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ECOLOGY AND CONSERVATION OF MEDITERRANEAN TEMPORARY PONDS IN THE UK

by

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Abstract

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Ecology and Conservation of Mediterranean Temporary Ponds in the UK

Macroinvertebrate and plant assemblage composition and abiotic habitat characteristics were examined in seventy-six ponds, in the New Forest (Hampshire, UK) and on the Lizard Peninsula (Cornwall, UK), in order to unravel the ecological processes influencing ponds at a range of spatial scales and provide a clear definition of Mediterranean Temporary Pond (MTP) habitat (92/43/EEC) in the UK. In addition, a set of newly created experimental ponds were monitored on the Lizard to examine patterns of colonisation and evaluate the use of habitat creation in temporary pond conservation. The findings are synthesised into a number of management recommendations for ponds in the regions, with a particular focus on MTPs.

MTPs equated to ephemeral, winter-flooded ponds occurring in shallow depressions on the Lizard, which had some floristic similarities to other western Atlantic fringe sites. They were dominated by low growing grasses, rushes and rare annual species of the *Nanocyperion* alliance along with a depauperate macroinvertebrate assemblage comprising Coleoptera (including characteristic rare taxa), Trichoptera and Chironomidae.

The strength of physicochemical and spatial pattern in assemblage composition varied between the regions. Lizard macroinvertebrate assemblage similarity was spatially autocorrelated and related to water chemistry and pond area but New Forest macroinvertebrate similarity was not related to any of the measured physicochemical parameters. Plant assemblage composition was only weakly related to wet phase physicochemistry. Pond vegetation structured macroinvertebrate assemblages in different ways at different spatial scales. At large-scales, macrophyte richness and composition affected macroinvertebrate assemblage composition in both regions, whereas, at smaller-scales, macrophyte structural complexity (measured using fractals) influenced body size scaling and overall biomass of macroinvertebrates.

Assemblages in both regions were significantly nested, indicating that species-poor sites tended to be subsets of rich sites. Macroinvertebrate nesting, on the Lizard, was not due to passive sampling, and was best explained by pond area, with habitat parameters and isolation being of secondary importance. Nested and idiosyncratic taxa differed in their spatial response to factors which structured assemblage-level nestedness; idiosyncratic taxa tended to possess broad ecological tolerance and good dispersal capacity, whilst nested species had narrower tolerance or limited powers of dispersal.

Experimental pond macroinvertebrate assemblage similarity converged with pond age, despite continued variation in physicochemistry, and the assemblages that developed were not significantly different from small natural ponds in the region. Augmentation of current MTP habitat could therefore be achieved by creating new sites in close proximity to existing water bodies.

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Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

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Publications

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Meetings & Conferences

Oral Presentations:

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British Ecological Society Winter Meeting, Warwick, UK December 2001: Assemblage composition and nestedness in UK Mediterranean Temporary Ponds.

IX European Ecological Congress, Lund, Sweden, July 2002: Unravelling spatial patterns in temporary pond assemblages

Botanical Society of the British Isles AGM, Cambourne, UK May 2003: How can nestedness analysis inform ecological management?

Poster Presentations:

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Second Symposium for European Freshwater Sciences, Toulouse, France July 2001: Macrophyte assemblage composition and nestedness in UK Mediterranean Temporary Ponds

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1 Introduction

Overview

A central theme of ecological research is the search for mechanisms underlying general patterns in species occurrence and richness across different systems and scales. Historically much work has focussed on small scale models examining niche space and co-existence, but more recently attention has been diverted to understanding ecological patterns and processes occurring at meso and macroecological scales (Okamura & Freeland 2002, Williamson 2002, Hanski 2001, Gaston & Blackburn 2000, Hanski 1999, Brown 1995).

Species distribution patterns at a regional or landscape scale are governed by both local and regional processes. Local processes, which occur within a habitat, such as competition, predation and abiotic intolerance, may reduce abundance or cause extinction of taxa and thus limit the species diversity of local assemblages. Contrastingly, regional processes such as dispersal, can balance these local extinctions (Ricklefs & Schluter 1993). Other factors, acting at a regional level, which affect the spatial distribution of species, include long term and seasonal changes in climate, (e.g. drought and storms) and anthropogenic activities that cause habitat fragmentation and pollution (Bohonak & Jenkins 2003).

This thesis deals with factors shaping the ecology and conservation of ponds in two regions of southern England, where a high density of small water bodies still occurs across the landscape. Most of the water bodies in these regions are small, seasonally fluctuating and often temporary in nature. The study concentrates on these temporary ponds, in particular the so-called 'Mediterranean Temporary Ponds', an EU priority habitat type whose status and ecology in the UK is poorly understood.

Temporary ponds form spatially discrete habitat islands in the terrestrial landscape (Bilton *et al.* 2001b) which are heterogeneous in their abiotic characteristics, such as hydroperiod and water chemistry. These local physicochemical attributes may affect the diversity and structural complexity of pond vegetation (Heegaard *et al.* 2001, Stace 1997) and pond physicochemistry and vegetation are, in turn, likely to influence the invertebrate assemblages that develop within ponds (Williams

1996, Dvorak & Best 1982). Ponds therefore form a spatial and temporal mosaic of patches in the landscape with very different biotic and abiotic attributes.

The life history strategies of macroinvertebrate taxa that utilise temporary ponds range from species which have transient populations in the landscape, that are regularly linked by dispersal, to species which can tolerate drought and therefore remain in the dry pond basin throughout their life cycle (Williams 1987, Wiggins *et al.* 1980). Macroinvertebrate assemblage composition is, therefore, also likely to be spatially and temporally dynamic, as species disperse to new habitat patches as ponds dry or avoid the effects of drying by entering a diapause phase. Temporary ponds are, therefore, excellent systems in which to examine factors that govern patterns in assemblage composition. In addition to being good model systems for addressing important ecological questions, temporary ponds often support rare populations of invertebrate and plant species (Nicolet 2002, Collinson *et al.* 1995). Hence, an understanding of the factors that structure the distribution of plant and macroinvertebrate species across temporary pond habitats is also an important prerequisite for their successful conservation.

In this thesis I aim to explore ecological patterns and processes (discussed more fully below) at a range of spatial scales, in ponds situated in two regions of Britain: the Lizard Peninsula, Cornwall, and the New Forest, Hampshire. Ponds in these regions have been highlighted as being of high conservation importance for their fauna and flora, although their ecology has been poorly studied (McLeod *et al.* 2002). This work examines the relative influence of local and regional factors on the plant and macroinvertebrate assemblages of these freshwater habitat islands and explores the influence that pond habitat heterogeneity, including macrophyte diversity and complexity, has on macroinvertebrate assemblage structure. Alongside it examines whether such processes culminate in spatially autocorrelated pattern in assemblage composition and whether pond assemblages form nested subsets of decreasing species richness. The broad aim of this thesis was therefore to examine factors that structure patterns in temporary pond assemblage composition across inter-regional to intra-pond scales and synthesise these ecological findings into a conservation strategy for the habitat.

1.1 Temporary pond habitats

Williams (1987) gives a straightforward definition of temporary ponds as '...natural bodies of water which experience a recurrent dry phase of varying duration...' Such ponds form a continuum in size and permanence and different types of pond can be distinguished by the length, timing and predictability of the dry phase and the assemblages of marginal and aquatic vegetation (Williams 1987, Wiggins *et al.* 1980). Temporary ponds are a common feature of landscapes in much of the world; from highly ephemeral rain filled puddles in sub-Saharan Africa (e.g. Hildrew 1985, McLachlan & Cantrell 1980) to boreal snow melt pools in northern Sweden (Nilsson & Svensson 1994) and North America, ponds in alder woodland in Poland (Williams *et al.* 2001) and large shallow lakes within Mediterranean temporary marshes (Grillas & Roché 1997) and on stabilised dunes (Serrano & Toja 1995).

Energy from ponds enters the terrestrial system when insect larvae emerge (Batzer & Wissinger 1996) and through herbivore grazing of pond vegetation. During the dry phase nutrients are remineralised and organic matter oxidized which increases wet phase productivity (Schneider & Frost 1996, Collinson *et al.* 1995). This means that temporary ponds are spatially predictable in the landscape, despite their temporal variability, because the rate of infilling is slowed by the breakdown of plant material during the dry phase and individual temporary ponds sometimes persist for thousands of years (Williams *et al.* 2001). Pond formation is dependent on suitable substrate conditions, these often occur in areas subject to podsolization (the development of an impermeable iron pan layer within the soil). Since iron is deposited more deeply in waterlogged and anaerobic soils ponds frequently develop in such areas.

Regular drying affects pond temperature regime (Blaustein *et al.* 1999) as well as water chemistry by increasing conductivity, decreasing available oxygen and altering pH (Williams 1996). The harsh physicochemical nature of temporary ponds therefore excludes many predators and competitors, making them ideal habitats for competitively inferior species, which are often otherwise scarce (Collinson *et al.* 1995). The length and predictability of pond hydroperiod limits assemblage composition as only those species of animal and plant with suitable life history strategies are able to survive and reproduce.

1.2 Life history strategies of temporary pond invertebrates and plants

Given the environmental challenges of temporary ponds, the organisms that inhabit them have evolved dispersal and diapause strategies to avoid physiological stress. Selection pressure favours life histories that: (i) allow rapid colonisation and growth rates; (ii) minimise competition, predation and desiccation and (iii) have a mechanism that allows flexible timing of metamorphosis in order to maximise growth but minimise risk (Wilbur 1997). Optimisation of life history strategies in a variable habitat is predicted to depend upon the spatial and temporal fluctuations in habitat availability, which leads to a trade off between the costs and benefits of reproducing immediately in the present habitat patch compared with those of dispersing to a different patch and reproducing later (Southwood 1977). Many temporary pond invertebrates and plants, exhibit r-selected life history strategies, having rapid growth rates and spreading reproductive effort amongst a large number of propagules. Both invertebrates and plants utilise dispersal and diapause as strategies to avoid adverse conditions and maximise reproductive success in a variable environment (Olivieri 2001). Wiggins *et al.* (1980) divide the life history strategies of temporary pond invertebrates into four main groups (Table 1.1).

	Life history strategy	Taxonomic groups that exhibit strategy
Group 1:	Year round residents incapable of active dispersal, remain in the pond basin throughout summer as desiccation resistant stages	Cladocera, Copepoda, Ostracoda, Mollusca, Isopoda and Amphipoda
Group 2	Spring recruits which oviposit in water but subsequently have drought resistant life stages	Ephemeroptera, Trichoptera, Coleoptera and Chironomidae,
Group3	Summer recruits which oviposit in the dry pond basin	Odonata, Trichoptera, Chironomidae and other Diptera
Group 4	Active dispersers that utilise the pond during the wet phase, reproduce in temporary water but returning to more permanent waters before pond dries	Coleoptera, Hemiptera, Ephemeroptera, Chironomidae and Amphibia

Table 1.1: Main life history strategies of temporary pond invertebrates highlighted by Wiggins *et al.* (1980)

Many of the species in temporary pond assemblages are ecological generalists that occur in a wide range of aquatic habitats but also possess the necessary adaptations to cope with the adverse effects of pond drying. Temporary pond insects often retain flight throughout the life cycle so they can 'escape' when the ponds dries, although the directionality and scale of such dispersal movements are still unclear (Bohonak & Jenkins 2003). Many species can also 'escape in time' (Lahr 1999) by having a life stage that is capable of drought resistance or diapause (e.g. rotifers, microcrustaceans) or is semi terrestrial (e.g. *Helophorus* beetle larvae, Williams 1987) and so can remain in the pond basin throughout the dry phase. Actively dispersing species that colonise newly wet temporary ponds might be regarded as 'super-tramp' or 'fugitive' species (Townsend *et al.* 2000) which gain freedom from competition by tracking such habitats across a landscape.

Amongst temporary pond invertebrates the dispersal behaviour of Coleoptera and Hemiptera has been most widely studied (e.g. Svenssen 1998, 1999, Landin 1980, Vepsäläinen 1978, Landin & Stark 1973, Pajunen & Jansson 1969, Fernando 1958). Polymorphism or polyphenism in wing length and flight musculature have been observed in a number of species (e.g. Fairburn & Desranleau 1987, Vepsalainen 1978, Jackson 1950) and, in general, short winged morphs have been found to be more common in more permanent habitats (Sheldon 1984, Landin 1980, Brown 1951). Species typical of temporary habitats such as *Corixa punctata* have also been shown to have an increased tendency to fly compared to long winged relatives (e.g. *Sigara striata*) which live in more permanent habitats (Brown 1951). *Callicorixa producta* and *Arctocorisa carinata* exhibit interspecific and seasonal variation in dispersal rate as they fly during the spring in order to take up suitable breeding sites before returning to deeper overwintering sites in late autumn (Pajunen & Jansson 1969).

Rotifers and other zooplankton produce amictic resting eggs when environmental conditions become severe (Gilbert 2002, Medland & Taylor 2001, Gilbert & Schreiber 1998). Such zooplankton species are therefore analogous to plants which have seed banks. Subsequent hatching of the eggs, when conditions ameliorate, can change the assemblage composition and seasonal dynamics of zooplankton communities (Hairston *et al.* 2000). Macroinvertebrates such as Culicidae (Lang 2003), Chironomidae (Chou *et al.* 1999, McLachlan & Cantrell 1980) and Limnephilidae (Wissinger *et al.* 2003) can also produce desiccation resistant eggs, and so can also leave dormant life stages in pond sediments. The dispersal of encysted zooplankton stages by wind or phoresy may also be a common phenomenon (Bohonak & Jenkins 2003, Bilton *et al.* 2001b).

Many temporary pond organisms exhibit phenotypic plasticity in developmental rate and/or time of hatching/germination, e.g. fairy shrimps (Hildrew 1985) and annual plants (Simovia & Hathaway 1997, Bonis *et al.* 1996). Such strategies are termed 'bet hedging' as they spread the risks of mortality amongst the progeny, optimising reproductive fitness across the years rather than maximising it within years (Williams 1996). Environmental cues such as pond drying, temperature, reduction in resources and unfavourable physicochemical conditions are believed to trigger trait plasticity.

1.3 Factors affecting temporary pond assemblage composition

1.3.1 The relative importance of local and regional processes

Patterns in assemblage composition are usually attributed to an interaction between regional and local factors (Tokeshi 1999, Gaston & Spicer 1998, Cornell & Lawton 1992) and chance (Gotelli & Graves 1996). Dispersal mediates the pool of potential colonists available and local environment restrains species establishment, so together they determine an 'ecological species pool' that biotic interactions may later regulate (Belyea & Lancaster 1999). Order and timing of colonisation are dictated by dispersal constraints, which depend on species-specific traits, landscape structure and chance (Delettre & Morvan 2000, Belyea & Lancaster 1999).

The relative influence of regional and local factors on community assembly remains relatively elusive (Havel & Shurin 2004, Jeffries 2003, Belyea & Lancaster 1999, Poff 1997), although local factors are predicted to prevail in systems where dispersal occurs more often than extinction (Cohen & Shurin 2003). The relative importance of regional and local processes on temporary pond assemblages is, therefore, likely to be mediated by habitat parameters that govern local extinction *i.e.* the regularity and predictability of pond drying (Kiflawi *et al.* 2003, Schneider 1997, Schneider & Frost 1996, Wellborn *et al.* 1996).

Kholin and Nilsson (1998) show that a positive relationship exists between local and regional richness of predatory water beetles in Sweden. Some authors have used this form of the relationship (type I community, Cornell & Lawton 1992) to infer that local assemblage membership is limited by dispersal, as local assemblages are not saturated with species. Most authors, however, believe that a positive regional-local diversity relationship does not preclude the influence of biotic interactions (Tokeshi 1999) and it has been shown, for example, that local predation could in fact increase local zooplankton diversity (Shurin & Allen 2001, Shurin 2000, Shurin *et al.* 2000). Although there is much evidence for competition and predation amongst macroinvertebrates in temporary pond systems (Finke & Denno 2002, Bilton *et al.* 2001a, Wibur 1997, Blaunstein *et al.* 1996, Hildrew 1985) these interactions are generally thought to be of lesser importance in shaping assemblage structure and dynamics than habitat permanence (Schneider 1997, Schneider & Frost 1996, Wellborn *et al.* 1996).

As well as being mediated by habitat permanence it is likely that the balance of local and regional influences on species distribution patterns in temporary ponds also differ depending on the life history strategy of taxa. Local processes are expected to play a more dominant role when extinction is rare (Cohen & Shurin 2003), which may be true for species, like zooplankton (Cáceres & Soluk 2002) and annual plants, which have an egg/seed bank that maintains the population throughout dry phases and can disperse passively (group 1 & 2 species, Table 1.1). In contrast, distributions of macroinvertebrate taxa, which become locally extinct in ponds as they dry (group 3 & 4 species), are likely to be constrained by the regional process of dispersal.

Other studies suggest that biotic interactions are not necessary for the local co-existence of species in ephemeral habitats (McGradySteed & Morin 1996, King *et al.* 1996, Shorrocks & Rosewell 1987) and models of community assembly (Lockwood *et al.* 1997) show that high rates of invasion minimise the influence of chance historical events (priority effects) on assemblages and lead to dynamic assemblage composition. Biotic interactions may still, however, be important in shaping abundance patterns within more permanent ponds (Schneider & Frost 1996) and during the summer months, when pond habitat is scarce in the landscape (Foggo, Bilton and Rundle in prep.).

1.3.2 Temporary ponds as habitat islands

The equilibrium theory of island biogeography (MacArthur & Wilson 1967) suggests that the number of species inhabiting an oceanic or habitat-island results from a dynamic equilibrium between the processes of colonisation and extinction. Colonisation rates are assumed to decrease with increasing isolation from a source of colonists, whereas, extinction rate is expected to decrease with increasing island size. Temporary pond species, however, are influenced by both the spatial distribution of ponds and their temporal permanence (Williams 1987). MacArthur and Wilson's (1967) model is therefore overly simplistic as it assumes: (i) that islands are constant throughout time; (ii) that species do not interact; and (iii) that islands of the same size are equally favourable habitats.

Ponds have been shown to be non-equilibrium systems, as the pool of available colonists is subject to seasonal variation and succession (Wilbur 1997, Barnes 1983, Wiggins *et al.* 1980). In addition, regular pond drying means that the colonisation process undergoes cycles, which prevent temporary pond systems from ever reaching equilibrium and may promote co-existence rather than niche saturation (Wilbur 1997, McGradysteed & Morin 1996, Ward & Blaunstein 1994). However, recent work by Kiflawi *et al.* (2003) shows that an island-biogeography model incorporating pond area and permanence can explain ca. 60% of the variation in pond local species richness. Colonisation rate was independent of pond permanence in the model, as the study modelled the occurrence of passively dispersing invertebrates which, it was assumed, could successfully colonise dry pond basins.

Some studies suggest that populations of pond macroinvertebrate species are governed by metapopulation dynamics (Caudill 2003, Briers & Warren 2000, Jeffries 1994, Svensson 1992). True metapopulation dynamics occur where species' populations are spatially discrete but are connected by dispersal and therefore persist in balance between local extinction and colonisation (Tokeshi 1999, Harrison 1991). Few systems have been shown to exhibit true metapopulation structure as the assumptions on which the model is based are rather stringent, *i.e.* there should be no correlation of events at each habitat patch, which is unlikely because environmental conditions are often autocorrelated, at least at small scales (Bohonak & Jenkins 2003, Bullock *et al.* 2002), and populations should be at equilibrium (Harrison 1991). Temporary ponds species are therefore unlikely to behave as true metapopulations and are more likely to be analogous to source-sink metapopulations, where persistence depends upon one or more extinction resistant populations remaining in the landscape (e.g. in more permanent water bodies), or a patchy population in which dispersal between patches is so high the system is effectively extinction resistant (Hanski 1999, Harrison 1991).

1.3.3 Effect of habitat heterogeneity on assemblage richness & composition

Habitat patches often vary in their temporal and spatial predictability as well as their size, complexity and abiotic conditions. Temporary ponds are usually spatially predictable (see section 1.2) but habitat heterogeneity varies as ponds form a continuum of size, permanence, water chemistry and macrophyte complexity throughout the landscape. Permanence has been shown to affect the relative influence of regional and local processes on local assemblage richness and composition. This is because pond hydroperiod regulates the biotic interactions which affect population density and the relative fitness of individuals (Wilbur 1997). The order and timing of colonisation may also be affected by short wet phase duration as it limits the window of opportunity for pond detection and oviposition. Hydroperiod has been shown to affect the distribution of freshwater Coleoptera adults and larvae (Eyre *et al.* 1992) and many other studies show variation in assemblage composition and species richness with pond duration (e.g. Kiflawi *et al.* 2003, Bilton *et al.* 2001a, Collinson *et al.* 1995).

Modelling studies have demonstrated that species can coexist in ephemeral habitats without the need for resource partitioning (Shorrocks & Rosewell 1987). It might therefore be expected that functionally similar congeners could coexist in ponds where the disturbance regime is high enough to render interspecific competition low. To date, there are limited data regarding this assertion, although Nilsson and Svensson's (1994) limited data dispute this, showing that larger ponds, which dry less frequently, have increased within-guild diversity.

The physical structure of a habitat has two major components; size and complexity (Lawton 1986). The relationship between habitat size and species richness is well documented (e.g. Harte & Kinzig 1997 Connor & McCoy 1979, Williams 1943) and may be a result of (i) passive sampling, because larger habitat patches often have more sampling effort invested in them, (ii) area *per se*, as large habitats are effectively bigger 'nets' with which to sample species from the environment or (iii) habitat heterogeneity, as the variety of microhabitats often increases with area. Pond area, like permanence, has been shown to affect both species richness and assemblage composition in a number of studies (e.g. Kiflawi *et al.* 2003, Spencer *et al.* 1999, Jeffries 1994).

The structural complexity of a habitat also limits the distribution of species (Holling 1992) and both species richness and abundance are frequently reported to increase with habitat complexity (e.g.

Kelt & Brown 1999, Downes *et al.* 1998). This may be because more complex habitats provide better refugia from predators (Bartholomew *et al.* 2000, Mosknes *et al.* 1998), greater habitat area for surface dwelling organisms, or simply more microhabitats (McNett & Rypstra 2000). Changing patterns in body size distribution with complexity have also been reported (Schmid *et al.* 2002, Raffaelli *et al.* 2000, Gee & Warwick 1994a, 1994b, Morse *et al.* 1985).

Pond substrate characteristics and assemblages of aquatic macrophytes contribute to the heterogeneity of pond habitat (Harper *et al.* 1997) and lotic freshwater invertebrates are more abundant and have higher richness in habitat patches with more complex sediment structure (Schmid *et al.* 2002, Schmid 2000). However, previous studies of the diversity, density and complexity of pond macrophytes have shown these factors to have mixed effects on macroinvertebrate abundance and diversity (e.g. Cheruvelil *et al.* 2002, Jeffries 1993, Cyr & Downing 1988, Rooke 1984, Dvorak & Best 1982), with no consensus in the literature.

The final components of pond heterogeneity, local abiotic conditions, include water and soil chemistry and temperature which also influence the distribution of macroinvertebrates (Blaunstein *et al.* 1999, Poff 1997, Bechara 1996, Malmqvist & Eriksson 1995, Barnes 1983) and macrophytes (Heegaard *et al.* 2001). Ponds with short hydroperiod have greater conductivity because they evaporate more quickly (McKee *et al.* 2003) and the resulting high concentrations of ions could cause osmotic problems for some insects (Buchwalter *et al.* 2003), although these have yet to be studied thoroughly (Williams 1996). Low pH has been shown to limit colonisation of acid intolerant species and to retard pond floral succession (Barnes 1983). It can also affect detrivore feeding, as the rate of leaf litter conditioning is reduced because bacterial action is slowed (Kok & Vanderveld 1994). Many temporary pond plant species also require specific physicochemical conditions for their survival and germination (Bonis *et al.* 1996, Bonis *et al.* 1995) so can only inhabit a subset of sites where these conditions are met. For example, *Juncus pygmaeus* occurs in shallow mineral soils compared to *Isoetes histrix* which favours organic/peaty soils and *Cicendia filiformis*, which grows in bare, sandy, gravely or peaty track microhabitats (Hopkins pers. comm.).

1.4 Commonly observed patterns in assemblage composition

1.4.1 Spatial autocorrelation

Spatial pattern is a theme of increasing general interest in ecology and conservation biology (Collinge 2001, Legendre & Legendre 1998). Environmental conditions, such as water chemistry, which affect the abundance and distribution of species, tend to be correlated through space, so sites in close proximity tend to have more similar abiotic and biotic characteristics than more distant sites, i.e. they are *spatially autocorrelated* in the landscape (Legendre & Legendre 1998, Brown 1995). Spatial autocorrelation in habitat suitability is, in turn, likely to affect metapopulation dynamics and therefore the persistence of species in the landscape (Bohonak & Jenkins 2003).

Even when spatial patterns in habitat heterogeneity are ignored, assemblages are likely to have intrinsic spatial structure, because communities that are close together in geographical space would be expected to be more similar than those more widely spread in the landscape as a consequence of dispersal limitation (Wilson 1999). Assemblage similarity might, therefore, be expected to show spatial pattern through the landscape which may be attributed to local habitat conditions and/or dispersal constraints, and spatially explicit analyses should be used in order to untangle their separate effects.

1.4.2 Nested subsets

The combined effect of local and regional processes leads to turnover of species between habitat patches (β diversity) (Ricklefs & Schluter 1993), as species vary in their levels of occupancy and abundance between sites due to habitat suitability, level of vagility, reproductive rates and biotic interactions (Gaston & Blackburn 2000). Interspecific differences in site occupancy therefore contribute to differences in species richness between sites. Species distributions may overlap or form checkerboards if local processes exclude one or other species from certain sites. The degree of overlap in species' site occupancy can be described by a measure called 'nestedness'.

Nestedness is one of the most commonly observed properties of a regional collection of local biotas (Gaston & Blackburn 2000). Perfect nesting occurs when species-poor sites contain subsets of the assemblages found in species-rich sites; most local assemblages occurring in insular habitats have been shown to exhibit nestedness (Wright *et al.* 1998, Boecklen 1997).

Passive sampling and differences in habitat distribution, isolation and area are all hypothesised to generate nestedness (Fischer & Lindenmayer 2002, Wright *et al.* 1998, Boecklen 1997, Honnay *et al.* 1999, Patterson & Atmar 1986; see chapter 3), whereas frequent between patch dispersal has been proposed to erode nested patterns (e.g. aquatic invertebrates, Wright *et al.* 1998, Boecklen 1997).

Studies of nested subsets in freshwater systems have found assemblages of lacustrine macrophytes (Weiher & Boylen 1994), pond amphibians (Beja & Alcazar 2003, Hecnar & MCloskey 1997) and stream (Malmqvist & Hoffsten 2000) and pond (Kholin & Nilsson 1998) macroinvertebrates to be significantly nested. In contrast, other work examining lotic macroinvertebrates (Malmqvist, *et al.* 1999, Malmqvist 1999, Malmqvist, *et al.* 1997, Malmqvist & Eriksson 1995) have failed to find significantly nested distributions. This indicates that there is mixed evidence for Boecklen's (1997) and Wright *et al.*'s (1998) proposition that there are low levels of nestedness within aquatic invertebrate assemblages.

The taxonomic resolution and the method of analysis used within a study affect whether nestedness is detected. Malmqvist and Hoffsten (2000) found lotic macroinvertebrates to have significant nested subset pattern when the nestedness temperature calculator (Atmar & Patterson 1995; see chapter 3) was used. However, earlier studies of freshwater macroinvertebrates that have failed to find significant nestedness have used alternative methods with different underlying null models. Care should be taken over the choice of technique used to assess nestedness, in order to ensure the null model used is appropriate (Fischer & Lindenmayer 2002, Jonsson 2001). As yet, there have been no studies of nestedness among temporary pond macroinvertebrate assemblages and only one study examining the nested subset pattern of temporary pond amphibians (Beja & Alcazar 2003).

1.5 The conservation importance of temporary ponds in Europe

Temporary ponds are common and widespread throughout all European biogeographic provinces (Willams *et al.* 2001) and have been recognised as an important habitat for many scarce invertebrate and plant species (Grillas & Roché 1997, King *et al.* 1996, Collinson *et al.* 1995). In addition, they are important for amphibian populations which are in decline in many areas (Semlitsch 2000, Bellemakers & van Dam 1992, Diaz-Paniagua 1990). When compared with permanent ponds temporary pond assemblages are often found to be depauperate, however, they frequently support a greater proportion of rare taxa (Collinson *et al.* 1995, Bratton 1990, Whitten 1990). For example, Nicolet (2001) showed that 80% of the 70 UK temporary ponds surveyed supported one or more nationally scarce species.

The main threat to pond biotas is habitat loss. The density of ponds in many European countries was reduced by 40-90% in the twentieth century (Oertli *et al.* 2000); the main reasons for this decline have been land drainage, water abstraction, intensification of agriculture and increased urbanisation (Maier *et al.* 1998, Oertli *et al.* 2002). Barr *et al.* (1994), estimate that 4-12% of ponds were lost in the UK between 1984 and 1990, showing habitat loss to be an ongoing problem. Small, shallow ponds are also particularly vulnerable to changes in disturbance regime, invasive species, acidification, eutrophication and pollution (Powell 2001). Agricultural run off and changes in grazing regime and land use also contribute to changes in pond physicochemistry and floral succession, which can lead to the local extinction of rare taxa (e.g. Maier *et al.* 1998), stressing the importance of increased habitat protection (including appropriate management of the wider landscape) and, where feasible, creation (e.g. Gee *et al.* 1997). However, even when the conservation importance of sites is recognised, the introduction of inappropriate management regimes, such as pond deepening, and the conflicting management requirements of different taxonomic groups have made conservation efforts problematic (Biggs *et al.* 2001, Gee *et al.* 1997, Collinson *et al.* 1995, Bellemakers & van Dam 1992).

Some areas of the UK still support a high density of ponds, and in these landscapes it may be impractical to gain detailed biological survey data for all sites (Briers & Biggs 2003). In addition, some invertebrate and amphibian species utilise more than one pond throughout their life cycle so the conservation importance of individual ponds may be underestimated (Boothby 1997). This highlights the importance of conserving a heterogeneous mosaic of waters in the landscape (Powell 2001). Within such a continuum of freshwater habitat, temporary ponds have been shown to support regionally unique faunas (Williams *et al.* 2004, Harper *et al.* 1997).

