THE ECOLOGY AND CONSERVATION OF BEETLES (COLEOPTERA) LIVING ON EXPOSED RIVERINE SEDIMENTS

by

ADAM JAMES BATES

A thesis submitted to
The University of Birmingham
for the degree of
DOCTOR OF PHILOSOPHY

School of Geography and Environmental Science
The University of Birmingham
September 2005

ABSTRACT

Situated at the very juncture of the aquatic and terrestrial, exposed riverine sediments (ERS) are poorly vegetated alluvial deposits of silts, sands and gravels, which are habitat for a wide range of rare and highly specialised beetles. The thesis aimed to assess: (1) the conservation value of ERS beetles; (2) their changing habitat requirements and spatial population structure over a range of spatio-temporal scales; and (3) their vulnerability to anthropogenic threats, in particular, trampling by livestock. A database of British occurrence records was used to assess the conservation value of ERS specialist beetles. Beetle sampling implemented quadrat hand searches and modified dry pitfall traps, and spatial distribution and population structure in relation to a suite of environmental variables was analysed using correlation, SADIE analysis, and mark recapture methods. ERS beetles were found to have considerable conservation importance and their spatial distribution was related to habitat characteristics at the within-patch, patch, reach, and stream segment scales. These distributions varied temporally in response to flow level and trampling intensity, and trampling intensity was shown to reduce the conservation value of beetle assemblages. The likely responses to a variety of threats, such as regulation and channelization, mediated by varying inter-patch spatial population structure were evaluated.

ACKNOWLEDGEMENTS

I thank the Countryside Council for Wales, and the School of Geography, Earth and Environmental Sciences at the University of Birmingham for funding this research. I thank Cat Butcher, Dave Bell, Robert Francis, Richard Johnson, Mel Bickerton, Montse Auladell Mestre and Amanda Hewertson for help in the field, with equipment preparation and the final putting together of this thesis. I thank Alan Jones, Mike Jenkins, Nigel Stringer, Sarah Andrews, Clive Faulkner, and many enthusiastic landowners for obtaining landowner contact details and allowing site access respectively. I thank Kevin Burkhill and Anne Ankorn for the preparation of several diagrams. I am grateful to the British Atmospheric Data Centre, which provided me with access to the Met Office Land Surface Observation Stations Data and to the Environment Agency for stage data. I also thank Joe Perry, Jim Hynes, Randolf Manderbach, Peter Hammond, Max Barclay, Howard Mendel, Steve Hewitt, Jonty Denton, Darren Mann, Derek Lott and Garth Foster for their help, advice and kind provision of data. Thanks also to all those in 425 for a pleasant working environment and numerous bits of help with Excel, spelling etc. Many thanks also to my all my friends and family for their support throughout. Especial thanks are due to Adrian Fowles (CCW) for his advice, help and critical comments at all stages of this investigation and report preparation. And, and he will like me starting a sentence with and, thanks Jon (Jon Sadler, UB) for all your guidance and support throughout, you are a great supervisor and friend.

P.S. Thanks to any who deserve thanks, but I have forgotten to thank.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

CHAPTER 1

INTRODUCTION

1.3 Preamble

Exposed river gravels, sands and silts have long been the focus of meticulous scrutiny by British amateur coleopterists, who recognised the extensive array of rare species available for collection and developed a preliminary understanding of their natural history through their informal observations. Nevertheless, systematic research into the ecology and conservation potential of the beetles (Coleoptera) associated with these habitats did not begin until the pioneering research of Andersen (e.g. 1968; 1969) in the late 1960s, only to be taken up by other researchers in mainland Europe in the 1980s (e.g. Plachter 1986; Desender 1989), and in the UK in 1989 (Fowles 1989). In Australia and the US, research still remains either fairly elemental (Holeski and Graves 1978; Holeski 1984), or implemented by European researchers on sabbatical (Hering 1998; Framenau *et al.* 2002). The relatively late development of this research area is perhaps surprising given the large amount of recent research interest on this subject (e.g. Eyre *et al.* 2001a, 2001b; Eyre and Luff 2002; Eyre *et al.* 2002; Hering *et al.* 2004; Sadler *et al.* 2004; Bates *et al.* 2005; Paetzold and Tockner 2005; Andersen and Hanssen in press; Paetzold *et al.* in press; Tockner *et al.* in press), but can be partly explained by the very habitat characteristics that have attracted the current level of research interest. In order to shed light on this apparent quandary it is first necessary to define what are meant by exposed riverine sediments and then describe the characteristics of these habitats.

1.2 Exposed riverine sediments (ERS): definition and characteristics

A range of terms have been used to describe ERS including point, counter-point, lateral and braid, bars, berms and shoals, which can be further differentiated according to their dominant sediment size. To overcome problems associated with this variation in nomenclature, Adrian Fowles and members of the Environment Agency in 1993 coined ‘exposed riverine sediments’ as a term to describe the full scope of these related habitats. A precise definition of ERS, however, has never been given. Hereafter, the term ERS is used to describe exposed riverine sediments, which are defined as:

> *Exposed, within channel, fluvially deposited sediments (gravels, sands and silts) that lack continuous vegetation cover, whose vertical distribution lies between the levels of bankfull and the typical base flow of the river.*

Therefore, eroding river banks will generally qualify as ERS under this definition because they are usually composed of fluvially deposited sediment, even if the deposits are ancient. Exposed riffle crests and areas of the river bed do not qualify as ERS because they are only exposed when water levels are unusually low. Likewise, over-bank deposits do not qualify because they are more elevated than the bankfull level. Additionally, open sediments within ox-bows and cut-offs (e.g. Lott 1992, 1993) do not qualify because they only remain un-vegetated because of livestock pressure.

As can be appreciated from this definition, ERS are on the very boundary of the aquatic terrestrial ecotone (Naiman *et al.* 1988; Naiman and Déchamps 1997; Ward *et al.* 1999), being neither truly terrestrial, nor truly aquatic, and it is because of this weak association with these two traditional divisions of ecology that the ecology of ERS has been neglected until relatively recently. The current more holistic approach to lotic and riparian management and conservation, views rivers and their floodplains as one intimately connected landscape; a ‘riverine landscape’, or ‘riverscape’ (Ward 1998; Ward *et al.* 2002). Within this new paradigm, the ecology of ERS communities is developing into an important new area of research for three main reasons. The first is the strong reliance of ERS invertebrates on aquatic food subsidies (Hering and Plachter 1997; Hering 1998;

Paetzold *et al* in press), which recent research suggests may have a considerable impact on the success of emerging aquatic insects (Paetzold and Tockner 2005). The second is the fundamental importance of flood pulses (*sensu* Junk *et al.* 1989) for ERS communities (Plachter and Reich 1998), both for the way floods maintain habitat in early stages of succession (Figure 1.1), and the way that they influence the distribution (Andersen 1968), lifecycles (Andersen 1983a) and rates of mortality (Reich 1991; Stelter *et al.* 1997; Lude *et al.* 1999; Hering *et al.* 2004) of ERS invertebrates. The high level of adaptation required to utilise aquatic food subsidies, and best counteract disturbances from flood pulses may be the reason for the considerable conservation importance of ERS, which is cited as the third reason, and is the focus of the next section. Both aquatic terrestrial trophic exchanges and the effect of flood pulses demonstrate the strong interdependence of ERS and lotic habitats and so link the two main elements of the riverine landscape: the aquatic and the terrestrial. The importance of research into the ecology of ERS communities cannot therefore be overstated.

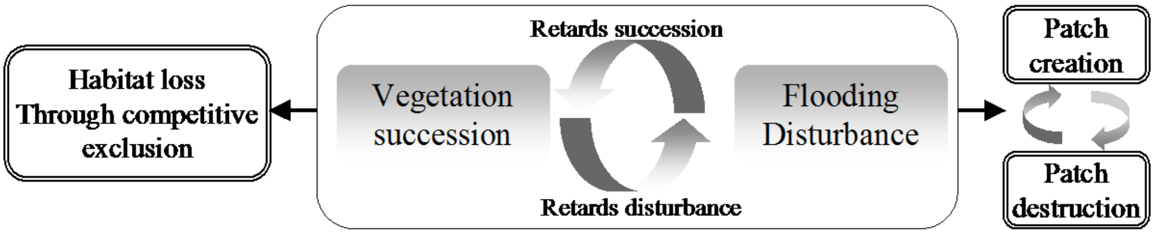


Figure 1.1 The succession: flood disturbance dynamic equilibrium. Any shift towards the left of the diagram due to either an enhanced rate of succession, or reduction in the frequency and intensity of flood disturbances will reduce the amount of available habitat as more generalist floodplain species competitively exclude ERS specialist, which are adapted to un-vegetated sediments.

1.3 Conservation importance of ERS beetles

ERS communities are not only valuable because of their key function within the riverine landscape; they also have considerable significance as conservation resources within the UK and Europe. ERS characteristically have little botanical interest (Eyre and Lott 1997), and, although they provide habitat for a few species of rare bird such as little ringed plover (*Charadrius dubius* Scopoli, 1786), oyster catchers (*Haematopus ostralegus* Linnaeus, 1758), and sandhill cranes [*Grus canadensis* (Linnaeus, 1758)] (Reich 1994; Herve Piegay pers comm.), it is the invertebrate fauna of ERS that is of particular value (e.g. Plachter 1986; Fowles 1989; Reich 1991; Stelter *et al.* 1997; Lude *et al.* 1999; Sadler *et al.* 2004; Andersen and Hanssen in press). In a UK context ERS are notable for both their spider (Araneae e.g. Sadler and Bell 2002) and true fly (Diptera e.g. Godfrey 1999) faunas. However, beetles (Coleoptera) dominate in terms of species richness and number of rare species (Eyre and Lott 1997; Sadler and Petts 2000). This dominance, together with the relatively stable taxonomy of beetles, led to the decision to focus on beetles throughout this investigation, although where appropriate, research on other ERS specialist invertebrates are considered. A focus solely on Carabidae (e.g. Boscaini *et al.* 2000) was rejected due to the comparatively limited number of ERS specialists in this group.

In the UK, of the 131 beetles considered by Fowles (2005) to be specialists of ERS, 86 (66%) have some conservation status, with 29 classified as red data book (RDB2, RDB3, RDB I and RDBK) and 57 classified as nationally notable (Na, Nb and N) by Hyman and Parsons (1992; 1994). Moreover, eight species (Carabidae: *Bembidion testaceum* (Duftschmid, 1812); *Lionychus quadrillum* (Duftschmid, 1812); *Perileptus areolatus* (Creutzer, 1799); *Dyschirius angustatus* (Ahrens, 1830); Staphylinidae: *Meotica anglica* Benick in Muona, 1991; *Thinobius newberyi* Scheerpeltz, 1925; Hydrophilidae: *Hydrochus nitidicollis* Mulsant, 1844; Dytiscidae: *Bidessus minutisimus* (Germar, 1824)) have biodiversity action plans (Anon. 1999). Additionally, the two staphylinids are classified as endemic to the UK, although *M. anglica* has now been found in the

Netherlands and *T. newberyi* is thought likely to be present in other parts of Europe (Hammond 1996; Bates and Sadler 2004a).

ERS specialist beetles, therefore, clearly represent an important conservation resource in the UK. However, since the early 1990s when the conservation status of British beetles was last reviewed, there has been a huge amount of survey work across the UK (e.g. Eyre and Lott 1997; Eyre 1998; Sadler and Petts 2000; Sadler and Bell 2002; Hammond 2003). As a result the designated conservation status of many ERS beetles is incorrect, with some species (e.g. Coccinellidae: *Coccinella quinquepunctata* Linnaeus, 1758) much more common, and others (e.g. *Bembidion testaceum*) much rarer than previously thought (Sadler and Bell 2002; Eyre *et al.* 1998; Eyre *et al.* 2000). No study that investigates the ecology and conservation of a group of species can proceed without first establishing which species are of most concern in terms of their rarity and/or rate of decline and which habitats are of most importance, and this is the aim of Chapter 3 of the thesis.

1.4 Justification for choices of research area

Despite the relatively recent origin of research into the ecology of ERS specialist beetles, quite a wide range of investigations have now been implemented. Early work examined the autecology of species in the tribe Bembidiini: specifically their, inundation responses and choice of hibernation sites (Andersen 1968), life cycles (Andersen 1969, 1983a), habitat distribution (Andersen 1969, 1983b), microhabitat selection (e.g. Andersen 1978, 1985) and interspecific interactions (Andersen 1988). Later research had a broader focus at a community level and included work on species ecomorphological adaptations (Desender 1989), feeding strategies (Hering and Plachter 1997; Hering 1998; Paetzold *et al* in press), microhabitat distribution (Desender 1989; Gurnell *et al.* 1998) and habitat associations (Eyre *et al.* 2001a, 2001b; Eyre and Luff 2002; Eyre *et al.* 2002; Sadler *et al.* 2004). The bulk of such studies have focused on ground beetles (Carabidae), particularly in work done in mainland Europe, but other families of beetles comprise an important component of ERS communities, principally the rove beetles (Staphylinidae), which are the most speciose group of ERS specialists.

Although all the above topics have been studied to some degree, few, if any, have been investigated to the extent that they do not require further consideration, particularly for the non-carabid families. The micro-distribution of ERS beetles for example, has only been studied over small transects towards the water's edge (Desender 1989), or inferred from two sets of pitfall traps situated at two distances from the water's edge (Gurnell *et al.* 1998). Furthermore, the research on community habitat associations (e.g. Eyre *et al.* 2001a, 2001b; Sadler *et al.* 2004), has focussed on ERS in a wide range of catchments and was therefore, unable to determine whether community attributes are responsive to bar, or catchment characteristics. Nevertheless, many important areas remain that had received little or no research attention at all, or were of such complexity and importance that an extensive amount of additional research was required to fully comprehend them.

Given the conservation importance of ERS beetles, it seemed clear from the outset that particular focus should be placed on their response to anthropogenic threats. Such threats can be subdivided into two groups: (1) those that directly negatively influence individuals or their immediate microhabitat, and (2) those that indirectly negatively influence communities via changes to sediment and/or flow regimes (Figure 1.2). Although some operations will have both direct and indirect threats, such as channelisation, which will locally cause direct damage to sediments and ERS communities, but will be likely to indirectly influence the flow and sediment regime downstream. Direct threats to ERS beetle communities include livestock trampling and aggregate extraction and are likely to operate over smaller spatio-temporal scales, whilst indirect threats include river regulation and channelisation, which can potentially operate over a larger range of spatio-temporal scales.

Lotic and riparian biological communities are likely to respond to both direct and indirect threats, or to changes in physical habitat caused by these threats, and in some cases (e.g. Gurnell *et al.* 2005) might in turn influence the physical habitat.

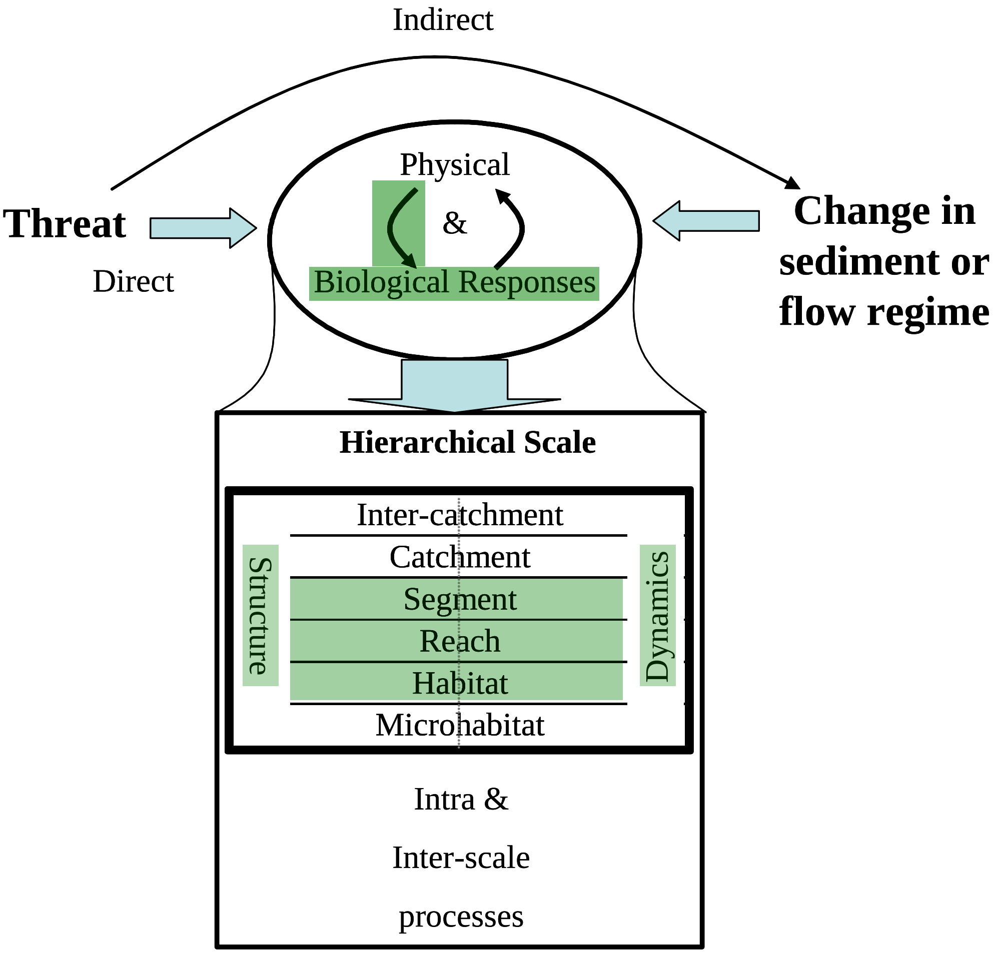


Figure 1.2 Top down hierarchical conceptual framework used to describe the interrelationship between the various elements of the thesis. External processes such as threats or changing sediment or flow regimes either directly or indirectly elicit physical and biological responses in the lotic and riparian system that cause changes in the structure and dynamics of ERS assemblages (indicated by the boxed area) at several distinct, or interacting scales (scales based on Frissel *et al.* 1986; Poole 2002). The shading illustrates areas practically investigated in the thesis.

The specific biological responses of ERS beetle communities are boxed in Figure 1.2. Responses are likely to operate over single, or multiple spatio-temporal scales, and will be manifest in community structure and dynamics. Responses at one spatio-temporal scale may influence community structure and dynamics at other scales either due to top down, or bottom up responses.

Investigating the structure and dynamics of ERS beetle communities over six distinct spatio-temporal scales and understanding their response to the full range of direct and indirect anthropogenic threats will necessarily be beyond the scope of any single thesis. Accordingly, choices had to be made regarding the selection of which anthropogenic threat(s) to focus on and the scales at which the structure and dynamics of ERS beetles should be studied. The nature of direct threats is likely to vary markedly with the type of operation, for example, beetles are likely to respond very differently to having their habitat permanently flooded by reservoir impoundment, partly removed by aggregate extraction, or disturbed and compacted by livestock trampling.

The two main candidates for the study of direct effects were aggregate extraction and livestock trampling. The negative effects of gravel extraction on river geomorphological stability are fairly well-known (e.g. Kondolf 1997, 1998; Sear and Archer 1998), and because of this, within-channel aggregate extraction licences are no longer issued in the UK (Sear and Archer 1998). Although unlicensed extraction continues on many British rivers, it is typically on a relatively small scale. In contrast, livestock trampling is widespread on ERS throughout the country, which both increases its potential threat to ERS beetles, and also renders it more conducive to study. As a consequence, the influence of livestock trampling on ERS communities was subjected to particular focus.

The habitat and ERS beetle response to changes in sediment or flow regime are likely to be complex and multi-faceted; influencing habitat availability, quality and disturbance regime, the responses to which, are likely to vary for different groups of species. As such, practical investigation into ERS beetle community response to such changes in sediment and flow regime seemed pre-emptive before more detailed investigations of the structure and dynamics of ERS beetle communities were completed. Within-habitat, within-reach, and within-stream segment population structure and dynamics were chosen for practical investigation because this range of scales seemed likely to encompass the entire lifecycle of the majority of individuals. Particular focus was given to understanding the dynamic spatial population structure (e.g. metapopulation, patchy population) of ERS beetles because it was considered to be a key determinant of the vulnerability of species to particular threats (Bates *et al.* 2005).

1.5 Thesis structure

The thesis structure and the interrelationships between the chapters are summarised in Figure 1.3. Section A provides a context for the rest of the PhD. Section B comprises the practical elements of the PhD, which map onto the shaded sections of Figure 1.2. Section C integrates findings from the scientific literature, the findings of Section B, and conceptual ideas to examine all the elements of Figure 1.2.

More specifically, Chapter two describes and justifies the selection of the study sites and the methods that are common to several chapters. Chapter three revises the conservation status of the British specialist ERS beetles, analyses their importance as a conservation resource, and provides a hierarchy of British rivers in terms of the ‘quality’ of their ERS beetle fauna assessed by an ERS species quality score (ERSQS) and ERS quality index (ERSQI). Chapter four investigates the effect of livestock trampling on ERS beetles across a wide range of trampling intensity. Chapter five investigates the effects of weather, flow level and the distribution of microhabitat and interspecifics on the dynamic microspatial distribution of several ERS beetles. Chapter six presents results from the mark recapture work done in 2002, which studied three species of ERS specialist. Chapter seven presents results from the mark recapture work done in 2003, which used methods refined from the 2002 study and largely focused on *Bembidion atrocaeruleum* (Stephens 1828), specifically its response to habitat inundation and trampling. Chapter eight investigates seasonal and annual changes in the density of *B. atrocaeruleum* across a ~6km stretch of river and relates these changes to environmental variation. Lastly, Chapter 9 concludes the thesis with an overall assessment of the conservation and management of ERS beetles.

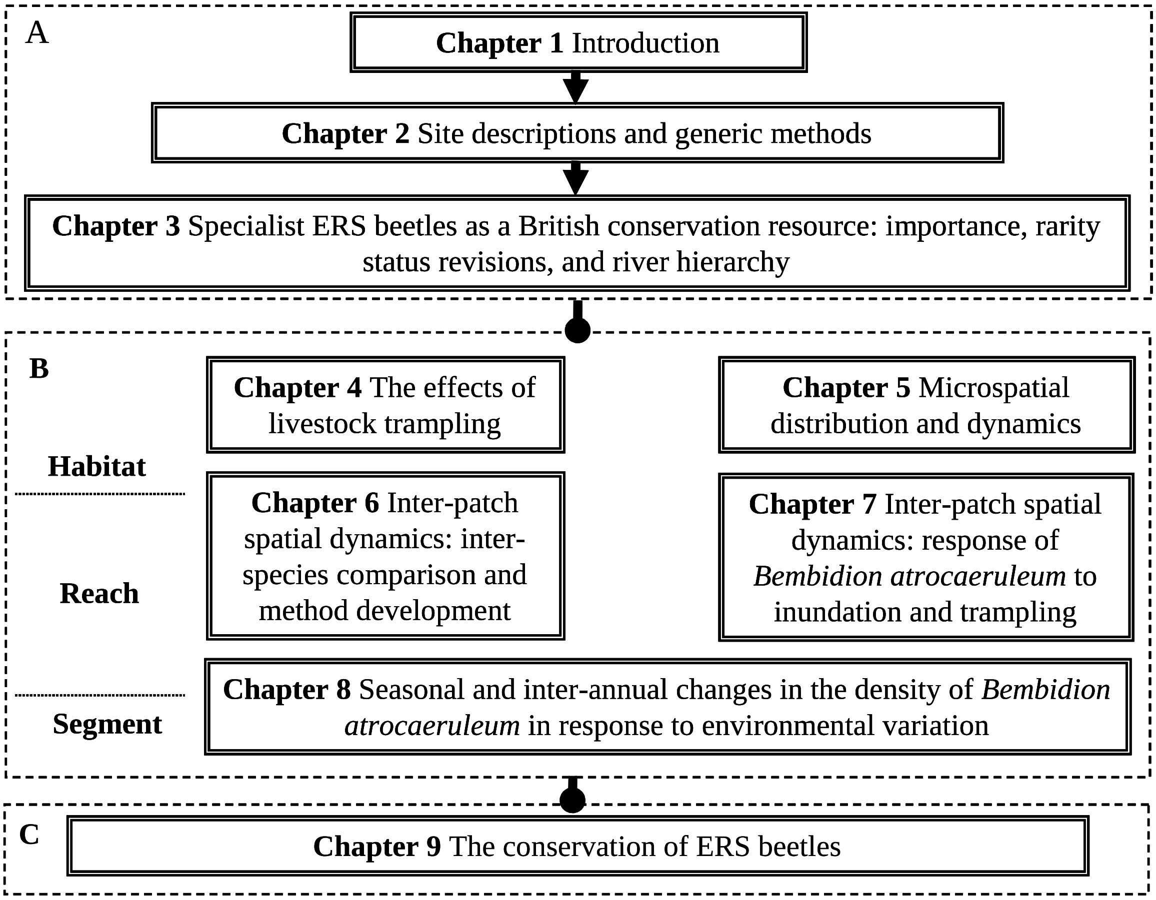


Figure 1.3 The thesis structure and association between chapters. Part A provides a context and generic methods for the rest of the thesis. Part B comprises practical investigations of ERS beetle community structure and dynamics at a range of scales (Chapters 6 and 7 bridge the habitat and reach scales; Chapter 8 bridges the reach and stream segment scales). Part C integrates findings from literature, the practical findings of the PhD and conceptual ideas, to provide general conclusions for the conservation management of ERS beetles and suggest further work.

1.6 Broad aims

The broad aims of the investigation were:

1. To bring the conservation status of specialist ERS beetles up-to-date to allow the appropriate assessment of the conservation value of ERS beetles and their habitats.

2. To assess the effects of livestock trampling on ERS beetle communities.
3. To assess the responses of ERS beetles to habitat characteristics.
4. To assess the structure and dynamics of ERS beetles at several spatio-temporal scales.
5. To assess the likely response of ERS beetles to all of the main threats and suggest management strategies for their conservation.

Specific objectives that relate to individual chapters are detailed therein.

CHAPTER 2

SITE DESCRIPTIONS AND GENERIC METHODS

2.1 Introduction

This chapter describes the rivers and sites studied, and methods that were common to several parts of the PhD. The generic methods section is subdivided into three main sections (a) sampling methods and justification (Chapters 4-8), (b) mark-recapture methods (Chapters 5-7), and (c) measurement of environmental variables (Chapters 4-8). Methods sections in subsequent chapters refer back to the descriptions and justifications used in this chapter, except where methods were specific to that chapter.

2.2 River and site selection and descriptions

Many welsh rivers are characterised as having very good ERS faunas in a national context, but the River Severn (Afon Hafren) and Afon Tywi (River Towi) are exceptional (Chapter 3; Bates and Sadler 2004a). The Tywi and the Welsh reaches (upstream of Welshpool) of the Severn (Upper Severn), although regulated to some degree, currently have a limited amount of channel engineering, which allows channel migration and the reworking of sediments (e.g. Leeks *et al.* 1988). Consequently they represent some of the best examples of semi-natural rivers in the UK. Although the Upper Severn is very geomorphologically active, its lower reaches have been engineered and stabilised. The river therefore lacks many of the ERS specialists associated with finer sediments, which are characteristic of more lowland ERS. In contrast, the Tywi has a relatively natural channel form right down to its tidal reaches, allowing the investigation of the beetle fauna of very sandy ERS, which represent some of the most threatened and relatively understudied ERS habitats (Eyre and Lott 1997).

2.2.1 The Upper Severn

Although the Upper Severn has a largely natural flow regime, the Afon Clywedog, one of the river's main tributaries, has been regulated since 1967, following the construction of the Clywedog dam (Brewer and Lewin 1998). Water from the reservoir (Llyn Clywedog) is used to offset downstream water extractions, so during dry periods water levels are higher than they would be naturally, although they remain lower than many other regulated rivers due to the lack of groundwater input from the impermeable geology (Wood 1987; Kirby *et al.* 1991). The use of the dam for flood protection has reduced flood magnitude and frequency by 25% and 31% respectively at Caersws (Higgs 1987).

Mean annual rainfall ranges from >2400mm at the Pumlumon watershed to 1400mm at the study site (LEAP- Severn Uplands; Lawler 1987). Land use within the catchment is mainly forestry, rough pasture and improved grassland (Higgs 1987). In the upland reaches the effects of afforestation on the hydrology, and sediment erosion and delivery have been intensely studied (Kirby *et al.* 1991). The reduction in water delivery due to afforestation was found to be balanced by increased rate of delivery due to drainage ditches. The delivery of both bed-load and suspended sediment was found to have increased due to drainage ditches, particularly after clearfelling (Kirby *et al.* 1991; Leeks and Marks 1997). Catchment geology is composed of Silurian and Ordovician siltstones, some of which contain lead, zinc and copper ores. Historically the river has been subject to heavy metal pollution from eighteen, mainly lead and copper mines, but copper and zinc levels are now low in the study segment (LEAP- Severn Uplands; EA 2004).

Bank erosion in the Upper Severn characteristically occurs during large, discrete high flow events, usually when coarser, more easily eroded sediments are eroded from beneath finer, more cohesive sediments, causing undercutting and a cantilever failure mechanism (Lawler *et al.* 1997). Geomorphologically active reaches, which contain large areas of ERS, are typically pre-conditioned for erosion because banks are composite (coarse sediments underlie finer sediments), high (higher banks are more likely to fail in this manner), and unvegetated (Lawler *et al.* 1997; Brewer and Lewin 1998; Winterbottom and Gilvear 2000). Other areas of instability are potentially associated with confluences, and macro (10^1-10^3m) or mega (>10^3m) sediment ‘waves’, or ‘slugs’ moving downstream, a process modified by the occurrence of ‘sedimentation zones’ (Hoey 1992; Passmore *et al.* 1993; Nicholas *et al.* 1995; Jacobson & Bobbitt Gran 1999). The Upper Severn is characterised by patchily distributed unstable sections of river in which there are large areas of ERS, often distributed in many discrete bars, interspersed by less dynamic reaches, typified by a relative paucity of ERS (Passmore *et al.* 1993; Brewer and Lewin 1998). In combining features of braided and meandering rivers, the Upper Severn can be classified as a ‘wandering gravel-bed river’, which are typically characterised by unstable ‘sedimentation zones’ separated by stable ‘transfer zones’ (Church 1983).

2.2.1.1 Severn study sites

An ~6km segment of the river next to the villages of Llandinam and Caersws (Figure 2.1) was selected for study. The water quality within the segment has been classified as ‘very good’ or a ‘natural ecosystem’ for several years (1999-2002) (EA 2004). Bank retreat 1km downstream of the Carno confluence averages 46cm a^{-1}, but can be as much as 1m in a single high flow event (Lawler *et al.* 1997). Similar rapid rates of bank retreat have been observed in sedimentation zones within the study segment (Paul Brewer pers. comm.). It is considered a prime example of a wandering gravel-bed river, and as a result lies within a proposed geomorphological special site of scientific interest (SSSI) (LEAP- Severn Uplands). A highly dynamic sedimentation zone situated at the river’s confluence with the River Carno (Afon Carno SO 028 916) was selected for the habitat and reach scale investigations (Chapters 5-7) because of the large number of distinct ERS bars, of varying size, and microhabitat heterogeneity.

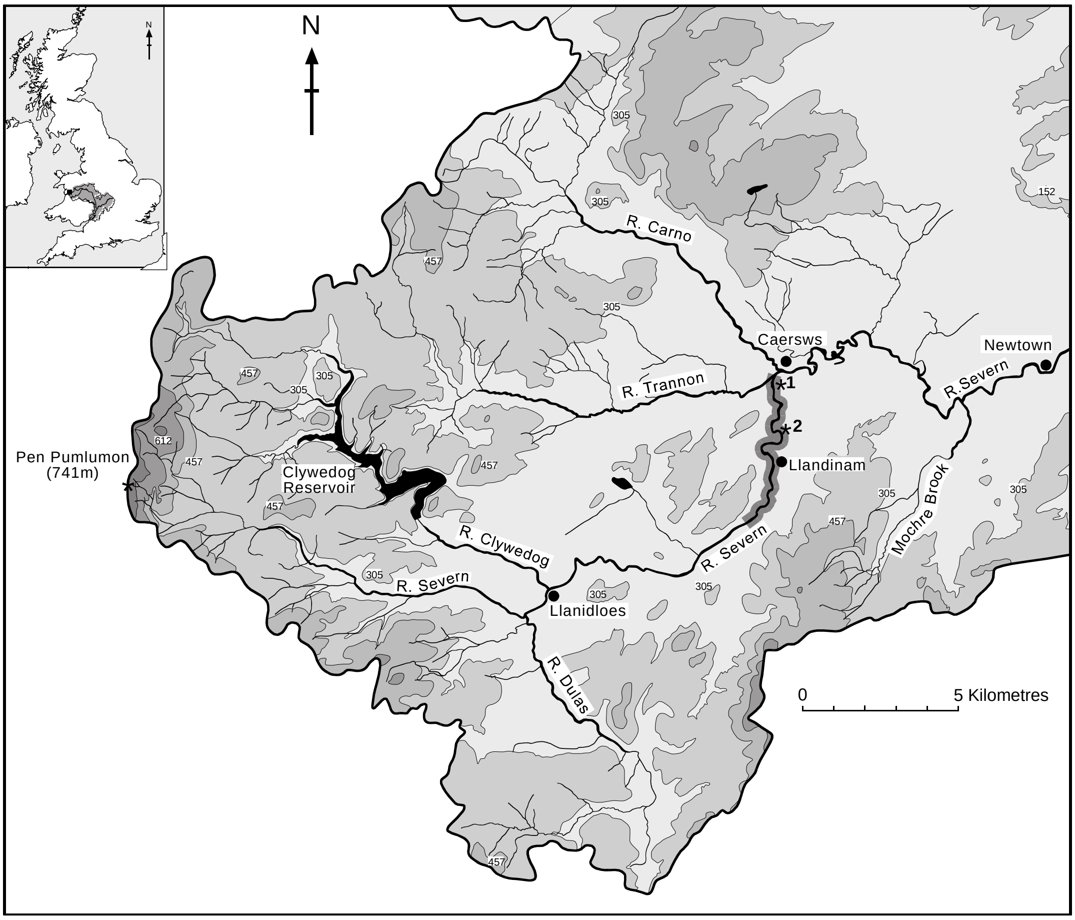


Figure 2.1 The Upper Severn catchment area (*1 = the reach studied in Chapters 5-7, *2 = the segment, marked by the shaded area, studied in Chapter 8).

2.2.2 The Afon Tywi

The Afon Tywi has been regulated since 1972, after the completion of the Brianne dam; which performs a similar role to the Clywedog dam on the Severn, reducing flood intensity, offsetting downstream water extractions and generating HEP. The river’s flow regime, however, is still relatively natural (Smith 1989). Impermeable Silurian and Ordovician shales, grits and mudstones dominate the catchment geology, but Devonian sandstones along the southern edge of the catchment input some groundwater into the river. Historically there have been a small number of lead, zinc and gold mines in the catchment but lead and zinc levels in the water are low (LEAP- Carmarthen area; EA

2004). Landuse within the catchment is mainly forestry, rough pasture and improved pasture (Whitehead *et al.* 1998), upstream of Carmarthen very little of the catchment is urbanised except for the small towns of Llandovery and Llandeilo (Figure 2.2). Average annual rainfall varies from <1400mm to >2000mm in the upper reaches (LEAP-Carmarthen area).

2.2.2.1 Tywi study sites

The investigation of the effects of livestock trampling (Chapter 4) sampled sites from within the area delimited upstream by the confluence with the Gwydderig (~1.5km d.s. of Llandovery) and downstream by the confluence with the Annell (~5km u.s. of Carmarthen), all of which is part of the Afon Tywi SSSI and candidate SAC (LEAP-Carmarthen area). Smith (1989) identified four main areas within this section of the Tywi according to their fluvio-geomorphology: (1) a ‘wandering gravel-bed’ (Church 1983) section between SN 754 334 (the most upstream point of Figure 2.2) and the confluence with the Afon Sawdde, in which similar geomorphological processes occur as on the Upper Severn; (2) a ‘stable’ (last 150 years) relatively straight section between the Sawdde confluence and SN 686 258 (the very bottom of the upper of the four sections in Figure 2.2), probably due to the stabilising effect of the River Sawdde alluvial fan; (3) an ‘active meandering’ section between SN 686 258 and Fferm Typicca (SN 537 205, the very bottom of the third section from the top in Figure 2.2), which consists of sequences of actively migrating bends, connected by relatively stable low-sinuosity segments; and (4) a ‘stable’ (last 150 years) but sinuous section from Fferm Typicca to the estuary at Carmarthen (Figure 2.2). Gravels generally dominate the ERS, but there is a distinct pattern of downstream fining, and in some of the lower reaches bars are dominated by sand (Smith 1989).

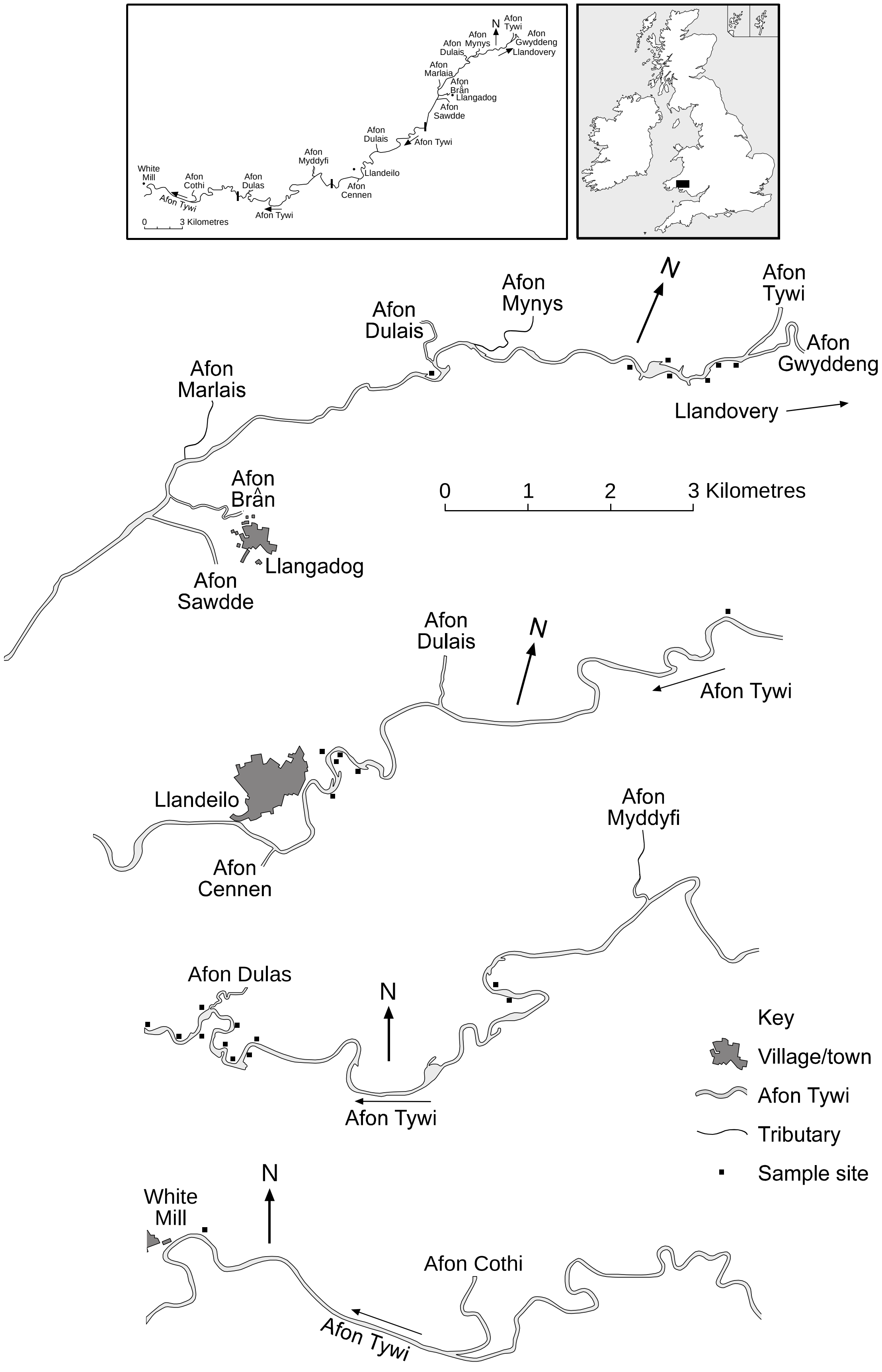


Figure 2.2 The Afon Tywi sampling sites (≥3rd order tributaries shown).

Despite several inputs from secondary sewage treated works, water quality is classed as very good (natural ecosystem) throughout the study area (EA 2004). Recent commercial gravel extraction is taking place at Llwynjack (SN 755 330) and was undertaken at Llanwrda station (SN 720 313) until ~1995. Both extraction sites are situated in the wandering gravel-bed section of the river. This has caused disruption of the surface ERS geomorphology at these sites, and there is some evidence for the enhanced deposition of fine sediments downstream from these sites as a result of the disruption to the surface armour layer (Newson and Leeks 1987).

2.3 Generic methods

2.3.1 Sampling methods and justification

Table 2.1 details the three overall methodological aims of the chapters involving practical investigation and lists the possible sampling methods that could be used to achieve this, and the final selection of sampling method. This section is subdivided into: (a) reasons for the rejection of alternative sampling methods, (b) description and justification of chosen sampling methods, and (c) method selection for the estimation of local population size.

Table 2.1 Methodological aims, possible methods, and the selected sampling methods used in Chapters 4-8.

		Possible methods		
Aim of method	**Chapters**	**Sampling**	**Est. Pop. Size**	**Selected method**
Measurement of microspatial distribution	5	Fatal pitfall traps Non-fatal pitfall traps Semi-quantitative hand searches	- - -	Non-fatal pitfall traps
Estimation of within-bar population density	4 & 8	Fatal pitfall traps Semi-quantitative hand searches Quadrat hand searches	- - -	Quadrat hand searches
Estimation of whole-bar population size and density	6 & 7	Fatal pitfall traps Non-fatal pitfall traps Semi-quantitative hand searches	Removal method Mark recapture	Non-fatal pitfall traps with mark recapture

2.3.1.1 Rejected sampling methods

Many of the considerations when using fatal and non-fatal pitfall traps are the same and semi-quantitative hand searches and quadrat hand searches are related methods that share many common elements. So a relatively broad critique is provided in this section despite the rejection of the use of fatal pitfall traps and semi-quantitative hand searches in the thesis.

2.3.1.1.1 Fatal pitfall traps

Pitfall trapping does not measure absolute abundance because it relies on a beetle's own movement to lead to capture, so pitfall trap returns are not only affected by the density of individuals but also their level of cursorial activity (Greenslade 1964a). When trapping is un-interrupted over a species entire reproductive period within the same habitat, pitfall traps can be used to reliably estimate inter-annual relative abundance (Baars 1979). However, pitfall trapping over smaller time periods, or between different habitats, is not a reliable measure of relative abundance for a variety of reasons (Adis 1979). For example, dense vegetation can markedly reduce pitfall returns, when compared to traps positioned in more open habitat (Greenslade 1964b; Adis 1979; Baars 1979), and hunger level can increase the movement rate of beetles, potentially causing higher rate of capture in unfavourable habitats (Wallin and Ekbom 1994; Andersen 1995). Furthermore, inter-species comparisons of relative abundance can be unreliable because individual species have differing propensities for capture due to differences in activity period (nocturnal or diurnal) (Greenslade 1964a; Andersen 1995) and size and mobility (Andersen 1995; Mommertz *et al.* 1996). Finally, inter-time period comparisons of relative abundance are also difficult because of varying capture efficiency due to changes in temperature and weather (Greenslade 1964a).

Therefore, pitfall trapping is not in itself a reliable method for inter-period, inter-species, or inter-habitat comparisons of absolute or relative population density at any scale (Table 2.1). Not surprisingly, fatal pitfall trapping cannot be combined with mark-recapture methods to estimate local population size, although it can be combined with removal methods for the estimation of population density. However, the application of the removal method was rejected for several reasons (Section 2.3.1.3), so fatal pitfall trapping had no application for the estimation of population size or density.

Pitfall trapping can, however, reasonably be used to measure the relative *distribution* of species, provided that differences in habitat across the area surveyed are small. ERS have relatively little structural diversity, with all micro-habitats providing few obstacles to movement, however, even on ERS, comparisons of relative distribution are problematic, because the ecomorphological adaptations of individual species allow more rapid cursorial activity on certain sediment types (Andersen 1978; Desender 1989). Nonetheless, when used with caution, the method is suitable for the study of micro-scale distribution within open habitats. Indeed, several studies have successfully used fatal pitfall trapping to investigate microscale distribution of beetles in ERS and other riparian habitats (Desender 1989; Bonn and Kleinwächter 1999; Antvogel and Bonn 2001; von Hofe and Gerstmeier 2001). However, a high density of fatal pitfall traps would cause unacceptable reductions of population size, given the conservation importance of ERS beetles. Therefore fatal pitfall trapping was not considered suitable for the investigation of the microscale distribution of ERS beetles.

2.3.1.1.2 Semi-quantitative hand searches

Semi-quantitative hand searches and quadrat hand searches are both types of hunting techniques where the researcher actively seeks and captures beetles (Lott and Eyre 1996). Both involve turning over stones and splashing sediments with water to find beetles, which are then collected using an aspirator (e.g. Sadler and Petts 2000; Bates and Sadler 2004a), and both methods can be affected by both the weather and the skill of the researcher (Murdoch 1966; Andersen 1969; Lott and Eyre 1996). The two methods mainly differ in the spatial extent of the hand searching. Semi-quantitative hand searches operate over relatively wide areas and are standardised either by searching for a given time-period, or searching for a given time-period over a given area (Andersen 1969).

Semi-quantitative hand searches cannot alone be used to estimate population density or size because large areas are left un-sampled (Table 2.1). However, they could potentially be combined with mark-recapture methods to estimate population size, even given the methods high dependency on weather conditions, because some mark-recapture models allow sample effort to be unequal between capture events. However, semi-quantitative hand searches were rejected for the measurement of local population size because: (1) there would be a very low capture rate during cold periods; (2) species that do not hand search well (e.g. *Fleutiauxellus maritimus* (Curtis, 1840)) could not be studied; (3) there would be a bias towards individuals which spend most of their time along the water's edge where hand searching is easiest; and (4) potentially there would be a bias towards marked individuals during re-captures because they might be more easily seen.

Semi-quantitative hand searches have previously been used to study the microspatial distribution of ERS beetles (Andersen 1969, 1983b), but only in order to establish species microhabitat associations. The searches can be implemented over large areas but the relatively small catches and labour intensive nature hinder its application to extensive micro-distributional studies. In addition, the large number of searches necessary would make standardisation impossible due to changing weather conditions and changing beetle distributions between searches so this method was rejected for the study of microscale distribution (Table 2.1).

2.3.1.2 Description and justification of chosen sampling methods

2.3.1.2.1 Quadrat hand searches

Variants of quadrat searches have been used by a number of workers to estimate the density of beetles in the area sampled (e.g. Andersen 1969, 1995; Holeski 1978; Desender and Segers 1985; Niemeier *et al.* 1997; Hering 1998). The method involves searching a known area of sediments for beetles, removing all of the surface armour (when present) and dousing the sediments with water in the process. The method is the most quantitative sampling method available and skilled workers can sample virtually all of the beetles in the quadrat (Andersen 1995). The method is the only available method of measuring absolute population density without the application of removal or mark-recapture methods (Table 2.1). The main disadvantage of the method is that it is very time consuming, so can only be implemented over relatively small areas, and as a consequence it needs to be carried out in areas of high beetle density in order to obtain reasonable results (i.e. at the water's edge).

2.3.1.2.2 Dry pitfall traps

Pitfall trapping is easy to implement, is more easily standardised than hand searching methods and can be used to capture very large numbers of individuals over relatively short periods (Lott 1996; Lott and Eyre 1996; Luff 1996). Pitfall traps can also be activated and emptied in quick succession and can therefore be used to sample wide areas over virtually the same time period. Therefore non-fatal pitfall traps were a good means of sampling ERS beetles both for the measurement of microspatial distribution and for use with mark-recapture methods to estimate whole-bar population size (Table 2.1). However, the use of non-fatal pitfall traps raises a number of additional considerations. These included: (1) escape from traps (e.g. Luff 1975; Halsall and Wratten 1998), (2) an unnatural response to being trapped due to within-trap stress (e.g. Greenslade 1964b); and (3) an unnatural level of mortality either within-traps, or shortly after release from traps.

The most likely causes of within-trap stress and mortality when used to sample ERS beetles were within-trap and aerial predation from arthropods and birds (Mitchell 1963; Baars 1979), desiccation due to high temperature, and drowning due to rainfall.

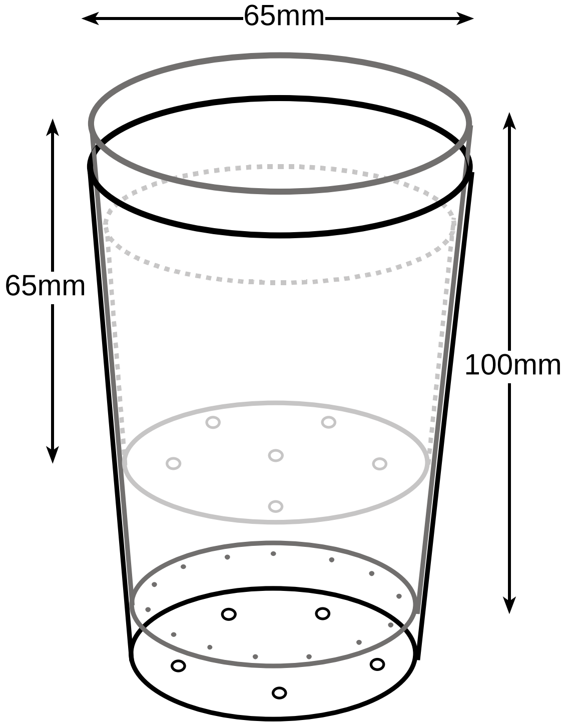


Figure 2.3 Design of the modified pitfall trap. The two outer section of the trap were 0.2L clear plastic cups, the innermost section was a 0.3L clear plastic cup with the upper part removed. Holes (3mm) in the bottom of the innermost and outmost sections allowed small beetles and water to pass through respectively. Pin-sized holes in the middle section allow the drainage of water, but not the passage of beetles. Damp sediment in the lower section reduced mortality due to desiccation.

A cheap, easily constructed pitfall trap was designed to overcome these problems (Figure 2.3). The traps were constructed using two 0.2L and one 0.3L clear plastic cups. The lower part of the 0.3L cups were cut off and slotted into the 0.2L cups. This separated the 0.2L cups into two compartments due to the wider diameter of the 0.3L cups. Small ERS specialist beetles could fall into the lower compartment via several 3mm diameter holes in the bottom of the upper cup. Once in the lower compartment beetles were prevented from escaping and protected from within-trap, and aerial predation, from large arthropods, birds and mammals. Damp sediment was placed within the lower section of the trap to reduce the level of stress and desiccation in captured beetles (Halsall and Wratten 1988). Water was allowed to drain out of the middle cup via several pin-sized holes, but these holes were too small to allow the passage of the beetles being studied. The lower cup when left in the ground during the emptying of traps would prevent the hole collapsing. This cup also had 3mm diameter holes in it to prevent it being pushed out of the ground by rising water levels, which meant that most traps would remain in place even when covered by water. Once in place, the dry pitfall traps could be rendered inactive, when not being used for sampling, using small polythene squares, which could be secured over the trap aperture using elastic bands.

2.3.1.3 Method selection for the estimation of local population size

Two distinct types of method can be used to estimate population size, the removal method (Moran 1951; Zippin 1956) and mark-recapture (mark-release-recapture) methods. The removal method is based on the idea that in a closed population, if animals are captured and removed, the size of catches will decline in a predictable way, so that the total population size can be estimated as the point at which catch per unit effort would be expected to equal zero. When used on rapidly moving species such as ERS beetles it requires the use of an enclosure to ensure the population is closed (e.g. Clark *et al.* 1995). The method could potentially be used to estimate the population density of a wide range of species, and could be used to estimate whole-bar population size if there were adequate numbers of enclosures of sufficient area, if the area of the bar was known. However, the method was rejected on the grounds that enclosures would be expensive to construct and would be liable to damage or loss through the activity of vandals, livestock or floods (Table 2.1).

The mark-recapture method follows the general premise that if a sample of a population is marked, released, and then after complete mixing within the original population, re-sampled, the proportion of marked individuals in the second sample will be the same as the proportion of the total number of marked individuals to the total population size. Since its conception (Petersen 1896; Lincoln 1930) it has been the focus of much more attention than the removal method, so that numerous refinements (e.g. Craig 1953; Jolly 1965; Burnham & Overton 1979; Wileyto *et al.* 1994) have allowed several of assumptions of the original method to be relaxed. A wide variety of different mark-recapture models (reviewed by Serber 1982; Greenwood 1996; Southwood and Henderson 2000) now allow population estimation for both open and closed populations and, for example, in situations when capture probability varies in time, or when there are deaths/emigrations in the study population. In contrast to the removal method, mark-recapture would only allow a limited number of species to be studied because of the large amount of field effort required, and the choice of study species would be limited to abundant, fairly large species that are identifiable in the field. Despite this, the flexibility of the mark-recapture approach, combined with the extra benefit of being able to study the movement dynamics of marked beetles, led to the choice of the mark-recapture method for the estimation of whole bar population size (Table 2.1).

2.3.2 Mark-recapture methods

Mark-recapture methods of estimating population size have a number of assumptions (Southwood and Henderson 2000): (1) marked animals are completely mixed in the population; (2) sampling is at discrete time intervals, which are small in relation to the time between samples; (3) the chance of capturing a marked individual is the same as that for an unmarked individual; and (4) marked animals are not affected in terms of life expectancy or behaviour, and marks are not lost. The needs of assumptions (1) and (2) had to be carefully balanced against each other, so that there was sufficient time between sampling periods for beetles to disperse naturally within the population, but sampling periods were still sufficiently close together. Marked beetles were released in the centre of bars after being marked, and within 0.5m of the point of capture when marking was not necessary, in order to increase the chances of complete mixing within the population. Mark-recapture schedules were carefully designed (Chapters 6 and 7) with assumption (2) in mind. Although common in vertebrates (e.g. Khan 1992; Tuyttens *et al.* 1999; Wegge *et al.* 2004), the occurrence of trap happiness and trap shyness in invertebrates is believed to be unlikely when using un-baited traps (Southwood and Henderson 2000). Therefore, the non-fatal pitfall traps used were not likely to violate assumption (3). Assumption (4) required the careful design and testing of the methods used to handle and mark beetles, and these are described in the following sections.

2.3.2.1 Handling live beetles for identification and marking

A method of controlling captured beetles was required in order to identify, and when necessary, mark them, but it was important to limit the amount of stress as far as possible. Options included ‘holding’ methods: restraining beetles with terylene netting (Murdoch 1963), fine hairs, dental floss, or some kind of suction; chilling them using iced water or dry ice to subdue them; or using ‘knock-out’ methods such as exposure to chloroform, or elevated levels of carbon dioxide (Southwood and Henderson 2000). However, the small size of ERS beetles, and the need to rapidly control large numbers of individuals, prohibited the use of ‘holding’ methods, and in order to reduce the amount of stress, chilling and ‘knock-out’ methods were rejected.

The method selected to control beetles was to drop them into water, whereby, beetles were separated from trap sediments, could be quickly identified, marks could be noted and beetles could be rapidly enumerated. When it was necessary to hold beetles still for identification or marking purposes beetles could be picked from the waters surface and their hind legs held firmly between thumb and forefinger (Plate 2.1). When beetles needed to be marked they were removed off-site in glass jars containing damp sediment, and were transferred to clear-lidded seed propagators containing damp sediment and food once they had been marked.

Plate 2.1 An individual *B. atrocaeruleum* held firm by a hind leg between thumb and forefinger whilst being marked with the 6 available colours of paint.

2.3.3.2 Method of marking live beetles

Methods of marking insects that are currently available, or in development, include tagging, mutilation marking, paint and ink marking, dust marking, elemental marking and protein marking (Hagler and Jackson 2001). A method of individually marking beetles was required because the application of stronger models for the estimation of population size (Otis *et al.* 1978a), and the identification of individual movements between bars, was then possible. A variety of methods have been used to mark beetles individually, including the application of different coloured paints (e.g. Mitchell 1963; Greenslade 1964a; Ohgushi and Sawada 1998), scratches (e.g. Murdoch 1963; García *et al.*, 2000), or burns (Nelemans *et al.* 1989), in unique codes. However, due to the relatively small size of ERS specialist beetles, a high rate of injury and mortality would be likely using ‘mutilation’ methods (e.g. scratching and branding) so the application of paint was preferred.

One of the problems with using paint-based marking systems is the loss of marks (Blinn 1963; Greenslade 1964b), and the abrasive nature of ERS habitats, together with the high level of activity in ERS specialist beetles accentuates this problem. Indeed, Wineriter and Walker (1984) tested the durability of 26 inks, pens and dyes and found that the longevity of virtually all materials was poor when used on the flour beetle *Tribolium castaneum* (Herbst, 1797). The only exception was paint extracted from the Mark-Tex Tech-Pen, the most modern version of which (the TexPen) was tested for its suitability. Another problem is that paints and thinners can potentially be toxic (e.g. Davey 1956; Dobson *et al.* 1958; Dobson and Morris 1961), causing mortality or behaviour alteration in marked individuals. Paint was extracted from the TexPen's by removing the nib section, and was thinned to an appropriate consistency with turpentine substitute (~5:1, paint: thinner). Fuse wire (five-amp) provided a suitable application method, allowing very small dots of paint to be applied. Six colours of paint were available and were applied in a six-dot code to the beetles' elytra (Plate 2.1).

2.3.3.2.1 Test of mark toxicity

Two species of carabid, *Bembidion atrocaeruleum* and *B. decorum* (Zenker in Panzer 1800), were used to test for mark toxicity (Bates and Sadler 2004b). Beetles were kept outside, in round white polypropylene paint kettles (internal diameter 172 mm, height 150 mm), which had holes in the bottom to allow drainage and 20-25 mm of sand and gravel substrate in which the beetles could hide and forage. White nylon netting (~0.5 mm diameter) was secured across the top of the container with glue continuously along ~40% of the container's circumference and elastic bands for the remainder. This allowed easy access into the containers for feeding and counting purposes. The sediment was initially heated overnight at 140^{o}C in order to kill beetle parasites (e.g. Laboulbeniales Fungi, Weir 1996). The beetles were fed with freeze-dried chironomids as required.

The survival of marked beetles of both species was compared with the survival of un-marked beetles over a period of 37 days in five replicate containers. Ten beetles were kept in each container and beetles were counted at two to four day intervals. Mann-Whitney U (Wilcoxon-Mann-Whitney) tests were used to determine if the number of marked and un-marked beetles surviving at each time period was significantly different.

Figure 2.4 illustrates the results of the mark toxicity experiment. At almost every time period, for both *B. atrocaeruleum* and *B. decorum*, the mean number of marked and un-marked beetles surviving were within 1 standard error of each other and none of the differences were significant even at the 10% level. The handling and marking process therefore did not increase mortality in *B. atrocaeruleum* and *B. decorum* over the period of study. The toxicity experiment was run over a longer time window than those used for the mark-recapture studies (Chapters 6 and 7). It was concluded that the marking method did not increase mortality and was therefore suitable for the investigation.

2.3.3.2.1 Mark longevity

Laboratory abrasion experiments were used to initially test if the paint adhered well to beetles and if it was likely to be durable in the highly abrasive ERS habitat. An abrasion experiment, in which dead *B. atrocaeruleum* (n = 10) and *F. maritimus* (n = 10) were glued to a card disc, submerged in ~2cm depth of sand and then put into a sediment shaker (≤1620 minutes, Heidolph promax 1020 shaker at speed 9, which was just enough to set all the sand in motion), showed that the paint was durable, that the different colours of paint were similarly durable, and that elytral marks were longer lasting than pronotal marks (Figures 2.4-6). The results of this experiment suggested that the marks were likely to last long enough for mark-recapture experiments to be run. Testing of actual mark longevity in field conditions was done using the results of the 2002 mark-recapture experiment (see Chapter 6).

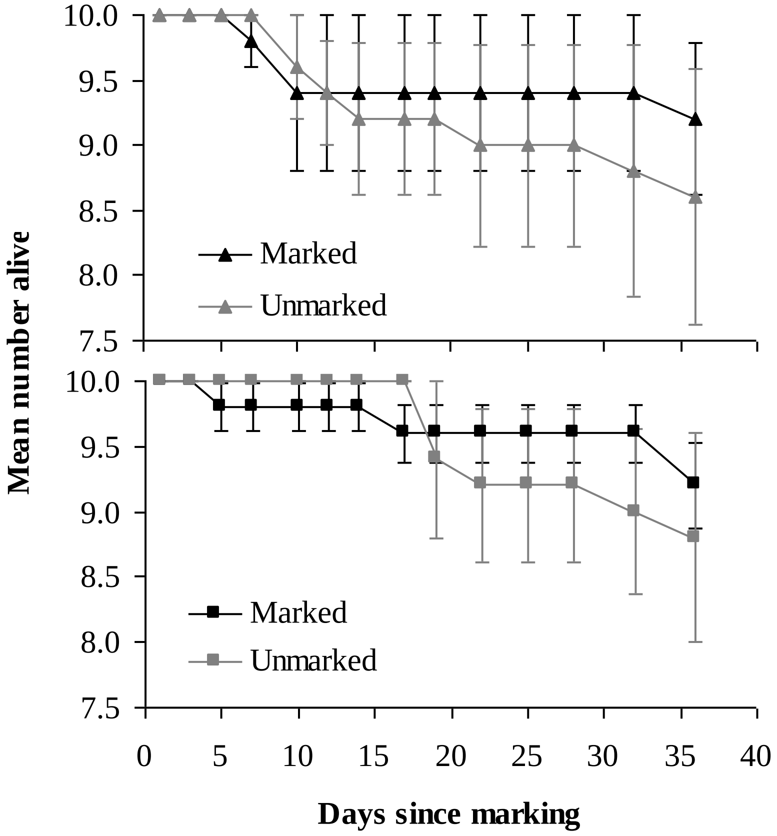


Figure 2.4 A comparison of the mean number of marked and unmarked *B. decorum* (top, triangles) and *B. atrocaeruleum* (bottom, squares) surviving in replicate (n = 5) gravel microcosms (error bars show $^{+}$/- 1SE)

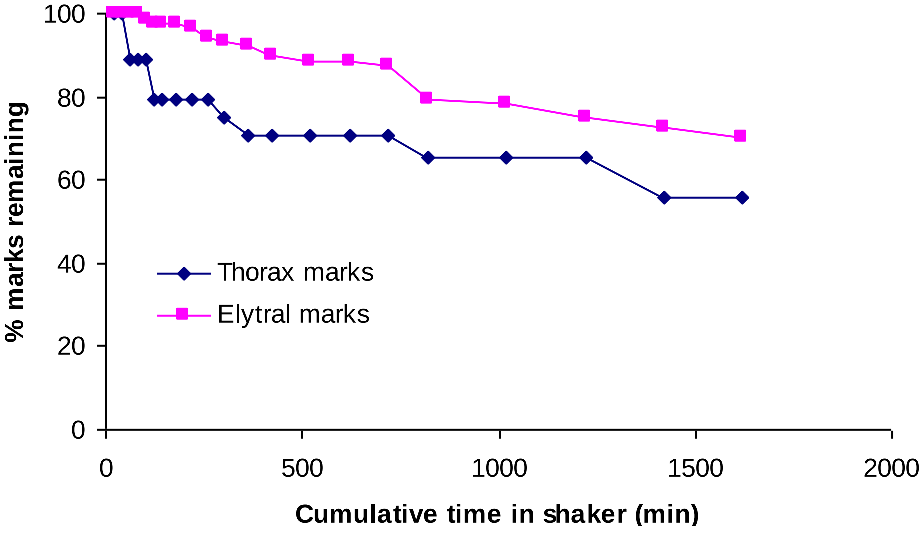


Figure 2.5 A comparison of the longevity of thorax and elytral marks in the shaker test (data from both *F. maritimus* and *B. atrocaeruleum* included).

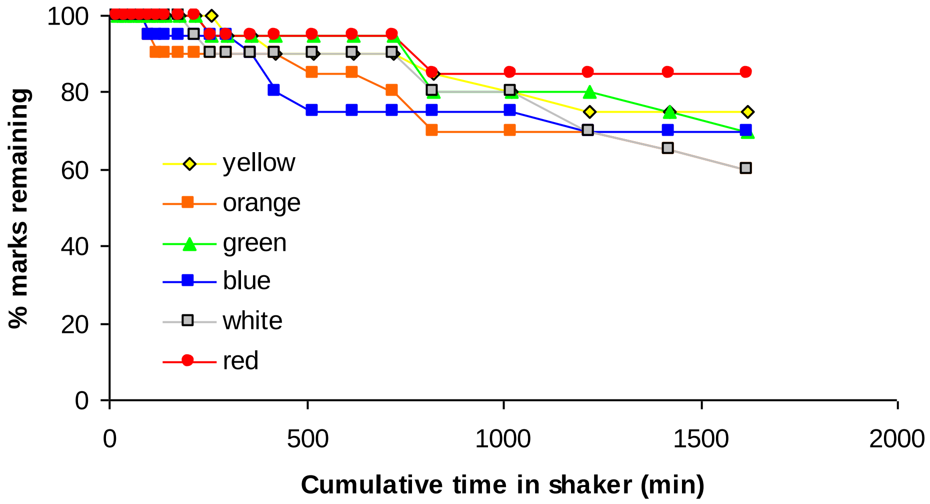


Figure 2.6 A comparison of the longevity of different coloured marks in the shaker test (data from both *F. maritimus* and *B. atrocaeruleum* included).

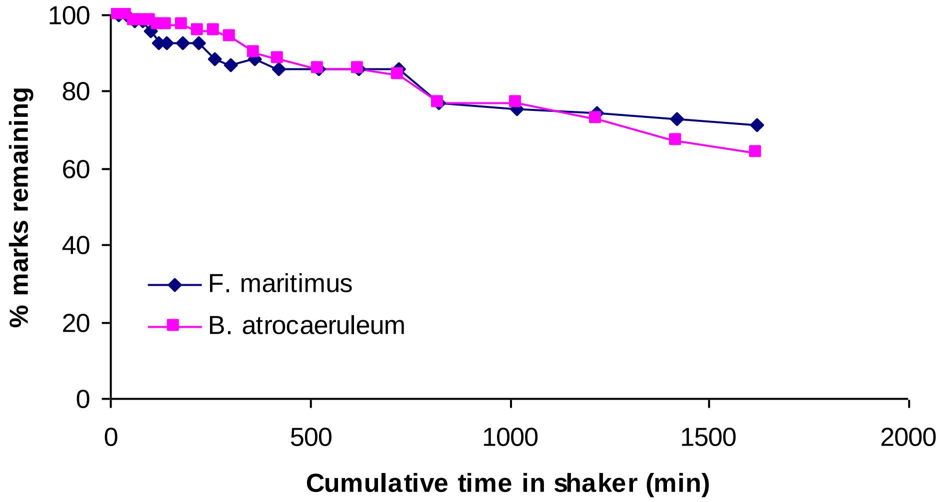


Figure 2.7 A comparison of the longevity of all marks between *F. maritimus* and *B. atrocaeruleum* in the shaker test.

2.3.3 Environmental variables

Every bar studied was surveyed using the methods of Sadler *et al.* (2004), which were based on the River Habitat Survey methodology (Fox *et al.* 1998; Raven *et al.* 1998) of the Environment Agency (Appendix 2.1 shows an example of a completed survey sheet). This was used as a basis for some of the environmental variables in Chapters 4-8. These surveys were designed to provide a quick snapshot of the environment of the studied ERS and the surrounding habitat and each variable was easily measurable in the field.

Vegetation type was categorised as (1) bare, (2) simple (predominantly annuals and short-lived perennial herbs), or (3) complex (other perennial species, e.g. gorse, and trees, in addition to 2). ERS profile was categorised as (1) flat (very low angled, low-lying ERS), (2) gentle (more elevated without avalanche faces at the bars edge), or (3) steep (avalanche faces at some point at the bars edge). ERS topography was categorised as (1) simple (flat and had no break of slope), (2) hummocky (clear mounds of sediment), and complex (flat areas, hummocks, and backwaters). Habitat heterogeneity was something of a summary variable of vegetation type, ERS profile, ERS topography and sediment diversity, and was based on the number of distinct microhabitats (e.g. downstream sandy areas, avalanche faces, silty fringes). Hibernation potential was scored on a scale of 1-3, where 1 showed the lowest hibernation potential and 3, the highest (in terms of the availability of grass tussocks, dead wood and dense vegetation). The availability of dead wood and grass tussocks both on the bar and on the bank was individually graded because of the known importance of these resources for hibernation (Luff 1966; Andersen 1968). Stocking densities were categorised as (1) light (livestock present but fairly limited damage to ERS), or (2) heavy (either heavy stocking relative to area, or light stocking but damage concentrated on ERS because, for example, ERS provide the only access to the water for drinking, leading to chronic heavy damage to ERS). If gravel had been extracted from the bar it was noted whether it was wide-scale, or from a limited discrete area, if the latter, the number of extraction area(s) was noted.

The importance of sediment size and diversity for habitat selection by ERS beetles has been recognised by a number of authors, and demonstrated in extensive field and intensive laboratory studies (e.g. Andersen 1969, 1978; Hammond 1998a; Eyre *et al.* 2001a; Eyre *et al.* 2001b; Sadler *et al.* 2004). Sediments are evidently one of the most important determinants of ERS beetle faunas, to the extent that many beetles show ecomorphological adaptations to living in particular sediment types (e.g. Andersen 1978; Desender 1989). As such, more sample effort was invested in the investigation of sediment grading and diversity. The methods of ‘photo-sieving’ here described were used for sediment analysis in Chapters 4-7.

The photo-sieving method used follows Petts *et al.* (2000), which was adapted from Adams (1979), and Ibbeken and Schleyer (1986). Coarse (≥ 8mm, -3phi) sediments were sampled *in situ* and further analyses of finer sediments were implemented in Chapter 6, but were not considered necessary in further investigations because there was found to be little difference in the finer sediment fraction’s *size distribution*, most heterogeneity having instead been found in the *amount* of fine sediment. The method involved placing a 0.25m^2 quadrat, marked with a scale, onto the surface of sediments and taking a photograph with the camera axis vertical to the surface plane (Plate 2.2).

Plate 2.2 Example photograph used for photo-sieving. The dots drawn onto the photograph were used to select clasts for measurement. The numbers prevented confusion when making measurements.

A hundred points were marked on the photograph, which lay at the intercepts of a 10x10 grid positioned over the photograph. The percentage of surface sediment <8mm was estimated as a percentage from these photographs. The b-axis of each of the marked clasts (>8mm) were measured from the photograph using the quadrat scale for reference. Quadrats containing numbered clasts, which were measured using a slide caliper, were photographed and calibrated with the b-axis measured from photographs. This was done on six sites on the Upper Severn study segment, and on six sites down the length of the Tywi, to create a calibration curve which could then be used to predict actual sediment sizes from those measured from photographs using linear regression. For the Upper Severn the relationship (N = 349, R^2 = 0.92) between the b-axis of particles estimated in the field and the actual b-axis (Figure 2.7) was described by the equation:

$$y = 0.9176x - 0.4985$$

where y = estimated particle size (phi) and x = particle size measured from photographs (phi)

For the Tywi the relationship (N = 617, R^2 = 0.91) between the b-axis of particles estimated in the field and the actual b-axis (Figure 2.8) was described by the equation:

$$y = 0.959x - 0.3086$$

where y = estimated particle size (phi) and x = particle size measured from photographs (phi)

The results from this method can be biased by (1) partial hiding of the clasts by fine sediment, shadows, or by other clasts, and by (2) imbrication of the clasts, but these methods are adequate in situations when a very high degree of accuracy is not required, especially considering the substantial amount of field effort saved (Church *et al.* 1987).

In the Upper Severn study area stage height was measured using a stilling well with shaft encoder at the Environment Agency stage measurement facility at Caersws (~250m downstream of the study area). Daily total rainfall data were taken from a Meteorological Office sampling station at Llandinam (SO 021 894, 131m asl). Daily temperature data (max/min) were taken from a Meteorological Office sampling station at Llanfair Caereinion (SJ 133 056, 243m asl, ~28km from the study area). The daily temperature data are likely to reflect the prevailing conditions at the study site less closely however, due to the distance between the sites and the elevational difference. The actual temperature at the study site would have been higher than that measured at Llanfair caereinion, probably by ~0.7^{o}C due to the difference in elevation (environmental lapse rate averages 0.65^{o}C in the troposphere). This stations distance from the study site was less of a problem than the difference in elevation because temperature is less spatially variable than rainfall. The rainfall data were from approximately the same elevation, which was very close to the study site, so these measurements would quite accurately reflect the amount of rainfall within the study area. Studies on the Afon Tywi all took place during similar flow levels and weather conditions and in addition, temperature was measured on site, therefore it was not considered necessary to obtain flow and weather data for the Tywi.

