monocots	% cover of emergent monocots, principally <i>Glyceria maxima</i> , <i>Phalaris arundinacea</i> , <i>Sparganium erectum</i> , <i>Iris pseudacorus</i> and <i>Carex</i> spp.
Submerged	% cover of submerged plants, <i>Ranunculus</i> spp., <i>Callitriche</i> spp. and others
Floating	% cover of floating plants, principally <i>Lemna minor</i>
Open water	% open water
Bankside vegetation	
Helophyte dicots	% cover of dicots typically associated with water's edge habitat, principally <i>Apium nodiflorum</i> , <i>Rorippa nasturtium-aquaticum</i> , <i>Veronica</i> spp., <i>Myosotis scorpioides</i> , <i>Mentha aquatica</i> , <i>Rumex hydrolapathum</i> and <i>Epilobium</i> spp.
Helophyte monocots	% cover of monocots typically associated with water's edge habitat, principally <i>Glyceria maxima</i> , <i>Phalaris arundinacea</i> , <i>Sparganium erectum</i> , <i>Iris pseudacorus</i> , <i>Carex</i> spp. and <i>Juncus</i> spp.
Forbs	% cover of terrestrial dicots, including <i>Urtica dioica</i> , <i>Montia sibirica</i> , <i>Solanum dulcamara</i> , <i>Rumex acetosa</i> , <i>Cirsium</i> 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 0–1 m	Direct measurement of vegetation height. Mean of four readings taken at water's edge, 0.25, 0.5 and 1 m from edge on both banks
Vegetation height 2–10 m	Direct measurement of vegetation height. Mean of three readings taken at 2, 5 and 10 m from water's edge on both banks

4.3 Results

4.3.1 Southern Damselfly density

The number of Southern Damselflies marked and recaptured at each site and sub-site is described in the previous chapter and shown in Table 3.1. This was then converted to a mean density for each 50 m by 50 m section. Figure 4.1 shows the frequency distribution of mean Southern Damselfly densities for each of the 82 sections for which we collected habitat data. Adult Southern Damselflies were recorded in 77 of these sections and the modal density was less than one damselfly per section per day. However, the data deviated from a Poisson distribution as there were more high density sections than expected, indicating that the Southern Damselfly 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.

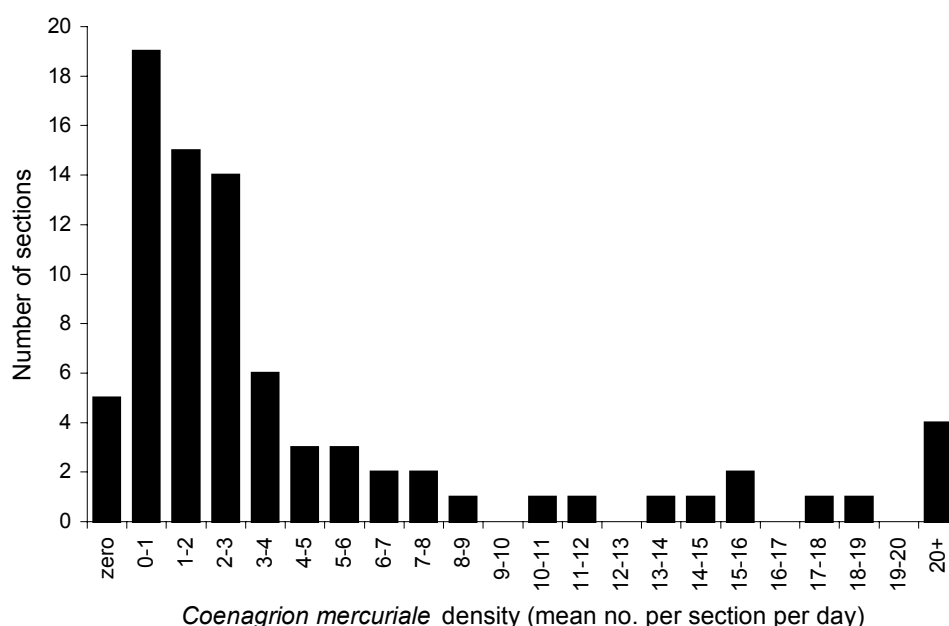


Figure 4.1. Frequency distribution of mean Southern Damselfly densities in 82 sections in the Itchen Valley, Hampshire.

4.3.2 Habitat associations

The single best predictor of high Southern Damselfly density was the presence of wide berms (Table 4.2 – Habitat model), and this factor alone explained 31.2% of the total variation in Southern Damselfly density. 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. Southern Damselflies were 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 to 10 m from the water's edge. Finally, an element of bare ground, usually caused by grazing livestock, was associated with higher densities.

Table 4.2. Significant predictors of Southern Damselfly 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 χ^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 Southern Damselflies in adjacent sections and a 'sub-sites' variable. For a fuller explanation of variables see Table 4.1 and text.

Model	Variable	χ^2	p	Parameter estimates	Standard Error
Habitat model Deviance = 158.49 d.f. = 68 Dev./d.f. = 2.33 $D^2 = 0.725$ Adj. $D^2 = 0.672$	Berm width B	44.73	***	1.336	0.200
	Vegetation height 2–10 m	15.91	***	-1.310	0.329
	Emergent dicots	12.12	***	0.0344	0.0099
	Bank width	11.97	***	0.0332	0.0096
	Vegetation height 0–1 m	11.82	***	1.420	0.413
	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 Deviance = 98.58 d.f. = 71 Dev./d.f. = 1.39 $D^2 = 0.829$ Adj. $D^2 = 0.805$	Adjacent mean density (\log_{10})	63.27	***	1.827	0.230
	Terrestrial monocots	27.85	***	0.0377	0.0071
	Substrate 1	16.67	***	0.562	0.138
	Helophyte monocots	13.84	***	0.0188	0.0050
	Berm width B	5.84	*	0.406	0.168
	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 three levels, but a much greater improvement on fitting a 'sub-sites' factor (Table 4.3). 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 4.3. The fit of Poisson regression models to explain Southern Damselfly density, incorporating (a) habitat variables only; (b) habitat variables and variables representing each site or sub-site; (c) habitat variables, sub-site 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 4.2. The habitat model from Table 4.2 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
+ \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

4.3.3 Effects of local population density

Density of Southern Damselflies 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 \log_{10} transformed mean density respectively. \log_{10} mean density provided the best fit to the data, with the worst fit provided by the maximum density (Table 4.3). An asymptotic response was, therefore, implied.

4.3.4 Final model

\log_{10} mean density was the single best predictor in the final model (Table 4.2). 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 Southern Damselfly 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, while bankside helophyte dicots showed a quadratic response, with greatest damselfly densities at intermediate percentage cover of this vegetation type.

4.3.5 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 10.1 m to 144.2 m with a median of 33.8 m.

Three habitat variables had a significant effect on Southern Damselfly movement (Table 4.4 – 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 Southern Damselfly density did significantly improve the model, with greatest movement occurring in sections with low densities of damselflies. \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 4.4. Significant predictors of mean Southern Damselfly 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 Southern Damselflies. For a fuller explanation of variables see Table 4.1 and text.

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

4.4 Discussion

4.4.1 Habitat associations

Mature adult Southern Damselflies are strongly associated with certain physical and vegetation characteristics of the water meadow 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. Southern Damselfly 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 Southern Damselflies 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 Southern Damselflies for a variety of purposes. They provide suitable perching sites close to the water's edge for basking, for 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 Southern Damselflies 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 Southern Damselflies 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 to 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 the Southern Damselfly 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, the Southern Damselfly occupied habitats with emergent vegetation cover ranging from 3 to 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 *et 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.

4.4.2 Local population size and habitat selection

Local population size has a major effect on Southern Damselfly 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 Southern Damselflies 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 the Southern Damselfly 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.

4.4.3 Southern Damselfly 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 Southern Damselflies, the shorter the average distance moved. This is the opposite effect to that found in most other species, but confirms the findings presented in the previous chapter. The most plausible explanations are likely to be once again, access to high quality habitat and to conspecifics in a species utilising 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 Southern Damselflies are 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 habitat 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.

4.4.4 Methodological considerations

Although our regression models uncovered statistically significant relationships between the predictor variables and Southern Damselfly density that appear to fit with the known ecology of the species, 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 the Southern Damselfly 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 normalised before analysis. Although the Southern Damselfly has been associated

with particular plant communities and functional types, it has never been associated with individual species. For example, Purse (2001) found that the Southern Damselfly 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.

4.4.5 Conservation implications

The results of this study have revealed a number of habitat features with which the Southern Damselfly 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 the Southern Damselfly should have an important bearing on the spatial scale of any planned management works. The majority of individuals move considerably less than 50 m 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 500 m are rare and the longest recorded lifetime movement is less than 2 km (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 reconnect populations and enable gene flow over large distances.

5. Adult roosting site selection

Chapter summary

In this chapter, the night-time roosting habitat of adult Southern Damselflies was investigated, a habitat that has often been overlooked in the past. Studies revealed that:

- **Individuals did not roost together and those that were recorded on more than one occasion did not return to the same spot each night.**
- **There is no apparent preference for roosting close to the watercourses.**
- **The Southern Damselflies roosted towards the top of the vegetation and this vegetation was considerably taller than the mean height of the vegetation in the study area.**
- **Adults are strongly associated with two tussock-forming monocots, *Juncus inflexus* (hard rush) and *Deschampsia cespitosa* (tufted hair grass). Differences in the abundance of these plants were shown to result in large differences in the numbers of Southern Damselflies roosting in different parts of the site.**

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. For the Odonata, a habitat must meet the ecological needs of all stages in the life cycle and 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 Southern Damselfly. 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, Southern Damselfly 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.

5.2 Methods

This study was performed in the Upper section of the Itchen Valley Country Park, one of the best areas for daytime observations of adult Southern Damselfly (Chapter 3). 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). Two other channels also cross the site, but were largely choked with vegetation and contained only small numbers of Southern Damselfly. The land use of the area is predominantly unimproved pasture, although the main channel is bounded for 220 m 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 50 m by 50 m 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 200 m 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.

Southern Damselflies were marked during the day as part of the large multi-site mark-release-recapture study described in 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 & Rehfeldt (1995) marked *Calopteryx haemorrhoidalis* with self-glowing fabric paint and Hunger & Röske (2001) successfully marked Southern Damselfly with UV fluorescent ink and relocated them with a UV lamp.

Nightly observations were carried out from 3 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 50 m by 50 m 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.

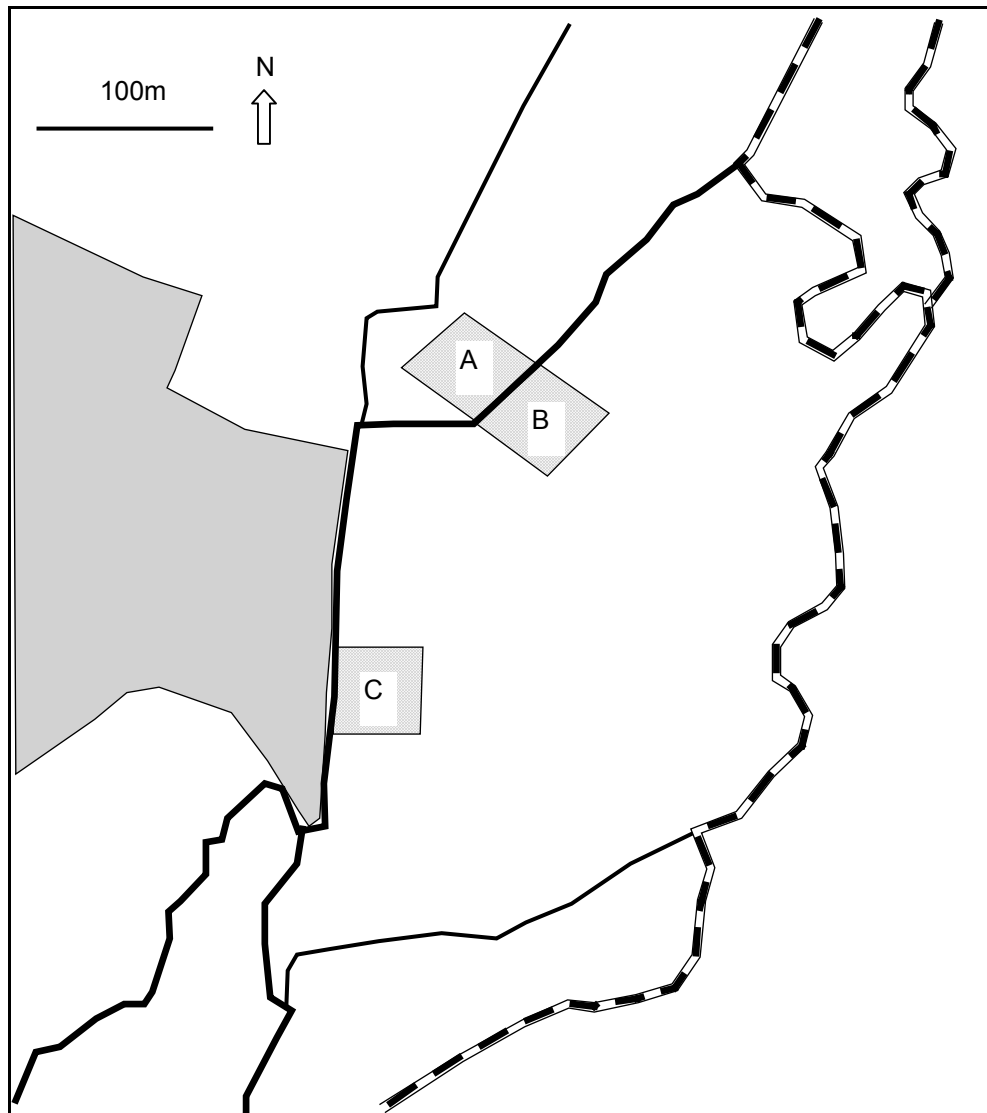


Figure 5.1. Study area in the Itchen Valley, Hampshire. The main channel where the Southern Damselfly was marked is represented by the thick black line, smaller channels are shown by the thinner black lines and the main River Itchen by the thick dashed line. Woodland is shown in grey, meadow in white. The location of the three 50 m by 50 m 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.

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

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

Southern Damselflies roosted more or less vertically, with the 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 head height of Southern Damselflies 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 nights 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 27 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 among 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.

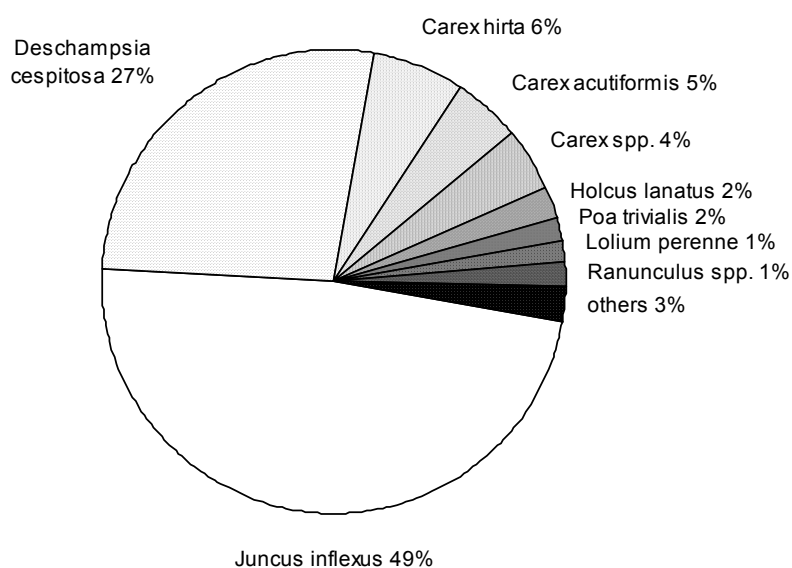


Figure 5.2. Plant species chosen for roosting by the Southern Damselfly, with percentage shown ($n = 273$).

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.

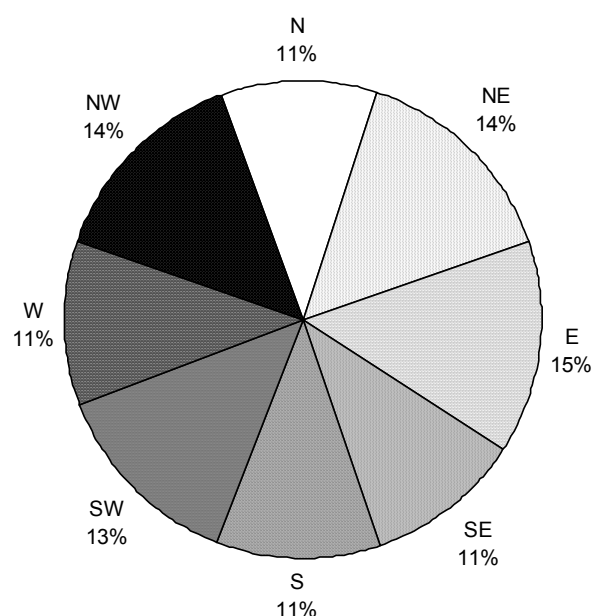


Figure 5.3. Orientation of the body during roosting, with percentage shown (n = 262).

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 & Röske (2001) used a similar method to study movement patterns of the Southern Damselfly 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 & Röske (2001) also reported similar recapture rates for both sexes.

5.4.2 Behaviour and habitat

The Southern Damselfly 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 the Southern Damselfly 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 & 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 & Grether, 2000). This species roosted in small groups with a mean of 5.6 individuals per roost and 13.7 individuals per m². However, it showed no preference for particular plant species and was found roosting 0.2–2 m above ground on most vegetation types.

The Southern Damselfly was usually found towards the top of the vegetation at a mean height of 46.5 cm. Hunger & Röske (2001) reported that Southern Damselflies were usually found at a height of about 20 cm, while roosting height of *Ischnura elegans*, *Coenagrion puella* and *Enallagma cyathigerum* was similar for all species at 75–83 cm (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 the Southern Damselfly 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 1.46 m during good weather conditions in southern France, but reduced roosting height to 0.79 m 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, Southern Damselflies were found throughout the 50 m by 50 m 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 & Röske (2001) who found 69.8% of Southern Damselfly within 5 m of water, and 96.4% within 25 m. 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, Southern Damselfly may have been forced to roost close to the water's edge if little suitable habitat had been available elsewhere.

The Southern Damselfly 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. Hunger & Röske (2001) reported that most Southern Damselflies 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 *Enallagma 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 2.17 mm 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 (2.1 mm) while *E. cyathigerum* preferred small and medium (3.1 mm) 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 and 2.13 mm respectively. Our results would seem to lend support to this hypothesis as the Southern Damselfly appears to be selecting plants with stems of a particular diameter, while 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 and 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 the Southern Damselfly is choosing *J. inflexus* and *Deschampsia 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 Southern Damselfly 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 and 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 Southern Damselfly 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 Southern Damselfly 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 watercourses 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 Southern Damselfly. 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. The Southern Damselfly 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.

6. Macroinvertebrate communities associated with late instar Southern Damselfly larvae

Chapter summary

Southern Damselfly larvae and the associated macroinvertebrate community are investigated in this chapter. Findings show that:

- Southern Damselfly larvae were captured at 53 out of the 100 sampling locations in the Itchen and Test Valleys on at least one occasion during the study, with the strongest populations occurring in the Itchen Valley Country Park. Larvae were also sampled in Oxfordshire and Anglesey.
- There were significant differences between the invertebrate communities at sites with and without the Southern Damselfly and using this information alone it was possible to correctly predict whether Southern Damselfly larvae were present or absent with reasonable accuracy.
- 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.
- An analysis of Southern Damselfly diet has found that it feeds predominantly on Chironomidae, *Gammarus* and Copepoda. The species appears to be an opportunistic feeder with a similar dietary prey composition to that available in its habitat and it is unlikely to be food limited.

6.1 Introduction

The focus of the investigations described in the earlier chapters of this report has been adult Southern Damselflies. In the following two chapters I shift attention onto Southern Damselfly larvae, an overlooked but critically important phase of the life cycle. In fact, the species lives for almost two years as a larva before emerging and living as an adult for only about two weeks. Although 95% of the life cycle occurs in the larval stage, little is known about the ecology of this phase 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 the larvae. The primary aim is to investigate the biological, physical and chemical attributes of all chalkstream and fen sites where the Southern Damselfly 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 Southern Damselfly larvae is investigated. I also address issues of taxonomic resolution, seasonal variation and Southern Damselfly diet. In the following chapter (Chapter 7) Southern Damselfly occurrence and abundance is related to physical, chemical and vegetation attributes.



Figure 6.1. Typical late instar Southern Damselfly larva.

6.2 Methods

6.2.1 Study sites

We were able to investigate all the major chalkstream and fen sites from which the Southern Damselfly has been recorded and, in addition, nearby sites where the species was thought not to occur. A description of all the sampling areas is provided in Chapter 2. The Itchen Valley was sampled at several sites between Winchester and Southampton, as is shown on Figure 2.2. Unfortunately, we were only allowed access to the River Test at one site close to King's Somborne, although this included all of the locations of Southern Damselfly in the Test Valley found prior to this study. In Oxfordshire, the only known Southern Damselfly site at Dry Sandford Pit was sampled, along with locations in the nearby Cothill Fen complex of sites. Finally, the only known Southern Damselfly site in Anglesey, at Cors Erddreiniog, was also sampled.

At each site, sampling locations were identified at approximately 150 m 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, 17 in the Test Valley, 9 in Oxfordshire and 5 in Anglesey.