Most species in natural assemblages are rare (Gotelli and Graves 1996) and these often form the focus of nature conservation efforts. In the context of this study rare taxa are those that occur at few sites with low or high density (i.e. they have restricted habitat breadth). The importance of including rare taxa in aquatic bioassessment as well as in conservation assessment is emphasised by Cao *et al.* (1998) and Cao and Larsen (2001), who show that species richness of the least impacted sites was disproportionately reduced compared to impacted sites when rare taxa were omitted, which led to reduced sensitivity of the multivariate method to detect ecological change due to anthropogenic effects. Some previous studies examining composition and structure of ecological assemblages have deleted rare species from data sets because they were thought to have little effect on the outcome of multivariate classification techniques, add noise to the statistical solution or violate statistical assumptions. Multivariate routines often underweight rare species, although this can be avoided by using appropriate data transformation and careful choice of similarity measure (Cao & Larsen 2001, Clarke and Warwick 2001, Legendre & Legendre 1998).

In the UK temporary ponds support important populations of Biodiversity Action Plan (BAP) and Red Data Book (RDB) plant species such as *Ranunculus tripartitus* (three-lobed crowsfoot), *Pilularia globulifera* (pillwort), *Juncus pygmaeus* (pygmy rush), *Mentha pulegium* (pennyroyal), *Luronium natans* (floating water plantain) and *Lycopodiella inundata* (marsh clubmoss) (Plantlife 2001, Edwards *et al.* 2000, Stewart *et al.* 2000; see appendices 7.3 & 7.4 for RDB status of taxa found in this study). Indeed it is thought that over 25% of wetland plant species given special protection in the UK are dependent on temporary pond habitat (Collinson *et al.* 1995). Many RDB and nationally scarce macroinvertebrate taxa are also supported in temporary or fluctuating waterbodies, these include many Coleoptera (e.g. *Haliplus variegatus Graptodytes flavipes, Hydroporus rufifrons, Hydroporus necopinatus, Enochrus nigritus, Aphodius niger*, *Dryops striatellus*, and *Bagous* spp), Odonata (*Coenagrion mercuriale* and *Sympetrum fonscolombei*) and some Mollusca (e.g. *Lymnaea glabra*; appendices 7.1 & 7.2 detail the conservation status of taxa found in this study).

The conservation importance of temporary ponds has been historically overlooked (e.g. Maitland & Morgan 1997, Ratcliffe 1977) and UK conservation bodies such as Plantlife, English Nature, the National Trust and Wildlife Trusts have recently put much effort into raising the profile of what are often inconspicuous patches of habitat. Wetlands in the New Forest, for example, until recently received less attention from the conservation bodies than the ancient and ornamental woodlands because they were less appreciated and less obviously under threat (Atkinson 1984). The Nature

Conservation review (Ratcliffe 1977) did much for wetland conservation in general but it took longer for temporary pond habitat to get the recognition it deserved.

A range of pond types are now protected under European Union Council legislation (92/43/EEC) commonly referred to as the 'Habitats Directive'. The directive aims to conserve biodiversity through the protection of habitats and species (Hopkins & Buck 1995). Biotopes for protection are listed under Annex I and species under Annex II. The following seven types of lentic water body are protected in Europe under Annex I:

- Oligotrophic waters containing very few minerals of the sandy plains (*Littorelletalia uniflorae*);
- Oligotrophic waters containing very few minerals generally on sandy soils of the West Mediterranean with *Isoetes* spp;
- Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletalia uniflorae* and/or *Isoeto-nanojuncetea*;
- Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp;
- Natural eutrophic lakes with *Magnopotamion* or *Hydropcharition* type vegetation;
- Natural dystrophic lakes and ponds;
- Mediterranean Temporary Ponds.

The last habitat type, 'Mediterranean Temporary Ponds' (MTPs) are a European priority biotope, which, despite the name, are not seen to be restricted to the Mediterranean basin. MTPs are reported to occur in two regions of the UK, in the New Forest, Hampshire and on the Lizard Peninsula, Cornwall. The status of MTP habitat is poorly understood, and this habitat forms the main focus of the thesis.

1.5.1 Current definition and distribution of Mediterranean Temporary Pond (MTP) habitat

The official definition of MTP habitat is (European Commission 2003, 92/43/EEC):

> 'Very shallow temporary ponds (a few centimeters) which exist only in winter or late spring with flora mainly composed of Mediterranean therophytic or geophytic species belonging to the alliances *Isoetion, Nanocyperion flavescentis, Preslion cervinae, Agrostion salmanticae, Helochloion* and *Lythrion tribracteeat."*

The Habitats Directive lists 41 plant species as being characteristic of MTPs, one of which is indicated as a European priority (*Lythrum flexosum*). Only about 30% of these species can be found in Britain, not all of which occur in the two nominated UK regions (Table 1.2). This means that if MTPs are considered to occur in the UK their flora would be depauperate in comparison to the rest of Europe. No invertebrate species or assemblages are yet listed in the Directive as characteristic of MTP habitat.

MTP Species (Europe)	Present in UK	Present In NF	Present on Liz
Agrostis pourretii			
Centaurium spicatum			
Chaetopogon fasciculatus			
Cicendia filiformis	●	●	●
Crypsis aculeata			
Crypsis alopecuroides			
Crypsis schoenoides			
Cyperus flavescens			
Cyperus fuscus	●	●	
Cyperus michelianus			
Damasonium alisma	●		
Elatine macropoda			
Eryngium corniculatum			
Eryngium galoides			
Exaculum pusillum	●		
Fimbristylis bisumbellata			
Glinus lotoides			
Gnaphalium uliginosum	●	●	●
Illecebrum verticillatum	●	●	
Isoetes boryana			
Isoetes delilei			
Isoetes duriei			
Isoetes heldreichii			
Isoetes histrix	●		●
Isoetes malinverniana			
Isoetes velata			
Juncus bufonius	●	●	●
Juncus capitatus	●		●
Juncus pygmaeus	●		●
Juncus tenageia	●		
Lythrum castellanum			
Lythrum flexosum			
Lythrum tribracteatum			
Marsilea batardae			
Marsilea strigosa			
Mentha cervina			
Ranunculus dichotomiflorus			
Ranunculus latiflorus			
Serapias lingua	●		
Serapia neglecta			
Serapia vomeracea			
41 species	12 species	5 species	6 species

Table 1.2: Plant species characteristic of MTP vegetation (European Commission 2003), with presence in the UK and the two sampling regions indicated (from Stace 1997). NF = New Forest; Liz = Lizard

The reported geographical range for MTPs extends from Greece through Italy, France, Spain and Portugal, with their occurrence in the New Forest and on the Lizard Peninsula being at the most northerly extreme of their global range. Twenty-one sites are proposed to support MTP habitat within the Atlantic biogeographic region (Fig 1.1).

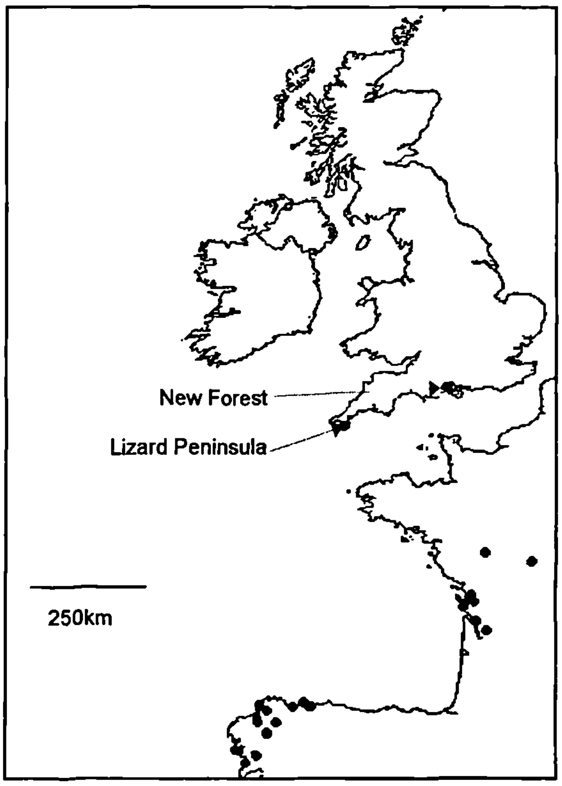


Figure 1.1: Location of MTP sites within the Atlantic Biogeographic region.

The working definition for MTPs in the UK has evolved and become simpler in recent years and the Special Area of Conservation (SAC) designation guidelines (McLeod *et al.* 2002) now describe them as:

> 'winter flooded areas that dry out to give vegetation rich in annuals; many of which are nationally rare species with southern European distribution, which are principally confined to this habitat type...'

The Joint Nature Conservation Committee (JNCC) defines two main types of MTP that are both restricted to the Lizard Peninsula, a more acid community of trampled and grazed areas often on flooded trackways, typically with one or more of *Juncus pygmaeus* (pygmy rush), *Ranunculus tripartitus* (three-lobed crowsfoot), *Mentha pulegium* (pennyroyal) and *Cicendia filiformis* (yellow centaury) and secondly a basic type in eroded serpentine pans that are subject to seepage with

Allium schoenoprasm (chives), *Juncus capitatus* (dwarf rush) and *Isoetes histrix* (land quillwort). However, the key species listed in the JNCC descriptions of MTP habitat include only a few from the EU list (Table 1.2).

Originally both the New Forest and the Lizard were deemed to support MTPs (Fitzgerald Holyoak & James 1999, JNCC 1997) but recent work has concluded that New Forest pond vegetation only contains elements of the MTP assemblage and is instead more similar to that of 'Oligotrophic to mesotrophic standing waters' (JNCC website, Sanderson 1998). Small New Forest sites are reported, however, to incorporate plants such as *Illecebrum verticillatum*, which is included in the European Commission MTP list (Table 1.2) and *Mentha pulgeium* which is found in Lizard MTP sites. In addition *Pillularia globulifera* (pillwort), (coral necklace), *Radiola linoides* (allseed) and *Anagallis minima* (chaffweed) occur in acidic sites with *Pulicaria vulgaris* in more eutrophic sites.

At present then there is confusion and controversy about the definition and classification of MTP habitat in the UK. This has largely arisen from the use of disparate definitions and classification schemes, which are often subjective, making it difficult to consistently characterise the habitat. The European definition in the Habitats Directive is loosely based around the Corine biotope classification system, since it is the only European level classification system available (EC 2003). In addition, the descriptions within the Directive often refer to phytosociological assemblages such as *Nanocyperion flavescentis* 'dwarf rush communities' (Rodwell 1994) which are not ubiquitous in their usage and often list a number of key species, many of which have restricted distributions. The JNCC have then distilled a working definition for UK MTP habitat which incorporates a number of nationally scare taxa associated with small ephemeral ponds, some of which do not occur in the European definition. Subsequent studies (e.g. Sanderson 1998) often try to fit pond vegetation into both the European Habitats Directive categories and the unrelated, but more familiar, National Vegetation Classification (NVC) scheme with limited success. This study aims to objectively classify pond vegetation in the New Forest and on the Lizard Peninsula, in order to define more rigorously MTP vegetation in a UK context and to examine the macroinvertebrate fauna of the ponds in order to clarify and augment the definition of this biotope.

1.6 Study Regions

1.6.1 New Forest

The geology of the Hampshire basin is dominated by Tertiary sediments. Eocene Barton Sands, Clays and Bracklesham beds dominate the north of the forest, giving rise to a complex of light sandy soils that underlie much of the heathland, and clay soils which lay beneath oak-woodland. The Eocene deposits are overlain, to the south, by Oligocene Headon Beds, which are comprised of clayey strata containing beds of fossil shells, which give rise to calcareous mires, whereas heathland dominates above superficial deposits of Pleistocene Gravels (Brewis *et al.* 1996).

Carbon dating of continuous peat deposits and examination of the pollen record indicate that during the Devensian interstadial (c12000 years BP) the vegetation in the New Forest area was dominated by tall-sedge and dwarf-birch fen. However, clay/charcoal strata indicate that fire disturbed succession after this time and the pollen record from 8000 years BP indicates that subsequent vegetation was dominated by oak-elm-hazel woodland. Later (c 5000 years BP) there is clear evidence for the *Alnus* and *Quercus* woodland and mire communities that are observed today (Clarke & Barber 1987). Woodland in the New Forest area was later fragmented by Neolithic anthropogenic activities, and so incorporated areas of grassland and heathland by 1500 years BP. Ponds sampled in this study lay predominantly in these areas of heathland and grassland, often above sandy or gravely soils which have developed a superficial impervious layer. In addition, several study sites were shallow marl pits which had seasonally fluctuating water levels.

Today the New Forest consists of 20,000 ha of unenclosed forest including: 12,500ha of heathland and acid grassland; 2,900ha of wet heath and valley mires; 3,700ha of ancient, unenclosed woodland open to grazing; 300ha of open short turf ‘lawn’; and 8,400ha of inclosures mostly in the main coniferous or broad leaved plantations. Much of the unenclosed area remains under commoner's rights and is still grazed by ponies, cattle, deer and, in autumn, pigs (Brewis *et al.* 1996, Putman *et al.* 1987, Edwards & Hollis 1982). The landscape management has therefore retained some of its medieval characteristics, despite increased anthropogenic impact (Angold 1997, Morgan 1987).

The New Forest is now a Special Area of Conservation (SAC) supporting 11 Annex I Habitats Directive biotopes; including two categories of pond (see section 1.6.3 below). An oceanic climate with high summer temperatures, mild winters and high rainfall along with varied topography and soil composition make Hampshire the most botanically rich UK County (Brewis *et al.* 1996). In addition, the region was never subjected to glaciation and so a natural mosaic of soil types and topography remains, which, along with the maintenance of traditional land management practices have resulted in a diversity of habitat types that are unmatched in the rest of the UK. The vascular plant species richness of acid bogs, fens and ponds forming on wet heaths and lawns makes the region particularly unique (Brewis *et al.* 1996).

1.6.2 Lizard Peninsula

The Lizard Peninsula comprises a Pliocene marine platform, its geology is comprised of an ophiolite sequence that was intruded and metamorphosed in the late Devonian. Much of the peninsula is underlain by tremolite and bastite serpentine, gabbro, hornblende schists and granite gneiss. The basic peridotite-gabbro-mafic assemblage is faulted against Devonian sediments to the north and overlain, in patches, by acidic, wind blown loess and Cretaceous Crousa gravels (Staines 1984, Flett 1946).

At the end of the last glaciation, Lizard vegetation, at least on the Devonian sediments, probably changed from open tundra to hazel and oak woodland, although it is unsure whether the serpentine plateau itself was ever wooded (Staines 1984). Pollen analysis suggests that open willow and hazel scrub and heathland existed above the serpentine around 1500 years BP. The area has a long history of agriculture and areas of heathland were taken in for crofts in recent centuries (maps exist from 1695) and much of the moorland was used for peat cutting activity. The effects of past cultivation still cause subtle variation in heathland assemblage composition (Rackham 1986).

The Lizard Peninsula is also now a SAC supporting six Annex I habitats. The unusual serpentine geology and the soil types derived from it have been shown to have an important influence on the Lizard's heathland, which have been studied extensively (Marrs & Proctor 1978, Malloch 1971, Proctor 1971, Coombe & Frost 1956). The heathland flora has been divided into four main associations (Coombe & Frost 1956) each of which have been found to occur on one of the three basic soil types (brown ranker, gley and pseudogley) which differ in mineralogy, drainage, humus content and podsolization (Kubiëna 1953). Rock heath (*Festuca ovina- Calluna* heath) formed on shallow stony, loamy soils, alongside serpentine outcrops. Mixed heath (*Erica vagans Ulex europaeus* heath) is associated with well drained brown earths and rankers around cliff tops and cover. Short heath (*Agrostis setacea* heath) develops where wind blown acid loess or Crousa gravel still overlay the serpentine, whereas Tall heath (*Erica vagans- Schoenus* heath) is wetter and has developed on homogeneous gleyed soils over large areas of the serpentine and gabbro plateau; most natural ponds occur in this latter heathland type. Cattle, pony and sheep grazing and controlled burning are all used to maintain a heathland mosaic (Lawman pers comm., Hughes 1988).

1.6.3 Ponds in the study regions

Both aquatic plants and invertebrates are relatively species-rich in both the New Forest and Lizard Peninsula regions. The diversity of the regional species pools largely results from the wide variety of waterbodies which vary in size, permanence, age and successional stage. Most ponds on the Lizard Peninsula appear man made (Hopkins 1978), some are believed to be ancient and may have been dug for cattle watering when areas of the Peninsula were enclosed during the Napoleonic wars (Hopkins pers. comm.), although some date back to the seventeenth century or earlier (Rackham 1986). Other more steep sided sites are a result of more recent small scale quarrying for serpentine, gabbro and schist (Staines 1984). Similarly, most New Forest ponds are man-made; some were created in the 18th and 19th centuries to supply mills whilst others were created through marl digging, which was permitted in some areas of the forest under Commoner's Rights.

Small, very ephemeral pools are particularly abundant on the Lizard, they are found along wet track-ways and hedgerows and are often no greater than 4-8m^2 in area. The ecological importance of the ancient cart tracks spanning the Lizard heathland was first highlighted by Hopkins (1978 & 1983), who reported populations of rare plant taxa in ephemeral ponds formed where tracks run through areas of wetter tall heath. The New Forest track ways have, in the main, been artificially surfaced to provide better access for residents and tourists, so the density of small temporary ponds has been much reduced. Examination of a 1920s map (Rackham 1986) shows that the Lizard Peninsula historically had a greater density of ponds than the New Forest and this disparity in the number and distribution of ponds is likely to have been recently exacerbated by the loss of small sites in the New Forest.

The international conservation importance of ponds in these two regions has been widely recognised (McLeod *et al.* 2002), and the ponds are believed to encompass four Annex I lentic freshwater habitat types (see section 1.5 & appendix 7.5). The JNCC designated Hatchett pond, in the New Forest, as an example of habitat 3110 'Oligotrophic waters containing very few minerals of the sandy plains'. Such ponds are generally large and acidic with soft water and are dominated by lawns of *Lobelia dortmanna* (water lobelia), *Littorella uniflora* (shoreweed) and/or *Isoetes lacustris* (quillwort). Only three other UK sites are currently recognised; Little Sea in Dorset, Oak Mere in Cheshire and acid lochs in the South Uist Machair complex on the Western Isles. In addition, the New Forest supports examples of habitat 3130 'Oligotrophic to mesotrophic standing waters' which are small, soft water ponds with *Littorella uniflora*, *Pilularia globulifera* (pillwort), *Illecebrum verticillatum* (coral necklace), *Cicendia filiformis* (yellow centaury), *Juncus bufonius* (toad rush) and *Anagallis minima* (chaffweed).

The Lizard Peninsula supports habitat 3140 'Hard oligo-mesotrophic waters with *Chara* spp'; unusually the high base status of these ponds is due to high concentration of magnesium, derived from the underlying serpentine geology. Other examples of this habitat in the UK have high calcium concentration, as the ponds are formed on shell sands or limestone. The fourth habitat, 'Mediterranean temporary ponds' (MTPs), has been reported to occur both in the New Forest, Hampshire and on the Lizard Peninsula, Cornwall (see section 1.5.1), although there are doubts over the status of New Forest sites.

1.7 Study aims

This thesis integrates descriptive and experimental approaches in an attempt to unravel the ecological processes influencing temporary ponds at a range of spatial scales. Macroinvertebrate and plant assemblage composition along with abiotic habitat characteristics were examined in ponds in the two study regions, the New Forest and the Lizard Peninsula, and a set of newly created experimental ponds were monitored on the Lizard. This allowed a number of interlinked ecological themes to be addressed simultaneously, many of which have, until now, remained unexplored within pond ecology. The thesis concentrated on temporary water bodies, including Mediterranean Temporary Ponds, but in order to examine these in context, a range of water bodies were studied in the two regions. The main ecological questions examined within the chapters of this thesis and representing a gradient from large to small scale are:

- Do similar physicochemical and spatial factors govern pond macroinvertebrate and plant assemblage composition in different geographical regions? (chapter 2)
- Do the distributions of temporary pond species within a region form nested subsets? If so which habitat parameters drive the pattern and do nested and non-nested taxa respond differently to these key parameters? (chapter 3)
- How fast are artificial temporary ponds colonised? Do differences in pond physicochemistry and plant assemblages affect colonisation and turnover? How quickly do man-made ponds resemble similar sized natural ponds? (chapter 4)
- Does small scale variation in the diversity, density and structural complexity of pond macrophyte stands effect the diversity and body size distributions of the macroinvertebrate fauna?(chapter 5)

The thesis also aimed to use these ecological data to inform the conservation management of ponds in the two regions, and specifically to: (i) provide a clear definition and classification of MTP habitat in the UK based on both plant and macroinvertebrate assemblages; (ii) understand what structures pond assemblage composition within these two UK landscapes; (iii) evaluate the potential use of habitat creation in temporary pond conservation; and (iv) synthesise the ecological information into a pond conservation management plan for the regions with a particular focus on MTPs (chapter 6).

2 Ecology of Lizard and New Forest pond assemblages in a national context

2.1 Abstract

Ponds in the New Forest and on the Lizard Peninsula support four vegetation types listed under the EU Habitats Directive. One of these categories, Mediterranean Temporary Pond (MTP) vegetation, is an EU priority habitat comprising ephemeral winter flooded areas, rich in wet ground annuals, the status and extent of which has remained obscure in the UK. This study examined plant and macroinvertebrate assemblage composition in the two regions in order to (i) examine whether similar physicochemical and spatial factors governed pond macroinvertebrate and plant assemblage composition in different geographical regions and (ii) gain a better understanding of the ecology and regional and national importance of these habitats by clearly defining and classifying MTP habitat in the UK.

Both New Forest and Lizard plant and macroinvertebrate assemblages were found to be distinct from similar assemblages recorded in ponds throughout England and Wales and contained a significantly greater number of Red Data Book (RDB) species. In total thirty two nationally scarce or RDB taxa were recorded across the two regions, twenty five of which were invertebrates. New Forest ponds had a significantly higher macroinvertebrate species rarity index (SRI) than UK ponds, whereas pond vegetation SRI was highest on the Lizard. Assessment of pond conservation status should, therefore, be based upon both plant and invertebrate assemblage composition.

Classification of the assemblages highlighted a strong influence of pond permanence on both macroinvertebrate and plant assemblage composition. The vegetation classification indicated that ponds fell into three Habitat's Directive categories (92/43/EEC). Depauperate vegetation of ephemeral Lizard ponds (groups 4, 5 & 6) with *Ranunculus tripartitus* and *Juncus bufonius* would best equate to MTPs. Macroinvertebrates associated with MTP vegetation were Coleoptera, Trichoptera and Chironomidae species that are active dispersers utilising small ephemeral sites for reproduction.

Macroinvertebrate and plant species richness were positively correlated with pond area on the Lizard, but not in the New Forest, whereas plant and invertebrate species richness were positively

correlated in both regions. Lizard macroinvertebrate and plant assemblage composition were correlated with pond physicochemistry; pond area, conductivity, depth and pH being the most important factors. Relationships between physicochemical factors and New Forest macroinvertebrate assemblage structure were weaker and non-significant for plants. Pond physicochemistry also showed weak relationships with the distribution of individual species in both regions.

When the effects of pond physicochemistry and spatial pattern were separated, using partial Mantel tests, assemblage similarity was correlated with different environmental, biotic and spatial factors in each region. Lizard macroinvertebrate assemblage similarity depended primarily on differences in pond area and proximity, although plant assemblage similarity and pond physicochemistry also had a significant effect. In contrast, New Forest macroinvertebrate similarity was unrelated to physicochemical or spatial factors, its sole correlate being plant assemblage similarity. Failure to detect spatial pattern in New Forest macroinvertebrate assemblage similarity may reflect regional differences in the relative strength of dispersal limitation, chance colonisation and biotic interactions.

2.2 Introduction

Temporary pond ecosystems in general have been recognised as an important habitat for many scarce animal and plant species (Collinson *et al.* 1995, Barr *et al.* 1994, Bratton 1990, Whitten 1990). Ponds in the New Forest and on the Lizard Peninsula highlight this as they incorporate four habitat types which fall in Annex I of the Habitats Directive (92/43/EEC; see chapter 1 and appendix 7.5). One of these, Mediterranean Temporary Pond habitat (MTP) is an EU priority biotope, comprising winter flooded areas, rich in low growing wet ground annual plant species, amongst which there are a number of internationally and nationally scarce or Red Data Book (RDB) taxa. Recently, effort has been made to characterise this vegetation type in the UK but this remains qualitative and somewhat subjective and there have been no studies of the possible conservation value of MTP fauna or the spatial and physicochemical factors that govern pond assemblages in the two regions (chapter 1).

Explaining non-random pattern in species occurrence is the underlying theme of many ecological studies. However, rules governing spatial patterns in community assembly at a regional scale remain elusive. Patterns in assemblage composition are usually attributed to a combination of (i) dispersal constraints, which limit the spatial distribution of individual species, (Belyea & Lancaster 1999, Palmer *et al.* 1996) (ii) environmental filtering, which causes correlations between species due to their shared response to the physical environment (Keddy & Weiher 1999, Wilson 1999, Poff 1997), (iii) internal dynamics, where species interactions structure assemblage composition (Belyea & Lancaster 1999) and (iv) chance (Jeffries 1989, Talling 1951).

Temporary ponds form habitat islands for aquatic macroinvertebrates, within an inhospitable terrestrial landscape (Bilton *et al* 2001b). Organisms that inhabit them must, however, possess characteristics which enable them to survive drought and/or give them good dispersal ability (Williams 1987, Wiggins *et al.* 1980). Environmental and dispersal constraints are therefore likely to play a primary role in structuring temporary pond assemblages, as they determine the ‘ecological species pool’ of potential colonists (Belyea & Lancaster 1999). The importance of biotic interactions is also thought to diminish in ponds with a short hydroperiod (Schneider 1997, Schneider & Frost 1996).

Many authors have shown pond assemblage structure to be influenced by both physical and chemical environmental constraints. Physical factors such as pond size and permanence (Kiflawi *et* *al.* 2003, Rundle *et al.* 2002, Wellborn *et al.* 1996, Jeffries 1994), affect the number of species in the assemblage, the identity of species (due to life history constraints imposed by short pond hydroperiod) and the proportion of predators within the assemblage (Bilton *et al.* 2001a, Spencer *et al.* 1999). Between pond variation in water chemistry also limits assemblage membership (Moss 1998), as macroinvertebrates and plants vary in their tolerance to pH, nutrient loading, turbidity and metal concentrations (e.g. Bechara 1996, Williams 1996, Malmqvist & Eriksson 1995, Campbell & Stokes 1985, Barnes 1983). Ponds can vary extensively in their physical and chemical characteristics across small spatial scales, which results in large variation in assemblage composition (Kiflawi, *et al.* 2003, Spencer *et al.* 2002).

The influence of dispersal constraints (Bilton *et al.* 2001b, Belyea & Lancaster 1999) and chance (Jeffries 1989) mean ponds that lie close together in geographical space are likely to have more similar species composition than those more widely spread in the landscape. Non-uniform spatial distribution in assemblage composition might equally be a consequence of similarity in neighbouring pond physical and chemical environment. Most studies of assemblage composition intrinsically contain both spatial structure (Wilson 1999) and environmental pattern, so should be examined using spatially explicit analyses that can separate the two effects (Keitt *et al.* 2002, Legendre *et al.* 2002); however, only two studies have examined pond assemblage composition in such a spatial context (Spencer *et al.* 2002, Stevens & Jenkins 2000). Understanding the relative importance of pond environment parameters and spatial pattern in structuring temporary pond assemblage composition is, therefore, important both for understanding their assembly dynamics and for making informed conservation and management decisions.

This chapter investigates ponds of varying size and permanence within two regions of the UK in order to examine the relative influence of inter-pond distance and pond physicochemistry on macroinvertebrate and plant assemblage composition. It aims to: (i) put the plant and macroinvertebrate assemblages into a UK context and assess their conservation status; (ii) classify both plant and animal assemblages in order to rigorously determine assemblage types in the two regions; (iii) provide a clear definition of MTPs based on plant and animal assemblages; and (iv) assess whether similar environmental and spatial factors govern pond assemblage structure in different geographical regions.

2.3 Methods

2.3.1 Study regions

Preliminary surveys, with local land managers, of both the New Forest (south Hampshire) and Lizard Peninsula (south-west Cornwall) were used to identify areas with a high density of temporary water bodies. Ponds were then sampled from these localities with a strategy aimed at including a wide range of temporary and seasonally fluctuating water bodies (see Figs 2.1 & 2.2). Ponds sampled varied substantially in area, permanence, vegetation composition and their proximity to neighbouring ponds in the landscape (see section 2.6. for examples). Physicochemical, spatial proximity and macroinvertebrate and plant assemblage composition data were generated for 45 ponds on the Lizard Peninsula and 31 ponds in the New Forest. Ponds on the Lizard were above ultra-basic serpentine geology in heathland/unimproved grassland, whereas New Forest ponds were in heathland/grassland above eroded sedimentary beds with superficial deposits of sand and gravel (see section 1.6 for detail).