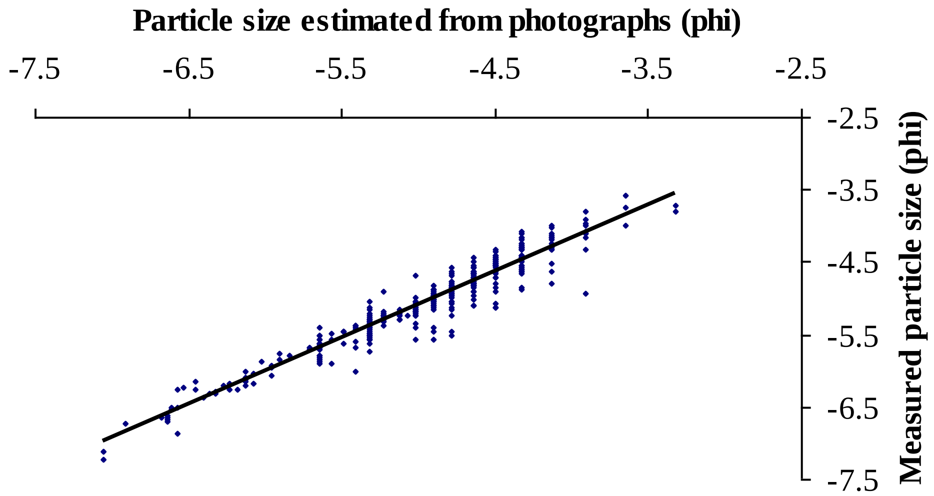


Figure 2.7 The relationship between the b-axis size of clasts estimated from photographs, with the actual measured b-axis for the Upper Severn.

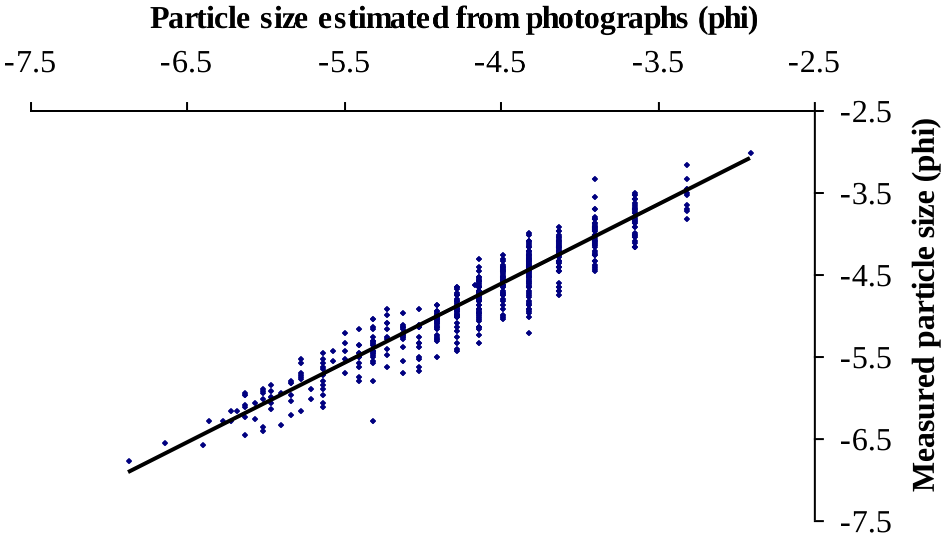


Figure 2.8 The relationship between the b-axis size of clasts estimated from photographs, with the actual measured b-axis for the Afon Tywi.

CHAPTER 3

SPECIALIST ERS BEETLES AS A BRITISH CONSERVATION RESOURCE: IMPORTANCE, RARITY STATUS REVISIONS, AND RIVER HIERARCHY

3.1 Introduction

This chapter details revisions to the rarity status of beetles that are considered to be British ERS specialists and assesses the importance of these beetles as a conservation resource. Initially, the chapter explains why it is important to carefully consider the definition and accurate allocation of: (1) habitat fidelity, and (2) accurate rarity statuses for the relative assessment of site conservation quality. It then describes the sources and methods used to allocate fidelity and revise the appropriate rarity statuses, before reporting these modifications. Illustrative examples of difficult and rare cases are included to aid the explanation of the process of assessing rarity status. Updates to the ERS quality scores and index are also presented and used to create a hierarchy of the best quality British rivers in terms of their ERS specialist beetle fauna. The chapter then concludes with a brief updated evaluation of the conservation importance of ERS beetles and their habitats, with particular focus on the species with biodiversity action plans (BAPs).

3.2 Background

This section expands on (1) the importance of habitat fidelity as a concept and of accurately allocating fidelity grades, (2) the importance of using up-to-date conservation statuses, and (3) describes the targets set in the BAPs for ERS beetles for subsequent examination of their likely success.

3.2.1 ERS habitat fidelity

Measurement of species diversity is one of the principal methods used in the assessment of site conservation quality (e.g. Wang and Young 2003; Wolters *et al.* 2005;

Bonn and Gaston 2005), and can be split into alpha (habitat diversity), beta (change in species between habitats), and gamma diversity (diversity of species in a region) (Noss 1990; Ricklefs and Schluter 1993). Any assessment of the diversity of an individual habitat (e.g. ERS, grey dunes, etc.) will be affected by the inclusion of species associated with adjoining habitats, and this will be particularly evident in areas with high beta diversity (e.g. riparian zones Ward *et al.* 1999) because species assemblages will differ more markedly in such areas.

The change in beetle assemblage between ERS and adjoining lotic and riparian habitats is particularly abrupt because of the very different characteristics of these habitats. Any assessment of the conservation quality of ERS based on species diversity will therefore be strongly affected by the proximity and quality of adjoining habitats. For example, consider two surveys of ERS of differing character based solely on the species diversity. The first is of a high quality piece of habitat (higher alpha diversity), with a large area (lower beta diversity) and poor quality adjoining habitats (lower gamma diversity). The second is of a low quality piece of habitat (lower alpha diversity), with a small area, and consequentially large ‘edge’ effect (higher beta diversity), and high quality adjoining habitat (higher gamma diversity). In this situation the beetle diversity measured on the ERS would most probably be higher in the second survey, despite its poorer habitat quality. This effect is common in ERS beetle surveys (Sadler *et al.* 2004) and was the reason for the development of a list of high fidelity, indicator species for ERS.

ERS beetle assemblages typically have a characteristic suite of species that are well adapted to un-vegetated sediments in close proximity to water. However, despite the considerable, and typically, primary importance of ERS as a habitat for these species, many are found in similar habitats such as exposed lacustrine sediments, coastal eroding cliffs, gravel pits, sand dunes, and even sewage works (Plachter 1986; Hammond 1998a;

Fowles 2005). As a consequence, the criteria for the inclusion as a fidelity 1 or 2 species were designed to include both species fairly fastidiously associated with ERS, and bare ground species for which ERS are very important habitats. Fowles (2005) defined fidelity 1 species as:

> *Species dependent for at least some stage in their life cycle on bare or sparsely vegetated sediments on the banks of rivers. Some of these species may also inhabit exposed lacustrine sediments, particularly where wave action forms banks of sediment on lake shores, as these features are in many ways ecologically similar to riverine shoals.*

and fidelity 2 species as:

> *Species strongly associated with exposed riverine sediments for at least some stage of their life cycle, but also occurring in a wide range of habitat types, such as flushes, seepages, pond margins, etc., where the presence of bare sediment is of fundamental importance for some stage of their life cycle.*

Species that are commonly found (sometimes in abundance) on ERS (e.g. *Bembidion tetracolum* Say, 1823; *Hypnoidus riparius* (Fabricius, 1792); and *Paranchus albipes* (Fabricius, 1796)), but which are also often found in less open habitats, or in bare ground habitats well away from water, were not included because they could easily reflect the quality of adjoining habitats rather than ERS *per se*.

The classification of a species within a certain fidelity class is influenced by the degree of understanding of that species' habitat requirements or habitat associations, and therefore is liable to change following additional research or survey work. Accordingly, the list of high fidelity ERS beetles has gone through many changes, the most recent of which, Fowles 2005, is available over the internet. This chapter presents necessary revisions to this list, obligated by increased understanding brought about by: (1) additional discussion with experts in the field, (2) later taxonomic revisions, and (3) additional survey work.

3.2.2 Rarity status

Information on the status and distribution of species underpins much of nature conservation practise (e.g. Luff 1987; Ball 1994; Cakan *et al.* 2005; Pierce *et al.* 2005). It is important for the assessment of site quality and change in species distribution in response to threats, environmental change, or conservation initiatives (e.g. Eyre 1994; Eyre *et al.* 1996; Cortes *et al.* 1998; Davies *et al.* 2005; Hickling *et al.* 2005). The emphasis here is the relative assessment of site quality, but clearly assessments are only as reliable as the species data upon which they are based. The relative assessment of conservation importance in other habitats using invertebrates, such as that undertaken for dead wood using saproxylic beetles (e.g. Harding and Alexander 1994; Fowles 1997; Fowles 1999), and for aquatic habitats using water beetles (Foster 1987; Foster and Eyre 1992), have been based on high fidelity indicator species which are relatively well studied. Until recently ERS beetles were relatively understudied in Britain and as a result their national rarity statuses (Hyman and Parsons 1992, 1994) are often inaccurate (Eyre *et al.* 1998; Eyre *et al.* 2000; Sadler and Bell 2002). The relative conservation quality of ERS habitats are assessed using the ERS quality score (ERSQS), and the ERS quality index (ERSQI) (e.g. Sadler and Bell 2002; Hewitt *et al.* 2005), which are based around the rarity of ERS specialist beetles. Without up-to-date rarity statuses, the relative assessment of ERS quality based on these indices will be erroneous.

3.2.3 Targets of ERS beetle Biodiversity Action Plans

The eight specialist ERS beetles that have BAPs are: (1) *Bembidion testaceum*, *Lionychus quadrillum*, *Perileptus areolatus*, *Meotica anglica*, *Thinobius newberyi*, *Hydrochus nitidicollis*, (2) *Dyschirius angustatus* and (3) *Bidessus minutisimus* (Anon.

1999). The aims of the BAP for the first six species are to (a) maintain viable populations within each of the catchments currently occupied by the species, and (b) enhance populations at selected sites by 2010. For *D. angustatus* the aim is simply to maintain its range. *Bidessus minutisimus* shares aim (a), and has a second aim which is to (c) ensure viable populations are maintained in a minimum of four Welsh and two Scottish catchments by 2010. The distributions of each of these species are presented with brief notes on their relative abundance and likely viability in the results.

3.2.4 Objectives

The specific objectives of this chapter were to:

1. Revise the rarity statuses of all the specialist ERS specialist beetles.
2. To use these revised statuses to produce a hierarchy of the best British rivers in terms of their ERS specialist beetle fauna.
3. To assess the British conservation importance of ERS beetles.

3.3 Methods

Due to the large amount of occurrence data associated with well over a hundred species across Britain, data was handled using the Recorder 2002 biological record collection, collation and reporting database. This section covers the selection of species for inclusion in the database, the operation of the database, the acquisition of all available occurrence data for these species, the criteria used to classify the rarity status of each species, a description of the indices used to assess ERS conservation quality, and the methods used to produce the hierarchy of British rivers according to their ERS quality.

3.3.1 Selection of specialist ERS beetles

Beetles have been selected for inclusion in the database, and given a fidelity of 1 or 2, using information in published sources, by consultation with experts in the field, and using experience obtained from survey work. Published sources include Lindroth (1974), Luff (1998), and Hyman and Parsons (1992, 1994). Experts consulted include Peter Hammond (responsible for the national Staphylinidae database, Natural History Museum), Adrian Fowles (Countryside Council for Wales), Jon Sadler (University of Birmingham), Howard Mendel (responsible for the national Elateridae database, Natural History Museum), Jonty Denton (responsible for the national Steninae database), Garth Foster (responsible for the national water beetle database, Balfour Brown Club), and Darren Mann (responsible for the national Scarabidae database, Oxford University Museum). Clearly, the assignment of fidelity classes to species is a subjective process, and will never lead to unanimous agreement across all coleopterists. However, all suggestions have been taken into account and every effort has been made to reach consensus for as many species as possible using all the available data.

3.3.2 The British specialist ERS beetle database

All data were input into Recorder 2002 (Version 2.3.7.8, National Biodiversity Network, Dorset Software Sources Ltd.) either manually using the recording card function, or through import from excel where data was available electronically. Record input fields used include: location, grid reference, date, sampling method, recorders, document from which record was taken, and important notes (e.g. description of habitat); thus enabling the full input of all available information for each record. The programme allows full filtering of the data by any desired criteria and data can be output to Microsoft Excel and DMAP. Data can also be displayed using the internal mapping device, although maps shown in this chapter were created using DMAP 7.0e (Dr Alan Morton).

3.3.3 Information sources for occurrence data

A wide variety of published and un-published sources were used in the database. There have been more than 100 intensive surveys of ERS beetles in Britain (e.g. Sadler and Petts 2000, Sadler and Bell 2002), the distribution of which are shown in Figure 3.1a. The distribution of these surveys is biased towards the north and west of Britain and this mirrors the distribution of the most extensive areas of ERS. Supplementary records were inserted from existing national recording schemes including those for: Carabidae (managed by Mark Telfer), Staphylinidae (managed by Peter hammond), water beetles (managed by Garth Foster and the Balfour Brown club), the Invertebrate Site Register (Ball 1994), the Cumbrian biodiversity database (Steve Hewitt, Tulliehouse Museum), and the existing ERS beetle database for Wales and the borders (managed by Adrian Fowles). Unpublished records were included from museum voucher specimens and various British coleopterists. Records were also incorporated from a large number of published and unpublished literature sources, which are listed in Table 3.1.

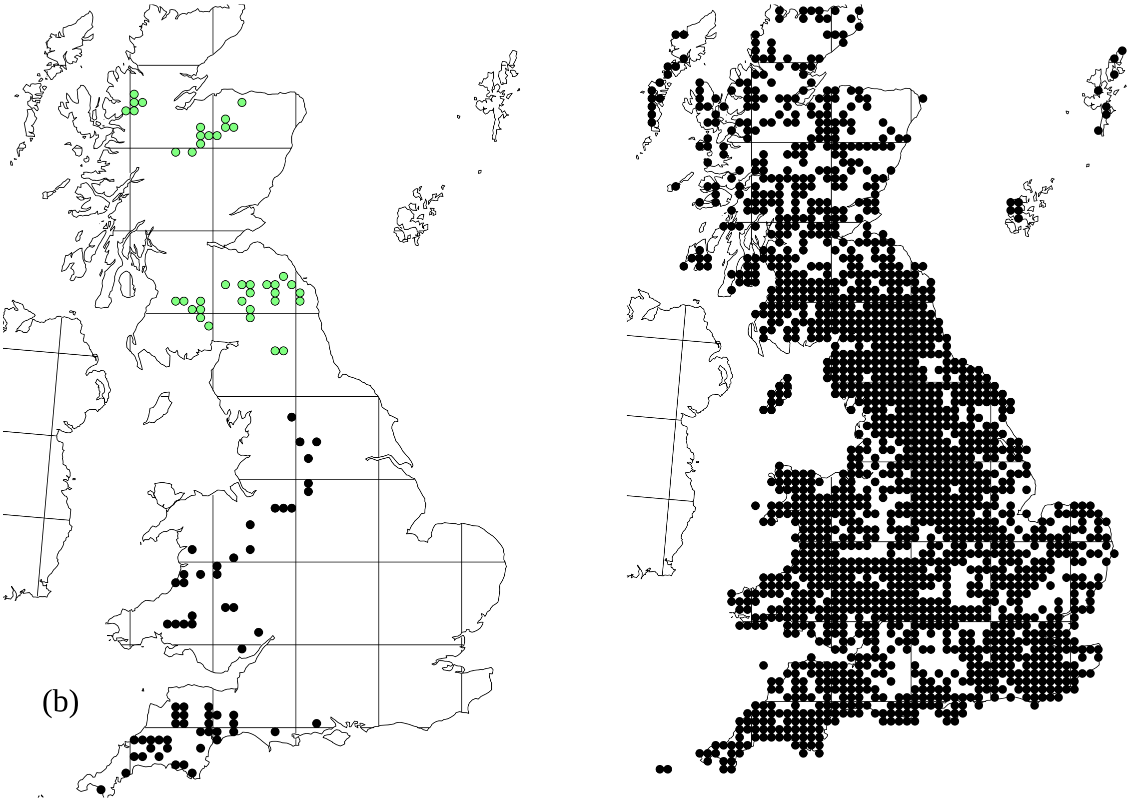


Figure 3.1 (a) Distribution of intensive surveys of ERS beetles across Britain. Light circles indicate surveys that have almost exclusively relied on pitfall trapping and have been carried out by Mick Eyre and co-workers. Black circles represent surveys that have also extensively employed hand searching. These have mainly been implemented by Jon Sadler and co-workers. (b) Distribution of all records in the database.

Table 3.1 List of published and unpublished sources from which records have been taken for the British ERS beetles database.

Alexander KNA. 1986. Local and rare Coleoptera from the Brecon Beacons. *Entomologist's Monthly Magazine* **122**: 71.
Allen JW. 1915. Records of Coleoptera from South wales district. *Entomological Research & Journal of Variation* **27**: 87-88.
Attlee HG. 1907. Coleoptera in wales in 1906. *Entomological Research & Journal of Variation* **19**: 94.
Bailey JH. 1903. *Hydroporus marginatus*, Duft., &c., in Shropshire. *Entomologist's Monthly Magazine* **39**: 203.
Bailey JH. 1903. *Perileptus areolatus*, Creutz, in Shropshire. *Entomologist's Monthly Magazine* **39**: 203.
Balfour-Browne F. 1949. The water beetles found in the counties of Cheshire, Flintshire, Denbighshire, Caernarvonshire, Anglesy, Merionethshire & Montgomeryshire. *Cheshire & North Wales Natural History* **3**: 81-134.
Bateman JA. 1974. Biological recording Group for Wales. Reports and records of field meetings. 1972-1973. National Museum of Wales, Cardiff.
Bates AJ, Sadler JP. 2004. Records of rare and notable species of beetle from exposed riverine sediments (ERS) on the rivers Tywi and Upper Severn. *Coleopterist* **13**: 125-132.
Bell D, Sadler JP, Drake CM. 2004. The invertebrate fauna of exposed riverine sediments in Devon: a survey report. EA & Devon County Council.
Bell D, Sadler JP. 2001. A survey report on the invertebrate fauna (Coleoptera and Araneae) of exposed riverine sediments in the River Camel catchment, Cornwall, UK.
Bell D, Sadler JP. 2002. The invertebrate fauna (Coleoptera and Araneae) of exposed riverine sediments in Cornwall and West Devon: a survey report.
Bell D, Sadler JP. 2003. Assessment of the river shingle invertebrate fauna at Llanelltyd on the Afon Mawddach, Merionydd. CCW.
Bell D, Sadler JP. 2003. The coleopteran fauna of exposed riverine sediments on the River Dane, Cheshire: a survey report. EA.
Bell D, Sadler JP. 2003. The coleopteran fauna of five exposed riverine sediment sites in Cornwall and West Devon: a survey report.
Bell D, Sadler JP. 2003. The invertebrate fauna (Coleoptera and Araneae) of coastal shingle at Loe Bar, Cornwall: a survey report.
Booth R. 2000. Exhibits: Coleoptera. *British Journal of Entomology & Natural History* **13**: 173-174.
Boyce DC. 1989. Coleoptera recording in Ceredigion in 1988. *Dyfed Invertebrate Group News***12**: 15-18.
Boyce DC. 1990. Coleoptera recording in Ceredigion (VC46) during 1989. *Dyfed Invertebrate Group News* **16**: 16-21.
Boyce DC. 1990. The beetles of Ynyslas Dunes (22/6094), Dyfi NNR, Ceredigion (VC46). *Dyfed Invertebrate Group News* **18**: 5-14.
Boyce DC. 1991. Coleoptera recording in Ceredigion during 1990. *Dyfed Invertebrate Group News* **20**: 15-20.
Boyce DC. 1998. Ceredigion Coleoptera records. *Dyfed Invertebrate Group News* **9**: 17-19.
Cooter J. 2002. Wales coastal soft cliff invertebrate survey Lleyn Peninsular, Gwynedd. Liverpool Museum.
Denton J. 1996. Notes on the Coleoptera of running water habitats in Surrey and North hampshire, including several new county records. *Coleopterist* **4**: 86.
Denton J. 2002. Rare and uncommon Coleoptera records, 2001. *Coleopterist* **11**: 29-30.

Denton JS. 1997. Recent records of notable Coleoptera in England and Wales. *Coleopterist* **6**: 70-71.

Denton JS. 1999. Rare and Notable Coleoptera in England, 1995-97. *Coleopterist* **8**: 20-22.

Denton JS. 2000. *Aegalia sabuleti* (Panzer) (Scarabidae) in Surrey. *Coleopterist* **9**: 24.

Dilwyn LW. 1829. Memoranda relating to coleopterous insects found in the neighbourhood of Swansea. Murray & Rees, Swansea.

Elliman EG. 1898. Coleoptera at Llanfairfechan, North Wales. *Entomologist's Monthly Magazine* **34**: 257-258.

Eyre MD, Luff ML, Lott DA. 1998. Rare and notable beetle species records from Scotland from survey work with pitfall traps, 1992 - 1996. *Coleopterist* **7**: 81-90.

Eyre MD, Luff ML, Lott DA. 2000. Records of rare and notable beetle species from riverine sediments in Scotland and Northern England. *Coleopterist* **9**: 25-38.

Eyre MD, Luff ML, Woodward J. 2002. Rare and notable Coleoptera from post-industrial and urban sites in England. *Coleopterist* **11**: 91-101.

Eyre MD, Luff ML. 1995. Coleoptera on post-industrial land: a conservation problem? *Land Contamination & reclamation* **3**: 132-134.

Eyre MD, Rushton SP. 1987. Allen Confluence and Doddington Bridge (R. Till). Report on the survey of proposed SSSI's on Northumberland rivers. EN.

Eyre MD, Rushton SP. 1992. An assessment of the invertebrates of the sandy riverbanks of the River Till, Northumberland. EN.

Eyre MD. 1998. Preliminary assessment of the invertebrate fauna of exposed riverine sediments in Scotland. SNH.

Fowles AP, Boyce DC. 1992. Rare and notable beetles from Cardiganshire (VC44) new to Wales. *Coleopterist* **1**: 7-15.

Hammond PM. 1998. Survey of invertebrates of exposed riverine sediments on the Rivers Teign and Bovey near their confluence. EA.

Hammond PM. 2003. Preliminary survey for the ground beetle *Bembidion testaceum* on the river Usk. CCW.

Harvey PR. 2005. Colne Point invertebrate survey and assessment 2004. Unpublished report for the Essex Wildlife Trust.

Hewitt S, Atty D, Parker J, Read J, Sinclair M. 2005. Survey of the insects of exposed riverine sediments on the rivers Eden and Derwent in Cumbria in 2004.

Hewitt SM, Atty DB, Parker JB, Sinclair M. 2000. Cumbrian river shingle invertebrates survey. Carlisle Natural History Society.

Hyder Consulting ltd. 2000. Gwent Europark - WDC2: reen flora and invertebrate monitoring 2000.

Lott D. 1992. A survey report on the terrestrial beetles of riparian habitats along the River Soar near Loughborough, Leicestershire, March - October, 1991. Leicestershire Museums Service.

Lott D. 1993. A study of the effects of the River Soar alleviation scheme upon the riparian beetle fauna - 1992. NRA, Severn Trent.

Lott DA. 1999. Riparian beetles on soft sediments by the River Teme, Worcestershire. *Coleopterist* **8**: 7-10.

Lott DA. 2004. Shingle invertebrate survey and condition assessment at Rheidol Shingles and Backwater's and Rheidol Gev Capel Bangor SSSI. CCW

Majerus MEN, Fowles AP. 1989. the rediscovery of the 5-spot ladybird (*Coccinella* 5-*punctata*L.) (Col. Coccinellidae) in Britain. *Entomologist's Monthly Magazine* **125**: 177-181.

Marsh RJ. 2002. Coleoptera report for 1995-2001. *The Naturalist* **127**: 69-80.

Mendel H. 2002. Notes on British Elateridae: *Dicronychus equisetiodes* Lohse, 1976 and *Negastrius arenicola* (Boheman, 1853) recorded from Britain. *Coleopterist* **11**: 77-80.

Sadler JP, Bell D, Hammond P. 2005. R&D assessment of the distribution of *Bembidion testaceum* and reasons for its decline. EA.

Sadler JP, Bell D, Skidmore P. 2000. A comparaitve assessment of ERS invertebrates in the catchment of the Upper Severn. CCW.

Sadler JP, Bell D. 2002. Invertebrates of exposed riverine sediments - Phase 3. EA & CCW.

Sadler JP, Bell, D. 1999. A comparative site assessment of exposed riverine sediment (ERS) beetle faunas in south-west England. EN.

Sadler JP, Petts GE. 1998. Invertebrates of exposed riverine sediments - Phase 2. EA.

Tomlin JRleB. 1921. Notes on the Coleoptera of Glamorgan, 1. *Entomologist's Monthly Magazine* **57**: 34-36.

The full distribution of all records in the database is shown in Figure 3.1b. All records that appear in the database are either from the public domain or included with the kind permission of those responsible for the data. Where data for a species is known or suspected of being incomplete, the advice of various coleopterists has been used to assign rarity status, or the current rarity status maintained, unless there was strong evidence to suggest that the status was incorrect.

3.3.4 Criteria for the classification of rarity status

The criteria for Red Data Book (RDB) categories 1-3 (1 = Endangered, 2 = Vulnerable, 3 = Rare) follow Shirt (1987). The criteria for the additional categories RDBK (Insufficiently Known) and RDBI (Indeterminate) follow Wells *et al.* (1983), and the criteria for Nationally Scarce (Notable) species follow Eversham (1983). Briefly, RDB1 species are those in danger of extinction in the UK; occurring in only one 10km square, in especially vulnerable habitats, or having undergone a rapid decline and now only occurring in <6, 10km squares. RDB2 species are those which could move into RDB1 if negative factors continue to operate; those declining throughout their range, and species in vulnerable habitats. RDB3 species are those with small populations that are not at present Endangered or Vulnerable, but are at risk; those *estimated* to exist in <16 10 km squares, or those that exist in more squares, but in small areas of especially vulnerable habitat. RDBI species are those considered to be in one of the RDB categories, but where there is insufficient information to definitively place them in one category or other. RDBK species are those which are suspected to belong to an RDB category, but it is not definitely known to be in one of the categories due to a lack of information. Na species are those not classified as RDB species but are *thought* to occur in 30 or fewer 10km squares. Nb species are those *thought* to occur between 31 and 100 10km squares. Notable species are those that are *estimated* to occur in 16 to 100 10km squares, but due to a lack of information, the subdivision of this category is not attempted. In contrast to Hyman and Parsons (1992, 1994), conservation status designations in this review are based on the number of post-1980 10km squares, rather than the number of post-1970 10km squares, due to the elapse of a decade or so since this review.

All of the conservation categories require a certain amount of subjective decision making, either during the assessment of the vulnerability of a species to certain threats, or for the estimation of the number of 10km squares a species is likely to occupy. Such decisions have been aided by experience and by discussion with various coleopterists. Few species have been studied in enough depth to make such decisions relatively straightforward. Examples of the decision making process are given in the Discussion section.

3.3.5 Indices of conservation quality

Indexes used to compare site conservation quality that are based on the rarity of the invertebrate community are many and varied (e.g. Alexander 1988; Eyre and Rushton 1989; Fowles *et al.* 1999). The ERS quality score (ERSQS), and ERS quality index (ERSQI) systems, currently used to assess the quality of ERS using the specialist beetle fauna (e.g. Sadler and Bell 2002; Hewitt *et al.* 2005) are typical of the geometric scoring indices generally used. The indices use the following scoring system: common species = 1; local species = 2; very local species = 4; N and Nb species = 8; Na and RDBK = 16; RDB3 and RDBI = 24; and RDB2 and RDB1 = 32. The ERSQS is the sum of these scores for the area (e.g. site, river, catchment) of interest. However, this index is very sensitive to the amount of survey work implemented on the area of interest (Fowles *et al.* 1999), which limits its applicability for site comparisons. The ERSQI corrects for differences in survey effort to some degree and is calculated as:

$$\text{ERSQI} = (\text{ERSQS}/N)*100$$

where N = the number of ERS specialist beetles in the area of interest

These indices use three levels of scores below Notable and RDB because there is still considerable variation in the distribution of sub-N species, which is important to capture in any assessment of the conservation potential of a site. The assignment of these categories has been assisted using the following criterion: *very local*, known from <22 100km British squares; *local*, known from 23-26 100km British squares; and *common*, known from >26 100km British squares. All known records of a species are used in this assessment as the idea is to get a measure of the national extent of their distribution. These criteria are used only as a guide, for less well recorded species (e.g. Staphylinidae), and for species very sparsely distributed in a large number of 100km squares, these rules can be relaxed. The method of assigning these statuses is therefore semi-quantitative because it takes into account extenuating factors.

3.3.6 Hierarchy of ERS quality for British rivers

There are records from over 200 rivers in the British specialist ERS beetle database, however many of these rivers have records for only a handful of species, which, because of the tendency of coleopterists to only publish records of rare species (Fowles 1997), often have high conservation status. The ERSQI is susceptible to inflation of site value when based on a few records of rare species from an area, so the conservation value of such rivers cannot reasonably be compared. As such, only rivers that have been intensively surveyed using pitfall traps (Figure 3.1a) were included in the analysis, together with the rivers Eden, Caldew, Irthing, Derwent and Kingwater in Cumbria which have been very intensively hand searched in recent years (Hewitt *et al.* 2000, 2005). An additional condition that the rivers had to have at least 15 scoring species was also imposed in order to prevent ERSQI inflation by a few high scoring species. Of the initial 73 rivers intensively surveyed this left 53 rivers in the analysis. Many records in the database are well over one hundred years old and the rivers conservation value would be likely to have changed since that time. Therefore in order to assess current conservation value only records from 1980 onwards were used in the analysis. It is recommended that site evaluation incorporate a combination of ERSQS and ERSQI (Sadler and Bell 2002; Hewitt *et al.* 2005), so rivers are ranked by both these indices.

3.4 Results

3.4.1 Changes to ERS fidelity, status and ERSQI

The revised fidelities, statuses and ERSQI scores for the 131 ERS specialists are shown in Table 3.2 together with information on their old statuses and fidelities, number of pre- post- and total 10km squares, and number of 100km squares.

3.4.2 Examples of the decision making process when assigning rarity statuses

Figure 3.2 shows the distribution of four species of carabid, namely *Bembidon geniculatum*, *B. fluviatile*, *Asaphidion flavipes*, and *Thalassophilus longicornis*. Carabids have been chosen as examples because they are the best recorded group in the database and have a relatively stable taxonomy. Nonetheless, these four species are good examples of: (a) the influence of under-recording from an area, (b) the influence of under-recording from a microhabitat, (c) the influence of taxonomic revisions, and (d) the influence of the ease of sampling of a species, respectively. These examples are considered in the Discussion section.

3.4.3 BAP species

The distribution of: (1) *Bembidion testaceum, Lionychus quadrillum, Perileptus areolatus, Meotica anglica, Thinobius newberyi*, *Hydrochus nitidicollis*, (2) *Dyschirius angustatus* and (3) *Bidessus minutisimus* are shown in Figures 3.3 and 3.4. The current status of *B. testaceum* (Figure 3.3) has been studied in considerable depth by Sadler *et al.* (2005).

Table 3.2 Revised fidelities, statuses and ERSQI scores for the 131 specialist ERS beetles. Current statuses are taken from Hyman and Parsons (1992, 1994). Old fidelities were taken from Fowles (2005). Species without an old status have been added to the list, species without a new status have been removed from the list. Agg. represents data for which accurate separation to species is not available. Statuses with the superscript 1 = those recommended by Peter Hammond (NHM); 2 = those recommended by Howard Mendel (NHM); and 3 = those for which due to a lack of information and input from those responsible for these databases, the former status has been retained unless there is strong evidence to the contrary.

Species	Current status	Old Fidelity	New Fidelity	Number 10km squares			Number 100km squares	Revised Status	ERSQI Score
				Pre 1980	Post 1980	Total			
Carabidae									
Acupalpus flavicollis (Sturm, 1825)	NA	2	2	26	5	30	-	RDB3	24
Agonum micans Nicolai, 1822	Local	2	2	79	91	156	27	Common	1
Amara fulva (Müller, O.F., 1776)	NB	2	2	86	62	132	-	NB	8
Amara quenseli (Schönherr, 1806)	NA	2	2	9	5	11	-	RDB3	24
Asaphidion flavipes (Linnaeus, 1761)	Common	2	2	0	7	7	-	Common^{3}	1
Asaphidion flavipes agg.	-	-	-	4	28	30	-	-	
Asaphidion pallipes (Duftschmid, 1812)	NB	2	2	39	20	50	-	NB	8
Bembidion andreae (Fabricius, 1787)	Very Local	2	2	55	72	116	25	Local	2
Bembidion articulatum (Panzer, 1795)	Local	2	2	144	130	240	20	V. Local	4
Bembidion atrocaeruleum (Stephens, 1828)	Local	1	1	104	237	303	29	Common	1
Bembidion bipunctatum (Linnaeus, 1761)	NB	2	2	66	47	106	-	NB	8
Bembidion decorum (Zenker in Panzer, 1800)	Common	1	1	110	175	245	29	Common	1
Bembidion dentellum (Thunberg, 1787)	Local	2	2	211	197	350	26	Local	2
Bembidion femoratum Sturm, 1825	Local	2	2	185	179	326	36	Common	1
Bembidion fluviatile Dejean, 1831	NB	2	2	30	16	41	-	NB	8
Bembidion geniculatum Heer, 1837/8	Very Local	1	1	68	33	91	-	NB	8
Bembidon gilvipes Sturm, 1825	NB	2	-	-	-	-	-	-	-
Bembidion lunatum (Duftschmid, 1812)	NB	2	2	48	33	71	-	NB	8
Bembidion monticola Sturm, 1825	NB	1	1	69	59	118	-	NB	8
Bembidion prasinum (Duftschmid, 1812)	Very Local	1	1	65	75	125	23	Local	2
Bembidion punctulatum Drapiez, 1821	Local	1	1	94	151	211	27	Common	1
Bembidion quadripustulatum Audinet-Serville, 1821	NB	2	2	32	17	46	-	NB	8
Bembidion saxatile Gyllenhal, 1827	NB	2	2	78	39	106	-	NB	8
Bembidion schueppeli Dejean, 1831	NA	1	1	12	34	44	-	NB	8

Bembidion semipunctatum Donovan, 1806	NA	1	1	9	5	12	-	RDB3	24
Bembidion stomoides Dejean, 1831	NB	1	1	44	12	55	-	NB	8
Bembidion testaceum (Duftschmid, 1812)	NB jBAP	1	1	26	7	30	-	RDB2	32
Bembidion tibiale (Duftschmid, 1812)	Common	1	1	216	298	431	33	Common	1
Bembidion virens Gyllenhal, 1827	RDB3	1	1	5	5	6	-	RDB3	24
Bracteon litorale (Olivier, 1791)	NB	1	1	46	52	85	-	NB	8
Chlaenius vestitus (Paykull, 1790)	Local	2	2	111	103	185	24	Local	2
Clivina collaris (Herbst, 1784)	Local	2	2	138	106	216	28	Common	1
Dyschirius aeneus (Dejean, 1825)	Local	2	2	92	43	118	-	NB	8
Dyschirius angustatus (Ahrens, 1830)	RDB3 BAP	2	2	5	9	12	-	RDB3	24
Elaphropus parvulus (Dejean, 1831)	NB	2	2	7	56	62	-	NB	8
Lasiotrechus discus (Fabricius, 1792)	NB	2	2	46	30	68	-	NB	8
Lionychus quadrillum (Duftschmid, 1812)	RDB3 jBAP	2	2	16	8	22	-	RDB3	24
Pelophila borealis (Paykull, 1790)	RDB3	2	2	6	4	8	-	RDB3	24
Perileptus areolatus (Creutzer, 1799)	NA jBAP	1	1	17	26	41	-	NB	8
Tachys bistriatus (Duftschmid, 1812)	NB	2	2	36	13	41	-	NB	8
Thalassophilus longicornis (Sturm, 1825)	NA	1	1	6	17	21	-	NA	16
Dytiscidae									
Bidessus minutissimus (Germar, 1824)	RDB3 BAP	1	1	14	10	21	-	RDB3	24
Hydrophilidae									
Georissus crenulatus (Rossi, 1794)	NA	2	2	26	50	70	-	NB	8
Hydrochus nitidicollis Mulsant, 1844	RDB3 jBAP	1	1	8	4	11	-	RDB3	24
Helophorus arvernicus Mulsant, 1846	NB	1	1	72	181	246	28	Common	1
Hydraenidae									
Hydraena gracilis Germar, 1824	Local	1	1	196	347	524	36	Common	1
Hydraena nigrita Germar, 1824	NB	1	1	88	122	207	26	Local	2
Hydraena rufipes Curtis, 1830	NB	2	2	34	64	95	-	NB	8
Ochthebius bicolon Germar, 1824	NB	2	2	97	140	230	35	Common	1
Heteroceridae									
Heterocerus marginatus (Fabricius, 1787)	Common	2	2	17	70	86	21	Local	2
Dryopidae									
Dryops nitidulus (Heer, 1841)	RDB3	2	2	19	13	30	-	RDB3	24

Ptilidae									
Actidium aterrimum (Motschulsky, 1845)	RDBK	1	1	1	1	2	-	RDBK[3]	16
Ptenidium brenskei Flach, 1887	N	1	1	1	10	10	-	N[3]	8
Ptenidium longicorne Fuss, 1868	Local	1	1	3	41	43	-	Local[3]	2
Staphylinidae									
Acronota exigua (Erichson, 1837)	Unknown	2	2	3	4	6	-	RDBK[1]	16
Aloconota cambrica (Wollaston, 1855)	Local	1	1	112	110	219	-	Local[1]	2
Aloconota currax (Kraatz, 1856)	Local	1	1	10	57	65	-	Local[1]	2
Aloconota eichhoffi (Scriba, 1867)	N	1	1	1	5	6	-	NA[1]	8
Aloconota insecta (Thomson, C.G. 1856)	Common	2	2	8	74	82	-	Local[1]	2
Aloconota planifrons (Waterhouse, G.R., 1864)	RDBK	2	2	1	2	3	-	RDBI[1]	24
Aloconota sulcifrons (Stephens, 1832)	Unknown	2	2	8	31	39	-	Local[1]	2
Bibloplectus minutissimus Aub E 1833	RDBK	2	2	1	6	7	-	RDBK[1]	16
Bledius annae Sharp, 1911	Local	1	1	6	23	29	-	NB[2]	8
Bledius arcticus Sahlberg, J., 1980	RDBI	1	1	20	9	27	-	N	8
Bledius defensus Fauvel, 1872	RDBK	1	1	16	3	18	-	N	8
Bledius erraticus Erichson, 1839	RDBK	2	2	14	0	14	-	RDBK	16
Bledius longulus Erichson, 1839	Local	2	-	-	-	-	-	-	-
Bledius pallipes (Gravenhorst 1806)	-	1	1	0	10	10	-	Common[2]	1
Bledius pallipes agg.	-	-	-	0	4	4	-	-	-
Bledius subterraneus Erichson, 1839	Local	2	2	53	53	94	25	Local	2
Bledius terebrans (Schiödte, 1866)	RDBK	2	2	14	3	15	-	RDBK	16
Brachygluta pandellei (Saulcy, 1876)	RDBK	1	1	1	12	12	-	NA[1]	16
Carpelimus obesus (Kiesenwetter, 1844)	N	2	2	0	3	3	-	N[1]	8
Carpelimus similis Smetan, 1967	N	2	2	1	31	32	-	NB[1]	8
Carpelimus subtilicornis (Roubal, 1946)	Very Local	2	2	1	15	16	-	NB[1]	8
Carpelimus subtilis (Erichson, 1839)	N	2	2	1	12	13	-	N[1]	8
Dasygnypeta velata (Erichson, 1837)	N	2	2	2	9	11	-	N[1]	8
Deleaster dichrous (Gravenhorst, 1802)	NB	2	2	8	103	111	-	Common[2]	1

Erichsonius signaticornis (Mulsant & Rey, 1853)	NB	2	2	5	21	26	-	NB[1]	8
Gabrius astutoides (Strand, A., 1946)	RDBI	2	2	6	10	16	-	RDB3	24
Gnypeta carbonaria (Mannerheim, 1830)	Local	2	2	12	22	34	-	Local[1]	2
Hydrosmecta delicatissima (Bernhauer, 1908)	RDBK	2	2	1	2	2	-	RDBK[1]	16
Hydrosmecta delicatula (Sharp, 1869)	RDBK	1	1	2	16	18	-	NA[1]	16
Hydrosmecta eximia (Sharp, 1869)	Very Local	1	1	4	51	54	-	NB[1]	8
Hydrosmecta fragilis (Kraatz, 1854)	N	1	1	5	23	27	-	NB[1]	8
Hydrosmecta longula (Heer, 1839)	N	1	1	5	65	69	-	Very local[1]	4
Hydrosmecta septentrionum (Benick, 1969)	N	1	1	6	47	52	-	NB[1]	8
Ilyobates bennetti Donisthorpe, 1914	Local	2	2	0	3	3	-	N[1]	8
Ilyobates propinquus Aub E 1850	N	2	2	1	6	7	-	N[1]	8
Ischnopoda atra (Gravenhorst, 1806)	Local	2	2	6	21	26	-	Very local[1]	4
Ischnopoda coarctata (Erichson, 1837)	N	1	1	4	10	14	-	NB[1]	8
Ischnopoda constricta (Erichson, 1837)	Local	1	1	1	52	53	-	Local[1]	2
Ischnopoda leucopus (Marsham, 1802)	Common	1	1	7	49	56	-	Local[1]	2
Ischnopoda scitula (Erichson, 1837)	RDBK	2	2	4	4	8	-	RDBK[1]	16
Ischnopoda umbratica Erichson, 1837)	Unknown	1	1	0	11	11	-	RDBK[1]	16
Lathrobium angusticolle Boisduval & Lacordaire, 1835	NB	1	1	4	23	26	-	NB[1]	8
Lathrobium dilutum Erichson, 1839	RDB3	1	1	3	5	7	-	RDB3[1]	24
Lathrobium pallidipenne Hochhuth, 1851	N	2	2	14	10	24	-	NB[1]	8
Medon ripicola (Kraatz, 1854)	N	2	2	2	11	12	-	NA[1]	16
Meotica anglica Benick in Muona, 1991	N jBAP END	1	1	2	8	10	-	RDB3	24
Neobisnius prolixus (Erichson, 1840)	RDBK	2	2	2	27	27	-	NA[1]	16
Ocalea latipennis Sharp, 1870	Local	1	1	6	2	8	-	N[1]	8
Ochthephilus andalusiacus (Fagel, 1957)	N	2	2	8	26	32	-	NB	8
Ochthephilus angustior (Bernhauer, 1943)	N	1	2	12	9	21	-	N	8
Ochthephilus aureus (Fauvel, 1871)	Local	2	2	88	52	132	27	Common	1
Ochthephilus omalinus (Erichson, 1840)	Local	2	2	22	56	75	20	Local	2
Ochthephilus omalinus agg.	-	-	-	21	13	33	-	-	-

Oxypoda exoleta Erichson, 1839	N	2	2	9	23	32	-	NB[1]	8
Parocyusa longitarsis (Erichson, 1837)	Common	2	2	1	26	27	-	Local[1]	2
Parocyusa rubicunda (Erichson, 1837)	N	1	1	5	4	9	-	N[1]	8
Philhygra debilis (Erichson, 1837)	Local	2	2	13	4	17	-	N[1]	8
Philhygra scotica (Elliman, 1909)	N	1	1	1	4	5	-	N[1]	8
Philonthus rubripennis Stephens, 1832	Very Local	1	1	7	61	66	-	Very local[1]	4
Quedius plancus Erichson, 1840	NA	2	2	5	0	5	-	NA[1]	16
Scopaeus gracilis (Sperk, 1835)	RDBK	1	1	1	9	10	-	RDB3[1]	24
Stenus asphaltinus Erichson, 1840	RDBI	2	-	-	-	-	-	-	-
Stenus biguttatus (Linnaeus, 1758)	-	-	2	14	40	52	-	NB	8
Stenus comma LeConte, 1863	Local	2	2	31	146	173	23	Local	2
Stenus guttula M Eler, P.W.J., 1821	Local	2	2	58	225	272	32	Common	1
Stenus incanus Erichson, 1839	RDBK	1	1	5	8	12	-	RDB3	24
Stenus nigritulus Gyllenhal, 1827	NB	2	-	-	-	-	-	-	-
Thinobius ciliatus Kiesenwetter, 1844	N	1	1	7	21	28	-	NA	16
Thinobius crinifer Smetana, 1960	N	1	1	14	8	21	-	NA	16
Thinobius linearis Kraatz, 1857	NA	1	1	14	18	32	-	NA	16
Thinobius longipennis Heer, 1841	Unknown	1	1	0	1	1	-	Unknown	1
Thinobius major Kraatz, 1857	RDBK	1	1	4	6	9	-	RDB3	24
Thinobius newberyi Scheerpeltz, 1925	RDBI jBAP END	1	1	2	3	5	-	RDB2	32
Thinodromus arcuatus (Stephens, 1834)	Local	1	1	59	45	98	22	Local	2
Scarabaeidae									
Psammoporus sabuleti (Panzer, 1797)	NB	2	2	6	37	42	-	NB	8
Elateridae									
Fleutiauxellus maritimus (Curtis, 1840)	NA	1	1	10	53	60	-	NB[2]	8
Negastrius arenicola (Boheman, 1852)	-	-	2	2	0	2	-	RDB2[2]	32
Negastrius pulchellus (Linnaeus, 1761)	RDB2	1	1	4	4	6	-	RDBI[2]	24
Negastrius sabulicola (Boheman, 1852)	RDB2	1	1	2	16	18	-	RDB3[2]	24
Zorochros minimus (Boisduval & Lacordaire, 1835)	Common	1	1	20	145	154	-	Common[2]	1

Coccinellidae									
Coccinella quinquepunctata Linnaeus, 1758	RDB3	1	1	5	38	42	-	NB	8
Curculionidae									
Baris lepidii Germar, 1824	NA	2	2	6	4	10	-	NA[3]	16

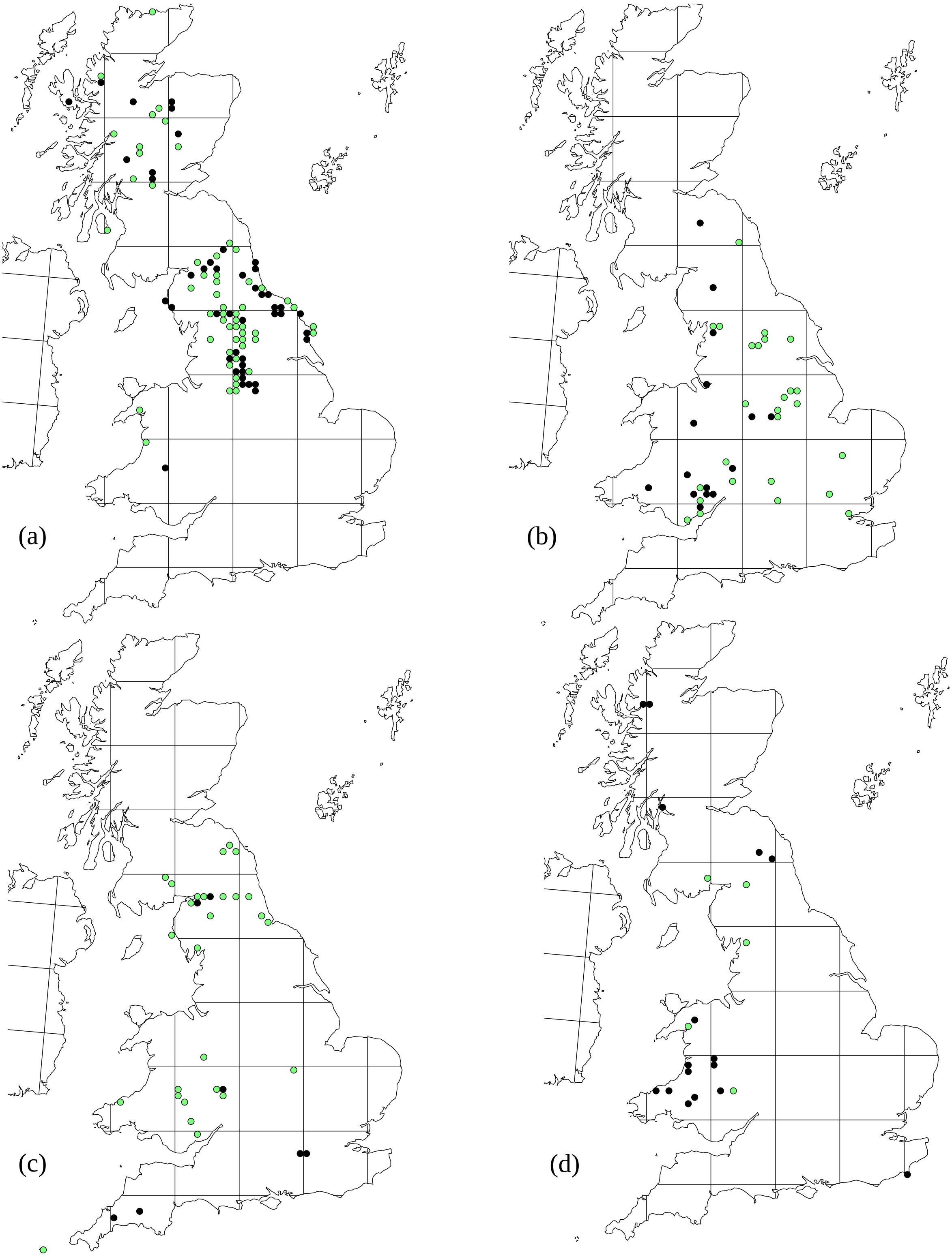


Figure 3.2 The British distribution of (a) *Bembidion geniculatum*, a species influenced by under-recording from an area, (b) *Bembidion fluviatile*, a species influenced by under-recording from a microhabitat, (c) *Asaphidion flavipes*, a species influenced by taxonomic revisions, and (d) *Thalassophilus longicornis*, a species influenced by difficulty of sampling (light circles represent pre-1980 records, dark circles represent post-1980 records, except in (c) where they represent aggregated and accurate records respectively).

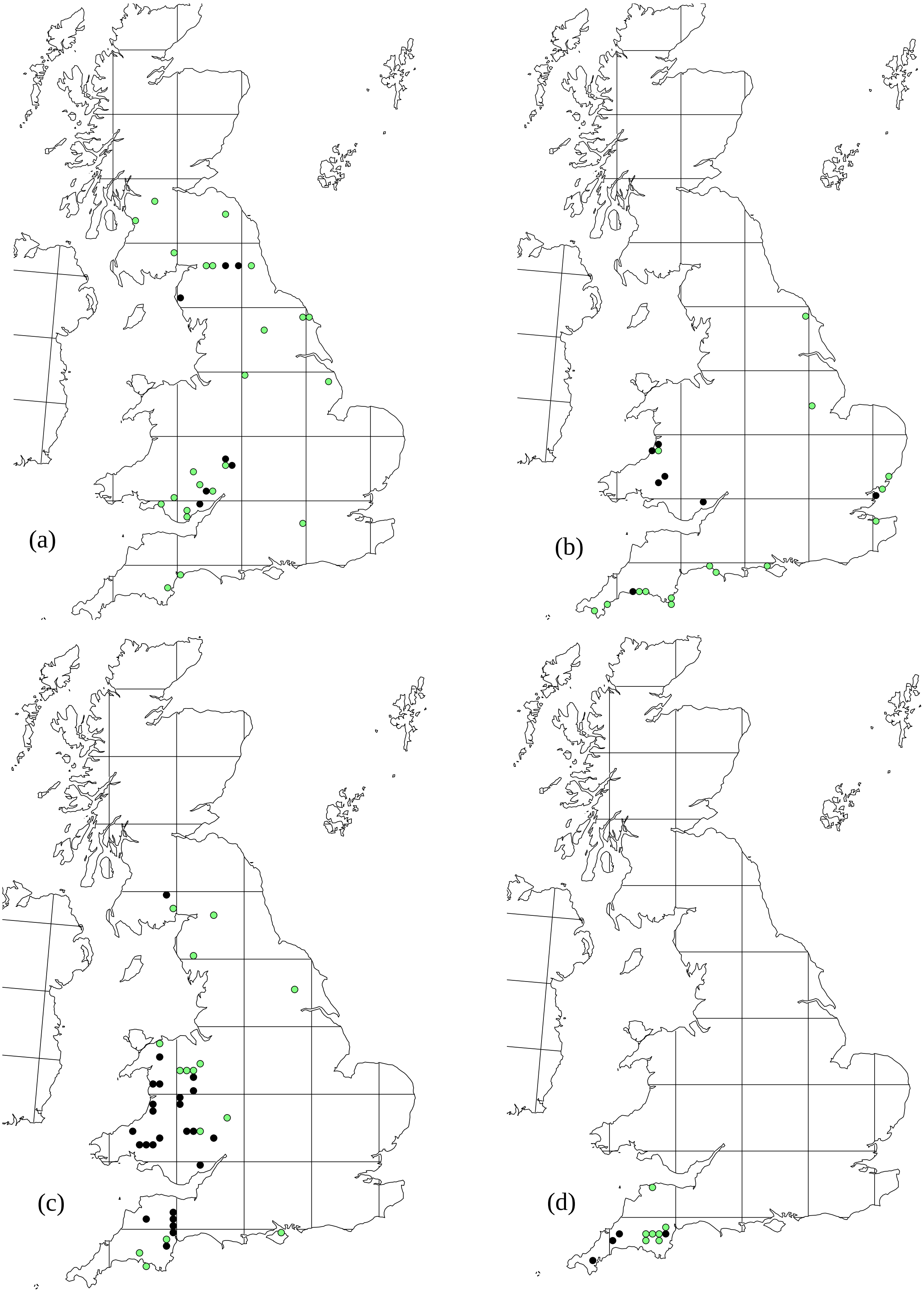


Figure 3.3 The British distribution of pre- (light) and post-1980 records of (a) *Bembidion testaceum*, (b) *Lionychus quadrillum*, (c) *Perileptus areolatus*, and (d) *Hydrochus nitidicollis*.

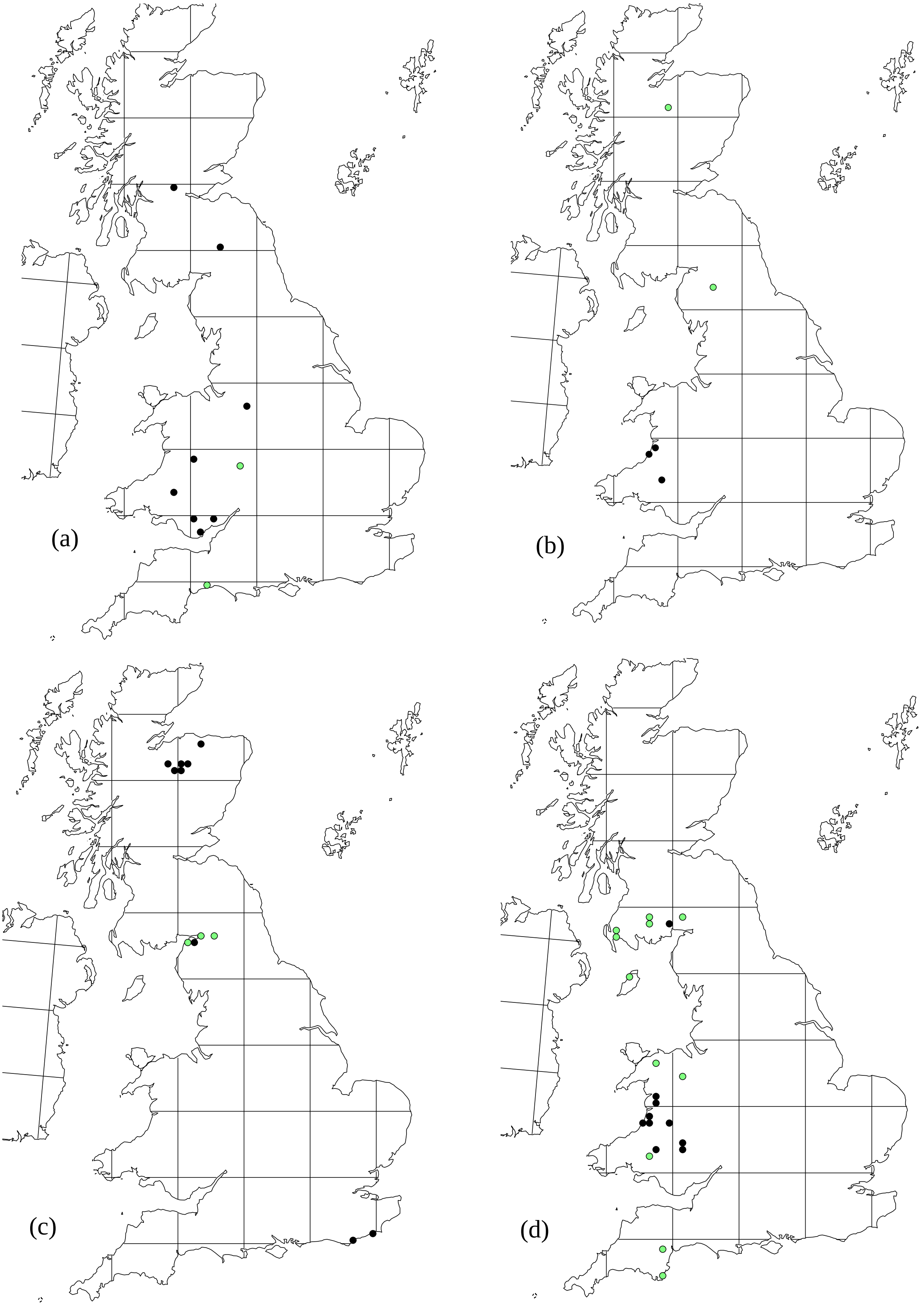


Figure 3.4 The British distribution of pre- (light) and post-1980 records of (a) *Meotica anglica*, (b) *Thinobius newberyi*, (c) *Dyschirius angustatus*, and (d) *Bidessus minutisimus*.

The identification of most records have been checked, and the vast majority of sites have been revisited, and targeted hand searches for *B. testaceum* implemented. The distribution shown in Figure 3.3 is therefore current and likely to be robust. Post 1980 records are mainly for small numbers of specimens from the rivers South Tyne, Devil's Water, Keekle, Monnow, Usk and Teme. Specimens have been consistently collected from the South Tyne over the last century over several sites in the catchment (including its tributary the Devil's Water). Specimens have also been taken from several areas of the Lower Usk, where it is sometimes present in some abundance.

Lionychus quadrillum (Figure 3.3) was historically quite well recorded from coastal localities, but has only recently been found at Seaton (Cornwall) and Colne Point (Essex). More recently it has mainly been found in association with ERS and has been consistently recorded from the rivers Usk, Tywi, Ystwyth and Rheidol. It is usually found in small numbers, but can occasionally be quite abundant. *Perileptus areolatus* (Figure 3.3) is currently known from many, good quality medium to large sized rivers in Wales and the West Country, and also from one location on the River Nith in Scotland. Historically it was more widespread, with records from the River Duddon (Cumbria) and the River Derwent (East Riding of Yorkshire). When present it is usually in some abundance.

Hydrochus nitidicollis is confined to Devon and Cornwall in Britain and is currently known from only 5, 10km squares (Figure 3.3). Usually this species is found in low numbers, but this may be due to the difficulty of sampling this species on the aquatic fringe of ERS and its very margins. The small cryptic staphylinid *Meotica anglica* is currently quite widely but sparsely distributed across Wales, the north of England and Scotland on the rivers Taff, Usk, Tywi, Severn, Dane, Northhouse Burn and Allan (Figure 3.4). This species usually occurs in low abundance, but can very occasionally be found in some numbers. The records of *T. newberyi* shown in Figure 3.4 represent its known world distribution as it has yet to be found in any other country. Historically it has been found on the River Druie (Spey catchment) and the River Eden (Cumbria), at the latter location several times between 1907-1911. Despite continuing visits to these sites by coleopterists no new specimens have been found. Current records are from just three bars on the rivers Tywi, Ystwyth and Rheidol in Wales, where the only repeat finds have been on the Ystwyth.

Dyschirius angustatus has an extensive but discontinuous distribution in Britain, with three centres of population in the eastern Scottish Highlands, the Solway estuary and Sussex Coast (Figure 3.4). It has been recently found from ERS in the Spey catchment on the rivers Nethy, Avon, Dorback Burn, Druie, Dulnain and Spey. When present it is usually in low abundance, and typically in association with the burrows of species of the staphylinid *Bledius*. The main recent centre of population for *B. minutisimus* (Figure 3.4) is Wales, being relatively consistently found on the rivers Tywi, Ystwyth, Wye and Rheidol, on the latter river often in some abundance. This species historically has a much wider distribution including the West Country, Isle of Mann, and southwest Scotland.

3.4.4 Hierarchical classification of the conservation quality of ERS on British rivers using specialist ERS beetles

The 53 rivers included in the analysis of conservation quality are ranked by ERSQS and ERSQI in Tables 3.3 and 3.4 respectively. In terms of ERSQS, the Tywi and the Severn were ranked first and second, and rivers in Wales and the Borders generally scored very highly, with the top six rivers (Tywi, Severn, Wye, Usk, Rheidol and Ystwyth). The remaining top ten rivers were the Teign and Bovey in the Southwest of England, the Dane in the North of England, and the Dorback Burn in the Spey catchment in Scotland. Scottish rivers generally ranked fairly lowly when classified by ERSQS (Table 3.3).

Table 3.3 ERS conservation quality of the 53 rivers analysed ranked by total ERSQS.

Position	River	Catchment	Sum ERSQS	ERSQI	Scoring spp.
1	Tywi	Tywi	442	749	59
2	Severn	Severn	403	672	60
3	Wye	Wye	355	657	54
4	Usk	Usk	336	646	52
5	Rheidol	Rheidol	317	834	38
6	Ystwyth	Ystwyth	279	845	33
7	Teign	Teign	277	577	48
8	Dorback Burn	Spey	244	841	29
9	Dane	Weaver	179	448	40
10	Bovey	Teign	176	476	37
11	Feshie	Spey	174	600	29
12	Till	Tweed	162	540	30
13	Exe	Exe	160	400	40
14	Culm	Exe	156	488	32
15	Spey	Spey	155	470	33
16	Tweed	Tweed	150	357	42
16	Carron	Carron	150	536	28
16	Yarty	Axe	150	385	39
19	Nith	Nith	143	421	34
20	Torridge	Torridge	142	418	34
21	Dulnain	Spey	138	657	21
22	Eden	Eden	129	445	29
23	Druie	Spey	125	568	22
24	Wharfe	Wharfe	124	443	28
25	Kings Water	Eden	123	439	28
26	Lew	Torridge	122	407	30
27	Irthing	Eden	121	390	31
27	Mawddach	Mawddach	121	637	19
29	Byrecleugh Burn	Tweed	120	600	20
30	Bray	Taw	119	458	26
31	Caldew	Eden	117	509	23
31	Avon (Scotland)	Spey	117	650	18
33	Camel	Camel	116	387	30
34	Otter	Otter	115	329	35
35	Cready Yeo	Exe	113	419	27
36	Allen	Tyne	109	574	19
37	Rankle Burn	Tweed	108	540	20
38	Northhouse burn	Tweed	104	578	18
39	Calder	Spey	103	572	18
40	Mole	Taw	98	408	24
41	Coly	Axe	92	400	23
42	Kale Water	Tweed	67	394	17
43	Carey	Tamar	65	433	15
44	Tamar	Tamar	60	286	21
45	Allan Water	Tweed	59	369	16
46	Glen Docherty Burn	Carron	58	341	17
47	Ottery	Tamar	57	317	18
48	Kelso Anna	Tweed	54	225	24
48	Erme	Erme	54	245	22
50	Avon (Devon)	Avon	49	272	18
51	Thrushel	Tamar	40	235	17
52	Ale Water	Tweed	36	240	15
53	Glen	Tweed	32	200	16

Table 3.4 ERS conservation quality of the 53 rivers analysed ranked by ERSQI.

Position	River	Catchment	Sum ERSQS	ERSQI	Scoring spp.
1	Ystwyth	Ystwyth	279	845	33
2	Dorback Burn	Spey	244	841	29
3	Rheidol	Rheidol	317	834	38
4	Tywi	Tywi	442	749	59
5	Severn	Severn	403	672	60
6	Wye	Wye	355	657	54
6	Dulnain	Spey	138	657	21
8	Avon (Scotland)	Spey	117	650	18
9	Usk	Usk	336	646	52
10	Mawddach	Mawddach	121	637	19
11	Feshie	Spey	174	600	29
11	Byrecleugh Burn	Tweed	120	600	20
13	Northhouse burn	Tweed	104	578	18
14	Teign	Teign	277	577	48
15	Allen	Tyne	109	574	19
16	Calder	Spey	103	572	18
17	Druie	Spey	125	568	22
18	Till	Tweed	162	540	30
18	Rankle Burn	Tweed	108	540	20
20	Carron	Carron	150	536	28
21	Caldew	Eden	117	509	23
22	Culm	Exe	156	488	32
23	Bovey	Teign	176	476	37
24	Spey	Spey	155	470	33
25	Bray	Taw	119	458	26
26	Dane	Weaver	179	448	40
27	Eden	Eden	129	445	29
28	Wharfe	Wharfe	124	443	28
29	Kings Water	Eden	123	439	28
30	Carey	Tamar	65	433	15
31	Nith	Nith	143	421	34
32	Cready Yeo	Exe	113	419	27
33	Torridge	Torridge	142	418	34
34	Mole	Taw	98	408	24
35	Lew	Torridge	122	407	30
36	Exe	Exe	160	400	40
36	Coly	Axe	92	400	23
38	Kale Water	Tweed	67	394	17
39	Irthing	Eden	121	390	31
40	Camel	Camel	116	387	30
41	Yarty	Axe	150	385	39
42	Allan Water	Tweed	59	369	16
43	Tweed	Tweed	150	357	42
44	Glen Docherty Burn	Carron	58	341	17
45	Otter	Otter	115	329	35
46	Ottery	Tamar	57	317	18
47	Tamar	Tamar	60	286	21
48	Avon (Devon)	Avon	49	272	18
49	Erme	Erme	54	245	22
50	Ale Water	Tweed	36	240	15
51	Thrushel	Tamar	40	235	17
52	Kelso Anna	Tweed	54	225	24
53	Glen	Tweed	32	200	16

In comparison, when ranked using the ERSQI, the rivers Tywi and Severn were ranked forth and fifth in terms of ERS quality and rivers in Wales and the Borders still ranked highly, with seven out of the top ten rivers. Scottish rivers, particularly those in the Spey catchment, faired better in this ranking system with three rivers in the top ten (Dorback Burn, Dulnain and Avon). There were no rivers from any other region in the top ten when ranked in this way. The ERSQS scores for the Dulnain, Scottish Avon and Mawddach, which were ranked in the top ten by ERSQI, were relatively low, and based on only around 20 scoring species.

3.4.5 Constancy of the overall conservation value of ERS specialists

A summary of the overall change in the distribution of status categories across the specialist ERS beetle fauna is shown in Figure 3.5. Generally there has been a move away from the more ambiguous RDBI, RDBK, N and unknown statuses because the large amount of survey work allows the more confident assignment of status categories for many groups. However, there still remain many species with these statuses, particularly the silt specialist staphylinids, which are under-recorded as a group, and which have received relatively poor survey coverage due to their distribution in the south and eastern parts of Britain (see Figure 3.1a). The statuses RDB3, Nb, and common are those that have shown the largest increases in the number of species allocated to them, mainly due to species being moved from RDBI and K; N; and very local and local respectively. Significantly, the overall distribution of rarity status has remained remarkably stable since the initial review (Hyman and Parsons 1992, 1994), with the total combined ERSQS score before, equalling 1303, and afterwards equalling 1222, only slightly reduced from the previous total.

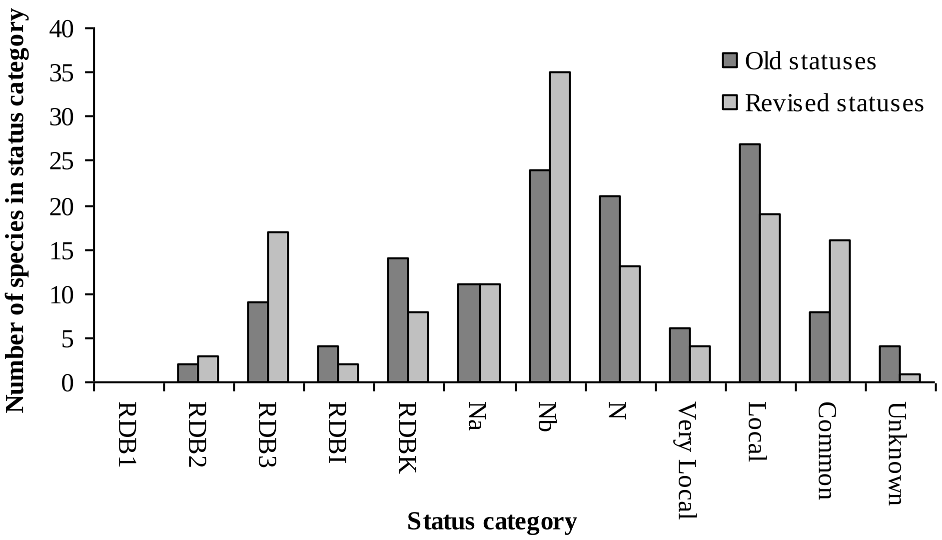


Figure 3.5 Summary changes in the distribution of status categories across the specialist ERS beetle fauna (Old statuses based on Hyman and Parsons (1992, 1994) and Fowles (2005), revised statuses from this review).

3.4 Discussion

3.4.1 Considerations in the review of rarity status: illustrated examples

Most of the records for *B. geniculatum* (Figure 3.2a) are pre-1980 (68), with relatively few (33) post-1980 records. It is possible to confuse this species with the closely related *B. atrocaeruleum* and *B. tibiale*, but generally this species is easily identifiable and, as a carabid, is potentially well recorded. However, there is an unusual concentration of pre-1980 records for this species in its main stronghold, the Pennine spine of northern England. It is possible that the reduced number of recent records from this area represents a real contraction of the range of this species. Nevertheless, in the absence of an obvious causal factor for such a decline, given the relative paucity of intensive survey work in this area (Figure 3.1a), it seems more probably that this is because of under-recording in the area. This species had no status in Hyman and Parsons (1992, 1994), but the number of post 1980 10km squares (Table 3.2) would suggest it should be an Nb species. However, the total number of 10km squares (pre- and post-1980) is nearly 100 for this species, so serious consideration was given to this revision, because it could be *thought*, given its spatial under-recording, to occupy >100 10km squares. In the end, its suggested status was changed to Nb, but this serves as a good example of the difficulty under-recording from an area can cause for the appropriate assignment of rarity status.

Bembidion fluviatile has a wide distribution of pre-1980 records, distributed over the Midlands, East Anglia, Wales, and the north of England (Figure 3.2b). There are, however, only 16 post-1980 10km squares, despite considerable sampling in rivers likely to contain suitable habitat for this species. As such, it would seem most sensible to give this species a rarity status of NA. However, *B. fluviatile* is associated with open eroding sand and silt banks rather than gravel and sand bars (Lindroth 1974, Luff 1998), and these were not included in early definitions of ERS. As a consequence, early intensive surveys did not find this species, even though subsequent hand searches have revealed it to be present in considerable abundance in nearby eroding banks. Furthermore, intensive surveys using only pitfall trapping were also unlikely to *detect* this species (see Figure 3.1a) because pitfall traps cannot easily be placed in eroding banks. Therefore the status of *B. fluviatile* was kept at Nb, despite the low number of post-1980 10km squares for this species. This is a good example of how the lack of sampling in a particular microhabitat can affect the perceived distribution of a species.

The British *Asaphidion flavipes* was shown in 1986 to be composed of three species: *A. flavipes* proper, *A. stierlini* (Heyden, 1880), and *A. curtum* (Heyden, 1870) (Focarile 1964; Speight *et al.* 1986). This meant that records of *A. flavipes* from before this date could be any one of these three species. Many records after this date could also be any one of these species, as the available British carabid keys still do not have these species split. As a consequence, many of the records can only be said to be an aggregation of one of these three species (Figure 3.2c). In such cases the best that can be done is to take the advice of experts in the field, in this case, giving it a status of common (Luff 1998).

Thalassophilous longicornis, although relatively large, is a fossorial species that is rarely collected by hand searching unless a considerable amount of effort is invested in this. As a consequence, most of the records for this species are recent, because intensive surveys employ pitfall trapping that favour the capture of these species. With 17 post-1980, and 6 pre-1980 10km squares, it is possible that this cryptic species could actually be distributed in over 30 10km squares. However, in this instance the status of Na was kept because on the whole this species has been found in high quality rivers (e.g. Rheidol, Severn, Tywi and Wye). This species is a good example of the problems associated with assigning rarity status to a species that is difficult to sample.