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, with the exception of Anglesey. At this site, difficulty with access meant that we only carried out fieldwork once, during the July 2002 sampling season. 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 three minutes with a 1.0 mm mesh pond net, with sampling effort allocated proportionally between the different habitat types present.

As the Southern Damselfly is a protected species, all samples were live-sorted for two hours on return to the laboratory. All damselfly (Zygoptera) larvae were separated for identification to species level and counted. Southern Damselfly larvae were then returned to their original sampling locations when feasible. 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 ten data sets were available for analysis.

A range of multivariate statistics was used to compare the community composition of sites where Southern Damselfly larvae were present with those where they were not. Technical details of the statistical tests used are given in Box 6.1. Please note that the samples taken from the fen sites in Oxfordshire and Anglesey were quite different from the chalkstream sites in the Itchen and Test Valleys and have been analysed separately.

Box 6.1: Statistical analysis

A range of multivariate statistics was used. As a first step, Bray-Curtis dissimilarities based on $\log(\log_{10} x + 1)$ transformed abundances were calculated using all taxa except for Southern Damselfly 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 maximise 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 Southern Damselfly, the Indicator Value method (IndVal) was used (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 Southern Damselfly 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 Southern Damselfly 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 Southern Damselfly larvae were present were compared to sites where they were absent using Mann-Whitney U-tests and correlations were performed against Southern Damselfly 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 λ 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 locations and abundance of Southern Damselfly

Southern Damselfly larvae were captured at 53 out of the 100 sampling locations in the Itchen and Test Valleys on at least one occasion during the study. During live sorting,

larvae were often found clinging to aquatic vegetation. 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 6.2–6.5 show the position of all sampling locations and indicate the number of seasons in which Southern Damselfly larvae were 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 6.2). Frequency of capture was reasonably high at Highbridge (Figure 6.3) and at some locations within the Mariner’s Meadow/Twyford Moors area (Figure 6.4). However, no larvae were captured at any of the sampling locations at Rosemary Leet or Compton Lock (Figure 6.4).

Table 6.1. Number of locations at which larval Southern Damselfly were captured in the Itchen and Test Valleys 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

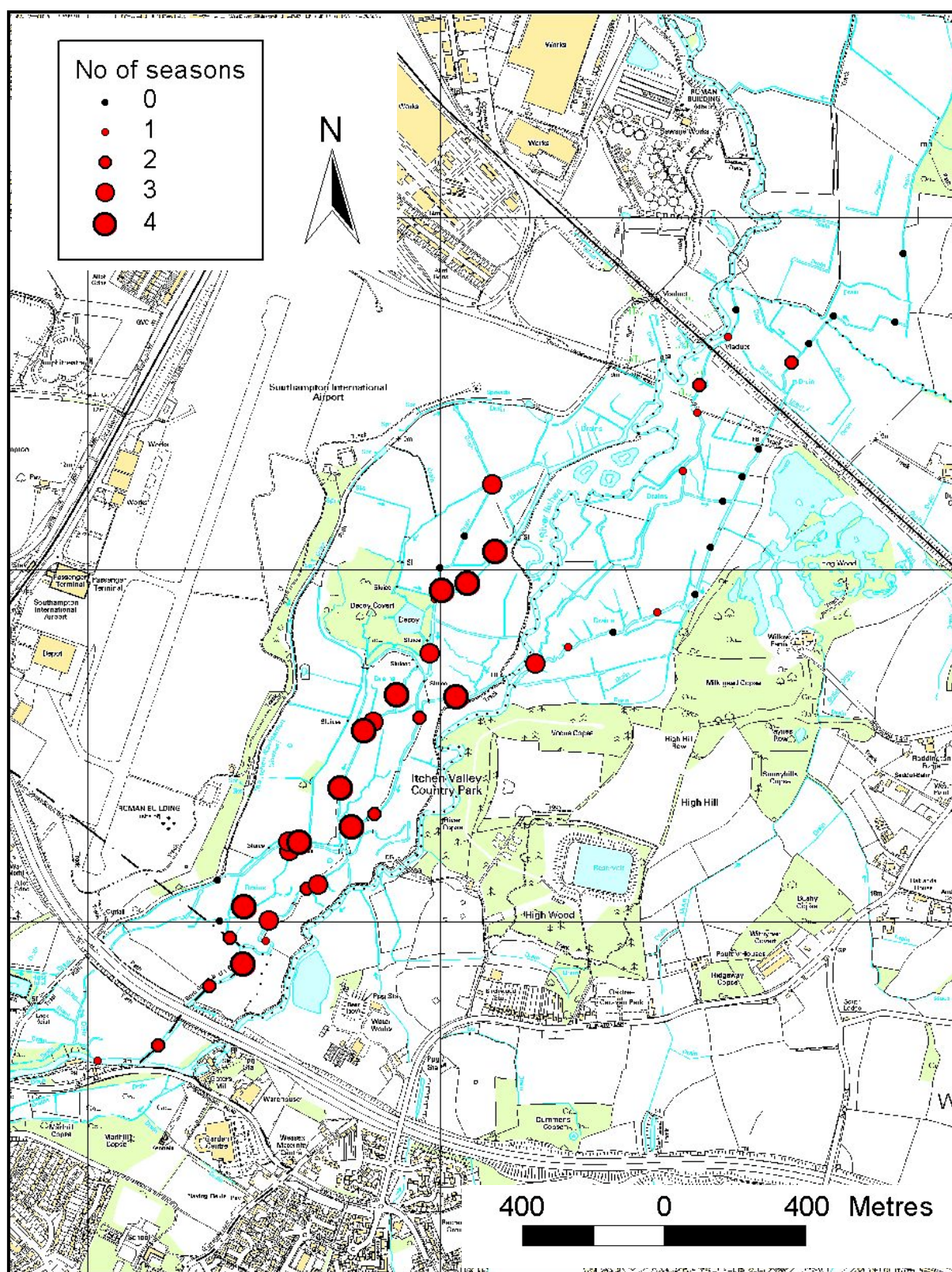


Figure 6.2. Itchen Valley from the Itchen Valley Country Park to West Horton Farm showing frequency of capture of Southern Damselfly larvae at each sampling location.

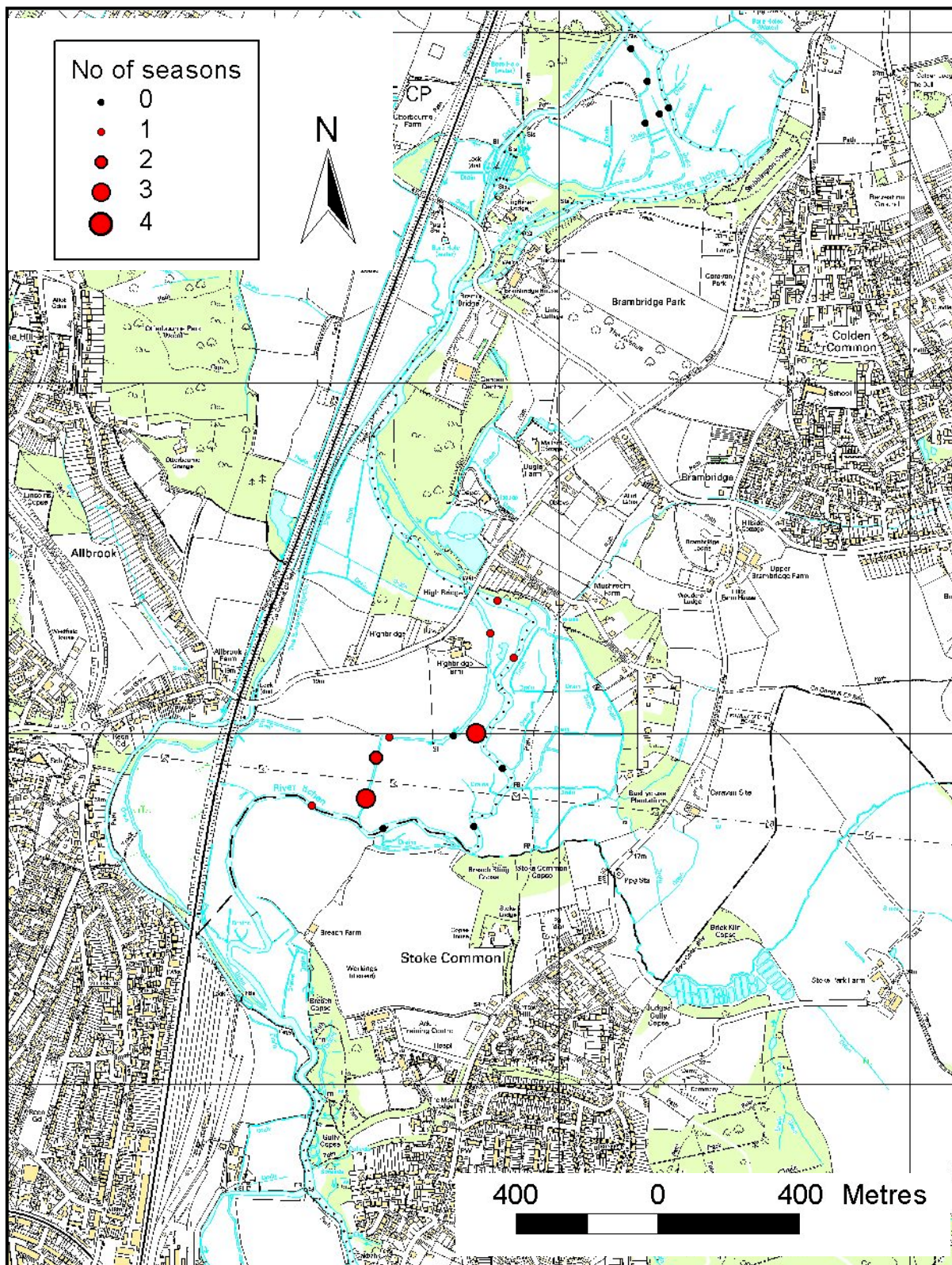


Figure 6.3. Itchen Valley from Highbridge to Rosemary Leet showing frequency of capture of Southern Damselfly larvae at each sampling location.

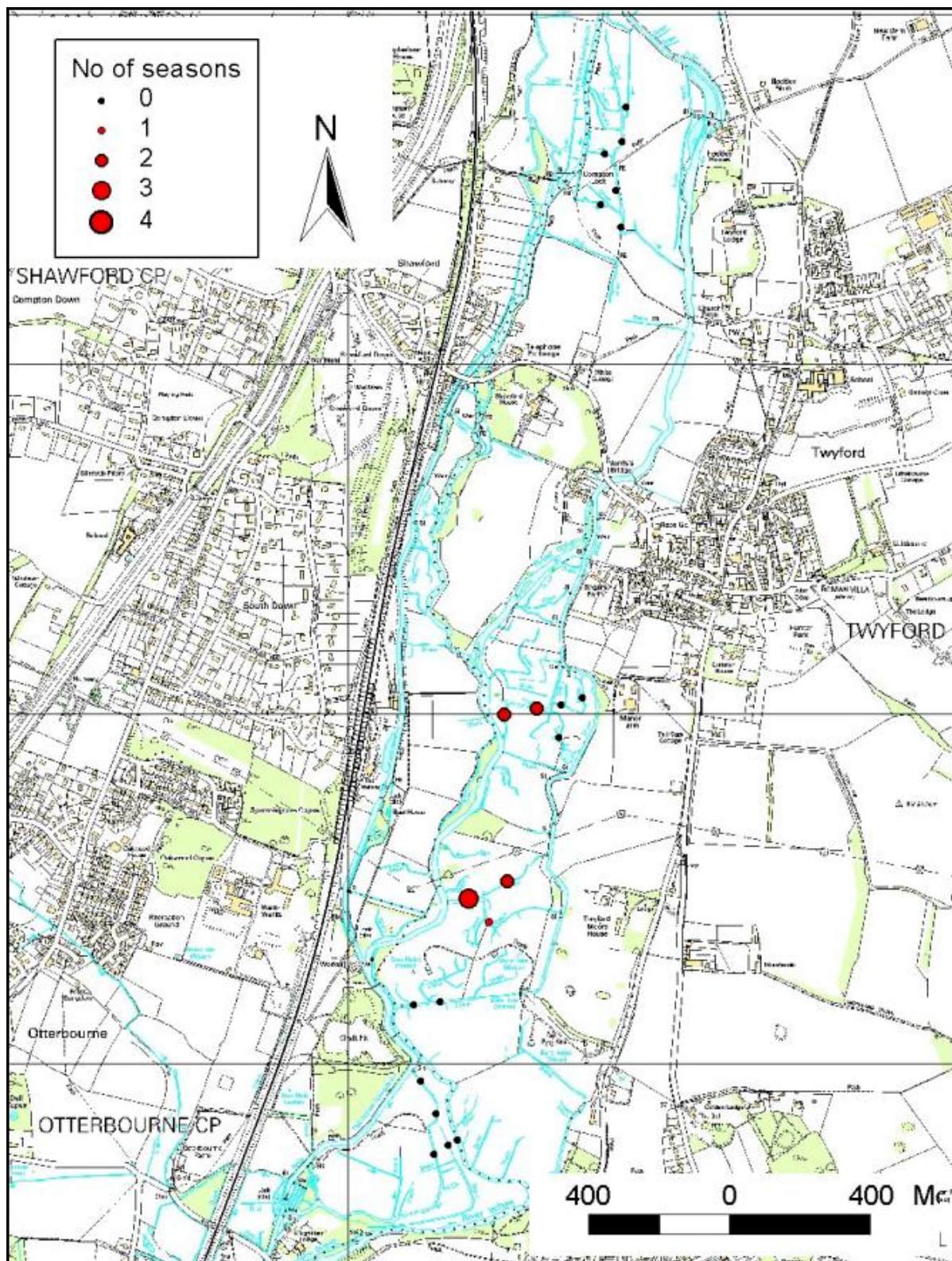


Figure 6.4. Itchen Valley from Rosemary Leet to Compton Lock showing frequency of capture of Southern Damselfly larvae at each sampling location.

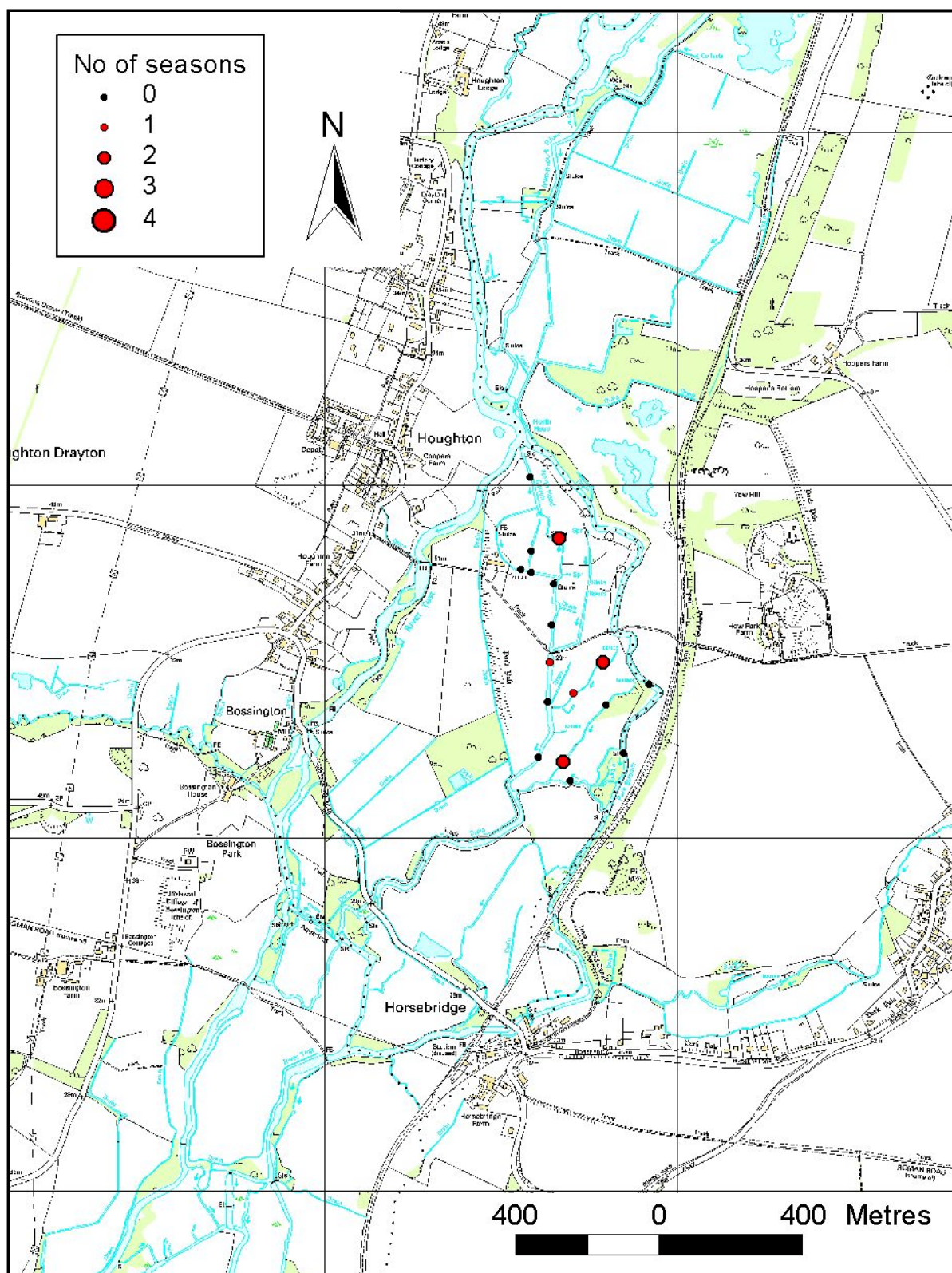


Figure 6.5. Test Valley from Horsebridge to Houghton showing frequency of capture of Southern Damselfly larvae at each sampling location.

6.3.2 Are there differences in the invertebrate communities at sites in the Itchen and Test Valleys with and without Southern Damselfly?

A comparison of the invertebrate communities at each site was made using PCoA ordination. Ordination plots can then be produced, which represent sample differences in two dimensions, with samples that are similar grouped closely together. In this study the ordination plots based on species-level data for the first three seasons were remarkably similar (Figure 6.6). There was a tendency for sites where Southern Damselfly was present to be located towards the lower left region of the ordination plots, although there was considerable overlap. This indicates that the sites where Southern Damselfly larvae occur contain similar assemblages of species and that sites that contain a very different community of species are less likely to also contain Southern Damselfly larvae, although these community differences are not clear-cut.

To test for the significance of these differences in invertebrate communities, two types of tests were run, ANOSIM and CDA (see Box 6.1 for an explanation of these tests and the differences between them). The results of the ANOSIM tests (Table 6.2a) revealed that the differences between sites with and without Southern Damselfly were significant for the first 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). In other words, using invertebrate data alone (excluding Southern Damselfly information), it was possible to correctly predict whether Southern Damselfly larvae were present or absent for at least 71% of sites.

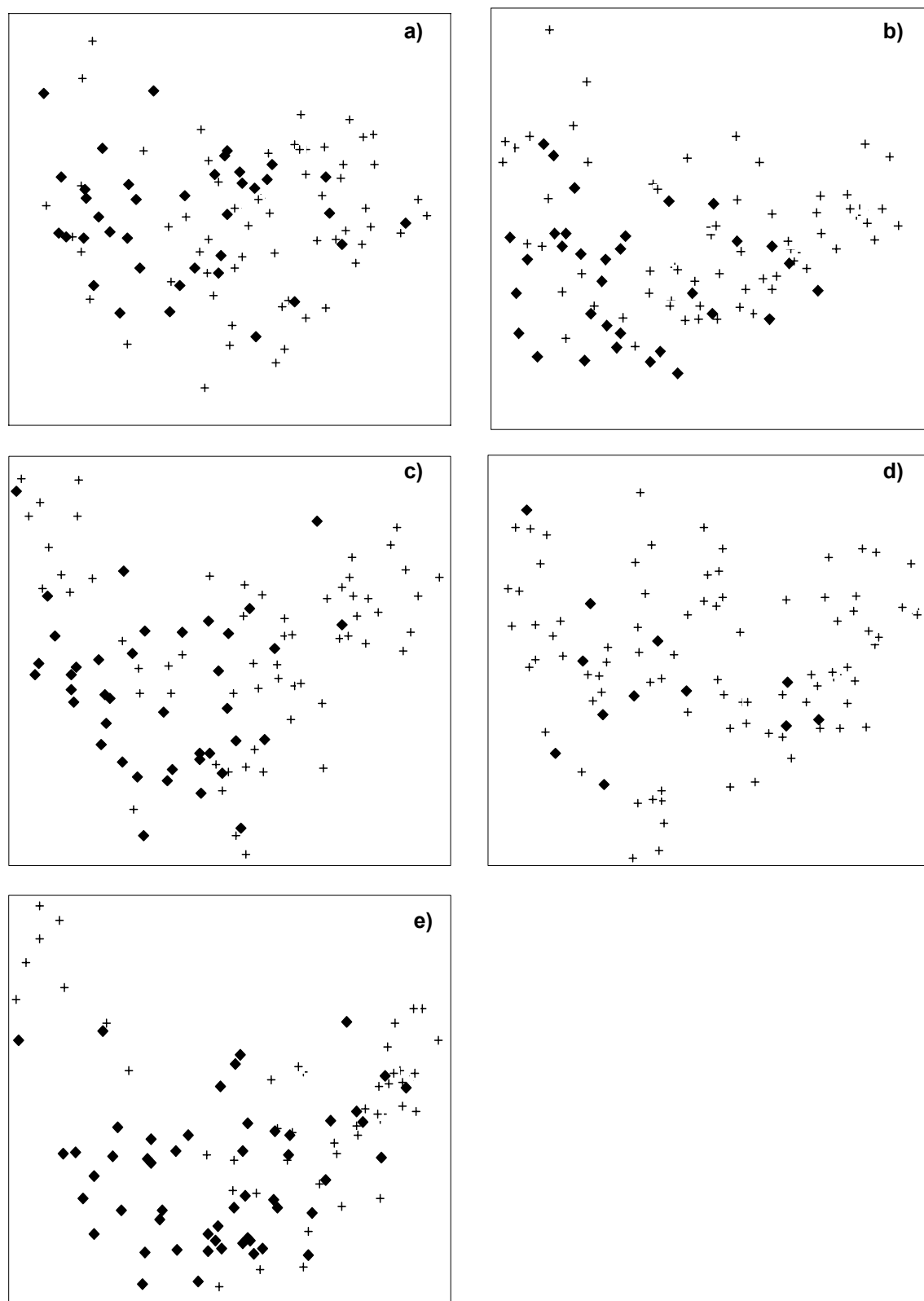


Figure 6.6. Ordination plots showing the first two axes of Principal Co-ordinate Analyses (PCoA) for (a) autumn season, (b) winter, (c) spring, (d) summer and (e) all seasons combined. Samples are log-transformed abundances of species-level data and show sites where Southern Damselfly larvae were present (diamonds) and sites where they were absent (+). Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

Table 6.2. Tests showing differences in the invertebrate communities at sites with and without Southern Damselfly larvae, using ANOSIM, CDA and CCorA for each season for (a) species-level data and (b) family-level data.