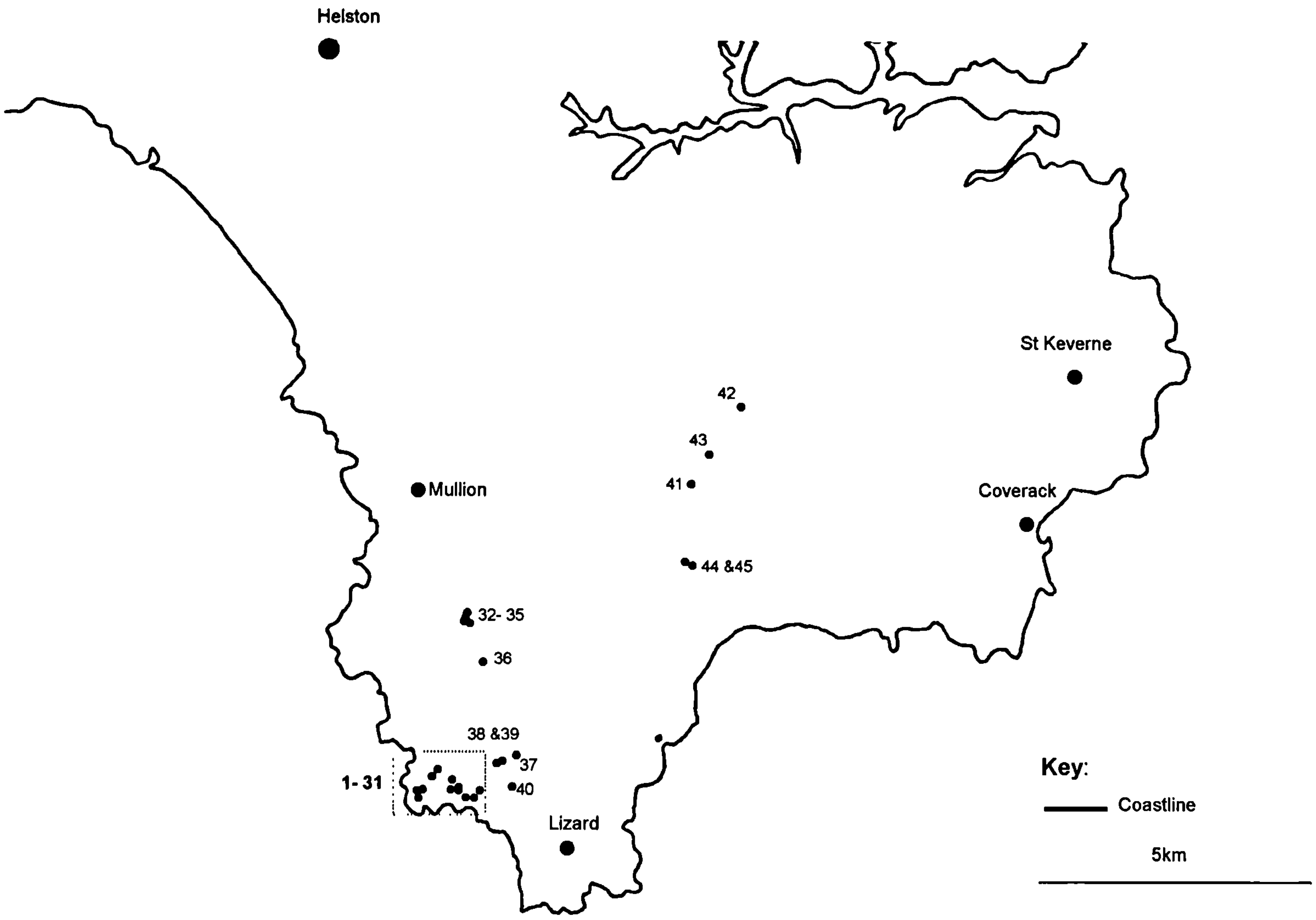


Figure 2.1: Overview map of Lizard pond locations (see Appendices 7.8 – 7.12 for detailed location maps)

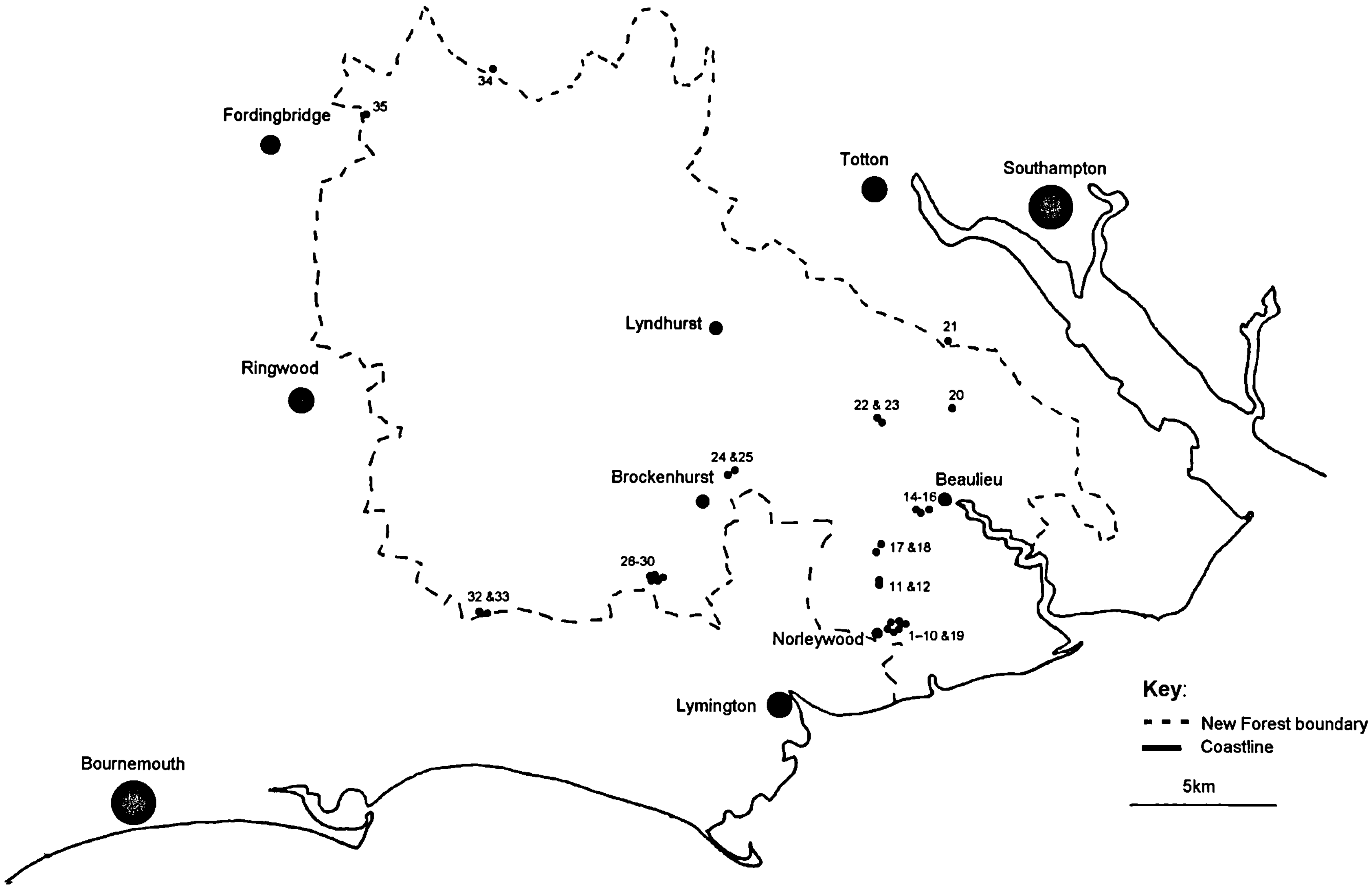


Figure 2.2: Overview map of New Forest pond locations (see Appendices 7.13 – 7.22 for detailed location maps)

2.3.2 Invertebrate assemblages

Invertebrates were sampled during February/March 2000, a time when temporary pond habitat was at maximum spatial extent and most macroinvertebrates occupy breeding sites. This ensured that most temporary waterbodies (including potential MTP habitat) were wet, allowing examination of their macroinvertebrate assemblage composition. Other studies have found that data from one season are often adequate to compare the relative assemblage composition of sites (e.g. Nicolet 2002) and Foggo *et al.* (in prep.) have shown Lizard pond assemblage richness and composition not to be significantly different between winter and summer samples. Ponds were sampled using a hand net (1mm mesh, dimensions 20 x 25cm), each sample comprised five standardised 1m sweeps which were stratified between beds of vegetation with different macrophyte species compositions. Two or three of such samples were taken from the largest sites according to their area Each 1m sweep involved approximately 10s of back and forth netting over the same area of habitat. This sampling strategy has been shown to give a reliable measure of the relative species richness of pond habitat, consistently sampling 60-80% of the macroinvertebrate species pool and allowing robust comparison of assemblage composition between sites (Foggo *et al.* 2003, Rundle *et al* 2002, Foggo *et al.* unpublished data). Sweeps were pooled (surface area for each sample 1.25m^2) and macroinvertebrates and detritus preserved in 70% ethanol. In the laboratory samples were sorted and Coleoptera, Hemiptera, Trichoptera, Mollusca, Ephemeroptera, Plecoptera, Zygoptera and Crustacea were identified to species, whereas early instar Anisoptera were identified to genus Chironomid larvae were sent to Dr Alan Bedford for identification to genus.

2.3.3 Plant assemblages

Macrophyte and semi-terrestrial vegetation species composition at sampling locations was examined in May/June of the same year; when most species were in flower and could be readily identified. Taxa present between the maximum winter flood level and 60cm deep were recorded from 1m^2 quadrats, the number of quadrats used being approximately proportional to the maximum surface area of the pond. The pond was also systematically surveyed for additional species that might have been missed from the quadrat samples. In very large ponds data recording was restricted to the region of the pond where macroinvertebrates had been sampled. Plant material from each quadrat and the survey was labelled, pressed and returned to the laboratory for identification. Most taxa were identified to species although Poaceae and *Rubus, Rumex, Pulicaria* and *Scilla* were identified to genus and *Callitriche* spp. were noted but not identified further. Charophytes were sent to Nick Stewart, the national referee, for identification

2.3.4 Pond environment and inter-pond distance

Before macroinvertebrates were sampled pH, temperature compensated conductivity and turbidity readings were taken on-site using a Solomat 520C probe. Five water depth measurements were also recorded from the area sampled for macroinvertebrates and the mean taken. Two water samples from each pond were collected in acid washed polypropylene bottles for analysis of metal cation and nutrient concentrations. Metal cation concentrations were analysed in the laboratory by atomic absorption spectroscopy. Cations measured included calcium, magnesium, aluminium, nickel, chromium, cobalt, iron, zinc and copper, which were chosen to represent the main differences between the underlying geology of the two regions. Water samples were also analysed for total organic nitrate (TON) and soluble reactive phosphorus (SRP) using a Dianex autoanalyser.

Accurate estimates of pond area were derived on the Lizard by using differential GPS (Trimble) to map the margin of each pond; in the New Forest area was estimated from either pacing pond perimeter or measurement from 1:10000 OS maps. dGPS mapping generated central point co-ordinates for each pond on the Lizard, which were then used to create an inter-pond distance matrix. The New Forest inter-pond distance matrix was created using six figure grid references which were accurate to 100m, which gave adequate resolution for examining spatial trends in this region, where ponds were relatively widely spaced (see section 2.3.9 below).

2.3.5 Other UK temporary pond data

Temporary pond plant and macroinvertebrate assemblages from the Lizard and New Forest regions were put into a UK context by comparison with similar presence absence species data collected from minimally impaired temporary ponds throughout England and Wales (data from Nicolet 2002, Ponds Conservation Trust: Policy and Research). The UK pond survey included plant data from 70 ponds and macroinvertebrate data from 65 ponds. Throughout this thesis Nicolet (2002) samples are referred to as 'UK pond' data. Forty eight of the UK temporary ponds were sampled during spring 1999 and 2000 with the remainder of the data being from the National Pond Survey (NPS; 1998) collected between 1990 and 1998 by the Ponds Conservation Trust. All of the UK ponds were located in semi-natural heathland, moorland, woodland or unimproved grassland habitat (Nicolet 2002).

UK, New Forest and Lizard data were firstly checked to ensure they covered the same taxonomic scope. Chironomids were not recorded for the UK sites so it was necessary to remove them from the Lizard and New Forest data sets, similarly flat worms, leeches and arachnids were removed from the UK pond data; in addition all recordings of *Sympetrum* species were amalgamated in the UK data. The taxonomic scope of the plant data was similarly standardised between the two studies. This process ensured that any observed difference between New Forest, Lizard and UK assemblages was not an artefact of differences in taxonomic resolution.

Macroinvertebrate sampling methods also differed between the two studies. The UK data (Nicolet 2002) was collected using a time limited method (3 minute sample), with sampling effort being distributed amongst different pond mesohabitats. However, this method has been shown to capture a similar proportion of species (>60%; Nicolet 2002, Pond Action 1994) as the standardised sweep method used in this study to sample New Forest and Lizard ponds (see section 2.3.2 above). By using presence absence data, rather than counts of relative abundance, and Bray-Curtis similarity for examining multivariate assemblage composition (see below), differences in assemblage composition resulting from discrepancies between the studies in sampling effort were minimised as far as possible. Nicolet's (2002) UK macroinvertebrate and plant data also included four New Forest ponds and one Lizard pond enabling multivariate analyses to be checked to see whether these ponds were similar in assemblage composition to the sites sampled as part of this study.

2.3.6 Context and conservation status of New Forest and Lizard ponds

In order to examine whether New Forest and Lizard pond plant and macroinvertebrate assemblages differed from other ponds in the UK, between pond variation in assemblage composition was examined using non-metric multidimensional scaling (MDS) analysis within the PRIMER v5 (Plymouth Routines In Multivariate Ecological Research) package (Clarke & Gorley 2001). Analyses were performed on Bray-Curtis similarity matrices (Bray & Curtis 1957) generated from the species presence absence data, ponds that were most similar in their assemblage composition being close together in ordination space. This method of ordination has two distinct advantages over other methods (i) Bray-Curtis similarity does not incorporate common absences in the calculation of between site similarity (Gamito & Raffaelli 1992) and (ii) the MDS ordination method makes few assumptions about the form of the data or the inter-relationship between samples and preserves between sample distance relationships in two dimensional space (Clarke & Warwick 2001). Inter-region (Lizard, New Forest and UK) differences in assemblage composition were assessed using one way ANalysis Of SIMilarities (ANOSIM). ANOSIM tests whether there is a statistically significant difference between two or more groups of samples based on the rank ordered similarity measures. If the groups are different in their assemblage composition between-group similarity might be expected to be smaller than the within-group similarity. The ANOSIM statistic, Global R, is therefore based on the difference in mean ranked similarity between versus within groups; statistical significance is then assessed by permutation of samples amongst groups in order to obtain the empirical distribution of R under the null-model (Clarke & Warwick 2001, Clark 1993). The method is regarded as a non-parametric, multivariate analogue of univariate analysis of variance (Somerfield *et al.* 2002).

Differences in the conservation value of macroinvertebrate and plant assemblages between UK, New Forest and Lizard ponds were assessed by giving each species a weighting depending on its rarity in the UK (Nicolet 2002, Foster 1996, Collinson *et al.* 1995; see appendices 7.1, 7.2, 7.3 & 7.4). Rarity scores were based on IUCN categories which take into account species distribution and/or perceived threat (Table 2.1). Species rarity scores were then summed for each pond to give a total rarity score and the mean taken to produce a species rarity index (SRI).

Score	IUCN category	Distribution/conservation status
1	Lower risk least concern (LRlc)	>100 hectads
2	Lower risk nationally scarce (LRnsA/B)	species occurring in 16-100 hectads
4	Lower risk nationally threatened (LRnt) or conservation dependent (LRcd) (Red data book status)	species occurring in <16 hectads or the focus of a continuing taxon-specific or habitat-specific conservation programme without which the species would become VU or EN
8	Vulnerable (VU) (Red data book status)	species facing a very high risk of extinction in the wild in the medium-term future
16	Endangered (EN) (Red data book status)	species facing a very high risk of extinction in the wild in the near future

Table 2.1: IUCN rarity categories and the species rarity scores applied for calculating Species Rarity Indices (SRI)

One way unbalanced analysis of variance was then used to examine differences between New Forest, Lizard and UK ponds in (i) taxon richness (ii) total rarity score (iii) SRI and (iv) total number of red data book (RDB) species (those species that scored a minimum of 4 points). As data were skewed and transformation failed to normalise the distributions H_0 was rejected at $\alpha = 0.01$ (Underwood 1997). Fisher's test for multiple comparisons was then used to establish which of the regions were significantly different at $\alpha = 0.01$.

2.3.7 Classification of New Forest and Lizard ponds

Differences between New Forest and Lizard pond assemblages were examined by classifying the plant and macroinvertebrate presence absence data separately using the Two Way INdicator SPecies ANalysis (TWINSPAN) module within PCord v4 (McCune & Mefford 1999). This hierarchical divisive method of classification is based upon correspondence analysis and has the advantage of listing the species most strongly associated with the subgroups created; these are commonly termed 'indicator' species. Tausch *et al.* (1995) and Oksanen and Minchin (1997) documented problems with the stability of the original TWINSPAN algorithm (Hill 1979a), reporting that the output changed with sample order. This 'bug' has been corrected in PCord v4 and Oksanen and Michnin's (1997) "super strict" convergence criteria have also been adopted. Three divisions split both the plant and macroinvertebrate assemblages into six sub-groups. Mann Whitney tests were then used to test for significant differences in median pond area, pH, conductivity, number of taxa and SRI at each division and the groups were then plotted in MDS ordination space, based on Bray-Curtis similarity.

2.3.8 Environmental factors

The effect of physicochemical parameters (area, pH, depth, conductivity and turbidity) on taxon richness of plants and macroinvertebrates in the two regions was first examined using Spearman rank correlation. The relationships between physicochemistry and assemblage composition, based on presence absence data, were then investigated with Canonical Correspondance Analysis (CCA; ter Braak & Šmilauer 1998) using CANOCO v4 (Microcomputer Power, NY) which has, like PCord, been corrected for instability (Oksanen & Minchin 1997) in the original algorithm (Hill 1979b).

All physicochemistry parameters were firstly log transformed and standardised. Many of the water cation and nutrient concentration measurements were found to be significantly correlated so these were subjected to Principle Components Analysis (PCA). First PCA axis score for each pond was then used as a summary measure of water cation and nutrient status in subsequent CCA analyses.

CCA variance inflation factors were checked for each physicochemical variable to ensure any correlations amongst the other variables were not affecting the analysis and 999 Monte Carlo simulations were used to test whether the relationship between physicochemistry and assemblage composition were significant ($\alpha < 0.05$). Species are given weightings within CCA, which indicate the strength of the correlation between their distribution patterns and physicochemistry. The positions of species with weightings over 15% in the CCA were also displayed on ordination axes in relation to the environmental variables.

2.3.9 The relative importance of spatial and environmental pattern

In order to examine the relative importance of physicochemical and spatial pattern on assemblage composition the relationships between inter-pond distance, assemblage and physicochemical similarity were examined using Mantel test statistics. Mantel tests are commonly used to correlate multivariate similarity/distance matrices (Dale *et al.* 2002, Mantel 1967). All analyses were based on the standardised Mantel statistic and performed using The R Package (Casgrain & Legendre 2001); significance was assessed by 999 random permutations of the first data matrix. Firstly euclidean *distance* matrices were created to describe inter-pond distance, physicochemistry (pH, turbidity, conductivity, depth and nutrient/cation PCA score) and pond area for each region. In addition Jaccard *similarity* matrices were produced for plant and macroinvertebrate data; Jaccard similarity is suitable for presence absence data and does not incorporate the common absence of species (Casgrain & Legendre 2001). Standardised Mantel's r was then calculated between all data matrix pairs for the New Forest and Lizard ponds separately. Ponds that were close together were expected to have more similar assemblage composition, which would result in a significant negative correlation between the inter-pond distance matrix and the assemblage similarity matrix. Partial Mantel tests were also used to unravel the relationships between assemblage similarity and pond area and inter-pond distance as the area and inter-pond distance matrices for Lizard ponds were found to be correlated.

Relationships between macroinvertebrate assemblage similarity and inter-pond distance were examined more closely by constructing a Mantel correlogram for each region, in order to highlight the spatial scale at which the relationship was significant. Correlograms were constructed by calculating Mantel's R statistic between all pond pairs that lie within a distance class or 'lag'. The Lizard correlogram was based on fourteen equal distance lag intervals in accordance with Yule's rule (Casgrain & Legendre 2001):

number of distance classes (lags) $= 2.5\sqrt[4]{n}$, where n is the number of distance pairs

number of distance pairs $= \frac{n-(n-1)}{2}$, where n is the number of sites

Inter-lag distance was, therefore, 675m as maximum inter-pond distance was 9.45km. Mantel's R was calculated between all pairs of ponds that were 0-675m apart for the first lag, 675-1350m apart for the second lag etc. The significance of Mantel's r at each lag was then corrected for multiple comparisons using the Bonferroni method. The relationship between inter-pond distance and assemblage similarity was confounded by a significant relationship between pond area and inter-pond distance so a partial Mantel correlogram was also constructed to remove the effect of pond area. Both Mantel and partial Mantel correlograms were plotted on the same axes to examine the change caused by the removal of the effect of pond area.

New Forest macroinvertebrate similarity was examined by constructing a similar Mantel correlogram (14 lags, inter-lag distance 1840m, max. inter-pond distance 25.76km) to ensure that a significant relationship with inter-pond distance was not remaining undetected by the overall Mantel test, which examines the average magnitude of the spatial response across the entire study area.

2.4 Results

2.4.1 Context and conservation status of New Forest and Lizard ponds

UK ponds supported 161 plant taxa whereas 87 were found in New Forest ponds and Lizard ponds supported 67. Plant assemblages formed three groups in MDS space although New Forest ponds were less variable in assemblage composition than Lizard or UK sites, being more tightly clustered (Fig. 2.3a). Macroinvertebrate richness followed a similar pattern, 229 taxa were recorded across the UK data set whereas 107 and 91 taxa were recorded respectively in New Forest and Lizard ponds (figures exclude chironomids, flatworms and leeches). Macroinvertebrate assemblages also formed three groups on the MDS plot (Fig. 2.3b). The three data sets were shown by ANOSIM to have small (low R^2) but significant overall differences in both plant (Global R = 0.252, $p< 0.001$; all pairwise comparisons $p <0.001$) and macroinvertebrate assemblage composition (Global R = 0.299, $p<0.001$; all pairwise comparisons $p <0.001$).

New Forest and Lizard assemblages included within the UK pond data set (Nicolet 2002) were shown to be similar to the New Forest and Lizard macroinvertebrate and plant data gathered for this study, being close together in MDS space (dotted circles in Fig. 2.3a and b). Some UK plant assemblages were more closely affiliated with New Forest and Lizard sites, these were in Radnorshire (Llandeilo Hill), Caernarvon (Sychnant Pass), Westmorland (Lad's Head Plantation), Cheviotland (Ross Links) and South Lancashire (Ainsdale). Two New Forest sites had plant assemblages that were more similar to Lizard sites (NF12 Crockford Bottom & NF34 Hope Cottage), whereas NF1 and NF2 (both near Norleywood) were more similar to UK ponds (Fig. 2.3a). A small subset of the UK macroinvertebrate assemblages were also shown to be more similar to New Forest and Lizard ponds than other UK sites. These ponds were in Radnorshire (Llandeilo Hill, Llandeilo Common & Whimble), Caernarvon (Sychnant Pass) Westmorland (Stickfell & Speel Bank), Brecknockshire (Brechfa Common), South Devon (Whitchurch Down) and Leicestershire (Beacon Hill).

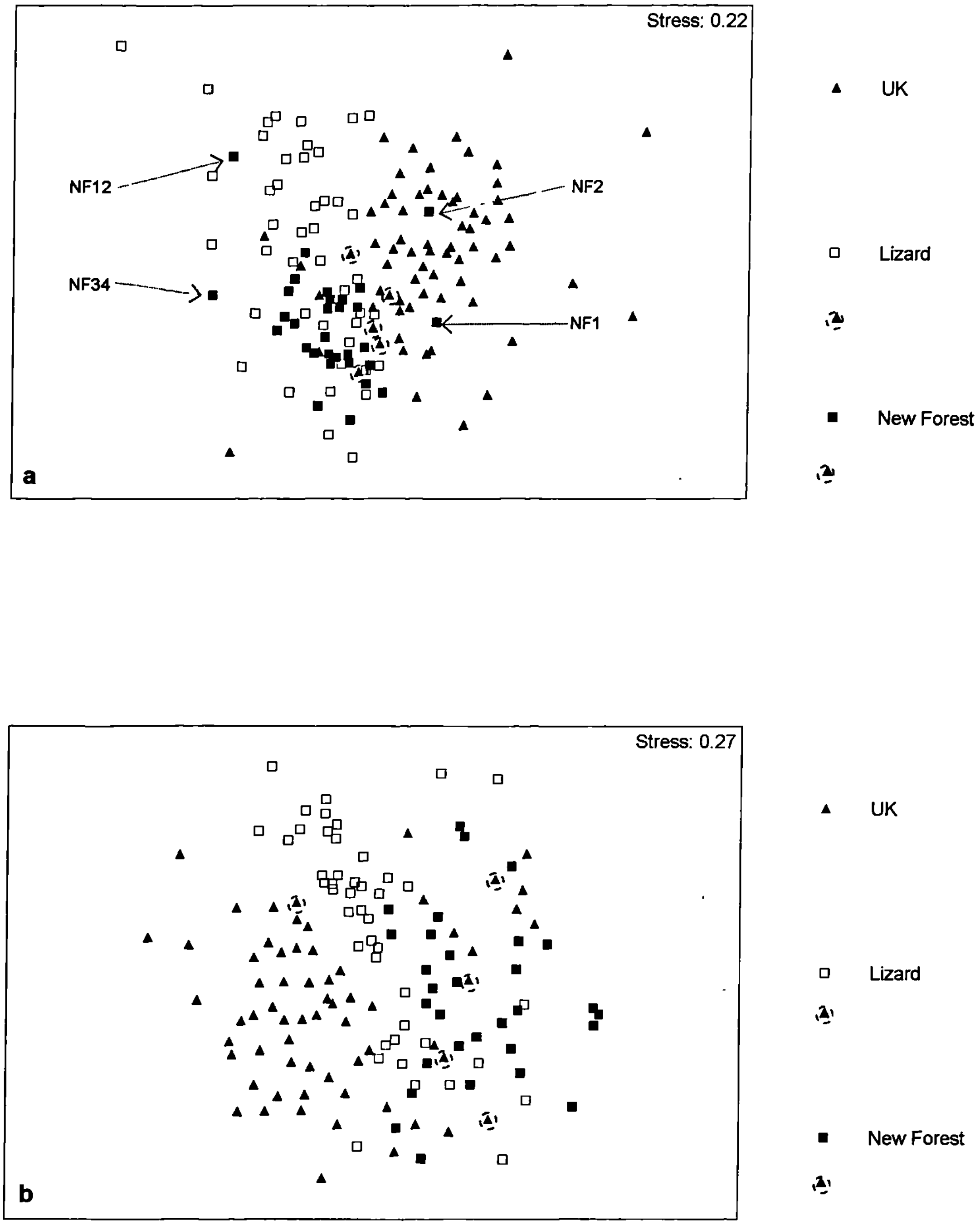


Figure 2.3: MDS plots of assemblages from UK, New Forest and Lizard ponds a) plants and b) macroinvertebrates. Dotted circles indicate New Forest (blue) and Lizard (red) ponds that form part of the UK data set. NF12 & NF34 plant assemblages were more similar to Lizard sites, whereas NF1 and NF2 were more similar to UK ponds.

UK ponds had greater total rarity scores than Lizard ponds ($F_{2,143}$ = 5.02, p <0.01; Fig. 2.4b). Despite this when SRI was examined Lizard ponds were shown to have significantly greater scores than UK and New Forest ponds ($F_{2,143}$ = 24.39, p <0.001; Fig. 2.4c). Macroinvertebrate taxon richness was significantly greater in the UK ponds ($F_{2,138}$ = 14.69, p <0.001; Fig. 2.4d), however there were no significant differences in total rarity score amongst the regions (Fig. 2.4e) and, when SRI was considered, New Forest ponds had significantly greater scores than UK ponds ($F_{2,138}$ = 8.38, p <0.001; Fig. 2.4f). The number of Red Data Book (RDB) plant and macroinvertebrate taxa was similar in New Forest (mean 1.04) and Lizard (mean 1.2) ponds whereas UK ponds on average supported significantly fewer RDB species (mean 0.4; $F_{2,137}$ = 10.09, p <0.001; Fig. 2.4g).

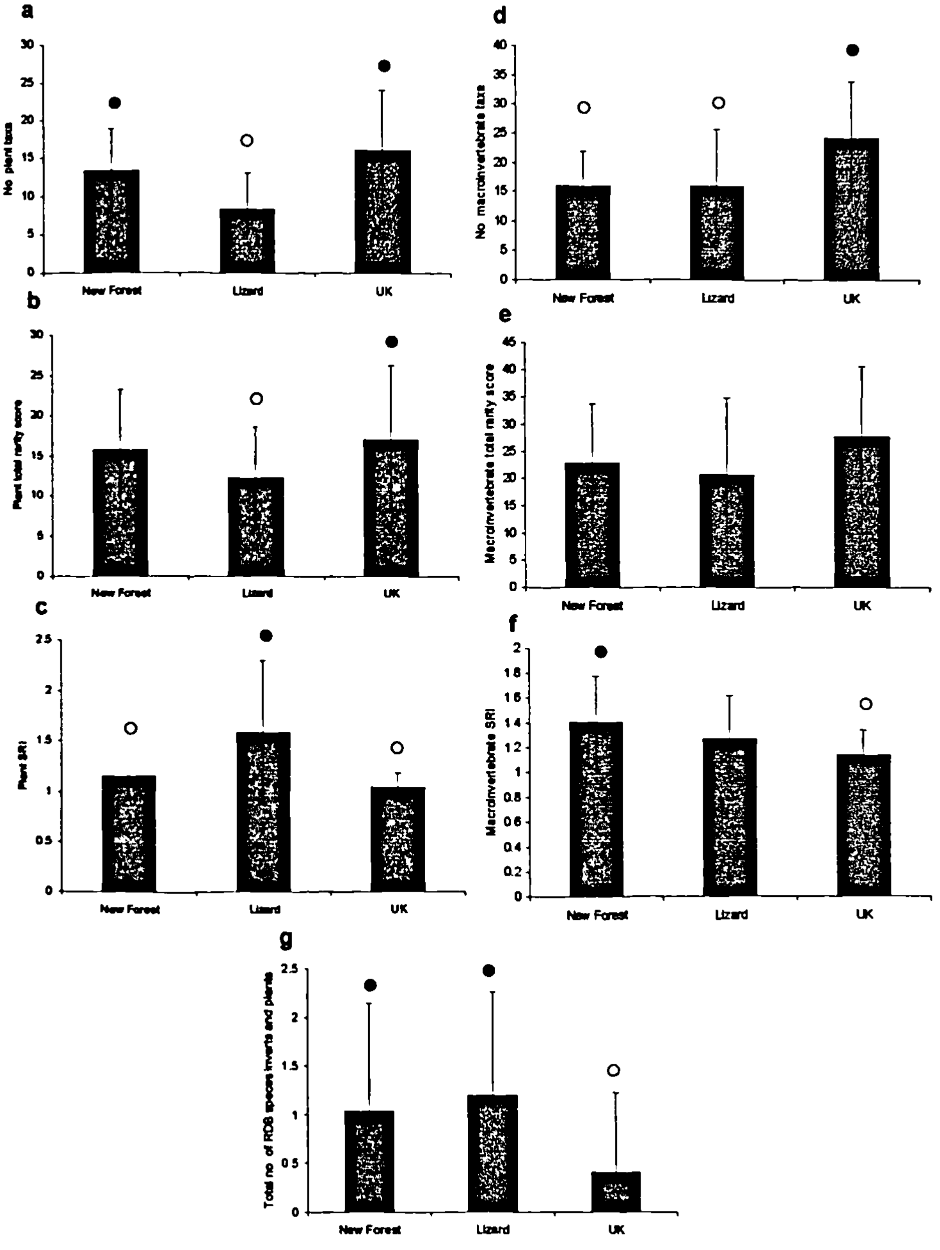


Figure 2.4: Comparison of taxon richness and rarity in UK, New Forest and Lizard ponds, different symbols indicate significant difference between means: mean number of taxa - a) plants and d) macroinvertebrates; total rarity score - b) plants and e) macroinvertebrates; species rarity index (SRI) - c) plants and f) macroinvertebrates; and mean number of RDB species - g) plants and macroinvertebrates combined.