These four examples serve to illustrate some of the considerations and problems involved with the assignment of rarity status. The Carabidae are perhaps the best studied family of beetles in the UK, and include the largest, most easily collected, and most easily identified species of ERS specialist. When considering other groups of ERS specialists, particularly the Staphylinidae and Ptiliidae, these problems are greatly inflated. For example, many species of *Bledius* (Staphylinidae) are also associated with open eroding banks and will cause similar problems to *Bembidion fluviatile*. There are a number of other fossorial species including *Trechus discus*, *Meotica anglica*, *Thinobius newberyi*, *Medon ripicola*, and *Scopaeus gracilis*. Whilst other species are just difficult to find on account of their small size, for example, *Ptenidium brenski*, *Hydrosmecta septentrionum*, *Brachygluta pandellei* and *Elaphropus parvulus*. Other groups of species are taxonomically highly unstable, such as the genus *Carpelimus*, or *Bledius*, whilst other taxa require considerable experience to be able to identify, such as the Alocharinae (Staphylinidae), often because of the lack of good, English taxonomic keys. The review of rarity statuses is clearly therefore a difficult undertaking, which requires the expertise of a large number of individuals.

3.4.2 Analysis of the status of ERS species with BAPs

The species of ERS beetles with BAPs have been focused on because of their enhanced status. However, these species are analysed with a view to providing examples of the relative fortunes of ERS beetles as a whole, using the BAP species in this wider context. The degree to which the distribution of *Bembidion testaceum* has been studied, checking the identification of voucher specimens associated with records, and then visiting the majority of sites to implement targeted hand searches for that particular species (Sadler *et al.* 2005), is unusually comprehensive. Although several historical records were found to be based on misidentified specimens, most historical records were found to be reliable (Hammond 2003; Sadler *et al.* 2005). Several sites formerly known to be habitat for *B. testaceum* (e.g. the River Taff, the River Derwent) were found to either no longer contain ERS, or contain extremely small amounts of ERS following channelisation. Several other sites, although they still contain significant amounts of ERS habitat (e.g. the River Wye, the River Nith, and River Irvine), have returned no specimens for over 50 years (Sadler *et al.* 2005). The extra amount of information available for this species has allowed the confident application of an RDB2 status, a large increase in status from its previous Nb status. This is a good example of a species that has clearly declined in Britain over the last century, and indeed, many of its current populations (the River Teme, the River Monnow, and River Keekle) are characterised by small abundance in very small sections of suitable habitat and may be under threat. The BAPs aim for this species of maintaining viable populations in all five catchments from where it is currently known may be difficult, and, with little knowledge of the autecology of even this heavily studied species, the aim of enhancing populations by 2010 at selected sites will be hard to achieve. The strongest population centres for this species seem to be on the Usk and South Tyne catchments, for which the River Usk is a candidate Special Area of Conservation (SAC) and the South Tyne is a SSSI at Hexham (one of the strongest population centres for *B. testaceum*) (Anon. 1999; JNCC 2005). Suggestions for the best ways of approaching these aims for this, and the other BAP species are made in Chapter 9.

Lionychus quadrillum is associated with some of the best quality ERS rivers in Britain, namely the Usk, Tywi, Rheidol and Ystwyth. Each of these rivers receives some protection in the form of candidate SAC's (Usk and Tywi) or SSSI's (Rheidol: Afon Rheidol ger Capel Bangor and Ystwyth: Gro Ty'n-yr-helyg and Gro Ystwyth) (Anon. 1999; JNCC 2005; Adrian Fowles pers comm.), and populations on each of these rivers appear reasonably robust. Over the near future the prospects for this species therefore seem good, and the maintainance of populations in these catchments, and the enhancement of populations at selected sites might be possible under management agreements given their protected status.

The south west of England, within which *Hydrochus nitidicollis* is exclusively found, has one of the densest concentrations of intensive ERS beetle surveys in the country (Figure 3.1a), and these surveys have been funded by English Nature, the Environment Agency and Devon County Council. This support was further demonstrated by the strong opposition by English nature to the extension of ball clay workings at a site where *H. nitidicollis* was present (Sadler and Bell 2000) and would suggest that multiple stake holders in this region are firmly committed to the conservation of ERS beetles. This suggests that the aim of maintaining viable populations of *H. nitidicollis* in Britain is quite likely to be successfull.

Meotica anglica is very small and probably fossorial (Bates and Sadler 2004a), which makes the accurate assessment of its distribution very difficult. It does continue to be detected in new surveys of ERS beetles (Bell and Sadler 2003) and could well be found in several other areas. It is quite possible therefore that we do not know its current distribution, which possibly renders the aims of its BAP fatuous. With so little information available about the habits of this species it is not possible to appropriately assess its fortunes. This lack of realism in many of the targets of BAPs is one of their considerable weak points, but has so far faced very limited criticism (c.f. Holloway *et al.* 2003).

Thinobius newberyi, like *M. anglica*, is very small and cryptic and very difficult to find even when an intensive survey is undertaken. However, the situation is slightly different for this species because it has only been taken from some of the very best examples of ERS in Britain, tentatively suggesting that it is genuinely rarer than *M. anglica*. The three recent records of this species are from only three individual bars, and it has not been found on nearby patches of habitat despite a good deal of searching. Much of the ERS on the River Rheidol at Glanafron despite receiving protection as a SSSI have become quite strongly vegetated following the development of a large-scale HEP scheme on the Afon Rheidol in 1961 (Greenwood *et al.* 1999), and *T. newberyi* has not been found there since 1990 despite intensive survey work since then (Sadler and Petts 2000; Lott 2004). This population may therefore be lost. The circumstances of the population on the Afon Ystwyth seem only a little less precarious as it has not been found since 1988, again despite intensive survey work on the site (Sadler and Bell 2002), and bars in close proximity are tentatively believed to be too coarse to support this species (Adrian Fowles pers comm.). Only the population on the Tywi is likely be robust due to its candidate SAC status, and large abundance of sediments that are believed to be suitable for *T. newberyi* for several kilometres up and downstream of the site where it was found. As a consequence of these considerations *T. newberyi* has been given an RDB2 status, which seems particularly prudent given its current British endemic status. Assessing the achievement of the aims of the BAP are again nearly impossible for this species due to the extreme difficulty in locating it, and lack of understanding of its ecological needs.

Dyschirius angustatus is a potentially unusual case in that it is reliant to some degree on the success of species of *Bledius*, which it preys upon and shares burrows (Luff 1998; Anon. 1999). It can be very locally distributed even in wide expanses of potentially suitable habitat. Most of the ERS where it is known to be present (River Spey catchment) are protected by the River Spey SAC (JNCC 2005), so the more broad aim of maintaining the range of this species is probably achievable, although this aim seems to be just to preserve the status quo for this species.

Water beetles such as *Bidessus minutisimus* are the focus of a relatively large amount of sampling through the efforts of the Balfour Brown club. So despite the small size of this species the lack of recent records from the Isle of Mann, West Country and Scotland are quite likely to be real so a status of RDB3 seems reasonable. Again, very little is known of its biology so it is difficult to assess the likely success of the aims of its BAP, although it must be noted that one is only a more specific version of the other.

3.4.3 Hierarchical classification of the conservation quality of ERS on British rivers

There was a marked difference in the relative placing of many of the Scottish rivers between the ranking based on ERSQS and ERSQI. This could be because these rivers genuinely have a low number ERS specialists, most of which are quite rare, or could be an artefact of only using pitfall traps to sample the ERS beetles (Section 3.3.3). However, this will remain unclear without supplementary hand searching in the Spey, Tweed, Nith and Carron catchments. The Spey, Tweed and Nith all have very large expanses of highly diverse ERS, so they have long been believed to be of considerable importance for ERS beetles. If this is true, then the ERSQI performed well by placing these rivers more highly than the ERSQS.

The Afon Tywi and River Severn have probably been subjected to more intensive survey work than any other British river, so the high number of scoring species associated with these rivers is perhaps not surprising. However, they still place highly when ranked according to ERSQI, demonstrating their extreme British conservation importance. It can be argued quite strongly however, that the Afon Tywi is of more conservation importance than the Afon Rheidol and Afon Ystwyth, which are both placed above it in the ranking based on ERSQI. The Afon Rheidol has 2 RDB and 2 Notable species, and the Afon Ystwyth has 3 RDB and 1 Notable species not known from the Afon Tywi. However, the Afon Tywi has 3 RDB and 11 Notable species not known from the Afon Rheidol, and 3 RDB and 13 Notable species not known from the Afon Ystwyth. Although the Rheidol and Ystwyth have not been quite as intensively surveyed as the Tywi, they have nonetheless been the focus of a great deal of intensive survey work (Fowles 1989; Sadler and Petts 2000; Lott 2004). The three rivers seem to mainly share the same RDB species, but the Tywi has a much larger pool of Notable species and more common ERS specialists. As this is unlikely to be purely the result of sampling artefact, the specialist ERS beetle fauna of the Afon Tywi has a larger conservation value than that of the Afon Rheidol or Afon Ystwyth. Therefore in this instance the ERSQS seemed to have performed better than the ERSQI. It is therefore important to consider the ranking based on ERSQS and ERSQI in tandem when assessing the conservation value of ERS.

Objective exact ranking of rivers according to their specialist ERS beetle fauna is therefore difficult. However, the rankings taken together show that the Tywi, Severn, Ystwyth, Rheidol and Wye in Wales and the Borders are of particular value. In Scotland, rivers in the Spey catchment seem to be of most conservation importance, and in the Southwest, the rivers Teign and Bovey seem to be of most value.

3.4.4 The ERS beetles as a conservation resource

The previous section on the ERS beetles with BAPs has shown that the outlook for various ERS specialist beetles is mixed. Some species show evidence of considerable vulnerability such as *Thinobius newberyi*; others show evidence of substantial decline across their UK range (*Bembidion testaceum*, *Bidessus minutisimus*); whilst others show evidence of sufficient population viability where they are distributed (*Perileptus areolatus*, *Lionychus quadrillum*); for others, such as *Meotica anglica*, the picture is far from clear. Clearly, individual species show different trends in terms of their British population viability. Given the myriad variation of likely resource requirements (Chapter 5), population structures (Chapter 7 and 8), and disturbance tolerances considering all 131 species of specialist ERS beetles, in twelve families of beetle; this is hardly surprising.

It has long been realised that the extreme number of rare and notable ERS specialist beetles might be due to the under-recording of these species to some extent. The example of the five-spot ladybird (*Coccinella quinquepunctata*), which was believed to be extinct in 1986 after not being found in Britain since 1953, but which now has been found in 38 post-1980 10km squares (Majerus and Fowles 1989; Eyre 1998; Sadler and Bell 2002), is a good case in point. However, following over 100 intensive surveys of ERS beetles and considerable effort in obtaining all available records for these species, the overall ERSQI score for all ERS specialist beetles has remained remarkably stable. This indicates that the extreme conservation importance of ERS beetles in the UK, suggested by the original findings of Fowles (1989), can be upheld. The newly assessed conservation importance of ERS specialist beetles (29 RDB, 59 National Notable species) is perhaps underestimated by the method of using 10km squares to assess rarity because of the thin and linear nature of lotic habitats relative to species of more extensive habitats (e.g. those of moorland, salt marsh, and fens) assessed in the same way (Howard Mendel pers comm.). This potentially adds to the extreme importance of ERS as an invertebrate conservation resource.

CHAPTER 4

THE EFFECT OF LIVESTOCK TRAMPLING

4.1 Introduction

This chapter examines the response of species assemblages to varying levels of livestock trampling intensity on the Afon Tywi. The chapter expands on the environmental measurements described in Chapter 2, especially the measures of trampling intensity. It uses the revised ERSQS from Chapter 3, together with richness and diversity indices to assess the impact of trampling on the conservation value of ERS beetle faunas. The management implications of these findings are reserved for the final chapter.

4.2 Background

The physico-chemical effects of riparian grazing are known to be very wide-ranging and include impacts on soils (e.g. reduction in infiltration rates and increased bulk density) (Wheeler *et al.* 2002), water table (e.g. lowering and contraction of the hyporheic zone) (Dobkin *et al.* 1998), stream channels (e.g. enhanced width-depth ratios, increased CPOM) (Magilligan and McDowell 1997; Clary 1999; Scrimgeour and Kendall 2003), stream banks (e.g. decreased stability) (Trimble and Mendel 1995; Clary 1999; Scrimgeour and Kendall 2003; Zaimes *et al.* 2004), and stream water (e.g. nutrient enrichment) (Agouridis *et al.* 2005). It has been associated with altered community composition and ecological function, and decreased diversity and conservation value for riparian vegetation (Clary 1999; Robertson and Rowling 2000; Scott *et al.* 2003; Holland *et al.* 2005), birds (Dobkin *et al.* 1998; Popotnik and Giuliano 2000; Scott *et al.* 2003), aquatic macroinvertebrates (Harrison and Harris 2002; Scrimgeour and Kendall 2003) and small mammals (Giuliano and Homyack 2004). Therefore livestock grazing is likely to have several indirect influences on ERS beetles as a result of changes to sediment delivery, vegetation cover, habitat shading, and aquatic food supply (Hering and Plachter 1997; Eyre *et al.* 2001a, b; Sadler *et al.* 2004; Paetzold *et al* in press).

The direct effects of trampling on ground-dwelling beetles have, however, rarely been studied (but see RiversMoore and Samways 1996), and almost nothing is known of its effect on ERS beetles. In a survey of 69 shingle ERS sites across England and Wales, Sadler *et al.* (2004) showed that livestock trampling explained a significant amount of the variation in ERS beetle assemblages. Contrary to expectations, trampling intensity was positively associated with the number of high fidelity ERS beetles with conservation status. The reason suggested for this apparent quandary was that trampling will destabilise ERS, suppressing vegetation succession, causing the availability of more habitat, which could be of particular significance in rivers with little available habitat (Sadler *et al.* 2004). In rivers towards the bottom of the ERS quality ranking (Chapter 3); that typically have small patches of shaded ERS due to either limited levels of hydrological disturbance or limited supply of sediments; the extra disturbance from livestock trampling may be beneficial in some instances.

The better quality (Chapter 3) ERS rivers however, typically already have high levels of hydrological disturbance and in such habitats, livestock trampling would be expected to reduce the conservation value of ERS beetle communities through the combined effects of (Sadler *et al.* 2004): (1) sediment compaction, which could cause direct mortality amongst ERS beetles and limit the availability of interstitial microhabitat; (2) defecation, which could enhance siltation of interstitial microhabitats and increase the amount of organic matter and nutrients in sediments, potentially increasing competition from non-ERS-specialist species; and (3) destruction of potential ERS beetle over-wintering sites, either through damage to grass tussocks (Luff 1966; Sotherton 1985), or through damage to interstitial hibernation sites (c.f. Andersen 1968).

This investigation examines beetle assemblages across a trampling gradient on the Afon Tywi, which is one of the very best ERS rivers in the UK (Chapter 3). It was expected therefore, that trampling intensity would have negative impacts on the conservation value of the ERS beetle communities. This negative impact might be observed: (1) as a direct reduction in the abundance of ERS specialist beetles, but with little alteration of community composition; or (2) as a reduction in the abundance of ERS specialist beetles, and an alteration of the community composition. This chapter therefore aims to investigate the effects of livestock trampling on specialist beetle communities in a high quality ERS system. The work addresses three linked objectives:

1. To determine if livestock trampling reduces the abundance of ERS specialist beetles.
2. To determine if livestock trampling affects the composition of ERS beetle assemblages.
3. To determine if livestock trampling negatively affects the conservation value of ERS beetle communities.

4.3 Methods

4.3.1 Description of sites

Twenty-five sites were sampled, which were distributed over ~47km of river, practically the entire range of the alluvial section of the Afon Tywi (Figure 2.2). These bars varied widely in heterogeneity, sediment size, bar size, and intensity of trampling, but varied little in the degree of shading due to their relatively large size and dynamic nature (Table 4.1).

4.3.2 Beetle sampling

Each bar was sampled twice using 1.5 by 1.5m (2.25m^2) quadrat hand searches (Chapter 2), one towards the upstream, and one towards the downstream end of the bar.

Quadrats were deliberately positioned to give as wide a possible range of trampling intensity over the whole study.

Table 4.1 Range of selected summary environmental variables for the survey bars.

	Minimum	Maximum
Distance downstream of source (km)	39.5	86.4
Vegetation cover (%)	2	65
Bar length (m)	77	396
Bar width (m)	8	64
Bar heterogeneity (1-3)	1	3
Tree shade (%)	0	15
Trampling damage (10-100)	10	84
Sediment size (phi)	5	-7.04

4.3.3 Environmental variables

Environmental variables were based on the generic site surveys and sediment sampling detailed in Chapter 2. Sediment photographs were taken just outside the sample quadrat to avoid disturbing the beetles before searching commenced. The high temporal specificity of the sampling method, the clear downstream gradient within the dataset, and the specific focus on trampling impact; required the measurement of additional variables. The extra field measurements were recorded on the form shown in Appendix 4.1 and were mainly associated with trampling damage.

Trampling damage was recorded from both within the quadrat and over the entire bar (Table 4.2). The method chosen allowed the estimation of the degree of trampling damage as a percentage of that possible. Due to the relative ubiquity of livestock on all bars, the minimum value was 10%; 100% indicated very heavy cattle trampling over the entirety of the quadrat or bar. Any such measure of trampling damage is subjective to some degree, but guidelines were created for the grading of damage according to the number of livestock footprints when this was possible (Table 4.2). This table was used directly for the grading of trampling damage within the sample quadrats; and for the whole bar, the percentage area of the bar for which each category was appropriate were summed to give an overall percentage trampling damage.

Table 4.2 Trampling damage categories.

Number	Code*1	Additional qualifiers
1	None	
2	Very light sheep	<20*2 sheep hoof prints, otherwise no damage to structure
3	Light sheep	<60*2 sheep hoof prints, otherwise no damage to structure
4	Very light cattle	<5*2 cattle hoof prints, otherwise no damage to structure
5	Medium sheep	Numerous sheep hoof prints, still some evidence of original structure
6	Light cattle	<15*2 cattle hoof prints, otherwise no damage to structure
7	Heavy sheep	Structure completely destroyed
8	Medium cattle	Numerous cattle hoof prints, still some evidence of original structure
9	Heavy cattle	Structure completely destroyed
10	Very heavy cattle	Structure completely destroyed + very heavily 'pitted'

*1 This is as far as the classification can go for coarse sediments because individual hoof prints cannot be discerned

*2 Numbers within 1.5 x 1.5m sample area and are only likely to apply to 'soft' sediments

Faeces counts were used as additional (and quantitative) measure of the level of trampling in the habitat. The method used was adapted from Sykes and Lane (1996), and Jansen and Robertson (2001); and involved the count of individual (one evacuation, rather than the number of faecal sub-sections) cattle or sheep faeces from both within the quadrat, and in two, 5m long, 2m wide ribbons extending from each corner of the quadrat into the bar interior. Despite the objective nature of such faecal measures, they are not direct measures of livestock habitat use because faeces can be distributed within an animals range in a heterogeneous manner, and their longevity will be highly dependent on factors such as the frequency of inundation and the rate of the degradation by arthropods (Jansen and Robertson 2001; Floate *et al.* 2005; Kryger *et al.* 2005).

Within the quadrat the amount of vegetation cover, the degree of compaction, and the angle of the ERS edge were all estimated on an ordinal scale (Table 4.3). Despite always implementing quadrat searches in the best weather possible, and within as short a temporal window as possible (13/7/03 to 28/8/03), there was likely to be some degree of unwanted variation between samples caused by these factors (Lott and Eyre 1996). Therefore, the temperature (^{o}C) and relative humidity (%) were measured at the time of sampling using a whirling hygrometer, and together with the time and date of sampling, were included in analyses. Because of the known importance of longitudinal gradients for ERS beetles (Fowles 1989; Framenau *et al.* 2002), the distance downstream from the river source and the stream order (Scheidegger 1965) at each site were measured from 1:50,000 British Ordnance Survey Landranger maps.

Table 4.3 Environmental variables used in the analyses, variable codes, variable types, data type, data transformation and scoring method.

Variable	Variable code	Variable type	Data type	Transformation	Scoring method
Date	Date	Covariable	Integer	-	Days from first
Time	Time	Covariable	Ordinal	-	Time 24 hour (<13:00 = 0.33, 13:00-16:00 = 0.66, >16:00 = 1)
Downstream or upstream	DS/US	Covariable	Binary	-	US = 1, DS = 0
Temperature (^{o}C)	Temp	Covariable	Decimal	-	Measured
Relative humidity (%)	Relhu	Covariable	Percentage	-	Measured
Grazing damage (quadrat)	Grazquad	Trampling	Percentage	Arcsine	See methods
Grazing damage (bar)	Grazbar	Trampling	Percentage	-	See methods
Faeces cattle quadrat	Facatqua	Trampling	Integer	Log10 + 1	Count
Faeces cattle ribbon	Facatrib	Trampling	Integer	Log10 + 1	Count
Faeces sheep quadrat	Facshqua	Trampling	Integer	Log10 + 1	Count
Faeces sheep ribbon	Facshrib	Trampling	Integer	Log10 + 1	Count
Stocking sheep	Stocksh	Trampling	Ordinal	-	None = 0, light = 1, heavy = 2
Stocking cattle	Stockca	Trampling	Ordinal	-	None = 0, light = 1, heavy = 2
Angle	Anglequ	Quadrat	Ordinal	-	Shallow = 1, medium = 2, steep = 3
Compaction	Compqu	Quadrat	Ordinal	-	Loose = 0, medium = 1, compact = 2, very compact = 3
Vegetation cover	Vegcovqu	Quadrat	Ordinal	-	None = 0, sparse = 1, medium = 2
Distance downstream of source (km)	Distds	Composite	Decimal	-	Measured from map
Stream order	Streord	Composite	Decimal	-	Measured from map
Vegetation type	Vegtyp	Bar	Ordinal	-	Bare = 0, simple = 1, complex = 2
Vegetation cover	Vegcov	Bar	Percentage	Arcsine	Estimated
Bar length (m)	Barlen	Bar	Integer	-	Measured
Bar width (m)	Barwid	Bar	Integer	-	Measured
ERS profile	ERSprof	Bar	Ordinal	-	Flat = 1, gentle = 2, steep = 3
ERS topography	ERStop	Bar	Ordinal	-	Simple = 1, humped = 2, complex = 3
Habitat heterogeneity	Habhet	Bar	Ordinal	-	Low = 1, medium = 2, high = 3
Tree shade	Treesh	Bar	Percentage	Arcsine	Estimated
Median sediment size (phi)	Medsedqu	Quadrat	Decimal	-	Estimated from photographs
Percentage fine (less than 8mm)	Percfine	Quadrat	Percentage	-	Estimated from photographs

4.3.4 Assessment of conservation value

Three different measures of the ERS quality were used to assess the conservation value of the beetles sampled from each quadrat. The first was richness, and was simply the total number of taxa sampled. The second was diversity, measured with the Simpson's index (Simpson 1949):

$$1/D = \sum \left(n_i \left[n_i - 1 \right] / N \left[N - 1 \right] \right)$$

where $1/D$ is the reciprocal of the Simpson's index (larger number = higher more even community); n_i = the number of individuals in the ith species; and N = the total number of individuals.

which is a highly robust and meaningful index of diversity, largely influenced by dominance (evenness), as opposed to the richness component of diversity (Magurran 2004). The final variable was the sum of ERS quality scores (ERSQS) for each quadrat. ERSQS could be used rather than the ERS quality index (ERSQI), because the amount of sample effort was directly comparable between quadrats.

4.3.5 Data analysis

Multivariate techniques were considered the most appropriate means of understanding the relationships between the community composition and the suite of potentially inter-relating environmental gradients. Ordination was employed using Canoco for Windows version 4.51 (ter Braak and Šmilauer 1998). Environmental variables (those that were not ordinal or binary) were checked for normality using Kolmogorov-Smirnov tests in SPSS and by examination of frequency histograms. Non-normally distributed data were transformed logarithmically (base 10 adding 1 in data sets where 0's were present) when positively skewed, or for percentage data by using an arcsine transformation (divided by 10, square root taken, then arcsine transformed), in order to move the data towards statistical normality.

Two sets of analyses were performed: (1) analysis of the total counts in order to examine the relationship between species composition and environmental variation, including the effects of overall abundance; and (2) analysis of percentage abundance in order to examine this relationship with a greater focus on assemblage composition. Species data were transformed in the analysis by using square root transformations and down-weighting of rare species in order to reduce the influence of dominant and rare species respectively. Initial indirect ordinations using detrended correspondence analysis (DCA) were used to examine broad patterns in the dataset and to determine whether to use linear, or unimodal methods in further analyses. As the largest gradient lengths (a measure of beta diversity in community composition) on the ordination axes were long (>4) canonical correspondence analysis (CCA) was the preferred ordination technique (Legendre and Legendre 1998; Lepš and Šmilauer 2003).

In each analysis, the variables date, time, ‘downstream or upstream’, temperature, and relative humidity were used as co-variables (i.e. partial CCA was employed), as their influence on the dataset was not the focus of the investigation. CCA and partial CCA use environmental data to structure the analysis of species assemblage in a form of ‘direct gradient analyses’ (ter Braak 1986). Therefore, both techniques have to be used with caution because the inclusion of inappropriate environmental variables can distort gradients within the species assemblage structure (McCune 1997). The selection of environmental variables for inclusion into the analyses are consequentially of critical importance and the methods used to do this vary (Lepš and Šmilauer 2003; Warnaffe and Dufrêne 2004). This study initially used the automatic selection procedure in Canoco, using Monte Carlo analyses (1000 permutations) under the reduced model, to assess the significance of all variables. Variables that were shown to be significant ($P \leq 0.05$) by this procedure were used in the models with the additional proviso that these variables were also significant when analysed as independent ‘single’ variables (c.f. Warnaffe and Dufrêne 2004). This method seemed to best balance the need to maximise the amount of the species variation incorporated by the model, while preventing the inclusion of variables considered inappropriate because of their poor relationship with the species assemblage data. The level of co-variation in selected variables was analysed using Pearson's correlations in SPSS.

The measures of conservation value; richness, diversity and total ERSQS, were used in each analysis as supplementary variables. This allowed assessment of relationships between environmental variables and the conservation value of each species assemblage. Phi measurements of median sediment size were all negative, but the negative sign was removed for all analyses in order to prevent confusion in the interpretation of ordination diagrams. Ordination plots used biplot scaling by inter-species distance, and the reported significance of the first and all canonical axes are from the reduced model. Species that had the most weight in the ordinations were displayed in the ordination plots.

4.4 Results

The investigation recorded 2,456 individuals of 87 taxa, 34 of which were ERS specialists. The Staphylinidae and Carabidae dominated the assemblages both in terms of abundance of individuals and species richness (Table 4.4). Measured species richness ranged from 2 to 19, species diversity ranged from 0 to 13.14, and ERSQS ranged from 1 to 51.

4.4.1 Effect on abundance: analysis of assemblage count data

4.4.1.1 Environment species relationship

Five variables were selected for inclusion into the partial CCA (Table 4.5), namely the number of sheep faeces in the quadrat (Facshqua) and ribbons (Facshrib), cattle stocking (Stockca), the median sediment size in the quadrat (Medsedqu) and distance downstream (Distds). These variables explained a significant proportion; 6.5% (F = 3.04, P = 0.025) and 20% (F = 2.50, P = 0.001) of the variation in species assemblage on the first and all four canonical axes respectively (Table 4.6).

Table 4.4 List of species sampled, their families, sources and ordination codes (nomenclature and sources follow Coleopterist 2005).

Taxa	Taxa code	Taxa	Taxa code
Staphylinidae		*Bembidion punctulatum* Drapiez, 1821	B.punct
A. Acrotona aterrima (Gravenhorst, 1802)	A.A.ater	*Bembidion quadrimaculatum* (Linnaeus, 1761)	B.quadri
A. Philhygra hygrotopora (Kraatz, 1856)	A.P.hygr	*Bembidion tetracolum* Say, 1823	B.tetrac
A. Philhygra malleus (Joy, 1913)	A.P.mall	*Bembidion tibiale* (Duftschmid, 1812)	B.tibiale
A. Philhygra melanocera (Thomson, C.C., 1856)	A.P.mela	*Chlaenius vestitus* (Paykull, 1790)	C.vestit
Aloconota cambrica (Wollaston, 1855)	A.camb	*Elaphropus parvulus* (Dejean, 1831)	E.parv
Aloconota currax (Kraatz, 1856)	A.currax	*Lionychus quadrillum* (Duftschmid, 1812)	L.quad
Brachygluta pandellei (Saulcy, 1876)	B.pande	*Loricera pilicornis* (Fabricius, 1775)	L.pilic
Carpelimus bilineatus Stephens, 1834	C.biline	*Paranchus albipes* (Fabricius, 1796)	P.albip
Carpelimus corticinus (Gravenhorst, 1806)	C.cortic	*Perileptus areolatus* (Creutzer, 1799)	P.areo
Carpelimus rivularis (Molschulsky, 1860)	C.rivula	*Pterostichus strenuus* (Panzer, 1796)	P.stren
Carpellimus pusillus (Gravenhorst, 1802)	C.pusill	*Pterostichus vernalis* (Panzer, 1795)	P.vern
Deleaster dichrous (Fabricius, 1775)	D.dichr	**Hydrophilidae**	
Gnypeta carbonaria (Mannerheim, 1830)	G.carbo	*Anacaena lutescens* (Stephens, 1829)	A.lutes
Gnypeta rubrior Tottenham, 1939	G.rubrio	*Cryptopleurum minutum* (Fabricius, 1775)	C.minut
Hydrosmecta fragilis (Kraatz, 1854)	H.frag	*Helophorus arvernicus* Mulsant, 1846	H.arver
Hydrosmecta longula (Heer, 1839)	H.longu	*Helophorus brevipalpis* Bedel, 1881	H.brevi
Hydrosmectina septentrionum (Benick, 1969)	H.sept	*Laccobius atrocephalus* Reitter, 1872	L.atroc
Ischnopoda atra (Gravenhurst, 1806)	I.atra	*Laccobius striatulus* (Fabricius, 1801)	L.stria
Ischnopoda leucopus (Marsham, 1802)	I.leuc	**Chrysomelidae**	
Lathrobium angusticolle Boisduval & Lacordaire, 1835	L.angu	*Gastrophysa viridula* (De Geer, 1775)	G.viridul
Myllaena elongata (Matthews, A.H., 1838)	M.elong	*Phaedon armoraciae* (Linnaeus, 1758)	P.armo
Neobisnius prolixus (Erichson, 1840)	N.proli	*Phyllotreta flexuosa* (Illiger, 1794)	P.flexu
Ochthephilus omalinus (Erichson, 1840)	O.omal	*Phyllotreta vittula* (Redtenbacher, 1849)	P.vittu
Oxytelus laqueatus (Marsham, 1802)	O.laqu	**Hydraenidae**	
Philonthus cruentatus (Gmelin, 1790)	P.crue	*Hydraena nigrita* Germar, 1824	H.nigri
Philonthus quisquiliarius (Gyllenhal, 1802)	P.quis	*Hydraena rufipes* Curtis, 1830	H.rufip
Philonthus rubripennis Stephens, 1832	P.rubri	*Limnebius truncatellus* (Thunberg, 1794)	L.trunc
Philonthus varians (Paykull, 1789)	P.vari	**Curculionidae**	
Platystethus cornutus (Gravenhorst, 1802)	P.corn	*Rhinoncus bruchoides* (Herbst, 1784)	R.bruc
Stenus comma Le Conte, 1863	S.com	*Sitona ambiguus* Gyllenhal, 1834	S.ambi
Stenus guttula M Eler, P.W.J., 1821	S.gutt	*Sitona lepidus* Gyllenhal, 1834	S.lepi
Stenus melanarius Stephens, 1833	S.mel	**Coccinellidae**	
Stenus tarsalis Ljungh, 1810	S.tars	*Coccinella quincepunctata* Linnaeus, 1758	C.quince
Thinobius ciliatus Kiesenwetter, 1844	T.cilia	*Coccinella semptempunctata* Linnaeus, 1758	C.septem
Unidentified *Atheta* Thomson, C.G., 1858: 1	A.F1	**Dryopidae**	
Unidentified *Atheta* Thomson, C.G., 1858: 2	A.F2	*Dryops luridus* (Erichson, 1847)	D.luridus
Carabidae		*Pomatinus substriatus* (Ph. Muller, 1806)	P.subst
Agonum marginatum (Linnaeus, 1758)	A.margin	**Dytiscidae**	
Agonum muelleri (Herbst, 1784)	A.muell	*Oreodytes davisii* (Curtis, 1831)	O.davi
Agonum viduum (Panzer, 1796)	A.viduum	*Oreodytes septentrionalis* (Gyllenhal, 1826)	O.sept
Bembidion andreae (Fabricius, 1787)	B.andrea	**Elmidae**	
Bembidion atrocaeruleum (Stephens, 1828)	B.atroc	*Elmis aenea* (Muller, 1806)	E.aenea
Bembidion biguttatum (Fabricius, 1779)	B.bigutt	*Limnius volkmari* (Panzer, 1793)	L.volk
Bembidion decorum (Zenker in Panzer, 1800)	B.decor	**Elateridae**	
Bembidion femoratum Sturm, 1825	B.femor	*Zorochros minimus* (Boisduval & Lacordaire, 1835)	Z.min
Bembidion fluviatile Dejean, 1831	B.fluviat	**Heteroceridae**	
Bembidion guttula (Fabricius, 1779)	B.guttu	*Heterocerus fenestratus* (Thunberg, 1784)	H.fene
Bembidion prasinum (Duftschmid, 1812)	B.prasi	**Scarabaeidae**	
Bembidion properans (Stephens, 1828)	B.prope	*Aphodius prodromus* (Brahm, 1790)	A.prodro

The relationship between species assemblage and selected environmental variables is shown in Figure 4.1. Variables were found to be aligned on two main planes: (1) off-horizontal, with distance downstream and the number of sheep faeces in the ribbons directly opposed, and (2) off-vertical, with cattle stocking and number of sheep faeces in the quadrat explaining similar, but distinct gradients in the species assemblage data and the median sediment size explaining a smaller amount of variation in roughly the opposite direction. The position of specialist ERS species within the ordination showed no clear alignment with the off-horizontal variables, but some tendency away from the intensity of cattle stocking and the number of sheep faeces in the quadrat (Figure 4.1).

Table 4.5 Automatic forward selection summary for the count data (environmental variables in bold were selected for inclusion into the model).

Variable	*F* ratio	*P* value	Variable	*F* ratio	*P* value
Facshrib	**3.00**	**0.004**	ERSprof	1.09	0.349
Facshqua	**2.64**	**0.049**	Compqu	1.02	0.425
Stockca	**2.12**	**0.001**	Vegcov	1.02	0.428
Distds	**2.45**	**0.001**	Facatqua	1.02	0.420
Medsedqu	**1.57**	**0.020**	Streord	0.97	0.484
Vegcovqu	1.33	0.125	Grazbar	0.96	0.506
Vegtyp	1.44	0.065	Treesh	0.91	0.530
Habhet	1.29	0.147	Grazquad	0.83	0.658
Anglequ	1.25	0.162	Barlen	0.68	0.770
Barwid	1.19	0.246	ERStop	0.64	0.835
Percfine	1.17	0.249	Facatrib	0.44	0.984
Stocksh	1.09	0.332			

Table 4.6 Eigenvalues, cumulative percentage of variance explained by axes (1-4) and significance of the first and all canonical axes in the canonical correspondence analysis (CCA) for the count data.

Axes	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.25	0.21	0.16	0.14
Cumulative percentage variance				
Species data	6.5	12.0	16.3	20.0
Species-environment relation	28.7	53.1	72.0	88.4
Significance of first canonical axis	*F* ratio = 3.04		*P* = 0.025	
Significance of all canonical axes	*F* ratio = 2.50		*P* = 0.001	

4.4.1.2 Environment conservation value relationship

All three measures of assemblage conservation value were clearly aligned with the off-vertical environmental variables (Figure 4.1). Taxonomic richness and diversity both increased with the level of cattle stocking and number of quadrat sheep faeces, although the length of the diversity arrow indicates that it varied little in this dataset. In contrast, the ERSQS score was negatively associated with these two trampling variables and more positively associated with more coarse sediments, thus following a similar trend to the distribution of ERS specialists in the ordination.

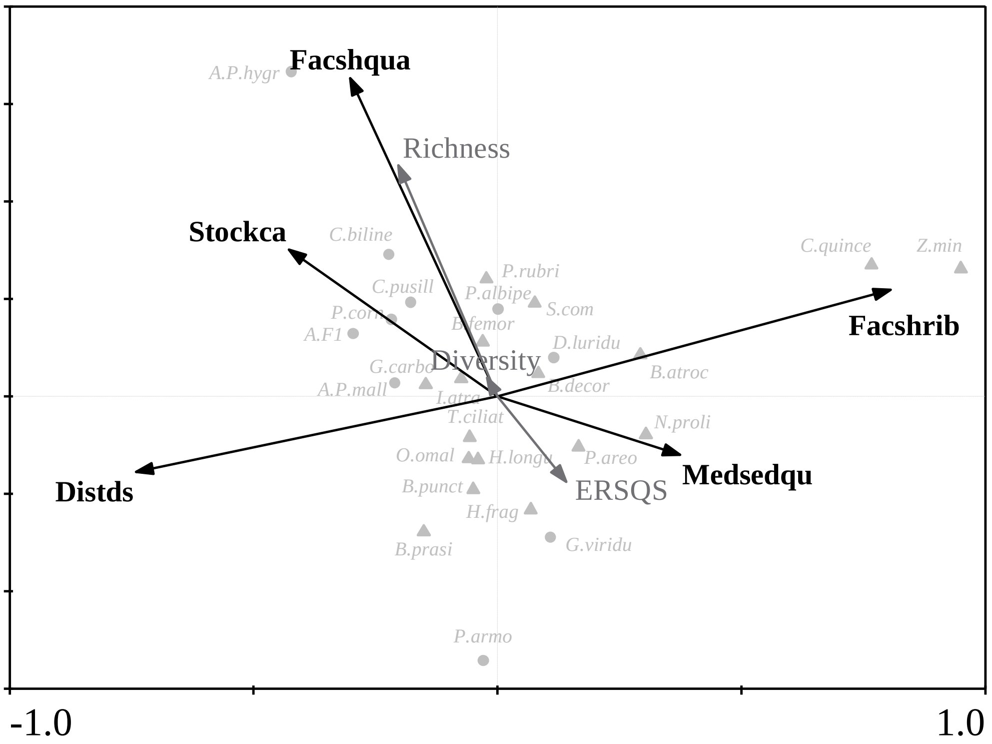


Figure 4.1 Partial canonical correspondence analysis (pCCA) of the count data. Only selected environmental variables are displayed (see Table 4.3 for variable codes). The direction of variation in the supplementary variables richness, diversity and ERSQS are displayed. Species with the most weight are shown in the ordination diagram; with ERS specialists displayed using triangular symbols (see Table 4.4 for species codes).

4.4.2 Effect on assemblage composition: analysis of assemblage percentage data

4.4.2.1 Environment species relationship

Four variables were selected for inclusion into the partial CCA (Table 4.7), three were common to both analyses, namely the number of sheep faeces in the ribbons (Facshrib), cattle stocking (Stockca) and distance downstream (Distds). The percentage of fine sediments in the quadrats (Percfine) was also selected. Although found to be significant in the automatic selection, the compaction of the quadrat (Compqu) was not significant when analysed as an independent single variable, so was not included in the model. These variables explained a significant proportion; 6.5% (*F* = 2.76, P = 0.012) and 18.4% (*F* = 2.25, P = 0.001) of the variation in species assemblage on the first and all four canonical axes respectively (Table 4.8).

Table 4.7 Automatic forward selection summary for the percent data (environmental variables in bold were selected for inclusion into the model).

Variable	*F* ratio	*P* value	Variable	*F* ratio	*P* value
Distds	**2.58**	**0.001**	ERSprof	1.09	0.346
Percfine	**2.20**	**0.003**	Facatqua	1.08	0.380
Facshqua	2.05	0.074	Vegcov	1.01	0.454
Facshrib	**2.02**	**0.041**	Medsedqu	0.99	0.452
Stockca	**1.97**	**0.003**	Treesh	0.88	0.588
Barwid	1.50	0.065	Grazbar	0.84	0.638
Compqu	1.47	0.048	ERStop	0.79	0.730
Vegcovqu	1.39	0.111	Streord	0.78	0.712
Vegtyp	1.31	0.132	Grazquad	0.70	0.799
Stocksh	1.27	0.169	Habhet	0.65	0.859
Barlen	1.25	0.192	Facatrib	0.50	0.952
Anglequ	1.18	0.228			

Table 4.8 Eigenvalues, cumulative percentage of variance explained by axes (1-4) and significance of the first and all canonical axes in the canonical correspondence analysis (CCA) for the percentage data.

Axes	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.25	0.19	0.16	0.11
Cumulative percentage variance				
Species data	6.5	11.4	15.6	18.4
Species-environment relation	35.2	62.0	84.9	100.0
Significance of first canonical axis	*F* ratio = 2.76		*P* = 0.012	
Significance of all canonical axes	*F* ratio = 2.25		*P* = 0.001	

The relationship between species assemblage and selected environmental variables is shown in Figure 4.2. Again there was a strong and roughly horizontal opposite alignment of the variables distance downstream and number of quadrat sheep faeces. The percentage of fines gradient was approximately aligned at right angles to this off-horizontal gradient. The gradient of cattle stocking this time ran between the off-horizontal and off-vertical gradients, mid-way between the direction of the distance downstream and percentage fine gradients (Figure 4.2). Specialist ERS species were again largely associated with lower cattle stocking levels, but in this instance also showed some evidence of a negative association with distance downstream.

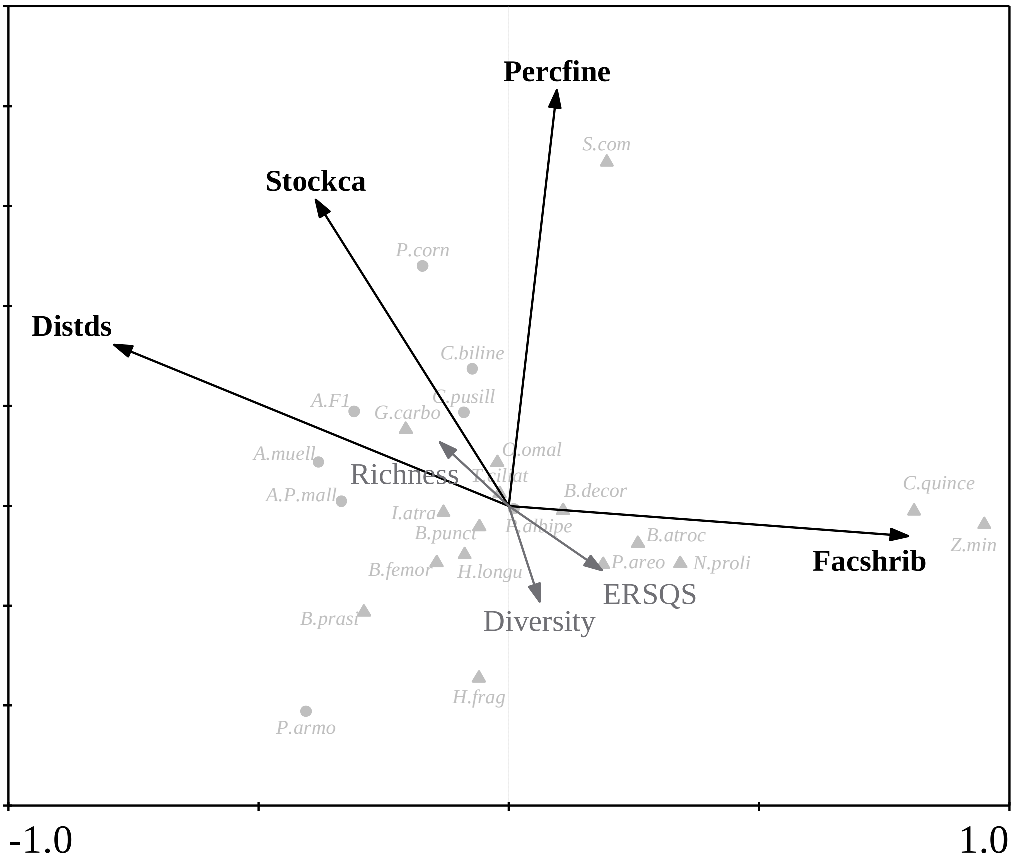


Figure 4.2 Partial canonical correspondence analysis (pCCA) of the percent data. Only selected environmental variables are displayed (see Table 4.3 for variable codes, Table 4.4 for species codes, and Figure 4.1 for diagram description). The direction of variation in the supplementary variables richness, diversity and ERSQS are displayed. Species with the most weight are shown in the ordination diagram; with ERS specialists displayed using triangular symbols (see Table 4.4 for species codes).

4.4.2.2 Environment conservation value relationship

Taxonomic richness was positively associated with cattle stocking and distance downstream (Figure 4.2). Gradients in diversity and ERSQS both ran in the opposite direction to species richness, with diversity negatively related to cattle stocking and percentage fine, and ERSQS negatively related to cattle stocking and distance downstream. ERSQS again followed a similar trend to the distribution of ERS specialists in the ordination.

4.4.3 Co-variation in selected variables

Table 4.9 shows the strength of correlation between the selected variables. Those correlations highlighted as significant all result from a longitudinal trend (distance downstream) in the data due to downstream increases in cattle stocking and sediment fining.

Table 4.9 Pearson correlations between selected environmental variables. Significant positive correlations are in bold, significant negative correlations are underlined (see Table 4.3 for variable abbreviations).

		Percfine	Medsedqu	Distds	Stockca	Facshrib
Facshqua	Pearson Correlation	0.11	-0.15	0.16	0.14	-0.05
	Sig. (2-tailed)	0.443	0.311	0.275	0.322	0.736
Facshrib	Pearson Correlation	0.02	0.06	-0.38	-0.21	
	Sig. (2-tailed)	0.878	0.698	0.007	0.147	
Stockca	Pearson Correlation	**0.42**	-0.41	**0.66**		
	Sig. (2-tailed)	**0.003**	0.003	**<0.001**		
Distds	Pearson Correlation	**0.36**	-0.48			
	Sig. (2-tailed)	**0.010**	<0.001			
Medsedqu	Pearson Correlation	-0.81				
	Sig. (2-tailed)	<0.001				

4.5 Discussion

4.5.1 Trampling effects on the abundance of ERS specialist beetles

The count data encapsulates both variation in the effects of the environmental gradients on the composition of the ERS beetle assemblages, as well as the overall abundance of ERS beetles. However, because the effects on composition are more clearly tested on the percentage data, the count data are considered to best represent effects on abundance and are discussed in this section.

General downstream decreases in sediment size are typical of most river systems (e.g. Seal and Paola 1995; Petts *et al.* 2000; Moussavi-Harami *et al.* 2004) as is the general upland lowland transition from sheep to cattle farming in Wales. Therefore, some co-variation in these factors was impossible to avoid within this investigation. On many sites surveyed on the Afon Tywi, however, there were both sheep and cattle, and a wide range of sediment calibres within each bar. This allowed sufficient dissimilarity in these variables to allow their effects on taxonomic assemblage to be tested, despite the strong longitudinal gradient in the dataset. It was also partly the purpose of this investigation to look at the interaction between sediment calibre and trampling effect, because the physical damage caused by trampling is clearly more intensive when sediments are finer. The ordination results confirm that, despite the level of co-variation, the level of cattle stocking and median sediment size explained significant variation in the species assemblage data that was not associated with distance downstream (Figure 4.1).

The lack of association between the number of sheep faeces in the quadrats and in the ribbons was a little surprising because the two measures would be expected to correlate quite closely. However, the negative correlation between the number in ribbons and distance downstream (Table 4.9) suggests a reason why this was the case. Typically, the frequency of low-magnitude flow events increases downstream (Benda *et al.* 2004a, b), and indeed, in a flow event shortly before the study was implemented downstream bars were largely inundated, whilst water levels further upstream hardly rose. Therefore it was likely that further upstream, sheep faeces in more elevated sections of bars had been accumulating for a longer period of time than those at the same elevation above the base flow downstream. At all sites, faeces close to the water's edge (in quadrats) would probably have been removed by this event. As a consequence, faeces in quadrats were likely to provide an indication of trampling intensity over the short term (2-3 weeks), and faeces counts in ribbons were likely to be a relatively unreliable indication of trampling intensity. The same argument can be made for the trampling indices, that they were only likely to be a reliable indicator of short-term impacts of trampling. The appearance of ribbon sheep faeces in the ordination is therefore most probably an artefact of its correlation with longitudinal variation.

The faeces counts from quadrats and overall stocking levels were more likely therefore to provide reliable short and medium-term indications of trampling intensity, respectively. Gradients in both cattle stocking levels and the abundance of sheep faeces in quadrats were negatively associated with specialist ERS beetles, thus suggesting that trampling by both sheep and cattle reduce the abundance of ERS specialist beetles. In contrast, specialist ERS beetles were positively associated with coarser sediments (Figure 4.2), and this may partly have been because coarser sediments are more resistant to trampling damage. Indeed, the amount of trampling damage in quadrats was negatively related to median sediment size, but this variable was not selected for inclusion due to the larger amount of variation explained by cattle stocking in the same direction. It is, however, difficult to be sure that this sediment size trampling intensity interaction was present in the data because of the co-variation of these factors along the longitudinal gradient.

4.5.2 Trampling effects on the composition of ERS beetle assemblages

The analysis of the percentage data allowed the effects of environmental variables on the composition of ERS beetle assemblages to be tested without the influence of overall abundances in the dataset. Despite this, the results of the analysis of the percentage data were fairly consistent with the findings of the analysis of the count data (Figures 4.1 and

4.2). The main differences were: (1) the inclusion of percentage fine into the ordination instead of median sediment size, and (2) the exclusion of quadrat sheep faeces from the ordination. Percentage fine was so strongly correlated with median sediment size (Table 4.9) that these variables mainly describe the same gradient, except in opposite directions; so this represented little change from the ordination of the count data. The amount of quadrat sheep faeces was only just significant in the analysis of count data, but its removal in the analysis of percentage data did not change the overall pattern of the ordination. ERS specialists were again negatively associated with cattle stocking, suggesting that trampling also reduced the proportion of ERS specialists in the beetle assemblages.

4.5.3 Trampling effects on the conservation value of ERS beetle communities

Taxonomic richness was shown to be greater for both datasets where the level of trampling was higher (Stockca Facshqua) (Figures 4.1 and 4.2). Species richness has previously been shown to be a poor indicator of conservation value for survey data, and particularly pitfall data, because of edge effects in narrow pieces of habitat (Chapter 3, Sadler *et al.* 2004). The use of the quadrat hand searching technique on ERS at the water's edge should strongly reduce such edge effects. However, even using this technique, species richness failed to follow the same gradient as the rarity based ERSQS. This was not likely to be the result of an edge effect, but rather the result of greater species richness in association with enhanced levels of organic matter and silt due to heavy grazing. Relatively little is known about the habitat requirements of most of the beetles sampled, but some of the species associated with trampling in the ordinations are associated with silty sediments (e.g. *A. Philhygra hygrotopora* and *Philonthus quisquilarius*) or high amounts of organic matter (e.g. *Philonthus cruenatus*) (Joy 1932).

The relationship between the evenness based Simpson's diversity index and the environmental variables changed between the two analyses. In the analysis of the count data it showed almost no relationship with any variable, but was slightly positively associated with the trampling variables. In the analyses of the percentage data on the other hand, it was found to be negatively associated with cattle stocking. It is therefore difficult to draw any firm conclusions about the effect of trampling on the diversity of ERS beetle assemblages.

High ERSQS were associated with low levels of trampling in both the analysis of the count and percentage data (Figures 4.1 and 4.2). Some of the highest scores (minimum 1, maximum 51) were higher than the scores for whole rivers that have been intensively surveyed for ERS beetles (e.g. River Avon in Devon 49, River Thrushel 40), so the gradient of quality scores was of sufficient length to act as a flexible indicator of conservation value. The ERSQS is a much better indicator of ERS beetle conservation value than species richness, because it both focuses on specialists of ERS and takes into account the rarity of each species. Livestock trampling does therefore reduce the conservation value of ERS beetle communities.

CHAPTER 5

MICROSPATIAL DISTRIBUTION AND DYNAMICS

5.1 Introduction

This chapter describes an investigation of the microspatial distribution of several species across three distinct bars, and explores the influences of weather, flow level and the distribution of microhabitat and interspecifics on these distributions. Additional information from the 2003 mark-recapture study (Chapter 7), which was run concurrently over the same area, was utilized to further the understanding of these distributions.

5.1.1 Background

At the whole-bar scale, ERS with a greater diversity of microhabitats have been shown to support more speciose beetle communities that contain a larger number of rare, ERS specialist species (Sadler *et al.* 2004). This was to be expected as individual species have previously been shown to be associated with particular microhabitats and are thus spatially segregated in terms of niche space. For example, Andersen (1969, 1978, 1983, 1985, 1988, 1989) demonstrated that species of the tribe Bembidiini are spatially segregated by their preference for ERS microhabitats that differ with respect to elevation/moisture content, sediment characteristics and vegetation cover due to ecomorphological adaptations to these habitats. Desender (1989) also showed how the microhabitat distribution and ecomorphological adaptation of species of *Bembidion* on ERS are related to gradients in microclimate and disturbance frequency, and sediment characteristics. Additionally, the propensity of different species to handle diverse food types and the range of temporally variable lifecycles (Anderson 1983), further partition species of ERS beetles along resource and temporal niche gradients. Such niche segregation may be important in sustaining species richness in ERS habitats. A more thorough understanding of the niche segregation of ERS beetles along spatial, temporal and resource partitioning gradients should provide an essential insight into the processes that are responsible for the maintenance of community function and diversity in ERS and riparian systems.

The utilisation of microhabitats by ERS beetles is likely to be dynamic and respond to changes in weather, flow level and the distribution of food, and these ideas are outlined in the ERS dynamic microhabitat utilisation model (Figure 5.1). The potential influence of temperature and moisture level on the spatial distribution of beetles have been previously demonstrated (e.g. Gereben 1995; Ottesen 1996), but in riparian habitats weather is also a principle determinant of water level, which has been shown to influence microhabitat choice (Andersen 1969). During hot, dry weather, temperatures at the surface of ERS are extreme, whilst moisture levels are very low (Hannah unpublished; Tockner *et al.* in press). At the water's edge, however, there is a well-defined zone of reduced temperature and increased humidity, which becomes more marked as ambient temperature increases (Desender 1989). The position of this zone will track water level closely and one might hypothesise that the beetles associated with it will move in response to its changing position as observed by Antvogel and Bonn (2001) in an alluvial forest. However, following prolonged or heavy rainfall this zone will become less distinct, and may even disappear completely, beetles may demonstrate a markedly different microspatial distribution in this instance (Figure 5.1). Moreover, aquatic invertebrates and algae, which likely provide important food sources for ERS carabids (e.g. Hering and Plachter 1997; Paetzold *et al.* in press) and small staphylinids (Lott 2003) respectively, will be concentrated at the water's edge during stable low water levels but will be distributed more widely as a flow pulse (*sensu* Tockner *et al.* 2000) recedes. Beetles that feed on these aquatic food resources may be expected to respond to such changes in the distribution of food as has been observed in arable habitats (e.g. Bryan and Wratten 1984; Wallin and Ekbom 1994; Bohan *et al.* 2000).

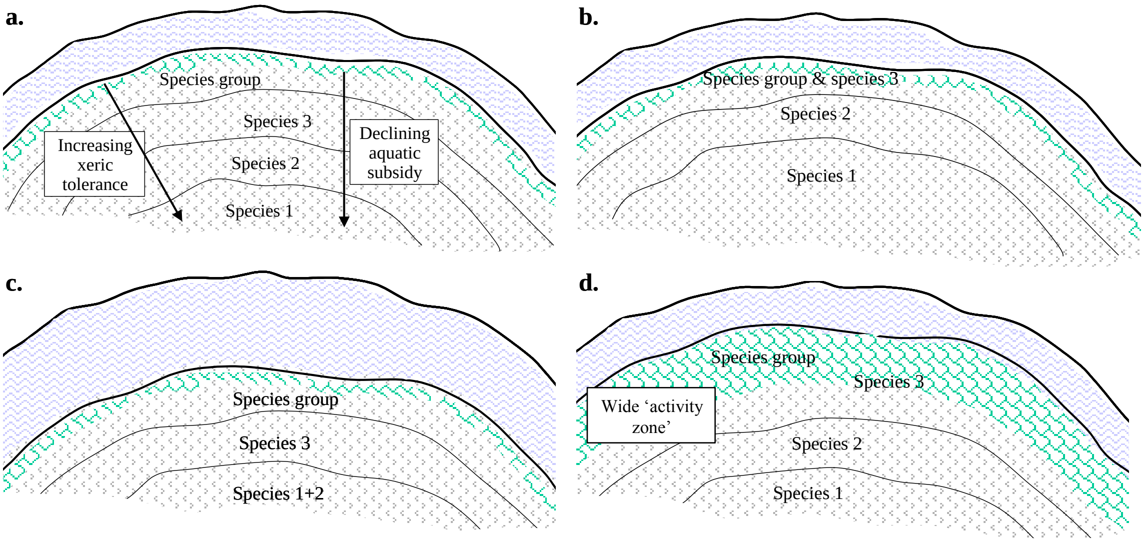


Figure 5.1 The ERS dynamic microhabitat utilization model. Sub-figures (a) to (d) represent the likely microspatial distributions during: (a) 'typical' conditions of base-flow water level and reasonably warm and wet weather; (b) hot and dry weather with low water level; (c) a flow pulse (*sensu* Tockner *et al.* 2000); and (d) after a flow pulse has receded. Species 1-3 represent hypothetical species with decreasing xeric tolerance and an increasing reliance on aquatic food subsidies. The species group represents several hypothetical species that are strongly associated with the water's edge. In the model, species alter their microspatial distributions due to: (a → b) a drying and warming of the ERS, which causes individuals to move towards the water to track their favoured microclimate; (a → c) the inundation of part of the ERS, which causes individuals to move away from the water to higher elevations; (c → d) the deposition of aquatic food resources (in green), raising of humidity levels, and lowering of temperature over a wider area, which causes an expansion of the distribution of species that find these conditions favourable.

In contrast with this investigation, previous studies of the microspatial distribution of riparian beetles (e.g. Bonn and Kleinwächter 1999; Antvogel and Bonn 2001) used correlation and multi-variate techniques to identify species' affinity to different microsites and the environmental variables driving that distribution. Although these methods are valid, they do not explicitly use the available spatial information in the data. SADIE (Perry 1998; Perry *et al.* 1999; Perry and Dixon 2002) allows both the measurement of local and overall spatial pattern for a dataset, and the measurement of the spatial association between two data sets from the same sampling locations.

5.1.2 Aim and objectives

The broad aim of this study was to investigate the microspatial (within-habitat) structure of ERS beetle assemblages and postulate reasons for that pattern, with a view to identifying the factors sustaining community diversity and function. The objectives were to:

1. Determine whether species showed significantly non-random spatial patterns.
2. Determine whether species showed significant positive or negative associations with environmental variables.
3. Determine whether different species were significantly spatially aggregated/separated with/from each other.
4. To investigate the way these patterns and spatial interactions changed over time, particularly with respect to changing weather conditions and flow levels.
5. Evaluate which variables were most likely to be responsible for any observed patterns.

5.2 Methods

5.2.1 Site description

This investigation was located within the Upper Severn study area around the river's confluence with the Afon Carno (Chapter 2). Three bars (Bars 2, 3 and 3d) were chosen for this study (Figure 5.2). Environmental characteristics (e.g. vegetation cover and sediment type) differed widely both between and within the study patches, so a wide range of variables were measured and spatially referenced to produce habitat maps for each patch (Figures 5.3-5).

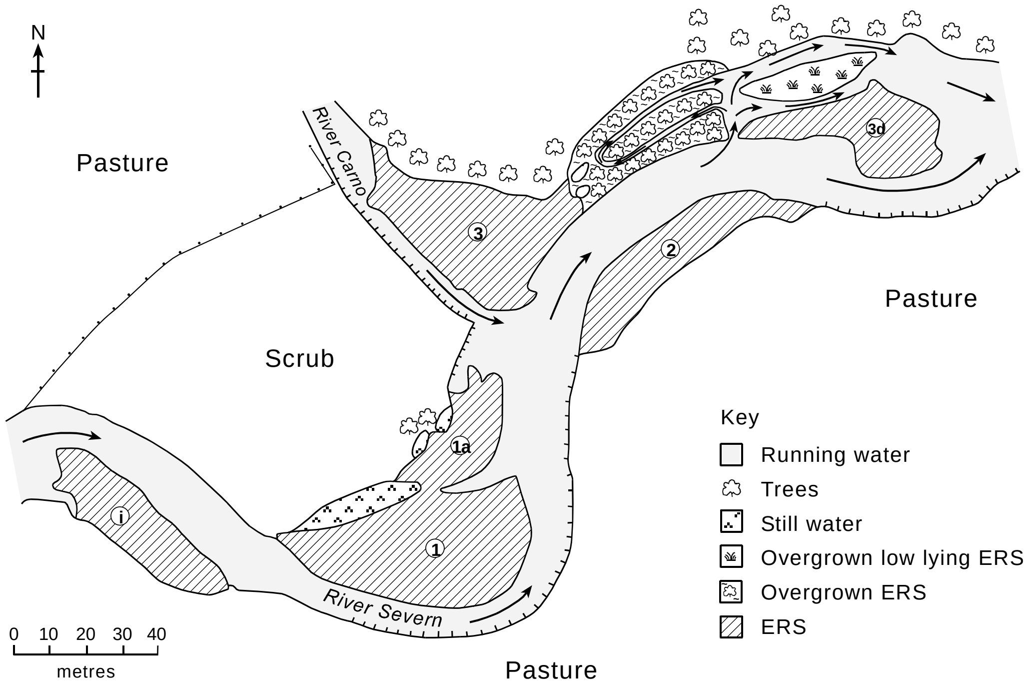


Figure 5.2 The study reach. Bars 2, 3 and 3d were sampled for this chapters study of microspatial distribution (Chapter 5), and all coded bars were sampled for the 2003 mark-recapture study (Chapter 7).

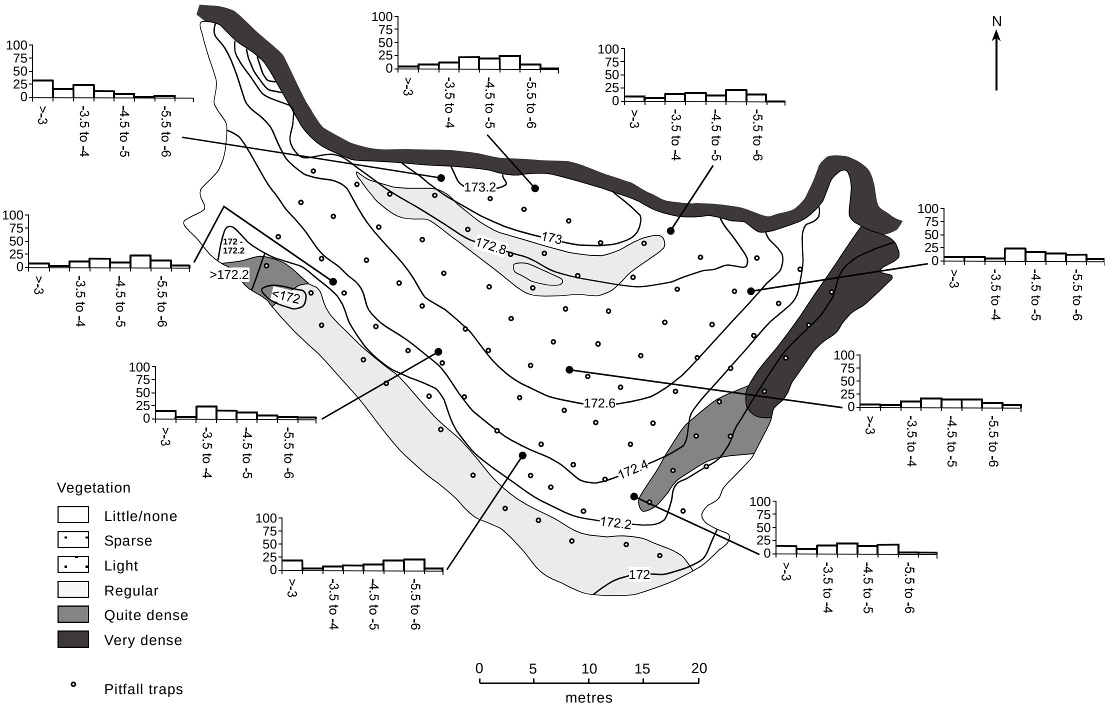


Figure 5.3 Map of Bar 3 showing the density of vegetation, elevation (contours m asl), trap positions, and sediment type at various positions around the bar. Sediment graphs show the percentage of sediments in each phi size class (missing classes, from left to right, are –3 to –3.5, -4 to –4.5, -5 to –5.5, and >-6), no distinct sediment zones were identified on Bar 3.

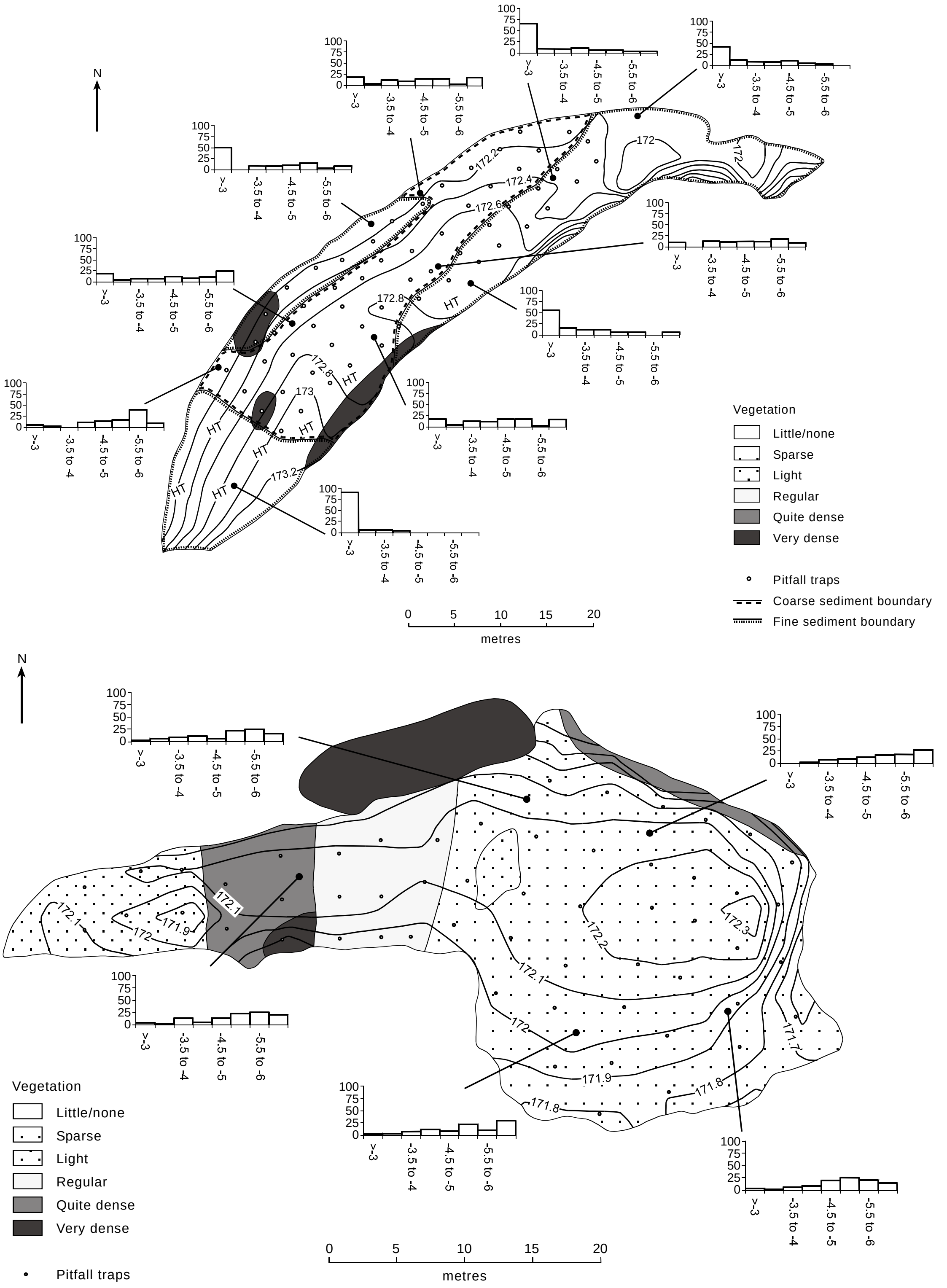


Figure 5.4 & 5.5 Map of Bar 2 (above) and Bar 3d (below) showing the density of vegetation, elevation (contours, m asl), trap positions, and sediment type at various positions around the bars. Sediment graphs show the percentage of sediments in each phi size class (missing classes, from left to right, are –3 to –3.5, -4 to –4.5, -5 to –5.5, and >-6). Two distinct sediment zones were identified on Bar 2: fine zones and a coarse zone (see text), on Bar 3d no distinct sediment zones were identified. The areas marked HT, show areas heavily trampled by cattle.

5.2.2 Environmental variables

Coarse sediment size distributions were estimated at several points (Figures 5.3-5) chosen to sufficiently map the diversity of sediments across each bar using the photo-sieving method (Chapter 2). When the results supported the existence of distinct sediment zones, this information was used in SADIE analyses. The degree of vegetation cover was estimated using the following scale: (1) bare/very sparse, (2) sparse, (3) light, (4) regular, (5) quite dense, (6) very dense. The degree of vegetation cover both within which an individual trap was situated and the densest vegetation within 3m (~1 trap distance away) of an individual trap were noted. Daily total rainfall and maximum and minimum temperature data were used together with information on stage height (Chapter 2). Water levels that flooded traps, thus reducing the effective sampling area were considered to be flow pulses (stage height of >1.40m at the gauging station).

A digital elevation model (DEM) of the study reach was created using a Leica differential global positioning system (dGPS) in kinematic mode for measurements of elevation, and manual mode for reach mapping and logging trap positions (e.g. Brasington 2000). A distance interval of 0.5m was used for the survey of elevation, and all areas of the study bars, a short distance into the adjoining banks and in areas of the river where the depth and velocity allowed. The model was used to estimate the distance of traps from the water's edge, together with their elevation.

5.2.3 Trapping method and choice of study species

Grids of modified dry pitfall traps (Chapter 2) were set over the entirety of each bar (~3m between traps and rows of traps) except for very heavily vegetated areas and areas where there was a very high intensity of cattle trampling. A total of 204 traps: 90 on Bar 3 (density $0.058m^2$), 58 on Bar 2 (density $0.060m^2$) and 56 on Bar 3d (density $0.067m^2$) were set and maintained (replaced when crushed or removed by livestock, high water or vandals, or when dirty) across the study area. When using non-fatal pitfall traps for the study of microspatial distribution, there is an additional consideration to those stated in Chapter 2, namely that animals can be trapped more than once on the same sampling occasion, thereby potentially altering the observed pattern of spatial distribution. The occurrence of individually recognisable *B. atrocaeruleum* (Chapter 7) was used to study the extent of this error. The vast majority of beetles captured could be identified to species level in the field (with the aid of a hand lens if necessary). Some small staphylinids and maculated *Bembidion* in the sub-genus *Peryphus* Dejean, 1821 could not be identified, but these were not common.

The three most abundant species were used to analyse spatial distribution on individual sample dates, namely the carabids *B. atrocaeruleum* (all bars), *B. decorum* (Bar 3d) and the elaterid *Z. minimus* (all bars, over all sample dates on Bar 3, but only in the second half of sampling for Bars 2 and 3d). However, numbers of some species were too small (<50) to allow sensible analysis of spatial distribution on individual dates. For these species, if a preliminary ‘eyeballing’ of the data in Surfer 7® (Golden Software, Inc) using the kriging interpolation process, showed spatial distribution to be fairly constant temporally, then counts were grouped across the entire sampling period. This was similar to the method used by Holland *et al.* (1999) to measure ‘activity’, except that because individuals could be captured more than once in this study, activity was over-estimated by grouped counts. Grouped data in this study can therefore be considered an indication of the spatial range of activity, rather than activity *per se*. If an ‘eyeballing’ of data for the less abundant species revealed temporally dynamic spatial distributions, or if, although spatially stable, counts were still considered too small (<50) to allow informative spatial analyses, then data for these species were not considered. Grouped data on one or more bars were analysed for the carabids *B. decorum*, *B. punctulatum*, *B. tibiale*, *C. collaris* and

Agonum muelleri (Herbst, 1784), and the elaterid *F. maritimus*. Grouped data for the more abundant species were also considered for comparative purposes.

5.2.4 Temporal distribution of sampling

Trap lids were removed in the sequence: Bar 3d, Bar 3 and Bar 2, and traps were emptied in the same sequence the following day (except traps opened on 17/7/03 see below), so were open for ~24 hours over the day and night. Sampling took place on 16-17/6/03, 23-24/6/03, 28-29/6/03, 3-4/7/03, 17-19/7/03, 22-23/7/03, 27-28/7/03 and 1-2/8/03. Heavy rain on 17/7/03, combined with very large catches of beetles in this, and the mark-recapture study meant that traps were only emptied on time (18/7/03) on Bar 2, on Bar 3d and Bar 3, traps remained open for 2 days. On Bar 3 there was insufficient time to count the beetles from all traps so these results are not presented.