	Autumn	Winter	Spring	Summer	All seasons combined
a) Species-level analysis:					
ANOSIM: Global R	0.106	0.082	0.159	-0.041	0.182
<i>p</i>	0.0017	0.0284	<0.0001	0.67	<0.0001
CDA: correlation (<i>d</i>)	0.621	0.533	0.762	0.632	0.831
<i>d</i> ²	0.386	0.284	0.580	0.400	0.691
<i>p</i>	0.0005	0.0018	<0.0001	0.0048	0.0001
total correct	71.7%	72.0%	84.0%	91.0%	80.0%
CCorA: correlation (<i>d</i>)	0.732	0.630	0.713	0.592	0.674
<i>d</i> ²	0.535	0.396	0.508	0.350	0.455
<i>p</i>	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
<i>p</i>	0.0078	0.0608	<0.0001	0.511	<0.0001
CDA: correlation (<i>d</i>)	0.553	0.475	0.792	0.614	0.678
<i>d</i> ²	0.305	0.226	0.627	0.377	0.460
<i>p</i>	<0.0001	0.0011	<0.0001	0.0035	0.0001
total correct	74.8%	71.0%	81.0%	85.0%	78.0%
CCorA: correlation (<i>d</i>)	0.765	0.583	0.645	0.535	0.761
<i>d</i> ²	0.585	0.340	0.416	0.287	0.579
<i>p</i>	<0.0001	0.0556	0.0057	0.0591	0.0031

N.B. ANOSIM and CDA compare sites with and without Southern Damselfly. CCorA shows the correlation with Southern Damselfly 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.

6.3.3 What are the species that are the best indicators of Southern Damselfly presence or absence?

Taxa that were the best indicators of Southern Damselfly presence or absence were assessed using the Indicator Value method (IndVal), and are shown in Table 6.3. There were 25 taxa significantly associated with Southern Damselfly 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 the Southern Damselfly 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).

Table 6.3. Taxa that are indicators of locations where Southern Damselfly larvae are present (Group 1) or absent (Group 2) for each season, based on **species-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 IndVal of at least 25 and a p -value < 0.05 are included.

Group	Taxa	Family	Autumn		Winter		Spring		Summer		Combined	
			IV	p	IV	p	IV	p	IV	p	IV	p
1	<i>Dixa nebulosa</i>	Dixidae	69.5	***	45.5	***			67.0	***	71.3	***
	<i>Calopteryx splendens</i>	Calopterygidae	61.1	**					60.7	***		
	<i>Lymnaea peregra</i>	Lymnaeidae	33.5	**	31.8	***	35.1	***	41.4	**	53.2	***
	<i>Ischnura elegans</i>	Coenagrionidae	30.7	***	35.1	***	41.7	***			39.4	***
	<i>Pericoma trivialis</i> group	Pscyodidae	26.3	*	28.0	**						
	<i>Cloeon dipterum</i>	Baetidae	25.1	***							27.9	*
	<i>Asellus aquaticus</i>	Asellidae			70.4	***					60.4	**
	<i>Gammarus/Crangonyx</i>				59.9	*			68.4	**		
	<i>Physa fontinalis</i>	Physidae			49.0	**	35.8	*			61.1	**
	<i>Limnephilus marmoratus</i>	Limnephilidae			44.3	***					39.3	***
	Ostracoda				38.0	*	37.0	**			57.4	***
	<i>Limnephilus rhombicus</i>	Limnephilidae			35.0	*						
	<i>Pisidium milium</i>	Pisidiidae			25.2	***	34.1	***				
	<i>Pisidium subtruncatum</i>	Pisidiidae					56.7	***	53.7	*	59.2	*
	<i>Erpobdella octoculata</i>	Erpobdellidae					55.9	***	62.8	**	63.7	*
	<i>Glossiphonia complanata</i>	Glossiphoniidae							48.9	*		
	Succineidae								48.6	***		
	<i>Halesus radiatus</i>	Limnephilidae							31.2	***		
	<i>Gerris</i>	Gerridae							30.8	***		
	<i>Nepa cinerea</i>	Nepidae							30.4	***		
	<i>Molanna angustata</i>	Molannidae							29.7	**	31.2	***
	<i>Bithynia tentaculata</i>	Hydrobiidae									54.9	*
	<i>Valvata piscinalis</i>	Valvatidae									33.2	***
	<i>Pisidium casertanum</i>	Pisidiidae									27.1	*
	<i>Ilybius fuliginosus</i>	Dytiscidae									26.8	**
2	<i>Ephemera danica</i>	Ephemeridae	70.5	***	61.6	**	71.2	***	67.8	**	66.1	***
	<i>Baetis rhodani</i>	Baetidae	62.6	**	58.6	**	47.3	*				
	<i>Potamophylax</i> group	Limnephilidae	53.9	**								
	<i>Heptagenia sulphurea</i>	Heptageniidae	40.7	*			49.2	***			61.6	***

Table 6.3 cont.

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

6.3.4 Which species correlate with Southern Damselfly abundance?

The invertebrate communities were correlated with Southern Damselfly abundance using Canonical Correlation Analysis (CCorA) of the principal co-ordinates. The correlation was significant in all analyses except for the winter season, which was almost significant (Table 6.2a). Taxa that were most highly correlated with Southern Damselfly 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 Southern Damselfly larval abundance and 26 taxa were negatively correlated. The positively correlated taxa are remarkably similar to those associated with Southern Damselfly presence (Table 6.3) and are dominated by members of the Odonata, Diptera, Sphaeriidae and Gastropoda. Likewise, the negatively correlated taxa are similar to those associated with Southern Damselfly absence and are dominated by members of the Trichoptera, Ephemeroptera and Coleoptera.

Table 6.4. Taxa that are positively (Group 1) or negatively (Group 2) correlated with Southern Damselfly larval 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	<i>Calopteryx splendens</i>	Calopterygidae	0.446	0.205		0.245	0.281
	<i>Pyrrhosoma nymphula</i>	Coenagrionidae	0.356	0.345			0.374
	<i>Gammarus/Crangonyx</i>		0.334	0.207		0.279	0.321
	<i>Ischnura elegans</i>	Coenagrionidae	0.289	0.270	0.367		0.316
	<i>Nepa cinerea</i>	Nepidae	0.248			0.410	0.305
	Ostracoda		0.227	0.296	0.41		0.291
	<i>Dixa nebulosa</i>	Dixidae		0.563			0.380
	<i>Pisidium pulchellum</i>	Pisidiidae		0.555			0.240
	<i>Pisidium amnicum</i>	Pisidiidae		0.416			
	<i>Asellus aquaticus</i>	Asellidae		0.365			
	<i>Physa fontinalis</i>	Physidae		0.352	0.347		0.245
	<i>Pisidium subtruncatum</i>	Pisidiidae		0.341	0.438	0.250	0.402
	<i>Pisidium nitidum</i>	Pisidiidae		0.293	0.250		
	<i>Pisidium casertanum</i>	Pisidiidae		0.287	0.455		0.310
	<i>Pisidium milium</i>	Pisidiidae		0.275	0.466		0.337
	<i>Bithynia tentaculata</i>	Hydrobiidae		0.259	0.232		
	<i>Lymnaea stagnalis</i>	Lymnaeidae		0.231	0.250		
	<i>Erpobdella octoculata</i>	Erpobdellidae		0.210	0.393	0.304	0.295
	<i>Lymnaea peregra</i>	Lymnaeidae			0.392	0.387	0.232
	<i>Hydroporus palustris</i>	Dytiscidae			0.323		
	<i>Phryganea</i>	Phryganeidae				0.408	
	<i>Halesus radiatus</i>	Limnephilidae				0.393	
	<i>Hesperocorixa sahlbergi</i>	Corixidae				0.369	
	<i>Notonecta glauca</i>	Notonectidae					0.358
	<i>Notonecta</i>	Notonectidae					0.245

Table 6.4 cont.

Group Taxa	Family	Autumn	Winter	Spring	Summer	Combined
2 <i>Ephemera danica</i>	Ephemeridae	-0.590	-0.255	-0.379	-0.235	-0.525
<i>Elmis aenea</i>	Elmidae	-0.388		-0.276		-0.360
Limnephilidae		-0.342				-0.234
<i>Potamophylax</i> group	Limnephilidae	-0.321				-0.274
<i>Sericostoma personatum</i>	Sericostomatidae	-0.319	-0.228	-0.341		-0.429
<i>Limnius volckmari</i>	Elmidae	-0.316	-0.241	-0.315		-0.368
<i>Baetis scambus/fuscatus</i>	Baetidae	-0.302		-0.227	-0.207	-0.249
Hydracarina		-0.300	-0.243		-0.258	-0.383
<i>Heptagenia sulphurea</i>	Heptageniidae	-0.268	-0.283	-0.295		-0.458
Oligochaeta		-0.249	-0.270			
<i>Paraleptophlebia submarginata</i>	Leptophlebiidae	-0.250		-0.221		-0.465
<i>Rhyacophila</i>	Rhyacophilidae	-0.233	-0.202	-0.225		-0.375
<i>Silo nigricornis</i>	Goeridae	-0.217		-0.286	-0.213	-0.341
<i>Orectochilus villosus</i>	Gyrinidae		-0.270	-0.227		-0.357
<i>Hydropsyche siltalai</i>	Hydropsychidae			-0.347		-0.422
<i>Hydropsyche pellucidula</i>	Hydropsychidae					-0.383
<i>Rhyacophila dorsalis</i>	Rhyacophilidae					-0.350
<i>Agapetus</i>	Glossosomatidae					-0.353
<i>Ithytrichia</i>	Hydroptilidae					-0.346
<i>Baetis rhodani</i>	Baetidae					-0.343
<i>Centroptilum luteolum</i>	Baetidae					-0.327
<i>Leuctra</i>	Leuctridae					-0.326
<i>Simulium</i>	Simuliidae					-0.324
<i>Polycentropus flavomaculatus</i>	Polycentropidae					-0.318
<i>Dicranota</i>	Tipulidae					-0.315
<i>Isoperla grammatica</i>	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 eight 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 6.7 and results for the other seasons were similar. Differences in the community structure between sites where Southern Damselfly larvae were 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 Southern Damselfly 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 Southern Damselfly abundance 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 Southern Damselfly abundance (Table 6.6) strongly reflect the species that were correlated (Table 6.4).

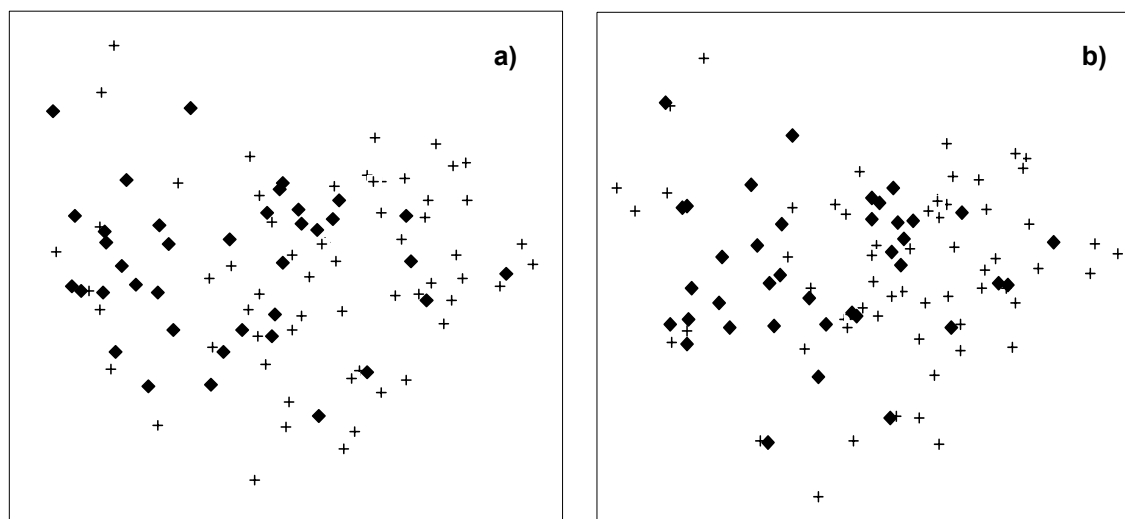


Figure 6.7. Ordination plots showing the first two axes of Principal Co-ordinate Analyses (PCoA) for the autumn season. Samples are log-transformed abundances of (a) species-level data and (b) family-level data, and show sites where Southern Damselfly larvae were present (diamonds) and sites where they were absent (+). 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 Southern Damselfly larvae are 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	<i>p</i>	IV	<i>p</i>	IV	<i>p</i>	IV	<i>p</i>	IV	<i>p</i>
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	***
	Leptophlebiae									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 Southern Damselfly larval 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
	Leptophlebiae		-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 Southern Damselfly larvae 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 Southern Damselfly larvae 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 Southern Damselfly occurred had lower flow velocities than sites from which it was absent. BMWP was lower in the winter and spring seasons at locations with Southern Damselfly larvae, while ASPT was lower in the autumn, winter and spring seasons.

When the diversity and biotic indices were correlated against Southern Damselfly larval abundance (Table 6.7d), 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 6.6). Indeed, if all samples were considered to be independent and analysed at the same time (Figure 6.8, 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 Southern Damselfly larvae were present, (b) the mean value where they were absent (c) the *p*-value of Mann-Whitney U-tests to compare these sites and d) the *p*-value of Spearman's Correlation with Southern Damselfly larval abundance (* *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001, n.s. not significant, N.A. not available).

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.	N.A.
LIFE (family level)	**	***	***	n.s.	N.A.
BMWP	n.s.	*	**	n.s.	N.A.
ASPT	***	***	***	n.s.	N.A.
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.	N.A.
LIFE (family level)	***	***	***	n.s.	N.A.
BMWP	*	n.s.	**	n.s.	N.A.
ASPT	***	***	***	n.s.	N.A.

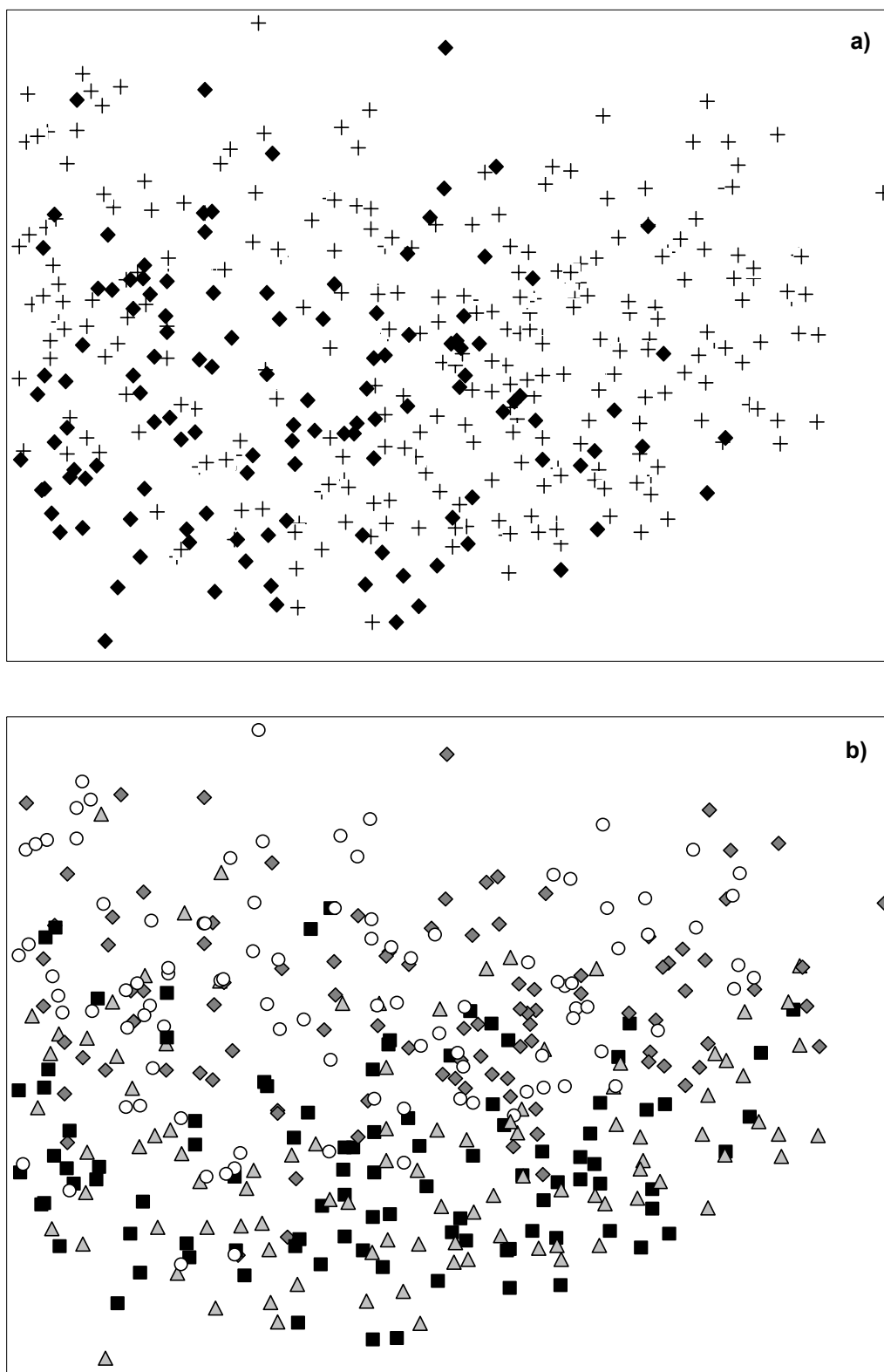


Figure 6.8. PCoA ordination plot of all samples from all four seasons showing (a) sampling locations where Southern Damselfly larvae were present (diamonds) or absent (+) and (b) the same plot highlighting the location of autumn (■), winter (△), spring (◆) and summer (○) samples. Samples are log-transformed abundances of species-level data.

6.3.8 Oxfordshire

Five locations were sampled in Dry Sandford Pit, two in Parsonage Moor, and one in Lashford Lane Fen at the northern end off the Cothill Fen complex. Over the course of the four seasons, Southern Damselfly larvae were found in three of the sampling locations at Dry Sandford Pit but never away from this site (see Figure 6.10). Larvae were much more abundant at one location on the north-east side of Dry Sandford Pit, where 18 larvae were found over the course of three seasons. At the two other locations, larvae were discovered in one season only and abundance was lower (only two individuals discovered on each occasion).

Ordination of the invertebrate communities revealed that differences in water flow caused the largest differences between the communities in different locations. Samples from locations where water flow was still or almost still appear on the right side of the ordination plot, while samples from locations with more stream-like conditions appear on the left side (Figure 6.9a). Locations containing Southern Damselfly larvae were situated in the middle of these extremes and are relatively close to each other, indicating that they contain relatively similar invertebrate communities. However, differences between sites with and without the Southern Damselfly were not significant, although this may be due to the relatively small number of sites compared (nine). Only three species were significant indicators of Southern Damselfly occurrence, and these were *Oxycera formosa* (Diptera), *Limnephilus lunatus* (Trichoptera) and *Sialis lutaria* (Neuroptera). The correlation of the invertebrate communities with Southern Damselfly abundance was not significant.