2.4.2 Classification of New Forest and Lizard ponds

2.4.2.1 Vegetation

Six types of wetland plant assemblage were generated by the TWINSPAN classification at the third level of division (Fig. 2.5); further divisions made group size small (<3 sites) and ill defined, as the additional groups had no indicator species. The groups represent a gradient in pond size and permanence, groups 1-3 were significantly larger than groups 4-6 and had lower conductivity (Tables 2.2 & 2.3). Indicator species for the first division reflect the difference in size and permanence of the ponds, group 1-3 indicators were aquatic floating and emergent species *Juncus bulbosus, Hydrocotyle vulgaris* and *Eleogiton fluitans* which are typical of UK wetlands (Stace 1997), whereas indicators for groups 4-6 include *Ranunculus tripartitus, Agrostis* and *Juncus* species that are typical of wet mud (Stace 1997) and terrestrial taxa such as *Potentilla anserina* and *Ranunculus repens.* Plant assemblage composition therefore spanned a continuum from well developed aquatic vegetation in the large seasonally fluctuating waterbodies of group 1 through to depauperate, semi-terrestrial damp grassland communities in small ephemeral ponds (groups 5 & 6).

Indicator species for groups 1 and 2 included *Potamogeton polygonifolius* and *Carex viridula*, which are typical of acid soils (Stace 1997). Group 1 ponds had higher mean conductivity (Table 2.3) and were dominated by submerged, floating and emergent aquatic plants. The indicator species for the group was *Eleocharis palustris* a widespread wetland species (Stace 1997). Occasional taxa included the Charophyte species *Chara fragifera,* usually associated with base rich ponds and lakes as well as *Pilularia globulifera* and *Littorella uniflora* which are more usually associated with acidic waters (Stace 1997). In contrast, ponds in group 2 were of lower conductivity, but had greater species richness than group 1 (Tables 2.2 & 2.3). They were again dominated by aquatic taxa, but indicator species for the group were the acidophilic emergents *Eleocharis multicaulis, Hypericum elodes,* and *Anagallis tenella* (Stace 1997). In addition *Molinia caerulea* and *Ludwigia palustris* were common and *Eriophorum augustifolium*, *P. globulifera* and *L. uniflora,* also of acidic soils (Stace 1997), were occasional.

Plant assemblages in group 3 were characterised by open ground and wet mud species, *Lythrum portula, Apium inundatum* and *Glyceria fluitans* (Stace 1997). Ponds in this group were on average smaller than those in Groups 1 and 2 (Table 2.2) but submerged and emergent taxa still had high constancy. *Illecebrum verticillatum*, a species of damp sandy open ground (Stace 1997) was occasional along with *P. globulifera, L. uniflora* and, *L. palustris.*

Ponds in groups 4, 5 and 6 were smaller and more temporary, being found along wet track-ways and hedgerows on the Lizard Peninsula. The sites had higher conductivity and were generally depauperate being dominated by damp grassland species, however SRI was high in groups 4 and 5 due to the frequent occurrence of *Ranunculus tripartitus* (Tables 2.2 & 2.3). Indicator taxa for group 4 included *Ranunculus tripartitus, Agrostis* spp and *Juncus articulatus* which are typical of wet mud (Stace 1997). The assemblages were dominated by grasses, rushes and *Ranunculus flammula,* a species also commonly found in groups 1-3. The smallest sites in groups 5 and 6 were characterised by the presence of terrestrial *Potentilla anserina* and *Ranunculus repens* and were dominated by grasses. Indicator species for sites in group 5 included *Juncus bufonius* and *Chamaemelum nobile* typical of grazed grassland, *R. tripartitus* was also of high constancy. Group 6 ponds were species-poor and had no specific indicator taxa, as the assemblages were composed of a number of common wet grassland species not found in other groups; they also had lower SRI due to the absence of *R. tripartitus.*

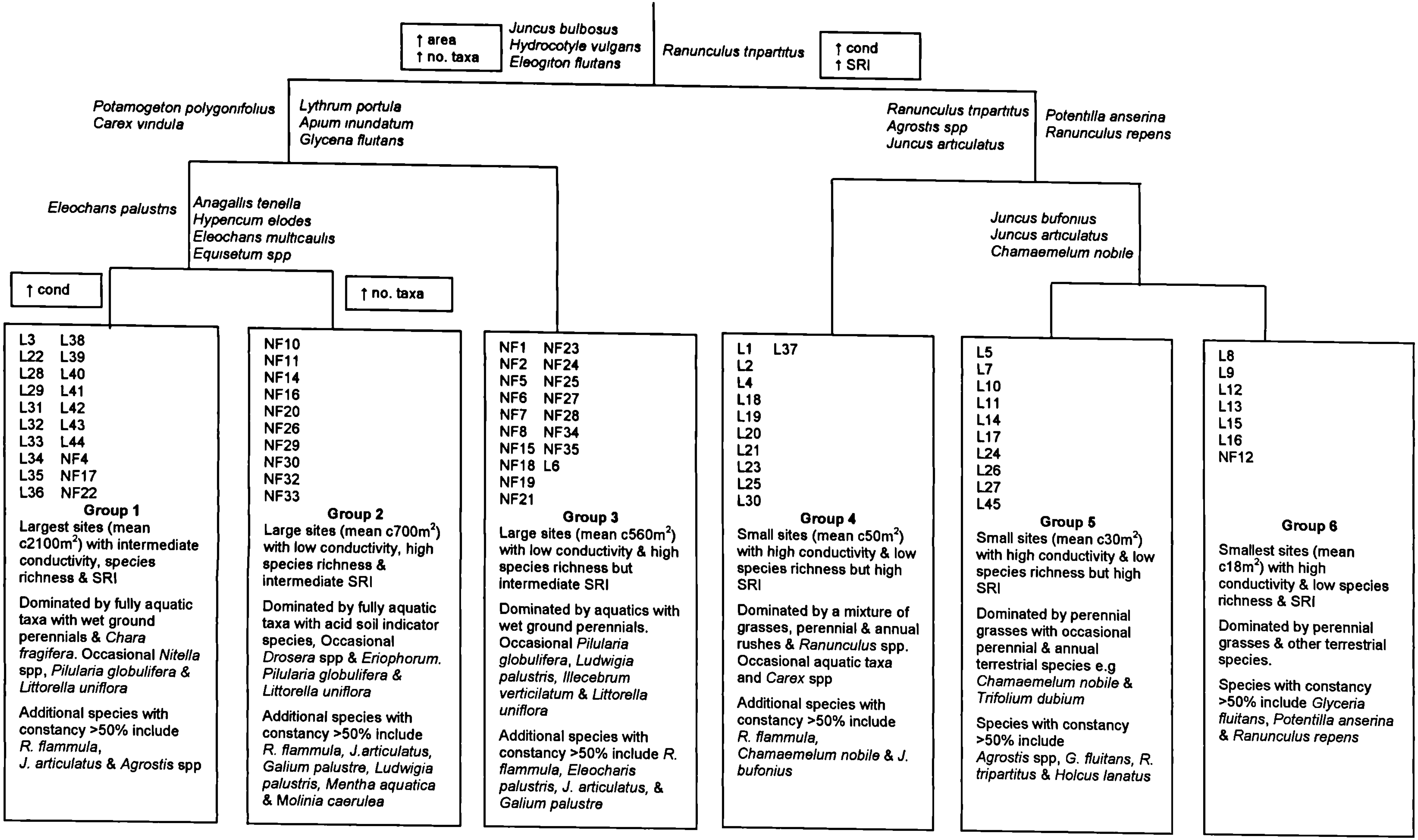
Plants	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Mean area m^2	2139.1 ±855.	706.6 ±524.2	561.0 ±252.2	54.2 ±18.2	33.3 ±14.1	18.0 ±7.5
Mean pH	6.41 ±0.17	6.06 ±0.40	6.21 ±0.24	5.78 ±0.22	6.13 ±0.25	6.05 ±0.21
Mean conductivity µS	410.6 ±52.3	235.0 ±42.9	268.0 ±42.2	676.3 ±74.7	756.1 ±68.7	733.6 ±99.8
Mean no. taxa	10.7 ±1.09	16.1 ±1.27	13.2 ±1.2	7.9 ±1.13	5.7 ±1.21	5.0 ±1.09
Mean SRI	1.15 ±0.04	1.16 ±0.07	1.22 ±0.06	2.02 ±0.18	2.12 ±0.29	1 ±0.00

Table 2.2: Mean (± s.e.m.) area, conductivity, pH, taxon richness and Species Rarity Index for each of the plant assemblage TWINSPAN end groups

Plant TWINSPAN end groups	area	conductivity	pH	No taxa	SRI
Division 1					
groups 1,2 & 3 vs 4,5 & 6	W = 2212.0, p < 0.001	W = 1311.0, p <0.001	W = 2010.0, ns	W = 2914.5, p < 0.001	W =1617.5, p < 0.001
Division 2					
groups 1 & 2 vs 3	W = 812.0, ns	W = 812.0, ns	W = 770.0, ns	W = 711.0, ns	W = 689.0, ns
group 4 vs 5 & 6	W = 183.0, ns	W = 141.0, ns	W = 133.0, ns	W = 195.5, ns	W = 205.0, ns
Division 3					
group 1 vs 2	W = 127.0, ns	W = 146.0, p <0.05	W = 131.0, ns	W = 213.0, p <0.05	W = 153.0, ns
group 5 vs 6	W = 95.0, ns	W = 332.0, ns	W = 96.0, ns	W = 93.0, ns	no test

Table 2.3: Mann Whitney tests of differences in median pond physicochemistry for each of the three plant assemblage TWINSPAN divisions

Figure 2.5: TWINSPAN dendrogram for Lizard and New Forest plant assemblages, indicator species and end groups shown with significant differences in physicochemistry, species richness and SRI indicated in boxes at each division



L3 L38
L22 L39
L28 L40
L29 L41
L31 L42
L32 L43
L33 L44
L34 NF4
L35 NF17
L36 NF22

Group 1

Largest sites (mean c2100m^2) with intermediate conductivity, species richness & SRI

Dominated by fully aquatic taxa with wet ground perennials & *Chara fragifera*. Occasional *Nitella* spp, *Pilularia globulifera* & *Littorella uniflora*

Additional species with constancy >50% include *R. flammula*, *J. articulatus* & *Agrostis* spp

NF10
NF11
NF14
NF16
NF20
NF26
NF29
NF30
NF32
NF33

Group 2

Large sites (mean c700m^2) with low conductivity, high species richness & intermediate SRI

Dominated by fully aquatic taxa with acid soil indicator species, Occasional *Drosera* spp & *Eriophorum. Pilularia globulifera & Littorella uniflora*

Additional species with constancy >50% include *R. flammula, J.articulatus, Galium palustre, Ludwigia palustris, Mentha aquatica & Molinia caerulea*

NF1 NF23
NF2 NF24
NF5 NF25
NF6 NF27
NF7 NF28
NF8 NF34
NF15 NF35
NF18 L6
NF19
NF21

Group 3

Large sites (mean c560m^2) with low conductivity & high species richness but intermediate SRI

Dominated by aquatics with wet ground perennials. Occasional *Pilularia globulifera, Ludwigia palustris, Illecebrum verticilatum & Littorella uniflora*

Additional species with constancy >50% include *R. flammula, Eleocharis palustris, J. articulatus, & Galium palustre*

L1 L37
L2
L4
L18
L19
L20
L21
L23
L25
L30

Group 4

Small sites (mean c50m^2) with high conductivity & low species richness but high SRI

Dominated by a mixture of grasses, perennial & annual rushes & *Ranunculus* spp. Occasional aquatic taxa and *Carex* spp

Additional species with constancy >50% include *R. flammula, Chamaemelum nobile & J. bufonius*

L5
L7
L10
L11
L14
L17
L24
L26
L27
L45

Group 5

Small sites (mean c30m^2) with high conductivity & low species richness but high SRI

Dominated by perennial grasses with occasional perennial & annual terrestrial species e.g *Chamaemelum nobile & Trifolium dubium*

Species with constancy >50% include *Agrostis* spp, *G. fluitans, R. tripartitus & Holcus lanatus*

L8
L9
L12
L13
L15
L16
NF12

Group 6

Smallest sites (mean c18m^2) with high conductivity & low species richness & SRI

Dominated by perennial grasses & other terrestrial species.

Species with constancy >50% include *Glyceria fluitans, Potentilla anserina & Ranunculus repens*

2.4.2.2 Macroinvertebrates

Six groups were also recognised from the TWINSPAN classification of invertebrate assemblages after three divisions (Fig. 2.6); further division again resulted in small ill defined groups. The groups represent a gradient in pond size and permanence in a similar way to the plant assemblages. Differences in pond area, conductivity and pH were, however, more marked between the groups than they were for the vegetation classification (Table 2.5). Ponds in groups 1-3 were larger and had greater pH and lower conductivity than groups 4-6 (Tables 2.4 & 2.5). Indicator species reflected differences in pond permanence, the group 1-3 indicator, *Sympetrum* spp, require prolonged hydroperiod for larval survival, whereas indicators for groups 4-6, *Helophorus* spp and *Ilybius montanus*, utilise temporary water for reproduction (Eyre *et al.* 1992, Carr & Nilsson 1988). The macroinvertebrate assemblage continuum mirrors that seen for the plant assemblages, varying from semi-permanent, species rich ponds in group 1 which support a range of taxonomic groups with different life history strategies through to small highly ephemeral ponds in group 6 which have a depauperate fauna comprised of species that can cope with a short hydroperiod

Ponds in group 1 were circum-neutral and the largest and most species rich, with all insect orders and molluscs being well represented. Indicator species were typical of sites which dry infrequently (*Lymnaea peregra* (Mollusca) and *Limnephilus lunatus* (Trichoptera)) and the RDB coleopteran species *Dryops auriculatus* and *Haliplus variegatus,* typical of seasonally fluctuating, permanent water bodies, were occasional. Group 2 ponds were smaller and Odonata species were less constant although other groups, particularly molluscs, were well represented. *Pisidium* spp and *Potamopyrgus antipodarum* were indicator taxa and *Lymnaea glabra* (RDB) was occasional. In contrast, macroinvertebrate assemblages in group 3 had fewer mollusc species; perhaps due to ponds having lower pH. The calcifuge *L. glabra* still occurred in a subset of these ponds, however. *Helochares punctatus*, a beetle typical of acidic peat and *Sphagnum* ponds (Friday 1988), was an indicator species for this group and *Dryops striatellus* (RDB) had high constancy.

Ponds in groups 4-6 were mainly formed on flooded trackways and in hedgerows in the Kynance area of the Lizard Peninsula (27/33 sites). However, three large Kynance sites (L3, L22 and L25) were also incorporated in group 4. More ephemeral sites in groups 4-6 were dominated by

Coleoptera, Trichoptera and Chironomidae (Diptera) and occasional species across the groups included the *Dryops striatellus* and *Graptodytes flavipes* (RDB).

Ilybius montanus and *Hydrobius fuscipes* were indicator beetle species for groups 4 and 5, and are typical of ephemeral acidic and detritus rich ponds respectively (Friday 1988). Group four ponds had larger mean area and *Asellus aquaticus* (Isopoda) and *Pisidium* spp as indicators and *Anisus leucostoma* and *Lymnaea truncatula* (molluscs) at high constancy. In comparison molluscs were less common across group 5 sites, which were rather ill-defined as they did not have specific indicator species and tended to contain a depauperate subset of the species found in group 4. Group 6 ponds were small and had lower conductivity than groups 4 and 5 (Table 4). They tended to contain the chironomids *Macropelopia* spp and *Microspectra* spp and had high constancy of *Limnephilus vittatus*, a caddis fly commonly found in temporary waters (Wallace *et al.* 2003). The classifications clearly show that there is a discrepancy in the frequency of both vegetation and macroinvertebrate assemblage types between the two regions (Figs 2.5 & 2.6) as groups 1, 4, 5 and 6 are dominated by Lizard ponds whereas groups 2 and 3 comprise predominantly New Forest sites. Overall both macroinvertebrate and plant TWINSPAN groups generally represented assemblage composition faithfully as MDS showed that the groups plotted separately in multidimensional space (Fig. 2.7).

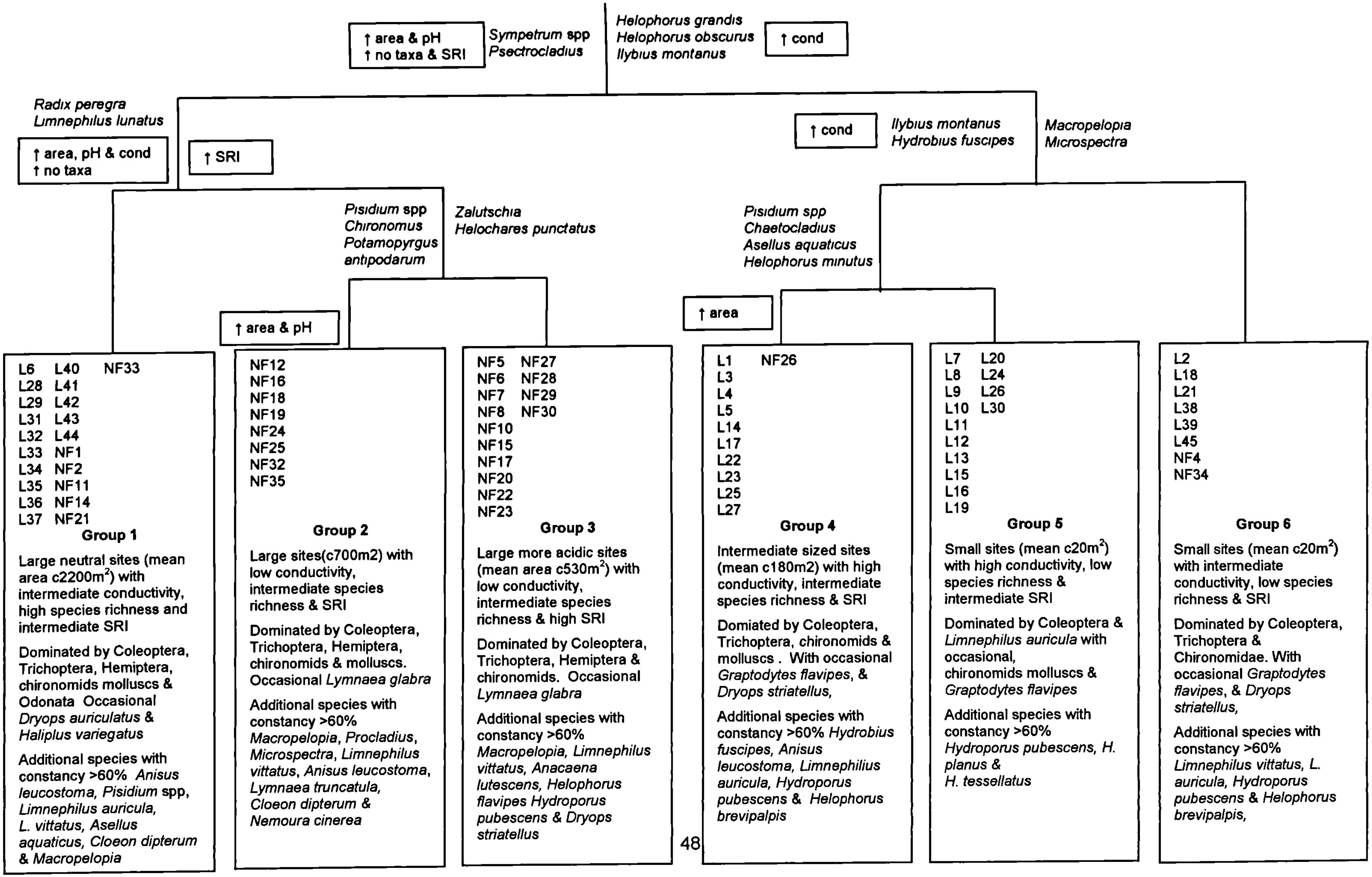
Macroinvertebrates	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Mean area m^2	2170.8 ±819.4	690.3 ±356 5	531.5 ±390.0	178 5 ±84.3	21.3 ±8.9	23.6 ±10.8
Mean pH	6.72 ±0.06	6.40 ±0.41	5.70±0.35	5.79 ±0 24	5.87 ±0.17	6.22 ±0.15
Mean conductivity µS	380.0 ±34.5	297.7 ±81.7	193.3 ±27.7	739.3 ±84.9	773.5 ±60.3	411.3 ±84.4
Mean no. taxa	22.7 ±2.15	16.5 ±2.35	15.4 ±1.45	15.2 ±1.78	10.1 ±0.80	10.6 ±2.36
Mean SRI	1.25 ±0.07	1.28 ±0.10	1.61 ±0.10	1.26 ±0.08	1.22 ±0.10	1.13 ±0.15

Table 2.4: Mean (± s.e.m.) area, conductivity, pH, taxon richness and Species Rarity Index for each of the macroinvertebrate assemblage TWINSPAN end groups

Macroinvertebrate TWINSPAN end groups	area	conductivity	pH	No taxa	SRI
Division 1					
groups 1,2 & 3 vs 4,5 & 6	W = 2039.5, p < 0.001	W = 1154.0, p < 0.001	W = 1914.0, p < 0.01	W = 2027.0, p < 0.001	W = 1841.5, p < 0.05
Division 2					
groups 1 vs 2 & 3	W = 363.0, p < 0.01	W = 342.0, p < 0.001	W = 390.5, p < 0.05	W = 386.0, p <0.05	W = 587.0 , p < 0.05
group 4 & 5 vs 6	W = 124.0, ns	W = 65.0, p < 0.01	W = 172.0, ns	W = 120.5, ns	W = 145.5, ns
Division 3					
group 2 vs 3	W = 125.0, p < 0.05	W = 102.0, ns	W = 105.0, ns	W = 97.5, ns	W = 63.0, ns
group 4 vs 5	W = 184.0, p < 0.05	W = 139.0, ns	W = 137.0, ns	W = 188.0, ns	W = 157.0, ns

Table 2.5: Mann Whitney tests of differences in median pond physicochemistry for each of the three macroinvertebrate assemblage TWINSPAN divisions.

Figure 2.6: TWINSPAN dendrogram for Lizard and New Forest macroinvertebrate assemblages, indicator species and end groups shown with significant differences in physicochemistry, species richness and SRI indicated in boxes at each division



L6 L28 L29 L31 L32 L33 L34 L35 L36 L37 L40 L41 L42 L43 L44 NF1 NF2 NF11 NF14 NF21 NF33

Group 1

Large neutral sites (mean area c2200m^2) with intermediate conductivity, high species richness and intermediate SRI

Dominated by Coleoptera, Trichoptera, Hemiptera, chironomids molluscs & Odonata Occasional *Dryops auriculatus* & *Haliplus variegatus*

Additional species with constancy >60% *Anisus leucostoma*, *Pisidium* spp, *Limnephilus auricula*, *L. vittatus*, *Asellus aquaticus*, *Cloeon dipterum* & *Macropelopia*

NF12 NF16 NF18 NF19 NF24 NF25 NF32 NF35

Group 2

Large sites(c700m2) with low conductivity, intermediate species richness & SRI

Dominated by Coleoptera, Trichoptera, Hemiptera, chironomids & molluscs. Occasional *Lymnaea glabra*

Additional species with constancy >60% *Macropelopia*, *Procladius*, *Microspectra*, *Limnephilus vittatus*, *Anisus leucostoma*, *Lymnaea truncatula*, *Cloeon dipterum* & *Nemoura cinerea*

NF5 NF6 NF7 NF8 NF10 NF15 NF17 NF20 NF22 NF23 NF27 NF28 NF29 NF30

Group 3

Large more acidic sites (mean area c530m^2) with low conductivity, intermediate species richness & high SRI

Dominated by Coleoptera, Trichoptera, Hemiptera & chironomids. Occasional *Lymnaea glabra*

Additional species with constancy >60% *Macropelopia*, *Limnephilus vittatus*, *Anacaena lutescens*, *Helophorus flavipes* *Hydroporus pubescens* & *Dryops striatellus*

L1 L3 L4 L5 L14 L17 L22 L23 L25 L27 NF26

Group 4

Intermediate sized sites (mean c180m2) with high conductivity, intermediate species richness & SRI

Domiated by Coleoptera, Trichoptera, chironomids & molluscs . With occasional *Graptodytes flavipes*, & *Dryops striatellus*,

Additional species with constancy >60% *Hydrobius fuscipes*, *Anisus leucostoma*, *Limnephilius auricula*, *Hydroporus pubescens* & *Helophorus brevipalpis*

L7 L8 L9 L10 L11 L12 L13 L15 L16 L19 L20 L24 L26 L30

Group 5

Small sites (mean c20m^2) with high conductivity, low species richness & intermediate SRI

Dominated by Coleoptera & *Limnephilus auricula* with occasional, chironomids molluscs & *Graptodytes flavipes*

Additional species with constancy >60% *Hydroporus pubescens*, *H. planus* & *H. tessellatus*

L2 L18 L21 L38 L39 L45 NF4 NF34

Group 6

Small sites (mean c20m^2) with intermediate conductivity, low species richness & SRI

Dominated by Coleoptera, Trichoptera & Chironomidae. With occasional *Graptodytes flavipes*, & *Dryops striatellus*,

Additional species with constancy >60% *Limnephilus vittatus*, *L. auricula*, *Hydroporus pubescens* & *Helophorus brevipalpis*,

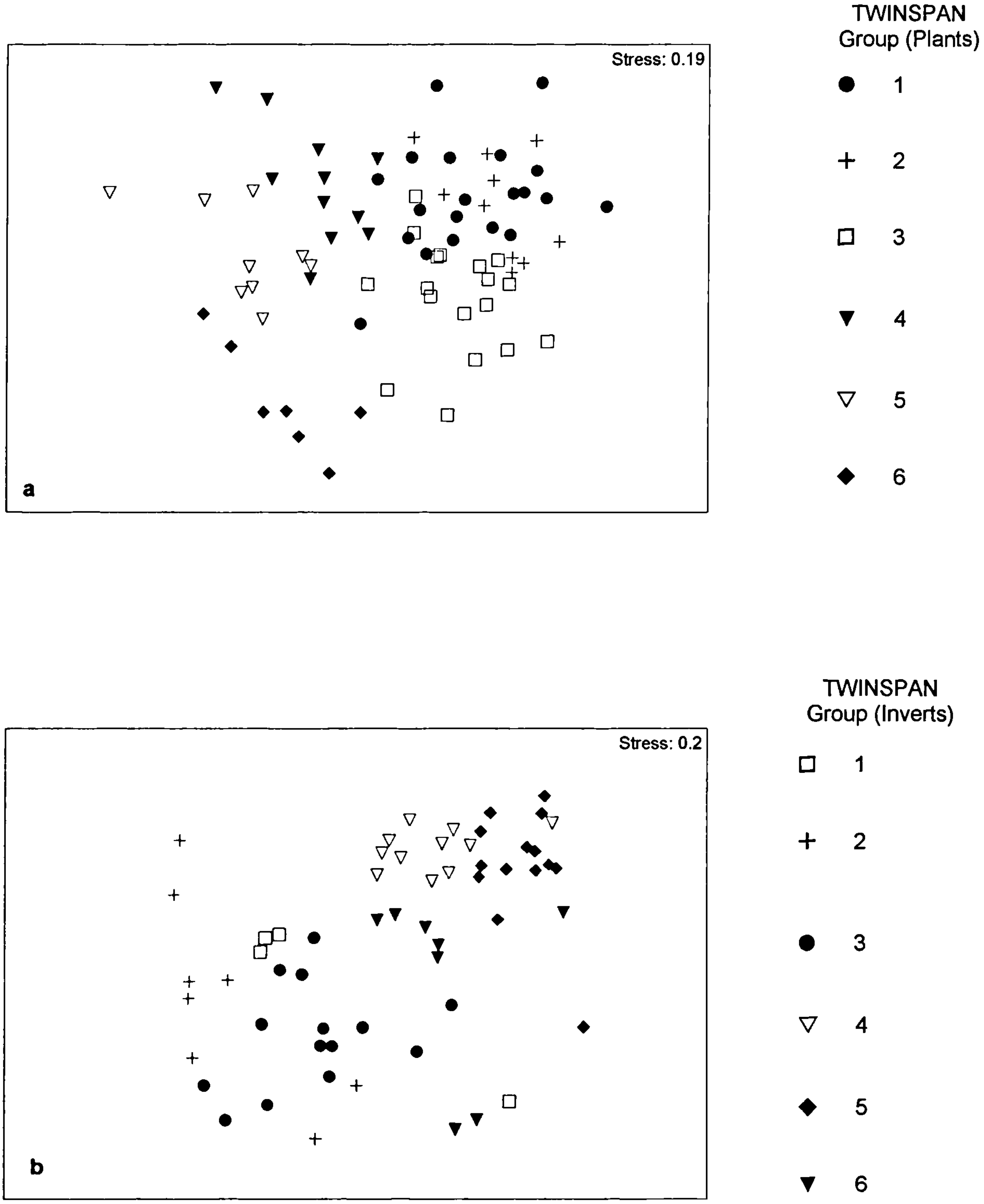


Figure 2.7: MDS plots of New Forest and Lizard assemblages with TWINSPAN end groups indicated a) macroinvertebrates and b) plants, based on Bray-Curtis similarity.

2.4.3 Environmental factors

Lizard macroinvertebrate taxon richness was significantly correlated with pond area and pH (Table 2.6). Richness also correlated with depth and conductivity variables, but these were themselves significantly correlated with pond area. Taxon richness of macroinvertebrates in the New Forest was not significantly related to any of the measured physicochemical variables (Table 2.6). Plant taxon richness was related to pond area and its correlate conductivity in Lizard ponds and pH and turbidity (which were also significantly correlated) in New Forest ponds.