5.2.5 SADIE analyses

SADIE (see Perry 1995; Perry 1998; Holland *et al.* 1999; Perry *et al.* 1999; Perry and Dixon 2002; Perry 2003) relies on the concept of distance to regularity (D), the smallest possible value of the total distance that individuals must move so that each sampling unit has the same number of individuals in it. For example, consider 5 pitfall traps equally spaced along a 4m line, in which the counts of a particular species of beetle are 10, 8, 2, 0 and 0. SADIE uses a transportation algorithm (Kennington and Helgason 1980) to calculate the minimum number of moves required so that they are arranged as regularly as possible along the line, in this case 4, 4, 4, 4 and 4 (D = 28m). SADIE tests if the sample D is unusually high or low using simulations, whereby a number of counts are randomly redistributed between sampling units and D_{rand} is calculated for each, for example 6, 8, 4, 2 and 0 could be one randomisation (D_{rand} = 18m). The average value of D_{rand}, denoted E_a is used to calculate the index of aggregation (I_a) from the ratio of the observed (D), to expected (E_a) distance to regularity:

$$I_a = D / E_a$$

For the example 10, 8, 2, 0 and 0, E_a (5967 randomisations) was 15.99m, so I_a was 1.75. Values of $I_a = 1$, indicate random distribution; values of $I_a < 1$, indicate a sample more regularly distributed than random; and values of $I_a > 1$, indicate samples less regularly distributed (aggregated) than random. So the example given can be considered aggregated. SADIE calculates the associated probability (P_a) that I_a is significantly more aggregated than random from a comparison of D with the frequency distribution of the simulated D_{rand} (Besag and Diggle 1977). In this example only 224 of the 5967 values of D_{rand} are more aggregated than D, so $P_a = 224 / 5967 = 0.038$. So therefore the data is significantly aggregated at the 5% level.

This method was extended by Perry *et al.* (1999) to quantify and easily visualise the degree to which the count at each sample unit contributes towards overall clustering and to compare the spatial distribution of different data sets. The methodology uses information on the strength (magnitude and distance) of individual outflows (Y_i) and inflows ($-Y_j$) during the transportation of individuals during movements to regularity. Randomisations are used to calculate the expected value of the average flow strength for observed individual counts (e.g. 8 in the above example), ${}_cY$, and the expected value of the average flow strength for an individual sampling position (e.g. 2m along the line in the above example), ${}_iY$. The average value of ${}_cY$ over all the counts (or ${}_\mathrm{i}Y$, they are the same) is denoted ${}_oY$. A standardised, dimensionless index of clustering (v_i) for outflows can then be calculated using:

$$v_i = Y_i \, {}_oY / {}_iY \, {}_cY$$

Clustering of inflows (v_j) is calculated in the same way, except that a negative sign is used. The indices v_i and v_j indicate the degree to which an individual sample point contributes to clustering into a patch or gap respectively. Large values of v_i (>1.5), show that the point is part of a patch, small values of v_j (<-1.5), show that the point is part of a gap. The mean values of all outflows ($\bar{v}_i$) and inflows ($\bar{v}_j$) can also be compared against data from randomisations, to produce associated probabilities (*P*) of departure from randomness. These tests based on clustering indices can be more powerful at detecting departure from randomness than the overall clustering index (I_a), especially when there are large counts around the boundaries of the sample area (Perry *et al.* 1999).

SADIE can also be used to measure the spatial association of two data sets sampled in exactly the same locations (Perry and Dixon 2002). This allows investigation of the way the spatial distribution of a species relates to environmental variables and to the distribution of other species, and how a species' spatial distribution changes over time. The programme tests for spatial association, or disassociation in the clustering indices (v_i and v_j) of the two data sets to produce a measure of local association (χ_p) for each sampling point, and a mean of these values for overall spatial association, X. The significance of X is tested against values of X_{rand}, generated from a randomisation test and estimates critical values for χ_p. Critical values for X and χ_p are adjusted for the effects of autocorrelation using a Dutilleul adjustment (Clifford *et al.* 1989; Dutilleul 1993) of sample size.

In this study, the maximum number of randomisations (5967 for initial analyses, and 9999 for tests of association) and random integer seeds were used in all analyses. All analyses met the recommendation of Holland *et al.* (1999) by containing at least 36 units.

5.3 Results

5.3.1 Environmental variables

Bar 3 was a point bar situated at the confluence of the Carno and Severn (Figures 5.2 and 5.3), and was the largest bar studied. Although the size distribution of sediments differed across the bar (Figure 5.3) no distinct sediment zones could be identified. As on the other bars, sediments were bimodal with a sand matrix. On this bar the larger clasts were relatively fine, mainly between –3.5 to –6 phi and sediments were mainly matrix supported. Vegetation was distributed in two areas: along the water's edge and in a long strip towards the top of the bar. At the back of the bar (northern edge) there was a smooth altitudinal transition to heavily vegetated, overgrown gravels. SADIE statistics for the measured environmental variables on each bar are shown in Table 5.1.

Table 5.1 SADIE statistics for the spatial distribution of measured environmental variables on Bars 3, 2 and 3d. The indices of aggregation, I_a, illustrate the overall degree of clustering ($I_a = 1$ indicates randomly arranged counts, $I_a > 1$ indicates aggregation of counts into clusters). The means of the standardised clustering indices over inflows ($\bar{v}_j$) and outflows ($\bar{v}_i$) indicate the presence of clustering into gaps, and clustering into patches respectively. The associated probabilities of departure from randomness for each statistic (P_a, P_j and P_i) are shown. Numbers in bold are significant at the 5% level.

	Bar	I_a	P_a	v_j	P_j	v_i	P_i
Vegetation trap within	3	1.143	0.1748	-1.139	0.1755	1.092	0.2298
Densest vegetation <1 traps distance away	3	**1.623**	**0.0107**	**-1.488**	**0.0196**	**1.628**	**0.0072**
Distance from water (m)	3	**2.529**	**0.0002**	**-2.451**	**<0.0001**	**2.008**	**0.0003**
Height above lowest trap (cm)	3	**2.513**	**0.0002**	**-2.484**	**<0.0001**	**1.844**	**0.0012**
Vegetation trap within	2	**1.856**	**0.0144**	-1.847	0.1740	**1.856**	**0.0149**
Densest vegetation <1 traps distance away	2	**3.577**	**0.0002**	**-3.564**	**<0.0001**	**3.800**	**<0.0001**
Distance from water (m)	2	**1.891**	**0.0121**	**-1.765**	**0.0226**	**1.590**	**0.0401**
Height above lowest trap (cm)	2	**3.044**	**0.0002**	**-2.895**	**<0.0001**	**2.985**	**<0.0001**
Sediment type	2	**2.039**	**0.0050**	**-2.004**	**0.0062**	**2.085**	**0.0032**
Vegetation trap within	3d	**3.811**	**0.0002**	**-4.058**	**<0.0001**	**4.006**	**<0.0001**
Densest vegetation <1 traps distance away	3d	**2.972**	**0.0002**	**-2.716**	**<0.0001**	**2.851**	**<0.0001**
Distance from water (m)	3d	**2.022**	**0.0047**	**-1.875**	**0.0072**	**1.746**	**0.0268**
Height above lowest trap (cm)	3d	1.264	0.1369	-1.133	0.2204	1.325	0.1046

Bar 2 was a narrow point bar that was comparatively heavily trampled by cattle, particularly across the back (southern edge) of the bar where cattle used the low cliff to scratch; and the upstream tip of the bar where cattle descended to drink (Figures 5.2 and 5.4). There was comparatively little vegetation except for a few patches towards the upstream end of the bar, and the river bank running along the back of the bar sharply separated the ERS from the adjoining pasture. On Bar 2 there were well-defined areas of differing sediment type. Situated along the bar centre from upstream to downstream ran an area of increasingly fine, matrix supported, clast dominated sediments. Upstream, and to either side of this zone were areas of much finer sediment with only a few larger clasts dotted on the surface.

In comparison with the other two bars, Bar 3d was a within-channel bar of much lower relief, which consequentially would be inundated much more often (Figures 5.2 and 5.5). The sediment size distribution was fairly uniformly coarse across the whole bar, and sediments were clast supported. Vegetation density was very low across the majority of the bar, but high along the narrow upstream end. There was a dense area of vegetation at the back (northern edge) of the bar growing on frequently inundated overgrown sediments.

5.3.2 Weather conditions and water level

Figure 5.6 summarises changes in weather conditions and the timing of flow pulses from May to the start of August. June was generally warm and dry and when there was quite heavy rain at the end of the month there was no resulting flow pulse. The weather during the first sampling event (16-17/6/03) was warm and dry and followed a long period of relatively little rain. There was a little rain in the second sampling period (23-24/6/03), but generally the weather was still warm and dry, whilst the third sampling period (28-29/6/03) was much wetter and followed three days of rainfall. The fourth sampling period (3-4/7/03) was cooler and dry, but fairly closely followed the wet period at the end of June.

The entire latter half of July could be classified as warm and wet, with rain on almost all days and three distinct flow pulses. The first was during the hot and dry period around mid July and was due to water released from the reservoir. The second and third pulses were due to rainfall, the second pulse following a fairly extreme summer rainfall event, which, relative to the other pulses was very large and very nearly completely inundated Bar 3d. The fifth sampling period (17-19/7/03) although warm, coincided with the first flood pulse, and the water level rose rapidly in response to some very heavy rainfall on 17/7/03. The sixth (22-23/7/03) and seventh (22-23/7/03) sampling periods were wet and cool. The final sampling period was warmer and dry, but closely followed several days of rainfall.

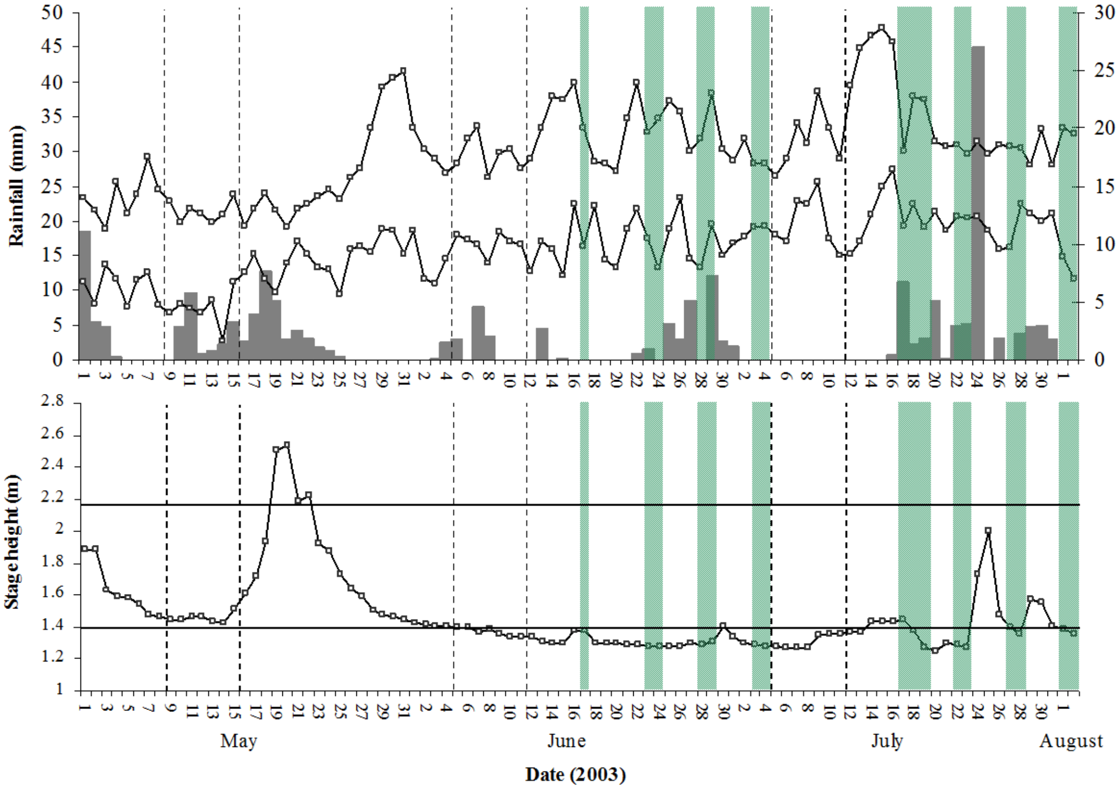


Figure 5.6 Weather and stage data over the study period. On the top section of the diagram the dark grey bars are the total daily rainfall, the upper and lower lines are daily maximum and minimum temperatures respectively. The lower section shows the stage height at Caersws, the lower horizontal line is the height at which edge pitfalls started to flood (a flow pulse) and the upper horizontal line represents the approximate level at which all bars were inundated. The dashed vertical lines show periods in which beetles were marked, and the light grey bars show recapture periods. All data cover the period from 9am on the date displayed until 9am the following day.

5.3.3 Information from the 2003 mark-recapture study (Chapter 7)

The presence of individually identifiable *B. atrocaeruleum* on the study bars provided supplementary information when considering the distribution of this species. There were, however, dangers in using the movements of marked beetles to interpret the distribution of unmarked beetles because marked beetles may respond to distributional cues in a different way. Although marked and unmarked *B. atrocaeruleum* showed no discernible difference in behaviour during handling or after they were released, it was considered necessary to test for differences in their spatial distribution. The relatively low number of marked individuals prohibited comparison on individual sampling days, so the distribution of marked *B. atrocaeruleum* and unmarked *B. atrocaeruleum* was compared over all sampling occasions. The spatial distribution of marked and unmarked *B. atrocaeruleum* was shown to be similar on all study bars (Figure 5.7) and the distributions were found to show strong, and significantly positive spatial associations (Table 5.2). On the strength of this evidence, the data for marked and unmarked *B. atrocaeruleum* were combined and analysed together. It was also considered reasonable to use information on the movements of marked *B. atrocaeruleum* to help interpret the spatial distribution of unmarked *B. atrocaeruleum*.

Individual marked *B. atrocaeruleum* were shown to range widely over all bars between sampling events. Figure 5.8 illustrates all known movements on Bar 3d as an example. The data show that individuals often changed their within-patch position on multiple occasions, sometimes using short movements and sometimes using long movements. This demonstrates that, at least over the time period between sampling, *B. atrocaeruleum* were capable of moving to any part of the bar, and therefore their distributions were not constrained by their rate of movement. They could potentially respond to distributional cues and position themselves in the most suitable habitat, wherever it was on the bar.

Marked *B. atrocaeruleum* were also used to evaluate the degree of error in the observed spatial distributions due to capture of individuals more than once on the same sampling occasion. Averaged over all bars and dates only 0.55% of the 687 individually identifiable marked *B. atrocaeruleum* were captured more than once on the same sampling occasion. Assuming that marked and unmarked *B. atrocaeruleum* have an equal chance of being recaptured more than once then the amount of error due to multiple recaptures on the same sampling occasion was negligible.

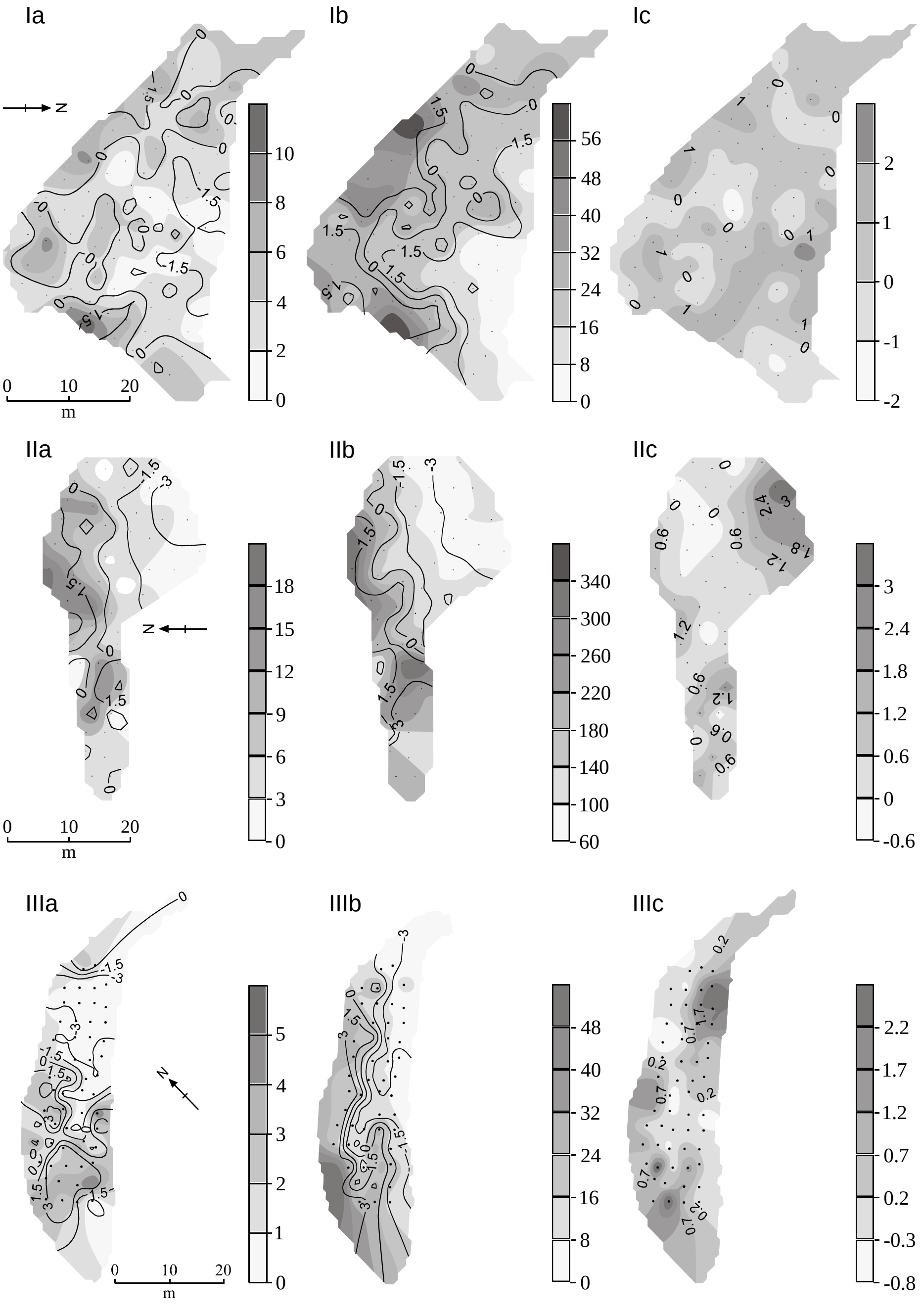


Figure 5.7 Microdistribution and local clustering of marked and unmarked *B. atrocaeruleum* over all sampling periods. In Ia, Ib, IIa, IIb, IIIa and IIIb the shading represents the interpolated numbers captured (note different scales); and the contours represent interpolated SADIE local clustering indices (v_i and v_j), where strong clustering into patches is indicated by areas >1.5, and strong clustering into gaps is indicated by areas <-1.5 (Holland *et al.* 1999). Ia, IIa, IIIa show the position of marked *B. atrocaeruleum* on Bars 3, 3d, and 2 respectively, and Ib, IIb, IIIb show the position of unmarked *B. atrocaeruleum* on Bars 3, 3d, and 2 respectively. Ic, IIc and IIIc show the degree of local association between the marked and unmarked *B. atrocaeruleum* on Bars 3, 3d and 2 respectively, where positive values represent positive association and negative values represent negative association (see scale bar). The position of traps is represented by the black dots.

Table 5.2 SADIE statistics describing and comparing the distribution of marked and unmarked *B. atrocaeruleum* on Bars 3, 3d and 2 (X = measure of overall association between the distribution of marked and unmarked beetles, P_X = Dutilleul adjusted probability level, see Table 5.1 for definition of other terms). Significant at a 5% level are highlighted in bold.

	Bar	Total count	I_a	P_a	v_j	P_j	v_i	P_i	X	P_X
Marked	3	329	1.236	0.1099	-1.222	0.2100	1.256	0.0863	**0.3195**	**0.0009**
Unmarked	3	2816	**1.983**	**0.0007**	**-1.545**	**0.0102**	**1.910**	**0.0007**	**-**	**-**
Marked	3d	403	**1.859**	**0.0075**	**-1.602**	**0.0271**	**1.731**	**0.0131**	**0.6670**	**<0.0001**
Unmarked	3d	9057	**2.743**	**0.0002**	**-2.371**	**0.0003**	**3.047**	**<0.0001**	**-**	**-**
Marked	2	84	**2.951**	**0.0002**	**-3.066**	**<0.0001**	**3.381**	**<0.0001**	**0.5136**	**0.0001**
Unmarked	2	932	**2.795**	**0.0002**	**-2.527**	**0.0005**	**3.221**	**<0.0001**	**-**	**-**

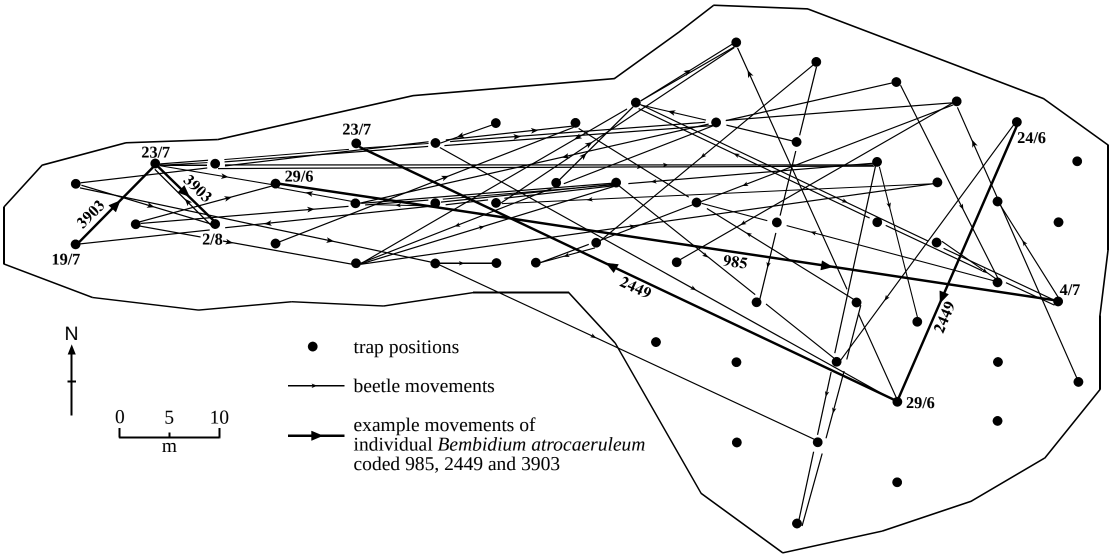


Figure 5.8 Known intra-patch movements of marked *B. atrocaeruleum* on Bar 3d. Example movements by three numbered individual beetles are highlighted in bold.

5.3.4 Beetle distribution on Bar 3

5.3.4.1 Spatial distribution of species

Zorochros minimus showed significant spatial patchiness on Bar 3 over all of the study dates, as indicated by significant values of I_a, v_j, and v_i (Table 5.3). On 17/6/03 there were four, nearly contiguous patches (local clustering into patches v_i >1.5) situated around the water's edge (south and eastern edges of the bar), whilst there was a large gap (local clustering into gaps $v_j > -1.5$) generally situated away from the water (northern part of the bar) (Figure 5.9). This pattern was markedly different from that on all other study dates, upon which patches were situated on the upper (northern) section of the bar. However, only the distributions on 17/6/03 and 23/7/03 were actually significantly negatively correlated with one another (Table 5.4). There was some indication that the distribution on 24/6/03 was transitional to that on 17/6/03 and the 29/6/03 (Figure 5.9).

Bembidion atrocaeruleum showed significant spatial patchiness on 17/6/03, 24/6/03, 4/7/03, 23/7/03, 28/7/03 and for the grouped data for all dates (Table 5.3). In contrast to *Z. minimus* the distributional pattern of *B. atrocaeruleum* distinctly changed on several occasions (Figure 5.10). On 17/6/03 there was a distinct patch situated at the southern foot of Bar 3 around the area where the Carno and Severn meet (Figures 5.2 and 5.10) and there were very few individuals in the upper portion of the bar. The distribution was considerably different on 24/6/03, when the main patches were situated in the mid to upper section of the bar, away from the water's edge (Figure 5.10). The distribution was again different on 4/7/03 when there were significant patches at the eastern and western ends of the bar at the water's edge. On 23/7/03 there were three significant patches, all situated away from the water's edge, whilst on 28/7/03 there was a significant patch running around the water's edge (Figure 5.10). Although all these distributions were somewhat different from each other, only 24/6/03 and 23/7/03 were significantly negatively correlated (Table 5.4). Significant positive correlations were shown between adjacent sampling dates in July; and between 4/7/03 and 2/8/03, and 17/6/03 and 28/7/03 (Table 5.4). These differences in distribution between dates demonstrate the danger of using data from captures over a long period without information on the temporal change in distribution. Based solely on the grouped data, the investigator would conclude that *B.*

atrocaeruleum were generally distributed at the water's edge, when in fact this was not the case.

The grouped data for *B. punctulatum*, *B. decorum*, *F. maritimus, C. collaris,* and *A. muelleri* were all found to have had significantly patchy distributions. *Bembidion punctulatum* and *B. decorum* were mainly distributed along the water's edge, especially along the Carno (Figures 5.2 and 5.11). *Fleutiauxellus maritimus* in contrast, was mainly distributed away from the water's edge, in one fairly large patch just west of the bar centre. *Clivina collaris* was mainly grouped along the back (northern edge) of the bar, and in a small area at the water's edge in the north-eastern corner (Figure 5.11). *Agonum muelleri* were mainly found in one fairly small area in the bars north-eastern corner.

Table 5.3 SADIE statistics for the spatial distribution of species grouped over all dates (*Bembidion atrocaeruleum*, *B. punctulatum*, *B. decorum*, *Zorochros minimus*, *Fleutiauxellus maritimus*, *Clivina collaris* and *Agonum muelleri*), and on individual sampling occasions (*Bembidion atrocaeruleum* and *Zorochros minimus*) for Bar 3 (see Table 5.1 for definitions of terms used).

Species	Date	Total count	I_a	P_a	v_j	P_j	v_i	P_i
B. atrocaeruleum	17/06/2003	332	**1.956**	**0.0010**	**-1.720**	**0.0047**	**2.058**	**<0.0001**
B. atrocaeruleum	24/06/2003	491	**1.496**	**0.0206**	**-1.426**	**0.0293**	**1.359**	**0.0431**
B. atrocaeruleum	29/06/2003	543	1.101	0.2336	-1.043	0.3280	1.125	0.2021
B. atrocaeruleum	04/07/2003	344	**1.452**	**0.0282**	**-1.415**	**0.0347**	**1.423**	**0.0292**
B. atrocaeruleum	23/07/2003	426	**1.466**	**0.0245**	-1.274	0.0801	**1.487**	**0.0193**
B. atrocaeruleum	28/07/2003	626	**2.165**	**0.0002**	**-1.924**	**0.0012**	**2.288**	**<0.0001**
B. atrocaeruleum	02/08/2003	383	1.245	0.1059	-1.054	0.3042	1.095	0.2338
All *B. atrocaeruleum*	All dates	3145	**1.974**	**0.0002**	**-1.591**	**0.0116**	**1.884**	**0.0010**
Z. minimus	17/06/2003	278	**2.112**	**0.0002**	**-1.822**	**0.0039**	**1.807**	**0.0025**
Z. minimus	24/06/2003	431	**2.460**	**0.0002**	**-2.425**	**<0.0001**	**2.185**	**<0.0001**
Z. minimus	29/06/2003	774	**2.672**	**0.0002**	**-2.660**	**<0.0001**	**2.535**	**<0.0001**
Z. minimus	04/07/2003	401	**2.407**	**0.0002**	**-2.347**	**<0.0001**	**2.289**	**<0.0001**
Z. minimus	23/07/2003	505	**1.886**	**0.0010**	**-1.843**	**0.0010**	**1.729**	**0.0035**
Z. minimus	28/07/2003	528	**2.588**	**0.0002**	**-2.485**	**<0.0001**	**2.329**	**<0.0001**
Z. minimus	02/08/2003	374	**2.329**	**0.0002**	**-2.114**	**0.0002**	**2.192**	**0.0003**
All *Z. minimus*	All dates	3290	**2.863**	**0.0002**	**-2.715**	**<0.0001**	**2.623**	**<0.0001**
All *B. punctulatum*	All dates	172	**2.041**	**0.0007**	**-1.978**	**0.0007**	**2.134**	**0.0003**
All *B. decorum*	All dates	186	**1.896**	**0.0018**	**-1.691**	**0.0050**	**1.949**	**0.0015**
All *F. maritimus*	All dates	108	**2.172**	**0.0002**	**-2.083**	**0.0002**	**2.189**	**<0.0001**
All *C. collaris*	All dates	193	**2.122**	**0.0002**	**-1.904**	**0.0012**	**1.931**	**0.0008**
All *A. muelleri*	All dates	85	**2.453**	**0.0002**	**-2.437**	**<0.0001**	**2.194**	**<0.0001**

Table 5.4 SADIE spatial associations between species (*B. atrocaeruleum*, *B. punctulatum*, *B. decorum*, *F. maritimus*, *Z. minimus*, *C. collaris*, and *A. muelleri*) on individual dates (17/6/03, 24/6/03, 29/6/03, 4/7/03, 23/7/03, 28/7/03, 2/8/03), or across all dates (-), and each other for Bar 3 (see Table 5.2 for a definition of the notation used). Significant (5% level in two-tailed test) positive associations are highlighted in bold, significant negative associations are underlined.

		Am -	Cc -	Fm -	Bd -	Bp -	Zm -	Zm2/8	Zm28/7	Zm23/7	Zm4/7	Zm29/6	Zm24/6	Zm17/6	Ba -	Ba2/8	Ba28/7	Ba23/7	Ba4/7	Ba29/6	Ba24/6
Ba17/6	X	-0.1930	-0.4406	0.1472	**0.4671**	**0.5201**	-0.5441	-0.5424	-0.4615	-0.5058	-0.5614	-0.5402	-0.4024	**0.3464**	**0.4962**	0.1839	**0.6025**	0.0691	-0.1030	0.1893	-0.0941
	P_X	0.9645	>0.9999	0.0868	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	0.9998	**0.0005**	**<0.0001**	0.0425	**<0.0001**	0.2664	0.8279	0.0375	0.8048
Ba24/6	X	-0.2474	-0.0913	**0.2876**	-0.2935	-0.0253	0.1037	0.0934	0.1431	0.0602	-0.0237	0.0233	0.1096	-0.1698	0.0185	-0.1642	-0.0877	-0.0852	-0.2562	0.1861	
	P_X	0.9825	0.7926	**0.0050**	0.9973	0.6029	0.1605	0.1943	0.0879	0.2834	0.5861	0.4190	0.1593	0.9479	0.4326	0.9355	0.7898	0.7954	0.9839	0.0399	
Ba29/6	X	-0.1540	-0.0412	0.0465	0.0573	0.0444	0.0234	-0.0788	-0.0391	-0.1200	-0.0272	-0.0530	-0.0151	0.1799	**0.3083**	0.1256	0.0428	0.0142	0.0073		
	P_X	0.5498	0.6361	0.3402	0.2986	0.3440	0.4062	0.7575	0.6346	0.8654	0.6002	0.6858	0.5565	0.0485	**0.0014**	0.1314	0.3508	0.4521	0.4793		
Ba4/7	X	-0.1312	0.0247	0.0745	0.1910	-0.0331	-0.1580	-0.1118	-0.2367	-0.1811	-0.0016	-0.1536	-0.1596	-0.0821	**0.3365**	**0.3248**	0.1869	**0.3223**			
	P_X	0.8714	0.4137	0.2534	0.0393	0.6016	0.9263	0.8565	0.9874	0.9461	0.5125	0.9143	0.9351	0.7812	**0.0010**	**0.0006**	0.0430	**0.0006**			
Ba23/7	X	-0.1217	-0.0940	0.1868	0.1159	0.0724	-0.2209	-0.0993	-0.2140	-0.1457	-0.1077	-0.1754	-0.2603	-0.2390	**0.2368**	0.0244	**0.2538**				
	P_X	0.8731	0.7898	0.0390	0.1369	0.2450	0.9825	0.8160	0.9782	0.9166	0.8391	0.9535	0.9913	0.9855	**0.0130**	0.4169	**0.0105**				
Ba28/7	X	-0.4906	-0.5646	**0.3131**	**0.6767**	**0.6916**	-0.7080	-0.6689	-0.6227	-0.7241	-0.6265	-0.6529	-0.5559	**0.2872**	**0.6956**	**0.2196**					
	P_X	>0.9999	>0.9999	**0.0029**	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	**0.0037**	**<0.0001**	**0.0194**					
Ba2/8	X	-0.0201	-0.0766	-0.0442	**0.3019**	0.1570	-0.1784	-0.1076	-0.1425	-0.1826	-0.1662	-0.2589	-0.1419	0.2165	**0.4442**						
	P_X	0.5785	0.7572	0.6549	**0.0024**	0.0702	0.9470	0.8362	0.8975	0.9508	0.9425	0.9938	0.9109	0.0267	**<0.0001**						
Ba -	X	-0.4490	-0.4360	**0.2950**	**0.4852**	**0.4912**	-0.5513	-0.4745	-0.4927	-0.5510	-0.4729	-0.5485	-0.4486	0.2173							
	P_X	>0.9999	>0.9999	**0.0018**	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	>0.9999	0.9998	0.0267							
Zm17/6	X	0.0121	-0.3409	-0.1318	**0.3116**	**0.2399**	-0.0821	-0.1202	-0.1576	-0.2938	-0.1701	-0.2500	-0.0010								
	P_X	0.4502	0.9991	0.8894	**0.0018**	**0.0134**	0.7618	0.8617	0.9183	0.9959	0.9319	0.5851	0.4991								
Zm24/6	X	**0.6031**	**0.3412**	-0.4754	-0.5535	-0.5651	**0.6871**	**0.5679**	**0.5954**	**0.4918**	**0.5678**	**0.6526**									
	P_X	**<0.0001**	**0.0013**	>0.9999	>0.9999	>0.9999	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**									
Zm29/6	X	**0.6222**	**0.5780**	-0.5014	-0.5460	-0.6582	**0.8533**	**0.6908**	**0.6983**	**0.6629**	**0.7813**										
	P_X	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**										
Zm4/7	X	**0.6273**	**0.5970**	-0.4322	-0.5099	-0.6874	**0.7585**	**0.7353**	**0.7066**	**0.6999**											
	P_X	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**											
Zm23/7	X	**0.5837**	**0.5740**	-0.3321	-0.5065	-0.7098	**0.7817**	**0.7084**	**0.7316**												
	P_X	**<0.0001**	**<0.0001**	0.9987	>0.9999	>0.9999	**<0.0001**	**<0.0001**	**<0.0001**												
Zm28/7	X	**0.6611**	**0.5444**	-0.4649	-0.5724	-0.7315	**0.8345**	**0.7548**													
	P_X	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999	**<0.0001**	**<0.0001**													
Zm2/8	X	**0.5850**	**0.5064**	-0.4128	-0.5591	-0.7223	**0.8196**														
	P_X	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999	**<0.0001**														
Zm -	X	**0.6706**	**0.5693**	-0.4772	-0.5808	-0.7884															
	P_X	**<0.0001**	**<0.0001**	>0.9999	>0.9999	>0.9999															
Bp -	X	-0.5921	-0.4526	**0.3818**	**0.6358**																
	P_X	>0.9999	>0.9999	**0.0001**	**<0.0001**																
Bd -	X	-0.3457	-0.4487	0.1204																	
	P_X	0.9996	>0.9999	0.1305																	
Fm -	X	-0.6190	-0.3200																		
	P_X	>0.9999	0.9985																		
Cc -	X	**0.5202**																			
	P_X	**<0.0001**																			

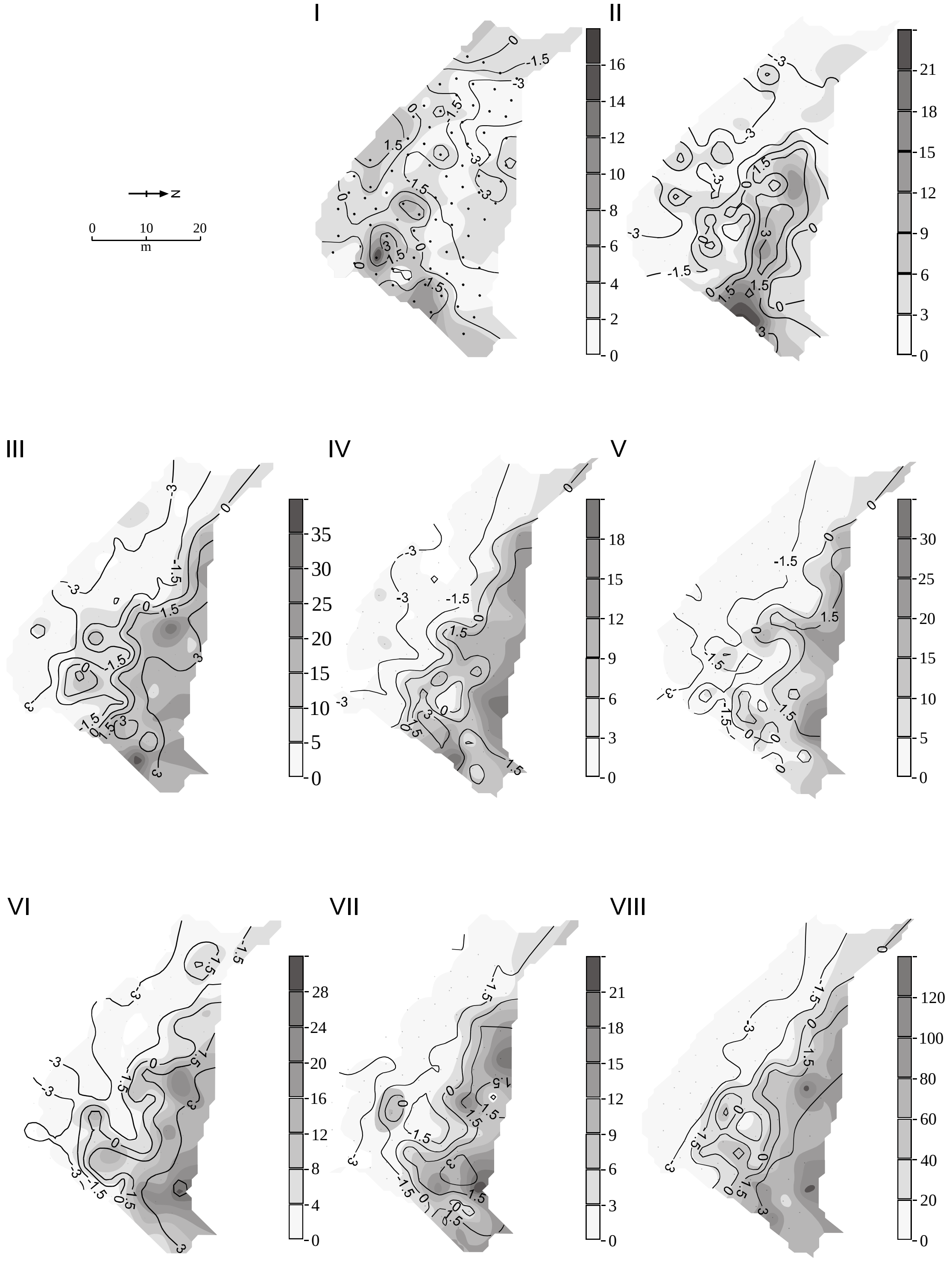


Figure 5.9 Temporal changes in the distribution and local clustering of *Z. minimus* on Bar 3. I = 17/6/03, II = 24/6/03, III = 29/6/03, IV = 4/7/03, V = 23/7/03, VI = 28/7/03, VII = 2/8/03 and VIII = data grouped across all dates (see Figure 5.7 for an explanation of the diagrams).

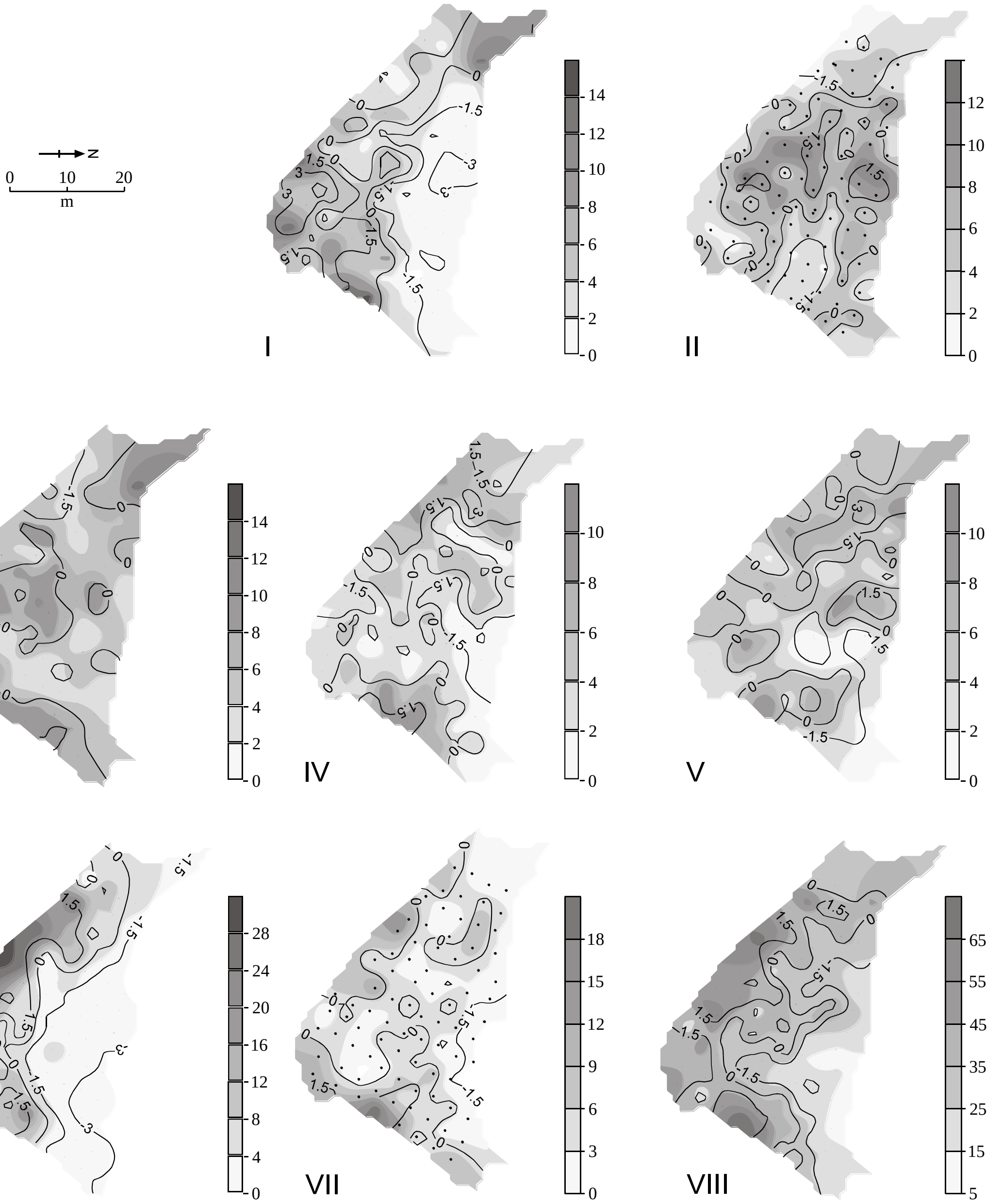


Figure 5.10 Temporal changes in the distribution and local clustering of *B. atrocaeruleum* on Bar 3. I = 17/6/03, II = 24/6/03, III = 29/6/03, IV = 4/7/03, V = 23/7/03, VI = 28/7/03, VII = 2/8/03 and VIII = data grouped across all dates (see Figure 5.7 for an explanation of the diagrams).

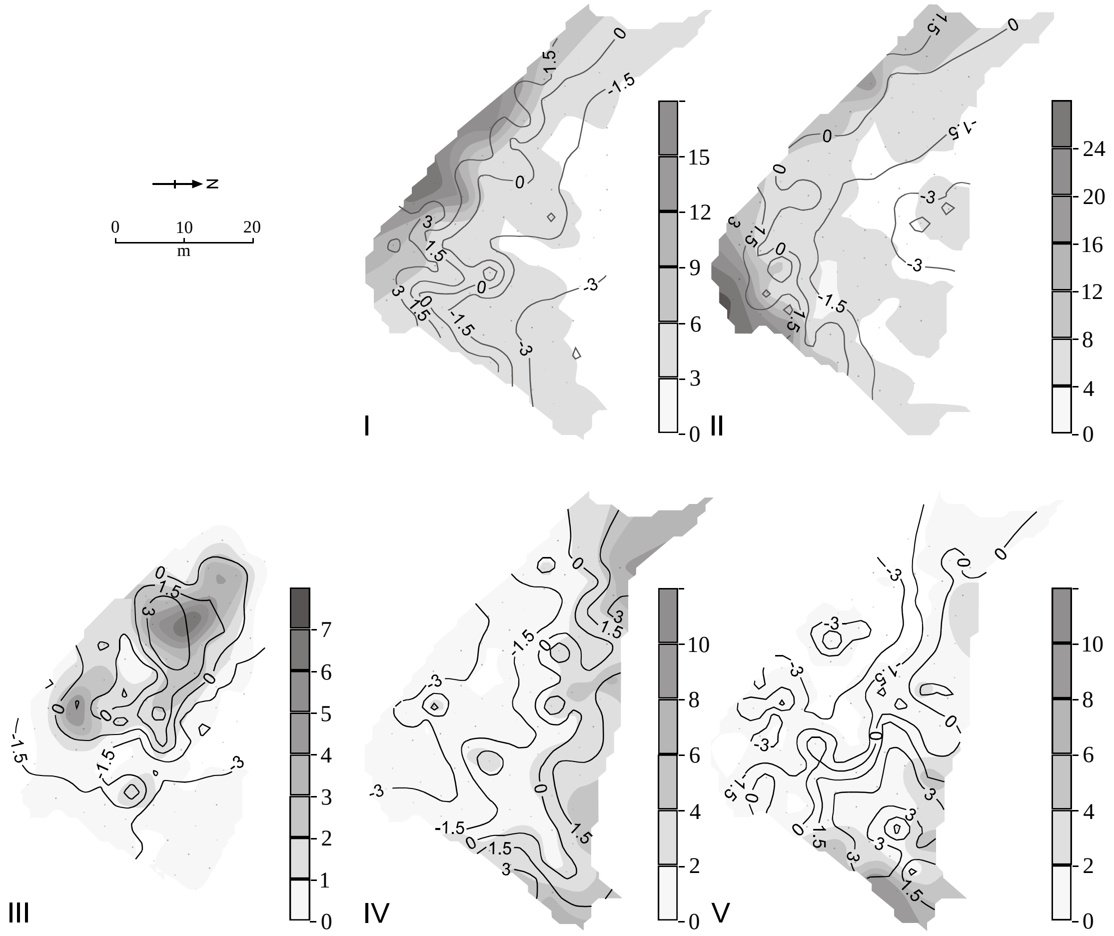


Figure 5.11 The distribution and local clustering of (I) *B. punctulatum*, (II) *B. decorum*, (III) *F. maritimus*, (IV) *C. collaris*, and (IV) *A. muelleri* across all sampling dates on Bar 3 (see Figure 5.7 for an explanation of the diagrams).

5.3.4.2 Spatial association with environmental variables

On 17/6/03 *Z. minimus* showed significant negative spatial associations with 'distance from water' (it was mainly close to the water) and elevation (it was mainly at low elevations). For the remaining sampling dates *Z. minimus* showed significant positive spatial associations with 'distance from water' and elevation (Table 5.5). On Bar 3, (1) the 'distance from water' and elevation are significantly positively correlated, and (2) 'vegetation near' and 'vegetation within' are positively correlated. Groups (1) and (2) are negatively correlated with each other, although the correlation with 'vegetation near' is not quite significant. This co-variation of environmental variables makes it difficult to evaluate

Table 5.5 SADIE spatial associations between species (*B. atrocaeruleum*, *B. punctulatum*, *B. decorum*, *F. maritimus*, *Z. minimus*, *C. collaris*, and *A. muelleri*) on individual dates (17/6/03, 24/6/03, 29/6/03, 4/7/03, 23/7/03, 28/7/03, 2/8/03), or across all dates (-), and measured environmental variables for Bar 3 (see Table 5.2 for a definition of the notation used). Significant (5% level in two-tailed test) positive associations are highlighted in bold, significant negative associations are underlined. Spatial associations between environmental variables are also shown.

		Vegetation within	Vegetation near	Distance from water	Elevation
Ba17/6	X	0.1058	0.0308	-0.5425	-0.5165
	P_X	0.1561	0.3841	>0.9999	>0.9999
Ba24/6	X	-0.1559	-0.2731	**0.3096**	**0.2921**
	P_X	0.9307	0.9937	**0.0020**	**0.0025**
Ba29/6	X	0.0072	0.0569	-0.1053	-0.1109
	P_X	0.4708	0.2998	0.7987	0.8301
Ba4/7	X	0.1805	0.0825	-0.2488	-0.2580
	P_X	0.0426	0.2122	0.9912	0.9940
Ba23/7	X	0.0033	-0.1345	-0.0577	-0.0501
	P_X	0.4937	0.8747	0.7016	0.6791
Ba28/7	X	**0.3276**	-0.1016	-0.5681	-0.6725
	P_X	**0.0009**	0.8175	>0.9999	>0.9999
Ba2/8	X	**0.2205**	0.1209	-0.3074	-0.4090
	P_X	**0.0191**	0.1457	0.9982	>0.9999
Ba -	X	**0.2992**	-0.0655	-0.4590	-0.5959
	P_X	**0.0061**	0.7127	0.9998	>0.9999
Bp -	X	**0.2187**	-0.2138	-0.4173	-0.5556
	P_X	**0.0189**	0.9764	>0.9999	>0.9999
Bd -	X	**0.3955**	0.1501	-0.6755	-0.7254
	P_X	**0.0001**	0.0788	>0.9999	>0.9999
Fm -	X	-0.1780	-0.5433	0.1032	-0.0219
	P_X	0.9508	>0.9999	0.1648	0.5821
Zm17/6	X	0.1379	0.1961	-0.4853	-0.4480
	P_X	0.1113	0.0426	>0.9999	0.9998
Zm24/6	X	-0.0744	0.2054	**0.2892**	**0.3464**
	P_X	0.7642	0.0251	**0.0031**	**0.0008**
Zm29/6	X	-0.1324	**0.3414**	**0.4124**	**0.5146**
	P_X	0.8896	**0.0013**	**0.0001**	**<0.0001**
Zm4/7	X	-0.0316	**0.4148**	**0.4050**	**0.4748**
	P_X	0.6145	**<0.0001**	**0.0001**	**<0.0001**
Zm23/7	X	-0.1841	**0.2541**	**0.5142**	**0.5633**
	P_X	0.9557	**0.0076**	**<0.0001**	**<0.0001**
Zm28/7	X	-0.0524	**0.3823**	**0.3517**	**0.4522**
	P_X	0.6778	**0.0003**	**0.0005**	**<0.0001**
Zm2/8	X	-0.0734	**0.2743**	**0.3922**	**0.4858**
	P_X	0.7359	**0.0086**	**0.0004**	**<0.0001**
Zm -	X	-0.0864	**0.3938**	**0.4032**	**0.5154**
	P_X	0.7942	**0.0002**	**0.0001**	**<0.0001**
Cc -	X	-0.0151	**0.3529**	**0.4139**	**0.3992**
	P_X	0.5585	**0.0003**	**0.0001**	**0.0001**
Am-	X	-0.0016	**0.5056**	0.1474	**0.2136**
	P_X	0.5126	**<0.0001**	0.0866	**0.021**
Elev	X	-0.5086	-0.1846	**0.8310**	
	P_X	>0.9999	0.9371	**<0.0001**	
Distw	X	-0.3928	-0.2262		
	P_X	0.9993	0.9610		
Vegn	X	**0.3659**			
	P_X	**0.0023**			

which (if any) variable is driving spatial distribution. Significant spatial association between a species and one environmental variable may be an artefact; a different environmental variable may be driving the distribution. The distribution of *Z. minimus* from 29/6/03 to 2/8/03 was also significantly positively associated with ‘vegetation near’, although it is possible that this might have been an artefact of the vegetation along the back edge of Bar 3 coinciding with the area of greatest elevation (Figure 5.3).

Agonum muelleri and *C. collaris* were both significantly positively associated with ‘vegetation near’ and elevation, but only *C. collaris* was positively associated with ‘distance from water’ (Table 5.5). *Fleutiauxellus maritimus* only showed significant negative association with ‘vegetation near’. The environmental spatial associations for *B. atrocaeruleum* changed over time, as might be expected given the species’ changing distribution. On 24/6/03 the species was significantly negatively associated with ‘vegetation near’ and significantly associated with ‘distance from water’ and elevation, this was the only occasion when this was the case. On four out of the six remaining dates *B. atrocaeruleum* was significantly negatively spatially associated with ‘distance from water’ and elevation, and on 28/7/03 and 2/8/03 there was also a significant positive association with ‘vegetation within’. *Bembidion punctulatum* and *B. decorum* were both significantly negatively associated with ‘distance from water’ and elevation, and positively associated with vegetation within.

5.3.4.3 Spatial association between species

Zorochros minimus was significantly positively spatially associated with *A. muelleri* and *C. collaris* on all dates except for 17/6/03, and the latter species was significantly negatively associated with *Z. minimus* in this instance (Table 5.4). *Zorochros minimus, C. collaris,* and *A. muelleri* were significantly negatively spatially associated with *F. maritimus, B. decorum,* and *B. punctulatum* on all dates, except for *Z. minimus* on

17/6/03. *Fleutiauxellus maritimus* was significantly negatively associated with *Z. minimus* on all dates except 17/6/03 and was positively associated with *B. punctulatum*. *Bembidion atrocaeruleum* did not show any consistent trend of either positive or negative association with any other species, although for the grouped *B. atrocaeruleum* data, there were significant negative associations with *Z. minimus* (on all dates except 17/6/03), *C. collaris* and *A. muelleri*; and significant positive associations with *F. maritimus*, *B. decorum* and *B. punctulatum* (Table 5.4).

5.3.5 Beetle distribution on Bar 2

5.3.5.1 Spatial distribution of species

Zorochros minimus only showed significant spatial patchiness on 18/7/03 and 28/7/03 (Table 5.6), despite showing a fairly obvious grouping of individuals towards the back (southern edge) of the bar (Figure 5.12). The distribution of *Z. minimus* was fairly stable over all sample dates between which there was always a positive spatial association, although this was not always significant (Table 5.7). *Bembidion punctulatum* showed significant spatial patchiness and was mainly distributed along the water's edge (Table 5.6 and Figure 5.12). Both of these distributions and the degree of between date association were similar to those for the same species on Bar 3.

Bembidion atrocaeruleum was significantly patchily distributed on all of the study dates except for 17/6/03 and 4/7/03 (Table 5.6). The distribution of *B. atrocaeruleum* showed much more temporal stability than on Bar 3, with the distributions on each date showing positive associations, which were mainly significant (Table 5.7). *Bembidion atrocaeruleum* had two distinct patches on 24/6/03, 29/6/03, 23/7/03 and 2/8/03 (Figure 5.13). The largest was always situated at the upstream (southwest) end of the bar and the smaller patch was generally situated towards the downstream end of the bar, usually near to the water (except on the 23/7/03 when it was removed from the water's edge and more towards the centre of the bar). On 18/7/03 there was only one patch at the upstream end of the bar, and on 28/7/03 there was one patch that was situated along the water's edge, from the upstream end, to the middle of the bar (Figure 5.13).

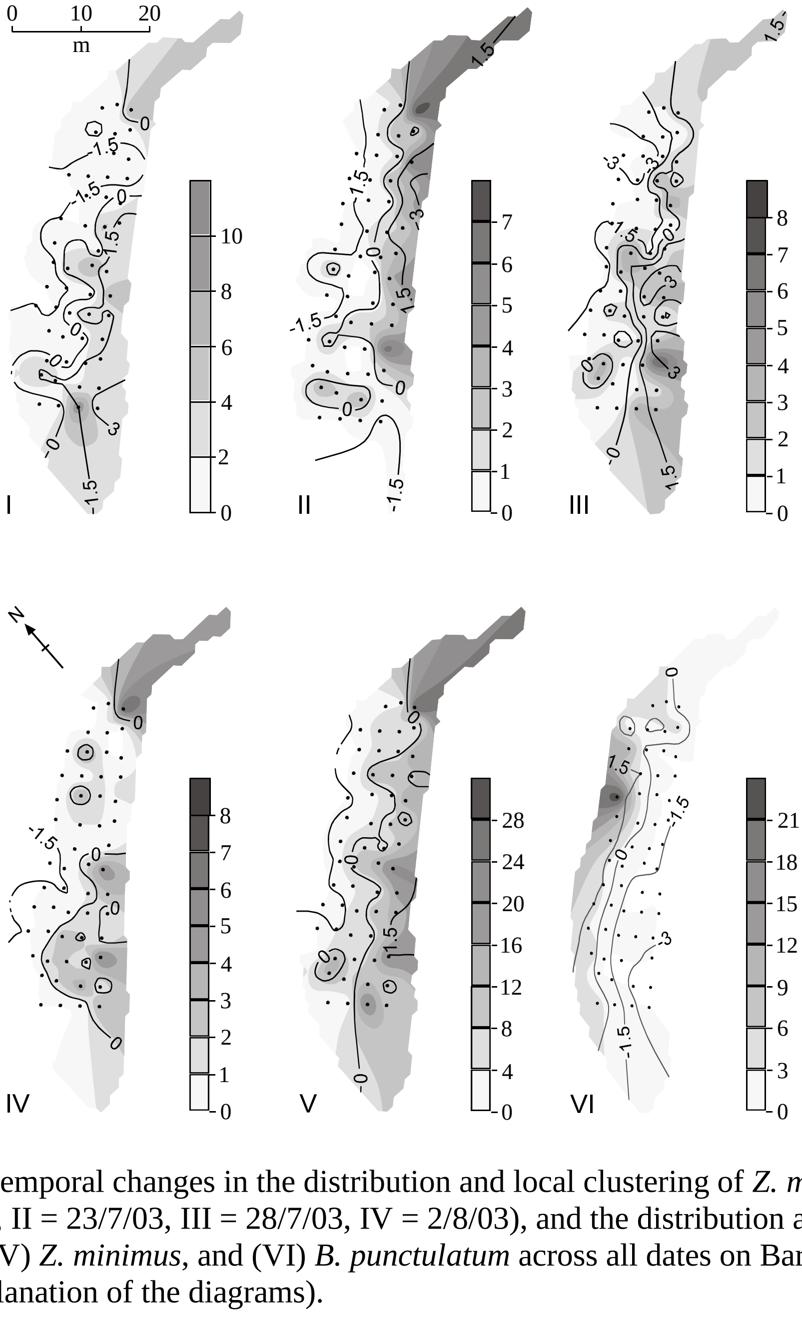


Figure 5.12 Temporal changes in the distribution and local clustering of *Z. minimus* on Bar 2 (I = 18/7/03, II = 23/7/03, III = 28/7/03, IV = 2/8/03), and the distribution and local clustering of (V) *Z. minimus*, and (VI) *B. punctulatum* across all dates on Bar 2 (see Figure 5.7 for an explanation of the diagrams).

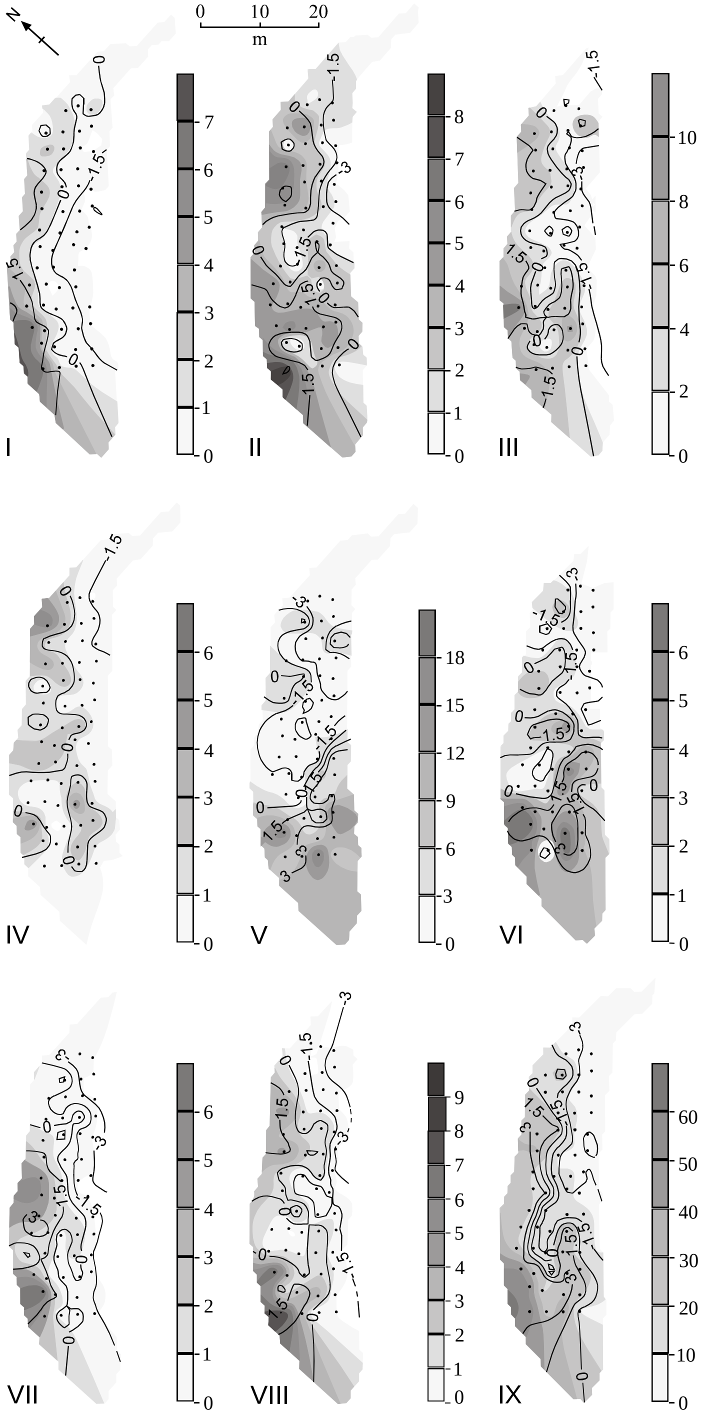


Figure 5.13 Temporal changes in the distribution and local clustering of *B. atrocaeruleum* on Bar 2. I = 17/6/03, II = 24/6/03, III = 29/6/03, IV = 4/7/03, V = 18/7/03, VI = 23/7/03, VII = 28/7/03, VIII = 2/8/03, and IX = data grouped across all dates (see Figure 5.9 for an explanation of the diagrams).

Table 5.6 SADIE statistics for the spatial distribution of species grouped over all dates (*B. atrocaeruleum*, *B. punctulatum* and *Z. minimus*), and on individual sampling occasions (*B. atrocaeruleum* and *Z. minimus*) for Bar 2 (see Table 5.1 for a description of the notation used).

Species	Date	Total count	I_a	P_a	v_j	P_j	v_i	P_i
B. atrocaeruleum	17/06/2003	104	1.465	0.0754	-1.364	0.1133	1.271	0.1455
B. atrocaeruleum	24/06/2003	148	**1.787**	**0.0209**	**-1.615**	**0.0412**	1.528	0.0509
B. atrocaeruleum	29/06/2003	166	**1.692**	**0.0305**	**-1.633**	**0.0347**	**1.539**	**0.0473**
B. atrocaeruleum	04/07/2003	80	0.762	0.8393	-0.774	0.8215	0.749	0.8829
B. atrocaeruleum	18/07/2003	220	**2.950**	**0.0002**	**-3.019**	**<0.0001**	**3.245**	**<0.0001**
B. atrocaeruleum	23/07/2003	103	**2.732**	**0.0003**	**-2.723**	**0.0002**	**2.112**	**0.0045**
B. atrocaeruleum	28/07/2003	112	**2.145**	**0.0027**	**-2.085**	**0.0065**	**1.833**	**0.0141**
B. atrocaeruleum	02/08/2003	83	**1.685**	**0.0332**	**-1.581**	**0.0473**	**1.617**	**0.0365**
All *B. atrocaeruleum*	All dates	1016	**3.048**	**0.0002**	**-2.806**	**<0.0001**	**3.550**	**<0.0001**
Z. minimus	18/07/2003	96	1.404	0.1037	-1.376	0.1104	**1.646**	**0.0307**
Z. minimus	23/07/2003	79	1.324	0.1255	-1.230	0.1735	1.340	0.1083
Z. minimus	28/07/2003	84	**1.808**	**0.0178**	**-1.748**	**0.0198**	**1.987**	**0.0065**
Z. minimus	02/08/2003	63	0.907	0.5214	-0.894	0.5643	1.021	0.3420
All *Z. minimus*	All dates	437	1.047	0.3214	-0.972	0.4205	1.085	0.2750
All *B. punctulatum*	All dates	114	**1.680**	**0.0300**	**-1.633**	**0.0411**	1.323	0.1165

5.3.5.2 Spatial association with environmental variables

Sediment size, elevation, 'vegetation within', and 'vegetation near' were all significantly positively associated with each other (Table 5.8). Elevation and 'distance from water' also co-varied making it difficult to distinguish which variables (if any) were responsible for the observed distributions. *Zorochros minimus* was significantly positively associated with every environmental measurement on 18/7/03, and generally showed positive associations with most variables with the exception of sediment size on 23/7/03. *Bembidion atrocaeruleum* showed most positive associations with sediment size and 'vegetation within' (Table 5.8). In contrast to *Z. minimus, B. atrocaeruleum* generally showed a negative association with 'distance from water', although this was not always significant and on 18/7/03 it was quite a strong positive association. *Bembidion punctulatum* showed a strongly significant negative association with all the measured environmental parameters (Table 5.8).

Table 5.7 SADIE spatial associations between species (*B. atrocaeruleum*, *B. punctulatum*, *Z. minimus*) on individual dates (17/6/03, 24/6/03, 29/6/03, 4/7/03, 23/7/03, 28/7/03, 2/8/03), or across all dates (-), and each other for Bar 2 (see Table 5.2 for a definition of the notations used). Significant (5% level in two-tailed test) positive associations are highlighted in bold, significant negative associations are underlined.

		Bp-	Zm -	Zm2/8	Zm28/7	Zm23/7	Zm18/7	Ba -	Ba2/8	Ba28/7	Ba23/7	Ba18/7	Ba4/7	Ba29/6	Ba24/6
Ba17/6	X	**0.5490**	-0.4066	-0.1126	-0.3315	-0.4817	-0.2813	**0.4939**	0.2559	**0.2990**	0.0779	0.0629	0.1266	**0.4558**	**0.4518**
	P_X	**<0.0001**	0.9995	0.7817	0.9942	>0.9999	0.9647	**0.0001**	0.0278	**0.0162**	0.2926	0.3251	0.1707	**<0.0001**	**0.0011**
Ba24/6	X	-0.0506	-0.1696	0.2358	-0.0560	-0.3472	-0.0443	**0.4265**	**0.3584**	**0.3028**	**0.4719**	**0.4376**	0.1845	**0.5620**	
	P_X	0.6259	0.8878	0.0501	0.6672	0.9952	0.5915	**0.0010**	**0.0039**	**0.0120**	**0.0002**	**0.0007**	0.0954	**<0.0001**	
Ba29/6	X	0.1886	-0.3437	0.1219	-0.1301	-0.5192	-0.0981	**0.5714**	**0.3852**	**0.4043**	**0.3791**	**0.2894**	**0.4171**		
	P_X	0.0807	0.9953	0.1809	0.8323	>0.9999	0.7546	**<0.0001**	**0.0011**	**0.0007**	**0.0023**	**0.0190**	**0.0006**		
Ba4/7	X	0.0863	-0.0350	0.0152	-0.0506	**0.6016**	0.0296	**0.4440**	**0.3268**	**0.4712**	**0.6016**	0.2100			
	P_X	0.2758	0.5971	0.4587	0.6458	**<0.0001**	0.4150	**0.0011**	**0.0060**	**0.0005**	**<0.0001**	0.0831			
Ba18/7	X	-0.5368	0.2031	**0.4369**	**0.3359**	-0.0431	**0.4754**	**0.5207**	**0.3974**	**0.3060**	**0.6901**				
	P_X	0.9998	0.0811	**0.0009**	**0.0112**	0.6156	**0.0002**	**0.0001**	**0.0033**	**0.0140**	**<0.0001**				
Ba23/7	X	**0.6731**	0.1522	0.2738	0.2002	-0.2124	**0.3912**	**0.6731**	**0.3874**	**0.5548**					
	P_X	**<0.0001**	0.1787	0.0281	0.0673	0.9406	**0.0019**	**<0.0001**	**0.0017**	**<0.0001**					
Ba28/7	X	0.1580	-0.2875	**0.4289**	0.0672	-0.3899	-0.1364	**0.6627**	**0.4289**						
	P_X	0.1232	0.9753	**0.0004**	0.3159	0.9984	0.8359	**<0.0001**	**0.0004**						
Ba2/8	X	0.0292	-0.2369	0.0520	-0.2136	-0.2345	-0.0153	**0.5026**							
	P_X	0.4143	0.9630	0.3490	0.9332	0.9541	0.5450	**<0.0001**							
Ba -	X	0.1013	-0.2074	0.0584	0.0477	-0.3682	0.1940								
	P_X	0.2525	0.9116	0.3386	0.3650	0.9974	0.1098								
Zm18/7	X	-0.6053	**0.5381**	**0.4302**	**0.5918**	0.2536									
	P_X	>0.9999	**<0.0001**	**0.0028**	**<0.0001**	0.0358									
Zm23/7	X	-0.3226	**0.4808**	0.0585	0.2664										
	P_X	0.9915	**0.0004**	0.3332	0.0256										
Zm28/7	X	-0.5691	**0.6452**	0.2326											
	P_X	>0.9999	**<0.0001**	0.0463											
Zm2/8	X	-0.4696	**0.3052**												
	P_X	0.9995	**0.0173**												
Zm-	X	-0.5541													
	P_X	0.9998													

Table 5.8 SADIE spatial associations between species (*B. atrocaeruleum*, *B. punctulatum*, *Z. minimus*) on individual dates (17/6/03, 24/6/03, 29/6/03, 4/7/03, 23/7/03, 28/7/03, 2/8/03), or across all dates (-), and measured environmental variables for Bar 2 (see Table 5.2 for a definition of the notation used). Spatial associations between environmental variables are shown.

		Vegetation within	Vegetation near	Distance from water	Elevation	Sediment
Ba17/6	X	**0.2886**	0.1049	-0.7263	-0.5593	0.0118
	P_X	**0.0239**	0.2140	>0.9999	>0.9999	0.4689
Ba24/6	X	**0.4117**	**0.2855**	-0.2466	0.0876	**0.5056**
	P_X	**0.0033**	**0.0160**	0.9553	0.2615	**<0.0001**
Ba29/6	X	**0.2935**	0.1408	-0.3427	-0.0203	**0.4457**
	P_X	**0.0121**	0.1510	0.9959	0.5527	**0.0003**
Ba4/7	X	0.2744	-0.0903	-0.2519	0.0290	**0.3102**
	P_X	0.0263	0.7365	0.9646	0.4147	**0.0186**
Ba18/7	X	**0.6748**	**0.7204**	0.2361	**0.4994**	**0.5908**
	P_X	**<0.0001**	**<0.0001**	0.0484	**0.0005**	**<0.0001**
Ba23/7	X	**0.6353**	**0.4858**	0.0050	**0.3522**	**0.5912**
	P_X	**<0.0001**	**0.0001**	0.4838	**0.0037**	**<0.0001**
Ba28/7	X	**0.5501**	**0.3267**	-0.3308	-0.0622	0.2232
	P_X	**<0.0001**	**0.0091**	0.9930	0.6657	0.0565
Ba2/8	X	**0.3529**	0.2687	-0.1910	0.0950	**0.3297**
	P_X	**0.0049**	0.0254	0.9189	0.2414	**0.0073**
Ba -	X	**0.6617**	**0.5070**	-0.3777	-0.0019	**0.3238**
	P_X	**<0.0001**	**<0.0001**	0.9976	0.5017	**0.0124**
Zm18/7	X	**0.4049**	**0.4889**	**0.4000**	**0.5726**	**0.3382**
	P_X	**0.0087**	**0.0002**	**0.0040**	**<0.0001**	**0.0218**
Zm23/7	X	-0.1426	0.0436	**0.4909**	**0.3087**	-0.3956
	P_X	0.8594	0.3796	**<0.0001**	**0.0147**	0.9989
Zm28/7	X	**0.3153**	**0.4431**	**0.4814**	**0.5391**	0.1613
	P_X	**0.0086**	**0.0006**	**<0.0001**	**<0.0001**	0.1150
Zm2/8	X	0.1320	0.2044	0.2414	**0.3669**	**0.3598**
	P_X	0.1797	0.0690	0.0424	**0.0035**	**0.0044**
Zm-	X	0.0443	0.2190	**0.5906**	**0.4727**	-0.0172
	P_X	0.3694	0.0590	**<0.0001**	**0.0001**	0.5474
Bp-	X	-0.3118	-0.4398	-0.7390	-0.7044	-0.4632
	P_X	0.9862	0.9997	>0.9999	>0.9999	0.9990
Sedi	X	**0.3775**	**0.3076**	0.0079	**0.3341**	
	P_X	**0.0040**	**0.0146**	0.4751	**0.0079**	
Elev	X	**0.3172**	**0.4225**	**0.7446**		
	P_X	**0.0069**	**0.0008**	**<0.0001**		
Distw	X	0.0124	0.2047			
	P_X	0.4655	0.0651			
Vegn	X	**0.7948**				
	P_X	**<0.0001**				

5.3.5.3 Spatial association between species

Zorochros minimus and *B. atrocaeruleum* showed some significant positive and negative associations, but these relationships were not consistent and, with the exception of 18/7/03, occurred on different dates (Table 5.7). *Bembidion atrocaeruleum* and *B. punctulatum* also showed no consistent spatial associations. The distributions of *Z.*

minimus and *B. punctulatum* were strongly and significantly negatively associated across all dates (Table 5.7).