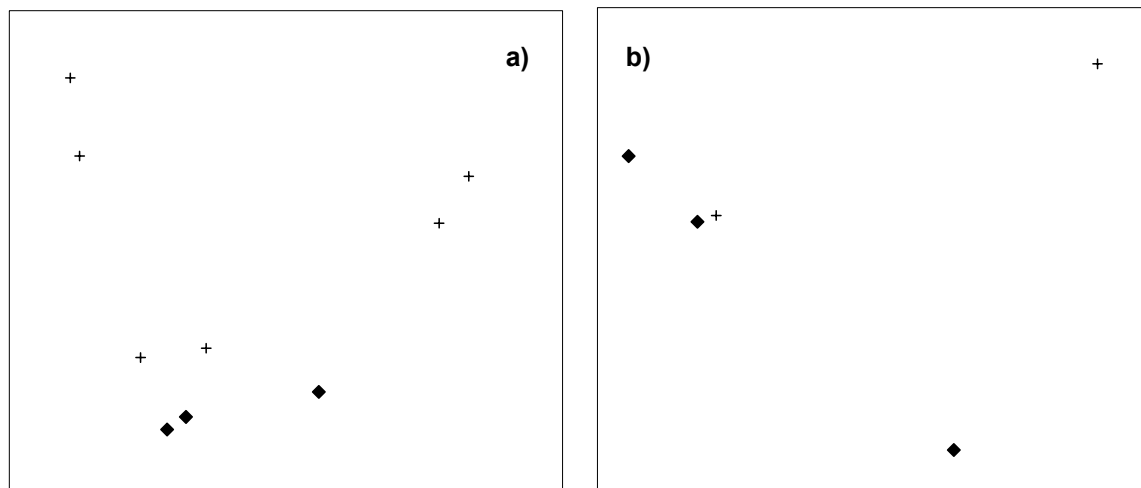


Figure 6.9. Ordination plot showing the first two axes of Principal Co-ordinate Analyses (PCoA) for (a) Oxfordshire sites, all seasons combined and (b) Anglesey sites, summer season only. Samples are log-transformed abundances of species-level data and show sites where Southern Damselfly larvae were present (diamonds) and sites where they were absent (+). Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

6.3.9 Anglesey

Five locations were sampled at Cors Erddreiniog, one in the main spring-fed ditch flowing through Nant Isaf, two in the area of springs and flushes slightly to the south, one in the larger stream that drains Nant Isaf to the west and one in Cors Nant Isaf, an area of small flushes 300 m to the west of Nant Isaf. During sampling in summer 2002 Southern Damselfly larvae were found at three of the sampling locations, as indicated on the map (Figure 6.11). The best site was the spring fed ditch in Nant Isaf, where five larvae were recorded. At each of the other two locations only one larva was discovered.

The three samples taken from Nant Isaf were similar in terms of their invertebrate communities and were located close together on the ordination plot (Figure 6.9b), even though one of these locations did not contain Southern Damselfly larvae. The remaining two sites were quite different from these and from each other. In consequence, it was not possible to use the invertebrate community to predict the occurrence or abundance of Southern Damselfly larvae (all results were not significant), and no species were significant indicators of Southern Damselfly occurrence. However, there were physical differences between these locations, which are examined in Chapter 7.

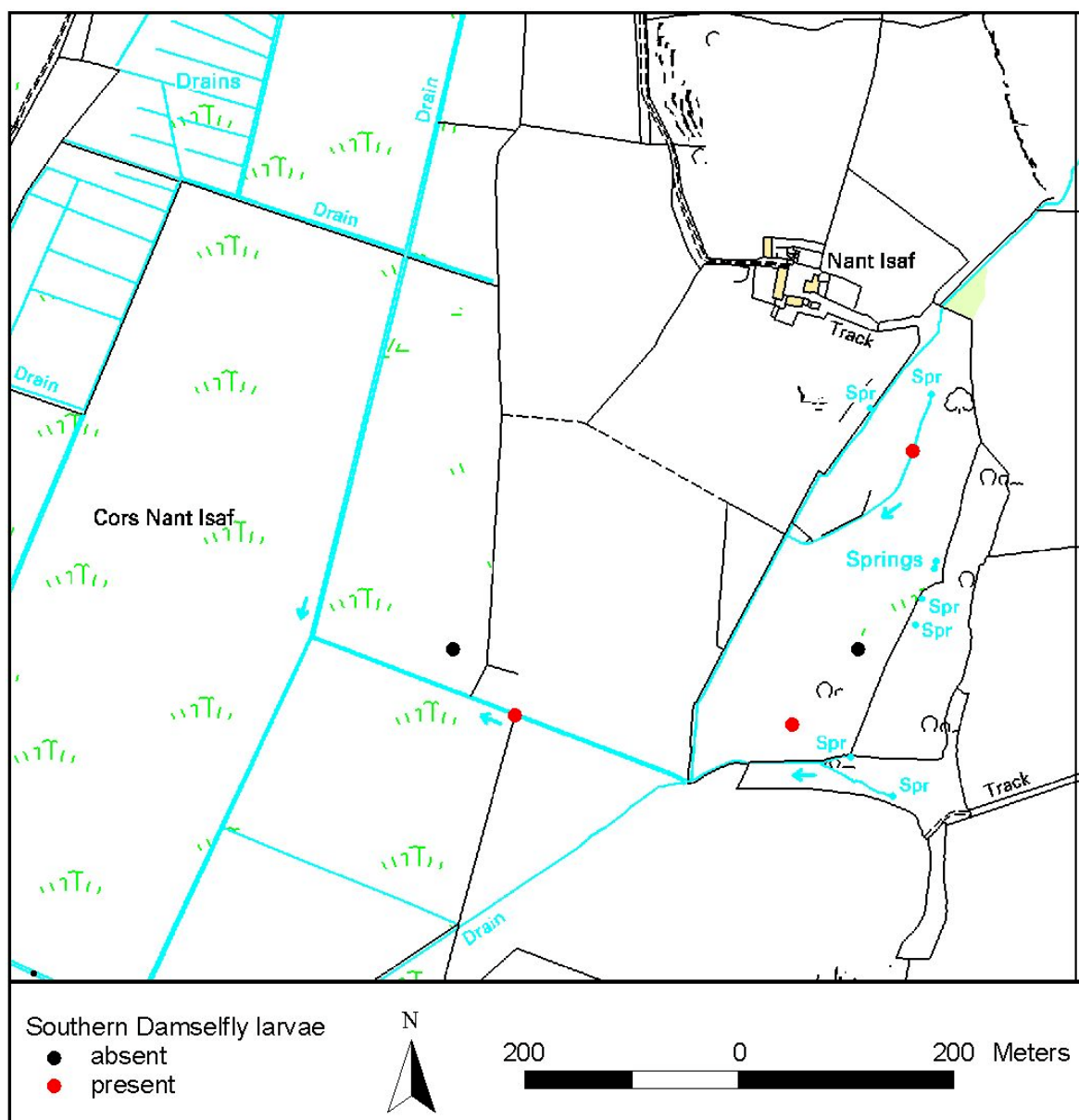


Figure 6.11. Sampling locations at Cors Erddreiniog in Anglesey, showing the presence or absence of Southern Damselfly larvae during sampling in summer 2002.

6.4 Discussion

6.4.1 Abundance of Southern Damselfly larvae and methodological issues

Although Southern Damselfly 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. Southern Damselfly 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 Southern Damselfly larvae from other members of the Coenagrionidae.

6.4.2 Associated species and community

This study has shown that Southern Damselfly larvae are 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 Southern Damselflies are 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 water-cress beds (Smith, 1989; Disney, 1999). Harrison (2000) reported that it was associated with marginal habitats in all seasons. *Phya 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 Southern Damselfly 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 Southern Damselfly larvae with those that are most highly correlated with its abundance. Additional taxa that are correlated with Southern Damselfly larval 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 Southern Damselfly larvae were abundant. It would seem that its optimum habitat requirements are similar to Southern Damselfly, but it is able to cope with a much wider range of conditions. *Pyrrhosoma nymphula* is a bottom-dweller, living among 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 Southern Damselfly 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 Southern Damselfly larvae. However, in some seasons there was a tendency for evenness and hence

diversity measures to be lower in sites containing Southern Damselfly, indicating that Southern Damselfly larvae 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 Southern Damselfly larvae are 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 Southern Damselfly larvae were 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 Southern Damselfly have a mean score of 3.76, while the group that are indicative of Southern Damselfly 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 Oxfordshire and Anglesey

At the Oxfordshire and Anglesey sites, Southern Damselfly larvae were also associated with slow flowing but not still conditions. The invertebrate communities at these sites were very different to that found in the Itchen and Test Valleys and so direct comparison is difficult. Furthermore, the relatively small number of sampling locations has precluded a more thorough analysis of these sites.

In Oxfordshire, the Southern Damselfly is only abundant in one relatively small area of Dry Sandford Pit, although it was also present at two other sampling locations. All three of these locations contain similar invertebrate communities, but the latter two are largely overshadowed, either by dense reeds or by overhanging trees. If management work was undertaken to open up these two locations it is likely that the Southern Damselfly populations would rapidly expand. It is also interesting to note that the invertebrate communities at Lashford Lane Fen and at one of the sampling locations in Parsonage Moor are similar to those from the sampling locations at Dry Sandford Pit where Southern Damselfly larvae occurred. It is possible, therefore, that these locations could become suitable for the Southern Damselfly, particularly as management work progresses to open up these sites. The long-term future of the Southern Damselfly in Oxfordshire would be far more assured if it were to establish colonies at two or three linked sites, rather than the present situation where it is entirely dependent upon just one site.

In Anglesey, Southern Damselfly larvae were most abundant in the main spring-fed ditch flowing through Nant Isaf. It still occurred in the more marginal area of springs and flushes slightly to the south, but it is clear that maintaining adequate water levels are vital for the long-term future of the Southern Damselfly on this site. This study is the first to find Southern Damselflies associated with the main stream that drains Nant Isaf, a habitat that is far more reminiscent of the water meadow ditches of the Itchen and Test Valleys.

6.4.4 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 Southern Damselfly larvae are 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 Southern Damselfly 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.

6.4.5 Diet of Southern Damselfly larvae

Bousfield (2003) examined the faecal pellets of approximately 40 of the Southern Damselfly 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. Bousfield 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 the Southern Damselfly 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 microinvertebrates and to see if there was any correlation with Southern Damselfly 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 they 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 middle to late instar larvae. It is likely that Copepoda and other microinvertebrates 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.

6.4.6 Conservation implications

This study has shown that Southern Damselfly larvae are clearly associated with particular species or groups of species and disassociated with others. They are 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. The study 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 Southern Damselfly 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 Southern Damselfly or the response of the community to new management practices.

This study, together with a study of the diet of Southern Damselfly (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 the species' 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 microinvertebrates across a range of sites.

7. Habitat associations of late instar larvae

Chapter summary

In this chapter the occurrence and abundance of Southern Damselfly larvae are related to physical, chemical and vegetation attributes. Investigations show that:

- Southern Damselfly 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* (fool's water-cress) and *Rorippa nasturtium-aquaticum* (water-cress) were found to be particularly important.
- Southern Damselfly larvae 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.
- In the fen sites in Oxfordshire and Anglesey, water flow, emergent dicots and a lack of shading were found to be key factors.

7.1 Introduction

The importance of understanding the habitat requirements of all stages of a species' life cycle has already been stated. The final section of research presented in this report is again concerned with the larval stage and continues on from Chapter 6.

In order to quantify the habitat preferences of Southern Damselfly larvae we have investigated the biological, physical and chemical attributes of all chalkstream and fen sites where the Southern Damselfly is present and nearby sites where it is not. The associated macroinvertebrates have been described in the previous chapter (Chapter 6). In this chapter Southern Damselfly 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

For full details of sampling locations, please refer to Chapter 6. Sampling locations were surveyed four times over the course of one year. 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 Southern Damselfly 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.

To investigate whether pesticides or metals were having a deleterious impact on Southern Damselfly larvae, we collected additional water samples from a sub-sample of 18 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).

Statistical approaches to measure the association between a species and its habitat generally fall into two classes: regression methods, including generalised linear models, and multivariate ordination. I used both these techniques to investigate the factors associated with the occurrence and abundance of Southern Damselfly larvae. Full details are provided in Box 7.1. Please note that the samples taken from the fen sites in Oxfordshire and Anglesey were quite different from the chalkstream sites in the Itchen and Test Valleys and have been analysed separately.

Box 7.1: Statistical analysis

Generalised linear models

Two types of generalised linear models (GLMs) were fitted to the data. Firstly, Southern Damselfly occurrence was modelled. This 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, Southern Damselfly larval abundance was modelled using a Poisson error structure and a logarithmic link function (Crawley, 1993; Dobson, 2002). In this case, however, the distribution of Southern Damselfly larvae was aggregated, showing marked under-dispersion, particularly in the autumn season, and so a quasi-likelihood function was used, as described in Box 4.1.

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 (PCAs) 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 each for the channel, bankside and chemical variables respectively. 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. This problem has been described in Box 4.1 and was dealt with by adding a series of dummy variables representing each sub-site.

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, as described in Box 4.1. A different GLM was run for each season. Thus four models were produced that related habitat variables to the occurrence of Southern Damselfly larvae and four more related habitat to the abundance of the larvae.

Multivariate ordination

Factors associated with Southern Damselfly 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 Southern Damselfly was present or absent were assessed using ANalysis Of SIMilarities (ANOSIM) and Canonical Discriminant Analysis (CDA) of the principal co-ordinates, as described in Box 6.1.

To identify the plants that were the best indicators of the presence or absence of Southern Damselfly larvae, we used the Indicator Value method (IndVal). However, it was not appropriate to use this 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 Southern Damselfly larval abundance, we used a Canonical Correlation Analysis (CCorA) of the principal co-ordinates, as described in Box 6.1.

7.3 Results

7.3.1 Distribution as a function of habitat – occurrence of Southern Damselfly larvae

Four different models were developed using logistic regression to model the presence or absence of Southern Damselfly larvae in each season for the Itchen and Test locations (Table 7.1). Each model was highly significant and was able to correctly classify a minimum of 79.8% of the sites. In other words, using habitat data alone it was possible to correctly predict whether Southern Damselfly larvae were present or absent for at least 79.8% of sites.

In the autumn season the abundance of emergent dicots was the single best predictor of Southern Damselfly presence, while the abundance of submerged macrophytes was a significant predictor of sites where the species did not occur. Occurrence of larvae was negatively related to bankside principal component 5 (PC5), 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.

In the winter season, seven variables were selected for inclusion in the final model. Channel PC1 and bankside PC1, were both negatively associated with the occurrence of Southern Damselfly larvae. 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 Southern Damselfly occurrence in this season. Southern Damselfly larvae were 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 Southern Damselfly 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, ten habitat parameters were included in this final model. Southern Damselfly 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. Southern Damselfly larvae were associated with low flows

and small substrate sizes (channel PC1), 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.

Table 7.1. Significant predictors of the occurrence of Southern Damselfly larvae, 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 χ^2 tests, parameter estimates and standard errors are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Model	Variable	χ^2	p	Parameter estimates	Standard error
Autumn Deviance = 79.75 $D^2 = 0.395$ Adj. $D^2 = 0.369$ % correct = 79.8	Intercept	4.94	*	-1.225	0.551
	Submerged	7.02	**	-0.0424	0.0160
	Emergent dicots	11.49	***	0.0752	0.0220
	Bankside PC5	7.05	**	-0.664	0.250
	Chemistry PC2	10.00	**	0.603	0.191
Winter Deviance = 74.59 $D^2 = 0.412$ Adj. $D^2 = 0.367$ % correct = 87.0	Intercept	19.27	***	-1.946	0.443
	Channel PC1	9.13	**	-0.409	0.135
	Bankside PC1	4.39	*	-0.417	0.199
	Chemistry PC1	8.04	**	-0.728	0.257
	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 Deviance = 41.93 $D^2 = 0.689$ Adj. $D^2 = 0.654$ % correct = 90.0	Intercept	11.14	***	-7.161	2.145
	Emergent dicots	10.10	**	0.438	0.138
	Channel PC1	4.34	*	0.586	0.281
	Channel PC2	7.74	**	-1.040	0.374
	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 Deviance = 45.83 $D^2 = 0.373$ Adj. $D^2 = 0.353$ % correct = 91.9	Intercept	23.08	***	-3.479	0.724
	Channel PC1	5.30	*	-0.548	0.238
	Chemistry PC2	12.05	***	1.012	0.292
	Site IVCP – Upper	5.15	**	2.033	0.896

7.3.2 Distribution as a function of habitat – abundance of Southern Damselfly larvae

A further four models were developed to relate habitat to Southern Damselfly larval abundance, using Poisson regression (Table 7.2). In the autumn season, Southern Damselfly larvae were more abundant at locations containing greater amounts of emergent dicots, and with channel features comprising 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). Southern Damselfly abundance was strongly negatively associated with bankside fencing (bankside PC4), but was weakly associated with trees on the bankface (bankside PC7). 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 Southern Damselfly 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.

Southern Damselfly larvae were 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 the Southern Damselfly 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 Southern Damselfly larvae tended to have higher levels of scrub on the adjacent land (bankside PC6), 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 7.2. Significant predictors of Southern Damselfly larval 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 χ^2 tests, parameter estimates and standard errors are shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. not significant).

Model	Variable	χ^2	p	Parameter estimates	Standard error
Autumn Deviance = 277.67 d.f. = 89 Dev./d.f. = 3.12 $D^2 = 0.844$ Adj. $D^2 = 0.828$	Intercept	12.52	***	-1.438	0.406
	Emergent dicots	36.73	***	0.0412	0.0068
	Channel PC2	7.33	**	-0.290	0.107
	Channel PC4	5.60	*	-0.329	0.139
	Channel PC5	9.31	**	0.462	0.151
	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 Deviance = 100.66 d.f. = 90 Dev./d.f. = 1.12 $D^2 = 0.875$ Adj. $D^2 = 0.863$	Intercept	33.49	***	-1.394	0.241
	Emergent dicots	37.61	***	0.0532	0.0087
	Channel PC1	6.45	*	-0.171	0.067
	Channel PC5	4.34	*	-0.258	0.124
	Bankside PC1	9.58	**	-0.272	0.088
	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 Deviance = 96.33 d.f. = 87 Dev./d.f. = 1.11 $D^2 = 0.822$ Adj. $D^2 = 0.797$	Intercept	0.92	n.s.	-0.460	0.479
	Submerged	32.53	***	-0.100	0.018
	Emergent dicots	17.47	***	0.100	0.024
	Emergent monocots	8.20	**	-0.035	0.012
	Channel PC5	6.78	**	0.386	0.148
	Channel PC6	8.14	**	-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 Deviance = 55.27 d.f. = 95 Dev./d.f. = 0.582 $D^2 = 0.759$ Adj. $D^2 = 0.751$	Intercept	12.68	***	-3.681	1.034
	Bankside PC6	4.46	*	-0.917	0.434
	Chemistry PC2	10.80	**	1.122	0.341
	Site IVCP – Upper	19.15	***	4.362	0.997

7.3.3 Multivariate ordination – vegetation

A comparison of the vegetation at each sampling location was made using PCoA ordination, and the plots for each season are shown in Figure 7.1. There was a tendency for sites where Southern Damselfly larvae were present to be located towards one side of the ordination plots, although there was considerable overlap. This indicates that the locations where Southern Damselfly larvae occur contain similar vegetation characteristics. Unconstrained ANOSIM tests (Table 7.3a) revealed that the differences between sites with and without the Southern Damselfly 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 7.3a).