	Lizard macroinvertebrate taxon richness	New Forest macroinvertebrate taxon richness	Lizard plant taxon richness	New Forest plant taxon richness
Area	$r_s = 0.673$ $p < 0.001$	$r_s = -0.008$ ns	$r_s = 0.698$ $p < 0.001$	$r_s = 0.077$ ns
pH	$r_s = 0.338$ $p < 0.05$	$r_s = 0.315$ ns	$r_s = 0.271$ ns	$r_s = 0.472$ $p < 0.01$
Conductivity	$r_s = -0.6$ $p < 0.001$	$r_s = 0.219$ ns	$r_s = -0.533$ $p < 0.001$	$r_s = 0.027$ ns
Turbidity	$r_s = 0.227$ ns	$r_s = 0.227$ ns	$r_s = 0.217$ ns	$r_s = -0.439$ $p < 0.05$
Depth	$r_s = 0.385$ $p < 0.01$	$r_s = 0.348$ ns	$r_s = 0.178$ ns	$r_s = 0.144$ ns
PCA cation and nutrient conc	$r_s = -0.23$ ns	$r_s = -0.12$ ns	$r_s = -0.212$ ns	$r_s = -0.288$ ns
Plant taxon richness	$r_s = 0.503$ $p < 0.001$	$r_s = 0.399$ $p < 0.05$		

Table 2.6: Spearman rank correlations between macroinvertebrate and plant species richness and pond physicochemistry parameters

Pond assemblage composition and physicochemistry were significantly correlated along the first CCA axis for both plants and macroinvertebrates on the Lizard Peninsula (Table 2.8). Physicochemical variables that best correlated with differences in assemblage composition were the same, (area and conductivity) for both plants and invertebrates (Table 2.8, Figs. 2.8a & 2.10a). The summary PCA axis describing water nutrient and cation concentrations (Table 2.7) had little influence on Lizard assemblage composition (Figs 2.8a & 2.10a). Overall the first two CCA axes explained a high proportion of the plant assemblage- physicochemistry and macroinvertebrate assemblage – physicochemistry relationships (60.7% and 64.1% respectively) and separated the assemblages of larger, deeper ponds in TWINSPAN end group 1 from those with lower pH and higher conductivity in groups 4, 5 and 6.

Variable	PCA axis 1 eigenvalue Lizard (36.9%)	PCA axis 1 eigenvalue New Forest (52.3%)
Total organic nitrate	0.67	0.04
Soluble reactive phosphorus	0.03	0.26
Calcium	0.07	0
Magnesium	0.01	0
Aluminium	0.07	0
Nickel	0.03	0.55
Chromium	0	0.57
Cobalt	0	0.55
Iron	0.19	0.07
Zinc	0.69	0.09
Copper	0.17	0.04

Table 2.7: Eigenvalues for Principle Component Analysis (PCA) of water cation and nutrient concentration parameters for New Forest and Lizard ponds.

When all four CCA axes were considered the New Forest macroinvertebrate assemblage-physicochemistry relationship was also significant (Table 2.8). Axes one and two explained 44.1% of the species-physicochemistry variation, whereas axes one two and three explained 61.3% of the relationship. Area and pH were the best correlates with axes 1 and 3 whereas conductivity and turbidity divided ponds on axis 2 (Fig. 2.9a). The summary nutrient and cation concentration PC axis (Table 7) had limited influence on New Forest macroinvertebrate assemblage composition (Fig 2 9a) and TWINSPAN groups were not well separated by the two dimensional summary of the data (Fig 2 9a). New Forest plant assemblage composition showed no significant relationship with pond physicochemistry (Table 2.8).

Lizard and New Forest pond physicochemistry predicted little of the variation in the occurrence of individual species (Table 2.9). CCA axes 1 and 2 explained 16.3% of the variation in Lizard macroinvertebrate species occurrence (Fig. 2.8b, Table 2.9), 11.1% of variation in New Forest macroinvertebrate occurrence (Fig. 2.9b) and 11.7% of variation in Lizard plant occurrence (Fig. 2.10b). Species therefore in general lie close to the origin of the CCA diagrams, indicating their weak association with trends in the physicochemical variables.

	Species-environment relationship				Correlations					
	Eigenvalue	% explained	Significance of axis one p<	Significance of all axes p<	Area	pH	Depth	Conductivity	Turbidity	PCA
Lizard Macroinvertebrates	0.467	47.6	0 001	0 001	-0.81	-0.59	-0.64	0.8	0.01	0.16
New Forest Macroinvertebrates	0.297	23 8	ns	0.001	-0.60	-0.56	-0.4	-0.54	0.1	0.09
Lizard Plants	0.471	41 2	0 001	0.001	-0.85	-0.42	-0.57	0.64	0.03	0.21
New Forest plants	0.28	31.1	ns	ns	0.59	0 47	0.64	0.6	-0.05	-0.23

Table 2.8: Summary data for the first axis of the CCA ordinations

New Forest			Lizard Peninsula						
Macroinvertebrates			Macroinvertebrates				Plants		
species	Indicator spp	weighting	number	species	Indicator spp	weighting	species	Indicator spp	weighting
Anacaena lutescens		20	1	*Ilybius montanus*	●	22	*Agrostis* spp	●	27
Hydroporus pubescens		16	2	*Helophorus brevipalpis*		22	*Glyceria fluitans*	●	22
Macropelopia	●	26	3	*Helophorus grandis*	●	29	*Juncus articulatus*	●	22
Procladius		19	4	*Helophorus minutus*	●	23	*Juncus bulbosus*		15
Psectrocladius	●	17	5	*Helophorus obscurus*	●	29	*Ranunculus flammula*		25
Micropsectra	●	19	6	*Hydrobius fuscipes*	●	33	*Ranunculus tripartitus*	●	17
Limnephilus vittatus		24	7	*Hydroporus pubescens*		32			
Sympetrum spp	●	22	8	*Hydroporus tessellatus*		21			
Anisus leucostoma		15	9	*Ochthebius dilatatus*		15			
Asellus aquaticus	●	16	10	*Macropelopia*	●	15			
Cloeon dipterum		18	11	*Chaetocladius*	●	16			
			12	*Metriocnemus*		15			
			13	*Limnephilus auricula*		33			
			14	*Limnephilus vittatus*		26			
			15	*Limnephilus lunatus*	●	17			
			16	*Anisus leucostoma*		26			
			17	*Pisidium* spp	●	20			
			18	*Asellus aquaticus*	●	17			

Table 2.9: Lizard and New Forest macroinvertebrate taxa and Lizard plant taxa with weightings greater than 15% in CCA analyses.

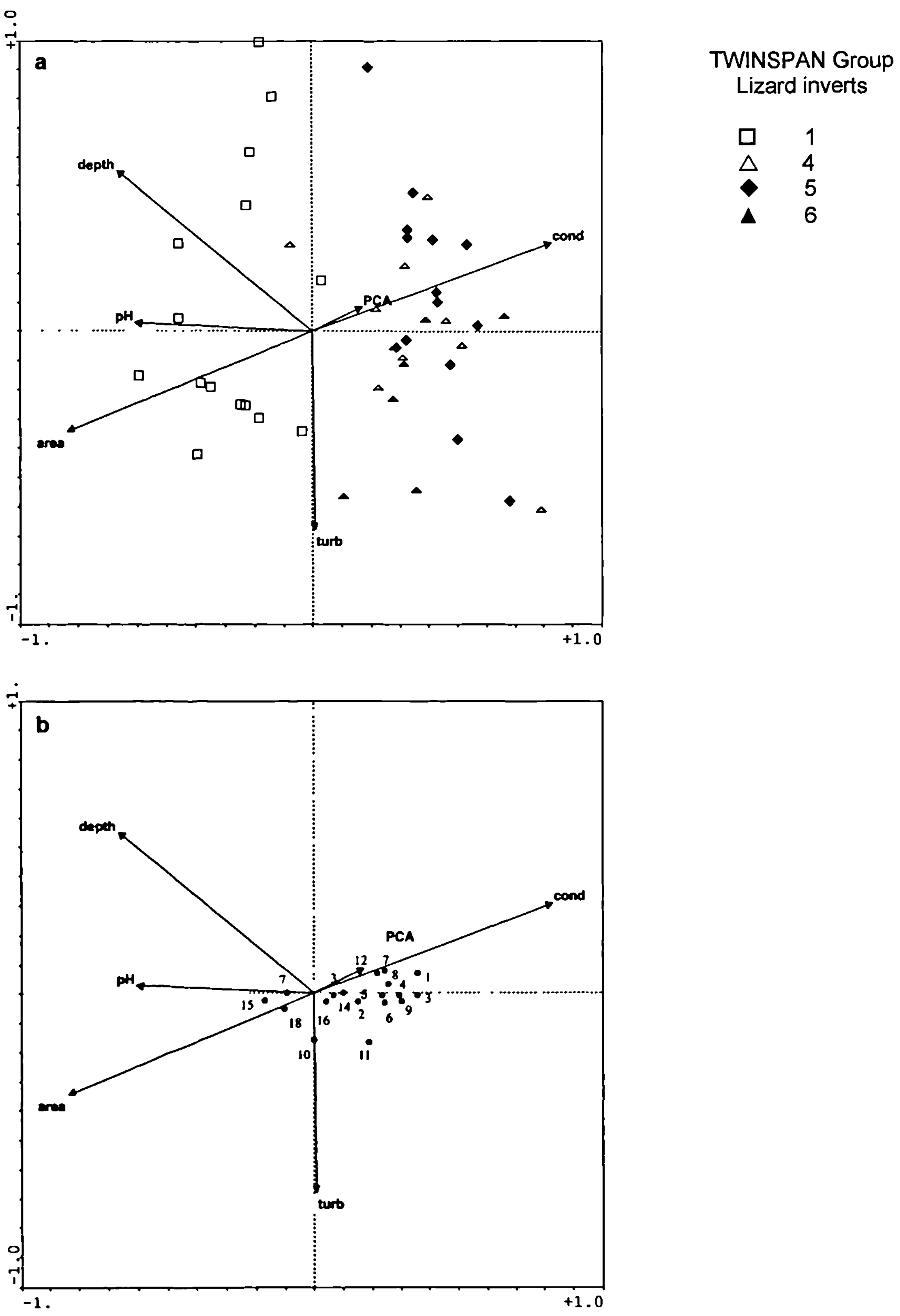


Figure 2.8: First two CCA axes for Lizard macroinvertebrate assemblages, arrows represent the direction and strength of environmental variables in analysis a) relevant TWINSPAN end groups shown (a subset of groups occurs in each region). Cumulative percentage of the species environment relationship explained by axes one and two 64.1%. b) species with weightings greater than 15% in the analysis shown (see Table 9 for key).

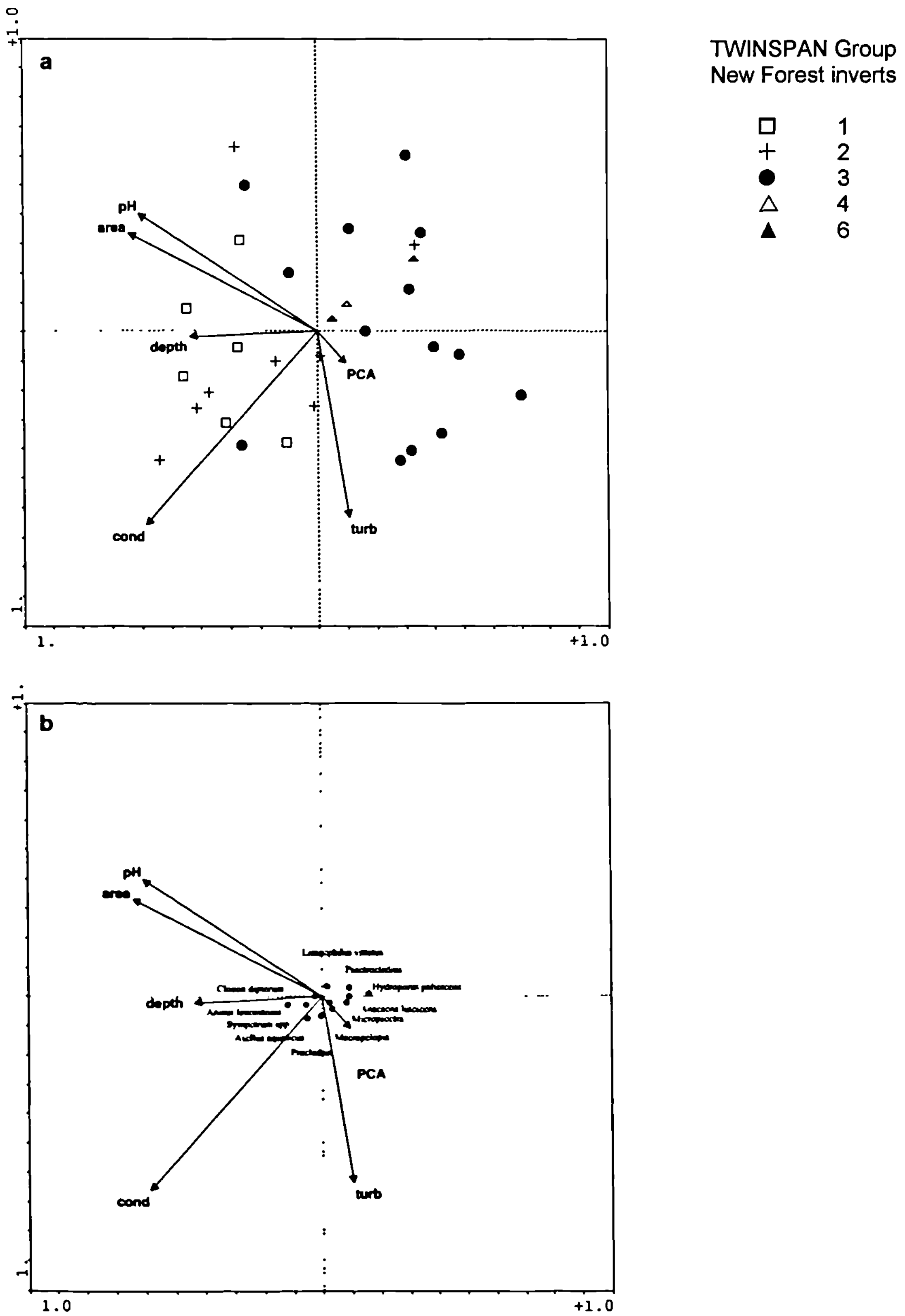


Figure 2.9: First two CCA axes for New Forest macroinvertebrate assemblages, arrows represent the direction and strength of environmental variables in analysis a) relevant TWINSPAN end groups shown (a subset of groups occurs in each region). Cumulative percentage of the species environment relationship explained by axes one and two 44.1%. b) species with weightings greater than 15% in the analysis shown.

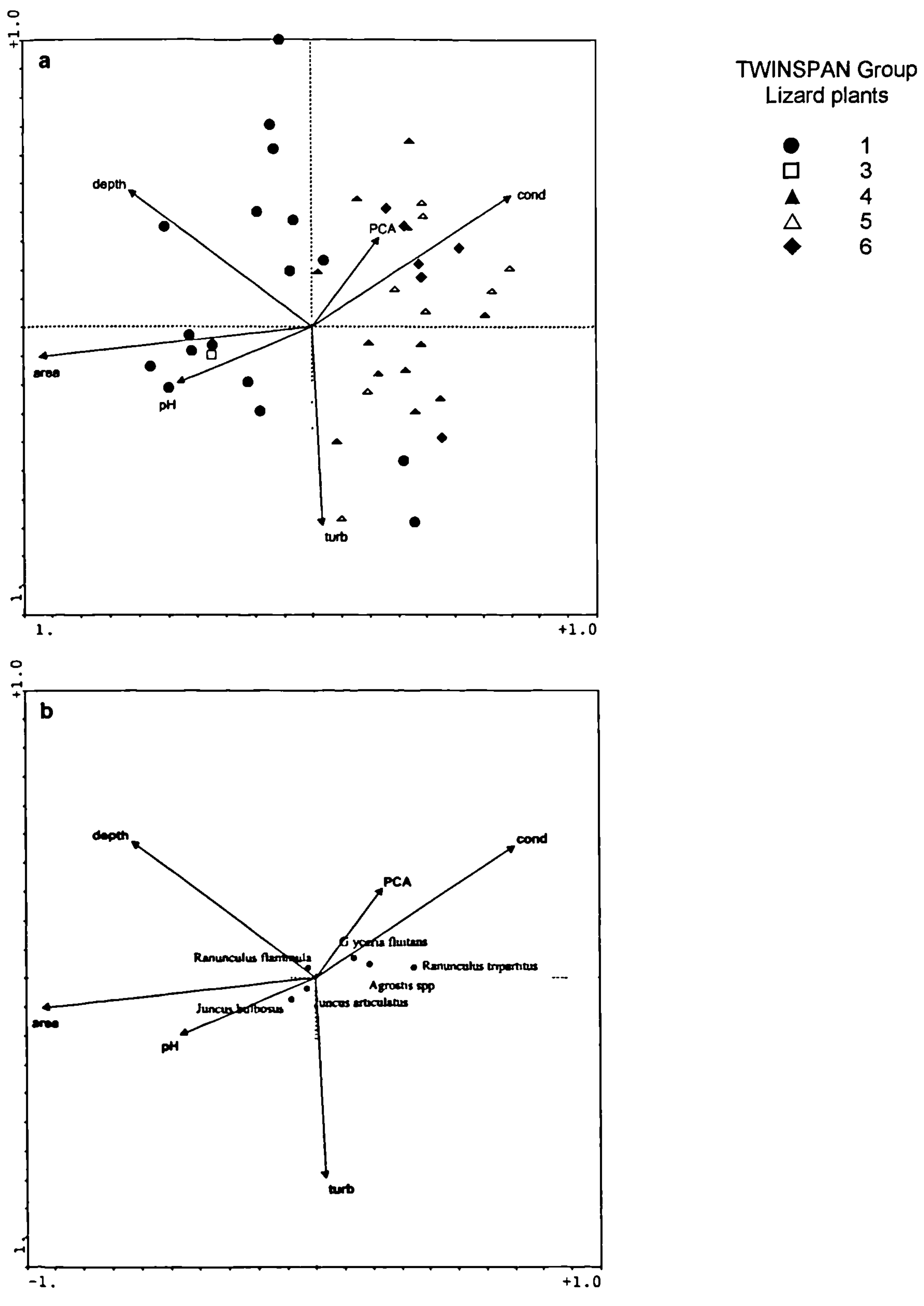


Figure 2.10: First two CCA axes for Lizard plant assemblages, arrows represent the direction and strength of environmental variables in analysis a) relevant TWINSPAN end groups shown (a subset of groups occurs in each region). Cumulative percentage of the species environment relationship explained by axes one and two 60.7%. b) species with weightings greater than 15% in the analysis shown.

2.4.4 The relative importance of spatial and environmental pattern

Preliminary pair-wise Mantel tests of Lizard pond matrices (Table 2.10) showed that there was a significant correlation between differences in pond area and inter-pond distance (r = 0.344, p <0.001) demonstrating that ponds that were close together tended to also be similar in size. It was therefore necessary to separate the effects of pond proximity and area on assemblage similarity, using partial Mantel tests (Fig. 2.11).

	Inter-pond distance (Euclidean)	Area (Euclidean)	Physicochemistry (Euclidean)	Plants (Jaccard similarity)
Area (Euclidean)	r = 0.344 p <0 001			
Physicochemistry (Euclidean)	r = 0.149 ns	r = 0.038 ns		
Plants (Jaccard similarity)	r = -0.174 p <0 05	r = -0.325 p <0.001	r = -0.101 ns	
Macroinvertebrates (Jaccard similarity)	r = -0.434 p <0.001	r = -0.501 p <0.001	r = -0.216 p <0.01	r = 0.371 p <0.001

Table 2.10: Mantel test results for relationships between inter pond distance, area, physicochemistry, plant and macroinvertebrates distance/similarity matrices for Lizard ponds.

	Inter-pond distance (Euclidean)	Area (Euclidean)	Physicochemistry (Euclidean)	Plants (Jaccard similarity)
Area (Euclidean)	r = -0.11 ns			
Physicochemistry (Euclidean)	r = -0.12 ns	r = 0.24 ns		
Plants (Jaccard similarity)	r = -0.16 ns	r = -0.03 ns	r = 0.18 p <0.05	
Macroinvertebrates (Jaccard similarity)	r = -0.14 ns	r = -0.15 ns	r = -0.15 ns	r = 0.22 p <0.05

Table 2.11: Mantel test results for relationships between inter pond distance, area, physicochemistry, plant and macroinvertebrates distance/similarity matrices for New Forest ponds.

Lizard pond macroinvertebrate assemblage similarity showed a significant negative correlation with inter-pond distance when the effect of area was removed using a partial Mantel test (Fig. 2.11a r = -0.32, p <0.001), indicating that adjacent ponds tend to have more similar macroinvertebrate assemblage composition. Plant assemblages however, were not affected by inter-pond distance when the effect of area was controlled for. Lizard ponds within 675m (1^{st} lag) of each other were shown by the Mantel correlogram (Fig. 2.12a) to have significantly similar macroinvertebrate assemblage compositions. However, ponds that were between 675-1350m (2^{nd} lag) apart were shown to have significantly dissimilar assemblages.

Lizard assemblage similarity was also significantly correlated with pond area when the effect of pond proximity was removed (Fig. 2.11a macroinvertebrates $r = -0.42$ $p < 0.001$, plants $r = -0.28$ $p < 0.001$) showing that similar sized ponds tended also to have similar assemblage composition. In addition physicochemical parameter dissimilarity and plant assemblage similarity also significantly affected macroinvertebrate composition (Fig. 2.11a physicochemistry $r = -0.22$, $p < 0.01$; plants $r = 0.26$, $p < 0.001$).

In contrast, inter-pond distance and differences in pond area had no significant effect on New Forest pond assemblage similarity (Table 2.11), although pond physicochemistry and plant assemblage composition were weakly correlated ($r = 0.18$, $p < 0.05$). Plant similarity was again correlated with macroinvertebrate assemblage similarity ($r = 0.25$, $p < 0.001$) when differences in physicochemistry were factored out (Fig. 2.11b). New Forest macroinvertebrate similarity showed no significant relationship with inter-pond distance at any lag distance (Fig. 2.12b).

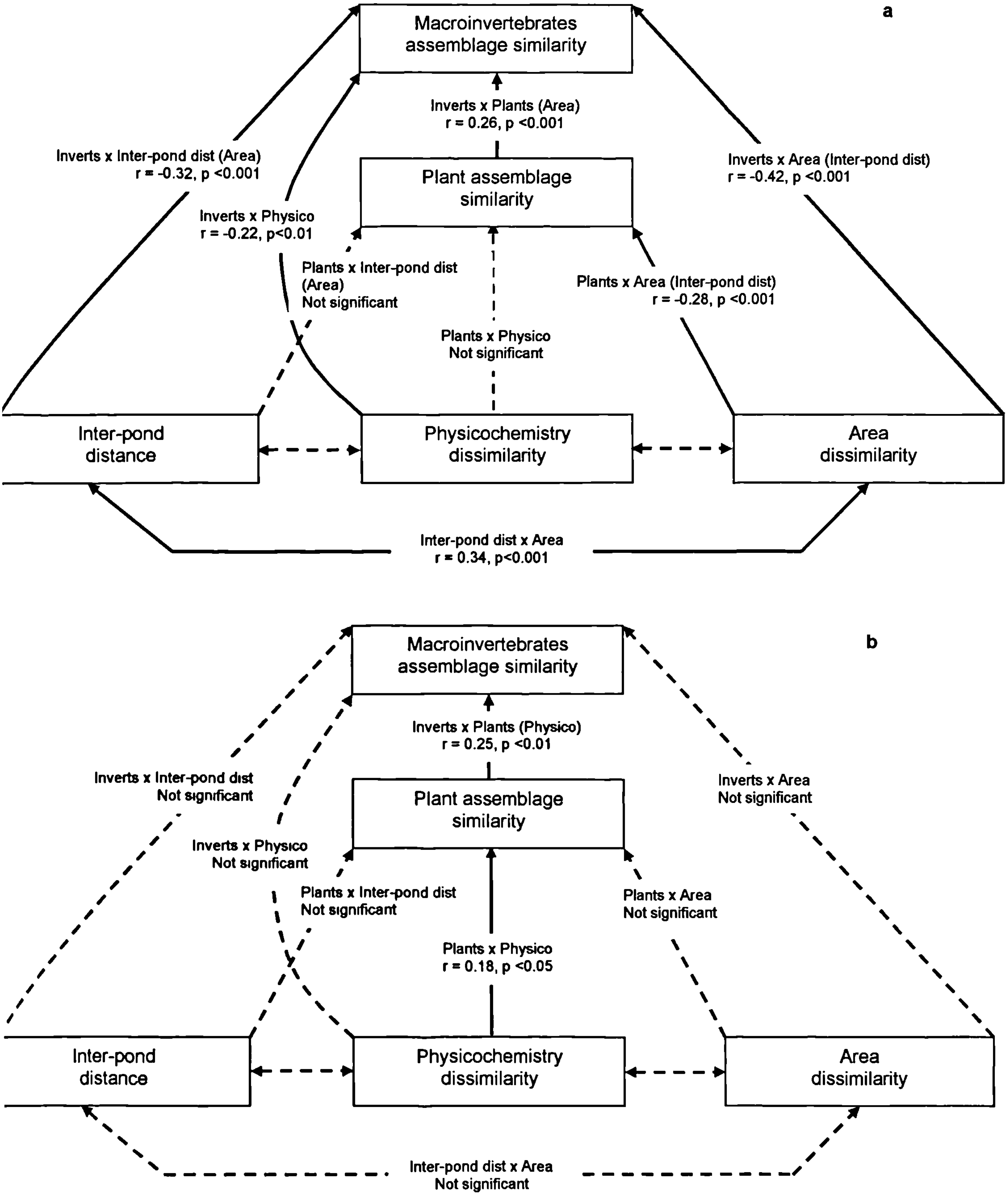


Figure 2.11: Summary diagrams of the relationship between similarity matrices based, where necessary, on partial Mantel tests, effect of matrix shown in brackets is removed. Dotted lines indicate non-significant relationship between matrices, a) Lizard ponds and b) New Forest ponds.

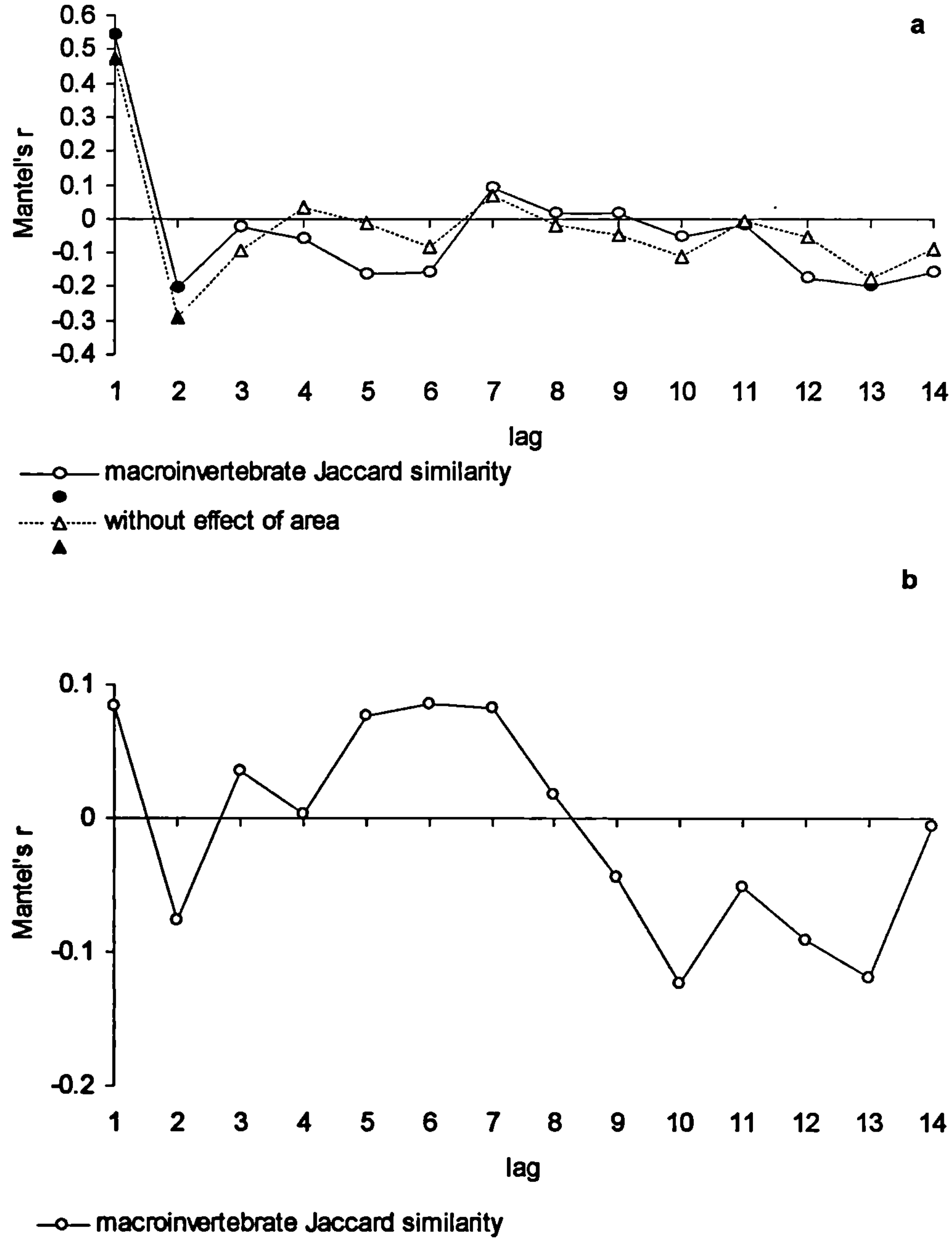


Figure 2.12: Mantel correlograms for a) Lizard macroinvertebrate assemblage similarity with the effect of pond area removed and b) New Forest macroinvertebrate assemblage similarity, significant lags represented by filled symbols.

Box 1: Interpreting the Lizard Mantel correlogram

Fig. 2.12a the filled symbol at the first lag distance shows significant positive spatial autocorrelation in macroinvertebrate assemblage similarity (positive Mantel's R value); this indicates that ponds that are closer together than 675m have similar assemblage composition. In contrast, ponds 675-1350m apart (lag 2) are significantly dissimilar (negative Mantel's R value). Between pond similarity is random when ponds are greater than 1350m apart (open symbols indicate insignificant relationship between interpond distance and assemblage similarity).