5.3.6 Beetle distribution on Bar 3d

5.3.6.1 Spatial distribution of species

The spatial distribution of *Z. minimus* was significantly patchy on all dates on Bar 3d (Table 5.9). Patches were mainly situated at the upstream finger (western end) of the bar and along the bar edge away (northwestern edge) from the main channel (Figure 5.14). There was a large, consistent gap in the distribution of *Z. minimus* in the main, downstream section of the bar, and the distribution of individuals was again stable throughout the sampling period (Table 5.10). *Bembidion tibiale* was also significantly patchily distributed (Table 5.9), and had a similar distribution to *Z. minimus* with a patch situated in the upstream finger of the bar and a large gap in the main downstream section of the bar (Figure 5.14). *Fleutiauxellus maritimus* was also significantly patchily distributed and had one fairly tight patch situated almost in the centre of the main downstream section of the bar (Table 5.9, Figure 5.14).

The distribution of *B. atrocaeruleum* was significantly patchily distributed on all dates except for the first (17/6/03) and final (2/8/03) sampling date (Table 5.9). On the consecutive sampling dates, 24/6/03 and 29/6/03 there was a fairly small patch situated halfway along the upstream finger of the bar (Figure 5.15). On 4/7/03 this patch had expanded to fill the whole of the upstream finger of the bar. By 19/7/03 there were two separate patches, one halfway along the upstream finger of the bar and another along the edge of the main downstream section of the bar on the opposite edge to the main channel (Figure 5.15). On 23/7/03 there was again one patch situated in the upstream toe of the bar, while on 28/7/03 there were two patches, one situated in the upstream tip of the bar, and another about halfway down the bar on the edge away from the main channel (28/7/03). On all these dates there was a large gap occupying the bulk of the main downstream section of the bar on the main channel side (Figure 5.15). Despite several small re-adjustments to the distribution of these patches, the distribution of *B. atrocaeruleum* was largely stable across all sampling dates, except for 17/6/03, which was often negatively associated with the distribution on the other sampling dates, although this was never significant (Table 5.10).

Table 5.9 SADIE statistics for the spatial distribution of species grouped over all dates (*B. atrocaeruleum*, *B. tibiale*, *B. decorum*, *Z. minimus* and *F. maritimus*), and on individual sampling occasions (*B. atrocaeruleum*, *B. decorum* and *Z. minimus*) for Bar 3d (see Table 5.1 for a description of the notation used).

Species	Date	Total count	I_a	P_a	v_j	P_j	v_i	P_i
B. atrocaeruleum	17/06/2003	516	1.051	0.3234	-1.090	0.2738	1.029	0.3585
B. atrocaeruleum	24/06/2003	955	**2.314**	**0.0008**	**-2.129**	**0.0018**	**2.139**	**0.0012**
B. atrocaeruleum	29/06/2003	1120	**2.588**	**0.0002**	**-2.556**	**<0.0001**	**2.005**	**0.0030**
B. atrocaeruleum	04/07/2003	1348	**3.431**	**0.0002**	**-3.478**	**<0.0001**	**3.829**	**<0.0001**
B. atrocaeruleum	19/07/2003	3487	**1.699**	**0.0255**	-1.413	0.0689	**1.641**	**0.0238**
B. atrocaeruleum	23/07/2003	900	**2.581**	**0.0002**	**-2.842**	**<0.0001**	**2.855**	**<0.0001**
B. atrocaeruleum	28/07/2003	739	**1.587**	**0.0390**	**-1.747**	**0.0173**	**1.640**	**0.0288**
B. atrocaeruleum	02/08/2003	395	1.058	0.3129	-1.150	0.1983	1.026	0.3454
All *B. atrocaeruleum*	All dates	9460	**2.722**	**0.0002**	**-2.339**	**0.0003**	**2.998**	**<0.0001**
B. decorum	17/06/2003	126	1.422	0.0771	-1.452	0.0523	1.136	0.2207
B. decorum	24/06/2003	178	1.030	0.3633	-1.046	0.3300	1.096	0.2683
B. decorum	29/06/2003	253	**2.045**	**0.0034**	**-1.834**	**0.0089**	**2.262**	**0.0007**
B. decorum	04/07/2003	306	1.336	0.1093	-1.236	0.1538	1.281	0.1168
B. decorum	19/07/2003	1135	**2.743**	**0.0002**	**-2.457**	**0.0003**	**2.432**	**0.0005**
B. decorum	23/07/2003	188	**1.642**	**0.0300**	**-1.708**	**0.0191**	1.229	0.1480
B. decorum	28/07/2003	364	**1.522**	**0.0473**	**-1.622**	**0.0270**	**1.546**	**0.0328**
B. decorum	02/08/2003	258	**1.535**	**0.0463**	**-1.689**	**0.0194**	1.339	0.0888
All *B. decorum*	All dates	2808	**2.239**	**0.0007**	**-1.860**	**0.0080**	**1.872**	**0.0070**
Z. minimus	19/07/2003	67	1.472	0.0650	-1.384	0.0850	**1.772**	**0.0136**
Z. minimus	23/07/2003	50	**2.921**	**0.0002**	**-3.069**	**<0.0001**	**3.146**	**<0.0001**
Z. minimus	28/07/2003	63	**2.642**	**0.0002**	**-2.396**	**0.0002**	**2.484**	**0.0002**
Z. minimus	02/08/2003	57	**2.201**	**0.0010**	**-2.036**	**0.0045**	**1.913**	**0.0087**
All *Z. minimus*	All dates	338	**2.959**	**0.0002**	**-2.414**	**0.0002**	**2.748**	**<0.0001**
All *B. tibiale*	All dates	56	**3.116**	**0.0002**	**-3.248**	**<0.0001**	**1.437**	**<0.0001**
All *F. maritimus*	All dates	86	**2.036**	**0.0028**	**-1.865**	**0.0064**	**1.797**	**0.0079**

The distribution of *B. decorum* was significantly patchy on 29/06/03, 19/7/03, 23/7/03, 28/7/03 and 2/8/03 (Table 5.9). Patches were situated on the edge of the main channel in the main downstream section of the bar on 29/6/03, 23/7/03, 28/7/03 and 2/8/03 (Figure 5.16). On 28/7/03 there was also a second patch on the edge of the base of the upstream finger of the bar away from the main channel. On 19/7/03 there was a fairly large patch situated in the main downstream section of Bar 3d on the edge away from the main channel (Figure 5.16). Although usually on the main-channel edge of the bar, the position of patches did alter somewhat between dates (Table 5.10), although the only significantly negative association was between the distribution on the consecutive sampling dates, 19/7/03 and 23/7/03.

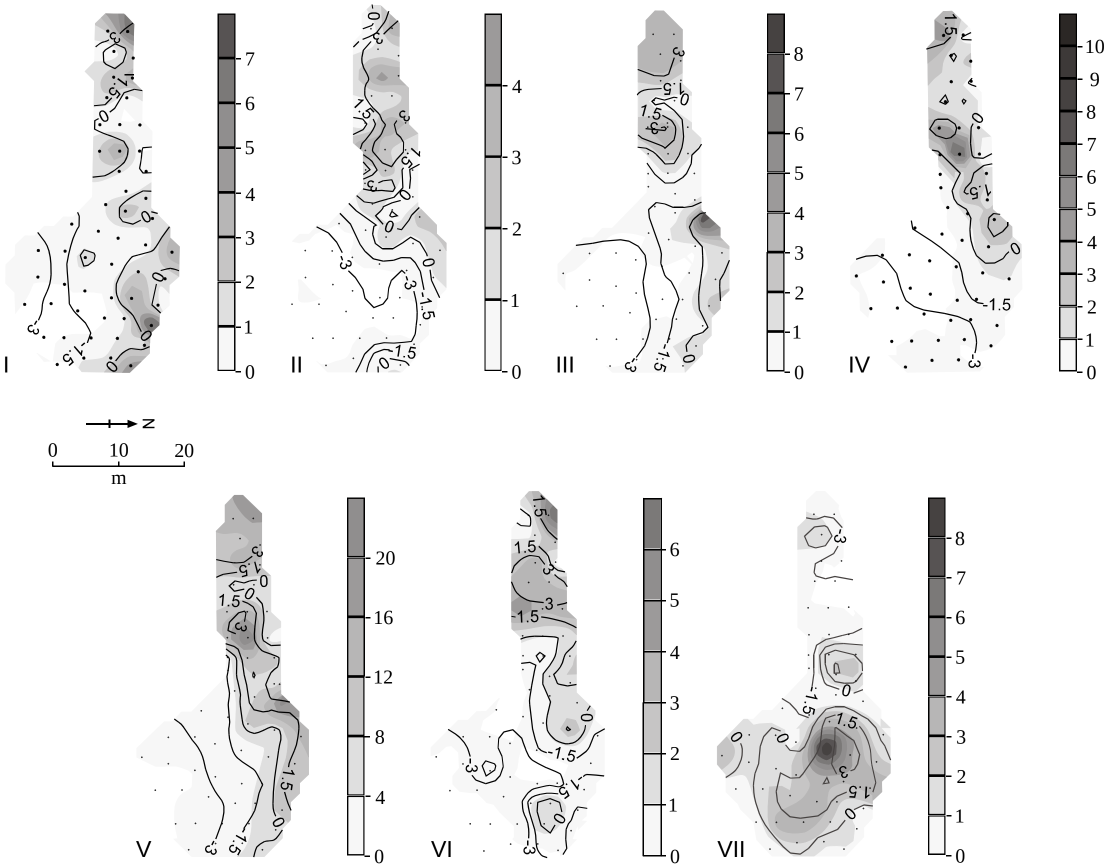


Figure 5.14 Temporal changes in the distribution and local clustering of *Z. minimus* on Bar 3d (I = 19/7/03, II = 23/7/03, III = 28/7/03, IV = 2/8/03), and the distribution and local clustering of (V) *Z. minimus*, (VI) *B. tibiale*, and (VII) *F. maritimus* across all dates on Bar 3d (see Figure 5.7 for an explanation of the diagrams).

5.3.6.2 Spatial association with environmental variables

Again there was strong significant spatial association between measured environmental variables. ‘Vegetation within’ and ‘vegetation near’ were significantly positively associated, as were elevation and ‘distance from water’, the latter was significantly negatively associated with both vegetation variables (Table 5.11). *Zorochros minimus* was significantly positively associated with both the vegetation variables and

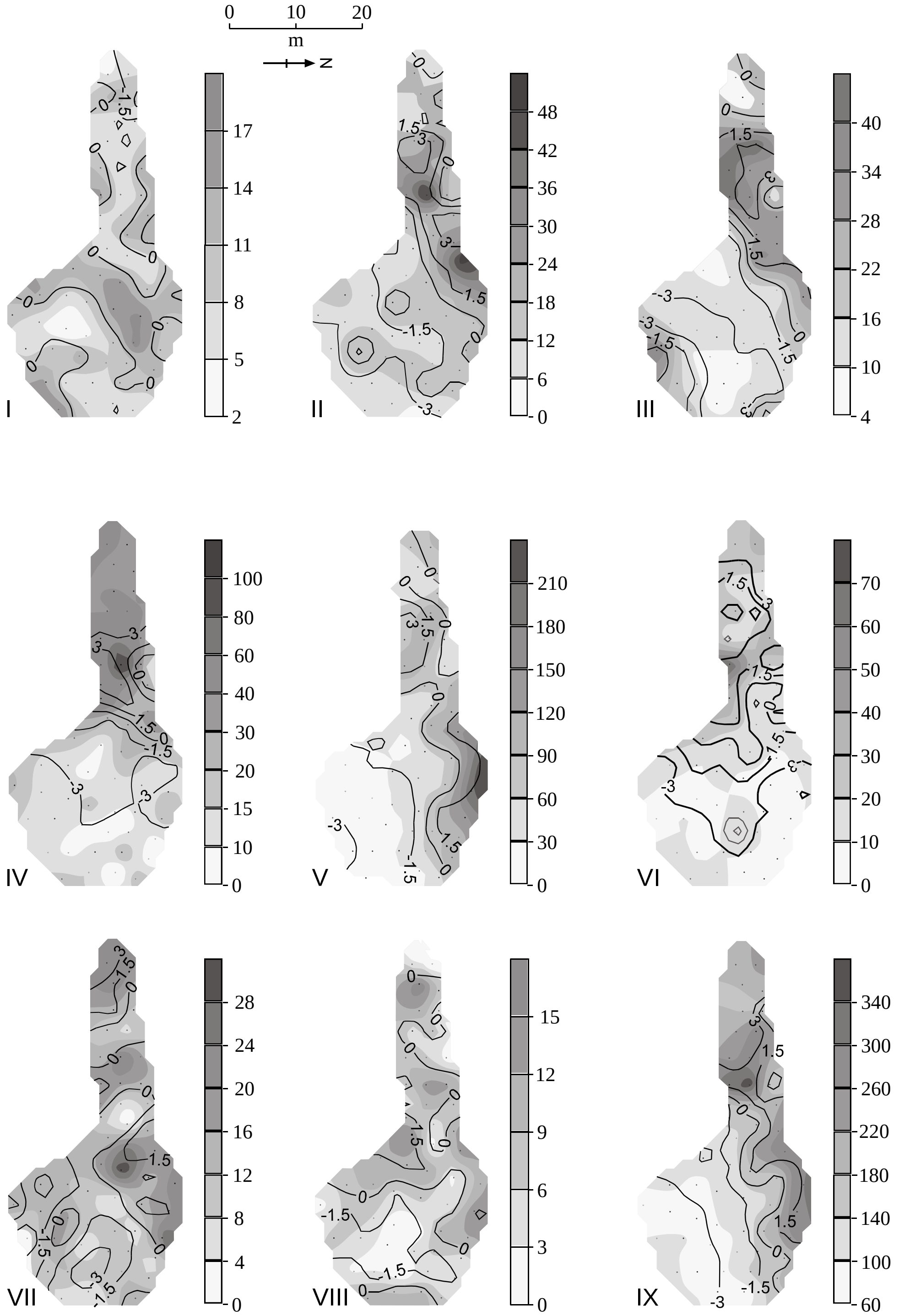


Figure 5.15 Temporal changes in the distribution and local clustering of *B. atrocaeruleum* on Bar 3d. I = 17/6/03, II = 24/6/03, III = 29/6/03, IV = 4/7/03, V = 19/7/03, VI = 23/7/03, VII = 28/7/03, VIII = 2/8/03, and IX = data grouped across all dates (see Figure 5.7 for an explanation of the diagrams).

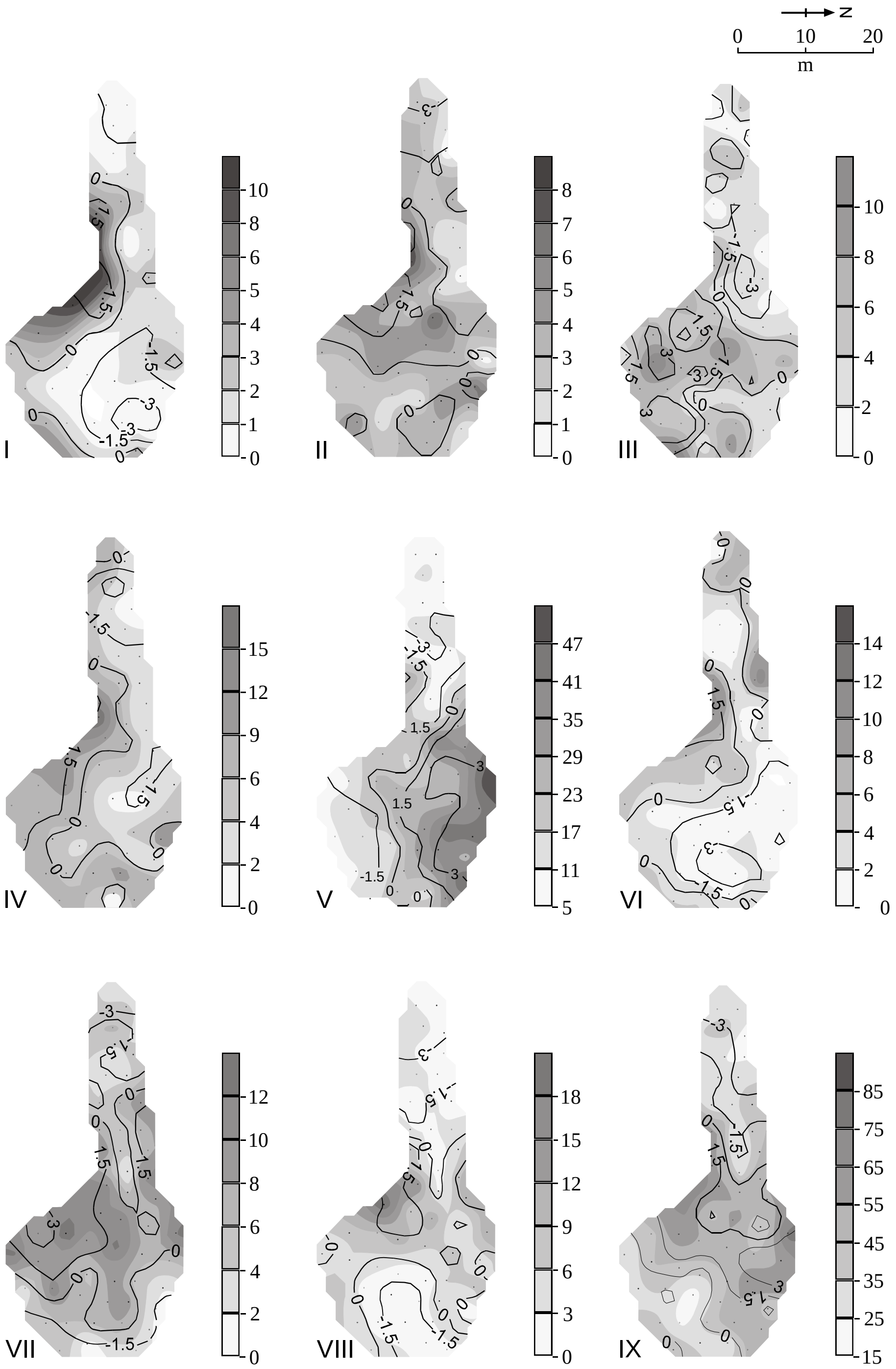


Figure 5.16 Temporal changes in the distribution and local clustering of *B. decorum* on Bar 3d. I = 17/6/03, II = 24/6/03, III = 29/6/03, IV = 4/7/03, V = 19/7/03, VI = 23/7/03, VII = 28/7/03, VIII = 2/8/03, and IX = data grouped across all dates (see Figure 5.7 for an explanation of the diagrams).

Table 5.10 SADIE spatial associations between species (*B. atrocaeruleum*, *B. tibiale*, *B. decorum*, *F. maritimus*, and *Z. minimus*) on individual dates (17/6/03, 24/6/03, 29/6/03, 4/7/03, 23/7/03, 28/7/03, 2/8/03), or across all dates (-), and each other for Bar 3d (see Table 5.2 for a definition of the notation used). Significant (5% level in two-tailed test) positive associations are highlighted in bold, significant negative associations are underlined.

		Bt -	Fm -	Zm -	Zm2/8	Zm28/7	Zm23/7	Zm19/7	Bd -	Bd2/8	Bd28/7	Bd23/7	Bd19/7	Bd4/7	Bd29/6	Bd24/6	Bd17/6	Ba -	Ba2/8	Ba28/7	Ba23/7	Ba19/7	Ba4/7	Ba29/6	Ba24/6
Ba17/6	X	-0.1302	**0.3785**	-0.1263	-0.0350	-0.2330	-0.3100	-0.1637	**0.3401**	**0.4002**	**0.3034**	0.0643	**0.3382**	0.0254	0.0823	**0.3859**	0.0813	-0.1691	0.0957	0.1199	-0.2367	-0.0222	-0.2296	-0.0045	0.0329
	P_X	0.8151	**0.0036**	0.8146	0.5965	0.9543	0.9897	0.8733	**0.0086**	**0.0010**	**0.0222**	0.3140	**0.0100**	0.5755	0.3019	**0.0026**	0.2771	0.8811	0.2426	0.2134	0.9572	0.5662	0.9423	0.5090	0.4110
Ba24/6	X	**0.6515**	-0.1848	**0.6614**	**0.8030**	**0.4917**	**0.6077**	**0.4261**	-0.2063	-0.0991	0.0135	0.0830	-0.0739	**-0.4424**	**-0.5866**	-0.1741	0.0226	**0.6700**	0.2322	**0.4097**	**0.4240**	**0.6651**	**0.6554**	**0.6949**	
	P_X	**<0.0001**	0.9104	**<0.0001**	**<0.0001**	**0.0001**	**<0.0001**	**0.0002**	0.9232	0.7654	0.4676	0.2640	0.6847	**0.9994**	**0.9998**	0.8891	0.4357	**<0.0001**	0.0411	**0.0007**	**0.0012**	**<0.0001**	**<0.0001**	**<0.0001**	
Ba29/6	X	**0.5858**	-0.3775	**0.5638**	**0.6993**	**0.4076**	**0.6392**	**0.3042**	-0.2814	-0.0946	-0.1519	**0.2972**	-0.2919	-0.2798	-0.4702	**0.6949**	0.2623	**0.5942**	**0.2671**	**0.4118**	**0.4522**	**0.5467**	**0.6618**		
	P_X	**<0.0001**	0.9979	**0.0001**	**<0.0001**	**0.0023**	**<0.0001**	**0.0197**	0.9812	0.7574	0.8696	**0.0151**	0.9774	0.9825	0.9996	**<0.0001**	0.0292	**<0.0001**	**0.0213**	**0.0009**	**0.0004**	**<0.0001**	**<0.0001**		
Ba4/7	X	**0.6447**	-0.4778	**0.7050**	**0.7313**	**0.6221**	**0.7813**	**0.5394**	-0.4485	-0.3240	-0.1801	**0.3931**	-0.5509	-0.4254	-0.5199	-0.3288	0.1408	**0.7775**	**0.3395**	**0.4508**	**0.7714**	**0.4784**			
	P_X	**<0.0001**	>0.9999	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9990	0.9916	0.8888	**0.0010**	>0.9999	0.9991	>0.9999	0.9933	0.1461	**<0.0001**	**0.0065**	**0.0015**	**<0.0001**	**0.0003**			
Ba19/7	X	**0.5817**	-0.2823	**0.6700**	**0.6170**	**0.6502**	**0.4586**	**0.5207**	0.0370	-0.0681	-0.1734	-0.0967	0.2144	-0.3043	-0.5634	-0.1636	-0.0873	**0.7204**	**0.3637**	**0.4091**	**0.2702**				
	P_X	**0.0001**	0.9697	**<0.0001**	**<0.0001**	**<0.0001**	**0.0003**	**<0.0001**	0.4032	0.6577	0.8887	0.7474	0.0803	0.9834	>0.9999	0.8713	0.7282	**<0.0001**	**0.0052**	**0.0039**	**0.0263**				
Ba23/7	X	**0.5104**	-0.5112	**0.4865**	**0.5436**	**0.4972**	**0.6664**	**0.4785**	-0.3741	-0.2737	**0.4011**	**0.5229**	-0.5217	-0.2561	-0.4739	-0.2278	0.2012	**0.5528**	**0.3793**	**0.4011**					
	P_X	**0.0002**	>0.9999	**0.0002**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0005**	0.9963	0.9772	**0.0014**	**0.0001**	>0.9999	0.964	>0.9999	0.9501	0.0669	**<0.0001**	**0.0045**	**0.0014**					
Ba28/7	X	**0.4517**	-0.2276	**0.5816**	**0.5086**	**0.5091**	**0.3903**	**0.6256**	0.0064	-0.0589	-0.0568	**0.2482**	-0.0502	-0.3023	-0.2999	-0.1550	0.0677	**0.5349**	**0.3429**						
	P_X	**0.0011**	0.9377	**<0.0001**	**0.0003**	**<0.0001**	**0.0014**	**<0.0001**	0.4781	0.6600	0.6515	**0.0357**	0.6273	0.9878	0.9868	0.8447	0.3222	**<0.0001**	**0.0076**						
Ba2/8	X	0.2178	-0.2387	**0.3611**	**0.3598**	**0.3513**	**0.4823**	0.2073	0.1667	0.1548	0.0323	**0.4920**	**0.3637**	-0.0511	-0.2278	0.1834	**0.5444**	**0.3703**							
	P_X	0.0546	0.9610	**0.0068**	**0.0030**	**0.0067**	**0.0002**	0.0682	0.1145	0.1496	0.4125	**0.0023**	**0.0058**	0.6222	0.9559	0.1030	**<0.0001**	**0.0022**							
Ba -	X	**0.7054**	-0.3730	**0.8741**	**0.7749**	**0.8494**	**0.6993**	**0.6343**	-0.3147	-0.3787	-0.3237	0.1079	-0.2226	-0.5140	-0.5871	-0.4703	-0.1229								
	P_X	**<0.0001**	0.9972	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.9888	0.9976	0.9881	0.2119	0.9280	0.9998	>0.9999	0.9996	0.8141								
Bd17/6	X	-0.0869	-0.2875	-0.1288	0.1005	-0.2330	0.1273	-0.0932	0.1001	0.2962	0.1959	**0.6210**	-0.2713	0.2812	0.1602	**0.2819**									
	P_X	0.7266	0.9826	0.7887	0.2264	0.9543	0.1744	0.7440	0.2315	0.0338	0.0817	**0.0002**	0.9741	0.0344	0.1194	**0.0234**									
Bd24/6	X	-0.1704	0.2538	-0.3425	-0.2702	-0.4117	-0.2905	-0.3461	**0.6428**	**0.5511**	**0.5210**	0.1001	**0.4297**	**0.4209**	0.2457										
	P_X	0.8925	0.0337	0.9952	0.9750	0.9990	0.9842	0.9942	**<0.0001**	**0.0001**	**0.0001**	0.2431	**0.0008**	**0.0023**	0.0379										
Bd29/6	X	-0.5427	0.1481	-0.6340	-0.6008	-0.5541	-0.5518	-0.4883	**0.2856**	**0.3336**	0.1826	-0.1103	0.0732	**0.3065**											
	P_X	>0.9999	0.1372	>0.9999	>0.9999	>0.9999	>0.9999	0.9997	**0.0212**	**0.0054**	0.1041	0.7890	0.3016	**0.0112**											
Bd4/7	X	-0.3626	-0.0034	-0.4644	-0.4562	-0.4461	-0.5049	-0.3451	**0.3468**	**0.2988**	0.1877	0.0890	0.1483												
	P_X	0.9946	0.5012	>0.9999	0.9996	0.9985	>0.9999	0.9931	**0.0049**	**0.0227**	0.0836	0.2974	0.1538												
Bd19/7	X	-0.1751	**0.5336**	-0.1414	-0.1784	-0.1689	-0.4440	-0.0932	**0.7173**	**0.5028**	0.2462	-0.4129													
	P_X	0.8712	**<0.0001**	0.8255	0.8841	0.8719	0.9993	0.7440	**<0.0001**	**0.0001**	0.0473	0.9993													
Bd23/7	X	0.0878	-0.3602	0.0513	0.1645	-0.0045	**0.3365**	0.0674	-0.1017	0.1548	0.1849														
	P_X	0.2576	0.9965	0.3653	0.1119	0.5130	**0.0082**	0.3179	0.7729	0.1961	0.0880														
Bd28/7	X	-0.0843	**0.2740**	-0.3317	-0.1193	-0.3871	-0.1844	-0.4432	**0.5125**	**0.5482**															
	P_X	0.7233	**0.0262**	0.9931	0.7958	0.9988	0.9113	0.9993	**<0.0001**	**<0.0001**															
Bd2/8	X	-0.2302	0.2630	-0.4079	-0.1066	-0.4106	-0.3966	-0.4184	**0.6904**																
	P_X	0.9551	0.0263	0.9975	0.7783	0.9989	0.9954	0.9987	**<0.0001**																
Bd -	X	-0.2946	**0.4064**	-0.2745	-0.2777	-0.2644	-0.4162	-0.1867																	
	P_X	0.9813	**0.0029**	0.9747	0.9751	0.9679	0.9995	0.9104																	
Zm19/7	X	**0.3926**	-0.3431	**0.6469**	**0.4971**	**0.6172**	**0.4493**																		
	P_X	**0.0021**	0.9950	**<0.0001**	**0.0002**	**<0.0001**	**0.0004**																		
Zm23/7	X	**0.6342**	-0.4587	**0.7003**	**0.6725**	**0.6441**																			
	P_X	**<0.0001**	0.9997	**<0.0001**	**<0.0001**	**<0.0001**																			
Zm28/7	X	**0.613**	-0.4019	**0.8751**	**0.6634**																				
	P_X	**<0.0001**	0.9991	**<0.0001**	**<0.0001**																				
Zm2/8	X	**0.6944**	-0.2783	**0.7546**																					
	P_X	**<0.0001**	0.9774	**<0.0001**																					
Zm -	X	**0.6141**	-0.2661																						
	P_X	**<0.0001**	0.9735																						
Fm -	X	-0.3389																							
	P_X	0.9922																							

Table 5.11 SADIE spatial associations between species (*B. atrocaeruleum*, *B. tibiale*, *B. decorum*, *F. maritimus*, and *Z. minimus*) on individual dates (17/6/03, 24/6/03, 29/6/03, 4/7/03, 23/7/03, 28/7/03, 2/8/03), or across all dates (-), and measured environmental variables for Bar 3d (see Table 5.2 for a definition of the notation used). Spatial associations between environmental variables are shown.

		Vegetation within	Vegetation near	Distance from water	Elevation
Ba17/6	X	-0.2206	-0.1170	0.1169	-0.5165
	P_X	0.9477	0.7934	0.2098	>0.9999
Ba24/6	X	**0.6327**	**0.6789**	-0.1789	**0.3276**
	P_X	**<0.0001**	**<0.0001**	0.9063	**0.0066**
Ba29/6	X	**0.6327**	**0.7131**	-0.2783	0.1146
	P_X	**<0.0001**	**<0.0001**	0.9826	0.2036
Ba4/7	X	**0.9546**	**0.6406**	-0.3649	0.1996
	P_X	**<0.0001**	**<0.0001**	0.9963	0.0754
Ba19/7	X	**0.4424**	**0.7303**	-0.3409	0.1817
	P_X	**0.0014**	**<0.0001**	0.9855	0.0973
Ba23/7	X	**0.8229**	**0.4493**	-0.4029	**0.2659**
	P_X	**<0.0001**	**0.0001**	0.9984	**0.0287**
Ba28/7	X	**0.4447**	**0.4174**	0.1735	0.1820
	P_X	**0.0009**	**0.0014**	0.8902	0.0893
Ba2/8	X	**0.2996**	**0.3997**	-0.2545	-0.0094
	P_X	**0.0231**	**0.0021**	0.9559	0.5291
Ba -	X	**0.7416**	**0.6561**	-0.3462	0.2597
	P_X	**<0.0001**	**<0.0001**	0.9954	0.0298
Zm19/7	X	**0.5041**	**0.4015**	-0.3420	0.2750
	P_X	**<0.0001**	**0.0016**	0.9904	0.0291
Zm23/7	X	**0.7761**	**0.6742**	-0.3144	0.1069
	P_X	**<0.000**	**<0.0001**	0.9883	0.2304
Zm28/7	X	**0.6059**	**0.6018**	-0.2955	0.1808
	P_X	**<0.0001**	**<0.0001**	0.9834	0.1041
Zm2/8	X	**0.7381**	**0.6957**	-0.2546	**0.2850**
	P_X	**<0.0001**	**<0.0001**	0.9708	**0.0186**
Zm -	X	**0.6752**	**0.6637**	-0.2109	0.2198
	P_X	**<0.0001**	**<0.0001**	0.9329	0.0524
Bt -	X	**0.6414**	**0.7006**	-0.3069	0.2181
	P_X	**<0.0001**	**<0.0001**	0.9864	0.0542
Fm -	X	-0.5125	-0.3747	**0.5792**	0.2016
	P_X	>0.9999	0.9967	**<0.0001**	0.0664
Bd17/6	X	0.1349	0.1019	-0.1264	-0.2672
	P_X	0.1714	0.2428	0.8102	0.9701
Bd24/6	X	-0.3549	-0.0818	0.2700	-0.1435
	P_X	0.9935	0.7286	0.0266	0.8488
Bd29/6	X	-0.5522	-0.6460	**0.3138**	-0.3325
	P_X	>0.9999	>0.9999	**0.0090**	0.9913
Bd4/7	X	-0.4112	-0.2680	0.0011	-0.4434
	P_X	0.9976	0.9805	0.4892	0.9998
Bd19/7	X	-0.5579	-0.0371	**0.2967**	0.2374
	P_X	0.9998	0.5935	**0.0199**	0.0503
Bd23/7	X	**0.4374**	0.1770	-0.3090	-0.1636
	P_X	**0.0003**	0.1391	0.9815	0.8637
Bd28/7	X	-0.1315	-0.0635	**0.3102**	0.0911
	P_X	0.8272	0.6753	**0.0156**	0.2593
Bd2/8	X	-0.3384	-0.0951	0.1927	0.0322
	P_X	0.9920	0.7207	0.0881	0.4174
Bd -	X	-0.4878	-0.1216	**0.3114**	-0.0133
	P_X	>0.9999	0.8153	**0.0139**	0.5361
Elev	X	0.1748	0.1978	**0.2795**	
	P_X	0.1031	0.0941	**0.0176**	
Distw	X	-0.4091	-0.2723		
	P_X	0.9993	0.9761		
Vegn	X	**0.6620**			
	P_X	**<0.0001**			

negatively associated with ‘distance from water’ on all dates, the latter was, however, only significant on 19/7/03, 23/7/03 and 28/7/03 (Table 5.11). The relative strengths of these associations, together with the distribution away from the water’s edge on Bars 2 and 3, would suggest that the distribution of *Z. minimus* was affected in this instance by the proximity of vegetation. *Bembidion tibiale* was also significantly positively associated with the two vegetation variables and significantly negatively associated with ‘distance from water’ (Table 5.11). *Fleutiauxellus maritimus* was found to show the opposite pattern, showing a significant negative association with the vegetation variables, and a significant positive association with elevation.

The distribution of *B. atrocaeruleum* was significantly positively associated with the vegetation variables on all sample dates except for 17/6/03, and was significantly negatively associated with distance from the water on 29/6/03, 4/7/03, 19/7/03 and 23/7/03 (Table 5.11). Again, the stronger association with vegetation than distance from water suggests that vegetation proximity might be more important to *B. atrocaeruleum* than ‘distance from water’ in this instance. There was a significant positive association with elevation on 24/6/03 and 23/7/03, and interestingly a negative relationship with elevation on 17/6/03.

Bembidion decorum was mainly found to be significantly negatively associated with ‘vegetation within’ (24/6/03, 29/6/03, 4/7/03, 19/7/03 and 2/8/03), but showed no significant relationship on 17/6/03 and 28/7/03, and a significant positive association on 23/7/03 (Table 5.11). *Bembidion decorum* was also significantly negatively correlated with ‘vegetation near’ on 29/6/03 and 4/7/03. The ‘distance from water’ was found to show significant positive association with *B. decorum* on 29/6/03, 19/7/03 and 28/7/03 (Table 5.11), although this was a result of the shape of the bar (Figure 5.16), as patches situated within the downstream, wider section of the bar are likely to show a significantly positive association with ‘distance from water’ even when it did not exist. There were also significant positive associations between *B. decorum* and elevation on 29/6/03 and 4/7/03.

5.3.6.3 Spatial association between species

Bembidion atrocaeruleum, *B. tibiale* and *Z. minimus* were found to show significant positive associations on almost all dates with very few exceptions. Only the distribution of *B. atrocaeruleum* on 17/6/03 showed negative associations with the distributions of *B. tibiale* and *Z. minimus* and this was only significant for the latter on 23/7/03 (Table 5.10). *Zorochros minimus* was generally negatively associated with *B. decorum* and many of these associations were significant, the main exception was on 23/7/03, when their distributions were significantly positively associated (Table 5.10). The distributions of *B. atrocaeruleum* and *B. decorum* demonstrated a mix of negative and positive associations, many of which were significant. The distribution of *B. atrocaeruleum* on 17/6/03 was mainly positively associated with *B. decorum*, whilst the distribution of *B. atrocaeruleum* on 4/7/03 was mainly negatively associated with *B. decorum* (Table 5.10). *Bembidion tibiale*, *Z. minimus* and *B. atrocaeruleum* all showed negative associations with the distribution of *F. maritimus*, which were often significant, the only exception was *B. atrocaeruleum* on 17/6/03, which was significantly positively associated with the distribution of *F. maritimus*. *Bembidion decorum* and *F. maritimus* showed no strong negative or positive association over time, the pattern was mixed, with significant negative associations on some dates, but significant positive associations on others (Table 5.10).

5.4 Discussion

5.4.1 Performance of SADIE

Xu (2003) has recently shown that it is not just the relative position of patches in a survey area that influences the results of SADIE, but also the absolute position. There are furthermore, other limitations to the use of SADIE analyses highlighted by this research. The distribution of *Z. minimus* on Bar 2 for example, visually showed a clear pattern of distribution along the back edge of the bar on all dates (Figure 5.12), but this was only found to be significant for two dates (Table 5.6). Holland *et al.* (1999) noted that clusters are generally not detected by SADIE unless more than ~6 neighbouring sample units all have above or below average counts. The long thin shape of Bar 2 therefore made it difficult to detect linear clustering along the edge of the bar. In most situations however, the SADIE methodology proved a good method for detecting spatial heterogeneity and establishing spatial associations.

5.4.2 General patterns of species distribution

Zorochros minimus showed a generally stable distribution on all bars studied. It was grouped towards the upper, dryer section of Bars 3 and 2, and although it was found to be distributed close to the water on Bar 3d this seems to have been due to a positive association with vegetation in the absence of any elevated, dryer conditions. It was also associated with vegetation cover on Bar 3. Perhaps not surprisingly due to the limited amount of vegetation, there was no regular effect of vegetation cover on Bar 2. This ERS specialist species of elaterid is associated with the drier, less frequently inundated microhabitats of ERS, and it seems probable that vegetation cover is important possibly because of its effects on microclimate (Thiele 1977), or food, perhaps in the form of seeds, detritus, or invertebrates associated with the vegetation. Although the feeding habits of *Z. minimus* are not yet fully understood (Howard Mendel pers. comm.). Sadler *et al.* (2004)

found that *Z. minimus* was associated with larger, wider ERS bars, which had greater area of drier, less frequently inundated microhabitats.

Bembidion atrocaeruleum was characterised by a less temporally stable distribution, with patches that occupied large areas of ERS. The evidence from the observation of the movements of marked individuals also showed that this species ranged widely *within* bars. On Bars 2 and 3, it was mainly distributed in the mid- to lower-sections of the bars, avoiding the upper drier sections of the bar preferred by *Z. minimus*. Desender (1989) also found this species to have a similar distribution in a river system in Belgium. *Bembidion atrocaeruleum* is by far the most numerous species of beetle on ERS in this system (Sadler *et al.* unpublished), and the large areas occupied by this species cover a number of ERS microhabitats, so it can be considered a generalist of ERS, although at a national scale it is exclusively confined to ERS. The distribution of *B. atrocaeruleum* on Bar 3d is interesting, as it is quite different than on Bars 3 and 2, which were more elevated bars. On Bar 3d it occupied the same microhabitats as *Z. minimus,* and was characterised by a relatively temporally stable distribution within vegetation that did not cover a large area. Many species in the genus *Bembidion* have been shown to exclusively feed on aquatic invertebrates (Hering and Plachter 1997; Hering 1998; Paetzold *et al.* in press), which suggests that the positive association with vegetation observed on Bar 3d was not because the vegetation provided a food resource.

Bembidion decorum was distributed along the water's edge on Bar 3. On the coarser and more low-lying Bar 3d where it was far more abundant, it ranged over a much wider area possibly because the habitat characteristics were more favourable. Desender (1989) found that *B. decorum* was mainly distributed very close to the water's edge, as observed on Bar 3. *Bembidion punctulatum* was also found to be tightly associated with the water's edge on Bars 3 and 2. This was also noted by Desender (1989), who observed that

B. punctulatum was mainly associated with finer sediments. Indeed, it was found to be associated with finer sediments on Bar 2, and the low numbers of this species on Bar 3d lends further support to notion that *B. punctulatum* was associated with finer sediments.

Fleutiauxellus maritimus was distributed in small, quite tightly packed patches in the mid sections of Bars 3 and 3d, away from vegetation. No other species showed the same distribution. *Clivina collaris* was distributed in the upper section of Bar 3, and might have been affected by the distribution of nearby vegetation. *Agonum muelleri* was the only non ERS-specialist beetle captured in sufficient numbers to analyse spatial distribution. This species was also distributed along the back edge of Bar 3, in close proximity to vegetation.

5.4.3 Effect of weather and flow pulses

The ERS dynamic microhabitat utilisation model hypothesised that changing weather conditions and water level would alter the microspatial distribution of ERS beetles (Figure 5.1). Species distributions did change over time, but generally species stayed within fairly well defined areas within the bar. Only two sampling dates showed some evidence for a departure from the standard situation, in response to hot dry weather and a flow pulse.

Sampling on 17/6/03 took place during a relatively dry and warm period, so the ERS ‘activity’ zone would be expected to be narrow (Desender 1989), and species that are usually situated farther up the bar would be expected to move closer to the water if they wished to remain in similar microclimatic conditions. *Zorochros minimus* on Bar 3 was distributed in the mid section of the bar, in contrast to all other dates when it was distributed in the upper section of the bar. Unfortunately, numbers of *Z. minimus* were too low on 17/6/03 to reasonably establish the distribution on Bars 2 and 3d. *Bembidion atrocaeruleum* on 17/6/03 was distributed towards the water’s edge on Bar 3, but this was not as marked as on some other dates (e.g. 28/7/03, during a wet period). On Bar 3d on 17/6/03 *B. atrocaeruleum* was captured in relatively small numbers, and did not show any perceivable or significant spatial pattern. Likewise, *B. decorum* was also captured in low numbers and did not show any significant spatial pattern, although visually there was a fairly strong tendency to be captured it the traps closest to the water's edge. The problem with pitfall traps is that they cannot be used to sample extremely close to the water's edge because they get flooded. On this occasion it was possible that both *B. atrocaeruleum* and *B. decorum* were distributed very close to the water's edge, and were not sampled adequately by pitfall traps. The 17/6/03 was the first date upon which the microspatial distribution was determined, but the observed altered distributional patterns were not likely to be due to a reaction of the beetles to their first capture because beetles had already been trapped over two months for marking in the 2003 mark-recapture study (Chapter 7).

The 17-19/7/03 was the only sampling period that coincided with a flow pulse, initially because of releases from the reservoir during a very hot, dry period, and then due to heavy rain on the day the traps were opened. The ERS dynamic microhabitat utilisation model suggests that the long, hot and dry period would cause species to aggregate more closely to the water's edge. As the water rose due to the heavy, prolonged rainfall, beetles at the water's edge would need to move up the bar or be submerged. A sampling method such as pitfall trapping, which relies on a beetle's own movements to induce capture, might in this case be expected to sample far more individuals than it usually would. This proved to be the case. The number of *B. atrocaeruleum* and *B. decorum* captured on the five bars sampled in the microspatial distribution and mark-recapture (Chapter 7) studies was so extreme that it was not possible to complete the counts for Bar 3, and traps on Bar 3d were emptied a day late. Despite this increased level of locomotory activity the patterns of distribution on Bars 2 and 3d were only unusual for *B. decorum* on Bar 3d. In this case, the main patch of *B. decorum* switched from the low-lying area of ERS near to the main channel, to the more elevated area of ERS next to the secondary channel. This may have been a response that reduced the chance of being washed away by the flow pulse. The lack of an observed change in distribution by other species might have been due to the long sampling window masking changing distributions that occurred over temporal scales less than one day.

The evidence to support the ERS dynamic microhabitat utilisation model from this investigation was not strong. This may have partly resulted from fairly unchangeable weather conditions throughout most of the sampling periods. However there were some valuable initial glimpses of changing species microdistributions, which suggest that the approach may yield important information about the dynamics of ERS beetle microdistirbution. Suggestions for further work on this topic are given in Chapter 9.

5.4.4 Did microhabitat characteristics or interspecific competition cause the patchy distribution of species?

Patchy distributions of ERS beetle species have been observed previously (e.g. Andersen 1969; Desender 1989), and have been explained by individual responses to environmental cues, and for some species, by interspecific competition (Andersen 1988). The co-varying nature of the environmental measurements made in this study made interpretation difficult. Although it has been shown in this study that different species show significantly different spatial distributions, descriptive studies such as this one cannot provide strong evidence for the existence of interspecific competition, they can only provide hints as to where such competition may exist (Hastings 1987). In order to conclusively show the existence of interspecific competition, experimental manipulations have to be implemented, such as the manipulation of the density of a species and examination of the response of possible competitors (Niemelä 1993). Clearly demonstrating the existence of spatial dissociation between species is however an important tool for highlighting areas where competition is likely to exist (Niemelä 1993). This investigation was therefore a valuable initial step towards understanding the structure and diversity of ERS beetle communities. Chapter 9 highlights areas of further research that should lead to a fuller understanding of the underlying processes sustaining diversity in ERS habitats.

CHAPTER 6

INTER-PATCH SPATIAL DYNAMICS: INTER-SPECIES COMPARISON AND METHOD DEVELOPMENT

6.1 Introduction

This chapter describes the initial mark-recapture study from the summer of 2002. The investigation tested the applicability of the mark-recapture methods for ERS beetles, which were further refined for the 2003 study (Chapter 7). This work focused on three species in order to examine possible differences in spatial population structure. The potential influence of spatial population structure on the response to threats is explored in Chapter 9.

6.2 Background

The processes driving population structure and dynamics strongly alter over different spatio-temporal scales and there is no single ‘correct’ scale at which populations and communities should be studied (Wiens 1989; Levin 1992; Blackburn and Gaston 2002). Rather, multi-scale investigations are encouraged as they can elucidate processes, and population and community responses at different scales, and highlight interactions between them. A considerable amount of recent research has investigated the spatial population structure at scales that encompass multiple distinct patches of available habitat and focus on the transfer of individuals between them (e.g. Matter 1996; Förare and Solbreck 1997; Sutcliffe *et al.* 1997a). Such studies have typically described these inter-patch population dynamics within the conceptual framework provided by ideas of ‘metapopulation’ (Levins 1969, 1970; Hanski and Gilpin 1991), and ‘patchy population’ (Harrison 1991), and have highlighted the integral importance of understanding inter-patch spatial population structure for successful conservation management (Shaffer 1981;

Collinge *et al.* 2001; Baguette and Schtickzelle 2003; Purse *et al.* 2003). Spatial population structure can be determined by (1) inter-patch habitat structure and movement patterns alone; or (2) in combination with the effects of local habitat quality (Bowne and Bowers 2004). The latter situation has increasingly been shown to be the case from many studies of spatial population structure (Harrison 1991; Thomas *et al.* 2001; Fleishman *et al.* 2002; Franken and Hik 2004; Bonte *et al.* 2004), and the importance of process interactions between the intra and inter-patch scales has thus been highlighted.

ERS are characterised by a high rate of habitat turnover (e.g. Brewer and Lewin 1998; Brewer *et al.* 2000), which necessitates the transfer of individuals between patches in order to prevent the eradication of populations as patches are destroyed. Therefore, ERS beetles cannot persist as ‘separate’ populations where no individuals migrate between patches. Similarly, ‘core’ ‘satellite’ systems, where small peripheral (satellite) patches are only maintained from a large stable ‘core’ patch (MacArthur and Wilson 1967; Boorman and Levitt 1973) are not possible because ‘core’ patches cannot be constantly present. Consequently, populations of ERS beetles must instead have a spatial population structure something akin to a ‘metapopulation’ (Hanski and Gilpin 1991) or ‘patchy population’ (Harrison 1991). Most populations do not easily fit into either of these categories of dynamic spatial population structure (Harrison 1991; Sutcliffe *et al.* 1997a), but rather, are best represented along continuous gradients of type of spatial population structure (Thomas and Kunin 1999). Therefore, the type of spatial population structure will typically be species specific (e.g. Baguette *et al.* 2000).

Typically, direct threats to ERS habitat will lower the habitat quality of the affected patch (e.g. Chapter 4), whilst indirect threats may reduce patch quality and will reduce the connectivity and availability of ERS habitat (Bates *et al.* 2005; Chapter 9), which can both have important implications for spatially structured populations (e.g. Hill *et al.* 1996;

Fleishman *et al.* 2002; Fahrig 2003; Franken and Hik 2004). The species specific nature of spatial population structure will mean that individual species will respond to these effects in different ways. This chapter investigates and compares the underlying spatial population structure of three species of ERS specialist beetle: the common carabids *Bembidion atrocaeruleum* and *B. decorum* and the Nationally Notable (Nb) elaterid *Fleutiauxellus maritimus* (rarity statuses based on Chapter 3) with a view to understanding the likely response of each, to the various activities that threaten ERS habitats and communities (Chapter 9). The work addresses the following objectives:

1. To test the efficacy of the developed mark recapture methods.
2. To preliminarily investigate the effects of patch characteristics (quality) on the spatial population structure of the three study species.
3. To compare the spatial population structure of the three study species.

6.3 Methods

6.3.1 Site description and environmental variability

Patches of ERS are easily spatially delineated from the unsuitable surrounding habitat matrix by water, or very heavily vegetated areas. In total, nine such patches from a one sedimentation zone (Church 1983) were used in this investigation, although two sets of two patches (Bar 1 and 1a; and Bar 3c and 3d) became connected due to low water levels (Figure 6.1). Seven environmental variables were measured in the investigation (Chapter 2), namely bar length, width, and area, tree shade, vegetation cover, sediment heterogeneity and dominant sediment size. Sediment heterogeneity (1-5, with 5 most heterogeneous) and dominant sediment size were estimated from ≤5 sediment photographs placed to encapsulate as much sediment diversity across the bar as possible. Samples of fine sediment were taken and proportions of different phi classes measured using dry sieving and laser particle sizing using a Malvern Mastersizer 2000MU. The investigation studied the spatial population structure during stable weather conditions at base flow level.

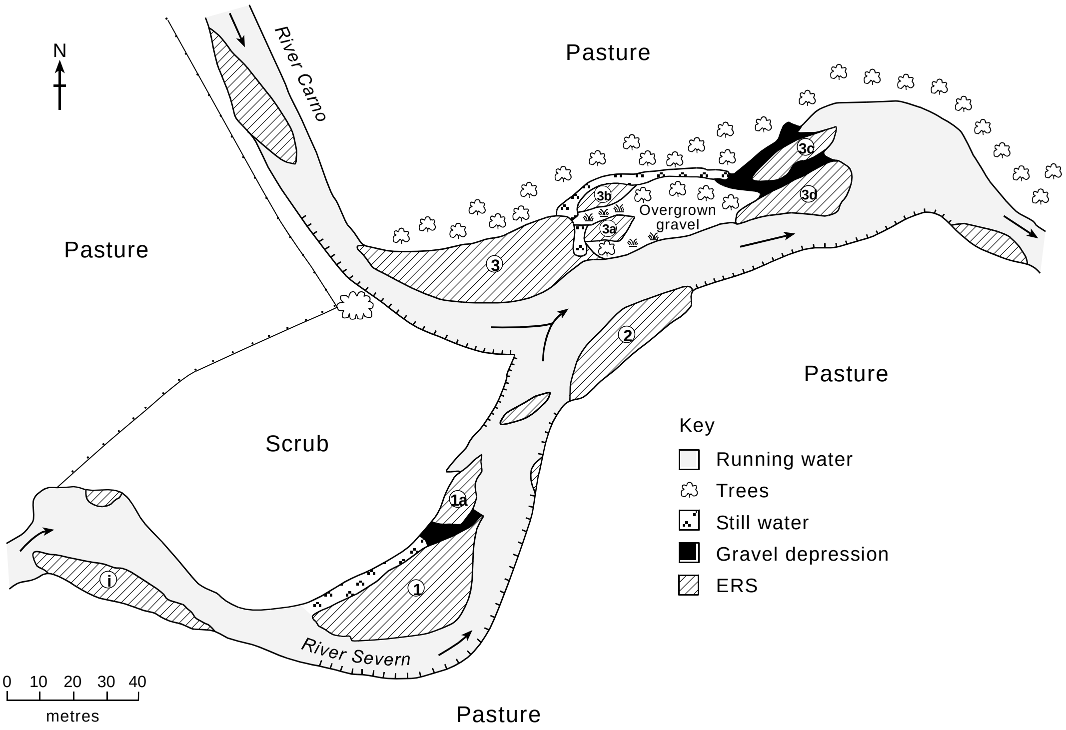


Figure 6.1 The mark recapture study site. The numbers highlight bars that were sampled.

6.3.2 Scale of study

Measured dispersal parameters in investigations of spatial population structure are highly dependent on the size of the study area over which the investigation takes place (Koenig et al. 1996; Schneider 2003), so it is important to state the scale of investigation. Within sedimentation zones the distribution of ERS patches are typically regularly and closely spaced, having a distribution that is analogous to beads threaded along a necklace. This natural habitat distribution allowed the spatial population structure within sedimentation zones to be satisfactorily assessed by the scale (~300m of river) of this study. Longer distance upstream dispersal between the study area sedimentation zone and other sedimentation zones was assessed to some degree by additional sampling for ~6km upstream (Chapter 8).

6.3.3 Study species

The three study species (*B. atrocaeruleum*, *B. decorum*, *F. maritimus*) were large enough to be marked (4.5-5.5, 5.6-6 and 4-6mm in length respectively), were known to be abundant on Upper Severn ERS (Sadler *et al.* 2004), and were readily identifiable in the field. The carabids are known to breed in the early spring in the UK, with larvae, and teneral adults present during the summer (June to August inclusive), and over-winter as adults. Both species are constantly macropterous (full-winged), and are always in possession of functional flight muscles, and so are constantly capable of flight (Desender 1989). Less is known about *F. maritimus*, but it is believed to have a similar lifecycle, has full wings and is likely to always be capable of flight. Beetle larvae are capable of limited dispersal (Traugott 2002), but the marked separation of ERS patches by water or unsuitable heavily vegetated habitat almost certainly prohibits inter-patch dispersal by larvae, although no data exist to substantiate this assertion.

6.3.4 Sampling design

Beetles were captured, handled and marked using the methods described in Chapter 2. Trap lids were removed in the morning and beetles were collected from the traps ~24 hours later.

Two periods of mark-recapture were undertaken, one in June and one in August. In the first period, trapping took place on 4-5/6/02, 12-13/6/02, 13-14/6/02, 18-19/6/02, 19-20/6/02, 20-21/6/02 and 25-26/6/02, and beetles were marked and released on 5, 13, 14, 19 and 20/6/02. On 26/6/02 beetles were released without marking. A total of 123 traps were set for the first six sampling periods, with an additional 67 traps for the final re-capture session. The traps were roughly divided between the numbered study bars according to their area, and placed in grids, covering as much of the bar as possible.

Between the June and August period of mark-recapture, Bars 3a, 3b and 3c became overgrown and were not used in the second study. To compensate, an extra bar, Bar i, was trapped. In the second period of mark-recapture half the bars were usually trapped on one day and half the following day so that Bars 1, i and 2 were trapped on 6-7/8/02, 13-14/8/02, 20-21/8/02 and 21-22/8/02, and Bars 1a, 3 and 3d were trapped on 7-8/8/02, 14-15/8/02, 20-21/8/02 and 21-22/8/02. A total of 200 traps were set across all the bars.

6.3.5 Estimation of population size

Fleutiauxellus maritimus showed no evidence of inter-patch movement during the study period, no teneral specimens were captured, and the short period of study restricted the potential for mortality, so the closed population programme CAPTURE (Otis *et al.* 1978b) was selected to estimate population size. CAPTURE (Otis *et al.* 1978a; Rexstad and Burnham 1992) comprises nine models that estimate population size under different assumptions. The programme objectively guides the user to select the most parsimonious model that best fits the data.

Bembidion atrocaeruleum and *B. decorum* were shown to migrate between bars over the period of study. The assumption of population closure was therefore rejected and the open population programme JOLLY (Pollock *et al.* 1990a, 1990b) was selected for data analysis. The programme uses variants of the Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965), and calculates the goodness of fit for each. Tests of goodness of fit often had poor power to reject models due to low recapture probability, so models were rejected on the grounds of unrealistic parameter estimates (e.g. survival estimates >1) and unrealistic assumptions (e.g. constant capture rate).

6.4 Results

6.4.1 Environmental variables

The bars studied demonstrated an array of different sediment sizes both between and within bars (Figure 6.2). Bars 1a, 3c and 3d were found to have fairly uniform surface sediments, which were quite fine in the case of 1a and 3c and coarse in 3d. Bars i, 1, 2, 3, 3a and 3b in contrast, showed more within-patch diversity because of the presence of finer sediments at the downstream end or elevated areas of the bars. The percentage organic matter in samples was highly variable (Figure 6.2), and showed no relationship to sediment size, or the presence of trampling. Information from Figure 6.2 is summarised in terms of sediment heterogeneity and dominant size in Table 6.1, together with the remaining environmental variables. Study bars showed a diversity of sediment heterogeneity, dominant sediment size, percentage tree shading, vegetation cover and trampling damage.

Table 6.1 Selected environmental variables for each study bar.

Bar code	ERS length (m)	ERS width (m)	Sediment heterogeneity	Dominant sediment size (phi)	Tree shade (%)	Vegetation cover (%)	Heavily grazed	Area (m^2)
1	54	24	3	-5	0	5	N	2062.25
1a	20	10	1	-4.6	0	10	N	535.45
2	47	11	3	-5.2	0	2	Y	831.03
3	68	22	2	-4.6	0	5	N	1371.60
3a	7	2	2	-4.6	100	10	N	89.46
3b	8	3	2	-4.7	100	5	N	86.10
3c	32	10	2	-4.6	20	20	N	289.56
3d	40	12	2	-5.6	10	5	N	809.61
i	59	12	2	-4.9	0	5	Y	771.05

6.4.2 Mark longevity

When marks were missing, illegible, misread, or misapplied, the complete capture history of an individual could not always be determined. Of the 262 *B. atrocaeroleum* recaptured during June and August 2002, 37 (14.1%) could not be individually identified (Figure 6.3). Nevertheless, of those 37 only five (13.5%) did not have a legible date of release mark, so the date upon which the individual was released and recaptured was usually known. As only 30 *B. atrocaeroleum* were recaptured more than once, and none of the erroneous colour codes appeared in recapture data more than once, it was assumed that individuals recaptured with only a legible date of release mark were only recaptured once. Of the 30 *F. maritimus* recaptured during June and August 2002, only one (3.3%) could not be individually identified (Figure 6.4). That individual did have a legible date of release mark and this was again assumed to be its only recapture. Of the 12 *B. decorum* recaptured during June and August 2002, two (16.7%) could not be identified individually or to date of capture.

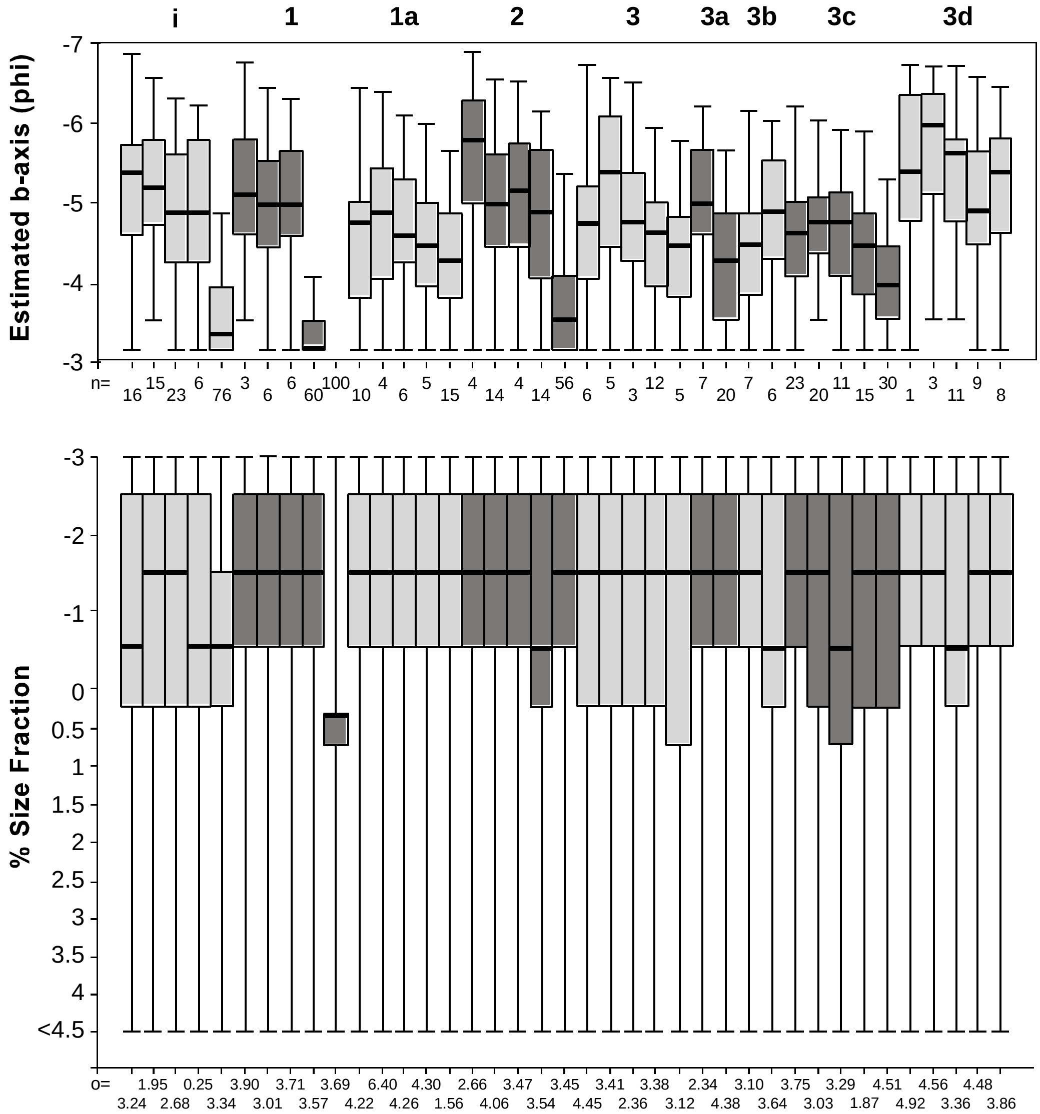


Figure 6.2 Sediment diversity within each study patch. The upper boxplot shows the size distribution of sediments with a b-axis >8mm estimated from photographs. The lower boxplot shows the size distribution of sediments smaller than >8mm measured using dry sieving and a laser particle sizing. N = the percentage of surface sediments finer than 8mm as estimated from photographs, and O = the percentage organic matter from sub-samples of the >1mm fraction of the sediment. The 10, 25, 50 (median), 75, and 90 percentiles are displayed in each boxplot.

The main drawback of the loss of marks was that inter-bar movements of unidentified individuals could not be detected, but this seems unavoidable to some extent. Total loss of all marks was possible, but usually only one or two marks were missing so it seems unlikely that it occurred to any large extent over the short study periods. For *F. maritimus* marks may be more durable, probably due to the paint adhering more easily to the hairs on the beetles' elytra. It was concluded, therefore, that the marks used were sufficiently durable for use in mark-recapture studies of *B. atrocaeruleum* and *F. maritimus* living on ERS, provided that the individual studies were only run for a period of around one month.

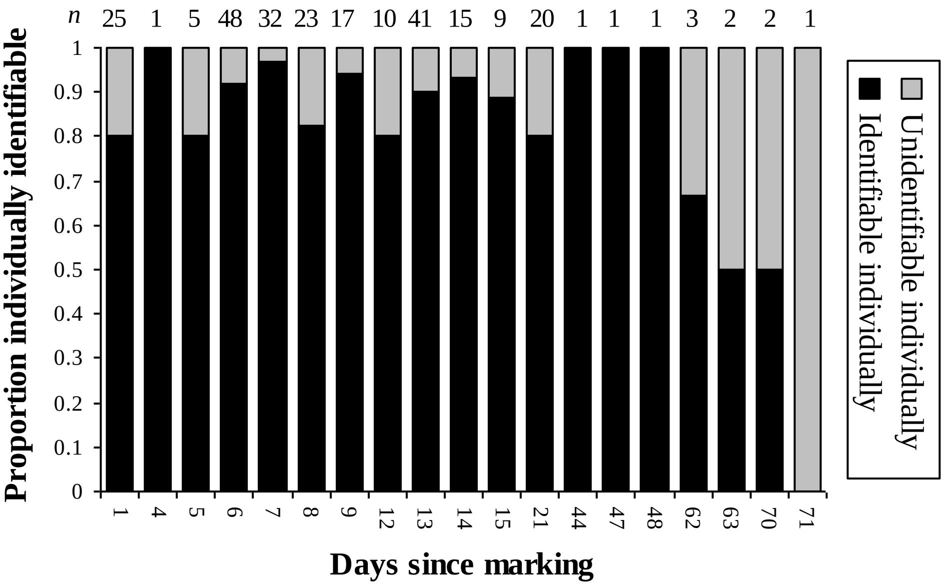


Figure 6.3 Relationship between the proportion of identifiable mark codes for recaptures of *Bembidion atrocaeruleum* and time (*n* = number of recaptures on which the proportion is based).

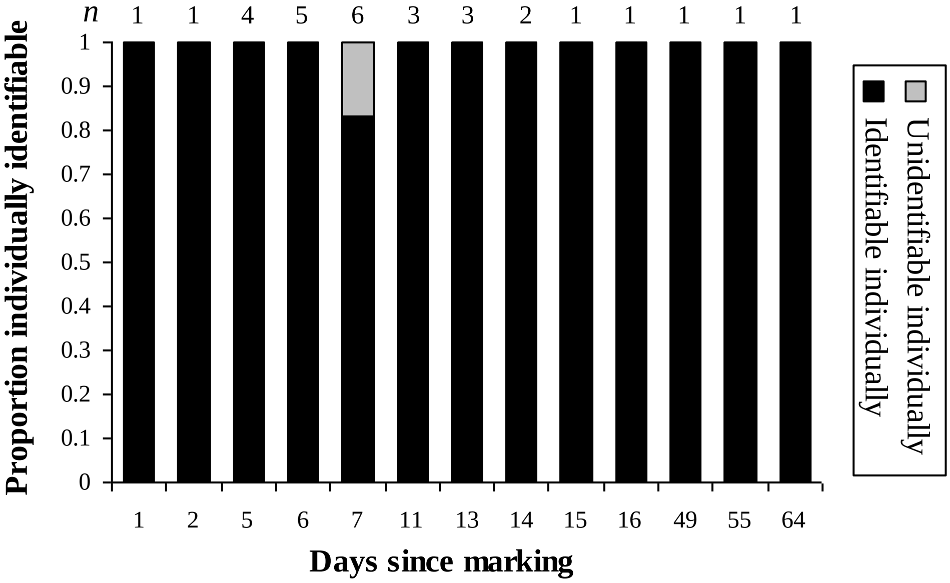


Figure 6.4 Relationship between the proportion of identifiable mark codes for recaptures of *Fleutiauxellus maritimus* and time (*n* = number of recaptures on which the proportion is based).

6.4.3 Inter-patch movements

Only beetles that could be identified individually were considered in the analysis of inter-patch movements. Of 157 *B. atrocaeruleum* marked in June and recaptured in both the June and August 2002 sampling periods, 27 (17.2%) were shown to have moved between bars (Table 6.2). This figure is artificially high because Bars 1 and 1a, and Bars 3c and 3d were connected due to low water levels throughout most of the study, so were no longer distinct patches. Nine *B. atrocaeruleum* (5.7%) were shown to have moved between bars over a real barrier to movement, three through thick vegetation and six over water. Of the 10, marked *B. decorum* recaptured, two (20%) were shown to have moved between bars, one between patches that had become connected and one over water. The greatest distance moved by *B. atrocaeruleum* and *B. decorum* was ≥65m and ≥135m respectively. None of the 29 *F. maritimus* marked in June and recaptured in both the June and August 2002 sampling periods was shown to have moved between bars.

Out of the 33 marked *B. atrocaeruleum* released and recaptured in the August 2002 sampling period, only one was shown to have moved between bars, but this individual did move over water (Table 6.2). If the movement rate were the same as in those released in June 2002 (17.2%) the expected number of *B. atrocaeruleum* shown to move between bars would be 5.7. The one recognisable *F. maritimus* both released and recaptured in August 2002 did not move between bars. No marked *B. decorum* were recaptured in August.

6.4.4 Population size estimates and effect of environmental variables

Due to the low probability of recapture, reasonable estimates of population size could only be made for *B. atrocaeruleum* and *F. maritimus* for some of the bars in June 2002 (Table 6.3). JOLLY model A', which allows for deaths/emigration, but no births/immigration, was selected as the most appropriate model for *B. atrocaeruleum*. No teneral individuals were captured during the June study period, and although there was immigration it showed no discernable direction, so this model was considered suitable. For *F. maritimus*, CAPTURE models M_t Chao and M_{th} Chao were selected for Bars 1 and 2 respectively. M_t Chao allows capture probabilities to vary with time and is preferred to M_t Darroch because it reduces the amount of bias due to small samples (Rexstad and Burnham 1992). M_{th} Chao allows capture probabilities to vary by time and by individual animal. Time-varying capture probabilities were expected because of changes in activity due to temperature (e.g. Greenslade 1964b) and because of the varying sampling intensity in the June study. No estimates could be made for *B. decorum* during both studies and for *B. atrocaeruleum* and *F. maritimus* during the August study due to limited recaptures. This was because during warm periods *B. decorum* activity aggregated at the water's edge (see Chapter 5), and the low water level meant that traps were not effectively positioned to capture this species.

Table 6.2 Known movements of individual *Bembidion atrocaeruleum* and *B. decorum* during the 2002 mark-recapture study. Data in bold represent individuals that were recaptured in August.

Species	Bar marked	Date marked	Bar captured	Date captured	Bar recap	Date recap	Bar recap 2	Date recap 2	Bar recap 3	Date recap 3
B. atrocaeruleum	1	05/06/2002	1a	26/06/2002	-	-	-	-	-	-
B. atrocaeruleum	1	05/06/2002	1a	14/06/2002	-	-	-	-	-	-
B. atrocaeruleum	1	13/06/2002	1a	26/06/2002	-	-	-	-	-	-
B. atrocaeruleum	2	05/06/2002	3c	20/06/2002	3c	26/06/2002	-	-	-	-
B. atrocaeruleum	3	05/06/2002	1	19/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3	05/06/2002	3d	14/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3a	13/06/2002	3a	19/06/2002	1	20/06/2002	-	-	-	-
B. atrocaeruleum	3a	13/06/2002	3b	20/06/2002	3b	26/06/2002	-	-	-	-
B. atrocaeruleum	3b	05/06/2002	3a	14/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3b	13/06/2002	3b	19/06/2002	3a	20/06/2002	-	-	-	-
B. atrocaeruleum	3c	05/06/2002	3d	14/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3c	05/06/2002	3d	21/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3c	05/06/2002	3d	14/06/2002	3c	20/06/2002	3c	26/06/2002	-	-
B. atrocaeruleum	3c	13/06/2002	3d	20/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3c	13/06/2002	3d	26/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3c	20/06/2002	3d	26/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3c	20/06/2002	3d	26/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3d	05/06/2002	3c	13/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3d	05/06/2002	3c	19/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3d	05/06/2002	3c	13/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3d	13/06/2002	3c	26/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3d	13/06/2002	3d	19/06/2002	-	-	-	-	-	-
B. atrocaeruleum	3d	13/06/2002	3d	20/06/2002	3c	26/06/2002	-	-	-	-
B. atrocaeruleum	3d	13/06/2002	3c	21/06/2002	3d	26/06/2002	-	-	-	-
B. atrocaeruleum	3d	13/06/2002	3d	19/06/2002	3c	21/06/2002	-	-	-	-
B. atrocaeruleum	3d	13/06/2002	3d	20/06/2002	3c	26/06/2002	-	-	-	-
B. atrocaeruleum	3d	13/06/2002	3d	14/06/2002	3d	19/06/2002	3b	20/06/2002	3b	26/06/2002
B. atrocaeruleum	**3d**	**20/06/2002**	**3c**	**03/08/2002**	**-**	**-**	**-**	**-**	**-**	**-**
B. atrocaeruleum	**3c**	**20/06/2002**	**3d**	**22/08/2002**	**-**	**-**	**-**	**-**	**-**	**-**
B. atrocaeruleum	**3**	**08/08/2002**	**3d**	**17/08/2002**	**-**	**-**	**-**	**-**	**-**	**-**
B. decorum	3c	13/06/2002	3d	26/06/2002	-	-	-	-	-	-
B. decorum	3c	13/06/2002	1	26/06/2002	-	-	-	-	-	-

Table 6.3 Population size and density estimates for *Bembidion atrocaeruleum* and *Fleutiauxellus maritimus* on individual bars for 5-21 June 2002.