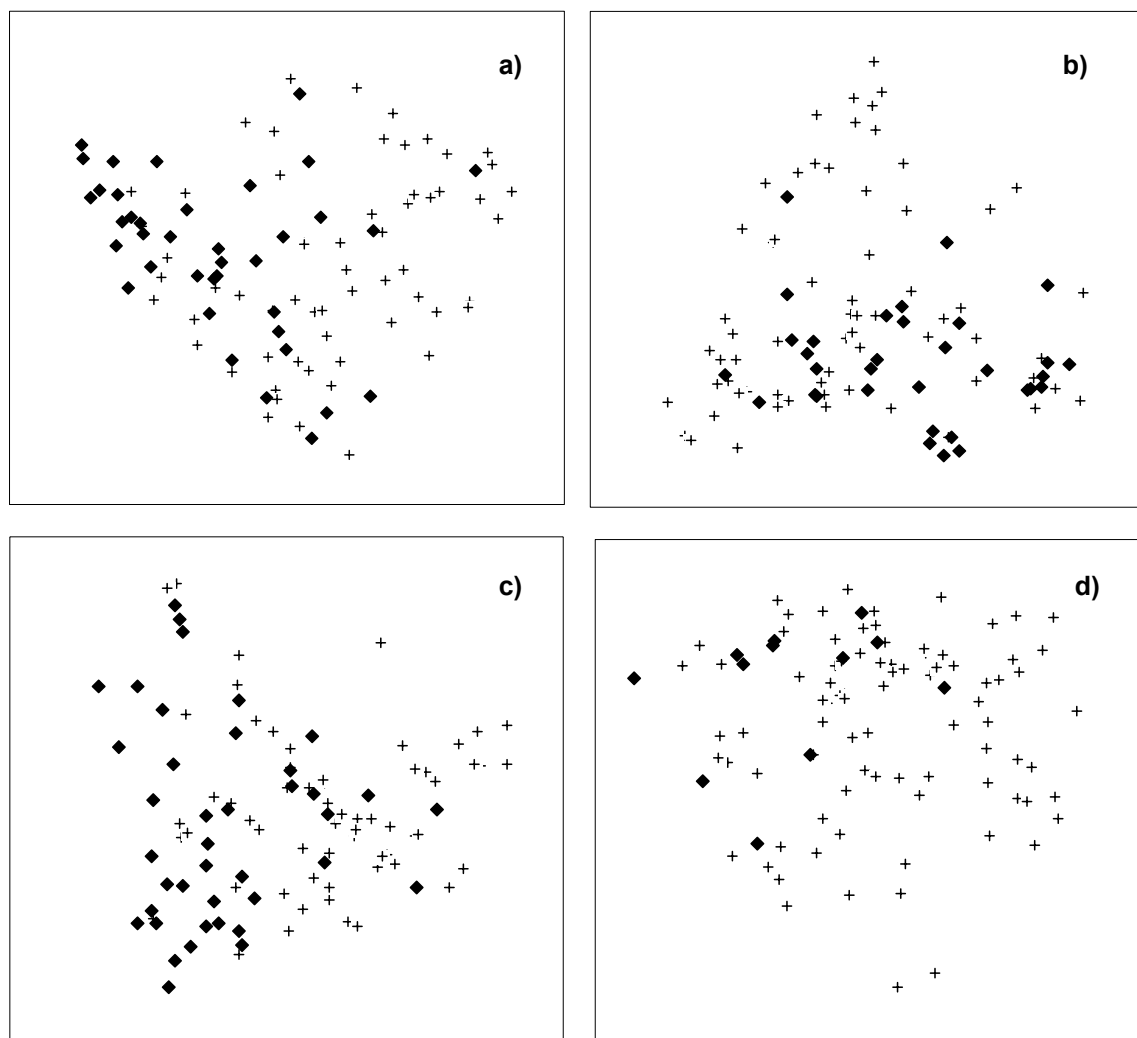


Figure 7.1. Ordination plots showing the first two axes of Principal Co-ordinate Analyses (PCoA) of **vegetation** data for (a) autumn season, (b) winter, (c) spring and (d) summer. Samples are arcsine-transformed percentage cover data and show sites where Southern Damselfly larvae were present (diamonds) and sites where they were absent (+). Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

Table 7.3. ANOSIM, CDA and CCorA results for each season for (a) vegetation data and (b) habitat data. ANOSIM and CDA compare sites with and without Southern Damselfly larvae. CCorA shows the correlation with Southern Damselfly larval 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
<i>p</i>	<0.0001	0.108	0.0017	0.631
CDA: correlation (<i>d</i>)	0.612	0.443	0.586	0.463
<i>d</i> ²	0.375	0.196	0.343	0.214
<i>p</i>	<0.0001	0.0052	<0.0001	0.0167
total correct	73.7%	69.0%	78.0%	77.0%
CCorA: correlation (<i>d</i>)	0.501	0.390	0.465	0.305
<i>d</i> ²	0.251	0.152	0.216	0.093
<i>p</i>	<0.0001	0.2053	0.0038	0.4086
b) Habitat analysis:				
ANOSIM: Global R	0.037	-0.014	0.013	0.169
<i>p</i>	0.125	0.605	0.310	0.0626
CDA: correlation (<i>d</i>)	0.856	0.581	0.910	0.720
<i>d</i> ²	0.733	0.338	0.829	0.519
<i>p</i>	0.0006	0.0005	<0.0001	0.0017
total correct	77.8%	73.0%	82.0%	85.9%
CCorA: correlation (<i>d</i>)	0.549	0.463	0.561	0.903
<i>d</i> ²	0.302	0.215	0.315	0.815
<i>p</i>	0.0053	0.0777	0.0273	0.0297

Table 7.4. Taxa that are indicators of locations where Southern Damselfly larvae were 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	<i>p</i>	IV	<i>p</i>	IV	<i>p</i>	IV	<i>p</i>
1	<i>Apium nodiflorum</i>	Emergent	64.8	***	37.3	***				
	<i>Rorippa nasturtium-aquaticum</i>	Emergent	25.9	*	13.6	**				
	<i>Lemna minor</i> group	Floating			32.5	*				
	<i>Glyceria maxima</i>	Emergent			30.4	*				
	<i>Apium nodiflorum</i>	Submerged			24.0	*				
	<i>Juncus</i> spp.	Emergent			13.3	**	12.5	***	32.5	***
	<i>Glyceria maxima</i>	Submerged			9.0	*				
	<i>Sparganium erectum</i>	Emergent					49.1	**		
	<i>Rumex hydrolapathum</i>	Emergent					39.3	***	24.2	***
	<i>Sparganium erectum</i>	Submerged					13.9	*		
	<i>Phalaris arundinacea</i>	Emergent							59.5	**
2	<i>Callitriche</i> spp.	Submerged	43.2	***						
	<i>Ranunculus</i> spp.	Submerged	40.1	***			32.9	***		
	<i>Sparganium emersum</i>	Submerged	16.4	**						
	<i>Carex</i> spp.	Emergent					37.6	*		

Vegetation taxa that were significant indicators of Southern Damselfly presence or absence are shown in Table 7.4. There were 11 taxa significantly associated with Southern Damselfly larvae, 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 form. Only four taxa were significant indicators of sites where Southern Damselfly larvae were 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.

The plant communities were correlated with Southern Damselfly larval 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 7.3a). Taxa that were most highly correlated with Southern Damselfly larval abundance and occurred in at least 10% of the samples are shown in Table 7.5. The positively correlated taxa are similar to those associated with Southern Damselfly presence (Table 7.4) and included the emergents *Apium nodiflorum*, *Rorippa nasturtium-aquaticum*, *Sparganium erectum* and *Phalaris arundinacea*. Similarly, the negatively correlated taxa included all those associated with Southern Damselfly absence and mostly have a submerged growth form.

Table 7.5. Taxa that are positively (Group 1) or negatively (Group 2) correlated with Southern Damselfly larval 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	<i>Apium nodiflorum</i>	Emergent	0.866	0.891	0.217	0.275
	<i>Sparganium erectum</i>	Emergent	0.356		0.417	0.379
	<i>Lemna minor</i> group	Floating	0.257			
	<i>Veronica anagallis-aquatica</i>	Submerged	0.212			
	<i>Juncus</i> spp.	Emergent			0.299	
	<i>Phalaris arundinacea</i>	Emergent			0.696	0.441
	<i>Rumex hydrolapathum</i>	Emergent			0.318	
	<i>Rorippa nasturtium-aquaticum</i>	Emergent			0.241	0.221
	<i>Ranunculus</i> spp.	Submerged				0.324
2	<i>Ranunculus</i> spp.	Submerged	-0.309		-0.349	
	<i>Callitriche</i> spp.	Submerged	-0.270		-0.265	
	<i>Cladophora</i>	Submerged	-0.246			
	<i>Carex</i> spp.	Emergent	-0.238		-0.314	-0.320
	<i>Sparganium emersum</i>	Submerged	-0.210			-0.370
	<i>Berula erecta</i>	Submerged	-0.209		-0.384	-0.245
	<i>Rorippa nasturtium-aquaticum</i>	Emergent		-0.236		

7.3.4 Multivariate ordination – habitat

The PCoA ordination plots of habitat data for each season are shown in Figure 7.2. The separation of sites where Southern Damsfly larvae were present or absent was less distinct than in the vegetation analysis, and this is reflected in the results of the ANOSIM tests (Table 7.3b). Differences between sites with and without Southern Damsfly larvae were not significant for any season, although differences did become apparent when CDA was performed. In other words, there were real and significant differences between sites with and without the Southern Damsfly, but these differences were not a major source of variation within the data structure. 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 7.3b).

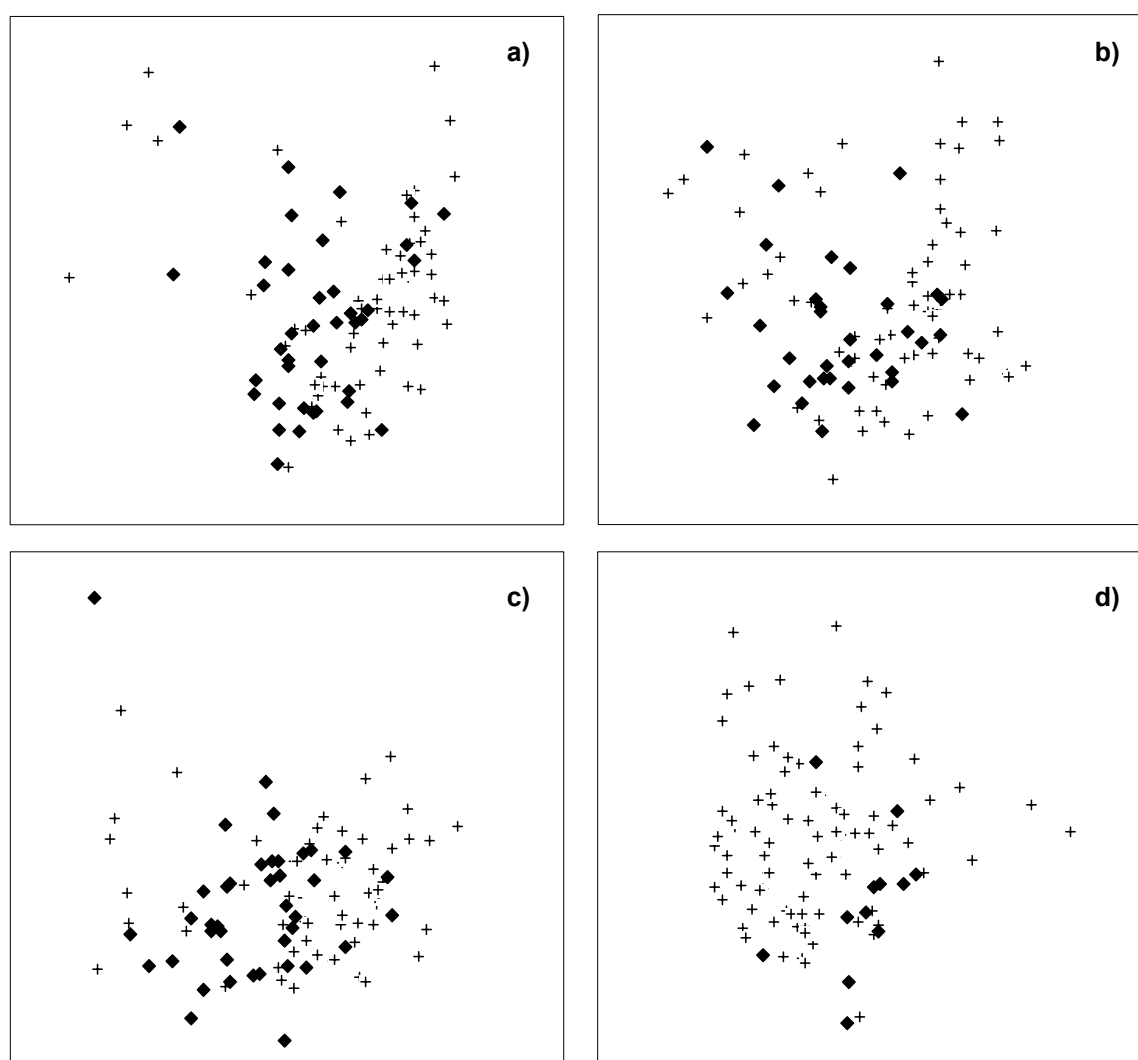


Figure 7.2. Ordination plots showing the first two axes of PCoAs of **habitat** data for (a) autumn season, (b) winter, (c) spring and (d) summer. Samples show sites where Southern Damsfly larvae were present (diamonds) and sites where they were absent (+). Plots represent sample differences in two dimensions, with samples that are similar grouped closely together.

Table 7.6. Variables that are positively (Group 1) or negatively (Group 2) correlated with Southern Damselfly larval 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 (Mean SUBstrate size)	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 and detritus depth > 30 cm		0.363		
	Chloride		0.329	0.472	0.462
	Conductivity		0.283	0.409	
	Water depth 0–5 cm		0.233		
	Salinity			0.417	0.241
	5–50 m – tall herbs and grasses			0.282	0.330
	5–50 m – scrub			0.248	
	Mean water depth			0.228	
	0–5 m – 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
	0–5 m – short herbs and grasses	-0.256		-0.201	
	Silt	-0.203			
	Mean flow		-0.514		-0.254
	Discharge		-0.484		-0.246
	0–5 m – 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
	5–50 m – bare ground		-0.298	-0.236	
	Bankface – bare ground		-0.286	-0.288	
	Silt and detritus depth – 0–5 cm		-0.285		
	Mean water width		-0.259		-0.202
	5–50 m – scrub		-0.204		
	Water depth – 5–30 cm			-0.263	

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 7.6, which includes 24 variables positively correlated with Southern Damselfly 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 Southern Damselfly occurrence included pebbles (four seasons), boulders, gravel, sand, 'run' (three 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 (two 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 Southern Damselfly larval abundance using CCorA was significant in the autumn, spring and summer seasons (at $p < 0.05$), but not in the winter season (Table 7.3b). The positively correlated variables (Table 7.7) 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 Southern Damselfly larval 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			
	5–50 m – bare ground	0.276			
	Bankface – tall herbs and grasses	0.272		0.273	
	5–50 m – scrub	0.247			
	0–5 m – bare ground	0.245			
	Salinity	0.227		0.311	
	5 m – scrub	0.224			
	Nitrite		0.601	0.620	
	0–5 m – tall herbs and grasses		0.445	0.581	
	Conductivity		0.394	0.296	
	Silt		0.374	0.444	
	Ammonia		0.330	0.265	
	5–50 m – tall herbs and grasses		0.303	0.520	
	Silt and detritus depth > 30 cm		0.302	0.287	
	Chloride		0.302	0.367	0.443
	Water depth – 0–5 cm		0.289		
	Alkalinity		0.249		

Table 7.7 cont.

Group	Variable	Autumn	Winter	Spring	Summer
	Water depth – 5–30 cm		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			
	0–5 m – tall herbs and grasses	-0.253			
	5–50 m – short herbs and grasses	-0.243		-0.341	
	Run	-0.234	-0.239		
	Bankface – scrub	-0.231			
	Silt and detritus depth – 5–30 cm	-0.210			
	Bankface – short herbs and grasses	-0.209			
	Discharge		-0.513		
	Mean flow		-0.456	-0.206	
	Mean water width		-0.415		
	5–50 m – bare ground		-0.381		
	0–5 m – bare ground		-0.333	-0.229	
	Suspended solids		-0.290		
	Bankface – bare ground		-0.278		
	Turbidity		-0.277		
	0–5 m – short herbs and grasses		-0.250	-0.506	
	Pebbles		-0.224	-0.338	
	Silt and detritus depth – 0–5 cm		-0.207	-0.218	
	Water depth > 30 cm		-0.204		
	5–50 m – scrub		-0.204		
	Boulders			-0.421	
	Bankfull height			-0.277	

7.3.5 Oxfordshire and Anglesey

Ordination of the vegetation at the Oxfordshire sites revealed that all three locations where Southern Damselfly larvae were present had a similar vegetation composition and that this was somewhat different to most of the locations without larvae. All three occupied locations contained a high percentage cover of emergent dicots in general, and high levels of emergent *Apium nodiflorum* in particular. Two of these sites were adjacent, but one was shaded by a high percentage cover of *Phragmites communis* (common reed). This site contained a far lower abundance of larvae than the open location nearby. Emergent dicots were also in greater abundance at two of the three locations containing Southern Damselfly larvae in Anglesey, although *Apium nodiflorum* and *Rorippa nasturtium-aquaticum* were only present at one of these locations.

The Oxfordshire locations with Southern Damselfly larvae all had intermediate levels of flow compared to the other locations, which were characteristically slow but not stagnant.

Chemical inputs were generally lower than the locations with no flow and the channel substrate consisted almost exclusively of silt and detritus.

At Anglesey, flow also seems to have been the major habitat difference between locations with and without the Southern Damselfly. Flow was extremely limited in the centre of the main area of springs and flushes in Nant Isaf, and in Cors Nant Isaf, and larvae were not found in these two places. Larvae appeared to prefer parts of the fen where distinct channels with a permanent water flow were present. No locations in Anglesey were shaded and all had a silt or organic substrate.

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 Southern Damselfly larvae. 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 Southern Damselfly presence or abundance.

7.4 Discussion

7.4.1 Habitat associations

Southern Damselfly larvae were associated with certain physical, chemical and vegetation characteristics of their habitat in the Itchen and Test Valleys. Generalised linear modelling and multivariate ordination have revealed similar variables with which the larvae are associated, although details vary from season to season and on which method is used. The most consistent variables associated with the occurrence of Southern Damselfly larvae 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 Southern Damselfly larval abundance, the most consistent variables were once again the abundance of emergent dicots, high levels of chloride, nitrite and phosphate, a lack of trees. The species was not associated with deep silt banks (> 30 cm 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 larval 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 Southern Damselfly larvae are associated. Both statistical techniques have shown that the Southern Damselfly 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 larval 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 the Southern Damselfly 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 and 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 Southern Damselfly larvae were apparent using multivariate ordination, as these chemicals were higher in the slow flowing, silt-impacted, vegetation-rich locations favoured by Southern Damselfly larvae. However, larvae 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 Southern Damselfly larvae 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 the Southern Damselfly 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 Southern Damselfly larvae did not occur or were 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 Southern Damselfly larvae were 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.

Southern Damselfly larvae occurred more frequently and were 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 Southern Damselfly 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 Southern Damselfly 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 the Southern Damselfly. Larvae may be associated with these species because the plants offer a refuge from predation, or the larvae's prey is more abundant, or simply because the plants 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 Southern Damselfly larvae were 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 Southern Damselfly larvae 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. The Southern Damselfly 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 among emergent dicots and submerged species were consistent with the above generalisations. However, the

pattern for emergent monocots was less clear, as several species were associated with Southern Damselfly larvae (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 Oxfordshire and Anglesey

The habitat at the Oxfordshire and Anglesey sites was generally different to that found in the Itchen and Test Valleys, and the relatively small number of sampling locations has precluded a more thorough analysis of these sites. However, the habitat features of most importance in determining the occurrence and abundance of Southern Damselfly larvae show remarkable similarity to the chalkstream sites. The most important features are slow, but not still-water flow, the presence of abundant emergent dicots, and a lack of shade. *Apium nodiflorum* has once again proved to be of particular importance for larvae at the Oxfordshire sites, although it is not predominant at the Anglesey locations.

7.4.4 Methodological issues

Habitat variables have been used to predict the occurrence or abundance of a species 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.

Colonisation 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 Southern Damselfly 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.

7.4.5 Conservation implications

The previous chapter showed that Southern Damselfly larvae are 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 the Southern Damselfly 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.

8. Conclusion

Chapter summary

Key conclusions:

- **Itchen Valley:** The Itchen Valley Country Park is one of the most important sites for Southern Damselfly in the UK. To the north of this site, however, the area is largely suboptimal, with only short reaches of good habitat. This has led to the isolation of these populations, putting them at increased risk of extinction in the medium to long term. Successful conservation will involve active management of existing sites, together with the creation (or recreation) of a series of new sites to reconnect populations.
- **Test Valley:** The status and distribution of the species in the Test Valley is far less clear and more comprehensive surveys should be conducted as a matter of urgency.
- **Oxfordshire:** The population in Oxfordshire is faring relatively well at the moment but is at risk in the longer term. Key conservation actions include expansion of the area of suitable habitat in Dry Sandford Pit and the creation of suitable areas in the Cothill Fen complex and other nearby sites.
- **Anglesey:** The Southern Damselfly population at Cors Erddreiniog in Anglesey remains viable, but it is clear that maintaining adequate water levels is vital for the long-term future of the species on this site.

Key recommendations:

- **Monitoring:** Southern Damselflies should be monitored directly by walking a transect to record adult males, and indirectly through habitat monitoring. A list of key habitat attributes is provided.
- **Landscape:** New habitat should be created within 500 m to 1 km of existing sites, to create a series of 'stepping-stones' that would rejoin existing populations.
- **Habitat creation:** Sluice gates should be installed at some sites to enable proper control over water flow. The ditches created should be shallow and slow flowing throughout, or have ample shallow margins. Bank profiles should be shallow or stepped.
- **Ditch management:** Management operations should be carried out every few years on existing sites. Work should be performed on short sections of ditch in rotation or on one side of the channel only. In all deeper channels shallow berms should be created during dredging work.
- **Bankside management:** Banksides should be lightly grazed by cattle right to the water's edge whenever possible. Extensive shading should be avoided. Where ditches flow through arable land, a 10 m strip of land should be left fallow to either side of the channel.

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 the Southern Damselfly in the Itchen and Test Valleys and then review the findings of this report regarding the ecology of the Southern Damselfly in its chalkstream and fen habitats, before proposing some avenues for further research. I will end by providing recommendations regarding the monitoring, conservation and management of the Southern Damselfly.

8.1 The Southern Damselfly in the Itchen and Test Valleys

Knowledge of the distribution and status of the Southern Damselfly in the Itchen Valley has increased vastly in the last six years, due in part to the work presented in this report 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 Southern Damselfly 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 Southern Damselfly, with less than 10 individuals recorded per 100 m of ditch (Röske, 1995) and no sites had more than 50 per 100 m. In comparison, considerably more than 50 individuals per 100 m 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 the Southern Damselfly as my study has shown (Chapter 3).

Despite the strong position of the Southern Damselfly 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 suboptimal, 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 the Southern Damselfly 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 the Southern Damselfly in the Test Valley is far less clear. The species is present in a fairly extensive area close to King's Somborne. Outside this area, however, very little is known. It has not been found in any other locations during survey work, but these surveys have been extremely limited in their overall coverage. It is likely that Southern Damselfly 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 & 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 individuals 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 Southern Damselfly was dredged in the winter of 2003/04, 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 recolonise from nearby. This whole area would benefit from regular monitoring.