2.5 Discussion

These analyses show that both Lizard and New Forest plant and macroinvertebrate assemblages are distinct from those found in other temporary ponds in England and Wales (Fig. 2.3). Large variation in vegetation assemblage composition was seen for the Lizard and UK data, although there was much less variation amongst plant assemblages in the New Forest, which appear as a tight cluster between Lizard and UK ponds (Fig. 2.3a). This is likely to be a consequence of the variety of sites present in the two regions. Ponds on the Lizard ranged from small areas of flooded grassland and track-way through to large fluctuating water bodies with well developed submerged, floating and emergent aquatic vegetation. In contrast New Forest sites varied less in area, as highly ephemeral sites were not as prevalent in the region. Small New Forest sites tended to have more truly aquatic taxa than small Lizard sites and were therefore less distinct from large sites. Two ponds that were more similar to other UK sites (NF1 and NF2) were deeper and more species rich ponds with emergent stands of *Typha latifolia, Sparganium erectum* as well as floating *Lemna* spp, which are typical of more eutrophic ponds and were not recorded in any of the other Lizard or New Forest sites. In addition *Crassula helmsii*, (Australian swamp stonecrop) an exotic invasive species was present in NF1. UK sites most similar to Lizard and New Forest ponds included some sites from the western oceanic fringes, particularly Wales.

Macroinvertebrate assemblage composition of the three data sets overlapped, due to wide variation in the composition of New Forest and Lizard ponds, which was close to the magnitude of variation seen amongst the UK ponds (Fig. 2.3b). This was unexpected considering that New Forest and Lizard samples came from smaller areas of the UK, which would be predicted to have a more limited range of species than the whole UK. New Forest macroinvertebrate assemblages in general seem to be more distinct within the UK than those on the Lizard, lying on the opposite side of the MDS plot. However some sites from the UK wide data did fall out amongst New Forest and Lizard ponds; these were mostly western, oceanic heathland/coastal sites, many of which again are in Wales. The positions of individual ponds on the MDS plots should, however, be interpreted with caution as both the macroinvertebrate and plant assemblage ordinations had high stress values due to the high quantity of data being summarised in two dimensions (Clarke & Warwick 2001). The patterns revealed by the MDS plots do appear rigorous, however, as ANOSIM showed New Forest, Lizard and UK ponds to have significantly different assemblage composition.

Comparison between data collected during this study and Nicolet (2002) also seem robust, as New Forest and Lizard data from Nicolet (2002) lie close to my data (Fig. 2.3).

The mean numbers of plant and macroinvertebrate taxa recorded in the New Forest and the Lizard were lower than those recorded for ponds in the UK survey (Nicolet 2002; Fig. 2.4a and d). New Forest and Lizard ponds did, however, have a significantly greater number of rare species than the UK ponds (Fig 2.4g). Overall the Lizard and New Forest supported seven RDB and nationally scarce plant species and twenty four RDB and nationally scarce coleopteran species and one RDB mollusc (see appendices 7.1, 7.2, 7.3 & 7.4). The occurrence of internationally and nationally scarce species across all of the vegetation and macroinvertebrate classification end groups (Figs 2.5 & 2.6) highlights the importance of maintaining a range of temporary freshwater habitats in each of the regions. Ponds sampled from the New Forest and Lizard would fall into three of the Habitat's Directive Annex I categories, according to the present JNCC definitions (McLeod *et al.* 2002; appendix 7.5). The depauperate vegetation of small Lizard ponds in groups 4, 5 and 6 (Fig. 2.5) with *Ranunculus tripartitus* and *Juncus bufonius* as indicator species fit the JNCC interpretation of 'Mediterraenean Temporary Ponds' (see chapter 6 for further discussion of MTP vegetation), whereas a subset of the larger Lizard sites in group 1, supporting beds of *Chara fragifera*-dominated vegetation would correspond to 'Hard Oligo-Mesotrophic standing waters with benthic *Chara*' (HOM). In contrast, some New Forest ponds in groups 2 and 3, have softer water (mean hardness New Forest 14.2 mgL^{-1}±10.32, Lizard 84.4mgL^{-1} ±7.02), and support vegetation assemblages comprising *Littorella uniflora* along with a subset of *Potamogeton polygonifolius, Pilularia globulifera*, *Myriophyllum alterniflorum* and *Juncus bulbosus.* These would correspond to 'Oligotrophic to Mesotrophic standing waters of the *Littorelletea uniflora*' (OML; appendix 7.5).

The macroinvertebrate assemblages associated with MTP type vegetation are mainly those in groups 4, 5 and 6 (Fig. 2.6), which are chiefly composed of actively dispersing Coleoptera, Trichoptera and Chironomidae that can utilise small ephemeral sites for reproduction (see Fig. 2.6 for details). Characteristic rare taxa of these habitats are the beetles *Graptodytes flavipes* and *Dryops striatellus*, both of which are Mediterranean-Atlantic taxa, associated with shallow ephemeral waters throughout their range. The macroinvertebrate assemblages related to HOM and OML vegetation, however, fall in groups 1 and 2 and include taxa that are weaker dispersers and/or require a longer hydroperiod to reproduce. Rare species of such habitats include *Haliplus* *variegatus* and *Dryops auriculatus*, both of which are associated with fluctuating waterbodies throughout their European ranges. It should be noted that many sites with high SRI for invertebrates and/or plants do not fall within any of the Habitats Directive vegetation categories (e.g. Marlpit Oak ponds in the New Forest have a number of rare Coleoptera and ponds in Norleywood had high invertebrate and plant SRI scores), but should not have their conservation importance underestimated. The classification and conservation status of temporary pond habitat in the two regions is readdressed in chapter 6.

Physicochemical and spatial pattern in plant assemblage structure was weak for both regions (Fig 2.11). The effect of pond area on plant assemblage composition and richness was significant on the Lizard Peninsula but non significant in the New Forest, perhaps due to differences in the range of available pond sizes (New Forest 4-5300m^2 compared with Lizard ponds 2-15000m^2) and the more restricted variation in assemblage composition that was observed for New Forest ponds (Fig. 2.3a). Previous studies examining the macrophyte species-area relationship in lentic freshwater have also found conflicting results (Oertli *et al.* 2000, Jeffries 1998, Weiher & Boylen 1994). The weak, but positive relationship between New Forest plant assemblage similarity and physicochemical dissimilarity (Fig. 2.11b $r = +0.18$, $p < 0.05$), is rather counter intuitive and may be spurious due to a type I error. Neither local wet phase conditions nor the spatial configuration of ponds in the landscape was found to significantly affect vegetation composition in either region. The length and timing of dry phase, lottery of arrival and competitive interactions are therefore more likely to govern the distribution of plant species in temporary ponds.

The strength of physicochemical and spatial pattern in macroinvertebrate assemblage composition differed substantially between the regions (Fig. 2.11). Lizard assemblage similarity was related to pond area, inter-pond distance, physicochemical parameters and vegetation composition, whereas New Forest assemblages were not correlated with physicochemical or spatial parameters, being only affected by vegetation composition. Larger ponds on the Lizard might support more species because they provide: (i) increased habitable space (Preston 1960); (ii) longer hydroperiod so a greater range of species can utilise the pond; (iii) a larger 'target' for dispersing macroinvertebrates to locate (Schwind 1991, 1995); and (iv) increased diversity of microhabitats (Williams 1943). . Pond area also affected Lizard macroinvertebrate assemblage composition; perhaps due to the greater permanence of large ponds. Extended hydroperiod enables macroinvertebrate species with slower development times to utilise the habitat, resulting in a greater pool of potential colonists (Wiggins *et al.* 1980) and wider variation in assemblage composition. Rundle *et al.* (2002) and Bilton *et al.* (2001a) also found pond area and permanence to be the most important correlates with Lizard pond macroinvertebrate assemblage composition. No species-area relationship was seen, however, for New Forest macroinvertebrates and pond area was not related to assemblage composition either (Fig 2.11). This may have been because pond area varied less in the New Forest, which may have reduced the variation in pond hydroperiod. In addition, pond area and permanence appeared less well correlated, as marl diggings tended to be small in area but fairly deep.

The range of pH and turbidity was greater in New Forest ponds, yet there was no relationship between physicochemistry and macroinvertebrate species richness or assemblage composition. In contrast physicochemistry had a significant effect on Lizard macroinvertebrate assemblage composition. It may be that the combination of high conductivity and low pH in more ephemeral Lizard ponds caused this effect. Ponds which evaporate more quickly typical have higher conductivity (McKee *et al.* 2003) which can have osmotic consequences for insects (Buchwalter *et al.* 2003, Williams 1996) and low pH has also been shown to limit the number of species and assemblage structure of pond habitat (Nicolet 2002, Jeffries 1998, Friday 1987, Barnes 1983). Low pH might have direct effects on macroinvertebrate richness and composition due to changes in ionic balance, protein stability (Maltby *et.al.* 1997) and calcium carbonate availability (Rundle *et al.* 2004) as well as indirect effects on detritus palatability (Kok & Vanderveld 1994).

The only common factor found to correlate with both Lizard and New Forest macroinvertebrate assemblage composition and richness was plant composition. Macrophytes provide food (Jones *et al.* 2000, Lodge *et al.* 1998), shelter (Heck & Crowder 1991, Maurer & Brusven 1983) and oviposition sites (Welch 1935) for macroinvertebrates, resulting in a variety of microhabitats for macroinvertebrates with different life history characteristics. Macrophyte diversity has a positive effect on macroinvertebrate richness (Ward & Blaunstein 1994, Bazzanti *et al.* 2003, Oertli *et al.* 2002, Brown *et al.* 1988) and invertebrate assemblage composition can vary amongst vegetation stands with different species composition (Scheffer *et al.* 1984, Dvorak & Best 1982). The structural complexity of vegetation can also influence invertebrate assemblages (see chapter 5).

Significant spatial pattern in assemblage composition was only observed for Lizard macroinvertebrates. The detection of spatial pattern in pond assemblage structure is likely to be dependent on (i) the spatial scale of the study area and the number of sites surveyed, (ii) the number and relative position of large, permanent ponds within study region, (iii) the dispersal ecology of the pool of species being examined, (iv) the relative importance of biotic interactions or 'assembly rules' in structuring the assemblages and (v) the power of the spatially explicit analysis to detect significance. Failure to detect spatial pattern in New Forest macroinvertebrate assemblage similarity may therefore have been due to the difference in spatial scale at which ponds were sampled (approximately 480 km^2 compared with the Lizard study area of $38km^2$) and the number of ponds sampled (31 compared with 45 Lizard ponds), which could have resulted in spatial patterns in assemblage composition being inadequately resolved in the New Forest. However, the sampling regimes were naturally constrained by the relative availability of ponds in the two regions; the Lizard Peninsula comprises a relatively smaller geographical area than the New Forest and tends to have a greater density of small ponds (see chapter 1), whereas the New Forest has local clusters of ponds spread more widely through the landscape. The proximity of large, permanent ponds in relation to small ponds (which are used for winter reproduction by a number of taxa), therefore, also differed between the two regions, which might have important consequences for spatial patterns in colonisation. The spatial scale of survey area, number of sites sampled and the spatial configuration of those ponds sampled within the landscape also affect the power of spatial analysis to detect pattern, as the number of distance pairs in each equidistant lag interval differs. Spencer *et al.* (2002) found no evidence for spatial or environmental pattern in pond assemblage composition and argued that either dispersal was not limited in the system or that biotic interactions were masking spatial pattern. Similarly the lack of spatial pattern in the New Forest might be due to increased importance of biotic interactions or assembly rules that have no intrinsic spatial pattern, e.g. priority effects (Wilbur 1997), which could render local dispersal events unsuccessful and therefore blur spatial pattern. New Forest ponds were, in general, more permanent and widely spaced and biotic interactions have been shown to increase in importance in as hydroperiod increases and the availability of pond habitat decreases (Foggo, Bilton and Rundle in prep., Kiflawi *et al.* 2003, Wellborn *et al.* 1996, Schneider and Frost 1996).

It is likely that dispersal limitation, chance colonisation, local physicochemistry and biotic interactions all shape patterns in assemblage composition in each of the regions. However, the relative strength of each of these processes depends on the spatial scale and configuration of the ponds along with the available range of pond permanence in the regions, the result is patchy spatial pattern in Lizard macroinvertebrate assemblage composition and more random assemblage structure in New Forest ponds.

2.6 Appendices

2.6.1 Appendix 1: Examples of small Lizard sites


L45


L4


L28


L26


L38


L39

2.6.2 **Appendix 2**: Examples of larger Lizard sites

L3

L6

L25

2.6.3 **Appendix 3**: Examples of New Forest sites

NF1

NF4

NF5

NF6

NF10

NF15

NF16

NF19

NF33

NF34

NF35

3 Unravelling nestedness and spatial pattern in pond assemblages

3.1 Abstract

Nestedness is a composite property of many suites of biotas. Such nestedness patterns may be driven by dispersal limitation, species-area relationships, hierarchical niche requirements, or occur as an artefact of passive sampling. Despite its widespread occurrence, few studies have explored the factors underlying nested subset structure, and ecological distinctions between nested and non-nested (idiosyncratic) taxa within a region have been largely ignored.

Macroinvertebrate assemblages from 45 heathland ponds in southwest England were used to: (i) unravel the relative importance of processes underlying nested subset structure; and (ii) test spatially explicit hypotheses concerning the response of nested and idiosyncratic taxa to parameters shown to structure assemblage-level nestedness. Despite being dominated by taxa with good powers of inter-site dispersal, pond macroinvertebrate assemblages were found to be significantly nested. This nesting was not due to passive sampling, and was best explained by pond area, with habitat parameters and isolation being of secondary importance. The spatial responses of nested and idiosyncratic taxa matched predictions; nested taxa showed strong spatial structure, which was reduced when the effects of pond area and habitat were removed. In contrast a greater proportion of idiosyncratic taxa were completely spatially random and exhibited weaker responses to factors that structure assemblage level nestedness. Nested and idiosyncratic species generally differed ecologically; idiosyncratic taxa generally possess broad ecological tolerance and good dispersal capacity, whilst nested species are more likely to have narrow tolerances or limited powers of dispersal.

Factors structuring nestedness in ponds can be viewed as probabilistic filters which act to limit the spatial distribution of species with narrow ecological tolerance or low dispersal tendency. Nestedness analysis alone fails to elucidate processes that structure assemblage composition. The additional use of spatially explicit analyses is important if processes that generate nested pattern across a region are to be understood.

3.2 Introduction

Nestedness is one of the most commonly observed properties of a regional collection of local biotas (Gaston & Blackburn 2000). Perfect nesting occurs when species-poor sites contain subsets of the assemblages found in species-rich sites, and the degree of nestedness thus quantifies the overlap in species composition between high and low diversity sites. Most local assemblages occurring in patchy habitats have been shown to exhibit nestedness (Wright *et al.* 1998), with examples spanning fragmented forest patches (e.g. Berglund & Jonsson 2003, Honnay *et al.* 1999), island archipelagos (e.g. Davidar *et al.* 2002, Hadley & Maurer 2001, Millien-Parra & Loreau 2000), and lentic freshwaters (Hecnar & MCloskey 1997, Weiher & Boylen 1994). Despite attempts to unravel the generalities of nestedness pattern across systems (e.g. Wright *et al.* 1998, Boecklen 1997) and improve methodologies for assessing it (e.g. Fischer & Lindenmayer 2002, Jonsson 2001, Brualdi & Sanderson 1999), few studies have explored the relative importance of processes that may drive nestedness.

Nested subset patterns could be caused by several factors. Passive sampling could generate nestedness as an artefact of underlying stochastic principles, as rare species are less likely to be sampled in a given area than common species (Fischer & Lindenmayer 2002; Gaston & Blackburn 2000). Habitat isolation also creates nested subsets through dispersal limitation, as species differ in their ability to colonise distant sites (Patterson & Atmar 1986). Additionally, area may drive nestedness, since larger habitat patches support species with both large and small minimum area requirements, whilst smaller patches only support the latter (Wright *et al.* 1998, Boecklen 1997). Nested distribution of habitat types, disturbance regime and hierarchical niche relationships may also produce nested assemblages (Patterson & Atmar 2000, Honnay *et al.* 1999, Kolasa 1996). In contrast, frequent between patch dispersal has been proposed to erode nested patterns (e.g. in aquatic invertebrates, Wright *et al.* 1998, Boecklen 1997), serving to homogenise assemblage composition.

In addition to indicating the presence of nested subset structure, nestedness analysis enables the recognition of significantly non-nested distributions due to species or habitat checker boarding (Gotelli & McCabe 2002), or spatial turnover (Gaston & Blackburn 2000). Where significant nesting does exist, species that conform to the overall assemblage nestedness pattern can be differentiated from taxa which depart from nestedness (known as idiosyncratic taxa); these latter types have a tendency to occur in species poor sites (Atmar & Patterson 1993; 1995).

Studies of assemblage structure, including nestedness analysis often have inherent spatial components, and therefore demand the use of spatially explicit analyses (Wilson 1999). For example, Keitt *et al.* (2002) argue that the relative and absolute importance of environmental variables for species occurrence and abundance may be incorrectly assessed if spatial autocorrelation in their patterns is ignored. Despite the importance of accounting for spatial structure within analyses of assemblage composition, only a single study published to date has examined nestedness in a spatial context (Hausdorf & Hennig 2003). Factors that can structure nested subset patterns (e.g. habitat area and type) may be spatially autocorrelated in the landscape, and the occurrence of nested taxa might therefore show a similar pattern of autocorrelation. In contrast, idiosyncratic taxa, which depart from the nested pattern, might be expected to exhibit different spatial structure, showing either negative or random responses to factors that drive nestedness. If dispersal erodes nested structure, as suggested by Boecklen (1997), idiosyncratic taxa should tend to be species that are especially strong and active dispersers, and should therefore be more widely distributed and spatially random than nested taxa, which would tend to have locally clumped distributions. To date these predictions have not been tested explicitly.

This study is the first to determine the relative importance of factors driving nested subset structure in a spatial context and compare the response of nested taxa to those which depart from this pattern. We use macroinvertebrate assemblages in heathland ponds to: (i) unravel the processes that may underlie nested subset structure; and (ii) examine the spatial responses of idiosyncratic and nested taxa to parameters shown to structure assemblage-level nestedness. Ponds are an ideal model system as they form habitat islands for aquatic species (Bilton *et al.* 2001b), and can vary extensively in their physical characteristics and the richness of their biota across small spatial scales (Kiflawi *et al.* 2003). The fauna of small ponds is also dominated by mobile species, many of which are capable of dispersing between individual waterbodies repeatedly during their lives.

3.3 Methods

3.3.1 Study area

Data on macroinvertebrate assemblage composition were generated for 45 heathland ponds on the Lizard Peninsula, south-west Cornwall UK. Ponds varied substantially in area, permanence and vegetation composition, although all were above ultra-basic serpentine geology on heathland/unimproved grassland (see section 1.6 for detail).

3.3.2 Invertebrate sampling

Invertebrates were sampled with a 1mm mesh FBA hand net during February 2000. Five standardised 1m sweeps were stratified between beds of vegetation with different macrophyte species compositions. Sweeps were pooled and macroinvertebrates and detritus preserved in 70% alcohol. In the laboratory samples were sorted and animals identified to species, except for chironomids which were identified to genus (see section 2.3 for detail).

3.3.3 Pond chemistry, habitat, isolation and area

Water samples from each pond were collected in acid washed polypropylene bottles for later analysis of metal cation concentration. Mean water depth was recorded and pH readings taken on-site using a Solomat 520C probe. Water hardness was calculated as $2.5[Ca^{2+}] + 4.1[Mg^{2+}]$ (Gower *et al.* 1994). Macrophyte and semi-terrestrial vegetation species composition at sampling locations was examined in late May of the same year; when most species were in flower and could be readily identified. Taxa present in the area from which invertebrates were sampled were recorded and identified to species; bryophytes and *Callitriche* spp. were noted but not identified further.

In order to examine the relationship between nestedness and habitat parameters a summary of vegetation and physicochemical variables was produced. Number of macrophyte species, mean depth, pH and water hardness were normalised and standardised, and subjected to Principle Components Analysis (PCA). First PCA axis score was then used as a simplified measure of pond habitat (Honnay *et al.* 1999) in subsequent analyses.

Accurate estimates of pond area were derived by using differential GPS (Trimble) to map the margin of each pond; this process also generated central point co-ordinates for each pond, which were used to create a between-pond distance matrix. Pond isolation was calculated as the sum of all pair-wise distances to other ponds (Jeffries 2003).

3.3.4 Nested subset analysis

Nestedness was assessed using the nestedness temperature calculator (Atmar and Patterson 1993; 1995). The metric employed (T) has various advantages over other measures of nestedness including: (i) matrix size independence; (ii) easy identification of idiosyncratic taxa; and (iii) simultaneous maximal nesting across species and sites (Patterson & Atmar 2000). The lack of stringency of the underlying null model used by the temperature calculator has been the subject of recent criticism, particularly since matrices generated by passive sampling have been shown to be significantly nested (Fischer & Lindenmayer 2002, Jonsson 2001). In order to test the significance of the observed nestedness more rigorously, and to discount passive sampling and species richness effects as sources of nestedness, we used two additional null models. To examine passive sampling effects, we created random matrices fixing the values for species' overall occurrence to that in the observed matrix (Gotelli & Graves 1996). One hundred such matrices were generated and the nestedness temperature calculator was used to calculate the range of T values expected from such random sampling. If passive sampling structures nestedness, the observed matrix temperature should lie within this expected distribution (Fischer & Lindenmayer 2002).

A second algorithm was then used, to create an additional hundred matrices, fixing both species occurrence and number of species per site (Brualdi & Sanderson 1999). These null distributions were used to test the effects of species richness upon nestedness. If richness drives the nestedness pattern, the observed matrix temperature would again be predicted to lie within the expected distribution.

3.3.5 Correlates of nestedness

To examine the effects of area, habitat and isolation (factors purported to drive nestedness in many systems) upon nestedness, we first calculated site nestedness order, using the matrix packing algorithm within the nestedness temperature calculator (Atmar & Patterson 1995). Second order partial correlation analysis (Sokal & Rohlf 1995) was then used to examine bivariate correlations between the nestedness order, and area, isolation and habitat PCA scores. Partial correlations were performed on ranked data as area and isolation were skewed and transformation failed to normalise their distribution.

The relationship between nestedness and area, isolation and habitat factors was also investigated using an approach developed by Lomolino (1996). Sites were ranked by species richness, and the number of departures from nestedness quantified by recording the number of times the absence of a species was followed by its presence in the next most species rich site, giving a basic measure of internal nestedness (Honnay *et al.* 1999). The same procedure was then repeated on the matrix after it had been reordered by rank pond area, rank isolation, and rank habitat (lowest PCA score first) respectively. The observed number of departures for each of these rankings was then compared with the range of values gained from 1,000 randomisations of the matrix. The matrix reorder variable resulting in the lowest number of departures is that which correlates best with observed nestedness structure.

3.3.6 Nested vs idiosyncratic taxa

To examine the spatial responses of taxa to correlates of nestedness, autocorrelation analyses were conducted using The R Package (Casgrain & Legendre 2001). Summed pair-wise inter-pond distances were used to generate fourteen equal distance lag intervals in accordance with Yule's rule (Casgrain & Legendre 2001); inter-lag distance was 675m with maximum inter-pond distance 9450m. Correlograms of total, nested and idiosyncratic species richness were produced using Moran's I computed for each distance class, with significance of Moran's I at each lag corrected for multiple comparisons using the Bonferroni method. The effect of pond area and habitat were determined using additional correlograms of residuals for each of the three richness measures regressed against pond area and habitat PCA scores respectively (P. Legendre pers. comm.). If pond area and/or habitat strongly influence the spatial structure of richness, these correlograms should show significant changes over the originals and indicate a lack of autocorrelation; if pond area or habitat has little influence, excluding their effects should leave the correlogram relatively unchanged.

Relative abundance data for taxa occurring in three or more ponds were also examined for autocorrelation, using correlograms to compare spatial structure in nested and idiosyncratic species. The numbers of lag distances with significant positive or negative autocorrelation were summed across all nested species, and the mean values per taxon taken as a measure of typical spatial structure. The same procedure was then performed for idiosyncratic taxa. Finally the effects of area and habitat on individual species' abundance distributions were examined, again by plotting correlograms of regression residuals as described above.

3.4 Results

3.4.1 Habitat variables

Principle component analysis (PCA) showed that axis one accounted for 41.2% of variation in the pond habitat data. Low PCA axis one scores represent ponds which were relatively deep, with approximately neutral pH, high macrophyte richness and low water hardness, typical of larger more permanent sites (Table 3.1).

Variable	PCA axis one eigenvector
log depth	-0.528
pH	-0.459
log number of plant taxa	-0.502
log water hardness	0.508

Table 3.1: Eigenvectors for Principle Component Analysis (PCA) of pond habitat parameters. Axis one accounted for 41.2% of variation in the data.

3.4.2 Nested subset analysis

The macroinvertebrate presence absence matrix had a temperature of 15.5° which was significantly nested when compared with all three null models (Table 3.2). Around a quarter (31/118) of taxa recorded were idiosyncratic in their distribution, with Coleoptera and chironomids making up 81% of these (Table 3.3) as opposed to 62% of nested species. Partial correlation indicated that the proportion of idiosyncratic taxa per site was negatively correlated with pond area (r_s = -0.695, p <

0.001), indicating that idiosyncratic taxa form a greater proportion of the total taxon richness in small ponds. The proportion of idiosyncratic taxa was also significantly correlated with the habitat PCA, (r_s = 0.494, $p < 0.001$), whereas the corresponding correlation with isolation was not significant. The absolute number of idiosyncratic taxa per pond was not significantly correlated with area, isolation or habitat.

Null model	Atmar and Patterson (1995) matrix temperature	Number of randomisations giving T < observed
Observed matrix temperature	**15.50°**	
(i) Default null model. Number of species occurrences and site species richness equiprobable (n = 1000)	mean 56.06°; sd 1.94° range 50.0° – 63.0°	0
(ii) Passive sampling effect. Number of species occurrences fixed and site species richness equiprobable (n = 100)	mean 34.25°; sd 1.32° range 30.86° – 37.26°	0
(iii) Species richness effect. Number of species occurrences fixed and site species richness fixed (n = 100)	mean 17.99°; sd 0.37° range 17.37° – 18.89°	0

Table 3.2: Observed and expected nestedness temperatures based on three different null models, (i) default model, species occurrence and site species richness are equiprobable, (ii) species occurrence fixed to that observed and (iii) species probability and site species richness fixed to that observed.

Taxon	Occurrence (Number of ponds)	Taxon	Occurrence (Number of ponds)
Coleoptera		**Chironomidae**	
Agabus bipustulatus	12	*Macropelopia*	15
Ilybius montanus	22	*Chaetocladius*	16
Anacaena lutescens	12	*Limnophyes*	11
Dryops striatellus	4	*Metriocnemus*	15
Gyrinus substriatus	2	*Chironomus*	7
Graptodytes flavipes	11	*Micropsectra*	13
Haliplus lineatocollis	11	*Paratanytarsus*	1
Haliplus fulvus	1	**Trichoptera**	
Helophorus aequalis	3	*Limnephilus vittatus*	26
Helophorus brevipalpis	22	**Hemiptera**	
Helophorus grandis	29	*Corixa punctata*	6
Helophorus minutus	23	*Corixa affinis*	2
Helophorus obscurus	29	**Mollusca**	
Hydroporus melanarius	1	*Lymnaea truncatula*	11
Hydroporus planus	13	**Crustacea**	
Hydroporus pubescens	32	*Crangonyx pseudogracilis*	2
Hydroporus tessellatus	21	**Odonata**	
Ochthebius dilatatus	15	*Enallagma cyanthigerum*	1

Table 3.3: Idiosyncratic taxa that are less nested than average, having temperatures greater than 15.5°.

3.4.3 Correlates of nestedness

Both the partial correlation and Lomolino (1996) methods indicated that nestedness order correlated with pond area (Tables 3.4 & 3.5). Nestedness order was also significantly related to pond isolation using Lomolino's technique (Table 3.5), but not using partial correlation (Table 3.4). Partial correlation indicated a significant relationship between nestedness and habitat PCA.

		Rank area	Rank isolation	Rank habitat
Pond nestedness ranked	Second order partial correlation r_s	-0.460	0.039	0.336
	p	<0.01	ns	<0.05
Pond species richness ranked	Second order partial correlation r_s	0.463	-0.082	-0.341
	p	<0.01	ns	<0.05

Table 3.4: Partial correlation between pond area, isolation and habitat PCA score and pond species richness and nestedness order.

	Number of departures D (Lomolino 1996)	Number of randomisations giving D < observed
Sites ranked by species richness	570	278
Sites ranked by area	452	0
Sites ranked by mean isolation	460	0
Sites ranked by habitat PCA score	602	815
Sites ranked randomly (n= 1000)	mean 581.9, sd 22.64 range 505 to 655	

Table 3.5: Lomolino (1996) departures for matrices reordered according to pond area, isolation and habitat PCA score compared with 1000 randomisations of site order.

3.4.4 Nested vs idiosyncratic species

The correlogram of total species richness (Fig. 3.1a) indicates that the total number of taxa was significantly structured through space (nine significant lag distances). The correlograms of the area and habitat PCA regression residuals were more spatially random, with only three significant lag distances each. This indicates that area and habitat are significantly structuring the spatial response of total species richness; this is particularly clear at low lag distances (675m to 4050m; Fig. 3.1a).

Richness of nested species shows a similar but stronger pattern to that for total species richness (Fig. 3.1b); with ten significant lag distances, whilst the correlograms of area and habitat residuals have only three. Idiosyncratic species richness (Fig. 3.1c) shows weaker spatial structure, with four significant lags; comparison of this correlogram with those of the habitat and area residuals reveals little change.