Species	Bar	No. unmarked captured	No. marked	No. marked captured	Selected model	Mean estimate	95% confidence interval	Density (m^2)	95% confidence interval
B. atrocaeruleum	1	469	181	21	A'-J	1930.29 (n=3)	1077.19 - 2783.39	0.94	0.52 - 1.35
B. atrocaeruleum	1a	210	103	14	A'-J	721.57 (n=3)	272.07 - 1171.07	1.35	0.51 - 2.19
B. atrocaeruleum	3a	73	36	16	A'-J	117.99 (n=3)	48.40 - 187.57	1.32	0.54 - 2.10
B. atrocaeruleum	3b	73	32	22	A'-J	95.27 (n=3)	67.50 - 123.03	1.11	0.78 - 1.43
B. atrocaeruleum	3c	304	113	46	A'-J	650.45 (n=3)	396.94 - 903.95	2.25	1.37 - 3.12
B. atrocaeruleum	3d	427	140	34	A'-J	1100.96 (n=3)	437.17 - 1764.74	1.36	0.54 - 2.18
F. maritimus	1	181	175	15	M(t) Chao	725 (n=1)	485 - 1152	0.35	0.24 - 0.56
F. maritimus	2	22	16	4	M(th) Chao	41 (n=1)	25 - 100	0.05	0.03 - 0.12

The 95% confidence intervals for population estimates of *F. maritimus* on Bars 1 and 2 do not overlap (Table 6.3) so the size of the population on Bar 1 can be considered significantly higher than that on Bar 2 at the 0.05 level. This difference was not simply an effect of bar size, as the population density was also significantly different ($p<0.05$, Table 6.3). Some other environmental variable, an effect of population structure, or a combination of factors must have influenced population density in this species.

Reasonable population estimates were made for *B. atrocaeruleum* on six bars in the June study period (Table 6.3). These were rank correlated, where possible, with the environmental variables shown in Table 6.1 (Table 6.4). Significant correlations were found between estimated population size and bar area (1.000**), bar length (0.886*), bar width (0.928**) and shading (-0.883*). However, shading and bar width (-0.821*), and shading and bar area (-0.883*) co-varied, as may be intuitively expected. Despite the wide variation of population size between bars, actual densities showed little variation, and all 95% confidence intervals for density over-lapped, with the exception of those for Bars 1 and 3c (Table 6.3), so it was not surprising that there were no significant relationships between the environmental variables and the density of *B. atrocaeruleum*. As such, it seems likely that the significant correlation between population size and percentage shading is, in this instance, an artefact of the relationship between bar size and shading. Of the variables measured therefore, bar size and, more specifically bar area, was the key determinant of the population size of *B. atrocaeruleum* in this investigation.

Table 6.4 Spearman's rank correlations between population size estimates and population density for *Bembidion atrocaeruleum*, and environmental variables.

		Sed. Size	T. sha.	% Veg.	Sed. Het.	Width	Leng.	Area	Dens.
Number estimated	Correlation coefficient	-0.516	-0.883*	-0.278	0.338	0.928**	0.886*	1.000**	-0.029
	Significance (2-tailed)	0.295	0.20	0.594	0.512	0.008	0.019	0.000	0.957
Density (m^{-2})	Correlation coefficient	0.273	0.029	0.617	0.507	-0.029	0.029	-0.029	1
	Significance (2-tailed)	0.600	0.956	0.192	0.305	0.957	0.957	0.957	.
Bar area (m^2)	Correlation coefficient	-0.516	-0.883*	-0.278	0.338	0.928**	0.886*	1	
	Significance (2-tailed)	0.295	0.20	0.594	0.512	0.008	0.019	.	
Length (m)	Correlation coefficient	-0.638	-0.736	-0.339	0.507	0.986**	1		
	Significance (2-tailed)	0.173	0.096	0.510	0.305	0.000	.		
Width (m)	Correlation coefficient	-0.647	-0.821*	-0.391	0.429	1			
	Significance (2-tailed)	0.165	0.045	0.443	0.396	.			
Sediment heterogeneity	Correlation coefficient	-0.539	0.000	-0.456	1				
	Significance (2-tailed)	0.270	1.000	0.363	.				
Vegetation cover (%)	Correlation coefficient	0.885*	0.127	1					
	Significance (2-tailed)	0.019	0.810	.					
Tree shade (%)	Correlation coefficient	0.250	1						
	Significance (2-tailed)	0.633	.						
Dominant sediment size	Correlation coefficient	1							
	Significance (2-tailed)	.							

6.5 Discussion

The findings of the 2002 study were preliminary in nature and used to better inform the following, larger scale, mark-recapture study run in 2003. In particular, because of the wide confidence intervals around local population size estimates (Table 6.3), the objective of investigating the effect of patch quality on the spatial population structure was not fully realised, particularly for *B. decorum*. Therefore, this discussion has been kept brief and focused on a comparison of likely spatial population structure between the three species and suggestions for methodological modifications, which were used in the 2003 study.

6.5.1 Comparison of spatial population structures and effects of patch quality

The ability of many specialist ERS beetles to swim strongly and survive underwater for long periods (Anderson 1968) suggests that downstream transfer by water flow is a likely dispersal mechanism. Indeed, high abundances of specialist ERS beetles can be found in stranded flood debris following high water levels (Hammond 1998a). In this study however, both *B. atrocaeruleum* and *B. decorum* moved upstream to other habitat patches and, given the relatively rapid flow at the study site, it seems highly improbably that these movements were achieved by swimming against the flow. Therefore dispersal by flight is important in *B. atrocaeruleum* and *B. decorum*, a finding supported by the highly developed wings (Desender 1989) in these and other ERS specialist carabid species.

When (a) local populations are subject to periodic turnover, and (b) when there is migration between local populations; populations can be classified as metapopulations (Hanski and Gilpin 1991). When (c) all suitable patches in a system are occupied because local extinctions are absent or not important due to high rates of dispersal, and (d) when on average, an individual inhabits more than one patch in its lifetime; populations can be classified as patchy (Harrison 1991). When (e) the rate of movement between habitat patches is so large that individuals occupy many patches throughout their lifetime, each patch cannot be said to support a local population. However, these exact classifications are unrealistic and most populations will combine features of both types of spatial population structure (Harrison 1991; Sutcliffe *et al.* 1997a). Populations can instead be classified along two axes: a 'mobility' axis, which describes the level of dispersal between subpopulations, and a 'compensation' axis, which describes the degree to which a local population exports or imports individuals (Thomas and Kunin 1999). Differentiation along the mobility axis is the main focus here.

All recaptures of *F. maritimus* were on the same bar upon which they were released, and although *B. atrocaeruleum* and *B. decorum* were shown to move between bars, for the most part beetles were recaptured on the same bar on which they were released. Thus during the 2002 study each bar could be considered to have a local population of each of these species.

Both species of carabid were found on every bar studied in every one of the three study years in the segment scale patch investigation (Chapter 8), and together with their relatively high rate of inter-patch migration, this suggests that their spatial population structures approximated a patchy population. In contrast, the dispersal rate of *F. maritimus* was found to be much lower than that demonstrated by the two ground beetles. This species was not found on all of the patches studied in Chapter 8, but the hand searching methods used in that study under-represent the abundance of *F. maritimus*. This suggests that *F. maritimus* can be placed lower down on the mobility axis of Thomas and Kunin (1999), and this species may quite closely approximate a metapopulation.

Population size in *F. maritimus* was not exclusively influenced by bar area in this investigation, and the micro-scale distribution of *F. maritimus* was found to be limited (Chapter 5). The lower rate of dispersal in *F. maritimus*, together with its less general habitat preferences are likely to make it more vulnerable to the various threats to ERS and may go some way to explaining its much more limited national distribution when compared with *B. atrocaeruleum* and *B. decorum*.

6.5.2 Methodological modifications for the 2003 mark-recapture study

Reasonable population estimates could not be made for all bars and species, and those that could be made have quite large confidence intervals due to the large population sizes and relatively small rates of re-capture. Furthermore, detection of individual movements was too low to allow detailed analysis of the timing and direction of movements. A mark-resight approach (e.g. Dreitz *et al.* 2002) in which all marking takes place over a preliminary period and no marking takes place during subsequent re-captures was recommended (Jim Hynes pers comm.), and was used in the 2003 study (Chapter 7). This allowed a much larger proportion of field effort to be devoted to re-capturing individuals and less time marking them. Furthermore, the large numbers of marked individuals present throughout the recapture period, and the higher re-capture rate, allow the more rigorous study of population movement dynamics.

The difficulties encountered with the low re-capture rate for *B. decorum* due to the separation between the position of traps, and the micro-scale distribution of individuals, suggested further necessary modifications to the mark-recapture design. Namely, that pitfall traps should cover as wide an area of the bar as possible, as evenly as possible, so that the sampling intensity is kept reasonably constant, whatever the micro-scale distribution of a species.

CHAPTER 7

INTER-PATCH SPATIAL DYNAMICS: RESPONSE OF BEMBIDION ATROCAERULEUM TO INUNDATION AND TRAMPLING

7.1 Introduction

This chapter details the 2003 mark recapture study and uses the refined mark recapture methodology outlined in Chapter 6. Both *Bembidion atrocaeruleum* and *Fleutiauxellus maritimus* were studied, but limited rates of recapture of the latter species meant that the principle focus of this chapter was *B. atrocaeruleum*. All habitats were completely inundated by a high flow event (18-23/5/03) in this study, which allowed the investigation of inundation effects on the dynamics of the spatial population structure. The methodological improvements allowed the detection of a far greater number of inter-patch migrations, and more precise estimation of population size. This allowed the effects of patch quality on the dynamics of the spatial population structure to be investigated far more rigorously.

7.2 Background

Spatial population structure can be classified along two axes: (1) the mobility axis, and (2) the compensation axis (Thomas and Kunin 1999). The mobility axis classifies populations according to their inter-patch population structure, ranging from no transfer of individuals in separate populations, to limited rates of transfer of individuals between local populations in metapopulations, to high rates of transfer between local populations in patchy populations. The position of a population on this axis will be determined by both the dispersal capabilities of the species and the distribution of suitable patches in the landscape (Addicott *et al*. 1987; Bowne and Bowers 2004). The separation of spatial population structure between the three species investigated in Chapter 6 was made along this axis.

The compensation axis operates at the scale of the local population and is related to the demography of the local population, both in terms of birth and death rate and immigration and emigration rate (Thomas and Kunin 1999). It thus describes whether local populations are net importers or exporters of individuals and is tied up in ideas of source-sink dynamics (Pulliam 1988; Watkinson and Sutherland 1995). Migration between local populations can be ‘condition dependent’ (Bowler and Benton 2005), and can be influenced by a wide variety of ‘conditions’, including patch quality, patch size, population density, matrix characteristics, ontogeny, and sex (e.g. Stamps *et al.* 1987; Hill *et al.* 1996; Albrectsen and Nachman 2001; Massot *et al.* 2002; Matter and Roland 2002; Amarasekare 2004; Bonte *et al.* 2004). These ‘conditions’ can operate at any of the three independent stages of migration: emigration, inter-patch movement, and immigration (Bowler and Benton 2005). In riparian environments, episodes of habitat inundation and exposure are likely to condition the migration between local habitat patches, as partly evidenced by carabid flight activity in relation to fluctuating flight levels (Bonn 2000).

Investigations into such condition dependent migrations between local populations were possible because of the higher quality data on local population size and inter-patch migration rates obtained from this (2003) mark recapture investigation. This enabled the following objectives to be addressed:

1. To investigate the influence of habitat inundation on the reach scale population structure, and local emigration and immigration rates for *B. atrocaeruleum*.
2. To investigate the influence of habitat characteristics on local emigration and immigration rates for *B. atrocaeruleum*.
3. To investigate the influence of local population size and density on local emigration and immigration rates for *B. atrocaeruleum*.

4. To confirm and refine the classification of spatial population structure for *F. maritimus* and *B. atrocaeruleum* at the reach scale.

A discussion of the full implications of the findings for the likely population responses to threats and conservation management is reserved for Chapter 9.

7.3 Materials and methods

The methods employed in this chapter largely follow those described in Chapters 2, 5 and 6 and only departures from these methods are described in this section.

7.3.1 Study area and environmental characteristics

Six distinct patches of ERS of varying size and isolation (Figure 5.2, Bar US not shown) were originally chosen for study (Bars 1 & 1a, 2, 3, 3d, i and US), but this was discontinued on Bar US midway through the investigation because it proved impossible to sample in the time available. Seven environmental variables were measured on each bar, namely ‘bar area’ (estimated from the DEM), ‘sediment heterogeneity’, ‘typical sediment size’, ‘vegetation cover’, heavy cattle trampling and ‘inundation potential’. Inundation potential describes the relative ease with which the study bars were completely inundated as water level rose, where a score of 1 represented bars that were not easily completely inundated, and 3 represented bars that were most easily inundated. Weather and stage data were also used in the investigation.

7.3.2 Sampling procedure

Beetles were captured using 381 modified dry pitfall traps which were arranged in grids across the bars at a density of ~$0.06m^2$ (Table 7.1). The mark-resight approach required sampling to be split into marking periods, when no population estimates were made; and recapture periods, when beetles were only captured and no marking took place. Three separate mark-recapture periods were conducted over May, June and July 2003 (Table 7.2), as mark losses after periods of >30 days would bias population estimates

(Chapter 2). During recapture periods all traps were open for ~24 hours except for the first recapture period in July when heavy rainfall and a large rate of capture meant that traps on Bars 1&1a, 3 and 3d were open for ≤48 hours. Furthermore, time only allowed half the traps on Bar 3 to be checked in this sampling period. The May marking period was not followed by any recapture periods because the study reach was completely inundated (Figure 5.6) shortly afterwards.

Table 7.1 Summary environmental variables and sampling intensity by bar.

Bar code	Area (m^2)	Total traps	Trap density (m^2)	Sediment heterogeneity	Typical sediment size (phi)	Vegetation cover (%)	Heavily trampled	Inudation potential
1 & 1a	2354.3	130	0.055	3	-4.96	35	0	1
2	969.4	58	0.060	2	-4.15	3	1	2
3	1539.1	90	0.058	2	-4.41	20	0	1
3d	837.5	56	0.067	1	-5.13	35	0	3
I	823.38	47	0.057	2	-4.73	20	1	2

Table 7.2 Sampling schedule for the mark and release of beetles.

	Bar 1 & 1a	**Bar 2**	**Bar 3**	**Bar 3d**	**Bar I**
May mark	9-15/5/03	9-15/5/03	9-15/5/03	9-15/5/03	9-15/5/03
June mark	5-11/6/03	5-11/6/03	5-11/6/03	5-11/6/03	5-11/6/03
1st recapture	17/6/03	17/6/03	17/6/03	17/6/03	17/6/03
2nd recapture	23/6/03	24/6/03	24/6/03	24/6/03	23/6/03
3rd recapture	28/6/03	29/6/03	29/6/03	29/6/03	28/6/03
4th recapture	3/7/03	4/7/03	4/7/03	4/7/03	3/7/03
July mark	5-11/7/03	5-11/7/03	5-11/7/03	5-11/7/03	5-11/7/03
1st recapture	17-18/7/03	18/7/03	18-19/7/03	18-19/7/03	17/7/03
2nd recapture	22/7/03	23/7/03	23/7/03	23/7/03	22/7/03
3rd recapture	27/7/03	28/7/03	28/7/03	28/7/03	27/7/03
4th recapture	1/8/03	2/8/03	2/8/03	2/8/03	1/8/03

7.3.3 Estimation of local population size and density

Bembidion atrocaeruleum was previously shown to migrate between ERS patches (Chapter 6), so closed population models were not considered appropriate. Therefore the open population programme JOLLY (Chapter 6) was used to estimate population size. Due to the more extensive nature of the data in this study the programme had much more power to reject inappropriate models on the basis of violation of their assumptions (e.g. equal capture probability between periods). When more than one model still remained after this initial model rejection stage, the most parsimonious model was selected as the most appropriate. As no further animals were marked after the initial marking period, unmarked *B. atrocaeruleum* were entered into the programme as animals that were not released after capture. Population densities (m^2) were calculated by dividing estimated local population size by patch area.

7.4 Results

7.4.1 Environmental variables

The study bars showed considerable differences in all environmental variables measured (Table 7.1). Bars ranged in character from small, easily inundated, relatively homogeneous patches of ERS (e.g. Bar 3d), to large, diverse, elevated, patches of ERS (e.g. Bar 1&1a). Air temperature, rainfall and flow level all varied markedly over the study period (Figure 5.6; Chapter 5). Two events were of particular significance for the patch-scale dynamics: (1) the complete, extended inundation of all bars following prolonged rainfall in mid May, which would compel beetles to evacuate bars by walking and/or flight, and/or would cause population reduction through removal downstream or direct mortality; and (2) the near inundation of bars following very heavy rainfall on 24/07/03 which may have instigated a movement response and/or population reduction.

7.4.2 Inter-patch migration dynamics

All known movements of *B. atrocaeruleum* released in the May, June, and July marking periods are shown in Table 7.3. The overall percentage rate of recapture was lowest for the May release (11.69%), when compared with the June (29.58%) and July (25.59%) releases, despite the longer time period over which recaptures could be made. Both the overall and daily percentage inter-patch migration rate was highest for the May release (39.47%, 0.46% per day) compared to June (6.43%, 0.11% per day) and July

(7.84%, 0.27% per day). The three highest rates of emigration were from the three most easily inundated bars (Tables 7.1 and 7.3), but this observation lacked the replication to test this statistically. The only known migration out of the study area were of two individuals released in May that were captured at least 488m upstream (measured in a straight line) of the mark-recapture area. These represented migrations to the nearest distinct sedimentation zone upstream. However, it was not known which bar they were released on because of mark loss.

Table 7.3 Known movements of *Bembidion atrocaeruleum* in each release period.

Release period	Bar released	Total released	Tot. individuals recaptured	% recaptured	Tot. individuals emigrated	% emigration	Immigration (% of tot. emigrated)				
							1 & 1a	2	3	3d	i
May	1 & 1a	311	38	12.2	10	26.3	-	0.0	30.0	50.0	20.0
	2	167	20	12.0	12	60.0	58.3	-	25.0	16.7	0.0
	3	359	70	19.5	14	20.0	92.9	0.0	-	7.1	0.0
	3d	349	37	10.6	16	43.2	58.8	5.9	17.6	-	11.8
	i	191	11	5.8	8	72.7	62.5	0.0	12.5	25.0	-
	US	249	14	5.6	14*	100.0	64.3	7.1	0.0	21.4	7.1
			Total immigration (% of all emigration)				**59.5**	**2.7**	**13.5**	**17.6**	**6.8**
June	1 & 1a	758	247	32.6	11	4.5	-	18.2	36.4	27.3	18.2
	2	134	26	19.4	5	19.2	40.0	-	20.0	20.0	20.0
	3	257	78	30.4	1	1.3	100.0	0.0	-	0.0	0.0
	3d	314	111	35.4	6	5.4	50.0	16.7	33.3	-	0.0
	i	175	75	42.9	6	8.0	100.0	0.0	0.0	0.0	-
	US	201	7	3.5	7*	100.0	57.1	0.0	0.0	0.0	42.9
			Total immigration (% of all emigration)				**44.4**	**8.3**	**19.4**	**11.1**	**16.7**
July	1 & 1a	487	148	30.4	13	8.8	-	23.1	53.8	0.0	23.1
	2	265	35	13.2	15	42.9	26.7	-	40.0	20.0	13.3
	3	294	81	27.6	3	3.7	33.3	33.3	-	33.3	0.0
	3d	500	135	27.0	4	3.0	50.0	0.0	50.0	-	0.0
	i	248	60	24.2	5	8.3	80.0	0.0	0.0	20.0	-
			Total immigration (% of all emigration)				**27.5**	**10.0**	**37.5**	**12.5**	**12.5**

*did not sample again after initial release

Summed across all bars, 121 marked *F. maritimus* were released in May, 123 in June and 147 in July. The lowest rate of recapture was for those released in May when no individuals were recaptured. In June and July, 9 (7.32%) and 10 (6.80%) individuals were recaptured respectively, all of which were recaptured on the bar they were released.

7.4.3 Local population size and density

Local population size was estimated for *B. atrocaeruleum* on each bar for the June and July mark-recapture periods, entering any known emigrations and immigrations of marked individuals into JOLLY as deaths and newly marked individuals respectively. Two models were selected as the most appropriate: (1) ‘Jolly A’, which is the standard Cormack-Jolly-Seber model; and (2) ‘Jolly B’, which is the Cormack-Jolly-Seber model with survival rate assumed constant per unit time and time-specific capture probability (Table 7.4).

Table 7.4 Mark-recapture model selection and summary input.

Release period	Bar	Total marked	Total unmarked captured	Total marked individuals captured	Model selected
June	1 & 1a	758	4973	206	Jolly A
	2	134	470	23	Jolly A
	3	257	1520	80	Jolly B
	3d	314	3816	89	Jolly B
	I	174	1561	64	Jolly B
July	1 & 1a	487	8251	163	Jolly B
	2	265	486	41	Jolly A
	3	294	2048	103	Jolly B
	3d	500	5312	166	Jolly B
	I	248	1838	71	Jolly A

The mean estimated population size on each bar for the June and July mark-recapture periods are shown in Figure 7.1, together with the mean estimated density for the June and July mark-recapture periods and sub-periods. The 95% confidence intervals around estimates were used to identify significantly different population densities. Although local population density is the main focus, the high level of correlation with local population size (Table 7.5) meant that trends in population size were very similar. Significant temporal differences in density were observed for Bar 1 & 1a, where the density was higher on 18/7/03 than on 17/6/03 and 22/7/03, and on Bar i, where the density was higher on 17/7/03 than on 23/6/03. There was a non-significant trend of estimated densities peaking around 28-29/6/03 and 17-19/7/03 on Bars 1 & 1a, 3, and i, and a generally upward trend in density estimates for Bar 3d. Density estimates were generally similar for Bars 1 & 1a, 3, and i, although the density on Bar 1 & 1a on 18/7/03 was significantly higher than many of the estimates on Bars 3 and i. Density on Bar 2 was particularly low, with the density estimated for 23/07/03 significantly lower than some density estimates on every other bar. The estimated density on Bar 3d was much higher than on all other bars, particularly during July, when it was significantly higher than most density estimates on the other bars (Figure 7.1).

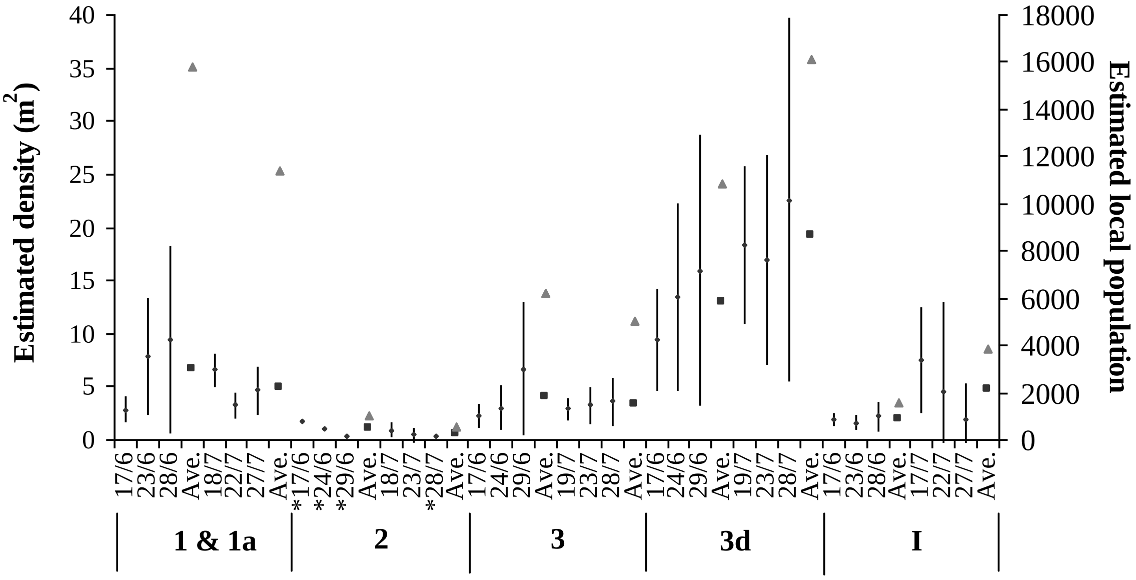


Figure 7.1 Estimated local population density and size for each study bar. Densities by date are represented by dashes, where error bars are 95% confidence intervals (not available on dates marked with an asterisk due to poor data), and squares for mean values for the June and July (2003) recapture periods. The mean estimated local population size for the June and July recapture periods are represented by the grey triangles.

7.4.4 Relationships between environmental variables, local population density and inter-patch migrations

Spearman’s rank correlations between estimated mean density and population size, migrations and environmental variables for *B. atrocaeruleum* are shown in Table 7.5. Local population density and population size were strongly positively correlated with each other and were significantly correlated with the same environmental variables. They were both positively correlated with vegetation cover and negatively correlated with heavy trampling and sediment size, although it should be noted that because the phi units are negatively scaled, the latter correlation showed that the densest local populations of *B.*

atrocaeruleum were associated with the coarsest sediments. Trampling and typical sediment size, were both significantly negatively correlated with vegetation cover. The percentage emigration was significantly positively correlated with heavy trampling, and significantly negatively correlated with population size.

Table 7.5 Spearman’s rank correlations between monthly average population density and local population estimates, inter-bar movements (Table 7.3), and summary environmental variables for the June and July 2004 releases (* = correlation significant at the 5% level, ** = correlation significant at the 1% level).

		He. tr.	Veg. co.	Sed. si.	Sed. het.	Area	Pop. si.	Den	Em. %
Total immigration (%)	Corr. Coef.	-0.606	0.495	-0.272	0.580	0.580	0.541	0.310	-0.535
	Sig. (2-tailed)	0.063	0.146	0.448	0.079	0.079	0.106	0.383	0.111
Emigration (%)	Corr. Coef.	0.711*	-0.467	0.394	0.275	-0.123	-0.636*	-0.539	1
	Sig. (2-tailed)	0.021	0.173	0.260	0.441	0.735	0.048	0.108	.
Density (m^2)	Corr. Coef.	-0.711*	0.934**	-0.935**	-0.220	0.049	0.927**	1	
	Sig. (2-tailed)	0.021	0.000	0.000	0.541	0.893	0.000	.	
Local population size	Corr. Coef.	-0.853**	0.934**	-0.837**	0.000	0.345	1		
	Sig. (2-tailed)	0.002	0.000	0.003	1.000	0.329	.		
Bar area (m^2)	Corr. Coef.	-0.577	0.211	0.100	0.671*	1			
	Sig. (2-tailed)	0.081	0.559	0.783	0.034	.			
Sediment heterogeneity	Corr. Coef.	0.000	0.000	0.224	1				
	Sig. (2-tailed)	1.000	1.000	0.535	.				
Typical sediment size (phi)	Corr. Coef.	0.577	-0.949**	1					
	Sig. (2-tailed)	0.081	0.000	.					
Vegetation cover (%)	Corr. Coef.	-0.761*	1						
	Sig. (2-tailed)	0.011	.						
Heavily trampled	Corr. Coef.	1							
	Sig. (2-tailed)	.							

7.5 Discussion

7.5.1 Effects of habitat inundation

Shortly after the May release of marked beetles all bars were completely inundated, and inter-patch migration by flight and mortality might have been expected to increase. Indeed, the inter-patch movement rate was highest for *B. atrocaeruleum* (39.47%), and the recapture rate was lowest for both study species released in the May mark-recapture period. The lower movement rate in successive captures of *B. atrocaeruleum* suggested that the higher rate of migration in May was coincident with the high water levels, and that inter-patch movement rate was reduced in June and July when water levels were lower. The rate of inter-patch migration of *B. atrocaeruleum* shown in this study during the relatively low water conditions in June (6.43%) and July (7.84%) were comparable with rates observed from the 2002 study (June 5.73% and August 3.03%) when water levels were also low. It is possible that earlier in the season *B. atrocaeruleum* have a condition dependent 'dispersal phase' associated with reproduction, or emergence from over-wintering diapause, or that flight conditions were favourable due to higher temperatures and low rainfall (Southwood 1962; Desender 2000), and that the enhanced migration rate following habitat inundation was coincidental. However, given the known higher rate of flight activity by riparian carabids during and after floods (Bonn 2000), and the low temperatures and high levels of rainfall during the early summer (Figure 5.6), this seems unlikely.

The complete lack of recaptures of *F. maritimus* and the low rate of recapture of *B. atrocaeruleum* from the May release could have been due to a variety of factors, either individually or in association: (1) enhanced mark loss over the longer time period over which recaptures could be made; (2) a longer time period over which the background rate of mortality can act; (3) enhanced migration of individuals from the study area during the inundation event; and (4) enhanced mortality during the inundation event. Large floods can markedly reduce the density of ERS specialist carabids (Hering *et al.* 2004) most probably through direct mortality, but it is unlikely that smaller inundation events cause substantial mortality in adult ERS specialist carabids because they can swim and survive inundation very well (Andersen 1968; Zulka 1994; Hammond 1998a). The ability of ERS specialist elaterids to survive inundations is less well known, but may be lower. However, if individuals did enter the stream as the water rose, many may have been carried downstream and out of the study area before they were able to get to shore. Two *B. atrocaeruleum* released in May were captured upstream of the study area, but no individuals released in June or July were captured outside of the study area. It seems probable therefore that at least some of the lower rate of recapture in May can be explained by migration out of the study area.

The incomplete inundation that occurred on 24/07/03 did not show any signs of reducing the population density of *B. atrocaeruleum* with two bars showing slight, non-significant reductions, and three bars showing slight non-significant increases in population density between 23/07/03 and 28/07/03 (Figure 7.1). There was also no obvious increase in the inter-patch migration rate after this event, although the overall percentage movement rate was higher in July (0.27% per day) than in June (0.11%). So there may have been a slight elevation of migration rate in response to this event, but it was certainly not as marked as after the May event.

7.5.2 Patch quality effects on population size, density and migration

Three environmental variables: trampling, vegetation cover, and sediment size, showed significant correlations with local population size and density, although vegetation cover co-varied with each (Table 7.5). *Bembidion atrocaeruleum* did not show consistent microspatial association with vegetation cover (Chapter 5), so it seems likely therefore, that the observed positive association between vegetation cover and population density was an artefact of the relationship between vegetation cover and sediment size/trampling. *Bembidion atrocaeruleum* tends to be associated with coarser sediments so the observed correlation between sediment size and population density might be expected. ERS damage by livestock was shown to reduce the abundance and diversity of ERS specialist beetles in Chapter 4. This investigation supported those findings, with significantly lower population densities of *B. atrocaeruleum* on the ERS patches that were heavily impacted by cattle (Bars 2 and i).

There was also a positive relationship between emigration rate and heavy trampling, which suggests that the low population densities on the trampled bars were due to a combination of direct mortality and migration away from the trampled bars. Migration from low quality or dangerous habitat due to an escape response can be advantageous because it enhances the chances of individuals finding more suitable habitat (e.g. Dixon 1958; den Boer 1983; Brodsky and Barlow 1986). It is unclear what cues are used to trigger such avoidance migrations, but the presence of conspecifics has been cited as one such possible determinant of habitat quality (Reed and Dobson 1993; Kuussaari *et al.* 1996). Such condition dependent dispersal in response to habitat quality has been reported for other several other species of invertebrate (e.g. Kuussaari *et al.* 1996; Matter and Roland 2002; Bonte *et al.* 2004).

7.5.3 Influence of population size and density on migration dynamics

Theoretical investigations of spatial population structure have rarely investigated the effects of population density on dispersal (e.g. Howe *et al.* 1991; Saether *et al.* 1999; Amarasekare 2004), despite fairly widespread evidence for increasing (e.g. Fonseca and Hart 1996; Aars and Ims 2000), and decreasing dispersal rate with increasing local population density (e.g. Hansson 1991; Kuussaari *et al.* 1996; Menéndez *et al.* 2002; Bonte *et al.* 2004). Such density dependent influences on dispersal are of major importance for the source sink dynamics of spatially structured populations as: (1) "*an increase in the emigration rate with increasing density will lead to <u>negative</u> density-dependent dispersal, which will strengthen self-limitation and increase a species' ability to increase when rare*", and (2) "*a decrease in the emigration rate with increasing density will lead to <u>positive</u> density-dependent dispersal, which will weaken self-limitation and reduce a species' ability to increase when rare*" (Amarasekare 2004, pp.159-160 emphasis my own).

The lack of theoretical studies on density dependent dispersal could partly have resulted from the difficulty of separating the effects of population density from the effects of patch quality, as high quality patches will typically support high population density and *vice versa*. This was also a problem in this investigation to some degree, because although emigration rate was positively correlated with heavy trampling and not population density, heavy trampling co-varied with population density (Table 7.5), so it is possible that emigration was *positively* density dependent. This potentially has important implications because such positive density dependence can cause migration mediated Allee (1949) effects (Menéndez *et al.* 2002; Bonte *et al.* 2004). The full effects of such positive density dependence on spatial population dynamics are currently unknown (Menéndez *et al.* 2002), but are likely to cause considerable temporal between patch instability in population density. However, because emigration rate was not shown to be directly correlated with local population density, it was assumed that reduced habitat quality due to livestock trampling was the main influence on emigration rates. This assumption is tested in Chapter 8 with an examination of long-term temporal stability of the local density of *B. atrocaeruleum* within the segment scale.

7.5.4 Re-analysis of the spatial population structures

In this (2003) investigation *Fleutiauxellus maritimus* was again never found to migrate between patches in a further 19 recaptures. The percentage rate of migration for *B. atrocaeruleum* from monthly releases (not including the May 2003 release) ranged from 3.03% in August 2002 to 7.84% in July 2003. If *F. maritimus* had the same rate of migration, of the 49 recaptures over both years, between 1.48 and 3.84 (1-4) individuals would be expected to have moved between bars. This suggests a lower rate of migration for *F. maritimus*, but clearly does not leave much room for error. However, the expected lower rate of patch occupancy, and lack of detected migrations between bars, do uphold the original (Chapter 6) conclusion that *F. maritimus* is situated lower down on the mobility axis of Thomas and Kunin (1999).

The slightly elevated rates of inter-patch migration observed from monthly releases in the 2003 study (June 6.43% and July 7.84%) compared to those in 2002 (June 5.73% and August 3.03%), much higher rates observed in May 2003 (39.47%), and large maximum distance moved (>488m), further support the conclusion of Chapter 6, that *B. atrocaeruleum* has a patchy population structure within sedimentation zones. The improved data on migration characteristics, and local population size and density, however, allow a more detailed synopsis of the within sedimentation zone spatial population structure of the patchy population of *B. atrocaeruleum*. This synopsis is broken into three areas: (1) the position of the population along the compensation axis of Thomas and Kunin (1999), (2) the impact of livestock trampling, and (3) the impact of inundation.

7.5.4.1 Position along the compensation axis

The compensation axis runs from local source populations, through classical populations (neither source, nor sink), and local pseudo-sink populations, to true sink populations (Pulliam 1988; Watkinson and Sutherland 1995). Sources are typified by a high population density and rate of emigration, and sinks typified by a low population density and high rate of immigration. The un-trampled local populations in this study are likely to occupy the area around a classic population on this gradient, as there was no evidence to suggest that they were either net importers or exporters of individuals over the period of this study. The low density, heavily trampled local populations do not fit easily onto the compensation axis, because of one of two exceptions described by Thomas and Kunin (1999): either (a) these local populations are not in equilibrium, which is thought likely to be a common situation in unstable habitats, or (b) they occupy a low density equilibrium that suffers from Allee type effects and do not fit onto the compensation axis. Over a longer period of study these populations would be expected to move towards the compensation axis, or to extinction, until there was a new founder event.

7.5.4.2 The impact of livestock trampling

The avoidance migration to escape the effects of livestock trampling is an example of a condition dependent emigration (Bowler and Benton 2005). This shows that the patchy population structure within the sedimentation zone was influenced by quality of habitat at the lower, patch, or habitat scale. Such influences of patch quality on larger-scale spatial population structure have important implications for the robustness of the population in response to direct threats and these are further discussed in Chapter 9.

7.5.4.3 The impact of inundation

The inundation induced migration pulse is another example of a condition dependent migration, this time influencing the temporal distribution of migrations. There was limited evidence to suggest that emigration was highest from more easily inundated bars but this cannot be stated with confidence. However, it seems likely that beetles will migrate to any nearby available habitat once their original habitat patch is inundated. The less easily inundated patches will have remained available for a longer period during the May inundation, so might have attracted migrants from inundated patches. Although beetles clearly returned to these patches following the exposure of the habitat there may have been a net movement towards the less easily inundated patches. There might be expected to be a more marked shift away from easily inundated habitats during flow pulses that inundate some bars completely, but leave some areas of others uncovered. Therefore, the inundation induced migration pulses are patchily distributed temporally, and may also influence the spatial population structure in a patchy manner. Flights to and from over-wintering habitat are also temporally patchy although less stochastic, and might have similar effects to those of inundation induced migration pulses.

CHAPTER 8

SEASONAL AND INTER-ANNUAL CHANGES IN THE DENSITY OF BEMBIDION ATROCAERULEUM IN RESPONSE TO ENVIRONMENTAL VARIATION

8.1 Introduction

This chapter analyses variation in density of *Bembidion atrocaeruleum* on 18 bars over three years (2002-2004), over the Upper Severn stream segment using data generated from quadrat hand searches. This was the most extensive spatio-temporal scale of study implemented in the thesis, and the findings were used together with those from Chapters 4-7 to produce a multi-scale overall exposition of the population and movement dynamics of *Bembidion atrocaeruleum* in Chapter 9.

8.2 Background

There is a fairly substantial body of research that relates ERS beetle communities at the patch scale to patch scale environmental variables (Eyre *et al.* 2001a, b, 2002; Sadler *et al.* 2004). This is not surprising as individual ERS bars provide convenient sampling sub-divisions, are home to local populations of ERS beetles (Chapter 6 and 7), and are at the lowest level of spatial resolution for which any protection for conservation is likely to have any effect. However, all of these studies have been confounded by broader scale variation in, for example, climate, geology and hydrology, and temporal variation in community structure, because only one or a few patches were investigated in a river reach across different seasons and years. As a consequence, these studies have conflated variation acting at a reach, river, or catchment scale with the patch scale. This chapter studies 18 distinct ERS patches in the same segment of river at the same time, thereby (1) investigating habitat scale effects in the virtual absence of confounding spatial and temporal variation, and (2) investigating inter-habitat variation at the segment scale. The target organism was *Bembidion atrocaeruleum* because its microhabitat utilization (Chapter 5) and inter-patch spatial dynamics (Chapter 6-7) were well established, and this species was one of the most abundant across the study reach.

Population abundances vary both in space and time, and it is the spatial (inter-patch) variation and its causes that are the main interest of this chapter. However, of key importance is the question of whether abundance/environmental relationships are consistent seasonally and inter-annually, as any hypotheses or conservation initiatives have to be temporally robust. Therefore this chapter examines causes of temporal variation in the density of *B. atrocaeruleum* and its interaction with spatial patterns of variation.

As no population increases without limit it has been suggested that some sort of regulating factor must generally cause population density to increase when it is small and decrease when it is large (Haldane 1953), and this phenomenon is known as density dependence (Smith 1951). In a closed system, population density can thus be a function of abundance as well as exogenous environmental variation, acting as random noise (Tanner 1966), or driving population variation (e.g. Swetnam and Lynch 1993; Hunter and Price 1998), and conceptually can take the following form (c.f. Tanner 1966):

$$N_{t+x} = N_t[f(N_t, E_t)] \pm S$$

where N_{t+x} = estimated population size/density at a time t plus a time lag x; E_t = environmental conditions at time t; and S = sampling error in the estimation of N.

Three inclusive variables can therefore explain estimated population density in a closed population: (1) population size at some previous point in time; (2) exogenous environmental conditions at some previous point in time; and (3) sampling error in the estimation of population density. Typically populations will not be closed, so (4) exchanges of individuals between local populations, can be added as a factor influencing population density (Chapter 7).

Time series of inter-annual changes in population density have been the focus of a vast amount of research involving a very large number of different species, and patterns have variously been explained by density dependent processes and environmental variation (e.g. Moran 1952; Andrewartha and Birch 1954; Morris 1959; Swetnam and Lynch 1993). Although on occasion, small (<8 years) time series of annual population density have been used to infer density dependence and the associated concept of habitat carrying capacity (e.g. Baguette and Schtickzelle 2003), in reality, the three years worth of data presented in this chapter cannot be used to definitively test for density dependence or the existence of exogenous driving variables. Even across very long datasets it is difficult to conclusively test for the existence of density dependence because of problems of autocorrelation in the methods used to estimate population growth rate (R_t) such that random numbers can demonstrate density dependent tendencies. As a consequence, there has developed an extensive literature on the best methods to test for this (e.g. Morris 1959; Tanner 1966; Eberhardt 1970; Hassell 1975; Pollard *et al.* 1987; Dennis and Taper 1994). In view of this the objectives related to temporal variation are restricted to the following:

1. To test the validity of the quadrat method, thus testing the importance of sampling error in the estimation of density.
2. To test for the possible existence of negative density dependent emigration (Chapter 7) across the segment.
3. To suggest possible factors that could control temporal change in measured density.

Upon completion of the analysis of temporal variation in measured density it should then be possible to analyse the factors explaining spatial variation in measured density. This section will have the following objectives:

4. To examine correlations between environmental variables and measured density.
5. To examine the temporal stability of the environment density correlations.

8.3 Materials and methods

8.3.1 Study area and environmental characteristics

Daily maximum temperature, minimum temperature, rainfall and stage height data (Chapter 2) from 2001 to 2004 were used to examine possible reasons for inter-annual changes in measured density.

Eighteen bars in four (A, B, E and F) distinct ‘sediment storage zones’ (Church 1983) in the Upper Severn study area were sampled in this investigation (Figure 8.1). The 18 bars ranged widely in character providing the necessary variation needed to test for the patch scale effects of environmental variables. A total of 23 patch scale environmental variables were measured and estimated for each bar (Table 8.1). These variables either follow the description in Chapter 2 (sometimes with a few alterations), or were wholly new variables that were appropriate given the multi-patch nature of this investigation. In addition to the median sediment size measured in previous chapters, the largest clast from all five sediment quadrats was used as an indication of the range of sediment size on the bar. The ‘maximum <8mm’ variable was the maximum (of the five sediment quadrats) number of points (out of 100) in the sediment quadrat grid that overlay sediments less than 8mm. So, where one of the sediment quadrats was composed of sediments all less than 8mm, this figure would be 100. Similarly ‘minimum <8mm’ was the minimum number of points in the sediment quadrat grid overlying sediments less than 8mm. These later two variables act as an approximate range of fine sediment abundance. ‘Sorting’ (Table 8.1) was a visual summary variable of the degree of sediment sorting on each bar.

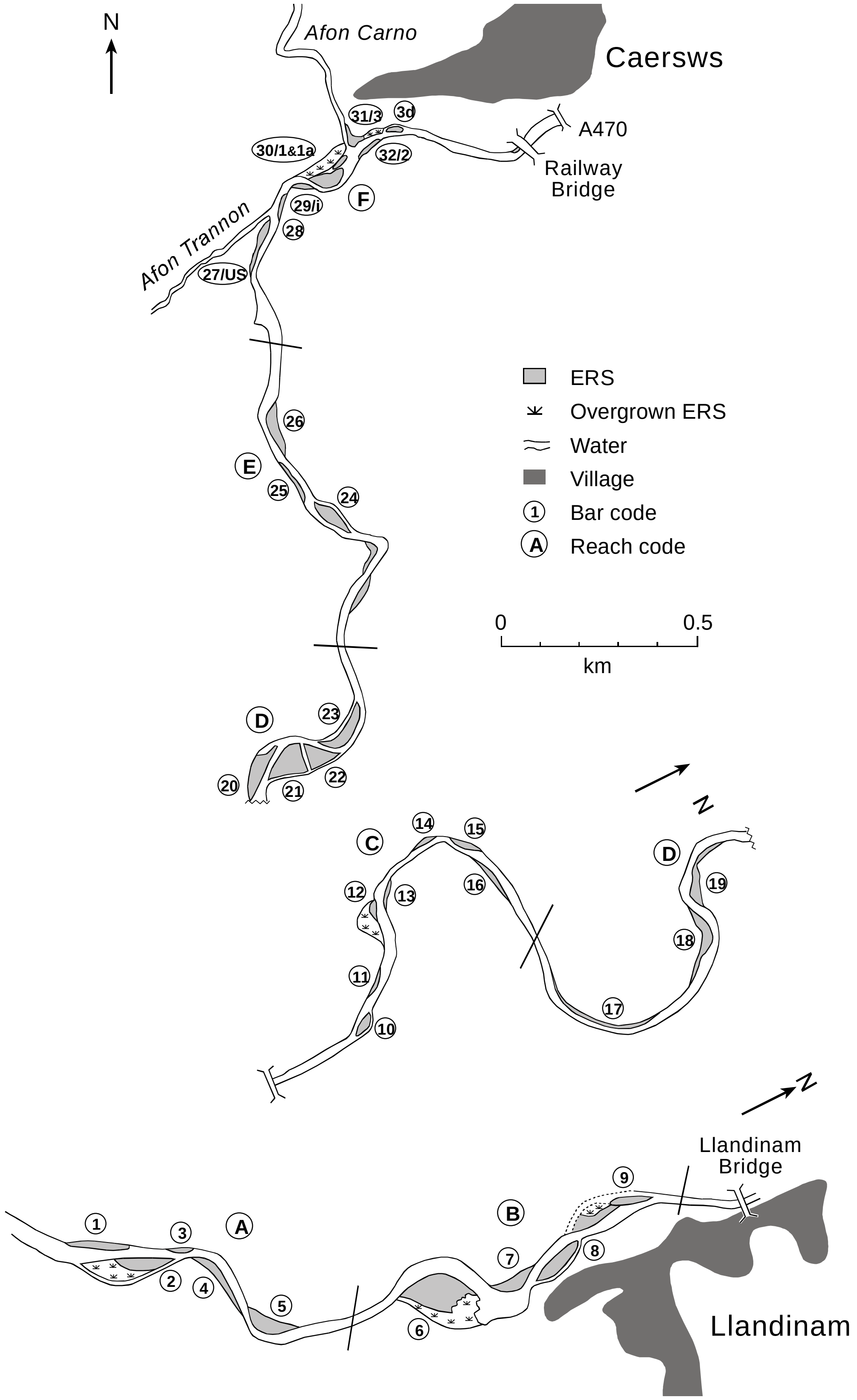


Figure 8.1 The study reach detailing the approximate position and size of all significant bars in the Upper Severn survey reach. Numbers represent individual bars, letters represent distinct reaches divided by ‘sediment transfer zones’ (Church 1983) with little ERS. All coded bars in reaches A, B, E and F were sampled for this investigation with the exception of Bar 3d.

Table 8.1 Whole patch environmental variables.

Type	Variable	Temporal precision	Description
Sediment	Median sediment	Whole study	Median clast in 'typical' sediment quadrat
	Largest clast	Whole study	Largest clast from all 5 sediment quadrats
	Maximum <8mm	Whole study	Maximum number of measured points with sediment <8mm from all sediment quadrats
	Minimum <8mm	Whole study	Minimum number of measured points with sediment <8mm from all sediment quadrats
	Sorting	Whole study	1-3, 1 = poorly sorted, 3 = well sorted
Bar type	Point bar	Whole study	Boolean number
	Lateral bar	Whole study	Boolean number
	Island bar	Whole study	Boolean number
	Inundation potential	Whole study	1-3, 1 = easily inundated, 3 = rarely inundated
Vegetation	Vegetation cover	Whole study	0-5, 0 = bare, 5 = very dense (follows Chapter 5)
	Vegetation type	Whole study	1-3, 1 = bare, 2 = simple, 3 = complex
	Shading	Whole study	% shaded
Trampling	Trampling index	Whole study	Overall (cattle, sheep, human) trampling damage (1-3)
	Cattle trampling	Whole study	Cattle trampling damage (0-2)
	Sheep trampling	Whole study	Sheep trampling damage (0-3)
Heterogeneity	Heterogeneity	Whole study	Overall heterogeneity (1-3)
	Profile	Whole study	1-3, 1 = flat, 2 = gentle, 3 = steep
	Backwater	Whole study	Slow moving/still backwater (boolean number)
Geographic	Bar area	Whole study	Total area of open sediments in that patch
	Wetted edge	Whole study	Total wetted edge
	Distance to nearest bar	Whole study	Straight line distance from the bar edge to the nearest bar edge
Weather	Maximum temperature	Daily	Maximum temperature on that 24 hour day (9am to 9am)
	Minimum temperature	Daily	Minimum temperature on that 24 hour day (9am to 9am)
	Rainfall	Daily	Total rainfall on that 24 hour day (9am to 9am)

Point bars were those that occurred on the inside of a meander bend, lateral bars occurred in relatively straight reaches, and island bars were those completely surrounded by water. ‘Inundation potential’ described the ease with which bars were inundated by rising water level. The trampling index was extended to a 1-3 scale because of the greater range of trampling levels observed, cattle and sheep trampling damage were independently estimated. All three trampling indices described typical conditions over all three study years. Bar area, distance to the nearest bar (from bar edge to edge), and wetted perimeter were estimated from dGPS surveys (Chapter 5) implemented in 2003 and 2004.

8.3.2 Sampling procedure

Two, 1 x 2m quadrats (2m^2, positioned with the long axis along the water’s edge) were searched for each bar sample. One quadrat was positioned towards the upstream (usually coarser) end of the bar, and one quadrat was positioned towards the downstream (typically finer) end of the bar. Quadrats were always positioned in an area that had not already been searched that year.

Three periods of sampling, centred around June, July and late August, were implemented in 2002, 2003 and 2004. As far as was practicable, sampling for any one month was completed over as short a period as possible in order to limit the effects of temporal variation due to changes in weather, flow level, and underlying population fluctuations. It was not always possible to implement all the sampling in as tight a temporal window as would have been ideal because weather conditions, flow level, and other sampling commitments sometimes made the work impossible. Therefore, the effects of changing weather conditions on capture rates were investigated. The full sampling schedule is shown in Table 8.2.

Table 8.2 Quadrat sampling schedule.

		2002			**2003**			**2004**	
Bar code	**June**	**July**	**August**	**June**	**July**	**August**	**June**	**July**	**August**
1	1.6	25.7	25.8	11.6	12.7	18.8	5.6	17.7	4.9
2	1.6	25.7	25.8	11.6	12.7	18.8	5.6	18.7	4.9
3	1.6	25.7	25.8	11.6	12.7	18.8	5.6	18.7	4.9
4	1.6	25.7	25.8	11.6	12.7	18.8	5.6	18.7	4.9
5	1.6	25.7	25.8	11.6	12.7	18.8	5.6	18.7	4.9
6	2.6	26.7	26.8	16.6	13.7	19.8	6.6	17.7	4.9
7	2.6	26.7	15.9	16.6	14.7	19.8	6.6	17.7	5.9
8	1.6	26.7	15.9	16.6	13.7	19.8	6.6	17.7	5.9
9	2.6	26.7	15.9	16.6	13.7	19.8	6.6	17.7	5.9
24	18.6	28.7	17.8	10.6	14.7	20.8	6.6	18.7	5.9
25	18.6	28.7	17.8	10.6	14.7	20.8	6.6	19.7	5.9
26	19.6	3.8	17.8	10.6	14.7	20.8	6.6	18.7	5.9
27	3.6	3.8	17.8	10.6	13.7	20.8	7.6	16.7	3.9
28/US	2.6	3.8	17.8	10.6	13.7	21.8	7.6	16.7	3.9
29/i	-	3.8	17.8	10.6	14.7	21.8	7.6	16.7	3.9
30/1&1a	2.6	3.8	17.8	9.6	15.7	20.8	7.6	16.7	3.9
31/3	2.6	3.8	17.8	9.6	15.7	19.8	7.6	16.7	3.9
32/2	2.6	3.8	17.8	9.6	14.7	21.8	7.6	16.7	3.9

8.3.3 Data analysis

Levenne's tests for differences in density between reaches, months and years showed that the variance between years were significantly heterogeneous even after square root, Ln and Log_{10} transformations to correct for the positive skew in the data, so Kruskal-

Wallis non-parametric analysis of variance was employed. Dunn's unequal sample size and Nemenyi equal sample size multiple comparisons tests were used to determine which groups were significantly different at the $P = 0.05$ level (Wheater and Cook 2000).

Population growth rate (R_t) was measured using the method of Pollard *et al.* (1987):

$$R_t = \ln N_{t+1} - \ln N_t$$

One was added to each of the measured densities to remove problems of negative densities when untransformed density was less than one. The conversion to logarithms has the advantages that it is more meaningful because of the typically geometric growth in animal populations, and that variances are stabilized to some extent (Morris 1959). Scatter graphs of growth rate (R_t) against measured density (N_t) were used to look for evidence of negative density dependence acting at an inter-annual time scale, tests of the significance of the relationship were not used, because they are meaningless (Eberhardt 1970). Data from all bars were plotted, because data from several sites can improve tests for density dependence (Langton *et al.* 2002), although this is only likely when high dispersal rates lead to inter-patch synchrony in their temporal patterns (Hastings 1993; Ray and Hastings 1996). The synchrony observed over many bars meant that using data from many bars was valid.

Much of the environmental data were measured on an ordinal scale and were not normally distributed upon graphical examination, therefore Spearman's rank correlation was used to analyse relationships between measured density and environmental variables. Due to the high number of correlations used for each period (24) there would be a 71% chance of finding one or more significant correlations within a period purely by chance. When considering all periods analysed (216) there would be a 100% chance of finding one or more significant correlations by chance (SISA 2005). So consideration was given to the consistency of the direction of correlations, to the chance of getting the same correlation more than once, to cross correlations in the data and to the ecological likelihood of the said correlation occurring.

8.4 Results

8.4.1 The quadrat method as a measure of population density

Figure 8.2 shows several relationships between mark recapture estimated whole bar population size (Chapter 7) and the quadrat measured ‘edge’ density for June and July 2004 on Bars 29/i, 30/1&1a, 31/3, and 32/2. The mark recapture density averaged for each month was poorly related to the density estimated from quadrats (Figure 8.2b, d & f). This was to be expected as the estimated population density changed quite markedly across both June and July 2004 (Chapter 7, Figure 7.1). Of the relationships between the closest date mark recapture estimates and the quadrat estimates, the downstream quadrat measurement (Figure 8.2c) and the averaged upstream and downstream measurement (Figure 8.2e) were found to be significant. Despite the stronger relationship with the downstream quadrat estimates, the mean quadrat estimates were selected for further analysis. This was because: (1) in the microhabitat investigations (Chapter 5) *B. atrocaeruleum* were not found to show any strong upstream/downstream bias in their distributions; (2) a mean value would offset, to some degree, any unusual, or spurious density measurements; and (3) the wide distribution of *B. atrocaeruleum* shown across most bars (Chapter 5) suggests that the wider an area sampled for them, the more likely density estimates are likely to be accurate.

Clearly, densities measured at the edge of bars over-estimate the population density of the whole bar (Figure 8.2) and this over-estimation seems to be about five fold in the 2003 data tested. This was to be expected due to the preferential distribution of *B. atrocaeruleum* towards the water’s edge (Chapter 5). The significant relationship between the density estimated by the two independent methods showed that the quadrat method was a good measure of relative population density and that any sampling bias was not large, or systematic.

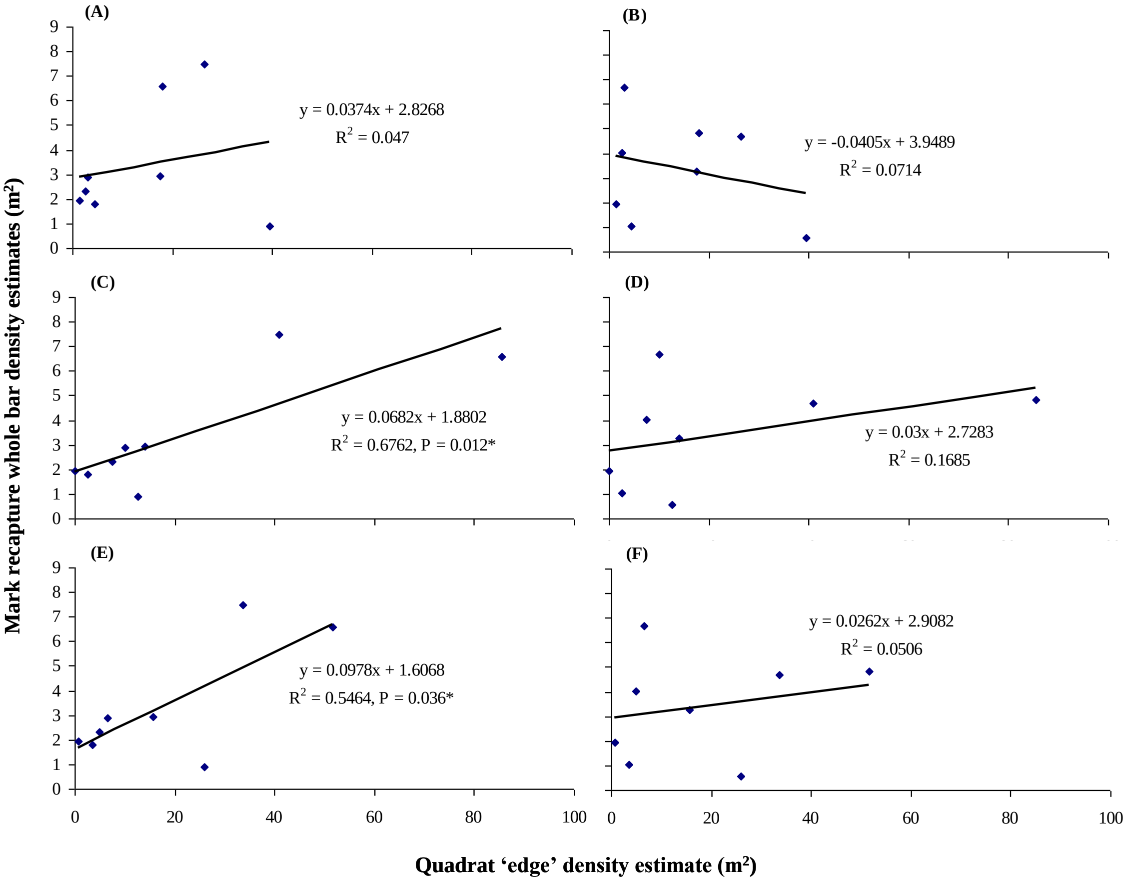


Figure 8.2 Relationship between quadrat 'edge' density estimates and mark recapture whole bar density estimates for *Bembidion atrocaeruleum* on Bars 29/i, 30/1&1a, 31/3, and 32/2 for June and July 2004. (A) = Mark recapture density estimates for 17/6/2004 and 17-19/7/2004 against density measured in the upstream quadrats. (B) = Mean mark recapture density estimates for June and July against density measured in the upstream quadrats. (C) = Mark recapture density estimates for 17/6/2004 and 17-19/7/2004 against density measured in the downstream quadrats. (D) = Mean mark recapture density estimates for June and July against density measured in the downstream quadrats. (E) = Mark recapture density estimates for 17/6/2004 and 17-19/7/2004 against the mean density from upstream and downstream quadrats. (F) = Mean mark recapture density estimates for June and July against the mean density from upstream and downstream quadrats.

8.4.2 Environmental variables

'Whole period' environmental variables are shown in Table 8.3, and their Spearman's rank cross correlations in Table 8.4. The latter is used in the consideration of significant correlations between these variables and measured density (8.4.5). Figure 8.3 illustrates the relationship between maximum temperature, minimum temperature and rainfall (when there was any) and measured density in each sampling period. The differences in weather are due to the sampling of bars on different days. In most sampling periods there seemed to be no indication of a weather artefact acting on the density data, with measured density having a similar distribution across a range of weather conditions. However in June 2003 there seemed to be a strong relationship both between minimum temperature and density, and maximum temperature and density. This was also the case in July 2004 for minimum temperature, but to a lesser extent. Therefore the correlation between weather variables and density were considered in later analyses (8.4.5). Water level was close to base level across all samples, so this was not considered in later analyses.

Table 8.3 ‘Whole period’ environmental variables.

Bar code	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Mark-recapture code	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**US**	**-**	**i**	**1&1a**	**3**	**2**
Median sediment	-5.93	-5.91	-5.39	-5.20	-5.69	-4.94	-5.43	-4.90	-5.14	-4.97	-5.52	-5.50	-5.00	-5.59	-5.39	-5.26	-4.77	-4.84
Largest clast	-6.85	-7.47	-6.61	-6.79	-7.06	-7.27	-6.23	-6.85	-6.96	-7.13	-6.85	-6.80	-6.82	-6.88	-6.88	-6.79	-6.76	-6.57
Maximum <8mm	22	50	33	100	100	100	69	19	100	100	100	100	100	76	100	100	32	85
Minimum <8mm	4	7	3	7	3	2	22	5	12	3	1	5	11	6	6	3	3	14
Sorting	2	3	2	2	3	3	1	3	2	3	3	2	2	2	2	3	3	2
Point bar (0-1)	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1
Lateral bar (0-1)	1	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0
Island bar (0-1)	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Inundation potential (1-3)	2	1	3	1	1	1	2	1	2	1	2	3	3	1	2	1	1	2
Vegetation (0-5)	1	1	1	0	2	2	1	3	2	4	2	2	3	0	1	2	1	0
Vegetation type (1-3)	1	3	1	1	3	3	1	3	2	2	3	1	1	1	1	1	3	1
Shading (%)	5	0	40	0	10	0	0	10	20	0	20	30	0	5	0	0	0	0
Trampling index (1-3)	3	1	1	1	2	1	3	1	1	1	1	1	2	3	3	1	1	3
Cattle trampling (0-2)	0	0	0	0	0	0	0	1	0	1	0	1	0	2	2	1	1	2
Sheep trampling (0-3)	3	2	1	1	1	1	3	1	1	1	1	1	2	1	1	0	0	1
Heterogeneity (1-3)	2	3	1	2	2	3	2	3	3	3	3	3	2	1	2	3	2	2
Profile	1	3	1	2	3	2	2	2	2	3	3	3	2	1	1	1	3	1
Backwater (0-1)	0	1	0	1	1	1	1	0	1	0	1	1	0	0	0	1	1	0
Area (m^2)	1459	3812	408	3575	2337	9696	3878	3958	2583	2158	808	1652	1843	275	823	2354	1539	969
Edge to edge (m^2)	17	17	17	19	19	23	11	4	4	7	7	22	19	11	11	19	15	15
Wetted edge (m)	165	145	57	198	147	372	164	295	198	205	112	147	177	51	89	221	117	95

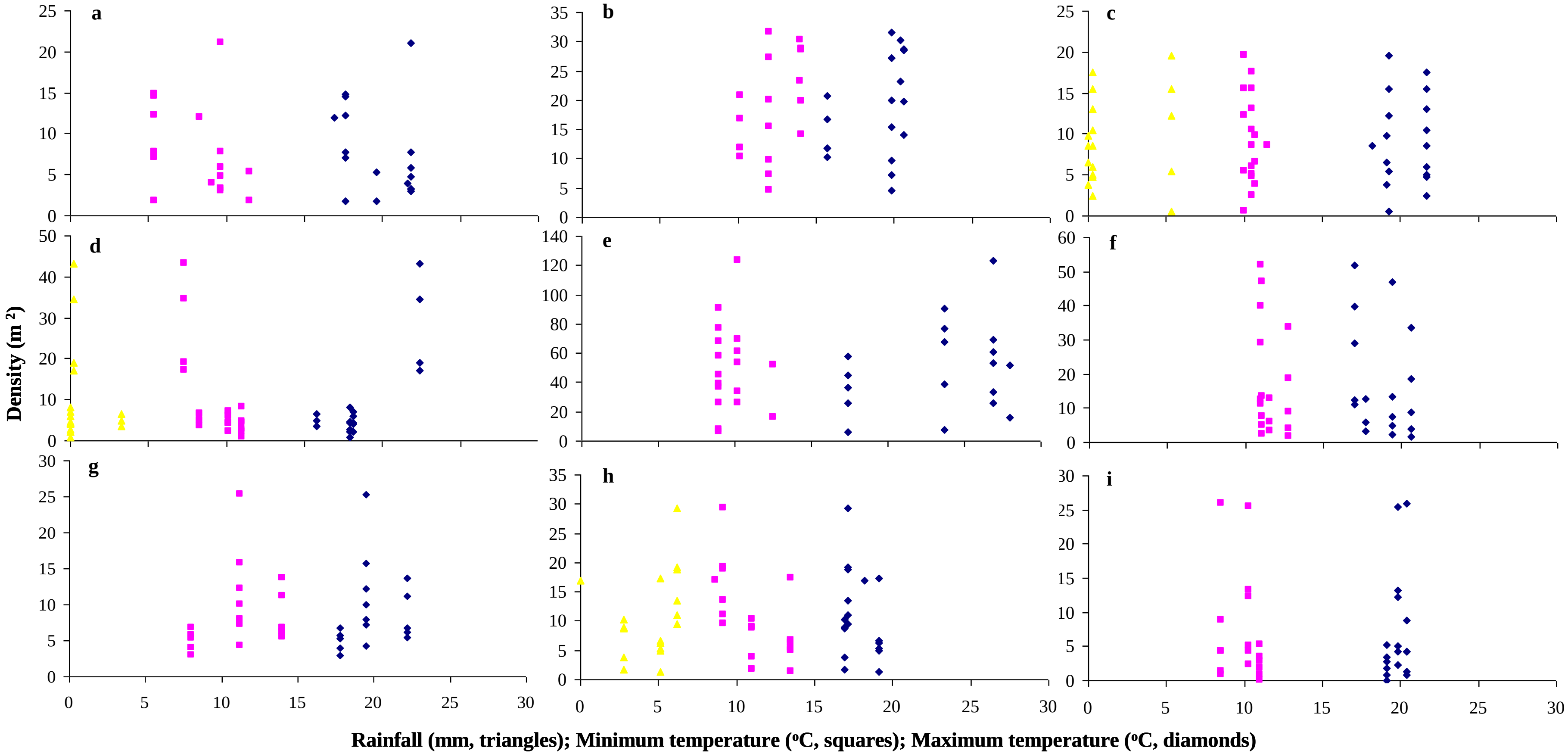
8.4.3 Population dynamics

Figure 8.4 illustrates changes in density between months, years and reaches across the study bars. There were significantly higher densities ($H = 31.60$, $df = 2$, $P = <0.001$) in the July sampling period across all years, but there was no significant difference between densities in June and August (Figure 8.5). Measured density (especially in July) was

Table 8.4 Spearman’s rank correlation coefficients between whole study environmental variables (significant correlation highlighted in bold, emboldened and underlined when correlations significant and negative).

	Wet	Edg	Are	Bac	Vet	Sor	Pro	Het	She	Cat	Tra	Sha	Veg	Isl	Lat	Poi	Inp	Min	Max	Lac
Median sediment	0.36	-0.14	0.24	-0.13	0.14	0.17	-0.01	0.15	**-0.47***	0.31	-0.28	-0.36	0.21	0.10	-0.35	0.27	-0.14	0.03	0.03	0.25
Largest clast	-0.21	0.10	-0.23	-0.04	**-0.55***	-0.49	-0.32	-0.43	-0.11	0.13	0.16	-0.02	-0.37	-0.45	0.18	0.16	0.41	0.25	-0.27	
Maximum <8mm	0.23	0.27	0.06	0.32	-0.07	0.06	0.20	0.32	-0.23	-0.06	-0.15	-0.10	0.34	-0.28	-0.17	0.38	0.07	-0.10		
Minimum <8mm	-0.10	-0.19	0.16	-0.14	-0.46	**-0.70****	-0.25	-0.24	**0.48***	0.07	0.46	-0.25	-0.37	-0.01	0.18	-0.16	0.28			
Inundation potential	-0.34	0.02	-0.43	-0.25	**-0.52***	**-0.65****	-0.22	-0.22	0.37	-0.15	0.25	0.39	0.01	-0.42	**0.54***	-0.21				
Point bar	0.04	**0.57***	0.06	0.35	-0.05	0.15	0.00	0.00	**-0.57***	0.32	-0.04	-0.30	-0.20	-0.40	**-0.71*****					
Lateral bar	-0.27	-0.30	-0.36	-0.20	-0.30	**-0.52***	-0.28	-0.36	**0.47***	-0.40	0.30	0.40	-0.08	-0.36						
Island bar	0.30	-0.37	0.39	-0.20	0.45	**0.49***	0.37	**0.47***	0.14	0.10	-0.35	-0.13	0.37							
Vegetation cover	**0.60****	-0.09	0.35	0.03	0.41	**0.48***	0.44	**0.64****	-0.07	-0.16	-0.43	0.17								
Shading	-0.23	-0.13	-0.32	-0.01	0.08	-0.08	0.07	0.02	-0.05	-0.18	-0.21									
Trampling index	-0.43	-0.10	-0.35	-0.46	**-0.50***	**-0.58***	**-0.51***	**-0.63****	0.46	0.25										
Cattle trampling	-0.27	-0.29	-0.38	-0.42	-0.24	0.01	-0.29	-0.08	**-0.49***											
Sheep trampling	-0.01	-0.02	0.15	-0.21	-0.20	-0.46	-0.03	-0.15												
Heterogeneity index	**0.62****	-0.10	**0.56***	0.43	**0.51***	**0.56***	**0.49***													
Profile	0.17	0.03	0.31	**0.55***	**0.68****	**0.50***														
Sorting	0.31	0.01	0.26	0.27	**0.80*****															
Vegetation type	0.22	-0.18	0.38	0.39																
Backwater	0.24	0.35	**0.47***																	
Area	**0.80*****	0.17																		
Edge to edge	0.16																			
Wetted edge																				

Figure 8.3 Relationship between weather and density in each sampling period (a = June 2002, b = July 2002, c = August 2003, d = June 2003, e = July 2003, f = August 2003, g = June 2004, h = July 2004, i = August 2004). Note different scales on the density axis.



particularly high in 2003 (Figure 8.6) and was significantly higher than that in 2004 (H = 10.87, df = 2, P = 0.004). There were also significant differences between reaches (Figure 8.7) with reach B and E having significantly higher overall densities than reach F (H = 17.87, df = 3, P = <0.001). There were, however, some clear interactions in these overall patterns, such as the enhanced densities in reach B in July 2003 when compared to the same levels in other reaches. Unfortunately, the heterogeneous variation across the dataset prohibited the application of parametric methods that would show the significance of the interactions. Nonetheless, the presence of interactions means that these overall patterns have to be interpreted with caution. Figure 8.8 illustrates overall differences between densities by patch. There were found to be significant differences in the mean ranks of each bar (H = 38.68, df = 17, P = 0.002), but the highly conservative Nemenyi multiple comparisons test did not show which overall densities were significantly different from the others.

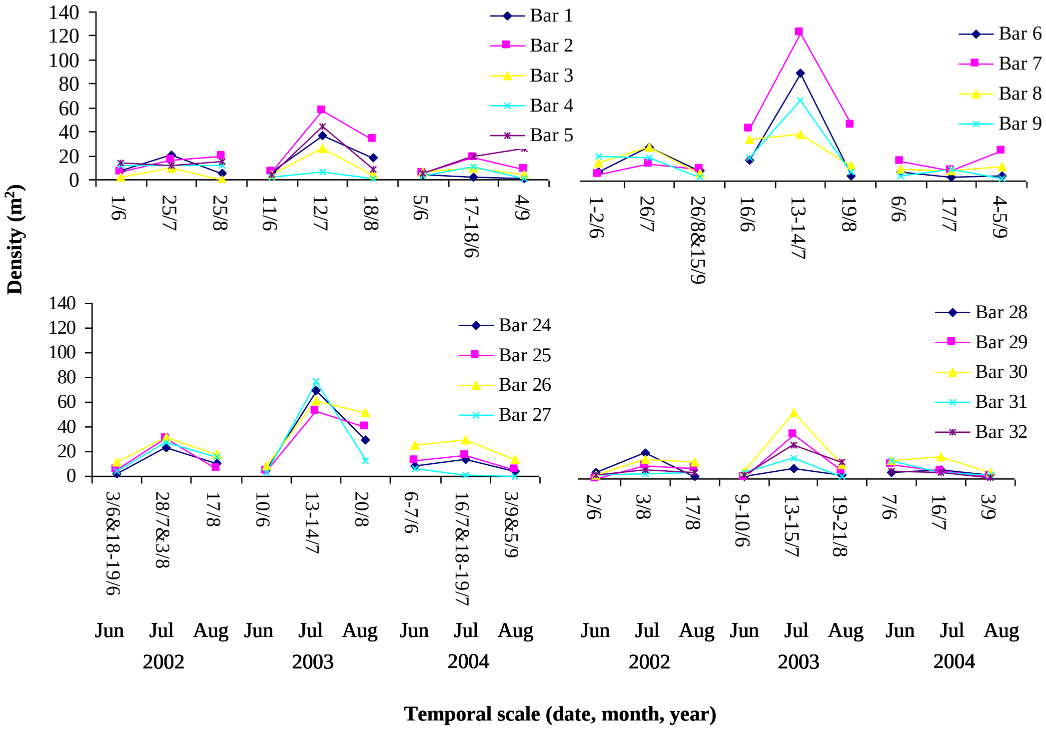


Figure 8.4 Temporal change in density by reach (top left = reach A; top right = reach B; bottom left = reach E; bottom right = reach F).