8.2 Ecology of the Southern Damselfly in chalkstream habitats

The Southern Damselfly 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 Southern Damselfly 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 Southern Damselfly sites in mainland Europe is similar to that in the Itchen and Test Valleys. All sites containing good populations of Southern Damselfly 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 the Southern Damselfly 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 the UK's historical 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 the Southern Damselfly. The species is extremely sedentary; lifetime movements of greater than 500 m were shown to be rare and only three 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 butterfly, Southern Damselfly movement declined with age. In butterflies, 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 dragonfly *Sympetrum danae* (Michiels & Dhondt, 1991). An

equivalent behavioural mechanism does not appear to be present in the Southern Damselfly, limiting its dispersal capabilities still further.

One of the most intriguing findings presented in this report is that Southern Damselfly 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. The Southern Damselfly will not readily colonise new areas unless they are close to existing sites, suboptimal sites are more likely to be abandoned, and small, isolated sites are at increased risk of extinction.

Inverse density dependent movement of adult Southern Damselflies 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.

Southern Damselfly 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, the larvae 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, Southern Damselfly 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 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 very 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 those 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 life cycle 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 Southern Damselfly 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, Southern Damselfly 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 Southern Damselfly 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 Southern Damselfly 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 the Southern Damselfly (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 report has also examined night-time roosting location of adult Southern Damselflies (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 Southern Damselflies 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 the Southern Damselfly.

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 the Southern Damselfly will involve active management of existing sites, together with the creation (or recreation) of a series of new sites to reconnect populations.

8.3 Status and ecology of the Southern Damselfly in fen habitats

The Southern Damselfly is only confirmed to be breeding at one site in Oxfordshire and one in Anglesey. These remain the only known fen sites in the UK, although the species does occur in similar habitat in other parts of Europe. Fortunately, the Southern Damselfly population in Oxfordshire is faring relatively well at the moment. At Dry Sandford Pit, the population has risen sharply from its first observation in 1996, with less than 10 recorded per visit until 1999, then over 20 in 2000 (Turner, 2000) and over 50 in a single visit in 2002 (J. Rouquette, pers. obs.). The population is clearly thriving at present and there are reports of recent sightings in parts of the nearby Cothill Fen complex of sites (D.J. Thompson, pers. comm.). However, the area of suitable habitat at Dry Sandford Pit is extremely limited and the long-term future of the Southern Damselfly in Oxfordshire is far from assured. Rapid population expansions following establishment at a new site are fairly frequent in insects, but these can often be followed by a crash if suitable habitat is limited. Furthermore, species that are reliant upon a single site are highly prone to extinction through natural, genetic or human pressures. The key to assuring the long-term future of the Southern Damselfly in Oxfordshire is expansion of the area of suitable habitat in Dry Sandford Pit and the creation of suitable areas in the Cothill Fen complex and other nearby sites.

At Cors Erddreiniog in Anglesey the Southern Damselfly population remains viable, but has fluctuated quite strongly in recent years. The peak count recorded on transect varied from 31 in 1997 to 11 the following year (Colley & Howe, 1999), but recovered to 80 in 2002 (J. Rouquette, pers. obs.). Indeed, smaller, more isolated and more northern populations of insects are known to be particularly prone to this type of large fluctuation. In recent years concern has been expressed that the management of the site may have contributed to this variation, although concerns over management appear to have been resolved for the time being. The main spring-fed ditch flowing through Nant Isaf is currently the stronghold for the Southern Damselfly. It still occurs in the more marginal area of springs and flushes slightly to the south, but it is clear that maintaining adequate water levels is vital for the long-term future of the Southern Damselfly on this site.

The habitats at Dry Sandford Pit and Cors Erddreiniog, although superficially very different from the chalkstream sites in the Itchen and Test Valleys, share a number of important characteristics. Water flow remains the single most important habitat feature at all these sites, along with an adequate cover of emergent dicots and a lack of shading. Recent efforts to introduce light grazing onto Dry Sandford Pit and Lashford Lane Fen should be encouraged and monitored closely. Maintaining adequate water levels, together with occasional management of the main spring-fed ditch flowing through Nant Isaf, are the priorities for conserving the Southern Damselfly in Anglesey.

8.4 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 teneral – Although movement patterns of mature adults have been well studied, movement by tenerals (newly emerged immature adults) remains a matter of conjecture. In the related species *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). The Southern Damselfly 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 the Southern Damselfly. 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 the Southern Damselfly 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 here (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 Southern Damselfly 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 the Southern Damselfly – 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 report. 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 the Southern Damselfly on the River Test – It is clear that large gaps remain in our knowledge of the Southern Damselfly in the Test Valley. More comprehensive surveys should be conducted as a matter of urgency to address this issue.

8.5 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 report (Thompson *et al.*, 2003b), detailing background and proposed methodology. Hence only a summary of the key points is provided here.

8.5.1 Monitoring of the Southern Damselfly directly

It would be possible to monitor the Southern Damselfly 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 Southern Damselfly 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).

8.5.2 Monitoring of Southern Damselfly habitat

Although monitoring of adults is being carried out more frequently, habitat monitoring is often ignored. This report has, however, revealed a number of key habitat attributes with which the Southern Damselfly 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 10 m strip of stream could be assessed per 50 m 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 Southern Damselfly 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 conditions for the Southern Damselfly 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.	<i>Lower and upper limit of extent on site:</i> 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 <i>Apium nodiflorum</i> and <i>Rorippa nasturtium-aquaticum</i> . May also include <i>Mentha aquatica</i> , <i>Veronica</i> spp. and <i>Myosotis scorpioides</i> .	<i>Lower and upper limit of cover:</i> 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.	<i>Lower and upper limit of cover:</i> 20–80% in summer, but with seasonal variations.
4. Bankside vegetation with heterogeneous sward of helophyte monocots, typically including <i>Glyceria maxima</i> , <i>Phalaris arundinacea</i> , <i>Sparganium erectum</i> , <i>Iris pseudacorus</i> , <i>Carex</i> spp. and <i>Juncus</i> spp.	<i>Lower and upper limit of extent on site:</i> 30–100% of bankside.
5. Ditch largely unshaded by bankside shrubs and trees.	<i>Lower and upper limit of scrub or trees shading ditch:</i> 0–40% cover.
6. Channel substrate consisting primarily of silt and detritus.	<i>Lower and upper limit of extent on site:</i> 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.	<i>Lower and upper limit of extent on site:</i> 0–10% of watercourse.
8. Ditch surrounded by lightly grazed meadow, containing tussocks of <i>Juncus inflexus</i> or <i>Deschampsia cespitosa</i> .	<i>Lower and upper limit of extent on site:</i> 50–100% meadow in surrounding area, containing 20–80% tussocks.

8.6 Conservation and management

8.6.1 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, the Southern Damselfly 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 suboptimal 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 Southern Damselfly movement parameters. In all studies of the Southern Damselfly, movements of up to 500 m 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 1 km 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 land use 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 the Southern Damselfly 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 Southern Damselfly populations and can be achieved by creating shallow, silty margins with abundant broad-leaved emergent vegetation.

8.6.2 Habitat creation/recreation

One of the most important ways in which Southern Damselfly 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 the Southern Damselfly.

All sites chosen for habitat recreation should be located within easy dispersal of existing colonies. An important prerequisite 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 colonisation 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.

8.6.3 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, Southern Damselfly populations should be monitored and management performed before numbers decline by much. Where healthy populations of Southern Damselfly already exist, management operations should be performed on short sections of ditch in rotation (perhaps 100 m 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 Southern Damselfly population. Dredging will also allow for some reprofiling of the channel. In all deeper channels (> 50 cm 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 the Southern Damselfly.

8.6.4 Bankside management

Bankside and adjacent land management has an important influence on Southern Damselfly 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 Southern Damselflies 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 & 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 the Southern Damselfly 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.



Figure 8.1. A channel in the Itchen Valley Country Park showing a wide fringe of emergent vegetation growing on an underwater berm and a bankside of mixed, lightly grazed vegetation.

8.6.5 Adjacent land use and water quality

All of the chalkstream sites containing good populations of Southern Damselfly 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 10 m 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 the Southern Damselfly in several parts of Europe (e.g. Buchwald, 1994; Goffart, 1995). Although the Southern Damselfly 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.



Figure 8.2. Southern Damselfly pair in copulation.

References

- Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, **84**, 511–525.
- Angelibert, S. & Giani, N. (2003) Dispersal characteristics of three odonate species in a patchy habitat. *Ecography*, **26**, 13–20.
- Anholt, B.R. (1990) Size-biased dispersal prior to breeding in a damselfly. *Oecologia*, **83**, 385–387.
- Anon. (2004a) Natura 2000: Recherche de sites par espèce: Agrion de mercure (*Coenagrion mercuriale*) [online]. Available from: <http://natura2000.environnement.gouv.fr/especes/1044.html>.
- Anon. (2004b) Natura 2000: Fiche du site: Marais Vernier et Basse Vallée de la Risle [online]. Available from: <http://natura2000.environnement.gouv.fr/sites/FR2300122.html>.
- Askew, R.R. (1982) Roosting and resting site selection by Coenagrionid damselflies. *Advances in Odonatology*, **1**, 1–8.
- Askew, R.R. (1988) *The Dragonflies of Europe*. Harley Books, Colchester.
- Banks, M.J. & Thompson, D.J. (1985) Emergence, longevity and breeding area fidelity in *Coenagrion puella* (L.) (Zygoptera: Coenagrionidae). *Odonatologica*, **14**, 279–286.
- Bass, J. (1998) *Last-Instar Larvae and Pupae of the Simuliidae of Britain and Ireland: A Key with Brief Ecological Notes*. Freshwater Biological Association Scientific Publication no. 55. FBA, Ambleside.
- Baur, A. & Baur, B. (1990) Are roads barriers to dispersal in the land snail *Arianta arbustorum*? *Canadian Journal of Zoology*, **68**, 613–617.
- Bennett, S. & Mill, P.J. (1995) Pre- and post-maturation survival in adults of the damselfly *Pyrrhosoma nymphula* (Zygoptera: Coenagrionidae). *Journal of Zoology*, **235**, 559–575.
- Bergman, K.O. & Landin, J. (2002) Population structure and movements of a threatened butterfly (*Lopinga achine*) in a fragmented landscape in Sweden. *Biological Conservation*, **108**, 361–369.
- Berrie, A.D. (1992) The chalk-stream environment. *Hydrobiologia*, **248**, 3–9.
- Betty, J. (1999) The development of water meadows in the southern counties. In *Water Management in the English Landscape: Field, Marsh and Meadow* (eds H. Cook & T. Williamson). Edinburgh University Press, Edinburgh.
- Beukema, J.J. (2002) Changing distribution patterns along a stream in adults of *Calopteryx haemorrhoidalis* (Odonata: Calopterygidae): a case of larval-drift compensation? *International Journal of Odonatology*, **5**, 1–14.
- Bhattacharya, M., Primack, R.B., & Gerwein, J. (2003) Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biological Conservation*, **109**, 37–45.
- Bilton, D.T., Freeland, J.R., & Okamura, B. (2001) Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, **32**, 159–181.
- Bousfield, L. (2003) *So you want to be a detective? What do the larvae of the Southern Damselfly, Coenagrion mercuriale (Odonata: Zygoptera) feed upon?* BSc. Thesis, University of Liverpool, Liverpool.

- Bowie, G.G.S. (1987) Watermeadows in Wessex – a re-evaluation for the period 1640–1850. *Agricultural History Review*, **35**, 151–158.
- Boyce, D.C. (2002) Southern Damselfly *Coenagrion mercuriale* GB Site Assessment Project. CCW Contract Science No. 537, Countryside Council for Wales.
- Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J., & Wilson, J.D. (2000) Habitat associations and breeding success of yellowhammers on lowland farmland. *Journal of Applied Ecology*, **37**, 789–805.
- Briers, R.A., Cariss, H.M., & Gee, J.H.R. (2002) Dispersal of adult stoneflies (Plecoptera) from upland streams draining catchments with contrasting land-use. *Archiv für Hydrobiologie*, **155**, 627–644.
- Briers, R.A., Gee, J.H.R., Cariss, H.M., & Geoghegan, R. (2004) Inter-population dispersal by adult stoneflies detected by stable isotope enrichment. *Freshwater Biology*, **49**, 425–431.
- Brooks, S.J. (1993) Review of a method to monitor adult dragonfly populations. *Journal of the British Dragonfly Society*, **9**, 1–4.
- Brooks, S., ed. (1997) *Field Guide to the Dragonflies and Damselflies of Great Britain and Ireland*. British Wildlife Publishing, Hampshire.
- Brown, I.L. & Ehrlich, P.R. (1980) Population biology of the checkerspot butterfly, *Euphydryas chalcedona*. Structure of the Jasper Ridge colony. *Oecologia*, **47**, 239–251.
- Buchwald, R. (1983) Kalkquellmoore und Kalkquellsümpfe als Lebensraum gefährdeter Libellenarten im westlichen Bodenseeraum. *Telma*, **13**, 91–98.
- Buchwald, R. (1989) Die Bedeutung der Vegetation für die Habitatbindung einiger Libellenarten der Quellmoore und Fließgewässer. *Phytocoenologia*, **17**, 307–448.
- Buchwald, R., Höppner, B., & Röske, W. (1989) Gefährdung und Schutzmöglichkeiten grundwasserbeeinflusster Wiesenbäche und -gräben in der Oberrheinebene. *Natur und Landschaft*, **64**, 398–403.
- Buchwald, R. (1994) Zur Bedeutung der Artenzusammensetzung und Struktur von Fließgewässer-Vegetation für die Libellenart *Coenagrion mercuriale* mit Bemerkungen zur Untersuchungsmethodik. *Ber. D. Reinh.-Tüxen-Ges.*, **6**, 61–81.
- Bullock, J.M., Kenward, R.E., & Hails, R.S., eds. (2002) *Dispersal Ecology*. Blackwell Publishing, Oxford.
- CCW (1988) *Agreed Management Policy Cors Erddreiniog*. The Countryside Council for Wales.
- Chamberlain, D.E., Wilson, A.M., Browne, S.J., & Vickery, J.A. (1999) Effects of habitat type and management on the abundance of skylarks in the breeding season. *Journal of Applied Ecology*, **36**, 856–870.
- Clarke, K.R. & Warwick, R.M. (1994) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Natural Environmental Research Council.
- Clobert, J., Danchin, E., Dhondt, A.A., & Nichols, J.D., eds. (2001) *Dispersal*. Oxford University Press, New York.
- Colley, L.T. (1983) *Coenagrion mercuriale* (Charpentier) in Anglesey, North Wales. *Journal of the British Dragonfly Society*, **1**, 27.
- Colley, L.T. (1993) *Coenagrion mercuriale* – Cors Erddreiniog. Filenote for CCW.
- Colley, L.T. & Howe, M.A. (1998) Monitoring of the southern damselfly (*Coenagrion mercuriale*) at Nant Isaf Spring Field, Cors Erddreiniog SSSI in 1997. Filenote for CCW.

- Colley, L.T. & Howe, M.A. (1999) Monitoring of the southern damselfly (*Coenagrion mercuriale*) at Nant Isaf Spring Field, Cors Erddreiniog SSSI in 1998. Filenote for CCW.
- Conrad, K.F. & Herman, T.B. (1990) Seasonal dynamics, movements and the effects of experimentally increased female densities on a population of imaginal *Calopteryx aequabilis* (Odonata: Calopterygidae). *Ecological Entomology*, **15**, 119–129.
- Conrad, K.F., Willson, K.H., Harvey, I.F., Thomas, C.J., & Sherratt, T.N. (1999) Dispersal characteristics of seven odonate species in an agricultural landscape. *Ecography*, **22**, 524–531.
- Conrad, K.F., Willson, K.H., Whitfield, K., Harvey, I.F., Thomas, C.J., & Sherratt, T.N. (2002) Characteristics of dispersing *Ischnura elegans* and *Coenagrion puella* (Odonata): age, sex, size, morph and ectoparasitism. *Ecography*, **25**, 439–445.
- Corbet, P.S. (1955) The larval stages of *Coenagrion mercuriale* (Charp.) (Odonata: Coenagriidae). *Proceedings of the Royal Entomological Society of London (A)*, **30**, 115–126.
- Corbet, P.S. (1957) The life-histories of two summer species of dragonfly (Odonata: Coenagriidae). *Proceedings of the Zoological Society of London*, **128**, 403–418.
- Corbet, P.S. (1999) *Dragonflies: Behaviour and Ecology of Odonata*. Harley Books, Colchester.
- Cordoba-Aguilar, A. (1994) Adult survival and movement in males of the damselfly *Hetaerina cruentata* (Odonata: Calopterygidae). *Florida Entomologist*, **77**, 256–264.
- Courchamp, F., Clutton-Brock, T., & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, **14**, 405–410.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Crawley, M.J. (2002) *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. Wiley, Chichester.
- Cutting, R. & Cummings, I. (1999) Water meadows: their form, operation and plant ecology. In *Water Management in the English Landscape: Field, Marsh and Meadow* (eds H. Cook & T. Williamson). Edinburgh University Press, Edinburgh.
- De Knijf, G. & Demolder, H. (2000) Een populatie van *Coenagrion mercuriale* en *Libellula fulva* in de Gaume (Belgisch Lotharingen). *Gomphus*, **16**, 115–122.
- Deliry, C. & Grand, D. (1998) L'Agrion de Mercure (*Coenagrion mercuriale*) dans la Moyenne Vallée du Rhône [online]. Available from: <http://cyrille.deliry.free.fr/odonates/mercure/mvrcoemer.htm>.
- Dennis, R.L.H. (2004) Just how important are structural elements as habitat components? Indications from a declining lycaenid butterfly with priority conservation status. *Journal of Insect Conservation*, **8**, 37–45.
- Denno, R.F. & Peterson, M.A. (1995) Density-dependent dispersal and its consequences for population dynamics. In *Population Dynamics: New Approaches and Synthesis* (eds N. Cappuccino & P.W. Price), pp. 113–130. Academic Press, London.
- Dieckmann, U., O'Hara, B., & Weisser, W. (1999) The evolutionary ecology of dispersal. *Trends in Ecology and Evolution*, **14**, 88–90.
- Disney, R.H.L. (1999) *British Dixidae (Meniscus Midges) and Thaumaleidae (Trickle Midges): Keys with Ecological Notes*. Freshwater Biological Association Scientific Publication no. 56. FBA, Ambleside.
- Dobson, A.J. (2002) *An Introduction to Generalized Linear Models* Chapman & Hall, London.

- Dover, J.W., Sparks, T.H., & Greatorex-Davies, J.N. (1997) The importance of shelter for butterflies in open landscapes. *Journal of Insect Conservation*, **1**, 89–97.
- Drake, C.M. (1995) The effects of cattle poaching on insects living at the margin of the River Itchen, Hampshire. *British Journal of Entomology and Natural History*, **8**, 165–169.
- Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.
- EBC (1995) Itchen Valley Nature Reserve Management Plan. Unpublished manuscript, Eastleigh Borough Council.
- Ecke, F., Lofgren, O., & Sorlin, D. (2002) Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *Journal of Applied Ecology*, **39**, 781–792.
- Elliott, J.M. & Mann, K.H. (1979) *A Key to the British Freshwater Leeches, with Notes on their Life Cycles and Ecology*. Freshwater Biological Association Scientific Publication no. 40. FBA, Ambleside.
- Elliott, J.M., Humpesch, U.H., & Macan, T.T. (1988) *Larvae of the British Ephemeroptera: A Key with Ecological Notes*. Freshwater Biological Association Scientific Publication no. 49. FBA, Ambleside.
- Elliott, J.M. (2003) A comparative study of the dispersal of 10 species of stream invertebrates. *Freshwater Biology*, **48**, 1652–1668.
- EN (1986) SSSI Notification: Dry Sandford Pit. English Nature.
- EN (1993) SSSI Notification: Cothill Fen. English Nature.
- EN (1996) SSSI Notification: River Test. English Nature.
- EN (2000a) SSSI Notification: River Itchen. English Nature.
- EN (2000b) Reasons for recommendation as a candidate Special Area of Conservation: River Itchen. English Nature.
- Environment Agency (1999) *Procedures for Collecting and Analysing Macroinvertebrate Samples*. BT001. Issue 2. Environment Agency, Bristol.
- Evans, F. (1989) A review of the management of lowland wet heath in Dyfed, west Wales, Rep. No. 42. Nature Conservancy Council, Peterborough.
- Extence, C.A., Balbi, D.M., & Chadd, R.P. (1999) River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. *Regulated Rivers: Research & Management*, **15**, 543–574.
- Fonseca, D.M. & Hart, D.D. (2001) Colonization history masks habitat preferences in local distributions of stream insects. *Ecology*, **82**, 2897–2910.
- Forman, R.T.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, **29**, 207–231.
- Fowles, A.P. & Colley, L.T. (1999) Southern Damselfly site dossier – Cors Erddreiniog (including Nant Isaf). CCW.
- Friday, L.E. (1988) *A Key to the Adults of British Water Beetles*. Field Studies Council Publication 189, Taunton.
- Garrison, R.W. (1978) A mark-recapture study of imaginal *Enallagma cyathigerum* (Charpentier) and *Argia vivida* Hagen (Zygoptera: Coenagrionidae). *Odonatologica*, **7**, 223–236.
- Gilbert, L.E. & Singer, M.C. (1973) Dispersal and gene flow in a butterfly species. *The American Naturalist*, **107**, 58–72.