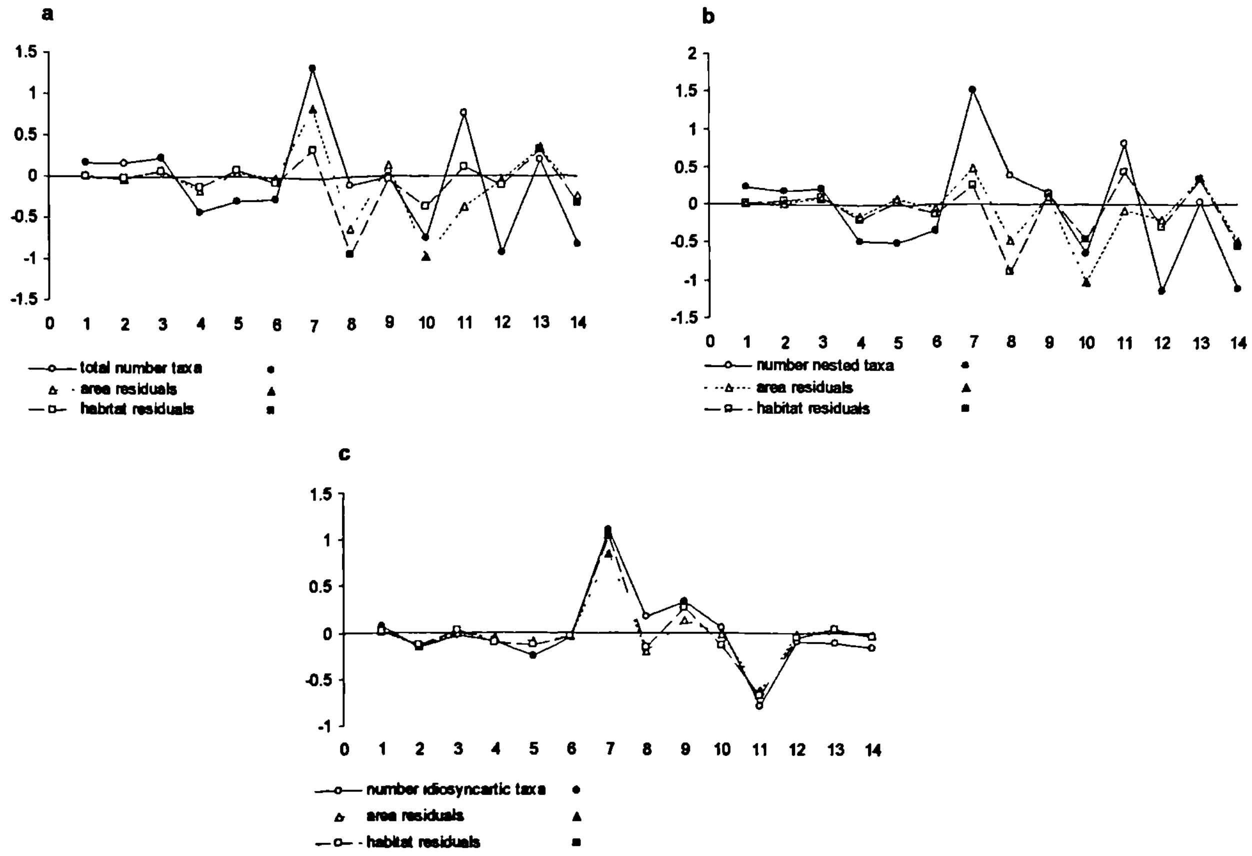


Figure 3.1: Correlograms of (a) total number of taxa (b) number of nested taxa and (c) number of idiosyncratic taxa. Dotted lines indicate correlograms of the residuals from regressions with pond area and habitat. Significant lags (Bonferroni correction p< α /14, where α =0.05) indicated by filled symbols, inter-lag distance is 675m.

On average individual idiosyncratic species showed less evidence of significant spatial structuring than nested species (Table 3.6) with means of 1.08 (n = 24) significant lag distances per taxon compared with 2.04 (n= 54; one tailed Mann Whitney test, W = 736, p < 0.01). The mean number of negative lags was significantly greater for nested than for idiosyncratic taxa (1.43 compared to 0.67; W= 692, p < 0.01). No significant difference in the number of significant positive lag distances was observed between idiosyncratic and nested taxa. The number of macroinvertebrate species that were completely spatially random (i.e. random at all lag distances) represented a greater proportion of idiosyncratic taxa (54.2%) than nested taxa (24.1%).

	No. taxa occurring in ≥ 3 ponds	Proportion of taxa that are completely spatially random (CSR)	Mean total no. of lags per taxon showing significant autocorrelation	Mean no. of lags per taxon showing significant negative autocorrelation	Mean no. of lags per taxon showing significant positive autocorrelation
Idiosyncratic taxa	24	54.2%	1.08*	0.67*	0.41
Nested taxa	54	24.1%	2.04*	1.43*	0.61

Table 3.6: Comparison of idiosyncratic and nested species spatial structure. Proportion of taxa showing completely spatially random (CSR) distributions and mean number of spatial lags per taxon showing significant autocorrelation after Bonferroni correction ($p < \alpha/14$, where $\alpha = 0.05$). Asterix indicates that idiosyncratic taxa have fewer significant lag distances than nested taxa (one tailed Mann Whitney $p<0.01$).

The spatial responses of individual species to pond area and habitat form a continuum (Fig. 3.2). Overall, idiosyncratic taxa (e.g. *Dryops striatellus,* (Fairmaire & Bristout); Fig. 3.2c) were more random in their spatial distribution and showed less response to pond area and habitat characteristics than nested taxa, (e.g. *Dryops luridus,* (Erichson); Fig. 3.2a) which showed stronger spatial autocorrelation. However, many idiosyncratic and nested species showed an intermediate level of response (e.g. nested *Dryops auriculatus,* (Geoffroy); Fig. 3.2b).

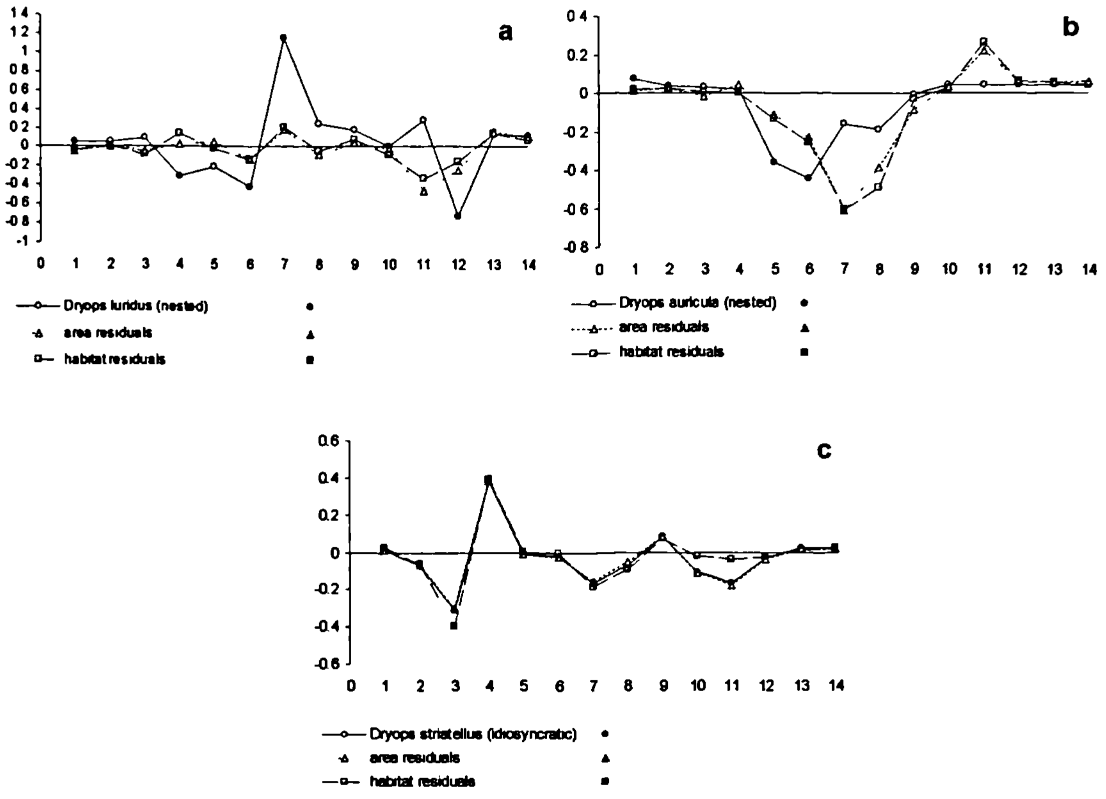


Figure 3.2: Relative abundance correlograms of (a) *Dryops luridus* (nested) (b) *Dryops auriculatus* (nested) and (c) *Dryops striatellus* (idiosyncratic). Dotted lines indicate correlograms of the residuals from regressions with pond area and habitat. Significant lags (Bonferroni correction $p < \alpha/14$, where $\alpha = 0.05$) indicated by filled symbols, inter-lag distance is 675m.

3.5 Discussion

This study shows that local assemblages within a region can show significant levels of nestedness despite being dominated by taxa with good powers of inter-locality dispersal (Rundle *et al.* 2002). This nested structure was not due to passive sampling or directly related to species richness (Tables 3.2 & 3.5).

Boecklen (1997) and Wright *et al.* (1998) showed that aquatic invertebrate assemblages exhibit lower degrees of nested subset structure than other taxonomic groups. They infer that high rates of dispersal amongst habitat islands might mask nested subset pattern by increasing the spatial turnover of species. This study suggests that a high level of inter-site dispersal does not always preclude the presence of nestedness in aquatic invertebrate systems. Significant nested subset structure has been shown for other taxonomic groups with high inter-patch dispersal, for example butterfly assemblages at both large and small spatial scales (Summerville *et al.* 2002, Fleishman & MacNally 2002, Fleishman *et al.* 2002).

Both of the techniques employed here show area to be the best correlate of nestedness, although pond habitat characteristics (Table 3.4) and isolation (Table 3.5) were also important. All three of these inter-related factors are likely to act together to shape nestedness. Large ponds with low habitat PCA scores (i.e. circum-neutral pH, higher macrophyte species richness with greater depth) and that are close to other ponds unsurprisingly tend to be the most species rich, and are basal to a pattern of nested pond assemblages throughout the landscape. Small sites with higher habitat PCA scores have lower total species richness, but support assemblages that contain a similar number of idiosyncratic taxa to that found in large ponds.

Patch-area dependent extinction processes are reported to shape nestedness when area correlates well with the observed pattern (Honnay *et al.* 1999, Wright *et al.* 1998, Atmar & Patterson 1993). This is particularly applicable for fragmented habitats where relaxation is occurring, and may similarly happen when ponds shrink as they dry. However, during February, temporary pond habitat is at maximum extent, and small ponds may instead have been depauperate because they: (i) provide less habitable space; (ii) have been wet for less time than larger water bodies, allowing less time for colonisation; and (iii) are risk prone for taxa without suitable adaptation to cope with or avoid drought.

Another factor that potentially structures nested subsets is the hierarchical distribution of niche space (Kolasa 1996). In this case, species well adapted to the temporary pond environment (usually referred to as temporary pond 'specialists') should in fact be ubiquitous generalists, and species more limited by pond hydro-period should be specialists occurring in a subset of sites. However, hierarchical niche relationships do not seem to be a major structuring force for nestedness in our system, as many species that could be considered generalists e.g. *Limnephilus vittatus* (Fabricius), *Helophorus brevipalpis* Bedel and *Corixa punctata* (Illiger) (Table 2) are idiosyncratic. These generalists are distributed across ponds of different species richness, area, isolation and habitat type, but because they occur in species poor sites the nestedness temperature calculator model expects them to be present in all assemblages of greater species richness. They are therefore idiosyncratic because they have unexpected gaps in their distribution.

Patterns in the number of nested species within individual assemblages (Fig 3.1a and b) are structured largely by the effects of pond area and habitat, whilst the number of idiosyncratic taxa is only weakly governed by pond characteristics (Fig. 3.1c). A similar effect is also evident in the spatial distribution of individual species. For instance, pond area and habitat are important in structuring the distribution of the nested water beetle *Dryops luridus* (Fig. 3.2a) but have little effect on the spatial distribution of its idiosyncratic relative *Dryops striatellus* (Fig. 3.2c). The pattern seen with individual taxa is sometimes less clear cut than that at the assemblage level, however, with a number of species such as the nested *Dryops auriculatus* (Fig. 3.2b) showing an intermediate response to pond area and habitat. Despite this continuum of response, nested taxa show greater spatial structure than idiosyncratic species as on average they have more significant negative spatial lags (Table 3.6). This indicates that nested taxa are more dispersed through the landscape, due to avoidance of unsuitable sites. In contrast the more random spatial distributions of idiosyncratic taxa indicate that they are not actively avoiding species rich sites but opportunistically colonise all types of pond.

The split into nested and idiosyncratic taxa in this study also appears related to differences in life history strategy. Idiosyncratic species tend to be active dispersers throughout adult life and possess adaptation to drought in one or more life stage, such as semi terrestrial larvae, short larval duration and/or aquatic larvae that can survive in moist mud (Williams 1987). Many are known to utilise small sites that fill during spring for reproduction (e.g. *Helophorus brevipalpis, Hydroporus planus* (Fabricius) and *Agabus bipustulatus* (L.); Landin & Stark 1973, Fernando 1958). Such species retain the ability to disperse throughout adult life and can track environmental change, dispersing to permanent refugia during the summer months (Svensson 1998; 1999, Landin & Stark 1973, Pajunen & Jansson 1969;). In comparison nested taxa (e.g. *Noterus clavicornis, Haliplus variegates,* and *Sigara nigrolineata*) are less frequently found in highly temporary water-bodies, and show reduced ability and/or tendency to fly (Young 1965, Brown 1951, Jackson 1950).

Factors structuring nested subsets in ponds might be viewed as probabilistic filters (Wright *et al.* 1998) which act at the individual species level to limit the spatial distribution of species with narrow ecological tolerance or low dispersal tendency. The degree of nestedness measured at assemblage-level summarises the response of species in the regional pool to these filters. Nestedness analysis alone, however, fails to elucidate processes that structure assemblage composition across a region. Approaches that utilise more stringent null models and examine the spatial response of nested and idiosyncratic taxa to ecological factors are essential if the processes that generate nested pattern are to be understood.

4 Colonisation dynamics in newly created temporary ponds

4.1 Abstract

Temporary ponds support many scarce animal and plant taxa. However, the density of temporary water bodies is declining across Europe, emphasising the need for successful habitat creation. In this study, fourteen small replicate ponds were created on grassland and heathland plots on the Lizard Peninsula (Cornwall, UK) to examine patterns in physicochemistry and plant and macroinvertebrate colonisation and evaluate the use of habitat creation in temporary pond conservation.

Ponds created on grassland and heathland had significantly different mean physicochemistry and plant assemblage composition. Physicochemical similarity between the ponds also varied over the three years following pond creation; seasonal variation within grassland and heathland plots was consistently greater than variation between plots. Mean macroinvertebrate assemblage composition was also significantly different between grassland and heathland sites. Initially grassland ponds accumulated more macroinvertebrate taxa on average, but after three years a total of 43 taxa had occurred in both grassland and heathland ponds. In the first year differences in the assemblage composition between heathland and grassland plots was greater than within plot seasonal variation. However, macroinvertebrate assemblage similarity converged with pond age, despite continued variation in physicochemistry, as both between and within-plot variation in assemblage composition was reduced in years two and three. Coleopteran assemblage similarity (based on abundance) was significantly correlated with both physicochemical and plant assemblage similarity. However the occurrence of coleopteran species was unrelated to physicochemistry or vegetation composition, suggesting that colonisation was independent of pond characteristics, but that subsequent larval survival might depend on these parameters.

The macroinvertebrate assemblages of grassland and heathland ponds were not significantly different from those found in small natural ponds in the region. Experimental sites were colonised by a high abundance of taxa found to be idiosyncratic in nestedness analysis, which are typical of small natural sites (e.g. *Helophorus* spp and *Graptodytes flavipes*), but were also sporadically colonised by a number of nested taxa, usually characteristic of more permanent waters (e.g. *Enochrus fuscipennis* and *Haliplus ruficollis*). Small ponds can therefore be successfully created on the Lizard, which rapidly resemble existing sites and increase habitat availability for taxa of conservation concern.

4.2 Introduction

Many organisms live in spatially and temporally discrete environments where regional processes, such as dispersal play a key role in determining individual fitness and influence population dynamics and assemblage succession (Cáceres & Soluk 2002, Rundle *et al.* 2002). In freshwaters both local and regional processes have been shown to be important in structuring assemblages (e.g. Kiflawi et al. 2003, Shurin 2001, Shurin 2000, Shurin *et al.* 2000, Blaunstein *et al.* 1999, Jenkins & Buikema 1998, Wilbur 1997, Schneider & Frost 1996, Jenkins 1995, Jeffries 1994, Sheldon 1984) although their relative importance is still not well understood (Havel & Shurin 2004). Local processes may be expected to play a more dominant role when dispersal occurs more often than extinction (Cohen & Shurin 2003, Okamura & Freeland 2002). Kiflawi *et al.*'s (2003) study of pond assemblage composition showed that pond permanence, which governs local extinction, mediated the relative importance of local and regional factors. Local processes are, therefore, more likely to structure permanent pond macroinvertebrate assemblages, where extinction is infrequent. In contrast, local assemblages of macroinvertebrates inhabiting small, highly ephemeral temporary ponds are likely to be governed by regional processes such as dispersal.

Temporary pond ecosystems have been recognised as an important habitat for numerous rare animal and plant species (Collinson *et al.* 1995, Bratton 1990, Whitten 1990). However, the density of temporary water bodies is declining throughout Europe due to land drainage, water abstraction, intensification of agriculture and increased urbanisation (Maier *et al.* 1998). The number of UK ponds has steadily fallen this century (Wood *et al.* 2003) and estimates of the proportion of ponds lost since 1945 vary between 28% (Barr et al. 1994) and 38% (Swan & Oldham 1989). This trend in habitat loss continued until 1990 (Barr *et al.* 1994), after which UK pond density apparently increased ca. 4% by 1998 (DEFRA Countryside survey 2000). Regional estimates show a similar picture; Essex is reported to have lost 55% of its ponds between 1870 and 1960, and a further 23% between 1960 and 1989 (Heath & Whitehead 1992) and losses of 21%, between 1977 and 1996, in Sussex (Beebee 1997) and 11%, between 1985 and 1994, in Cambridgeshire (Cambridgeshire Pond Habitat Action Plan, 2003) have also been reported.

In addition to direct habitat loss, pond ecosystems are also threatened by eutrophication, acidification, pollution and invasive species (Wood *et al.* 2003, Powell 2001, Bellemakers & van Dam 1992, Lahr 1999). Even in regions where these risks are minimised ponds can be endangered by alterations in land use which change the disturbance regime of ponds, with consequences for pond physicochemistry and floral succession which can reduce the distribution and abundance of rare taxa (e.g. Edwards *et al.* 2000, Maier *et al.* 1998, Grillas & Roché 1997). The diverse range of threats to pond ecosystems and the reduction in their national and regional density highlight the need for increased habitat protection and, where feasible, mitigation via habitat creation.

Formal studies of the creation and subsequent development of the assemblages of complexes of ponds are still relatively rare (e.g. Jenkins & Buikema 1998, Jenkins 1995, Layton & Voshell 1991, Fernando 1958). More often studies have compared the macroinvertebrate assemblages of ponds of different ages or successional stages (e.g. Gee *et al.* 1997, Barnes 1983) or have examined assemblage development in outdoor mesocosms (e.g. Wilbur 1997, Blaunstein *et al.* 1996, 1999). Studies of newly created temporary pond habitats are particularly infrequent but Lichko & Calhoun (2003) have found that man-made temporary pond habitats often do not replace the function of temporary ponds which have been lost from the landscape. The current trend of increased pond density in the UK is likely to be partially due to an increase in the number of garden ponds, but such urban increases are unlikely to mitigate the loss of pond complexes from the wider landscape (DEFRA Countryside survey 2000).

This study examines macroinvertebrate assemblage development in a complex of fourteen newly created temporary ponds. Ponds were created on heathland and unimproved grassland plots on the Lizard Peninsula; a region highlighted because of the presence of putative Mediterranean Temporary Ponds (MTPs), an EU priority habitat that is rare in the UK. Experimental ponds were small and highly ephemeral, mimicking the proposed MTP sites present in the landscape. The aims of the study were to: (i) compare the rate and contingency of colonisation of small temporary ponds on grassland and heathland; (ii) examine whether pond assemblage composition (within and between plots) becomes more similar through time, or whether community assembly was reset after dry down each year; (iii) test whether pond physicochemistry and plant assemblage composition were correlated with the macroinvertebrate assemblages that develop; and (iv) assess the potential use of habitat creation in temporary pond conservation by comparing the experimental pond assemblages with samples from similar sized natural ponds.

4.3 Methods

4.3.1 Pond creation

Fourteen small temporary ponds were created on two 50m by 50m plots 0.4km apart on heathland (SW680149) and grassland (SW678152) on the Lizard Peninsula. In each area, seven replicate ponds (4m^2 square with a maximum depth of 30cm; Figs 4.1 & 4.2), were dug at random co-ordinates. Each plot was approximately equidistant from potential sources of colonising species, as natural ponds were dotted throughout the landscape.

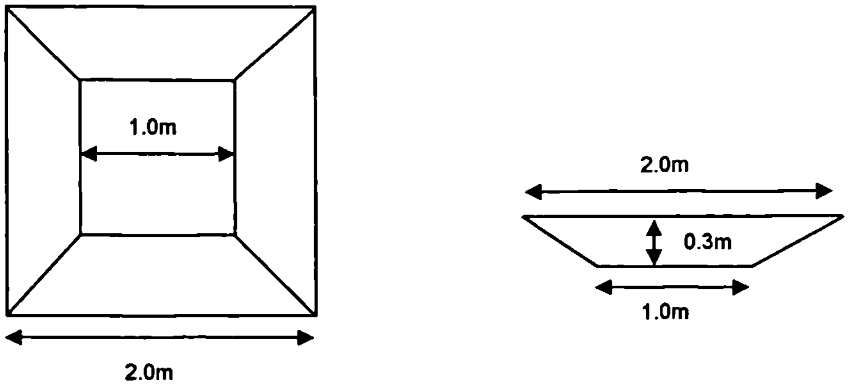


Figure 4.1: Experimental pond dimensions

4.3.2 Sampling

Ponds were sampled monthly/bimonthly when wet from April 2000 to April 2003 (appendix 4.6.1), although no data were collected between February and November 2001 due to Foot and Mouth restrictions preventing fieldwork access.

a) September 2000 grassland pond (G1)

b) September 2000 heathland pond (H5)

c) November 2000 grassland pond (G6)

d) November 2000 heathland pond (H3)

e) March 2001 grassland pond (G2)

f) March 2001 heathland pond (H5)

Figure 4.2: Example photographs of the experimental ponds

4.3.2.1 Physicochemistry

On each sampling occasion area and maximum water depth were measured and where the water was deep enough, pH, temperature and conductivity readings were taken on-site using a Solomat 520C probe. Pond permanence was measured as the proportion of sampling trips over the three year period that each pond had been wet. In order to further characterise initial colonisation conditions turbidity, metal cation and nutrient concentrations were also measured during the first year. Water samples from each pond were collected in acid washed, polypropylene bottles, refrigerated and vacuum filtrated using Whatman cellulose acetate filter papers within 24h. Metal cation concentrations were analysed in the laboratory by atomic absorption spectroscopy. Cations measured were magnesium, sodium, aluminium, nickel, chromium, cobalt, iron, zinc and copper. Water samples were also analysed for total organic nitrate (TON) and soluble reactive phosphorus (SRP) concentrations using a Dianex autoanalyser.

4.3.2.2 Biota

Macroinvertebrates were sampled using a hand net (1mm mesh, area 20 x 25cm). To prevent unintentional transfer of species the net was rinsed in 70% industrial methylated spirit followed by distilled water between ponds. Ponds were vigorously netted, the sample was then tipped into a white tray and sorted; netting continued until no new taxa were collected. All Coleoptera adults were identified to species and counted, other macroinvertebrate taxa and Coleoptera larvae were identified as far as possible in the field and recorded as present. All animals were returned to the pond after identification. The occurrence of plant taxa in each of the ponds was also recorded over the three years, on a presence/absence basis.

4.3.3 Physicochemical development

Differences in mean pond physicochemistry were compared in order to examine whether grassland and heathland pond conditions were similar. In addition within and between-plot differences in physicochemistry were compared through time to examine whether heathland and grassland pond physicochemistry became more similar through time.

Firstly, overall differences in grassland and heathland physicochemistry were examined by comparing mean physicochemistry (across sampling dates for each pond) using Principle Components Analysis (PCA). PCA is suitable for physicochemical data which can be described by euclidean distance (Clarke & Warwick 2001). Differences in the physicochemistry of grassland and heathland ponds were also assessed using ANalysis Of SIMilarity (ANOSIM; see section 2.3.6) and univariate t tests.

Changes in physicochemistry over the three years were then examined by calculating mean grassland and heathland physicochemistry parameters on each sampling occasion. Univariate trends in physicochemical variables were firstly examined in order to determine whether grassland and heathland physicochemistry varied in synchrony though time. Multivariate trajectories, for mean grassland and heathland physicochemistry were then plotted using PCA and distances between heathland and grassland ponds on each sampling occasion were calculated from the PCA co-ordinates. Means distance between grassland and heathland samples was then calculated for each wet phase (2000/1, 2001/2 & 2002/3) and compared. If grassland and heathland physicochemistry became more similar through time mean between plot distance would diminish. Finally, within-plot, or seasonal change, in physicochemistry was examined, by calculating and comparing the mean distance between consecutive samples in PC space for each wet phase, for grassland and heathland ponds separately.

Physicochemical data were checked for normality and heteroscedasticity of residuals prior to univariate statistical analysis and variables were transformed ($\log_{10}$ used for all variables except permanence which was arcsine transformed and pH which remained untransformed) and standardised before multivariate techniques were applied.

4.3.4 Macroinvertebrate assemblages

4.3.4.1 Univariate diversity and taxon accumulation

In order to compare the rate of colonisation of grassland and heathland ponds taxon accumulation curves were constructed. Grassland and heathland plots had different permanencies, so the number of ponds available for colonisation varied on each sampling date; the effects of differences in sampling intensities between the plots were therefore examined by plotting the cumulative number of species against the cumulative number of ponds wet. In addition the cumulative number of taxa was adjusted by the cumulative number of ponds wet and plotted against time.

The total numbers of taxa per pond were also corrected for the number of sampling occasions the pond remained wet (no. taxa/no. sampling occasions pond was wet) and compared between plots using t tests. One way unbalanced ANOVA was also used in conjunction with pair-wise Tukey tests to compare the total number of taxa recorded between months and years. Before univariate analyses macroinvertebrate data were checked for normality and heteroscedasticity of residuals.

4.3.4.2 Assemblage composition

Differences in macroinvertebrate assemblage composition were compared in order to examine whether grassland and heathland assemblages differed. In addition, within and between-plot differences in assemblage composition were compared through time to examine whether heathland and grassland pond assemblages became more similar as succession progressed.

Three data sets were generated (i) overall mean coleopteran abundance per pond, (ii) overall presence absence of Coleoptera per pond (as Coleoptera were the most species rich and abundant group in the ponds) and (iii) overall presence absence of all taxa per pond. An MDS plot based on Bray-Curtis similarity was produced for each data set (beetle abundance was 4th root transformed in order to down-weight the most abundant species; Clark & Warwick 2001) and then one-way ANOSIM was used to test each data set for significant differences in assemblage structure between grassland and heathland ponds.

Between-plot differences in assemblage composition were compared through time by generating three similar data sets, describing the mean assemblage structure for grassland and heathland ponds on each sampling occasion (mean Coleoptera abundance through time, presence absence of Coleoptera through time and presence absence of all taxa through time). Multivariate trajectories were plotted in MDS space, based on Bray-Curtis similarity, and the distance between heathland and grassland ponds on each sampling occasion was calculated from the MDS co-ordinates. The mean distances between grassland and heathland samples for each wet phase (2000/1, 2001/2 & 2002/3) could then be compared allowing trends in grassland and heathland similarity through time to be examined. Finally, within plot seasonal change in assemblage composition was inspected by calculating the mean distance between consecutive samples in MDS space for each wet phase, for grassland and heathland ponds separately.

4.3.5 Relationship between macroinvertebrates, plants & physicochemistry

In order to examine the influence of physicochemistry on species richness the relationship between physicochemical variables and the total number of taxa per pond were investigated using correlation. In addition the multivariate influence of pond physicochemistry and plant composition on macroinvertebrate assemblage structure was examined using Mantel test statistics. Mantel tests are commonly used to correlate multivariate similarity/distance matrices (Dale *et al.* 2002, Mantel 1967). All analyses were based on the standardised Mantel statistic and performed using The R Package (Casgrain & Legendre 2001); significance was assessed by comparison with 999 random permutations of the first data matrix.

Firstly three measures of macroinvertebrate assemblage similarity were calculated: Steinhaus similarity for mean coleopteran abundance and Jaccard similarity for presence absence of Coleoptera and all taxa. Jaccard similarity was also used to describe plant assemblages but physicochemical dissimilarity was described by euclidean distance. Jaccard similarity is suitable for presence absence data whereas Steinhaus similarity can be used for measures of abundance, neither measure incorporates the common absence of species (Casgrain & Legendre 2001). Plant similarity and physicochemical similarity were significantly correlated, so their effects on macroinvertebrate similarity were separated using partial Mantel tests (Dale *et al.* 2002, Mantel 1967). Partial Mantel statistics were therefore calculated between each of the three measures of macroinvertebrate similarity and: (i) physicochemical dissimilarity and (ii) plant assemblage similarity.

4.3.6 Comparison with natural pond assemblages

Presence absence assemblage data collected from experimental ponds during February 2001, 2002 and 2003 were compared with data from small natural ponds (area <10m^2) for February 2000 (see chapter 2). Although natural and experimental pond data were not strictly comparable (due to potential inter-annual variation between natural and experimental samples) this analysis allowed examination of how closely assemblages in man-made ponds resembled those in small natural sites.

Firstly, natural and experimental pond data were standardised to ensure they covered the same taxonomic scope (e.g. chironomids were not recorded for the experimental sites so they were removed from the natural pond data sets) so that any observed difference between natural and experimental pond assemblages was not an artefact of differences in taxonomic resolution. The mean number of taxa in ten natural sites (area $<10m^2$) was then compared with: (i) the number of taxa in the experimental ponds during February 2001, 2002 and 2003 and (ii) the taxon richness of grassland and heathland ponds, pooled across years, using unbalanced one-way ANOVA followed by pair-wise Tukey tests.