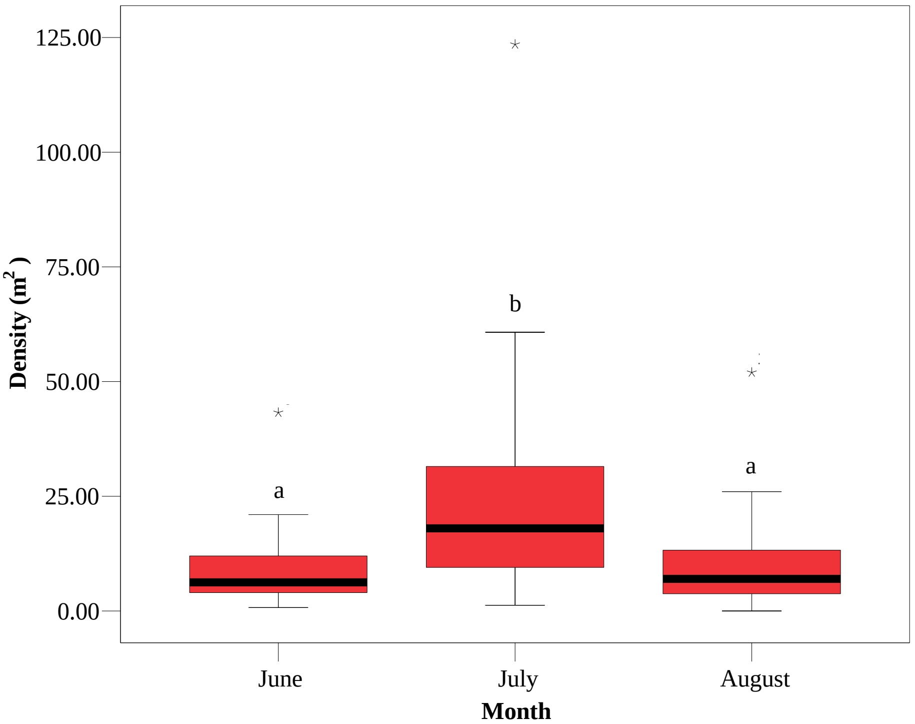


Figure 8.5 Box and whisker plot of differences in monthly density across all bars and all years (* = maximum value; whiskers = 10th and 90th percentiles; box range = 25th and 75th percentiles; thick bar = median; letters indicate significant differences between groups tested using Dunn's multiple comparison tests).

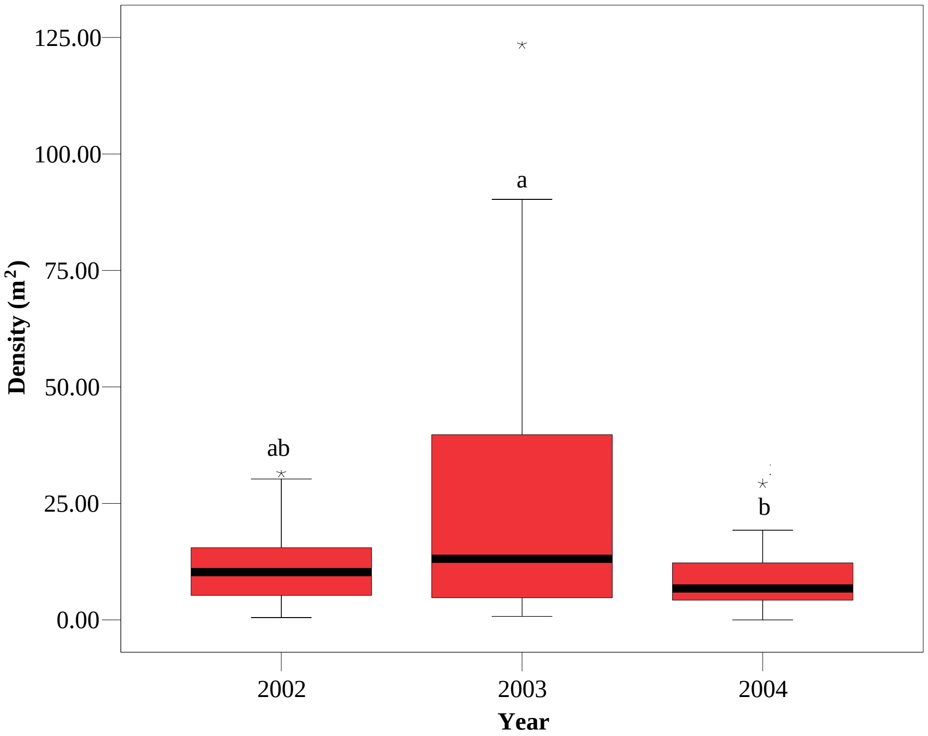


Figure 8.6 Box and whisker plot of differences in yearly density across all bars and all months (* = maximum value; whiskers = 10th and 90th percentiles; box range = 25th and 75th percentiles; thick bar = median; letters indicate significant differences between groups tested using Dunn's multiple comparison tests).

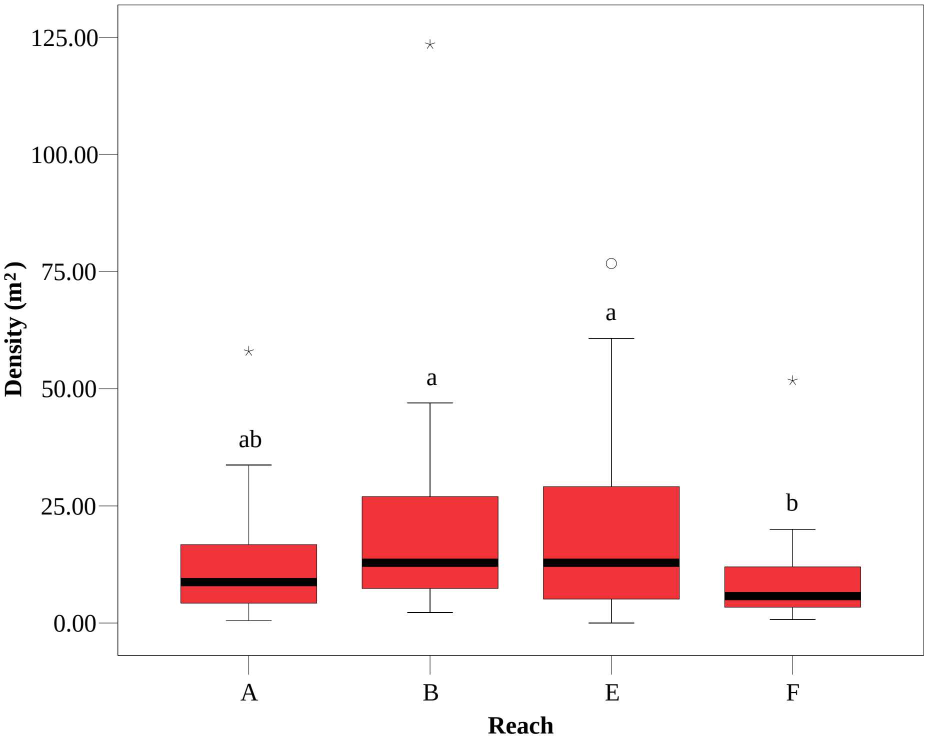


Figure 8.7 Box and whisker plot of differences in reach density across all years and all months (* & ^{o} = maximum value; whiskers = 10th and 90th percentiles; box range = 25th and 75th percentiles; thick bar = median; letters indicate significant differences between groups tested using Dunn’s multiple comparison tests).

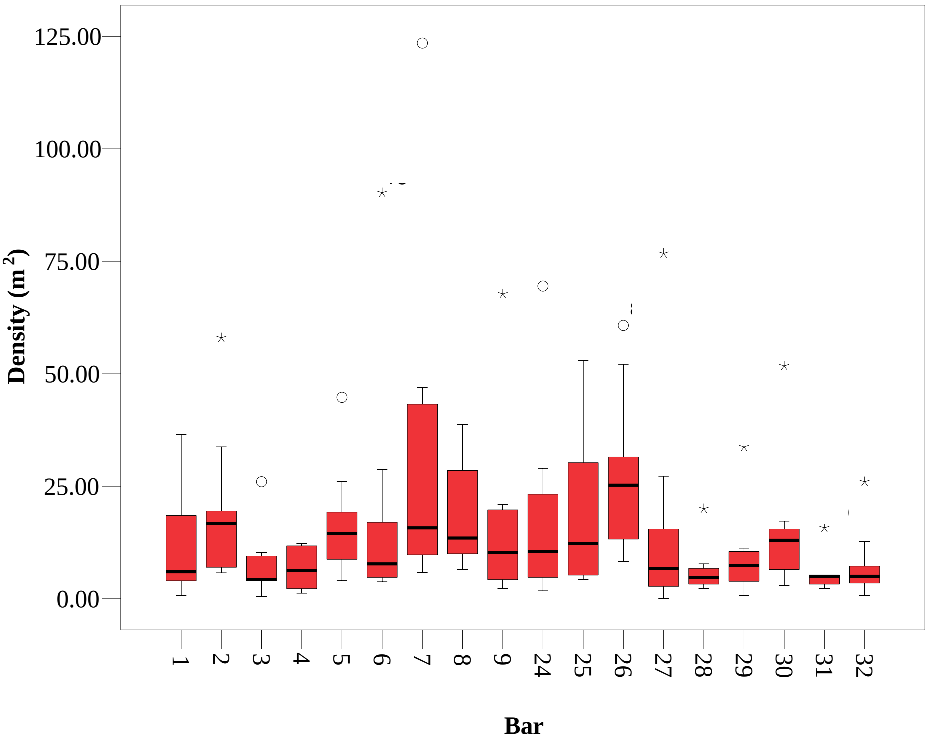


Figure 8.8 Box and whisker plot of differences in bar density across all years and all months (* & ^{o} = maximum value; whiskers = 10th and 90th percentiles; box range = 25th and 75th percentiles; thick bar = median).

8.4.4 Potential drivers of temporal variation between periods

Figure 8.9 illustrates changes in daily maximum and minimum temperature, daily rainfall, and daily stage data between 1/1/2001 and 31/12/2004. Five factors that might explain the significantly higher densities in 2003 are:

1. The comparatively high maximum temperatures in April 2003 when compared to maximum temperatures in other years.
2. High maximum temperatures in the late spring and summer of 2003.
    a. The comparatively high mean maximum temperatures in the 2003 sampling period compared to other years.
    b. The comparatively high range of maximum temperatures in the 2003 sampling period compared to other years. The summer of 2003 was noted for its exceptionally high temperatures, with temperatures in May and June described as “well above average”, and temperatures in July and August described as “very warm”. The maximum recorded UK temperature of 38.5^{o}C was recorded on 10/8/2003 at Brogdale near Faversham (Kent) (Met Office 2005).
3. Comparatively prolonged or extreme amounts of rainfall occurring through May and July in 2003.
4. A comparatively high number of summer high flow events in 2003. Unfortunately, complete stage data was not available in time. However, personal observations showed that there were more large flow pulses between May and late August in 2003 (3), than in 2002 (0) and 2004 (1).

For all months there was a clear negative relationship between growth rate and density, but this did not necessarily support the existence of density dependence (see above). The strongest relationship and steepest gradient occurred in July when populations were at their peak.

Figure 8.10 shows the relationships between density and inter-annual growth rate for each month.

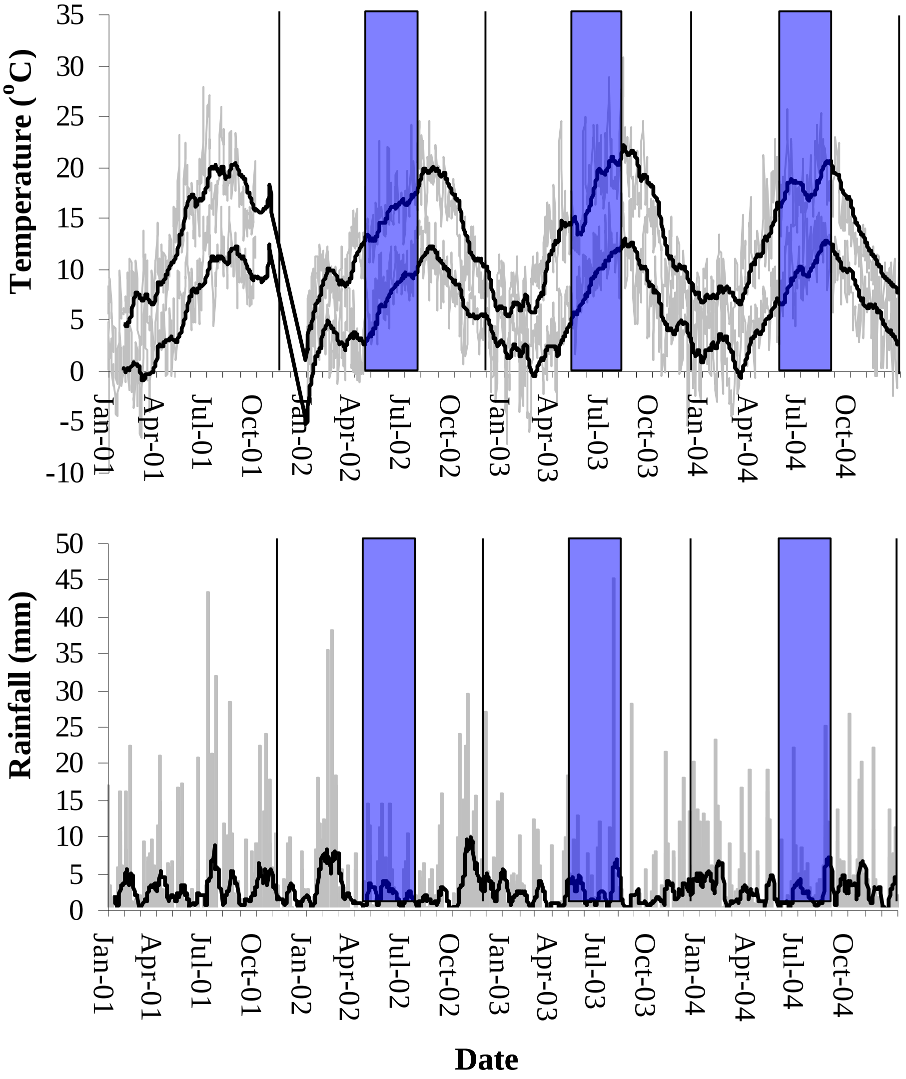


Figure 8.9 Variations in weather and stage height in the year preceding, and three study years (2001-2004). (a) Shows daily maximum and minimum temperatures (grey line), with a 30-day running average fitted (black line), the sampling months are highlighted by the grey bars (note the missing data between October and December 2002). (b) Shows daily rainfall (grey bars) with a 15-day running average fitted (black line), the sampling months are highlighted by the grey bars.

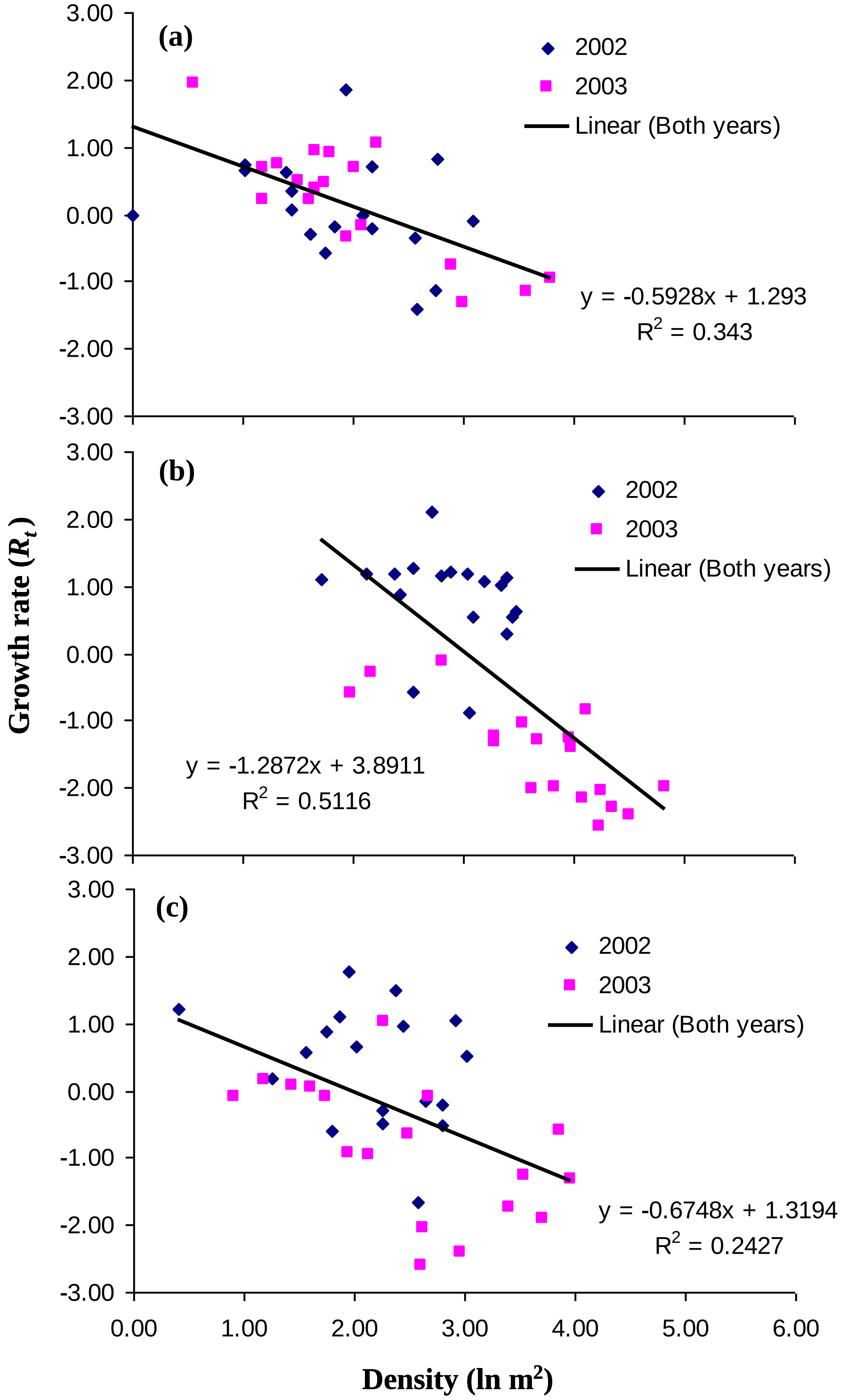


Figure 8.10 The relationship between measured density and inter-annual growth rate for (a) June, (b) July and (c) August.

8.4.5 Spatial variation in measured density

A total of 11 variables were significantly correlated with measured density at some point over the period of study although none showed consistently significant correlations with measured density over the whole sampling period (Table 8.5). The most consistently significant relationships with measured density were shown by area and heterogeneity, which were significantly positive on four occasions, and always showed positive correlations with density. Bar area positively co-varied with relatively few variables, namely, wetted edge, the heterogeneity index and ‘backwater’. Heterogeneity, in contrast, co-varied with eight variables (Table 8.4), as would be expected, as it is a summary variable of a variety of characteristics. Interestingly, it was negatively related to the trampling index.

Bar profile was significantly correlated with measured density on three instances out of the nine sampling periods and always showed quite a strong positive relationship with measured density on the other occasions. ‘Backwater’, vegetation cover and wetted edge were all significantly positively correlated with measured density on two occasions, and all were found to consistently show positive correlations (Table 8.5). All of these variables significantly positively co-vary with heterogeneity (Table 8.4).

The observations made from Figure 8.3 (8.4.2) were supported by the correlation analyses, with a significant positive correlation with maximum temperature in June 2003, and significant negative correlations with minimum temperature in June 2003 and July 2004. This suggests that clear sky, and consequent hotter daytime conditions favoured greater catch rates in these periods. The distance to the nearest bar was found to be significantly positively related to measured density on one occasion, but generally showed very poor correlations, so it would seem probable that this relationship occurred by chance (Table 8.5).

Table 8.5 Spearman's rank correlation coefficients (CC) and their associated probability values (P) between the measured density of *Bembidion atrocaeruleum* and environmental variables (significant correlations are highlighted in bold, and are in bold and underlined when correlations significant and negative).

	Jun-02		**Jul-02**		**Aug-02**		**Jun-03**		**Jul-03**		**Aug-03**		**Jun-04**		**Jul-04**		**Aug-04**		**Overall**	
	CC	**P**	**CC**	**P**	**CC**	**P**	**CC**	**P**	**CC**	**P**	**CC**	**P**	**CC**	**P**	**CC**	**P**	**CC**	**P**	**CC**	**P**
Area	**0.51***	**0.037**	0.21	0.411	**0.49***	**0.039**	**0.65****	**0.004**	**0.52***	**0.027**	0.15	0.559	0.01	0.958	0.15	0.559	0.37	0.133	**0.51***	**0.031**
Heterogeneity	0.28	0.281	**0.59****	**0.010**	0.41	0.092	**0.60****	**0.008**	**0.58***	**0.012**	**0.50***	**0.035**	0.31	0.214	0.44	0.067	0.38	0.124	**0.61****	**0.007**
Profile	0.22	0.398	0.31	0.213	**0.50***	**0.035**	0.27	0.280	0.38	0.119	0.35	0.149	0.23	0.359	**0.51***	**0.030**	**0.47***	**0.047**	**0.60****	**0.008**
Backwater	0.37	0.148	0.04	0.865	0.39	0.111	0.41	0.091	0.28	0.260	0.07	0.799	0.19	0.440	**0.52***	**0.028**	**0.48***	**0.046**	**0.47***	**0.047**
Vegetation cover	0.09	0.728	**0.62****	**0.006**	0.37	0.134	0.38	0.116	**0.67****	**0.003**	0.38	0.116	0.32	0.201	0.22	0.387	0.32	0.201	**0.56***	**0.015**
Wetted edge	0.33	0.192	0.44	0.066	0.38	0.115	**0.53***	**0.024**	**0.50***	**0.036**	0.12	0.639	0.02	0.951	0.03	0.913	0.11	0.665	0.34	0.163
Minimum temperature	-0.43	0.084	0.42	0.084	-0.18	0.471	**-0.66****	**0.003**	0.03	0.913	-0.39	0.108	0.45	0.061	**-0.66****	**0.003**	-0.29	0.244	-0.30	0.230
Maximum temperature	-0.33	0.197	0.42	0.084	0.07	0.795	**0.53***	**0.025**	0.15	0.547	-0.33	0.181	0.45	0.061	-0.081	0.749	0.29	0.244	-0.15	0.546
Distance to nearest bar	0.04	0.866	-0.01	0.977	**0.49***	**0.037**	-0.09	0.727	0.04	0.891	-0.16	0.519	-0.06	0.817	0.09	0.710	0.08	0.765	0.09	0.738
Trampling index	-0.05	0.838	-0.29	0.243	-0.17	0.496	-0.38	0.122	-0.15	0.565	0.04	0.862	-0.18	0.465	**-0.50***	**0.033**	-0.30	0.229	-0.24	0.329
Sheep	0.22	0.395	0.24	0.334	0.21	0.412	0.14	0.591	0.39	0.108	**0.49***	**0.041**	-0.29	0.252	-0.25	0.314	-0.075	0.766	0.28	0.263

Sheep trampling showed little stability in its correlation with measured density. They were positively correlated in 2002 and 2003, significantly so in August 2003, but weakly negatively correlated in 2004. The overall trampling index was generally negatively correlated with measured density, but this relationship was only significant once (Table 8.5). Interestingly, the trampling index was significantly negatively related to the vegetation type, sorting, and profile, which are all taken into account when estimating the heterogeneity index, which it was also negatively related to. Thus there seemed to be a general positive relationship between measured density and (1) area, (2) heterogeneity and related indices, and (3) daytime temperature. There is some weak support for a significant negative relationship with trampling intensity, but this is complicated by this variables co-variation with the heterogeneity variables (Table 8.4).

The lack of any clear temporal pattern in the by period measured density / environmental correlations allows an overall assessment of the relationship between measured density and environmental variables over all nine periods. Clearly, to just take mean densities over all these periods would allow July measurements, and particularly those in 2003, to dominate the observed correlations. Therefore, densities on each bar were converted to a percentage of the sum of all of the measured densities for that sample period. The results of this overall analysis are presented in the last column of Table 8.5. This overall correlation supports the results of the by period correlations, namely that measured density shows significant ‘real’ positive correlations with bar area and measures of bar heterogeneity. Trampling was negatively correlated with density, but was not significant (Table 8.5).

8.5 Discussion

8.5.1 An assessment of the quadrat method as a measure of population density

The findings of Section 8.4.1 suggested that the density measured by the quadrat method was a reasonable indication of overall population size on each bar, and this leant extra weight to the analyses that followed. This method has been used extensively to measure the population density of ERS beetles and, for example, has been used to construct conclusions about seasonal and inter-annual change in abundance and abundance patterns (e.g. Andersen 1969, 1995; Framenau *et. al* 2002; Hering *et al.* 2004). In lieu of mark-recapture estimates over many bars, over a very long time period (which is nearly impossible), quadrat hand searches are the best method available for estimating density.

8.5.2 Evidence for positive density dependent emigration?

Figure 8.4 illustrates that measured density showed a very high degree of temporal synchrony, which strongly suggests that inter-patch emigration was not positively density dependent, or was of insufficient magnitude to cause between patch instability. However, the estimates of inter-annual growth rate in population size are biased to some extent due to generational overlap, even if *Bembidion atrocaeruleum* exclusively only live for one year. The July data represent the maximum population size after larval maturation and therefore provide the best estimate of inter-annual population growth rate. The evidence from Figure 8.10, particularly from July, supports the observation of high temporal synchrony, showing no evidence for inter-annual positive density dependence.

8.5.3 Possible factors controlling temporal population dynamics

Clearly three years worth of data is insufficient to adequately test for negative density dependence and environmental influences on population size, a longer-term dataset would be necessary to do this more satisfactorily, and even in a long-term data set it is often very difficult to definitively show that there are density dependent effects (e.g.

Pollard *et al.* 1987; Dennis and Taper 1994; Reddingius 1996). Therefore this section discusses *possible* factors that could have controlled the temporal change in measured density and does not firmly conclude which factors were influencing changes in density.

Stubbs (1977), in a meta-analysis of 30 studies mainly on insects, found that more extreme density dependent fluctuations and over-compensating density dependence were more prevalent in unstable habitats. However, it is often the case that such density dependent effects only act at high population densities (Hassell 1975; Stubbs 1977), and in insects it is typically the juvenile stages most affected by such effects (Tanner 1966; Stubbs 1977). Density dependence has been observed in response to competition, predation and parasitism (e.g. Johnson *et al.* 1995; Ferguson and Joly 2002; Lane and Mills 2003). Therefore, without information on both larval and adult density and detailed information on the autecology of a species, confidently demonstrating density dependent effects is difficult. Such persistent, autecological work on a single ERS species is some way off, especially given the poor state of larval taxonomic identification at present. Consistent, inter-annual censuses of adults could provide a good foundation, and indication of whether density dependent effects are likely in the first instance. This study suggests that mid-July, when population density is at its peak is a good time to do this, particularly as July gives the best indirect indication of larval abundance.

Weather conditions, particularly temperature, are known to be key determinants of habitat preference and distribution at most spatial scales for beetles (e.g. Thiele 1977; Desender 1989; Butterfield 1996; Colombini *et al.* 1994; Eyre *et al.* 2005). Weather conditions have also been shown to strongly influence beetle population density at seasonal to inter-annual temporal scales (Klimetzek and Yue 1997; Frampton *et al.* 2000; Delippe *et al.* 2001). Given that beetles are ectothermic, temperatures would be expected *a priori* to influence population density, so the observed changes in measured population density could well have been due to the extreme temperatures observed in 2003. *Bembidion atrocaeruleum* is distributed across the full length of the UK however, so its distribution provides no evidence that would indicate that higher temperatures would be expected to necessarily lead to increases in population density.

Hering *et al.* (2004) compared baseline ERS beetle relative densities (timed hand searches) in 1995 and 1996, with conditions following a 1 in 100 year flood in 1999 and 2000 to determine the effects of extreme flooding on beetle abundance. They found the lowest densities ever recorded one month after the flood, followed by the highest densities recorded two months later, and concluded that extreme flow levels have considerable propensity to influence the density of ERS carabid beetles. It seems quite probable that the enhanced level of flow pulses observed in 2003 might well have had a similar effect, possibly enhancing population density by suppressing the abundance of predators or parasites, or increasing the amount of available food (Chapter 1, 5). However, it is folly to make any firm conclusions on this matter when both the enhanced temperatures in 2003 and possible density dependent responses could also explain the measured density patterns observed. Further years' data would be required to allow the selection of (1) enhanced summer temperatures, (2) enhanced number of flow pulses, or (3) neither (1) or (2) as the factor best explaining inter-annual changes in population density.

8.5.4 Environmental variable effects on inter-bar population density

Overall, area, and four heterogeneity related measures, namely 'backwater', profile, vegetation cover and heterogeneity were found to be significantly related to the measured density of *B. atrocaeruleum* (Table 8.5). Bar area was also found to be significantly related to percentage of *B. atrocaeruleum* migrating to a bar in Chapter 7 (Table 7.6), and has previously been shown to be strongly related to ERS beetle community structure (Sadler *et al.* 2004). As *B. atrocaeruleum* utilises large areas of a bar (Chapter 5) the local population size would be expected to be positively related to bar area, however, explaining the reasons for the positive association between bar area and measured density is more difficult. There are several possibilities, which include: (1) the possibility that larvae utilise more of the bar than adults, therefore increasing measured density when they emerge as adults and largely become distributed from the water's edge to the mid elevation of bars (Chapter 5); and (2) that larger bars allow *B. atrocaeruleum* to occupy their preferred microdistribution at a greater range of flow levels, and are therefore favourable. Deciphering the reasons for this relationship with bar area is not possible at this stage, but it is clear that the size of bars is of some importance for this species.

Heterogeneity was another significant environmental variable in the study of Sadler *et al.* (2004), but was not measured in Chapters 6 and 7, and in Chapter 4, the within-bar focus of the study probably prevented this variable from being significant. The significant positive effect of greater heterogeneity on density suggests that *B. atrocaeruleum* is favoured by a diversity of microhabitats, many of which it has previously been shown to utilise (Chapter 5). For a species so clearly capable of rapidly changing its microdistribution (Chapter 5) and therefore utilising the most favourable conditions available at all times (depending on, for example, weather, food availability and flow level), increased habitat heterogeneity is always likely to be favourable.

Of the related significant variables, 'backwater', is the most difficult to explain ecologically. The microdistribution of *B. atrocaeruleum* suggests that this species might be favoured by a greater wetted edge, with which the presence of a backwater is related, however, wetted edge is not a significant variable. It would seem most probable that the statistical significance of 'backwater' is the result of co-variation with bar profile or area (Table 8.4). Although vegetation cover and bar profile co-vary with several other variables they make more explanatory sense for *B. atrocaeruleum* than 'backwater', as vegetation cover can influence microclimate, and bar profile influences the availability of favourable microhabitat at different flow levels, and avalanche faces are often associated with high abundance of *B. atrocaeruleum* (pers obs.).

The lack of significant correlations with the sediment variables, and of consistent significant correlation with the trampling index, was surprising, as one or other of these variables have been shown to be important in other investigations (Andersen 1969, 1978; Hammond 1998a; Eyre *et al.* 2001a, b; Sadler *et al.* 2004; Chapter's 4 and 7). The scale at which density was measured was out of sync with the whole-bar scale at which the sediment variables were measured, and this might explain the lack of statistical significance of this variable. Regarding the sediment variables, the association with coarser sediments observed in Chapter 7 might have been due to co-variation with vegetation cover. Sediment variables were also not significant in Chapter 4, instead, stream order measurements, which strongly influenced sediment size were selected as significant. Although trampling intensity was always negatively associated with measured density there was no overall significant relationship, this may well have been due to the sampling methods used. Quadrats were typically positioned on the bar edge in areas that would be expected to maximise sample returns, because investigating the effects of trampling was not the main aim of this chapter. Therefore within-patch areas that were particularly heavily trampled were avoided to some degree.

CHAPTER 9

THE ECOLOGY AND CONSERVATION OF ERS BEETLES

9.1 Introduction

This final chapter integrates the findings of the previous chapters with conceptual ideas to analyse the likely response of ERS specialist invertebrates to various threats. It then provides a synopsis of the adaptations that allow *Bembidion atrocaeruleum* to be so successful in the ERS systems studied. There then follows a discussion of the general management implications of the findings for ERS species, and in particular, those with BAPs. Finally, it presents possible extensions to this research, and other investigations that would further advance the understanding of the ecology and conservation of ERS beetles.

9.2 Response to threats: integration of data with conceptual ideas

This section integrates information derived from this investigation and information from other research on ERS specialist invertebrates, within a conceptual examination of the likely response of different groups of ERS species to the various threats to ERS. It begins by considering the most appropriate scale in which to consider these effects.

9.2.1 Considerations of scale when investigating response to threats

This thesis has shown that the structure of a community, or the distribution and abundance of a species, and the processes influencing this structure, will vary with the scale of investigation. The scale within which a beetle perceives and moves within its environment will typically be small relative to the scale of human perception (e.g. Wiens and Milne 1989; Wallin and Ekbom 1994; Gereben 1995; Antvogel and Bonn 2001; but see Curtis Creighton and Schnell 1998), and this has important implications for: (1) the conservation and management of species and communities (see below), and (2) the investigation and consideration of the response to threats. Any such consideration has to focus on a scale that is both relevant to the organism studied, and viable for the management of the species or community (Wiens 1989; Levin 1992).

The inter-patch spatial structure of populations studied in Chapters 6 and 7 integrate microhabitat and habitat pattern and process within the notion of patch quality and patch size; and reach and segment scale variations in terms of patch connectivity. The spatial structure of a population therefore incorporates pattern and process over several scales. Given its multi-scalar properties, its relevance to the study organisms, and its ready recognition and comprehension by ecologists and environmental managers, the inter-patch spatial population structure of ERS invertebrates is used as a conceptual tool for the understanding of species responses to threats.

9.2.2 The inter-patch spatial population structure of ERS invertebrates

All previous studies of dispersal dynamics for ERS specialist invertebrates have demonstrated the transfer of individuals between ERS patches. Females of *Bryodema tuberculata* (Fabricius 1775), an endangered ERS specialist grasshopper, have limited dispersal abilities and only rarely move between bars, usually when the bars have become connected during periods of low flow (Reich 1991; Stelter *et al.* 1997). The spatial population structure of this species is akin to a classic metapopulation, situated low down on the mobility axis of Thomas and Kunin (1999). In contrast, research on the carabid *Nebria picicornis* (Fabricius 1801) showed that most individuals were recaptured >400m, and many >800m from their point of release (Manderbach and Plachter 1997); indeed, dispersal rates were so high in this species that running a successful mark-recapture study was impractical (Randolf Manderbach pers comm.). Re-colonisation of newly created ERS habitat by *Bracteon litorale* (formerly *Bembidion*) has been observed ~10km upstream from the nearest known population (Gunther and Assmann 2005). So it seems likely that many ERS specialist carabids are capable of widespread dispersal, and could be classified as having patchy spatial population structures. Such high inter-patch dispersal is a common trait of species living in unstable or transient habitats (Southwood 1962; Hanski 1987). ERS specialist invertebrates that exist as metapopulations, or which are situated lower down the population mobility axis, such as *B. tuberculata*, and *F. maritimus* are likely to be more vulnerable to threats than species such as *B. atrocaeruleum* and *B. decorum*, which exist as patchy populations. Other ERS specialists that are likely to have a limited ability to undertake inter-patch migrations, such as the Ptiliidae (feather-wing beetles), which are incapable of directional flight, despite their probable ability to travel long distances on the wind, are also likely to be more vulnerable to threats.

The discovery of a condition dependent migration, or escape response, in reaction to heavy livestock trampling by *B. atrocaeruleum*, has particular significance because it is likely to increase population robustness in the face of local degradation of habitat. If the negative effect of trampling on ERS beetle assemblages (Chapter 4) was brought about by similar escape responses in other ERS beetles, rather than direct mortality, then other species may have a similar robustness to such degradation. There would be strong evolutionary pressure amongst ERS specialist beetles to develop an escape response in reaction to vegetation succession, so other species might be expected to also show a similar response to degradation of habitat due to trampling.

9.2.3 The likely response of ERS beetles to potential threats

There are three main factors commonly believed to cause adverse impacts on spatially structured populations, these are (1) reductions in the availability of habitat, (2) reductions in the connectivity between available patches, and (3) reductions in patch quality (e.g. Hill *et al.* 1996; Thomas *et al.* 2001; Fleishman *et al.*, 2002; Baguette and Schtickzelle 2003; Johansson and Ehrlén 2003; Franken and Hik 2004). The effects of habitat loss are known to have large negative effects on most populations, whereas the effects of isolation are generally much less detrimental, and can sometimes be positive (Fahrig 2003). Unpicking the effects of habitat loss and isolation is difficult and typically, processes that reduce the availability of ERS habitat will reduce the connectivity between ERS patches, so these effects are considered concurrently and termed HAbitat Loss and ISolation (HALIS) effects. HALIS effects will usually be caused by indirect threats to ERS systems, mediated through (1) reduced sediment supply and (2) increased rate of vegetation succession, although these two processes will rarely be completely mutually exclusive. Reductions in patch quality can be caused by both direct and indirect threats to ERS, and will be often be associated with HALIS effects when caused by the latter type of threat.

The HALIS effects of the various threats influence these two processes, usually through modification of the hydrological regime. Reduced sediment supply can be the consequence of the disruption of longitudinal transfers (e.g. through impoundment and gravel extraction) or reductions in the rate of lateral supply through erosion (e.g. channel engineering). The supply of sediment from bank erosion can sometimes exceed that from upland erosion (e.g. Mount 2000). Increased rates of vegetation succession can occur through the reduction in flood frequency and intensity (e.g. Brewer *et al.* 2000; Gilvear *et al.* 2002), more favourable conditions for vegetation growth due to fewer low flow events (Plachter and Reich 1998; Hering *et al.* 2004) and enhanced sedimentation of sand and silt (Church 1995; Gurnell & Petts 2002). Figure 9.1 illustrates the likely response of a river reach or segment to indirect externally driven HALIS effects. The increased rate of vegetation succession and/or reduced rate of sediment supply perturb the natural dynamic equilibrium causing the transition to a new dynamic equilibrium, characterised by fewer patches of different character, with lower connectivity and smaller bar area.

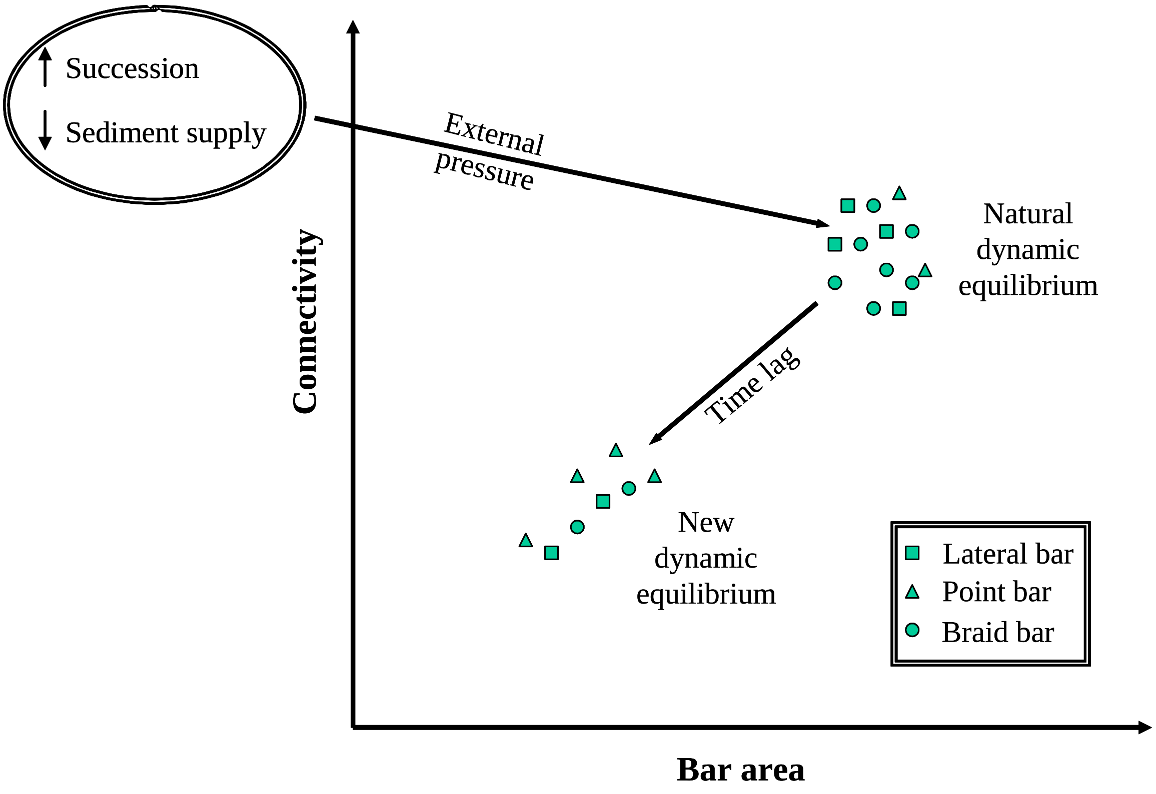


Figure 9.1 Hypothetical response of a river reach to the external pressure of reduced sediment supply and increased rate of vegetation succession. The natural dynamic equilibrium is disturbed and following a time lag, a new dynamic equilibrium is reached that has fewer bars, of different character, lower connectivity and smaller size.

Figure 9.2 illustrates the likely probability of survival for species with different types of inter-patch spatial population structure, depending on the scale of the negative impact. The survival probability should be greater for patchy populations than metapopulations because the greater dispersal capabilities of the former will limit their vulnerability to HALIS effects and might increase the chances of successful escape from local negative effects on habitat quality. The rate of decline of survival probability increases once more than one bar is affected, and continues to decline as a greater proportion of the formerly available habitat is affected for longer periods (Figure 9.2). Survival probability is shown to be reduced when source patches in particular are affected, because this will also impact the fitness of nearby sink populations. Linear declines in survival probability are shown together with declines that have a threshold, when survival probability drops sharply.

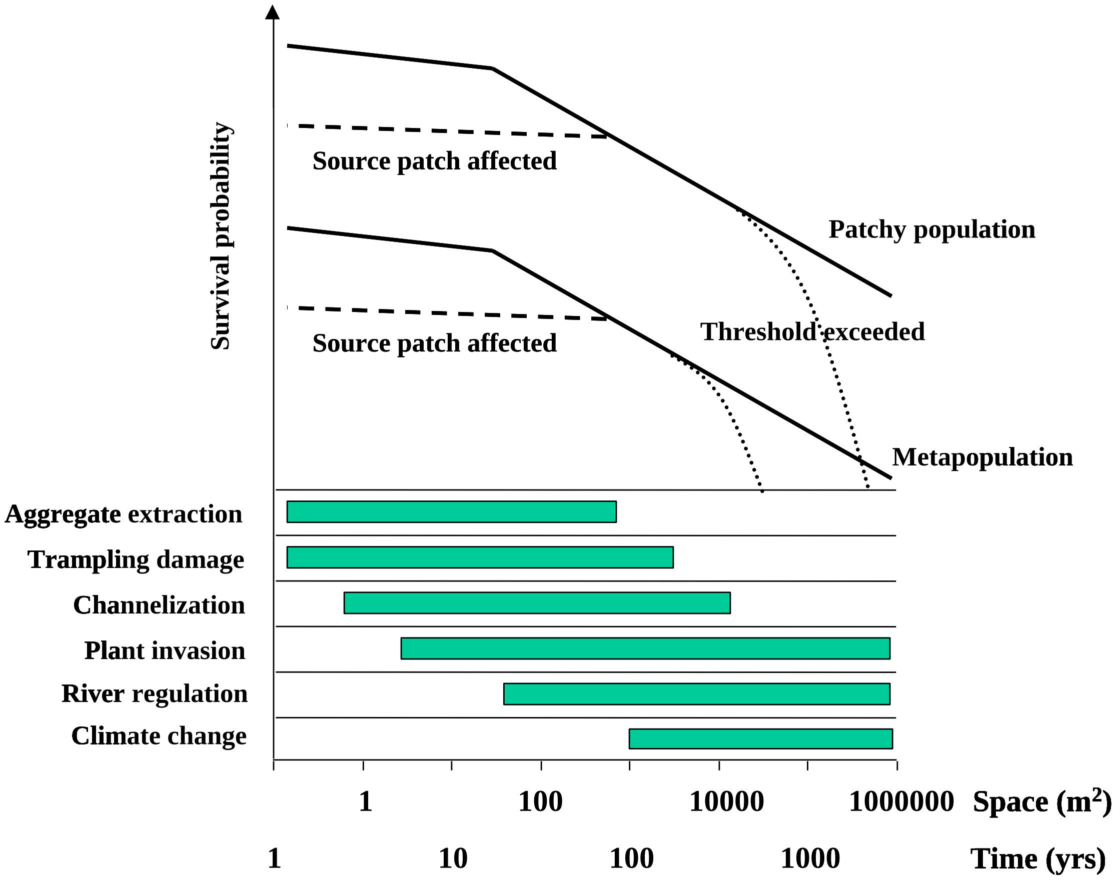


Figure 9.2 The likely survival probability of the various SPS when exposed to threats ranging from acute threats (e.g. aggregate extraction), acting over small spatiotemporal scales; to chronic threats (e.g. river regulation), acting over large spatiotemporal scales. The dashed lines represent the situation when a source patch within a patchy population or metapopulation is affected by the local acute threat. The dotted line represents the situation when HALIS effects exceed beyond the threshold of the species and the population crashes. Individual species are likely to show different survival probability curves.

The literature suggests that there are often thresholds in population survival probability (e.g. With and King 1998; Fahrig 2001, 2003). Accordingly, a minimal increase in HALIS effects or reduction in patch quality can cause large decreases in the survival probability of a population. For example, above a certain level of habitat loss the effect of habitat isolation on dispersal distances may become critical (Fahrig 2003), or populations may become reduced to a level where Allee effects are important (Boyce

1992). Alternatively, physical thresholds might be crossed, such as a shift between braided and single-thread plan forms (Leopold and Wolman 1957), causing large-scale HALIS effects (Figure 9.1). In this context, Werrity and Leys (2001) discuss the differences between robust and responsive river systems. In the former, large shifts in channel morphology might be expected, whilst in the latter, the fairly linear decline might be more realistic (see Figure 9.2).

Figure 9.2 also illustrates the likely spatio-temporal scale of several potential threats, including: river channelization and regulation, aggregate extraction, livestock damage, invasion by exotic plants, and climate change (Anon. 1999; Sadler *et al.* 2004; Bates *et al.* 2005). The threats operate over a diversity of spatio-temporal scales within the geomorphic hierarchy (Figure 9.3) and range from small scale acute effects (e.g. local aggregate extraction) to large scale chronic effects (e.g. river regulation). Each of these threats is considered in turn.

Aggregate extraction and livestock damage through trampling are both largely direct threats and will typically operate at small spatio-temporal scales in the UK (Figure 9.2). They can physically affect individual bars without heavily impacting other bars in close proximity. In many countries, aggregate extraction is often a large-scale, intensive operation; the effects of which spread both upstream and downstream of the extraction site (Kondolf 1997; Nicholas *et al.* 1999). For example, the disturbance to surface armouring can enhance mobilisation of fine sands and silts, causing downstream fining below gravel works (Newson and Leeks 1987), or can cause both upstream and downstream bed incision through the process of nick migration (Kondolf 1997, 1998; Sear and Archer 1998). However, the main effect of limited aggregate extraction is likely to be confined to the patches from which extraction takes place, except in a source-sink system when a source patch is impacted. In such a situation the likelihood of a large population decline or extinction is likely to increase significantly (Figure 9.2).

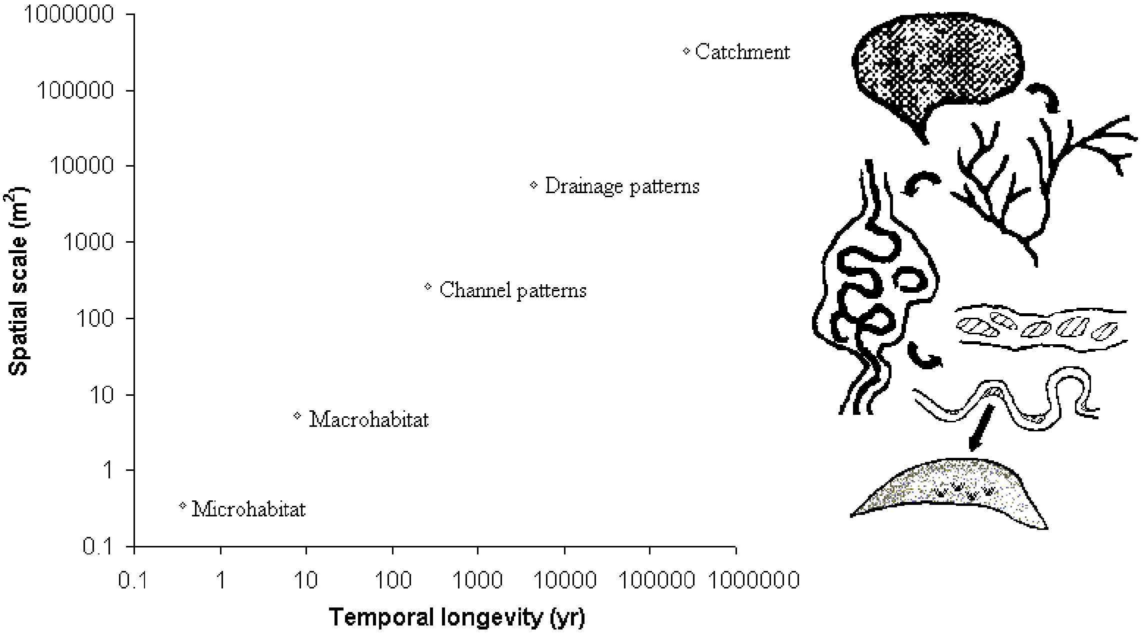


Figure 9.3 Spatio-temporal geomorphic heirachy of riparian landscapes (adapted from Naiman *et al.* 1992 and Ward 1998).

By grazing on vegetation (increasing erosion during high flows), and eroding banks through trampling, livestock (particularly cattle) increase the rate of lateral erosion, whilst reducing the rate of succession (Trimble and Mendel 1995; Jansen and Robertson 2001), possibly creating more ERS habitat. Trampling can therefore potentially act in a similar manner to floods in counter-acting succession (Figure 1.1), and may have a positive influence on ERS beetles in systems with limited available ERS (Sadler *et al.* 2004). In high quality systems, where there is a large availability of ERS, this investigation has shown that trampling reduces the conservation potential of ERS assemblages (Chapter 4), and can cause escape responses in some species. Although such responses may limit the negative impact on ERS beetles to some extent, trampling still reduces the quality of individual habitat patches in a system. In a UK context, pastoral farming is by far the dominant land use around rivers with an abundance of ERS, so grazing has the potential to impact large sections of ERS river. However, livestock typically only heavily impact a small number of bars in any one reach, unless stocking density is very high, especially when high banks, trees, or fencing limit the number of places that livestock can enter the river (Trimble and Mendel 1995). So the effect of livestock are likely to be a reduction in population density on individual bars, and are again (as in all situations) more likely to cause large population reduction or extinction if source bars are impacted in a source-sink system (Figure 9.2).

The broadest definition of river channelization (Brookes 1989) includes channel enlargement, channel realignment, embanking, and general channel maintenance (e.g. dredging and the removal of obstructions). Making generalisation about the effects of channelization is, therefore, difficult. Extreme forms of channelization, such as channel straightening and weir construction, evidently have devastating consequences for ERS communities in terms of both HALIS effects and individual patch effects (patch removal). More minor forms of channelization, such as protection of eroding banks by rip-rap or gabions, or more sensitive channel re-alignment (e.g. Vivash *et al.* 1998), are likely to have less extensive effects on ERS communities. As channelization typically reduces the rate of lateral erosion, and hence downstream sediment supply, more widespread HALIS effects are likely to arise over a larger scale than for trampling damage and aggregate extraction (Figure 9.2).

The three non-native, invasive, plant species which colonise ERS, and are considered the most problematic (Collingham *et al.* 2000; Holland 2000; Rotherham 2000) are: *Fallopia japonica* (Houtt.) (Japanese knotweed), *Heracleum mantegazzianum* Sommier et Levier (giant hogweed), and *Impatiens glandulifera* Royle (Himalayan balsam). *Impatiens glandulifera* and ‘other invasive species’ are mentioned in the grouped river shingle beetles BAP as a potential threat (Anon 1999), but unless these species colonise ERS habitat more quickly than native species, they are unlikely to negatively impact ERS beetles. Indeed, because all species are annual, and tend to competitively exclude perennial species, the bare riparian areas left by winter die-back might actually increase the rate of erosion (Dawson and Holland 1999; Holland 2000), potentially increasing the amount of available ERS. If these species do colonise ERS more quickly than native species then the effects are likely to be chronic, HALIS effects, which, given the propensity for these species to spread rapidly through hydrochory (e.g. Dawson and Holland 1999; Goodson *et al.* 2003), are likely to be large scale (Figure 9.2).

The effects of river regulation are extensive and widespread, with approximately two-thirds of the water flowing to the oceans controlled by dams (Petts 1984). However, the term river regulation describes a large suite of measures, each with markedly different effects on riparian habitats (Janssen *et al.* 2000). Types of regulation include: (1) reach dewatering (e.g. Klingeman *et al.* 1998), (2) run-of-river impoundments (e.g. Holubová 1998), and (3) upstream regulation (e.g. Brewer *et al.* 2000), which has the most limited environmental impacts (Jansson *et al.* 2000) and is the typical situation in the UK. The extent of impacts largely depend on the scale of regulation, with natural landscape processes expected to resume at some distance from the regulation in accordance with the serial discontinuity concept (Ward and Stanford 1995; Stanford and Ward 2001). Flooding a section of river containing ERS obviously will have disastrous consequences for the affected patches, and potentially for the whole population if source patches are affected. Although regulation may potentially influence the quality of patches, for example through the removal of fine sediments downstream of dams (Petts 1979), the main effects of regulation will be large-scale, chronic, HALIS effects (Figure 9.2).

Lastly, the effects of climatic change clearly act over large temporal and spatial scales, and could potentially have widespread negative, or positive, HALIS effects depending on the type of change (e.g. Passmore *et al.* 1993; Knox 1999; Werrity and Leys 2001). If flood magnitude or frequency were reduced, or if the rate of vegetation succession was accelerated by climate change, then one might expect negative effects. However, the current UK trend for wetter winters, with more intense rainfall (high confidence), and drier summers with less intense rainfall is expected (medium confidence) to continue through the 21st Century, regardless of the greenhouse gas release scenario (Hulme *et al.* 2002). It is, therefore, likely that the frequency and magnitude of flooding is going to increase (Werrity and Leys 2001). However, other climatic changes that are forecast (Hulme *et al.* 2002), such as a large reduction in snow cover, might have negative landscape effects if snow melt drives a large proportion of floods in the catchment. However, in Britain, even in the Cairngorms, relatively few floods are driven by snow melt (Werrity and Brazier 1991) so this seems unlikely.

9.3 The ecology of *Bembidion atrocaeruleum*: extensive adaptations to the ERS system

The previous section broadly categorises the inter-patch spatial population structure of species into metapopulations and patchy populations. When considering the likely responses of all ERS invertebrates to threats in such a comprehensive manner this is a necessary simplification, allowing broad trends to be identified and discussed without becoming fast in intricate detail, which would necessarily have to be extrapolated from relatively little understanding. However, response to HALIS effects and patch quality will be species specific, and when more detailed research has been implemented for a species, this extra information can greatly enhance the understanding of the study habitat. *Bembidion atrocaeruleum* is used here as such an example.

This section is configured along four distinct, but interrelated, conclusions about the dynamic population structure of *B. atrocaeruleum* in the study segment: (1) individuals make choices about their distribution; (2) the patchy structure of the population allows rapid response to variations in patch quality; (3) the species responds dynamically at multiple scales; and (4) its strong adaptations to the highly disturbed ERS environment make the population highly robust. To some degree these conclusions are specific to both the species, and the area studied, as within species population structure is known to vary spatially both with climate and habitat distribution, and between species (e.g. Thomas *et al.* 1999; Schneider *et al.* 2003; Purse *et al.* 2003). However, the dynamic characteristics which allow *B. atrocaeruleum* to be so successful are likely to be consistent both for this species across the study area, and for other ERS species in other systems (c.f. Plachter and Reich 1998).

9.3.1 Individuals make choices about their distribution

In a sequence of small-scale elegant experiments, Andersen (1978, 1985, 1989) showed that species of *Bembidion* respond to sensory and mechanical stimulation in the selection of the most appropriate microhabitat. At a slightly larger scale, *Bembidion obtusidens* has been shown to use gradients in humidity and the odour of cyanobacteria to orientate movements towards their favoured sea shoreline microhabitat (Evans 1984, 1997). The zonation of ERS is unlikely to be as strong as that for which marine shoreline specialist beetles (e.g. Colombini *et al.* 1994, 2002) are adapted to, so the orientation capacity of ERS beetles might not be as that exhibited by marine shoreline specialists. Nonetheless, individual *B. atrocaeruleum* showed considerable propensity to move some distance within bars, and this species was shown to considerably alter its distribution temporally (Chapter 5). Andersen (1968) also observed similar small-scale cursorial redistribution in response to changing flow levels. These micro-scale redistributions can be classified as ‘trivial’ movements, and are likely to be bought about by non-random alteration of the movement and turning rate in response to favourable or unfavourable habitat (e.g. Kennedy 1974; Hassell and Southwood 1978; Wallin and Ekbom 1994). The thresholds for response for such movements are typically low (Hassell and Southwood 1978), and are likely to be linear in response to rising water levels.

At some point, upon exceeding a threshold of unsuccessful attempts to find a suitable microhabitat, or in response to a stronger movement cue (e.g. complete flooding of the habitat); an individual will make a ‘migratory’, or escape, type movement redistribution by flight (e.g. Johnson 1969; Hassell and Southwood 1978). Such redistribution is quite likely to result in the migration to a different patch, and such condition dependent emigration has been observed in response to habitat inundation and livestock trampling (Chapter 7). Such redistribution will require the expenditure of much more energy and may not be possible during cool conditions (Southwood 1962). *Bembidion atrocaeruleum*, therefore, makes choices about the suitability of its microhabitat, and whether to use trivial or migratory movement, although it is unclear which cues cause these movements. Such abilities are likely to increase the fitness of individuals in dynamic ERS habitats.

9.3.2 The patchy structure of the population allows rapid response to patch quality

Sutcliffe *et al.* (1997b) suggest that the greater a species dispersal ability the less likely patch size and isolation will be important, and the more important habitat quality becomes. At the scale studied, isolation was clearly not an important determinant of population density, and all patches were occupied by *B. atrocaeruleum*. Given the highly connected nature of ERS systems, particularly in light of the migration capability shown by *B. atrocaeruleum*, this was to be expected. There was, however, a significant positive correlation between density and patch area, but this might have been an effect of patch quality or varying inundation potential (Chapter 8). This was also found to be the case by Förare and Solbreck (1997) for a patchily distributed moth, despite the clear importance of patch quality in their study. Variation in patch quality (e.g. bar heterogeneity and sediment size) was found to be important for *B. atrocaerulem*, and beetles were shown to move in response to trampling intensity. The density of *Bembidion atrocaeruleum* was therefore highest in the most favourable areas, as predicted by Sutcliffe *et al.* (1997b) when dispersal rate is high. This should lead to higher population fitness in ERS systems, where patches will become more or less favourable over time in response to succession, patch creation, patch rejuvenation.

9.3.3 The species responds dynamically at multiple scales

Figure 9.4 illustrates the spatio-temporal scale at which different dynamic processes mainly act, although many of these processes will also have effects at other scales. The spatial axis is divided into three scales and represents processes occurring within individual patches, between patches (but within the same sediment storage zone), and between sediment storage zones. Above this scale *B. atrocaeruleum* may also respond to other processes, for example, distributional changes in response to climate change (Thomas *et al.* 2004; Hickling *et al.* 2005); but such responses were not studied. The temporal scale is divided into four levels and represents processes occurring over periods shorter than that of a generation, from microscale redistribution to abundance recovery after high flow events; at the generational time scale (a process that occurs once per generation); and at inter-generational time scales. The scale assumes that *B. atrocaeruleum* generally lives for only one year.

Despite the wide range of scales over which these processes operate, all have the potential to influence the spatial density of *B. atrocaeruleum*. This transpires through two processes: (1) a response in terms of population abundance (high flow recovery, patch quality effects, density dependence, flow dynamics, and weather); or (2) a response in terms of redistribution (favourable microhabitat tracking, high flow response, escape response, and overwintering). However, all type 2 responses are likely to increase population fitness and therefore influence overall changes in population abundance.

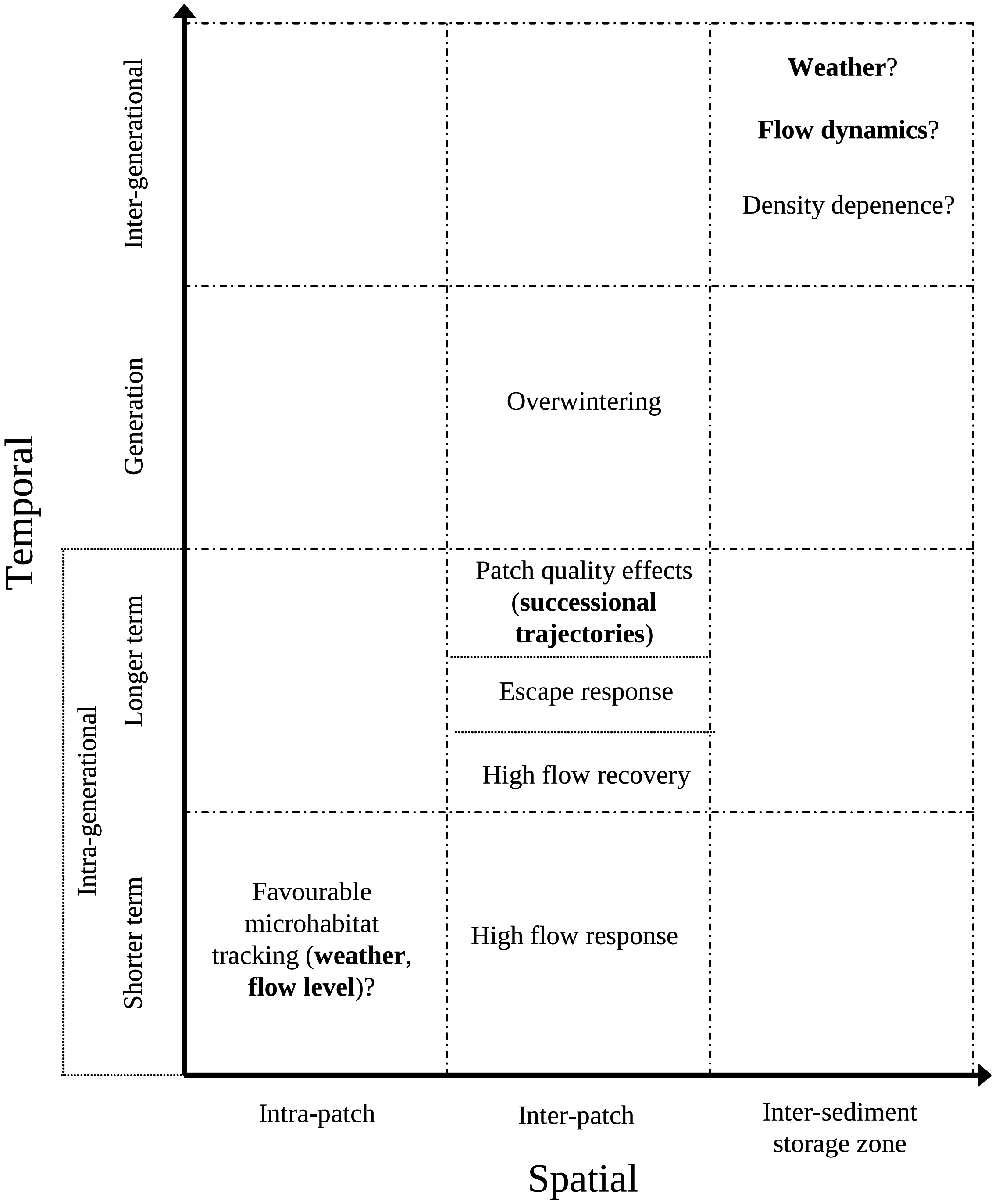


Figure 9.4 Dynamic responses of *Bembidion atrocaeruleum* at a variety of spatio-temporal scales (? = processes that may occur, **bold** = effects that are external to the ERS habitat and community).

9.3.4 Its strong adaptations to the highly disturbed ERS environment make the population highly robust

This population of *Bembidion atrocaeruleum* is markedly robust for several reasons: its broad range of ERS microhabitat use, its potentially flexible microhabitat distribution, its escape from unfavourable conditions (e.g. heavily trampled areas), and its temporal avoidance of unfavourable flow and weather conditions (overwintering). A lack of any one of these characteristics in other ERS specialists would be likely to increase their vulnerability, and so lead to greater rarity. *Bembidion atrocaeruleum* therefore provides a good example of a very highly adapted and successful ERS beetle with which to compare other rarer species (e.g. Chapter 6).

Most of the processes highlighted in Figure 9.4 only became apparent after intensive mark-recapture investigations and medium term (3 years) monitoring of the density of a single species. They would not have been identified by standard survey work alone. This investigation of *B. atrocaeruleum* therefore serves as a good example of the way intensive species specific studies (e.g. Manderbach and Plachter 1997) are necessary to fully appreciate the dynamic processes influencing species abundance in the complex ERS system.

9.4 Implications for the appropriate management of ERS

9.4.1 The creation of protected areas

In highly developed landscapes it is clearly impossible to preserve and protect every area of ERS because of limited availability of conservation resources and the overriding necessity to protect people and property from flooding and erosion. There is consequently a need to estimate the amount of habitat, or number of individuals, necessary to have a high chance of successfully conserving a species (e.g. Shaffer 1981; Boyce 1992; Hanski *et al.* 1996). The level of understanding needed to do this for any ERS species is not available at present (although see Stelter *et al.* 1997 for a related approach based on the amount of necessary flood disturbance). Nonetheless, implications for the creation of protected areas for ERS species can be derived from the findings of this thesis.

It is clearly not appropriate to just protect one bar when trying to preserve a community of ERS beetles, particularly as the bar can move out of the protected area. It is not clear exactly how much ERS is required in order to protect the ERS community living there, but a reasonable rule of thumb seems to be to protect reaches of river that have a fairly continuous occurrence of patches of ERS. Even rivers that contain large expanses of high quality ERS (Chapter 3), rarely have these sediments distributed throughout their lengths, some sections are laterally constrained by bedrock, or palaeo-alluvial fans, and when such sections are of 2km or more in length they provide convenient dividing reaches where the protection of ERS habitat is of a lower priority.

9.4.2 Management of threats

Livestock trampling has been shown to negatively impact the conservation value of ERS beetle communities, so some shielding from these effects is recommended for protected areas of ERS. Some of the best examples of ERS rivers (the Usk, Wye, Tywi and Spey) are, or are soon likely to be protected over a combined river length of hundreds of kilometres, assuming that their Special Areas of Conservation statuses are approved by the EU (JNCC 2005). However, it is not feasible to completely exclude livestock from large sections of river containing ERS because fencing is expensive and has a very limited lifespan on these highly dynamic rivers (Adrian Fowles pers. comm.). Furthermore, despite trampling damage across much of the Afon Tywi and River Severn, these rivers have still been shown to support ERS beetle faunas of considerable conservation status. It is therefore recommended that the best quality sections of ERS within these high quality rivers should be identified using the ERSQS and ERSQI (Chapter 3; Sadler and Bell 2002).

Bars with more fine sediment are likely to be more vulnerable to trampling impacts, so sites should be selected for fencing according to both their robustness and conservation value. Livestock impact can be reduced over wider areas by the careful rotation of grazing areas and the provision of more off-river sources of drinking water (e.g. Janson and Robertson 2001; McInnis and McIver 2001; Stillings *et al.* 2003).

Of the other threats discussed in this Chapter, river regulation and channelization are the most readily manageable. Although dams regulating rivers have sometimes been removed (e.g. Bednarek 2001), this is exceedingly rare in the UK, and is unlikely to be an option in the vast majority of cases. Careful management of reservoir releases could be used to benefit many riparian species (e.g. Tiegs *et al.* 2005; Tiegs and Pohl 2005), but at present the understanding of the flow requirements of ERS species is not sufficient to advise on this (but, see Section 9.5). However, it is strongly advised that deliberate control of the flow regime of the best quality British ERS rivers that further reduces the frequency and magnitude of floods, should be prohibited whenever possible. Plachter and Reich (1998) come to analogous conclusions regarding the regulation of the best quality sections of ERS rivers in Germany.

Similarly, channelization of the best quality British ERS rivers should be avoided whenever possible. However, in the highly populated British landscape, the lateral migration of river channels will often threaten constructions such as roads, railways and housing. In these instances, some channelization works, such as the use of gabions and rip-rap on the inside of eroding banks, are usually employed in the UK (Adrian Fowles pers. comm.). Such works should aim to be as minimal as possible, while still protecting the construction.

9.4.3 Direct manipulations of habitat and species distribution

In order to facilitate dispersal between areas of ERS that are highly spatially separated, it might be desirable to create small patches or ‘stepping stones’ of ERS in sections of river without any (c.f. Gilpin 1980, Fischer and Lindenmayer 2002; Baum 2004). Such methods have already been used in the UK with varying success on the Upper Trent and River Tame (Andrew Crawford pers. comm.), although with the aim of habitat creation, rather than dispersal facilitation. However, the creation of such stepping stones is not always appropriate because while functioning as corridors for movement they can sometimes act as sink habitats, and can increase the rate of emigration from source patches, potentially leading to the extinction of the source patch (Henein and Merrian 1990; Hess and Fischer 2001; Amarasekare 2004). In lieu of detailed information on such effects for ERS beetles, the construction of such stepping stones is not recommended, except in an experimental context.

There are numerous examples of deliberate re-introductions of species to areas where they were formerly known to be present for conservation purposes (e.g. Whatmough 1995; Fischer and Lindenmayer 2000; O’Toole *et al.* 2002). However, re-introductions of invertebrates are extremely rare (Fischer and Lindenmayer 2000), probably due to a combination of the generally limited general interest in the conservation of insects and the difficulty in assessing the necessary criteria for responsible re-introductions. Responsible re-introductions should: (1) have good historical evidence for former natural occurrence; (2) only re-introduce species lost through anthropogenic activity, that are unlikely to re-colonise naturally; (3) only be attempted when the factors causing the original loss have been rectified; (4) only be attempted when sufficient habitat is available; (5) re-introduce individuals from a population as genetically close as possible to that of the former population; (6) only be attempted when the loss of individuals will not risk the continued survival of the donor population (Centre Naturopa 1996). Currently, these criteria cannot be satisfactorily confirmed for species of ERS beetle, but they might be considered in the future once the level of understanding of ERS beetles has been increased. One species that might particularly benefit from such re-introductions is the BAP species *Bembidion testaceum*.

9.4.4 BAP species

There are two main aims of the BAP's for the eight specialist ERS beetles, namely: (a) to *maintain* viable populations, and to (b) *enhance* populations at some sites (Chapter 3). Despite the work implemented in this thesis and in other recent studies of ERS beetles in the UK (Eyre *et al.* 2001a, b; Sadler *et al.* 2004), some of which have focused specifically on BAP species (Sadler *et al.* 2005); the recommendations for the maintenance and enhancement of populations of species of BAP ERS beetles are very restricted. They are to: (1) preserve the *status quo* on sites for which population maintenance is desired, by not allowing any new potential threats to begin to operate; and (2) to reduce possible reductions in population size due to trampling by fencing sites that are currently damaged by livestock, especially when the aim is to *enhance* these populations. The limited nature of these recommendations does not reflect negatively on the quality of the research in these investigations, but rather on the unrealistic aims set out in the BAP's. The very large amount of research required to even assess the success of these aims, let alone determine the best course of management action to achieve them, was not envisioned when the aims were established, and for some of the BAP ERS beetles, the research may not be possible (Chapter 3).

9.5 Suggested further work

Although this work presents several significant findings relating to the ecology and conservation of ERS beetles; as the last section has suggested, much work remains to be done. This section is subdivided twice: (1) extension to research themes already encompassed in the thesis, and (2) other research themes that have not been broached in the thesis.