- Goffart, P. (1995) Situation actuelle de l'Agrion de Mercure (*Coenagrion mercuriale*) en Wallonie et propositions de mesures visant sa conservation. *Gomphus*, **11**, 27–40.
- Goffart, P., Testaert, D., & Paquay, M. (2001) Actualisation du statut de l'Agrion de Mercure (*Coenagrion mercuriale*) dans la plaine de Focant (Beauraing). *Gomphus*, **17**, 83–94.
- Grand, D. (1996) *Coenagrion mercuriale* (Charpentier, 1840). In *Background information on invertebrates of the Habitats Directive and the Bern Convention. Part II – Mantodea, Odonata, Orthoptera and Arachnida* (eds P.J.v. Helsdingen, L. Willemse & M.C.D. Speight), Vol. 80, pp. 245–253. Council of Europe Publishing.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Guisan, A., Edwards, T.C., & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157**, 89–100.
- Hagler, J.R. & Jackson, C.G. (2001) Methods for marking insects: current techniques and future prospects. *Annual Review of Entomology*, **46**, 511–543.
- Hall, D.L., Bergthold, B.S., & Sites, R.W. (2003) The influence of adjacent land uses on macroinvertebrate communities of prairie streams in Missouri. *Journal of Freshwater Ecology*, **18**, 55–68.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.
- Harrison, S.S.C. (2000) The importance of aquatic margins to invertebrates in English chalk streams. *Archiv für Hydrobiologie*, **149**, 213–240.
- Harrison, S.S.C. & Harris, I.T. (2002) The effects of bankside management on chalk stream invertebrate communities. *Freshwater Biology*, **47**, 2233–2245.
- Heikkinen, R.K. & Neuvonen, S. (1997) Species richness of vascular plants in the subarctic landscape of northern Finland: modelling relationships to the environment. *Biodiversity and Conservation*, **6**, 1181–1201.
- Henderson, I.G., Vickery, J.A., & Carter, N. (2004) The use of winter bird crops by farmland birds in lowland England. *Biological Conservation*, **118**, 21–32.
- Higashi, K. & Ueda, T. (1982) Territoriality and movement pattern in a population of *Calopteryx cornelia* (Selys) (Zygoptera: Calopterygidae). *Odonatologica*, **11**, 129–137.
- HMSO (1994) *Biodiversity: The UK Action Plan*. HMSO, London.
- HMSO (1995) *Biodiversity: The UK Steering Group Report – Volume 2: Action Plans*. HMSO, London.
- Hold, A.J. (1994) Itchen Valley Country Park Dragonfly Survey. Unpublished report.
- Hold, A.J. (1998) Survey of the Southern Damselfly (*Coenagrion mercuriale*), the Itchen Valley Country Park 1997. Unpublished report.
- Howe, M.A. (1997) Monitoring of the southern damselfly (*Coenagrion mercuriale*) at Nant Isaf Spring Field, Cors Erddreiniog. Filenote for CCW.
- Hunger, H. & Röske, W. (2001) Short-range dispersal of the southern damselfly (*Coenagrion mercuriale*, Odonata) defined experimentally using UV fluorescent ink. *Zeitschrift für Ökologie und Naturschutz*, **9**, 181–187.
- Jaberg, C. & Guisan, A. (2001) Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *Journal of Applied Ecology*, **38**, 1169–1181.

- Jacquemin, G. (1994) Odonata of the Rif, northern Morocco. *Odonatologica*, **23**, 217–237.
- Jenkins, D.K. (1987) A population study of *Coenagrion mercuriale* (Charpentier) at a New Forest site. Part 3. Diurnal variation. *Journal of the British Dragonfly Society*, **3**, 17–20.
- Jenkins, D.K., Parr, M.J., Moore, N.W., & Silsby, J. (1998) Management guidelines for the southern damselfly. In *Species Management in Aquatic Habitats* (ed C.P. Mainstone). Environment Agency, Bristol.
- Jenkins, D.K. (1998) A population study of *Coenagrion mercuriale* (Charpentier) at a New Forest site. Part 7. Mark/recapture used to determine the extent of local movement. *Journal of the British Dragonfly Society*, **14**, 1–4.
- Keller, I. & Lurgiader, C.R. (2003) Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Proceedings of the Royal Society of London Series B*, **270**, 417–423.
- Kerney, M. (1999) *Atlas of the Land and Freshwater Molluscs of Britain and Ireland*. Harley Books, Colchester.
- Killeen, I., Aldridge, D., & Oliver, G. (2004) *Freshwater Bivalves of Britain and Ireland*. Field Studies Council Occasional Publication 82, Shrewsbury.
- Kindvall, O., Vessby, K., Berggren, A., & Hartman, G. (1998) Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli*: an experimental study. *Oikos*, **81**, 449–457.
- Kuhn, K. (1998) *Coenagrion mercuriale* (Charpentier 1840). Unpublished manuscript.
- Kuussaari, M., Nieminen, M., & Hanski, I. (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology*, **65**, 791–801.
- Kuussaari, M., Saccheri, I., Camara, M., & Hanski, I. (1998) Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos*, **82**, 384–392.
- Laurance, W.F. (1997) A distributional survey and habitat model for the endangered northern bettong *Bettongia tropica* in tropical Queensland. *Biological Conservation*, **82**, 47–60.
- Lawton, J.H. (1970) Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata: Zygoptera). *Journal of Animal Ecology*, **39**, 669–689.
- Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm. *Ecology*, **74**, 1659–1673.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. 2nd English edition. Elsevier, Amsterdam.
- Lucas, W.J. (1900) *British Dragonflies (Odonata)*. L. Upcott Gill, London.
- Ludwig, J.A. & Reynolds, J.F. (1988) Diversity indices. In *Statistical Ecology: A Primer in Methods and Computing*, pp. 85–103. John Wiley & Sons.
- Macan, T.T. (1977) *A Key to the British Fresh- and Brackish-Water Gastropods with Notes on their Ecology*, 4th edition. Freshwater Biological Association Scientific Publication no. 13. FBA, Ambleside.
- MacNally, R., Fleishman, E., Fay, J.P., & Murphy, D.D. (2003) Modelling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin of western North America. *Biological Conservation*, **110**, 21–31.
- Mader, H.J. (1984) Animal habitat isolation by roads and agricultural fields. *Biological Conservation*, **29**, 81–96.

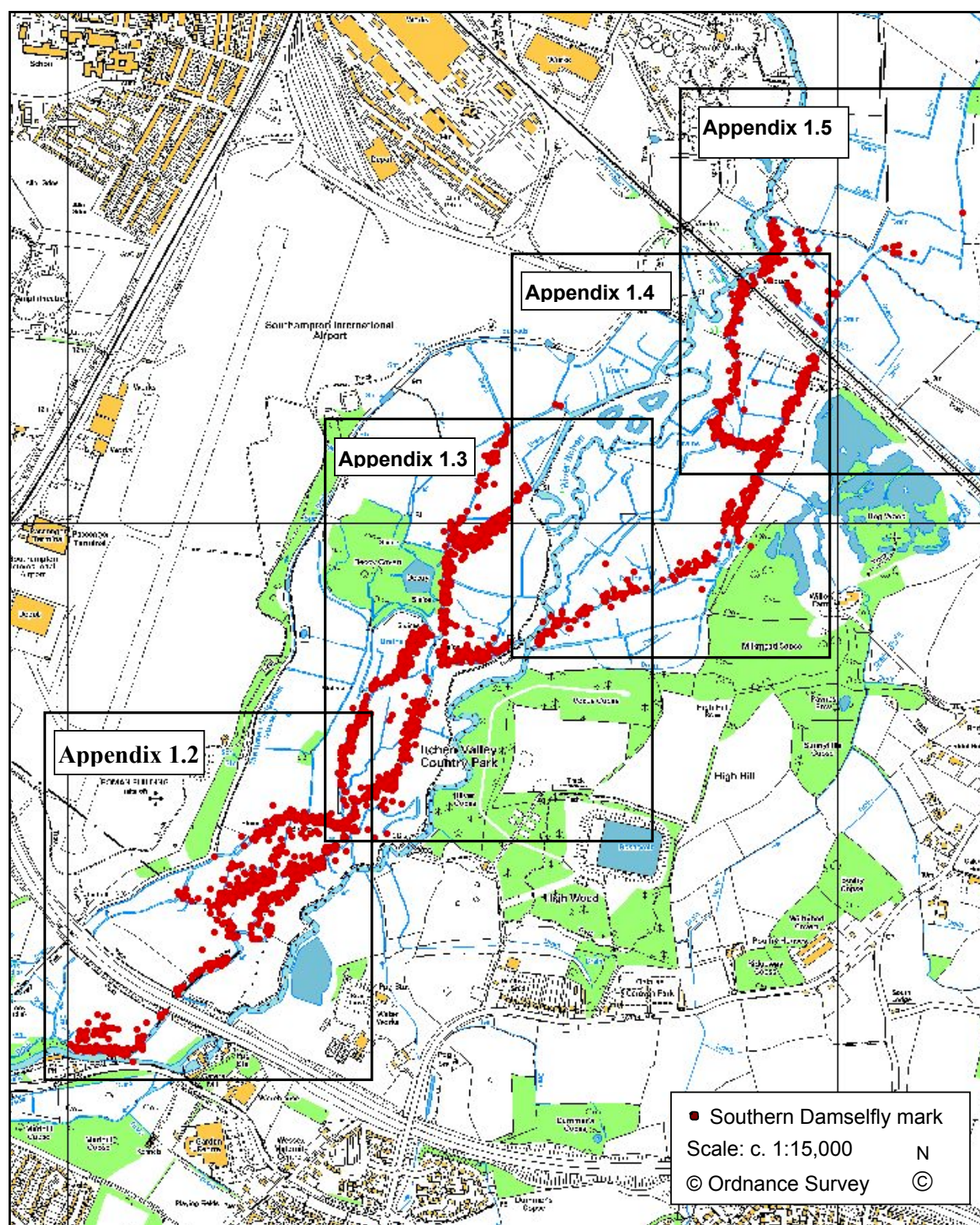
- Maggini, R., Guisan, A., & Cherix, D. (2002) A stratified approach for modeling the distribution of a threatened ant species in the Swiss National Park. *Biodiversity and Conservation*, **11**, 2117–2141.
- Mainstone, C.P. (1999) *Chalk Rivers – Nature Conservation and Management*. English Nature and Environment Agency, Peterborough.
- Manel, S., Buckton, S.T., & Ormerod, S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology*, **37**, 756–770.
- Martens, A. (2000) Group oviposition in *Coenagrion mercuriale* (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica*, **29**, 329–332.
- Matter, S.F. & Roland, J. (2002) An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. *Ecological Entomology*, **27**, 308–316.
- Mayo, M.C.A. & Welstead, A.R. (1983) *Coenagrion mercuriale* (Charpentier) on the flood plains of the River Itchen and River Test in Hampshire. *Journal of the British Dragonfly Society*, **1**, 20–21.
- McCullagh, P. & Nelder, J.A. (1983) *Generalized Linear Models*. Chapman & Hall, London.
- McGeoch, M.A. & Chown, S.L. (1998) Scaling up the value of bioindicators. *Trends in Ecology and Evolution*, **13**, 46–47.
- McKee, D., Harvey, I.F., Thompson, D.J., & Sherratt, T.N. (2005) Frequency of female colour morphs in populations of four coenagrionid damselflies. *Odonatologica*, **34**, 39–47.
- Meggs, J.M., Munks, S.A., Corkrey, R., & Richards, K. (2004) Development and evaluation of predictive habitat models to assist the conservation planning of a threatened lucanid beetle, *Hoplogonus simsoni*, in north-east Tasmania. *Biological Conservation*, **118**, 501–511.
- Menendez, R., Gutierrez, D., & Thomas, C.D. (2002) Migration and Allee effects in the six-spot burnet moth *Zygaena filipendulae*. *Ecological Entomology*, **27**, 317–325.
- Merritt, R. (1983) Scarce species status report. 1. *Coenagrion mercuriale* (Charpentier) with notes on habitat. *Journal of the British Dragonfly Society*, **1**, 9–12.
- Merritt, R., Moore, N.W., & Eversham, B.A. (1996) *Atlas of the Dragonflies of Britain and Ireland*. HMSO.
- Michiels, N.K. & Dhondt, A.A. (1991) Characteristics of dispersal in sexually mature dragonflies. *Ecological Entomology*, **16**, 449–459.
- Neubauer, K. & Rehfeldt, G. (1995) Roosting site selection in the damselfly species *Calopteryx haemorrhoidalis* (Odonata: Calopterygidae). *Entomologia Generalis*, **19**, 291–302.
- O'Farrell, A.F. (1971) Roosting and related activities in some Australian Zygoptera. *Journal of Entomology*, **46**, 79–87.
- Odendaal, F.J., Turchin, P., & Stermitz, F.R. (1988) An incidental-effect hypothesis explaining aggregation of males in a population of *Euphydryas anicia*. *The American Naturalist*, **132**, 735–749.
- Olsen, L.-H., Sunesen, J., & Pedersen, B.V. (2001) *Small Freshwater Creatures*. Oxford University Press, Oxford.
- Pardo, I. & Armitage, P.D. (1997) Species assemblages as descriptors of mesohabitats. *Hydrobiologia*, **344**, 111–128.
- Paul, J. (1998) On the mysterious occurrence of *Coenagrion mercuriale* (Charpentier) at Cothill. *Journal of the British Dragonfly Society*, **14**, 28–30.

- Pearce, J. & Ferrier, S. (2001) The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation*, **98**, 33–43.
- Pollard, E. (1977) A method of assessing changes in the abundance of butterflies. *Biological Conservation*, **12**, 115–134.
- Pollard, E. & Yates, T.J. (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London.
- Purse, B.V. (2001) *The Ecology and Conservation of the Southern Damselfly (Coenagrion mercuriale)*. PhD Thesis, University of Liverpool, Liverpool, UK.
- Purse, B.V. & Thompson, D.J. (2002) Voltinism and larval growth pattern in *Coenagrion mercuriale* (Odonata: Coenagrionidae) at its northern range margin. *European Journal of Entomology*, **99**, 11–18.
- Purse, B.V. & Thompson, D.J. (2003a) Emergence of the damselflies, *Coenagrion mercuriale* and *Ceriagrion tenellum* (Odonata: Coenagrionidae), at their northern range margins, in Britain. *European Journal of Entomology*, **100**, 93–99.
- Purse, B.V. & Thompson, D.J. (2003b) Reproductive morphology and behaviour in *Coenagrion mercuriale* (Charpentier) (Zygoptera: Coenagrionidae). *Odonatologica*, **32**, 29–37.
- Purse, B.V., Hopkins, G.W., Day, K.J., & Thompson, D.J. (2003) Dispersal characteristics and management of a rare damselfly. *Journal of Applied Ecology*, **40**, 716–728.
- Purse, B.V. & Thompson, D.J. (2005) Lifetime mating success in a marginal population of a damselfly, *Coenagrion mercuriale*. *Animal Behaviour*, **69**, 1303–1315.
- Robinson, R.A., Wilson, J.D., & Crick, H.Q.P. (2001) The importance of arable habitat for farmland birds in grassland landscapes. *Journal of Applied Ecology*, **38**, 1059–1069.
- Roland, J., Keyghobadi, N., & Fownes, S. (2000) Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology*, **81**, 1642–1653.
- Röske, W. (1995) Die Helm-Azurjungfer (*Coenagrion mercuriale*, Odonata) in Baden-Württemberg – Aktuelle Bestandssituation und erste Erfahrungen mit dem Artenhilfsprogramm. *Zeitschrift für Ökologie und Naturschutz*, **4**, 29–37.
- Rundle, S.D., Foggo, A., Choiseul, V., & Bilton, D.T. (2002) Are distribution patterns linked to dispersal mechanism? An investigation using pond invertebrate assemblages. *Freshwater Biology*, **47**, 1571–1581.
- Rushton, S.P., Ormerod, S.J., & Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology*, **41**, 193–200.
- Sagova-Mareckova, M. (2002) Interactions between crayfish, benthic invertebrates, macrophyte roots and sediment in a littoral zone. *Archiv für Hydrobiologie*, **155**, 645–665.
- SAS Institute Inc. (1999) *SAS OnlineDoc*. SAS Institute Inc., Cary, NC.
- Savage, A.A. (1989) *Adults of the British Aquatic Hemiptera Heteroptera: A Key with Ecological Notes*. Freshwater Biological Association Scientific Publication no. 50. FBA, Ambleside.
- Schneider, C. (2003) The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. *Ecological Entomology*, **28**, 252–256.
- Schutte, G., Reich, M., & Plachter, H. (1997) Mobility of the rheobiont damselfly *Calopteryx splendens* (Harris) in fragmented habitats (Zygoptera: Calopterygidae). *Odonatologica*, **26**, 317–327.
- Scott, J.A. (1973) Convergence of population biology and adult behaviour in two sympatric butterflies, *Neominois ridingsii* (Papilionoidea: Nymphalidae) and *Amblyscirtes simius* (Hesperioidae: Hesperiidae). *Journal of Animal Ecology*, **42**, 663–672.

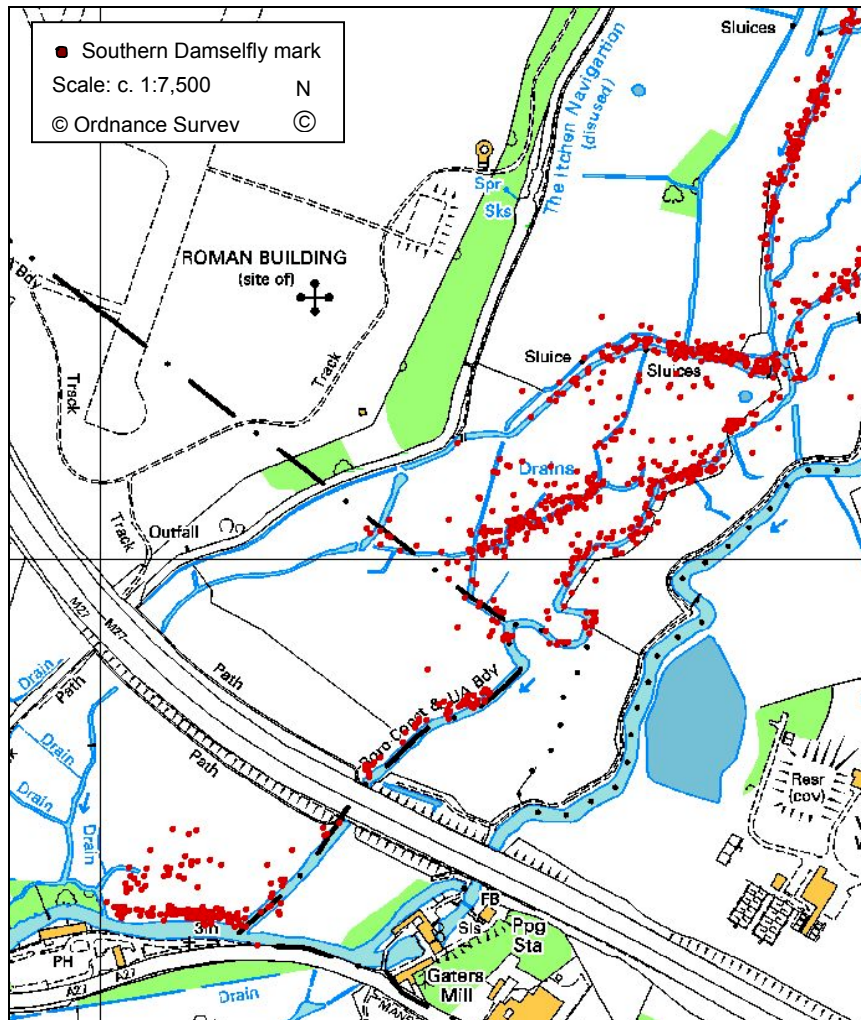
- Sherratt, T.N. (2001) The evolution of female-limited polymorphisms in damselflies: a signal detection model. *Ecology Letters*, **4**, 22–29.
- Shirt, D.B., ed. (1987) *British Red Data Books: 2. Insects*. Nature Conservancy Council, Peterborough.
- Smallshire, D. & Swash, A. (2004) *Britain's Dragonflies*. WILDGuides, Hampshire.
- Smith, K.G.V. (1989) *An Introduction to the Immature Stages of British Flies*. Handbooks for the Identification of British Insects: Volume 10, Part 14. Royal Entomological Society, London.
- Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biological Reviews*, **37**, 171–214.
- Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution*, **14**, 401–405.
- Stephens, P.A., Sutherland, W.J., & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.
- Sternberg, K., Buchwald, R., & Röske, W. (1999) *Coenagrion mercuriale*. In *Die Libellen Baden-Württemberg* (eds K. Sternberg & R. Buchwald), pp. 255–270. Eugen Ulmer Press, Stuttgart.
- Stettmer, C. (1996) Colonisation and dispersal patterns of banded (*Calopteryx splendens*) and beautiful demoiselles (*C. virgo*) (Odonata: Calopterygidae) in south-east German streams. *European Journal of Entomology*, **93**, 579–593.
- Stevens, J. & Thurner, M. (1999) *A 1998 Survey to Further Investigate the Status and Distribution of the Southern Damselfly (Coenagrion mercuriale) in Hampshire*. Environment Agency, Bristol.
- Stoks, R. (2001a) Male-biased sex ratios in mature damselfly populations: real or artefact? *Ecological Entomology*, **26**, 181–187.
- Stoks, R. (2001b) What causes male-biased sex ratios in mature damselfly populations? *Ecological Entomology*, **26**, 188–197.
- Strange, A. & Burt, S. (1998) Southern Damselfly *Coenagrion mercuriale* Survey at Itchen Valley Country Park. Unpublished report.
- Strange, A. (1999) *Distribution of Southern Damselfly on the River Itchen*. Ecological Planning and Research, Winchester.
- Strange, A. (2000) *Distribution of Southern Damselfly on the River Test*. Ecological Planning and Research, Winchester.
- Sutherland, W.J., Gill, J.A., & Norris, K. (2002) Density-dependent dispersal in animals: concepts, evidence, mechanisms and consequences. In *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R.S. Hails). Blackwell Publishing, Oxford.
- Switzer, P.V. & Grether, G.F. (2000) Characteristics and possible functions of traditional night roosting aggregations in rubyspot damselflies. *Behaviour*, **137**, 401–416.
- Telfer, S., Holt, A., Donaldson, R., & Lambin, X. (2001) Metapopulation processes and persistence in remnant water vole populations. *Oikos*, **95**, 31–42.
- Ternaat, T. (1999) Ontdekking van een populatie van *Coenagrion mercuriale* (Charpentier, 1840) nabij Virton. *Gomphus*, **15**, 29–31.
- Thomas, J.A. (1994) Why small cold-blooded insects pose different conservation problems to birds in modern landscapes. *Ibis*, **137**, S112–S119.
- Thompson, D.J. (1978) The natural prey of larvae of the damselfly *Ischnura elegans* (Odonata: Zygoptera). *Freshwater Biology*, **8**, 377–384.