9.5.1 Extensions to investigations in the thesis

9.5.1.1 Influence of trampling

The level of negative impact that livestock trampling has on ERS beetle communities will be partly dependent on whether the observed reduction in conservation value is due to escape from the trampled area, as observed for *B. atrocaeruleum*, or to direct mortality. This could be tested by establishing multiple plots within an un-trampled bar, some kept as controls and others with different degrees of simulated trampling; and testing the rate of movement from the affected area by cursorial movements using pitfall traps, and flight using interception traps. This would allow the existence of escape responses in several species to be tested, and could be used to determine whether individuals typically respond by walking to un-trampled sections of habitat, or by flight, potentially to a different patch. Interactions with weather could be tested for by repeating the experiment across a range of air temperatures.

9.5.1.2 Microspatial distribution

The dynamic microhabitat utilization model (Figure 5.1) suggests that the favoured microhabitat of a species continually shifts in response to changing weather conditions and flow level. Such dynamic shifts in the spatial distribution of niche space might reduce the potential for interspecific competition, thereby preventing the competitive exclusion of certain species. Several extensions to the investigation outlined in Chapter 5 are described below that should ascertain the validity of this model, and thereby investigate the underlying processes sustaining the biodiversity of ERS beetle communities. In Chapter 5 conditions on 17/6/03 were warm and dry and *Zorochros minimus* was shown to be distributed nearer to the water than on all other occasions, however, changes in the distribution of species associated more closely with the water's edge were not observed. This was possibly because species such as *B. decorum*, *B. punctulatum*, and *B. atrocaeruleum* were distributed so close to the water's edge that pitfall traps could not sample them effectively. It is therefore suggested that a combination of hand searching at the water's edge, and pitfall trapping over the remainder of the bar is the best way to sample the microspatial distribution of ERS beetles. Additional microhabitat measurements, such as surface temperature, humidity, and food availability would also improve further studies. Experimental manipulations of species density, microclimate and food availability could also be used to test the responsiveness of observed microspatial distributions to changing conditions, and could be used to more directly test for the presence of interspecific competition.

9.5.1.3 Spatial population structure

This investigation has shown that *B. atrocaeruleum* and *B. decorum* have a patchy spatial population structure at the within-sedimentation zone scale. At larger scales the spatial population structure of these species might better approximate metapopulations, or even separate populations when the distance separating systems of patches is very large. Information on the spatial population structure at much larger scales than studied in this thesis is important for understanding the viability of very isolated populations, or when re-creating ERS habitat many kilometres from the nearest ERS habitat (e.g. Klaassen *et al.* 1998). Such large scale studies cannot be implemented using the methods described in this thesis, they are too labour intensive. Over stream segment scales, short-term mark recapture studies for the estimation of dispersal might be possible using rapid methods of marking and detection, such as the adherence of dusts that glow under UV light sources (e.g. Hagler and Jackson 2001). However, over catchment and inter-catchment scales, the degree of exchange between population units can only realistically be investigated using analysis of variation DNA in combination with simulations of gene flow (e.g. Kumar *at al.* 2001; Mardulyn 2001; Laval and Excoffier 2004; Mardulyn and Milinkovitch 2005).

9.5.1.4 Longer-term investigations

ERS habitats and beetles are likely to be highly responsive to environmental changes that influence the hydrological regime and availability of habitat. To understand temporal variability of this nature it is necessary to collect longer term datasets (e.g. Burt 1994; Lane 1997; Scott and Anderson 2003). A viable baseline dataset is also necessary if changes due to, for example: the invasion of the habitat by plants (e.g. Himalayan balsam, giant hogweed), the effect of unusual hydrological events (e.g. Hering *et al.* 2004), or the appearance of invasive species of beetle (e.g. the harlequin ladybird, *Harmonia axyridis* (Pallas, 1773) Majerus and Roy 2005), are to be investigated. The continuation of the three-year density dataset for *B. atrocaeruleum* and other species (not included in this thesis) into the long-term is therefore recommended. Such a study would be likely to require downscaling of the sampling effort. Problems of changing patch characteristics could be minimised, but not excluded, by focusing on more stable, large point bars. Mid-July is recommended as the best period to sample when the focus is on long-term change, as population density is at its peak, and July gives the best indirect indication of larval abundance.

9.5.2 Other investigations

The detrimental effects of channelisation and flow regulation have been hypothesised (Plachter and Reich 1998), and comparisons between ERS communities in regulated and unregulated rivers have been made (Reich 1986). However, there remain no published investigations that directly study the effects of any of the threats described above except for this thesis' study of trampling effects. However, in a UK context, aggregate extraction is generally small-scale and localised, so is not considered a high research priority. Furthermore, investigations of the often wide-scale effects of the various indirect threats (e.g. channelisation, regulation) are likely to be subject to fairly intractable problems of spatio-temporal autocorrelation, and pseudo-replication, as they will necessarily take the form of ‘before and after’, or ‘upstream and downstream of’, type studies. Therefore, the effects of such broad-scale threats on ERS beetles and their habitat are best predicted by further ecological understanding of these communities. Two further areas of research of large importance for the comprehension of the ecology and conservation of ERS beetles are described below.

9.5.2.1 The importance of larvae and pupae for the ecology and conservation of ERS beetles

The main role of larvae in the life history of beetles is to eat and grow, whereas, the role of the adult phase of a beetle’s lifecycle is more concerned with breeding and dispersal (Linssen 1959; Thiele 1977). It is quite likely therefore, that competition (inter and intra-specific) occurs in the larvae of ERS species. Andersen (1988) showed how, upon contact, larvae of ERS species are aggressive towards other larvae, and that this will usually result in the death of the smallest larva. Other studies have shown that it is typically the larvae that are resource limited, and subject to density dependence (e.g. Tanner 1966; Stubbs 1977). Larval abundance might therefore be a better indicator of patch quality and competitive interactions than the abundance of adults. However, very little is known about the distribution, competitive interactions and resource requirements of beetle larvae and pupae (although see Andersen 1988; Manderbach and Plachter 1997 for notable exceptions) mainly because the taxonomic understanding to identify down to species level is not yet available. Detailed taxonomic work is required to fill this gap in the taxonomy of ERS beetles. Once this is achieved, studies of the microdistribution of ERS beetle larvae

(Chapter 5 and Section 9.5.1.2), and the long-term investigation of larval densities (Chapter 8 and Section 9.5.1.4) are likely to be particularly useful for enhancing the understanding of the factors sustaining ERS beetle biodiversity.

9.5.2.2 Which characteristics of the flow regime sustain the integrity of ERS beetle communities?

The importance of preserving the natural flow regime, and the overriding influence of flood pulses for ERS beetles are well appreciated (Plachter 1998; Plachter and Reich 1998; Tockner *et al.* 2003; Tockner *et al.* in press). However, the significance of the frequency distribution of lower magnitude flow pulses (*sensu* Tockner *et al.* 2000) and other characteristics of the flow regime are not fully comprehended. Nevertheless, they are of potentially large significance for the transfer of aquatic food resources (Tockner *et al.* in press), for the suppression of competing non-specialist species, and for the control of inter-specific interactions and niche packing. In essence, we understand that the preservation of the natural flow regime is important for the maintenance of community function and diversity, but we do not understand which *specific* characteristics of the natural flow regime are crucial for this. Manipulation of the flow regime for research purposes is only possible on regulated rivers and examples of this are very rare (e.g. Tiegs *et al.* 2005; Tiegs and Pohl 2005). It is probable that such research will have to measure the importance of flow regime indirectly by comparing the ERS beetle fauna of multiple rivers which have a variety of flow regimes, most probably using multivariate statistics.

REFERENCES

Aars J, Ims RA. 2000. Population dynamic and genetic consequence of spatial density-dependent dispersal in patchy populations. *American Naturalist* **155**: 252-265.

Adams J. 1979. Gravel size analysis from photographs. *Journal of the Hydraulics Division* **Oct.**: 1247-1255.

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA. 1987. Ecological neighbourhoods: scaling environmental patterns. *Oikos* **49**: 340-346.

Adis J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger* **202**: 177-184.

Agouridis CT, Workman SR, Warner RC, Jennings GD. 2005. Livestock grazing management impacts on stream water quality: A review. *Journal of the American Water Resources Association* **41**: 591-606.

Albrectsen B, Nachman G. 2001. Female-biased density-dependent dispersal of a tephritid fly in a fragmented habitat and its implications for population regulation. *Oikos* **94**: 263-272.

Alexander KNA. 1988. The development of an index of ecological continuity for deadwood associated beetles. *Antenna* **12**: 69-70.

Allee WC, Emerson AE, Park O, Park T, Schmidt KP. 1949. *Principles of animal ecology*. Saunders, Philadelphia.

Amarasekare P. 2004. The role of density-dependent dispersal in source-sink dynamics. *Journal of Theorectical Biology* **226**: 159-168.

Andersen J. 1968. The effect of inundation and choice of hibernation sites of Coleoptera living on river banks. *Norsk Entomologisk Tidsskrift* **15**: 115-133

Andersen J. 1969. Habitat choice and life history of Bembidiini (Col., Carabidae) on river banks in central and northern Norway. *Norsk Entomologisk Tidsskrift* **17**: 17-65.

Andersen J. 1978. The influence of the substratum on the habitat selection of Bembidiini (Col., Carabidae). *Norwegian Journal of Entomology* **25**: 119-138.

Andersen J. 1983a. The life cycles of the riparian species of Bembidion (Coleoptera, Carabidae) in northern Norway. *Notulae Entomologicae* **63**: 195-202.

Andersen J. 1983b. The habitat distribution of species of the tribe Bembidinni (Coleoptera, Carabidae) on banks and shores in northern Norway. *Notulae Entomologicae* **63**: 131-142.

Andersen J. 1985. Low thigmo-kinesis, a key mechanism in habitat selection by riparian Bembidion (Carabidae) species. *Oikos* **44**: 499-505.

Andersen J. 1988. Resource partitioning and interspecific interactions among riparian Bembidion species (Coleoptera: Carabidae). *Entomologia Generalis* **13**: 47-60.

Andersen J. 1989. Photoresponse of carabid beetles depends on experimental design. *Oikos* **54**: 195-200.

Andersen J. 1995. A comparison of pitfall trapping and quadrat sampling of Carabidae (Coleoptera) on river banks. *Entomologica Fennica* **6**: 65-77.

Andersen J, Hanssen O. in press. Riparian beetles, a unique, but vulnerable element in the fauna of Fennoscandia. *Biodiversity & Conservation.*

Andrewartha HG, Birch LC. 1954. *Distribution and abundance of animals*. University of Chicago Press, Chicago.

Anon. 1999. *Tranche 2 action plans volume 6- Terrestrial and freshwater species and habitats.* English Nature, Peterborough.

Antvogel H, Bonn A. 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography* **24**: 470-482.

Baars MA. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* **41**: 25-46.

Baguette M, Petit S, Queva F. 2000. Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology* **37**: 100-108.

Baguette M, Schtickzelle N. 2003. Local population dynamics are important to the conservation of metapopulations in highly fragmented landscapes. *Journal of Applied Ecology* **40**: 401-412.

Ball SG. 1994. The Invertebrate Site Register – objectives and achievements. *British Journal of Entomology & Natural History* **7** (supplement **1**): 2-11.

Bates AJ, Sadler JP. 2004a. Records of rare and notable species of beetle from exposed riverine sediments (ERS) on the rivers Tywi and Upper Severn. *The Coleopterist* **13**: 125-132.

Bates AJ, Sadler JP. 2004b. A long-lasting method for marking beetles (Coleoptera), which does not enhance mortality. *Entomological News* **115**: 49-51.

Bates AJ, Sadler JP, Fowles AP, Butcher CR. 2005. Spatial dynamics of beetles living on exposed riverine sediments in the Upper River Severn: Method development and preliminary results. *Aquatic Conservation: Marine and Freshwater Ecosytems* **15**: 159-174.

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT. 2004. The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* **85**: 2671-2676.

Bednarek AT. 2001. Undamming rivers: a review of the ecological impacts of dam removal. *Environmental Management* **27**: 803-814.

Bell D, Sadler JP. 2003. *The coleopteran fauna of exposed riverine sediments on the River Dane, Cheshire: a survey report*. Unpublished report for the Environment Agency.

Benda L, Poff NL. Miller D, Dunne T, Reeves G, Pess G, Pollock M. 2004a. The network dynamics hypothesis: how channel networks structure riverine habitats. *Bioscience* **54**: 413-427.

Benda L, Andras K, Miller D, Bigelow P. 2004b. Confluence effects in rivers: Interactions of basin scale, network geometry, and disturbance regimes. *Water Resources Research* **40**: W05402.

Besag J, Diggle PJ. 1977. Simple Monte Carlo tests for spatial pattern. *Applied Statistics* **26**: 327-333.

Blackburn TM, Gaston KJ. 2002. Scale in macroecology. *Global Ecology & Biogeography* **11**: 185-189.

Blinn WC. 1963. Ecology of the land snails Mesodon thyroidus and Allogona profunda. *Ecology* **44**: 498-505.

den Boer P.J. 1983. Dispersie als vluchtreatie. *Vakblad voor Biologen* **63**: 326-329.

Bohan DA, Bohan AC, Glen DM, Symondson OC, Wiltshire CW, Hughes L. 2000. Spatial dynamics of predation by carabid beetles on slugs. *Journal of Animal Ecology* **69**: 367-379.

Bonn A, Kleinwächter M. 1999. Microhabitat distribution of spider and ground beetle assemblages (Araneae, Carabidae) on frequently inundated river banks of the River Elbe. *Zeitschrift für Ökologie und Naturschutz* **8**: 109-123.

Bonn A. 2000. Flight activity of carabid beetles on a river margin in relation to fluctuating water levels. 147-160 *In* Brandmayr P, Lövei G, Brandmayr TZ, Casale A, Vigna Taglianti A (eds) *Natural history and applied ecology of Carabid beetles*. Pensoft Publishers, Sofia, Moscow.

Bonn A, Gaston KJ. 2005. Capturing biodiversity: selecting priority areas for conservation using different criteria. *Biodiversity and Conservation* **14**: 1083-1100.

Bonte D, Lens L, Maelfait J-P. 2004. Lack of homeward orientation and increased mobility result in high emigration rates from low-quality fragments in a dune wolf spider. *Journal of Animal Ecology* **73**: 643-650.

Boorman SA, Levitt PR. 1973. Group selection on the boundary of a stable population. *Theoretical Population Biology* **4**: 85-128.

Boscaini A, Franceschini A, Maiolini B. 2000. River ecotones: carabid beetles as a tool for quality assessment. *Hydrobiologia* **422/423**: 173-181.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* **80**: 205-225.

Bowne DR, Bowers MA. 2004. Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology* **19**: 1-20.

Boyce MS. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* **23**: 481-506.

ter Braak CFJ, Šmilauer P. 1998. *CANOCO reference manual and user's guide to Canoco for Windows: Software for canonical community ordination (version 4)*. Microcomputer Power, Ithaca.

ter Braak CFJ. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.

Brasington J, Rumsby BT, Mcvey RA. 2000. Monitoring and modelling morphological change in a braided gravel-bed river using high resolution GPS-based survey. *Earth Surface Processes and Landforms* **25**: 973-990.

Brewer PA, Lewin J. 1998. Planform cyclicity in an unstable reach: complex fluvial response to environmental change. *Earth Surface Processes & Landforms* **23**: 989-1008.

Brewer PA, Maas GS, Macklin MG. 2000. A fifty-year history of exposed riverine sediment dynamics on Welsh rivers. *BHS Occasional Paper* **11**: 245-252.

Brodsky LM, Barlow CA. 1986. Escape responses of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera, Aphididae) – influence of predator type and temperature. *Canadian Journal of Zoology* **64**: 937-939.

Brookes A. 1989. Alternative channelization procedures. 139-157. *In* Gore JA, Petts GE (eds.). *Alternatives in regulated river management*. CRC Press, Inc. Boca Raton, Florida.

Bryan KM, Wratten SD. 1984. The response of polyphagous predators to prey spatial heterogeneity: Aggregation by carabid and staphylinid beetles to their cereal aphid prey. *Ecological Entomology* **9**: 251-259.

Burnham KP, Overton WS. 1979. Robust estimates of population size when capture probabilities vary amongst animals. *Ecology* **60**: 927-936.

Burt TP. 1994. Long-term study of the natural-environment – Perceptive science or mindless monitoring. *Progress in Physical Geography* **18**: 475-496.

Butterfield J. 1996. Carabid life-cycle strategies and climate change: a study on an altitudinal transect. *Ecological Entomology* **21**: 9-16.

Cakan H, Yilmaz KT, Duzenli A. 2005. First comprehensive assessment of the conservation status of the flora of the Cukurova Deltas, southern Turkey. *Oryx* **39**: 17-21.

Centre Naturopa. 1996. *Reintroduction of species.* Naturopa No. 82, Centre Naturopa of the Council of Strasbourg.

Church M. 1983. Pattern of instability in a wandering gravel bed channel. In Collison JD, Lewin J (eds) Modern and Ancient Fluvial Systems. *International Association of Sedimentologists Special Publications* **6**: 169-180.

Church MA, McLean DG, Wolcott JF. 1987. River bed gravels: sampling and analysis. 43-78. *In* Thorne CR, Bathhurst JC, Hey RD (eds.) *Sediment transport in gravel rivers*. John Wiley: Chichester.

Church M. 1995. Geomorphic response to river flow regulation: Case studies and time scales. *Regulated Rivers: Research and Management* **11**: 3-22.

Clarke MS, Luna JM, Youngman RR. 1995. Estimation of adult carabid densities in a no-till corn field by removal sampling. *Applied Soil Ecology* **2**: 185-193.

Clary WP. 1999. Stream channel and vegetation responses to late spring cattle grazing. *Journal of Range Management* **52**: 218-227.

Clifford P, Richardson S, Hémon D. 1989. Assessing the significance of the correlation between two spatial processes. *Biometrics* **45**: 123-134.

Collinge SK, Holyoak M, Barr CB, Marty JT. 2001. Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California. *Biological Conservation* **100**: 103-113.

Collingham YC, Wadsworth RA, Huntley B, Hulme PE. 2000. Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. *Journal of Applied Ecology* **37**: 13-27.

Colombini I, Chelazzi L, Fallaci M, Palesse L. 1994. Zonation and surface activity of some Tenebrionid beetles living on a Mediterranean sandy beach. *Journal of Arid Environments* **28**: 215-230.

Colombini T, Aloia A, Bouslama MF, ElGtari M, Fallaci M, Ronconi L, Scapini F, Chelazzi L. 2002. Small-scale spatial and seasonal differences in the distribution of beach arthropods on the norwestern Tunisian coast. Are species evenly distributed along the shore? *Marine Biology* **140**: 1001-1012.

Cormack RM. 1964. Loglinear models for capture-recapture. *Biometrics* **45**: 395-413.

Cortes Y, Fernandez-Salvador R, Garcia FJ, Virgos E, Llorente M. 1998. Changes in otter Lutra lutra distribution in central Spain in the 1964-1995 period. *Biological Conservation* **86**: 179-183.

Craig CC. 1953. On the utilization of marked specimens in estimating populations of flying insects. *Biometrika* **40**: 170-176.

Curtis Creighton JC, Scnell GD. 1998. Short term movement patterns of the endangered American burying beetle *Nicrophorus americanus*. *Biological Conservation* **86**: 281-287.

Davey JT. 1956. A method of marking isolated adult locusts in large numbers as an aid to the study of their seasonal migrations. *Bulletin of Entomological Research* **46**: 797-802.

Davies ZG, Wilson RJ, Brereton TM, Thomas CD. 2005. The re-expansion and improving status of the silver-spotted skipper butterfly (Hesperia comma) in Britain: a metapopulation success story. *Biological Conservation* **124**: 189-198.

Dawson FH, Holland D. 1999. The distribution in bankside habitats of three alien invasive plants in the U.K. in relation to the development of control strategies. *Hydrobiologia* **415**: 193-201.

Dennis B, Taper ML. 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* **64**: 205-224.

Desender K, Segers R. 1985. A simple technique for quantitative sampling of riparian beetle populations with some carabid and staphylinid abundance estimates on different riparian habitats (Coleoptera). *Revue D'écologie et du Biologie du Sol* **22**: 497-506.

Desender K. 1986. On the relation between abundance and flight activity in carabid beetles from a heavily grazed pasture. *Journal of Applied Entomology* **102**: 225-231.

Desender K. 1989. Ecomorphological adaptations of riparian carabid beetles. 309-314. *In* Wouters K, Baert L (eds) *Comptes Rendus du Symposium 'Invertèbres de Belgique'*. Royal Institute of Natural Sciences, Brussels.

Desender K. 2000. Flight muscle development and dispersal in the life cycle of carabid beetles: Patterns and processes. *Bulletin de L'institut Royal des Sciences Naturelles de Belgique: Entomologie* **70**: 13-31.

Deslippe RJ, Salazar JR, Guo Y-J. 2001. A darkling beetle population in West Texas during the 1997-1998 El Niňo. *Journal of Arid Environments* **49**: 711-721.

Dixon AFG. 1958. The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). *Transactions of the Royal Entomological Society of London.* **110**: 319-334.

Dobkin DS, Rich AC, Pyle WH. 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. *Conservation Biology* **12**: 209-221.

Dobson RM, Stephenson JW, Lofty JR. 1958. A quantitative study of a population of wheat bulb fly, Leptohylemyia coarctata (Fall.), in the field. *Bulletin of Entomological Research* **49**: 95-111.

Dobson RM, Morris MG. 1961. Observations on the emergence and life-span of wheat bulb fly, Leptohylemyia coarctata (Fall.), under field-cage conditions. *Bulletin of Entomological Research* **51**: 803-821.

Dreitz VJ, Nichols JD, Hines JE, Bennetts RE, Kitchens WM, Deangelis DL. 2002. The use of resighting data to estimate the rate of population growth of the snail kite in Florida. *Journal of Applied Statistics* **29**: 609-623.

Dutilleul P. 1993. Modifying the t-test for assessing the correlation between two spatial processes. *Biometrics* **49**: 305-314.

EA. 2004. Available from the environment agency 'what's in your backyard' section of their webpage: http://www.environment-agency.gov.uk/maps/

Eberhardt LL. 1970. Correlation, regression and density dependence. *Ecology* **51**: 306-310.

Evans WG. 1984. Odor-mediated responses of Bembidion obtusidens (Coleoptera: Carabidae) in a wind tunnel. *Canadian Entomologist* **116**: 1653-1658.

Evans WG. 1997. Humidity-invoked upwind orientation of shore insects (Bembidion obtusidens, Coleoptera: Carabidae). *Journal of Insect Behaviour* **10**: 355-363.

Eversham B. 1983. *Defining Rare and Notable species – a discussion document*. Invertebrate Site Register report no 49. Nature Conservancy Council, unpublished. CSD report no. 35.

Eyre MD, Rushton SP. 1989. Quantification of conservation criteria using invertebrates. *Journal of Applied Ecology* **26**: 159-171.

Eyre MD. 1994. Invertebrates in monitoring environmental quality and change. *British Journal of Entomology & Natural History* **7** (supplement **1**): 27-35.

Eyre MD, Lott DA, Garside A. 1996. Assessing the potential for environmental monitoring using ground beetles (Coleoptera: Carabidae) with riverside and Scottish data. *Annales Zoologici Fennici* **33**: 157-163.

Eyre MD, Lott DA. 1997. *Invertebrates of exposed riverine sediments*. R&D Project Record W1/i525/1. Entomological Monitoring Services, Environment Agency, FWR.

Eyre MD. 1998. *Preliminary assessment of the invertebrate fauna of exposed riverine sediments in Scotland*. Scottish Natural Heritage, Edinburgh.

Eyre MD, Luff ML, Lott DA. 1998. Rare and notable beetle species records from Scotland from survey work with pitfall traps, 1992-1996. *Coleopterist* **7**: 81-90.

Eyre MD, Luff ML, Lott DA. 2000. Records of rare and notable beetle species from riverine sediments in Scotland and northern England. *The Coleopterist* **9**: 25-38.

Eyre MD, Luff ML, Phillips DA. 2001a. The ground beetles (Coleoptera: Carabidae) of exposed riverine sediments in Scotland and northern England. *Biodiversity & Conservation* **10**: 403-426.

Eyre MD, Lott DA, Luff ML. 2001b. The rove beetles (Coleoptera, Staphylinidae) of exposed riverine sediments in Scotland and northern England: Habitat classification and conservation aspects. *Journal of Insect Conservation* **5**: 173-186.

Eyre MD, Luff ML. 2002. The use of ground beetles (Coleoptera: Carabidae) in conservation assessments of exposed riverine sediment habitats in Scotland and northern England. *Journal of Insect Conservation* **6**: 25-38.

Eyre MD, Luff ML, Lott DA. 2002. The importance of exposed riverine sediments for phytophagous beetles (Coleoptera) in Scotland and northern England. *Aquatic Conservation: Marine & Freshwater Ecosystems* **12**: 553-566.

Eyre MD, Rushton SP, Luff ML, Telfer MG. 2005. Investigating the relationships between the distribution of British ground beetle species (Coleoptera, Carabdidae) and temperature, precipitation and altitude. *Journal of Biogeography* **32**: 973-983.

Fahrig L. 2001. How much habitat is enough? *Biological Conservation* **100**: 65-74.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution & Systematics* **34**: 487-515.

Ferguson SH, Joly DO. 2002. Dynamics of springtail and mite populations: the role of density dependence, predation, and weather. *Ecological Entomology* **27**: 565-573.

Fischer J, Lindenmayer DB. 2000. An assessment of the published results of animal relocations. *Biological Conservation* **96**: 1-11.

Fischer J, Lindenmayer DB. 2002. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. *Biodiversity & Conservation* **11**: 833-849.

Fleishman E, Ray C, Sjőgren-Gulve P, Boggs CL, Murphy DD. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conservation Biology* **16**: 706-716.

Floate KD, Wardhaugh KG, Boxall ABA, Sherratt TN. 2005. Fecal residues of veterinary parasiticides: Nontarget effects in the pasture environment. *Annual Review of Entomology* **50**: 153-179.

Focarile A. 1964. Gli Asaphidion del gruppo flavipes (L.), con particolare riguardo alla fauna Italiana. *Mem. Soc. Entomol. Italiana* **43**: 97-120.

Fonseca DM, Hart DD. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* **75**: 49-58.

Förare J, Solbreck C. 1997. Population structure of a monophagous moth in a patchy landscape. *Ecological Entomology* **22**: 256-263.

Foster GN. 1987. The use of Coleoptera records in assessing the conservation status of wetlands. 8-18. *In* Luff ML (ed.) *The use of invertebrates in site assessment for conservation*. University of Newcastle Upon Tyne: Agriculture Environment Group.

Foster GN, Eyre MD. 1992. Classification and ranking of water beetle communities. *UK Nature Conservation* **1**.

Fowles AP. 1989. The Coleoptera of shingle banks on the River Ystwyth, Dyfed. *Entomologist's Record* **101**: 209-221.

Fowles AP. 1997. The saproxylic quality index: an evaluation of dead wood habitats based on rarity scores, with examples from Wales. *Coleopterist* **6**: 61-66.

Fowles AP, Alexander KNA, Key RS. 1999. The Saproxylic Quality Index: evaluating wooded habitats for the conservation of dead-wood Coleoptera. *Coleopterist* **8**: 121-141.

Fowles AP. 2005. http://thasos.users.btopenworld.com/ersqi.htm (24/1/05)

Fox PJA, Naura M, Scarlett P. 1998. An account of the derivation and testing of a standard field method, River Habitat Survey. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 455-475.

Framenau VW, Manderbach R, Baehr M. 2002. Riparian gravel banks of upland and lowland rivers in Victoria (south-east Australia): arthropod community structure and life-history patterns along a longitudinal gradient. *Austrailian Journal of Zoology* **50**: 103-123.

Frampton GK, van den Brink PJ, Gould PJL. 2000. Effects of spring drought and irrigation on farmland arthropods in southern Britain. *Journal of Applied Ecology* **37**: 865-883.

Franken RJ, Hik DS. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas Ochotona collaris. *Journal of Animal Ecology* **73**: 889-896.

Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* **10**: 199-124.

García AF, Griffiths GJK, Thomas CFG. 2000. Density, distribution and dispersal of the carabid beetle Nebria brevicollis in two adjacent cereal fields. *Annals of Applied Biology* **137**: 89-97.

Gereben B-A. 1995. Co-occurrence and microhabitat distribution of six Nebria species (Coleoptera: Carabidae) in an alpine glacier retreat zone in the Alps, Austria. *Arctic and Alpine Research* **27**: 371-379.

Gilpin ME. 1980. The role of stepping-stone islands. *Theoretical Population Biology* **17**: 247-253.

Gilvear DJ, Heal KV, Stephen A. 2002. Hydrology and the ecological quality of Scottish river ecosystems. *The Science of the Total Environment* **294**: 131-159.

Giuliano WM, Homyack JD. 2004. Short-term exclusion effects on riparian small mammal communities. *Journal of Range Management* **57**: 346-350.

Godfrey A. 1999. A review of Diptera from exposed riverine sediments based on literature records. *Dipterists Digest* **6**: 63-82.

Goodson JM, Gurnell AM, Angold PG, Morrissey IP. 2003. Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: The River Dove, Derbyshire, UK. *River Research & Applications* **19**: 317-334.

Greenslade PJM. 1964a. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* **33**: 301-310.

Greenslade PJM. 1964b. The distribution, dispersal and size of a population of Nebria brevicollis (F.) with comparative studies on three other Carabidae. *Journal of Animal Ecology* **33**: 311-333.

Greenwood JJD. 1996. Basic techniques. 11-109 *In* Sutherland WJ. (Ed.). *Ecological Census Techniques*. Cambridge University Press.

Greenwood MT, Bickerton MA, Gurnell AM, Petts GE. 1999. Channel changes and invertebrate faunas below Nant-y-Môch dam, River Rheidol, Wales, UK: 35 years on. *Regulated Rivers: Research & Management* **15**: 99-112.

Günther J, Assmann T. 2005. Restoration ecology meets carabidology: Effects of floodplain restitution on ground beetles (Coleoptera, Carabidae). *Biodiversity & Conservation* **14**: 1583-1606.

Gurnell AM, Bickerton M, Angold P, Bell D, Morrissey I, Petts GE, Sadler J. 1998. Morphological and ecological change on a meander bend: the role of hydrological processes and the application of GIS. *Hydrological Processes* **12**: 981-993.

Gurnell AM, Petts GE. 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. *Freshwater Biology* **47**: 581-600.

Gurnell A, Tockner K, Edwards P, Petts G. 2005. Effects of deposited wood on biocomplexity of river corridors. *Frontiers in Ecology* **7**: 377-382.

Hagler JR, Jackson CG. 2001. Methods for marking insects: Current techniques and future prospects. *Annual Review of Entomology* **46**: 511-543.

Haldane JBS. 1953. Animal populations and their regulation. *New Biology* **15**: 9-24.

Halsall NB, Wratten SD. 1988. The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology* **13**: 293-299.

Hammond PM. 1996. *A taxonomic review of possibly endemic British non-marine invertebrates*. The Natural History Museum, London.

Hammond PM. 1998a. Riparian and floodplain arthropod assemblages: their characteristics and rapid assessment. 237-282. In Bailey RG, José PV, Sherwood BR (Eds.) United Kingdom Floodplains. Westbury Press: Otley.

Hammond PM. 1998b. *Survey of invertebrates of exposed riverine sediments on the rivers Teign and Bovey near their confluence*. NHM, London. Report to EA Devon Area.

Hammond PM. 2003. *Preliminary survey for the ground beetle Bembidion testaceum on the river Usk*. CCW contract report no. 608.

Hanski I. 1987. Colonization of ephemeral habitats. 155-186. *In* Gray A, Crawley M, Edwards P (eds) *Colonization, succession and stability*. Blackwell Scientific Publications, Oxford.

Hanski I, Gilpin M. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**: 3-16.

Hanski I, Moilanen A, Gyllenberg M. 1996. Minimum viable metapopulation size. *The American Naturalist* **147**: 527-541.

Hansson L. 1991. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society* **42**: 89-103.

Harding PT, Alexander KNA. 1994. The use of saproxylic invertebrates in the selection and evaluation of areas of relic forest in pasture-woodlands. *Journal of Entomology & Natural History* **7** (supplement **1**): 21-26.

Harrison S. 1991. Local extinction in a metapopulation context: An empirical evaluation. *Biological Journal of the Linnean Society* **42**: 73-88.

Harrison SSC, Harris IT. 2002. The effects of bankside management on chalk stream invertebrate communities. *Freshwater Biology* **47**: 2233-2245.

Hassell MP. 1975. Density-dependence in single-species populations. *Journal of Animal Ecology* **44**: 283-295.

Hassell MP, Southwood TRE. 1978. Foraging strategies of insects. *Annual Review of Ecology & Systematics* **9**: 75-98.

Hastings A. 1987. Can competition be detected using species co-occurrence data? *Ecology* **68**: 117-123.

Hastings A. 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* **74**: 1362-1372.

Henein KM, Merriam G. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecology* **4**: 157-170.

Hering D, Plachter H. 1997. Riparian ground beetles (Coleoptera, Carabidae) preying on aquatic invertebrates: A feeding strategy in alpine floodplains. *Oecologia* **111**: 261-270.

Hering D. 1998. Riparian beetles (Coleoptera) along a small stream in the Oregon Coast Range and their interactions with the aquatic environment. *The Coleopterists Bulletin* **52**: 161-170.

Hering D, Gerhard M, Manderbach R, Reich M. 2004. Impact of a 100-year flood on vegetation, benthic invertebrates, riparian fauna and large woody debris standing stock in an Alpine floodplain. *River Research & Applications* **20**: 445-457.

Hess GR, Fischer RA. 2001. Communicating clearly about conservation corridors. *Landscape & Urban Planning* **55**: 195-208.

Hewitt SM, Atty DB, Parker JB, Sinclair M. 2000. *Cumbrian rivers shingle invertebrates survey*. Carlisle Natural History Society.

Hewitt S, Atty D, Parker J, Read J, Sinclair M. 2005. *Survey of the insects of exposed riverine sediments on the rivers Eden and Derwent in Cumbria in 2004*. EN & EA.

Hickling R, Roy DB, Hill JK, Thomas CD. 2005. A northward shift of range margins in British Odonata. *Global Change Biology* **11**: 502-506.

Higgs G. 1987. Environmental change and hydrological response: Flooding in the Upper Severn catchment. 131-159. *In* Gregory KJ, Lewin J, Thornes JB. *Palaeohydrology in practice*. John Wiley & Sons Ltd, Chichester.

Hill JK, Thomas CD, Lewis OT. 1996. Effects of habitat patch size and isolation on dispersal by Heperia comma butterflies: implications for metapopulation structure. *Journal of Animal Ecology* **65**: 725-735.

Hoey T. 1992. Temproal variations in bedload transport rates and sediment storage in gravel-bed rivers. *Progress in Physical Geography* **16**: 319-338.

vom Hofe H, Gerstmeier R. 2001. Ecological preferences and movement patterns of carabid beetles along a river bank. *Revue D' ecologie – La Terre et la Vie* **56**: 313-320.

Holeski PM. 1978. A method of sampling shore beetles. *Entomological News* **89**: 191-192.

Holeski PM, Graves RC. 1978. An analysis of the shore beetle communities of some channelized streams in northwest Ohio (Coleoptera). *The Great Lakes Entomologist* **11**: 23-36.

Holeski PM. 1984. Possible colonization strategies of some carabid beetles inhabiting stream shores (Coleoptera: Carabidae). *The Great Lakes Entomologist* **17**: 1-7.

Holland DG. 2000. Giant hogweed and Japanese knotweed. 25-36. *In* Bradley P (ed.) *Exotic and invasive species: should we be concerned*. Proceedings of the 11th conference of the Institute of Ecology and Environmental Management. IEEM.

Holland JM, Perry JN, Winder L. 1999. The within-field spatial and temporal distribution of arthropods in winter wheat. *Bulletin of Entomological Research* **89**: 499-513.

Holland KA, Leininger WC, Trlica MJ. 2005. Grazing history affects willow communities in a montane riparian ecosystem. *Rangeland Ecology & Management* **58**: 148-154.

Holloway GL, Griffiths GH, Richardson P. 2003. Conservation strategy maps: a tool to facilitate biodiversity action planning illustrated using the heath fritillary butterfly. *Journal of Applied Ecology* **40**: 413-421.

Holubová K, Klúcovská J, Szolgay J. 1998. Environmental impact of hydroelectric power generation on an anastomosing reach of the river Danube. 293-312. *In* Klingeman PC, Beschta RL, Komar PD, Bradley JB (eds.) *Gravel-bed rivers in the environment*. Water Resources Publications, LLC.

Howe RW, Davis GJ, Mosca GJ. 1991. The demographic significance of sink populations. *Biological Conservation* **57**: 239-255.

Hulme M, Jenkins GJ, Lu X, Turnpenny JR, Mitchell TD, Jones RG, Lowe J, Murphy JM, Hassell D, Boorman P, McDonald R, Hill S. 2002. *Climate change scenarios for the*

United Kingdom. The UKCIP02 scientific report. Tyndall Centre for Climate Change Research, UEA.

Hunter MD, Price PW. 1998. Cycles in insect populations: delayed density dependence or exogenous driving variables? *Ecological Entomology* **23**: 216-222.

Hyman PS, Parsons MS. 1992. A review of the scarce and threatened Coleoptera of Great Britain: Part 1. *UK Nature Conservation* **3**: 1-483.

Hyman PS, Parsons MS. 1994. A review of the scarce and threatened Coleoptera of Great Britain. Part 2. *UK Nature Conservation* **12**: 1-248.

Ibbeken H, Schleyer R. 1986. Photo-sieving: A method for grain-size analysis of coarse-grained, unconsolidated bedding surfaces. *Earth Surface Processes and Landforms* **11**: 59-77.

Jacobson RB, Bobbitt Gran K. 1999. Gravel sediment routing from widespread, low-intensity landscape disturbance, Current river basin, Missouri. *Earth Surface Processes & Landforms* **24**: 897-917.

Jansen A, Robertson AI. 2001. Relationships between livestock management and the ecological condition of riparian habitats along an Australian floodplain river. *Journal of Applied Ecology* **38**: 63-75.

Janssen R, Nilsson C, Dynesius M, Andersson E. 2000. Effects of river regulation on river-margin vegetation: a comparison of eight boreal rivers. *Ecological Applications* **10**: 203-224.

JNCC 2005. List of SAC's and candidate SAC's in the UK. http://www.jncc.gov.uk/page-1458 20/5/05.

Johansson P, Ehrlén J. 2003. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. *Journal of Ecology* **91**: 213-221.

Johnson CG. 1969. *Migration and dispersal of insects by flight*. Methuen, London.

Jolly GM. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**: 225-247.

Joy NH. 1932. *A practical handbook of British Beetles*. The Riverside Press Ltd, Edinburgh.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. 110-127. *In* Dodge DP (ed.) Proceedings of the International Large River Symposium. *Canadian Special Publications of Fisheries & Aquatic Sciences* **106**

Kennedy JS. 1974. Insect dispersal. 103-119. *In* Pimental D (ed.) *Insects, science and society*. Academic Press, New York.

Kennington JL, Helgason RV. 1980. *Algorithms for network programming*. Wiley, New York.

Khan JA. 1992. Efficiency of wonder trap against roof rat, *Rattus rattus* L. *Applied Animal Behaviour Science* **34**: 175-180.

Kirby C, Newson MD, Gilman K. 1991. *Plynlimon research: The first two decades*. Institute of Hydrology report no. 109. Galliard, Great Yarmouth.

Klaassen GJ, Lambeek J, Mosselman E, Duizendstra HD, Nieuwenhuijzen ME. 1998. Re-naturalization of the Meuse river in the Netherlands. 655-674. *In* Klingeman PC, Beschta RL, Komar PD, Bradley JB. (eds.) *Gravel-bed rivers in the environment*. Water Resources Publications, Colorado.

Klimetzek D, Yue CF. 1997. Climate and forest insect outbreaks. *Biologia* **52**: 153-157.

Klingeman PC, Bravard J-P, Giuliani Y, Olivier J-M, Pautou G. 1998. Hydropower reach by-passing and dewatering impacts in gravel-bed rivers. 313-344. *In* Klingeman PC, Beschta RL, Komar PD, Bradley JB (eds.) *Gravel-bed rivers in the environment.* Water Resources Publications, LLC.

Knox JC. 1999. Long-term episodic changes in magnitudes and frequencies of floods in the Upper Mississippi river valley. 257-282. *In* Brown AG, Quine TA (eds.) *Fluvial processes and environmental change.* John Wiley & Sons, Chichester.

Koenig WD, Van Vuren D, Hooge PN. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution* **11**: 514-517

Kondolf GM. 1997. Hungry water: Effects of dams and gravel mining on river channels. *Environmental Management* **21**: 533-551.

Kondolf GM. 1998. Large-scale extraction of alluvial deposits from rivers in California: Geomorphic effects and regulatory strategies. 455-470. *In* Klingeman PC, Beschta RL, Komar PD, Bradley JB (eds.). *Gravel-bed rivers in the environment*. Water Resources Publications, LLC.

Kryger U, Deschodt C, Scholtz CH. 2005. Effects of fluazuron and ivermectin treatment of cattle on the structure of dung beetle communities. *Agriculture, Ecosystems & Environment* **105**: 649-656.

Kumar S, Tamura K, Jakobsen IB, Nei M. 2001. MEGA2: molecular evolutionary genetics analysis software. *Bioinformatics* **17**: 1244-1245.

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.

Lane AMJ. 1997. The UK environmental change network database: An integrated information resource for long-term monitoring and research. *Journal of Environmental Management* **51**: 87-105.

Lane SD, Mills NJ. 2003. Intraspecific competition and density dependence in an *Ephestia kuehniella Venturia canescens* laboratory system. *Oikos* **101**: 578-590.

Langton SD, Aebischer NJ, Robertson PA. 2002. The estimation of density dependence using census data from several sites. *Oecologia* **133**: 466-473.

Laval G, Excoffier L. 2004. SIMCOAL 2.0: a program to simulate genomic diversity over large recombining regions in a subdivided population with a complex history. *Bioinformatics* **20**: 2485-2487.

Lawler DM. 1987. Spatial variability in the climate of the Severn basin: A palaeohydrological perspective. 49-79. *In* Gregory KJ, Lewin J, Thornes JB. Palaeohydrology in Practice. John Wiley, Chichester.

Lawler DM, Couperthwaite LJ, Bull LJ, Harris NM. 1997. Bank erosion events and processes in the Upper Severn basin. *Hydrology and Earth System Sciences* **1**: 523-534.

LEAP- Carmarthen area. Available from the EA website at: http://www.environment-agency.gov.uk/regions/wales/426317/156731/161030/?lang=_e

LEAP- Severn uplands. Available from the EA website at: http://www.environment-agency.gov.uk/regions/wales/426317/156731/161084/?lang=_e

Leeks GJ, Lewin J, Newson MD. 1988. Channel change, fluvial geomorphology and river engineering: the case of the Afon Trannon, Mid-Wales. *Earth Surface Processes and Landforms* **13**: 207-223.

Leeks GJ, Marks SD. 1997. Dynamics of river sediments in forested headwater streams: Plynlimon. *Hydrology and Earth System Sciences* **1**: 483-497.

Legendre P, Legendre L. 1998. Numerical ecology (2nd English Ed.). *Developments in Environmental Modelling* **20**.

Leopold LB, Wolman MG. 1957. *River channel patterns: Braided, meandering and straight*. Geological Survey Professional Paper 282-B. United States Government Printing Office, Washington.

Lepš J, Šmilauer P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

Levin SA. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology* **73**: 1943-1967.

Levins RA. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**: 237-240.

Levins RA. 1970. Extinction. *Lectures on Mathematics in the Life Sciences* **2**: 75-107.

Lima SL, Zollner PA. 1996. Towards a behavioural ecology of ecological landscapes. *Trends in Ecology & Evolution* **11**: 131-135

Lincoln FC. 1930. *Calculating waterfowl abundances on the basis of banding returns*. U.S. Department of Agriculture, Circular 118.

Lindroth CH. 1974. *Coleoptera: Carabidae*. Handbooks for the identification of British Insects 4(2): 1-146. British Entomological Society, London.

Linssen EF. 1959. *Beetles of the British Isles*. Frederick Warne & Co. Ltd., London & New York.

Lott D. 1992. *A survey report on the terrestrial beetles of riparian habitats along the River Soar near Loughborough, Leicestershire, March – October, 1991*. Leicestershire Museum Service.

Lott D. 1993. *A study of the effects of the River Soar Alleviation Scheme upon the riparian beetle fauna – 1992.* Report to the National Rivers Authority (Severn – Trent region). Leicestershire County Council, Museums, Arts and Records Service.

Lott DA. 1996. Beetles by rivers and the conservation of riparian and floodplain habitats. 36- 41. *In* Eyre, M.D. (Ed.). *Environmental monitoring, surveillance and conservation using invertebrates*. EMS Publications.

Lott DA, Eyre MD. 1996. Invertebrate sampling methods. 9-13. *In* Eyre, M.D. (Ed.). *Environmental monitoring, surveillance and conservation using invertebrates*. EMS Publications.

Lott DA. 2003. *An annotated list of wetland ground beetles (Carabidae) and rove beetles (Staphylinidae) found in the British Isles including literature review of their ecology*. English Nature Research Reports 488, Peterborough.

Lott DA. 2004. *Shingle invertebrate survey and condition assessment at Rheidol Shingles and Backwater's and Rheidol Gev Capel Bangor SSSI*. CCW.

Lude A, Reich M, Plachter H. 1999. Life strategies of ants in unpredictable floodplain habitats of Alpine rivers (Hymenoptera: Formicidae). *Entomologica Generalis* **24**: 75-91.

Luff ML. 1966. The abundance and diversity of the beetle fauna of grass tussocks. *Journal of Animal Ecology* **35**: 189-208.

Luff ML. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* **19**: 345-357.

Luff ML. 1987. The use of invertebrates in site assessment for conservation. University of Newcastle Upon Tyne: Agriculture Environment Group.

Luff ML. 1996. Environmental assessments using ground beetles (Carabidae) and pitfall traps. 42- 47. *In* Eyre, M.D. (Ed.). *Environmental monitoring, surveillance and conservation using invertebrates.* EMS Publications.

Luff ML. 1998. *Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Great Britain*. Biological Records Centre, Monks Wood, Cambridgeshire.

MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogreography*. Princeton University Press, Princeton.

Magilligan FJ, McDowell PF. 1997. Stream channel adjustment following elimination of cattle grazing. *Journal of the American Water Resources Association* **33**: 867-878.

Magurran AE. 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford.

Majerus MEN, Fowles AP. 1989. The rediscovery of the 5-spot ladybird (Coccinella 5-punctata L.) (Col. Coccinellidae) in Britain. *Entomologist's Monthly Magazine* **125**: 177-181.

Majerus MEN, Roy HE. 2005. Scientific opportunities presented by the arrival of the harlequin ladybird, *Harmonia axyridis,* in Britain. *Antenna* **29**: 196-208.

Manderbach R, Plachter H. 1997. Life strategy of the carabid beetle Nebria picicornis (Fabr. 1801) (Coleoptera, Carabidae) on river banks. *Beitrage zur Őkologie* **3**: 17-27.

Mardulyn P. 2001. Phylogeography of the Vosges mountains population of *Gonioctena pallida* (Coleoptera: Chrysomelidae): a nested clade analysis of mitochondrial DNA haplotypes. *Molecular Ecology* **10**: 1751-1763.

Mardulyn P, Milinkovitch MC. 2005. Inferring contemporary levels of gene flow and demographic history in a local population of the leaf beetle *Gonioctena olivacea* from mitochondrial DNA sequence variation. *Molecular Ecology* **14**: 1641-1653.

Massot M, Clobert J, Lorenzon P, Rossi JM. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology* **71**: 253-261.

Matter SF. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. *Oecologia* **105**: 447-453.

Matter SF, 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.

McCune B. 1997. Influence of noisy environmental data on canonical correspondence analysis. *Ecology* **78**: 2617-2623.

McInnis ML, McIver J. 2001. Influence of off-stream supplements on streambanks of riparian pastures. *Journal of Range Management* **54**: 648-652.

Menéndez R, Gutiérrez D, Thomas CD. 2002. Migration and allee effects in the six-spot burnet moth Zygaena filipendulae. *Ecological Entomology* **27**: 317-325.

Met Office. 2005. http://www.metoffice.com/climate/uk/2003/index.html 26/5/05.

Mitchell B. 1963. Ecology of two carabid beetles, Bembidion lampros (Herbst) and Trechus quadristriatus (Schrank). *Journal of Animal Ecology* **32**: 377-392.

Mommertz S, Schauer C, Kösters N, Lang A, Filser J. 1996. A comparison of D-Vac suction, fenced and unfenced pitfall trap sampling of epigeal arthropods in agro-ecosystems. *Annales Zoologica Fennici* **33**: 117-124.

Moran PAP. 1951. A mathematical theory of animal trapping. *Biometrica* **38**: 307-311.

Moran PAP. 1952. The statistical analysis of game-bird records. *Journal of Animal Ecology* **21**: 154-158.

Morris RF. 1959. Single-factor analysis in population dynamics. *Ecology* **40**: 580-588.

Mount NJ. 2000. Medium-term response of lowland river reaches to changes in upland land use. Unpublished PhD thesis, Liverpool John Moores University.

Moussavi-Harami R, Mahboubi A, Khanehbad M. 2004. Analysis of controls on downstream fining along three gravel-bed rivers in the Band-e-Golestan drainage basin NE Iran. *Geomorphology* **61**: 143-153.

Murdoch WW. 1963. A method for marking carabidae (Col.). *Entomological Monthly Magazine* **99**: 22-24.

Murdoch WW. 1966. Aspects of the population dynamics of some marsh Carabidae (Coleoptera). *Journal of Animal Ecology* **35**: 127-156.

Naiman RJ, Décamps H, Pastor J, Johnston CA. 1988. The potential importance of boundaries to fluvial ecosystems. *Journal of the North American Benthological Society* **7**: 289-306.

Naiman RJ, Lonzarich DG, Beechie TJ, Ralph SC. 1992. General principles of classification and assessment of conservation potential in rivers. *In* Boon, P.J., Calow, P. & Petts, G.E. (eds.). *River conservation and management*. John Wiley & Sons.

Naiman RJ, Décamps H. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecological Systems* **28**: 621-658.

Nelemans MNE, den Boer PJ, Spee A. 1989. Recruitment and summer diapause in the dynamics of a population of Nebria brevicollis (Coleoptera: Carabidae). *Oikos* **56**: 157-169.

Newson MD, Leeks GJL. 1987. *Fluvial geomorphological effects of gravel extraction from the River Tywi*. Scientific Services, Welsh Water Authority.

Nicholas AP, Ashworth PJ, Kirkby MJ, Macklin MG, Murray T. 1995. Sediment slugs: large-scale fluctuations in fluvial sediment transport rates and storage volumes. *Progress in Physical Geography* **19**: 500-519.

Nicholas AP, Woodward JC, Christopoulos G, Macklin MG. 1999. Modelling and monitoring river response to environmental change: The impact of dam construction and alluvial gravel extraction on bank erosion rates in the lower Alfios basin, Greece. 117-137. *In* Brown AG, Quine TA (eds.) *Fluvial processes and environmental change*. John Wiley & Sons, Chichester.

Niemeier S, Reich M, Plachter H. 1997. Ground beetle communities (Coleoptera: Carabidae) on the banks of two rivers in the eastern Carpathians, the Ukraine. *Verhandlungen der Gesellschaft für Ökologie* **27**: 365-372.

Niemelä J. 1993. Interspecific competition in ground-beetle assemblages (Carabidae): What have we learned? *Oikos* **66**: 325-335.

Noss RF. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**: 355-364.

O’Toole L, Fielding AH, Haworth PF. 2002. Re-introduction of the golden eagle into the Republic of Ireland. *Biological Conservation* **103**: 303-312.

Otis DL, Burnham KP, White GC, Anderson DR. 1978a. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**.

Otis DL, Burnham KP, White GC, Anderson DR. 1978b. CAPTURE - Computes estimates of capture probability and population size for closed population capture-recapture data. US Geological Survey - Patuxent Wildlife Research Centre. http://www.mbr-pwrc.usgs.gov/software.html#capture

Ottesen PS. 1996. Niche segregation of terrestrial alpine beetles (Coleoptera) in relation to environmental gradients and phenology. *Journal of Biogeography* **23**: 353-369.

Paetzold A, Tockner K. 2005. Effects of riparian arthropod predation on the biomass and abundance of aquatic insect emergence. *Journal of the North American Benthological Society* **24**: 395-402.

Paetzold A, Schubert CJ & Tockner K (in press) Aquatic-terrestrial linkages along a braided-river: Riparian arthropods feeding on aquatic insects. *Ecosystems*

Passmore DG, Macklin MG, Brewer PA, Lewin J, Rumsby BT, Newson MD. 1993. Variability of late Holocene braiding in Britain. 205-229. *In* Best JL, Bristow CS (eds.). Braided rivers. Geological society special publication No. 75.

Perry JN. 1995. Spatial analysis by distance indices. *Journal of Animal Ecology* **64**: 303-314.

Perry JN. 1998. Measures of spatial pattern for counts. *Ecology* **79**: 1008-1017.

Perry JN, Winder L, Holland JM, Alston RD. 1999. Red-blue plots for detecting clusters in count data. *Ecology Letters* **2**: 106-113.

Perry JN, Dixon PM. 2002. A new method to measure spatial association for ecological count data. *Ecoscience* **9**: 133-141.

Perry JN. 2003. http://www.rothamsted.bbsrc.ac.uk/pie/sadie/SADIE_downloads_software_page_5_2.htm (1/12/03).

Petersen CGJ. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. *Report of the Danish Biological Station* **6**:1-77.

Petts GE. 1979. Complex response of river channel morphology subsequent to reservoir construction. *Progress in Physical Geography* **3**: 329-362.

Petts GE. 1984. *Impounded rivers: Perspectives for ecological management*. Wiley, Chichester.

Petts GE, Gurnell AM, Gerrard AJ, Hannah DM, Hansford B, Morrissey I, Edwards PJ, Kollmann J, Ward JV, Tockner K, Smith BPG. 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems* **10**: 249-266.

Pierce SM, Cowling RM, Knight AT, Lombard AT, Rouget M, Wolf T. 2005. Systematic conservation planning products for land-use planning: interpretation for implementation. *Biological Conservation* **125**: 441-458.

Plachter H. 1986. Composition of the carabid beetle fauna of natural riverbanks and man-made secondary habitats. 509-538. *In* den Boer, P.J., Luff, M.L., Mossakowski, D. & Weber, F. (eds.). *Carabid beetles: Their adaptations and dynamics*. G. Fischer Verlag, Stuttgart.

Plachter H, Reich M. 1998. *The significance of disturbance for populations and ecosystems in natural floodplains*. Proceedings of the International Symposium on River Restoration, May 26-27, Tokyo-Japan.

Pollard E, Lakhani KH, Rothery P. 1987. The detection of density-dependence from a series of annual censuses. *Ecology* **68**: 2046-2055.

Pollock KH, Nichols JD, Brownie C, Hines JE. 1990a. JOLLY - Computes estimates of survival and capture probability for 1-age class open population capture-recapture models. US Geological Survey - Patuxent Wildlife Research Centre. http://www.mbr-pwrc.usgs.gov/software.html#jolly

Pollock KH, Nichols JD, Brownie C, Hines JE. 1990b. Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**.

Poole GC. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. *Freshwater Biology* **47**: 641-660.

Popotnik GJ, Giuliano WM. 2000. Response of birds to grazing of riparian zones. *Journal of Wildlife Management* **64**: 976-982.

Pulliam HR. 1988. Sources, sinks, and population regulation. *The American Naturalist* **132**: 652-661.

Purse BV, Hopkins GW, Day KJ, Thompson DJ. 2003. Dispersal characteristics and management of a rare damselfly. *Journal of Applied Ecology* **40**: 716-728.

Raven PJ, Holmes NTH, Dawson FH, Everard M. 1998. Quality assessment using River Habitat Survey data. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 477-499.

Ray C, Hastings A. 1996. Density dependence: are we searching at the wrong spatial scale? *Journal of Animal Ecology* **65**: 556-566.

Reddingius J. 1996. Tests for density dependence. *Oecologia* **108**: 640-642.

Reed JM, Dobson AP. 1993. Behavioural constraints and conservation biology: Conspecific attraction and recruitment. *Trends in Ecology & Evolution* **8**: 253-256

Reich M. 1991. Grasshoppers (Orthoptera, Saltatoria) on alpine and dealpine riverbanks and their use as indicators for natural floodplain dynamics. *Regulated Rivers: Research & Management* **6**: 333-339.

Reich M. 1994. Kies- und schotterreiche Wildflußlandschaften – primäLebensräume des Flußregenpfeifers (Charadrius dubius). *Vogel und Umwelt* **8**: 43-52.

Rexstad E, Burnham K. 1992. Users' guide for interactive programme capture: Abundance estimation of closed animal populations. Colorado Cooperative Fish and Wildlife Research Unit. http://www.mbr-pwrc.usgs.gov/software.html#capture

Ricklefs RE, Schluter D. 1993. *Species diversity in ecological communities*. University of Chicago Press, Chicago.

RiversMoore NA, Samways MJ. 1996. Game and cattle trampling, and impacts of human dwellings on arthropods at a game park boundary. *Biodiversity & Conservation* **5**: 1545-1556.

Robertson AI, Rowling RW. 2000. Effects of livestock on riparian zone vegetation in an Australian dryland river. *Regulated Rivers – Research & Management* **16**: 527-541.

Rotherham ID. 2000. Himalayan balsam – the human touch. 41-50 *In* Bradley P (ed.) *Exotic and invasive species: should we be concerned*. Proceedings of the 11th conference of the Institute of Ecology and Environmental Management. IEEM.

Sadler J, Bell D. 2000. *A comparative assessment of exposed riverine sediment (ERS) beetle faunas in south-west England*. EN Research Reports 383.

Sadler JP, Petts GE. 2000. *Invertebrates of exposed riverine sediments: Phase 2. Technical Report* W196, WRc, Environment Agency, Swindon.

Sadler JP, Bell D. 2002. *Invertebrates of exposed riverine sediments: Phase 3 – baseline faunas*. Technical Report W1-034/TR, WRc, Environment Agency, Swindon.

Sadler JP, Bell D, Fowles AP. 2004. The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. *Biological Conservation* **118**: 41-56.

Sadler JP, Bell D, Hammond P. 2005. *R&D assessment of the distribution of Bembidion testaceum and reasons for its decline*. Environment Agency.

Saether B, Engen S, Lande R. 1999. Finite metapopulation models with density-dependent migration and stochastic local dynamics. *Proceedings of the Royal Society of London Series B* **266**: 113-118.

Scheidegger AE. 1965. The algebra of stream-order numbers. *US Geological Survey Professional Paper* **525B**: 187-189.

Schneider C. 2003. The influence of spatial scale on quantifying insect dispersal: An analysis of butterfly data. *Ecological Entomology* **28**: 252-256

Schneider C, Dover J, Fry GLA. 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of study area. *Ecological Entomology* **28**: 219-227.

Scott ML, Skagen SK, Merigliano MF. 2003. Relating geomorphic change and grazing to avian communities in riparian forests. *Conservation Biology* **17**: 284-296.

Scott WA, Anderson R. 2003. Temporal and spatial variation in carabid assemblages for the United Kingdom Environmental Change Network. *Biological Conservation* **110**: 197-210.

Scrimgeour GJ, Kendall S. 2003. Effects of livestock grazing on benthic invertebrates from a native grassland ecosystem. *Freshwater Biology* **48**: 347-362.

Seal R, Paola C. 1995. Observations of downstream fining on the North Fork Toutle River near Mount St. Helens, Washington. *Water Resources Research* **31**: 1409-1419.

Sear DA, Archer D. 1998. Effects of gravel extraction on stability of gravel-bed rivers: The Wooler Water, Northumberland, UK. 415-432. *In* Klingeman PC, Beschta RL, Komar PD, Bradley JB (eds.). *Gravel-bed rivers in the environment*. Water Resources Publications, LLC.

Seber GAF. 1965. A note on the multiple-recapture census. *Biometrika* **52**: 249-259.

Seber GAF. 1982. *The estimation of animal abundance and related parameters*. Charles Griffin, London.

Shaffer ML. 1981. Minimum viable population sizes for species conservation. *Bioscience* **31**: 131-134.

Shirt DB. 1987. *British Red Data Books: 2. Insects.* Nature Conservancy Council.

Simpson EH. 1949. Measurement of diversity. *Nature* **163**: 688.

SISA Simple Interactive Statistical Analysis. 2005. http://home.clara.net/sisa/bonfer.htm 20/6/2005.

Smith M. 1951. *The British reptiles and amphibians*. Collins, London.

Smith SA. 1989. Sedimentation in a meandering gravel-bed river: The river Tywi, South Wales. *Geological Journal* **24**: 193-204.

Sotherton NW. 1985. The distribution and abundance of predatory Coleoptera overwintering in field boundaries. *Annals of Applied Biology* **106**: 17-21.

Soulé ME. 1987. Introduction. 1-10. *In* Soulé ME. (ed.) *Viable populations for conservation*. Cambridge University Press.

Southwood TRE. 1962. Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* **37**: 171-214

Southwood TRE, Henderson PA. 2000. *Ecological Methods (3rd Ed.)*. Blackwell Science. 575pp.

Speight MCD, Martinez M, Luff ML. 1986. The Asaphidion (Col.: Carabidae) species occurring in Great Britain and Ireland. *Proceedings & Transactions of the British Entomological & Natural History Society* **19**: 17-21.

Stamps J, Buchner M, Krishnen V. 1987. The effects of edge permeability and habitat geometry on emigration from habitat patches. *American Naturalist* **129**: 533-552.

Stanford JA, Ward JV. 2001. Revisiting the serial discontinuity concept. *Regulated Rivers: Research & Management* **17**: 303-310.

Stelter C, Reich M, Grimm V, Wissel C. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper Bryodema tuberculata. *Journal of Animal Ecology* **66**: 508-518

Stillings AM, Tanaka JA, Rimbey NR, Delcurto T, Momont PA, Porath ML. 2003. Economic implications of off-stream water developments to improve riparian grazing. *Journal of Range Management* **56**: 418-424.

Stubbs M. 1977. Density dependence in the life-cycles of animals and its importance in K- and R-strategies. *Journal of Animal Ecology* **46**: 677-688.

Sutcliffe OL, Thomas CD, Peggie D. 1997. Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. *Oecologia* **109**: 229-234.

Sutcliffe OL, Thomas CD, Yates TJ, Greatorex-Davies JN. 1997. Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia* **109**: 235-241.

Swetnam TW, Lynch AM. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* **63**: 399-424.

Sykes JM, Lane AMJ. 1996. *The UK Environmental Change Network: Protocols for standard measurements at terrestrial sites*. Stationery Office, London.

Tanner JT. 1966. Effects of population density on growth rates of animal populations. *Ecology* **47**: 733-745.

Thiele HU. 1977. *Carabid beetles in their environments: A study on habitat selection by adaptation*. Springer-Verlag, Berlin, New York.

Thomas CD, Kunin WE. 1999. The spatial structure of populations. Journal of Animal *Ecology* **68**: 647-657.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beumont LJ, Collingham YC, Erasmus BFN, de Siqueria MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004. Extinction risk from climate change. *Nature* **427**: 145-148.

Thomas JA, Rose RJ, Clarke RT, Thomas CD, Webb NR. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Functional Ecology* **13**: 55-64.

Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger, B. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London: Series B* **268**: 1791-1796.

Tiegs SD, O'Leary JF, Pohl MM, Munill CL. 2005. Flood disturbance and riparian species diversity on the Colorado River Delta. *Biodiversity & Conservation* **14**: 1175-1194.

Tiegs SD, Pohl M. 2005. Planform channel dynamics of the lower Colorado River: 1976-2000. *Geomorphology* **69**: 14-27.

Tockner K, Malard F, Ward JV. 2000. An extension of the flood pulse concept. *Hydrological Processes* **14**: 2861-2883.

Tockner K, Paetzold A, Karaus U, Claret C, Zettel J. in press. Ecology of braided rivers. *In* Sambrook Smith GH, Best JL, Bristow CS, Petts GE. (eds.) *Braided Rivers: Process, Deposits, Ecology and Management.* IAS Special Publication 36, Blackwell Publishing.

Traugott M. 2001. Dispersal power, home range and habitat preference of cantharid larvae (Coleoptera: Cantharidae) in arable land. *European Journal of Soil Biology* **38**: 79-83

Trimble SW, Mendel AC. 1995. The cow as a geomorphic agent – A critical review. *Geomorphology* **13**: 233-253.

Tuyttens FAM, Macdonald DW, Delahay R, Rogers LM, Mallinson RJ, Donnelly CA, Newman C. 1999. Differences in trapability of European badgers Meles meles in three populations in England. *Journal of Applied Ecology* **36**: 1051-1062.

Vivash R, Ottosen O, Janes M, Sorenson HV. 1998. Restoration of the rivers Brede, Cole and Skerne: a joint Danish and British EU-LIFE demonstration project, II – The river restoration works and other related practical aspects. *Aquatic Conservation – Marine and Freshwater Ecosystems* **8**: 197-208.

Wallin H, Ekbom B. 1994. Influence of hunger level and prey densities on movement patterns in three species of Pterostichus beetles (Coleoptera: Carabidae). *Environmental Entomology* **23**: 1171-1181.

Wang ZJ, Young SS. 2003. Differences in bird diversity between two swidden agricultural sites in mountainous terrain, Xishuangbanna, Yunnan, China. *Biological Conservation* **110**: 231-243.

Ward JV, Stanford JA. 1995. The serial discontinuity concept: Extending the model to floodplain rivers. *Regulated Rivers: Research and Management* **10**: 159-168.

Ward JV. 1998. Riverine landscapes: Biodiversity patterns. Disturbance regimes, and aquatic conservation. *Biological Conservation* **83**: 269-278.

Ward JV, Tockner K, Schiemer F. 1999. Biodiversity of floodplain ecosystems: Ecotones and connectivity. *Regulated Rivers: Research & Management* **15**: 125-139.

Ward JV, Tockner K, Arscott B, Claret C. 2002. Riverine landscape diversity. *Freshwater Biology* **47**: 517-539.

Warnaffe G du Bus de, Dufrêne M. 2004. To what extent can management variables explain species assemblages? A study of carabid beetles in forests. *Ecography* **27**: 701-714.

Watkinson AR, Sutherland WJ. 1995. Sources, sinks and pseudo-sinks. *Journal of Animal Ecology* **64**: 126-130.

Wegge P, Pokheral CP, Jnawali SR. 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. *Animal Conservation* **7**: 251-256.

Weir A. 1996. A preliminary host-parasite list of British Laboulbeniales (Fungi, Ascomycotina). *The Entomologist* **115**: 50-58.

Wells SM, Pyle RM, Collins NM. 1983. *The IUCN Invertebrate Red Data Book*. Gland International Union for Conservation of Nature and Natural Resources.

Werrity A, Brazier V. 1991. The *geomorphology, conservation and management of the River Feshie SSSI*. NCC, University of St. Andrews.

Werritty A, Leys KF. 2001. The sensitivity of Scottish rivers and upland valley floors to recent environmental change. *CATENA* **42**: 251-273.

Whatmough JA. 1995. Grazing on sand dunes: The re-introduction of the rabbit *Oryctolagus cuniculus* L. to Murlough NNR, Co. Down. *Biological Journal of the Linnean Society* **56**: 39-43.

Wheater CP, Cook PA. 2000. *Using statistics to understand the environment*. Routledge, London & New York.

Wheeler MA, Trlica MJ, Frasier GW, Reeder JD. 2002. Seasonal grazing affects soil physical properties of a montane riparian community. *Journal of Range Management* **55**: 49-56.

Whitehead PG, Wilson EJ, Butterfield D, Seed K. 1998. A semi-distributed integrated flow and nitrogen model for multiple source assessment in catchments (INCA): Part II – application to large river basins in south Wales and eastern England. *The Science of the Total Environment* **210/211**: 559-583.

Wiens JA. 1989. Spatial scaling in ecology. *Functional Ecology* **3**: 385-397.

Wiens JA, Milne BT. 1989. Scaling of ‘landscapes’ in landscape ecology, or landscape ecology from a beetle’s perspective. *Landscape Ecology* **3**: 87-96.

Wileyto EP, Ewens WJ, Mullen MA. 1994. Markov-recapture population estimate: A tool for improving interpretation of trapping experiments. *Ecology* **75**: 1109-1117.

Wineriter SA, Walker TJ. 1984. Insect marking techniques: Durability of materials. *Entomological News* **95**: 117-123.

Winterbottom SJ, Gilvear DJ. 2000. A GIS-based approach to mapping probabilities of river bank erosion: regulated River Tummel, Scotland. *Regulated Rivers Research & Management* **16**: 127-140.

With KA, King AW. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* **13**: 314-326.

Wolters M, Garbutt A, Bakker JP. 2005. Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation* **123**: 249-268.

Wood TR. 1987. The present-day hydrology of the River Severn. 79-97. *In* Gregory KJ, Lewin J, Thornes JB (Eds.). *Palaeohydrology in practice*. John Wiley & Sons Ltd, Chichester.

Xu X. 2003. Considerations for the use of SADIE statistics to quantify spatial patterns. *Ecography* **26**: 821-830.

Zaimes GN, Schultz RC, Isenhart TM. 2004. Stream bank erosion adjacent to riparian forest buffers, row-crop fields, and continuously-grazed pastures along Bear Creek in central Iowa. *Journal of Soil and Water Conservation* **59**: 19-27.

Zippin C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* **12**: 163-169.

Zulka KP. 1994. Carabids in a central European floodplain: species distribution and survival during inundations. 399-405. *In* Desender K, Dufrene M, Loreau M, Luff ML, Maelfait JP (Eds.). *Carabid beetles: ecology and evolution*. Kluwer, Dordrecht.

Appendix 4.1 Example additional information survey.

Surveyors name	**Adam Bates**	**Site name**	**Ty Gwyn**
Survey date	**03/08/2003**	**Bar code**	**US4 (TG3)**
River	**Tywi**	**Grid reference**	**SN 63743 22813**
Catchment	**Tywi**	**Method (M/GPS)**	**GPS**

Areal code (US, DS) **DS**

Grazing damage (aerial hand searches) **8**

Number	Code*1	Additional qualifiers
1	None	
2	Very light sheep	<20*2 sheep hoof prints, otherwise no damage to structure
3	Light sheep	<60*2 sheep hoof prints, otherwise no damage to structure
4	Very light cattle	<5*2 cattle hoof prints, otherwise no damage to structure
5	Medium sheep	Numerous sheep hoof prints, still some evidence of original structure
6	Light cattle	<15*2 cattle hoof prints, otherwise no damage to structure
7	Heavy sheep	Structure completely destroyed
8	Medium cattle	Numerous cattle hoof prints, still some evidence of original structure
9	Heavy cattle	Structure completely destroyed
10	Very heavy cattle	Structure completely destroyed + very heavily 'pitted'

*1 This is as far as the classification can go for coarse sediments
because individual hoof prints cannot be discerned
*2 Numbers within 1.5 x 1.5m sample area and are only likely to apply to 'soft' sediments

Grazing damage (for the whole ERS patch) ((10% x 10) + (40% x 9) + (30% x 8) + (20% 6))/100 = **8.2**

Percentage of the patch that falls within each of the above classifications
Will be used to create grazing index (e.g. 20% 1, 40% 4 & 40% 6 = ((1*20)+(4*40)+(6*40))/100 = 4.2

Faecies index

Total number of individual (see ECN terrestrial protocol) within 1.5 x 1.5m sample area

No. of cattle faecies	**0**
No. of sheep faecies	**0**

Number of faecies in four 5x1m diagonal ribbons from the quadrat corners

No. of cattle faecies	**0**
No. of sheep faecies	**0**
Total no. of meters	**10**

Sediment photograph taken	Yes	Time:	12:30
Dry bulb	23	Wet bulb temp	18

Description: Medium sized sediment, gently sloping, quite compact

APPENDICES

Appendix 2.1 Example ERS environmental record sheet

Surveyors name	**Adam Bates**
Survey date	**03/08/2003**
River	**Tywi**
Catchment	**Tywi**

Site name	**Ty Gwyn**
Bar code	**US5**
Grid reference	**SN 63627 22668**
Method (M/GPS)	**GPS**

Vegetation	**Type (Bare, Simple, Complex)**	**C**
	Veg. Cover %	**65**
General	**ERS length (m)**	**172**
	ERS Width (m)	**20**
ERS profile	**Flat**	
	Gentle	**X**
	Steep	
ERS Topography	**Simple**	**X**
	Humped	
	Complex	
	Habitat heter. (1-3)	**1**
Hibernation	**Hibernation potential (1-3)**	**2**
	Grass on ERS (0-2)	**2**
	Grass on bank (0-2)	**1**
	Dead Wood on ERS (0-2)	**0**
	Dead wood on bank	**1**
Recreation	**Fishing**	**X**
	Boating	
Channel	**None**	**X**
	Dredging	
	Weed Cutting	
	Enhancement	

Bank Profile	**Natural/unmodified**	**X**
	Artificial/modified	
	Artificial levees	
	Gabions/riprap	
	Bankfull height (m)	**2**
	Bank height if diff. (m)	
	Embanked height (m)	
Land Use	**Mixed wood**	
	Con. Plant.	
	Moor/heath	
	Scrub/rough	
	Bog/marsh	
	Grazed semi/improved grass	**X**
	Ungrazed semi/improved grass	
	Arable	
	Suburban/Urban	
Stocking	**Cattle light**	**X**
	Cattle heavy	
	Sheep light	
	Sheep heavy	
Gravel extraction	**Area**	
	Point	
	Number	
	Tree shade %	**0**