- Thompson, D.J. & Purse, B.V. (1999) A search for long-distance dispersal in the southern damselfly *Coenagrion mercuriale* (Charpentier). *Journal of the British Dragonfly Society*, **15**, 46–50.
- Thompson, D.J., Rouquette, J.R., & Purse, B.V. (2003a) *Ecology of the Southern Damselfly, Coenagrion mercuriale*. Conserving Natura 2000 Rivers Ecology Series No. 8, English Nature, Peterborough.
- Thompson, D.J., Purse, B.V., & Rouquette, J.R. (2003b) *Monitoring the Southern Damselfly, Coenagrion mercuriale*. Conserving Natura 2000 Rivers Monitoring Series No. 8, English Nature, Peterborough.
- Thompson, D.J. & Rouquette, J.R. (2004) Variation in the ‘mercury mark’ of the Southern Damselfly *Coenagrion mercuriale* (Charpentier) in Britain. *Journal of the British Dragonfly Society*, **20**, 17–21.
- Turner, M. (2000) The status of southern damselfly *Coenagrion mercuriale* at selected Oxfordshire sites. Environment Agency and English Nature.
- UKBG (1999) *Tranche 2 Action Plans – Volume 1: Vertebrates and Vascular Plants*. UK Biodiversity Group.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.
- Van Tol, J. & Verdonk, M.J. (1988) *The Protection of Dragonflies (Odonata) and their Biotopes*. Nature and Environment Series No. 38, Council of Europe, Strasbourg.
- Wallace, I.D. (1991) *A Review of the Trichoptera of Great Britain*. Research and Survey in Nature Conservation 32: 1–59. Nature Conservancy Council, Peterborough.
- Warren, M.S. (1987) The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Adult population structure and mobility. *Journal of Applied Ecology*, **24**, 483–498.
- Watts, P.C., Rouquette, J.R., Saccheri, I.J., Kemp, S.J., & Thompson, D.J. (2004) Molecular and ecological evidence for small-scale isolation by distance in an endangered damselfly, *Coenagrion mercuriale*. *Molecular Ecology*, **13**, 2931–2945.
- Wildermuth, H. (1993) Habitat selection and oviposition site recognition by the dragonfly *Aeshna juncea* (L.): An experimental approach in natural habitats (Anisoptera: Aeshnidae). *Odonatologica*, **22**, 27–44.
- Winsland, D.C. (1985) Preliminary site and pH evaluation for assessing the distribution of *Coenagrion mercuriale* (Charp.) in the New Forest. *Journal of the British Dragonfly Society*, **1**, 89–93.
- Winsland, D. (1997) Southern Damselfly *Coenagrion mercuriale* (Charpentier). In *Field Guide to the Dragonflies and Damselflies of Great Britain and Ireland* (ed S. Brooks), pp. 74–75. British Wildlife Publishing, Hampshire.
- Wong, A., Smith, M.L., & Forbes, M.R. (2003) Differentiation between subpopulations of a polychromatic damselfly with respect to morph frequencies, but not neutral genetic markers. *Molecular Ecology*, **12**, 3505–3513.
- Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R., & Tylanakis, J.M. (2003) Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia*, **134**, 605–611.
- Wright, J.F., Hiley, P.D., Cameron, A.C., Wigham, M.E., & Berrie, A.D. (1983) A quantitative study of the macroinvertebrate fauna of five biotopes in the River Lambourn, Berkshire, England. *Archiv fur Hydrobiologie*, **96**, 271–292.
- Wright, J.F. (1992) Spatial and temporal occurrence of invertebrates in a chalk stream, Berkshire, England. *Hydrobiologia*, **248**, 11–30.

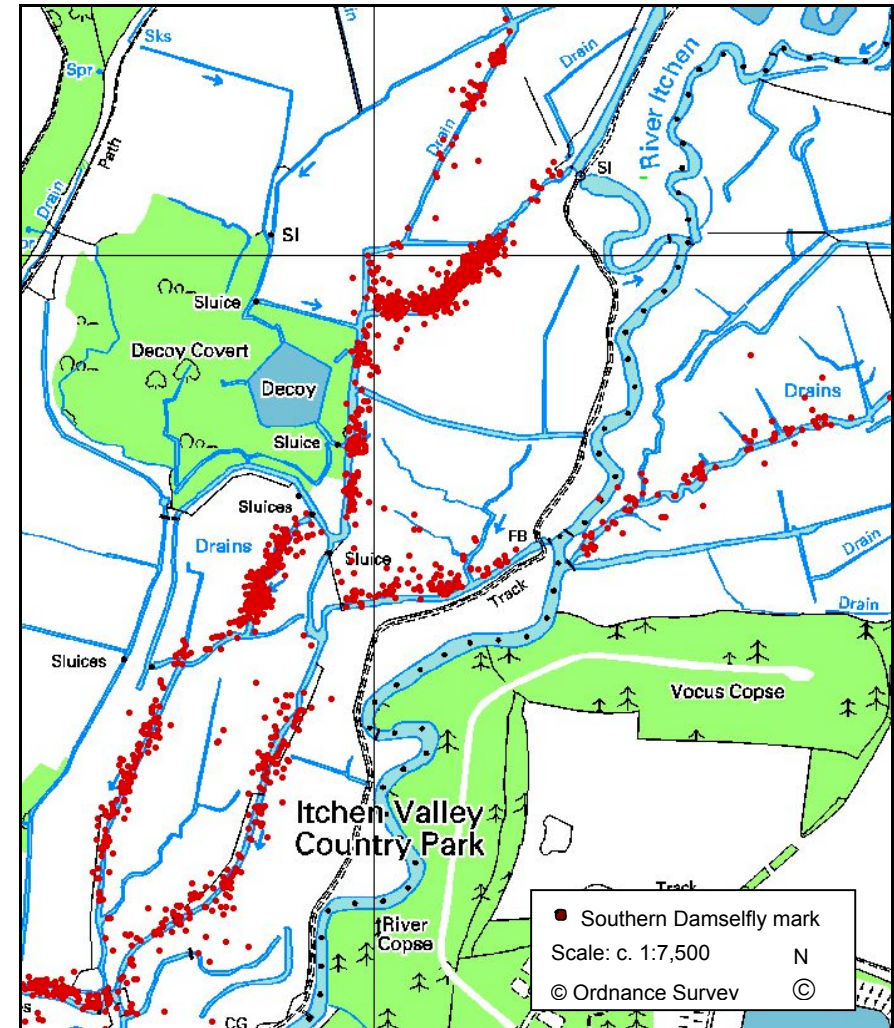
Appendix 1.1. Map of Lower Itchen Complex, showing site location and position of all adult Southern Damselflies marked during mark-release-recapture survey (Chapter 3).



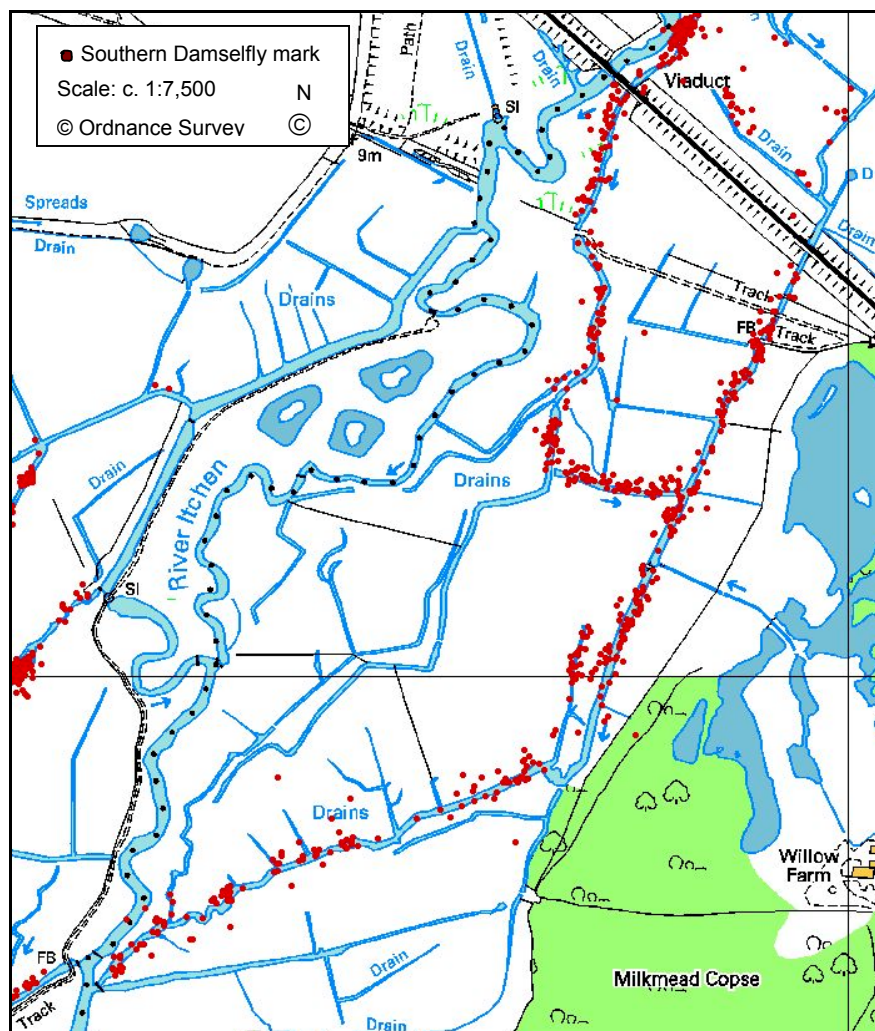
Appendix 1.2. Map of Itchen Valley Country Park (south), showing location of all marked Southern Damselflies. Note location of M27 motorway.



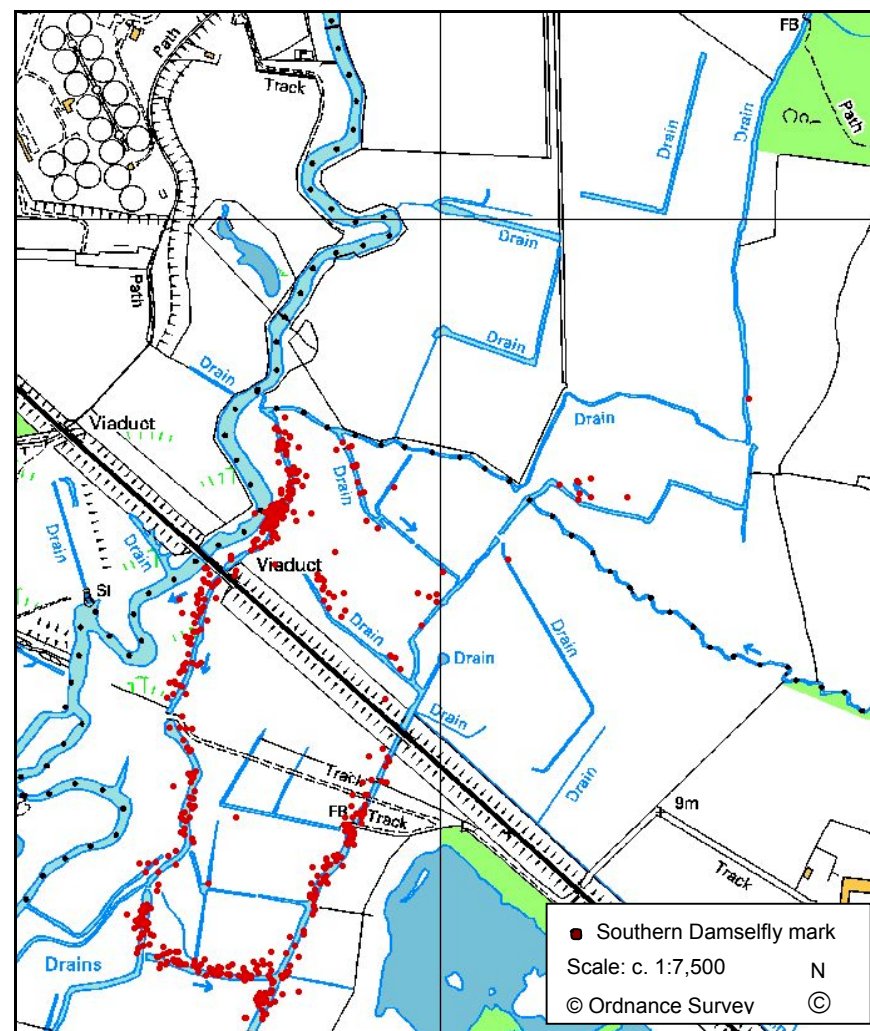
Appendix 1.3. Map of Itchen Valley Country Park (north), showing location of all marked Southern Damselflies.



Appendix 1.4. Map of Allington Manor Farm showing location of all marked Southern Damselflies. Note location of railway embankment.



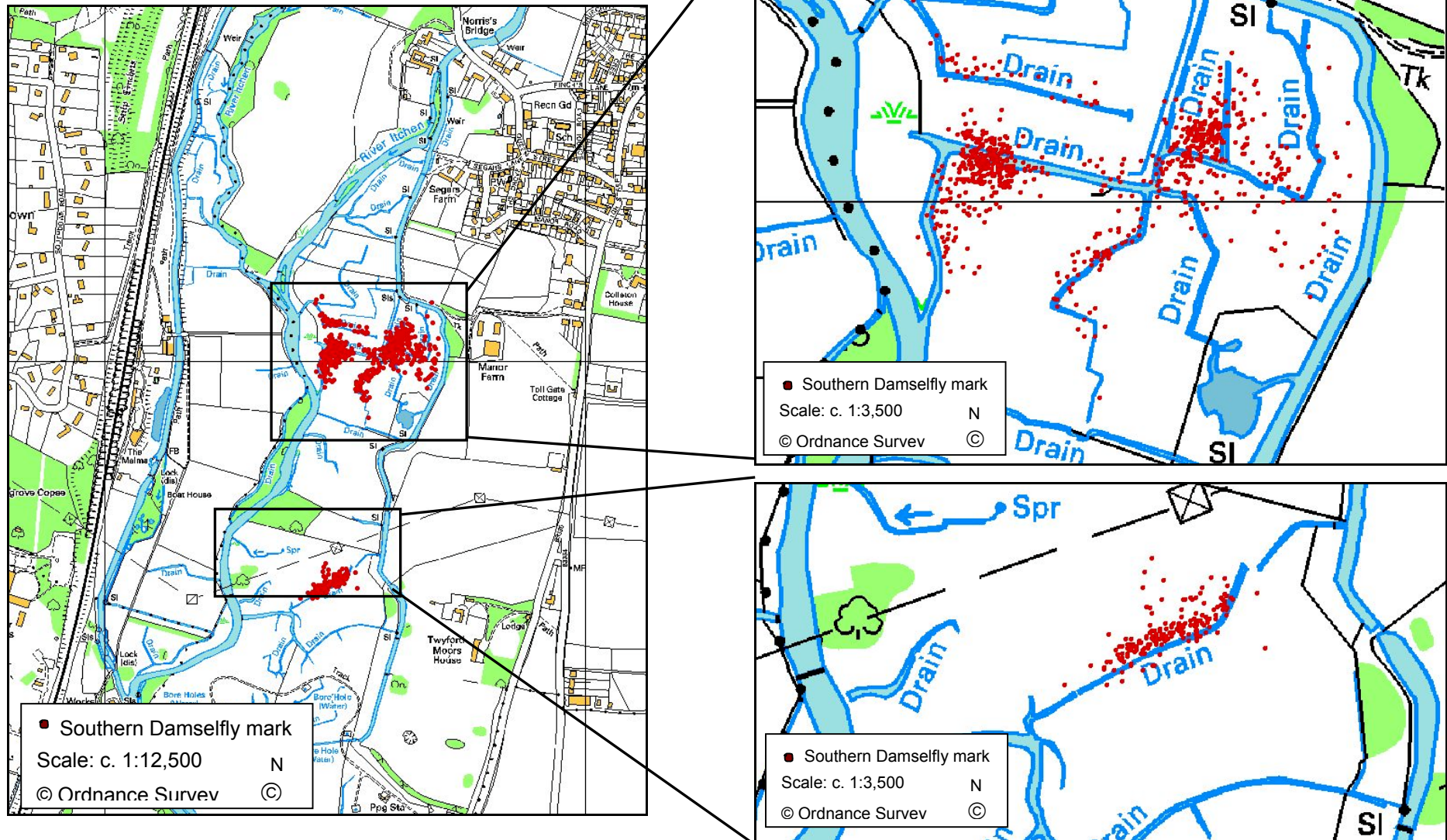
Appendix 1.5. Map of West Horton Farm showing location of all marked Southern Damselflies. Note location of railway embankment.



Conservation requirements of the Southern Damselfly in chalkstream and fen habitats



Appendix 1.7. Map of Mariner's Meadow, showing site location and position of all marked Southern Damselflies.



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

Variable	Variable
Channel variables	Bankside variables
Mean water width	Bankfull height
Mean water depth	Banktop height
Mean flow	Shade – none
Discharge	Shade – broken
Exposed silt	Shade – heavy
Water depth – 0–5 cm	Bankface – bare ground
Water depth – 5–30 cm	Bankface – bryophytes
Water depth > 30cm	Bankface – short herbs and grasses
Silt and detritus depth – 0–5 cm	Bankface – tall herbs and grasses
Silt and detritus depth – 5–30 cm	Bankface – scrub
Silt and detritus depth – > 30 cm	Bankface – trees
Boulders	0–5 m – bare ground
Pebbles	0–5 m – short herbs and grasses
Gravel	0–5 m – tall herbs and grasses
Sand	0–5 m – scrub
Silt	0–5 m – trees
MSUB (Mean SUBstrate size)	5–50 m – bare ground
Run or riffle	5–50 m – short herbs and grasses
Glide	5–50 m – tall herbs and grasses
Marginal deadwater	5–50 m – scrub
	5–50 m – trees
Chemical variables	Poaching
Alkalinity	Fenced
Ammonia	Grazed
BOD (Biological Oxygen Demand)	
Chloride	In-channel vegetation
COD (Chemical Oxygen Demand)	Emergent dicots
Nitrate	Emergent monocots
Nitrite	Submerged
Phosphate	Floating
Suspended solids	
Turbidity	
Conductivity	
Salinity	
pH	

Appendix 2.2. Metal and pesticide variables measured at 18 locations in the summer sampling season of the larval field study. See Chapter 7 for more details.

Variable	Variable
Metals	Organo-phosphorus pesticides
Calcium	Carbophenothion
Copper	Dichlorvos
Iron	Fenitrothion
Magnesium	Malathion
Sodium	Parathion (Parathion-ethyl)
Zinc	Demeton (Demeton-S-methyl)
Organo-chloride pesticides	Phenoxyalkanoic herbicides
Aldrin	Dichlorprop
Dieldrin	MCPA
Endrin	MCPB
Isodrin	Mecoprop
Hexachlorobenzene (HCB)	Trichlorophenoxyacetic Acid (2,4,5)
Hexachlorobutadiene (HCBD)	24D
Hexachlorocyclohexane (alpha)	Triazine and conazole herbicides
Hexachlorocyclohexane (beta)	Atrazine
Hexachlorocyclohexane (delta)	Simazine
Hexachlorocyclohexane (gamma)	Propazine
PCB 28	Redlist aromatic solvents
PCB 52	Benzene (1,2,3 Trichlorobenzene)
PCB 101	Benzene (1,2,4 Trichlorobenzene)
PCB 118	Benzene (1,3,5 Trichlorobenzene)
PCB 138	
PCB 153	Extended ECD
PCB 180	Triallate
DDT (o-p)	
DDT (p-p)	
Endosulphan (alpha)	
Endosulphan (beta)	
Heptachlor	
Trifluralin	

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 PhD supervisor Dave Thompson for his invaluable support throughout this project. Tim Sykes, from the Environment Agency and chairman of the UK Southern Damselfly Species Action Plan Steering Group, was instrumental in providing funding, enthusiasm and an ongoing commitment to this project.

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

I would like to thank all 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 and the Countryside Council for Wales.