Differences in macroinvertebrate assemblage structure between natural and experimental ponds were then examined by constructing an MDS plot of the natural and experimental pond data based on Bray-Curtis similarity. One way ANOSIM was then used to examine significant differences between the natural and experimental ponds. All MDS and ANOSIM analyses were performed using PRIMER v5 (Plymouth Routines In Multivariate Ecological Research; Clarke and Gorley 2001) and Minitab v13.0 was used for univariate statistics.

4.4 Results

4.4.1 Physicochemical development

Grassland and heathland ponds differed physicochemically (appendix 4.6.2). Grassland ponds were significantly deeper and less permanent and had higher mean turbidity and phosphate concentration but lower conductivity than heathland ponds (Table 4.1).

Variable	T	p	
area	-1.13	ns	
depth	3.4	<0.01	grass > heath
permanence	3.31	<0.01	heath > grass
pH	1.51	ns	
conductivity	-2.33	<0.05	heath > grass
turbidity	5.47	<0.001	grass > heath
temperature	0.04	ns	
nitrate	1.55	ns	
phosphate	3.33	<0.05	grass > heath

Table 4.1: Comparison of grassland and heathland physicochemistry based on transformed mean measures per pond replicate

These differences were reflected in the scores on axes 1 and 2 of the PCA (Fig. 4.3), which explained 55.1% of the variation in the physicochemical data (Table 4.2). One grassland pond (G1) had physicochemistry that was more similar to heathland ponds than other grassland replicates. ANOSIM analysis showed that the difference between mean heathland and grassland physicochemistry was significant (Global R = 0.624, p < 0.001).

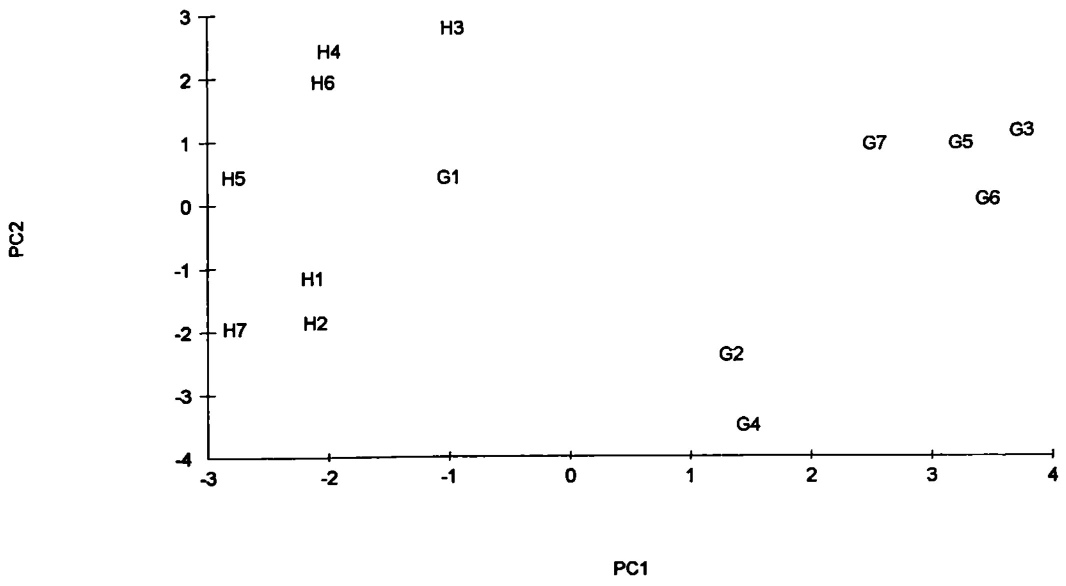


Figure 4.3: First two Principle Components of the transformed and standardised mean physicochemical data (55% of the variation explained)

Variable	PC1 34.9% variation	PC2 20.2% variation
area	-0.137	0.367
depth	0.325	0.214
permanence	-0.331	-0.094
pH	0.277	0.222
conductivity	-0.164	0.352
turbidity	0.258	-0.314
temperature	0.067	0.087
nitrate	0.081	-0.312
phosphate	0.344	-0.044
Cu	-0.232	0.107
Zn	-0.098	-0.409
Fe	-0.203	-0.251
Co	0.119	0.195
Cr	-0.35	-0.070
Ni	0.274	-0.169
Al	-0.292	-0.215
Mg	-0.212	0.230
Na	-0.144	0.143

Table 4.2: Eigenvalues for each physicochemical variable used in PCA

Mean grassland and heathland physicochemical variables, except turbidity, fluctuated in synchrony though time, despite differences in their absolute values (Figs 4.4). Turbidity was consistently greater in grassland ponds. Mean pH appeared to increase through the wet phase in both grassland and heathland ponds during 2000/1 and 2002/3, but during 2001/2 when pH was greater and more variable (Fig 4.4e).

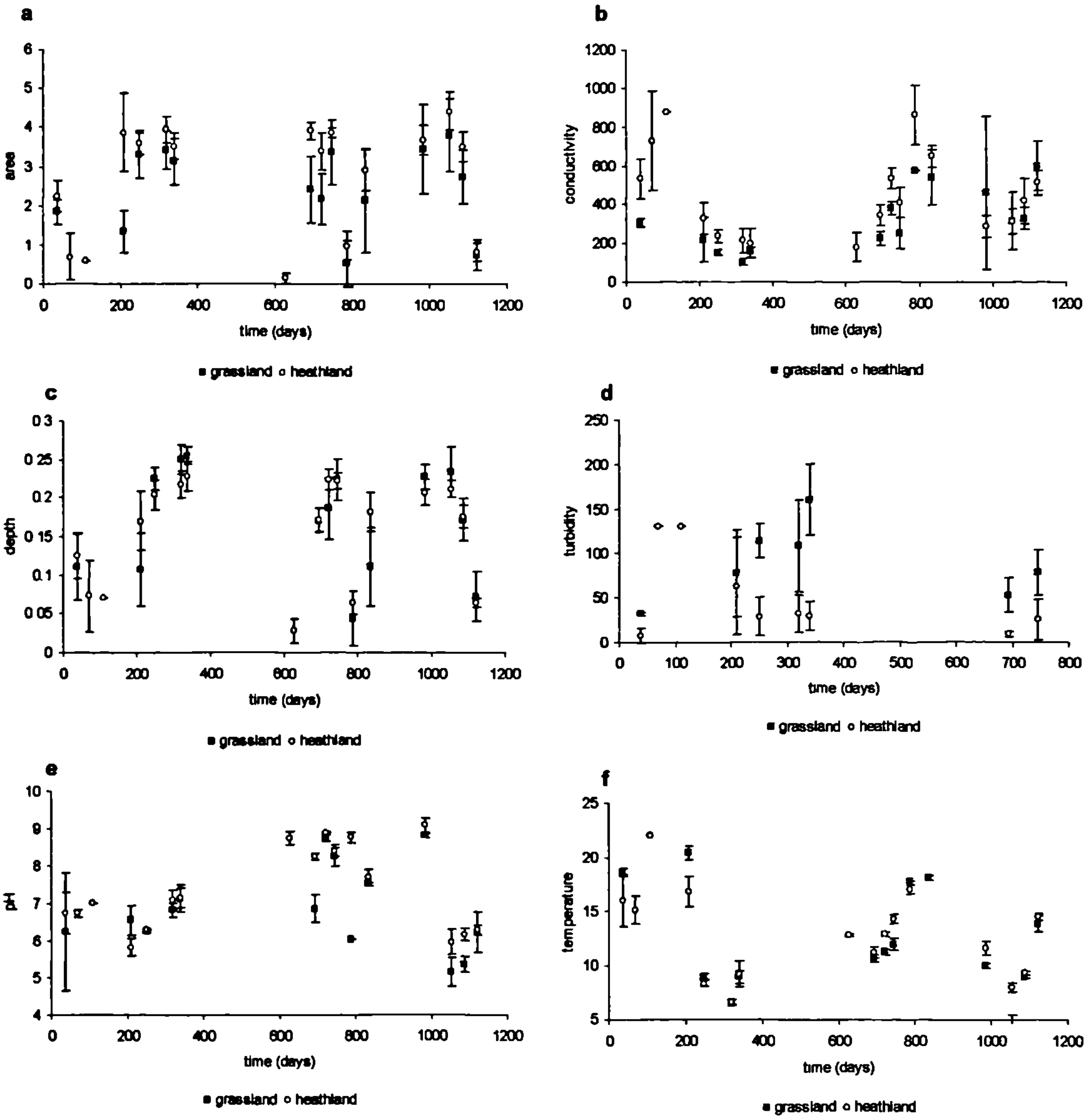


Figure 4.4: Comparison of mean (± sem) grassland and heathland physicochemistry through time. Means taken across all replicate ponds wet on each sampling occasion a) area, b) conductivity, c) depth, d) turbidity, e) pH, f) temperature

Axes 1 and 2 of the PCA of mean physicochemistry through time explained 76.2% of the variation in the data and temporal variation was primarily related to changes in pond depth, area and pH

(Table 4.3). Within plot (seasonal) variation in pond physicochemistry was greater than between plot variation in physicochemistry in all years (Fig. 4.5). Neither within or between plot variation showed a decreasing trend between years, indicating that physicochemical variation did not diminish as succession progressed (Fig. 4.5).

	PC1	PC2
Variable	54.1% variation	22.1% variation
area	0.525	-0.316
depth	0.556	-0.307
pH	-0.095	-0.798
cond	-0.416	-0.299
temp	-0.483	-0.281

Table 4.3: Eigenvalues for each of the physicochemical variables used in the Principle Components Analysis (PCA)

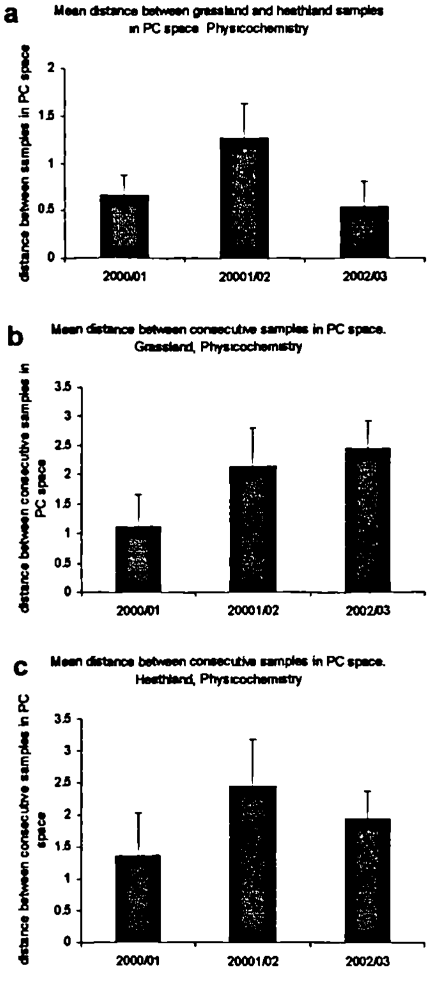


Figure 4.5: Mean variation in physicochemistry for each wet phase calculated from inter-sample principle component distances a) mean variation between grassland and heathland samples, b) mean seasonal variation within grassland ponds and c) mean variation within heathland ponds.

4.4.2 Plant assemblage composition

Heathland and grassland ponds differed in the occurrence of plant taxa (Table 4.4) and ANOSIM showed that heathland and grassland plant assemblages differed significantly (Global R = 0.597, p <0.01). Heathland ponds had greater incidence of *Juncus bulbosus, Glyceria fluitans, Ranunculus flammula* and *Callitriche* spp whereas grassland pond replicates were dominated by *Carex* and Poaceae species that encroached from the surrounding field. The Red Data Book species, *Ranunculus tripartitus* colonised one of the grassland ponds within a year, but did not occur in any of the heathland sites.

Plant taxa	H1	H2	H3	H4	H5	H6	H7	G1	G2	G3	G4	G5	G6	G7
Anagalis arvensis										1				
Bryophytes								1	1					
Callitriche spp		1	1	1	1			1						
Carex spp	1	1								1	1	1	1	1
Glyceria fluitans	1	1	1	1	1	1	1	1	1					
Poaceae	1	1						1	1	1	1	1	1	1
Juncus bulbosus		1	1	1	1	1	1	1						
Juncus articulatus		1												
Ranunculus flammula	1	1	1	1	1	1	1	1	1					
Ranunculus repens		1												1
Ranunculus tripartitus														1

Table 4.4: Occurrence of plant taxa found in grassland and heathland ponds over three years

4.4.3 Macroinvertebrate assemblages

In total, forty eight macroinvertebrate taxa were recorded, including 35 coleopteran species, three hemipteran genera, two mollusc species and four dipteran families (appendix 4.6.3). In addition *Triturus helveticus* (palmate newt), *Rana temporaria* (common frog) and *Bufo bufo* (common toad) were also present in a subset of the ponds and tadpoles of *R. temporaria* were observed in the heathland ponds each year (appendix 4.6.7). Twelve coleopteran species were found to be ubiquitous, occurring at least once in all fourteen ponds (appendix 4.6.3) and seventeen taxa were rare, occurring in <3 ponds.

4.4.3.1 Univariate diversity and taxon accumulation

No significant difference in overall taxon richness (i.e. total number observed over whole study) was observed between grassland and heathland pond replicates ($T_9 = -1.44$, $p > 0.05$) although there were significantly greater numbers of Coleoptera species in heathland ponds ($T_9 = -2.40$, $p < 0.05$). However, when the number of taxa per pond was corrected for pond permanence neither the total number of taxa or the number of Coleoptera species were significantly different between habitats ($T_9 = -0.79$, $p > 0.05$ and $T_9 = -0.22$, $p > 0.05$, respectively).

Overall taxon accumulation curves show that heathland ponds (23 taxa after 38 days) were colonised more quickly than grassland ponds (13 taxa), although after three years both grassland and heathland sites had accrued 43 taxa and the fitted exponential models show that both plots had accrued the same amount of taxa after 900 days (Fig. 4.6a). When the pattern of accumulation with sampling intensity was examined grassland and heathland plots fitted exponential models. Both plots accumulate the same number of taxa (37) after 53 pond samples which is equivalent to gaining 0.7 (37/53) extra species per additional pond sampled (Fig 4.6b). This rate of accrual was achieved after 590 days on the heathland plot and 760 days on the grassland plot (Fig 4.6c). The rate of taxon accrual per pond was greater throughout the study on the grassland plot (Fig 4.6c) but the greater permanence of heathland sites meant there was more available habitat for taxa to colonise, so greater heathland richness was observed at the start of the study (Fig 4.6a). Overall total taxon diversity was therefore similar across the two plots after three years but the rate at which colonisation proceeded differed.

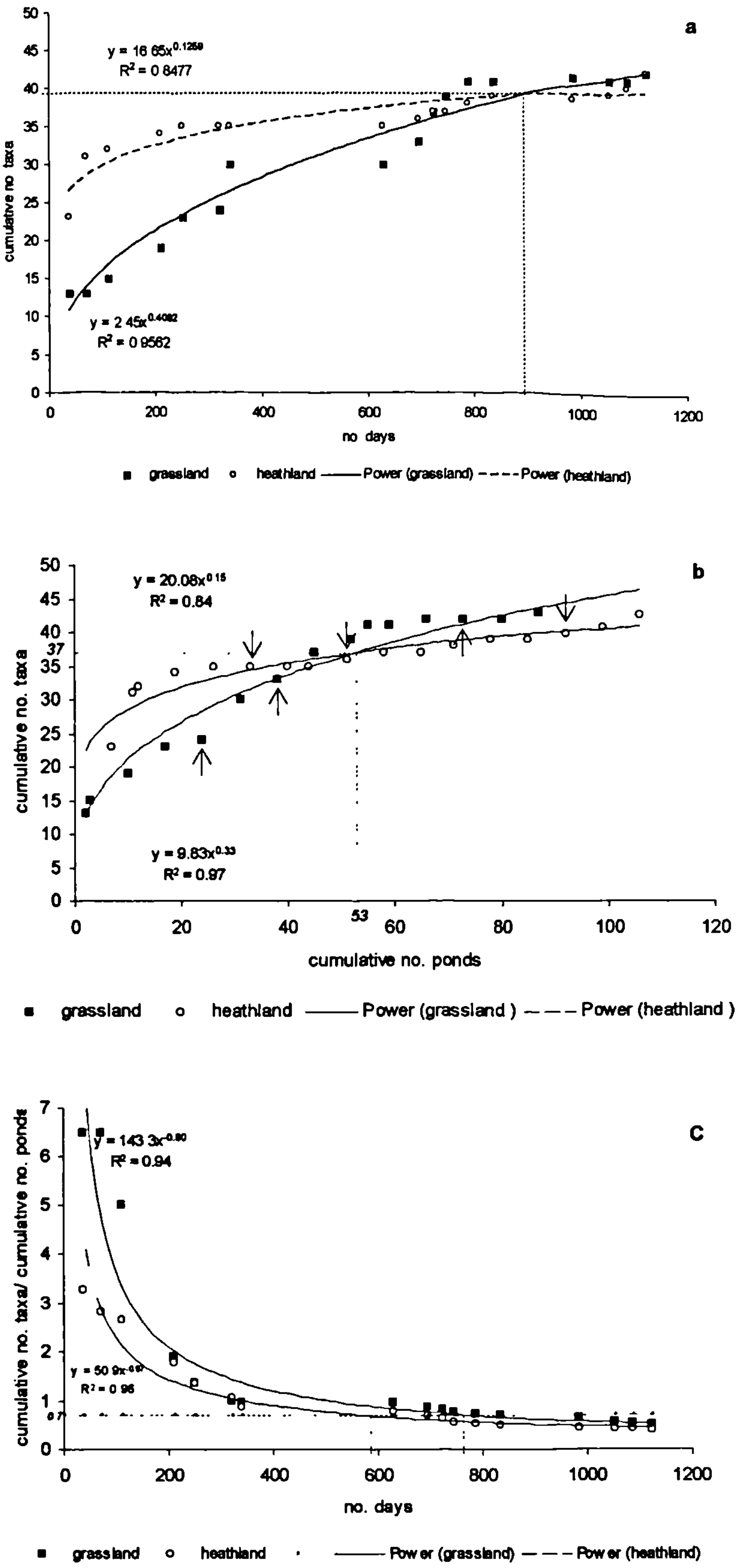


Figure 4.6: a) Cumulative no. of taxa recorded in heathland and grassland ponds through time b) Cumulative no. of taxa against no. ponds sampled - arrows indicate Jan 2001, Jan 2002 & Jan 2003 c) Cumulative no. of taxa corrected for the cumulative number of ponds remaining wet through time.

Order and timing of colonisation differed between grassland and heathland plots (appendices 4.6.4 & 4.6.5). All of the 13 initial colonisers of grassland ponds were Coleoptera species, including 8 of the 12 ubiquitous beetle species (appendix 4.6.3) plus *Ochthebius dilatatus, Hydroporus planus, Graptodytes flavipes, Dryops luridus* and *Agabus bipustulatus* (appendix 4.6.4). Heathland ponds were initially colonised by all the species found in grassland sites (including all 12 of the ubiquitous beetle species) plus *Helophorus alternans, Helophorus minutus, Hydroporus melanarius, Paracymus scutellaris, Limnephilus* spp and oliochaetes (appendix 4.6.5). Absolute species richness appeared to converge after ca. 200 days and after 320 days grassland and heathland species richness began to fluctuate in synchrony through time (Fig. 4.7).

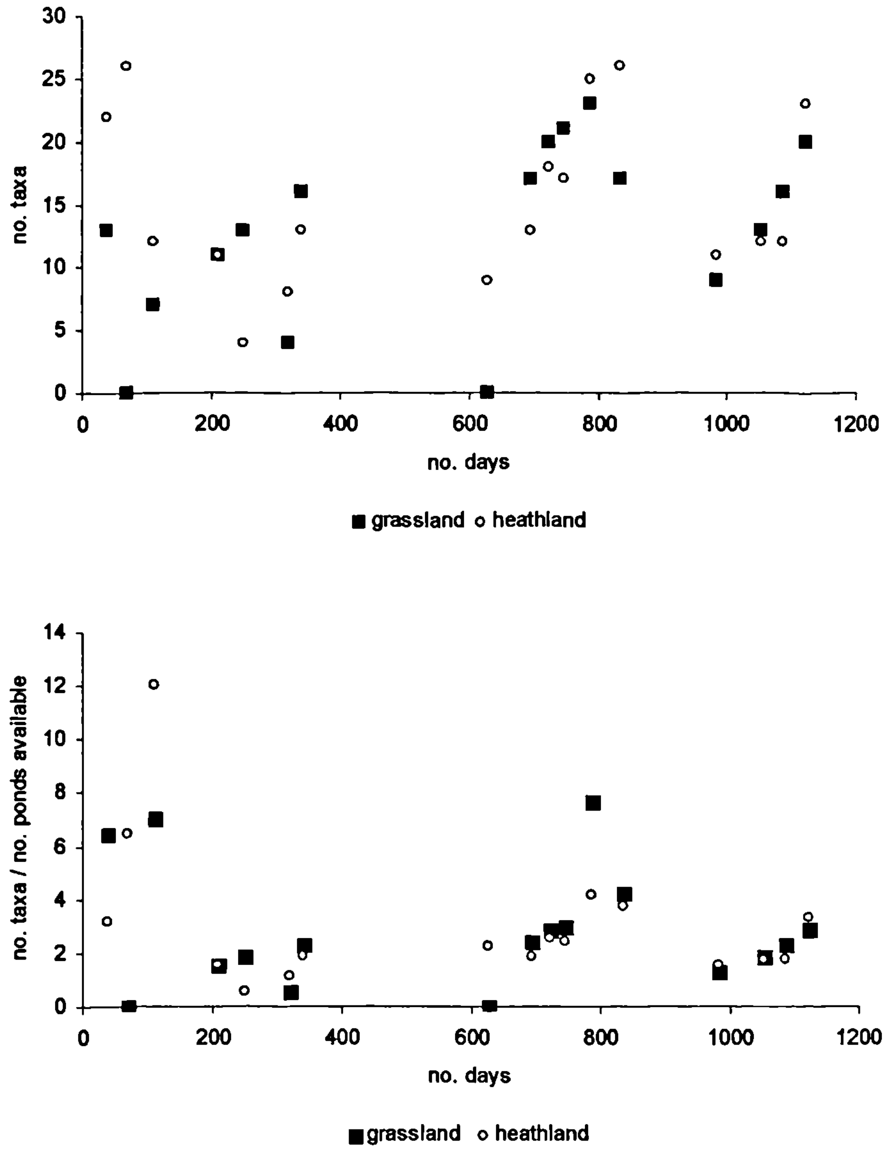


Figure 4.7: a) absolute number of taxa recorded in grassland and heathland ponds April 2000 to April 2003, b) absolute number of taxa recorded corrected for number of ponds wet on each sampling occasion.

There were significant increases in the mean number of taxa per pond between January 2001 and 2002//3 ($F_{2,39}$ = 21.32, $p < 0.001$) and February 2001 and 2002/3 ($F_{2,39}$ = 7.08, $p < 0.01$), however there was no significant differences in the mean number of tax per pond between years during November and April (Fig. 4.8). Mean taxon richness was shown to significantly increase throughout the wet phase from November/January to February and April across all years ($F_{3,149}$ = 14.88, $p < 0.001$; Fig. 4.8).

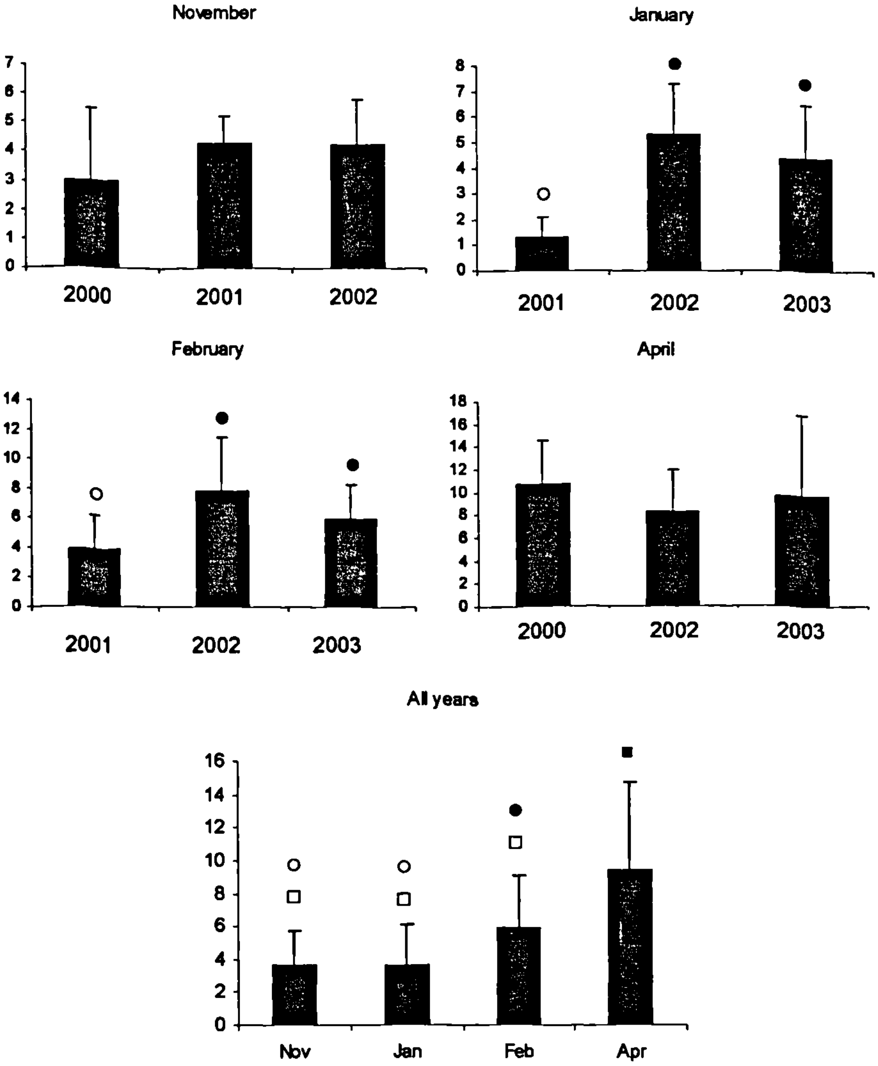


Figure 4.8: Mean number of taxa (± sd) across all wet ponds for each year November, January, February, April and mean for each month across all years, filled and open symbols indicate significant difference between means

4.4.3.2 Assemblage composition

Mean grassland and heathland assemblage composition was shown to be significantly different no matter which of the data sets were used (Fig. 4.9; Table 4.5), although the difference was most pronounced when coleopteran abundance (Fig. 4.9a) or presence/absence of all taxa (Fig. 4.9c) were used.

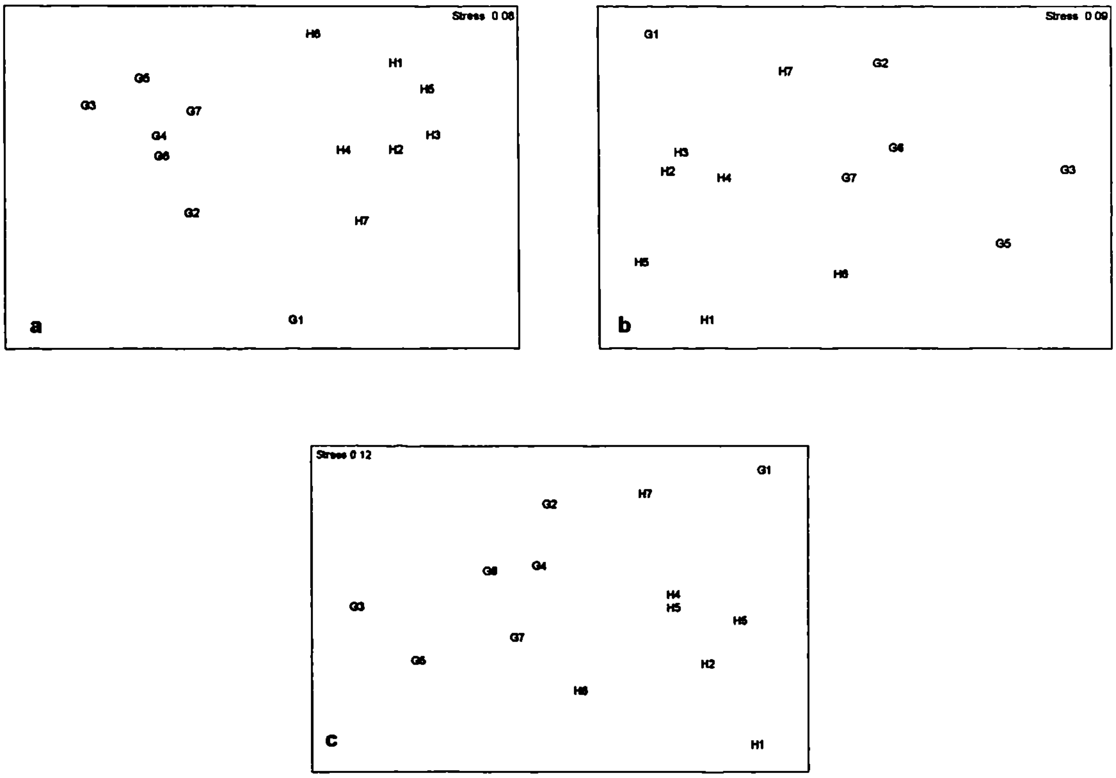


Figure 4.9: MDS plots of Bray-Curtis similarity for each pond replicate a) mean beetle abundance (fourth root transformed), b) presence absence of beetles and c) presence absence of all taxa

	Difference between grassland and heathland ponds	
Similarity matrix	Global R	p
(i) Coleoptera abundance	0.828	< 0.005
(ii) Coleoptera presence absence	0.447	< 0.005
(iii) All taxa presence absence	0.562	< 0.005

Table 4.5: ANOSIM results, significant differences between grassland and heathland pond assemblages

The MDS plots, summarising assemblage composition through time, failed to highlight any obvious temporal patterns between or within the grassland and heathland ponds (Fig. 4.10). However, all three data sets showed the same overall patterns in within and between plot variation in assemblage composition when distances between samples, in MDS space, were examined (Fig 4.11). Between plot variation in composition was greatest during the first wet phase, after which grassland and heathland sites became more similar, as between plot variation diminished (Fig. 4.11 a, b & c). Between plot variation was also greater than seasonal variation during the first wet phase, after this though within and between plot variation were of similar magnitude (Fig. 4.11) Seasonal variation was also shown to lessen through time, showing that macroinvertebrate assemblage structure became more homogeneous amongst ponds through both time and space as succession progressed (Fig. 4.11 d-i).

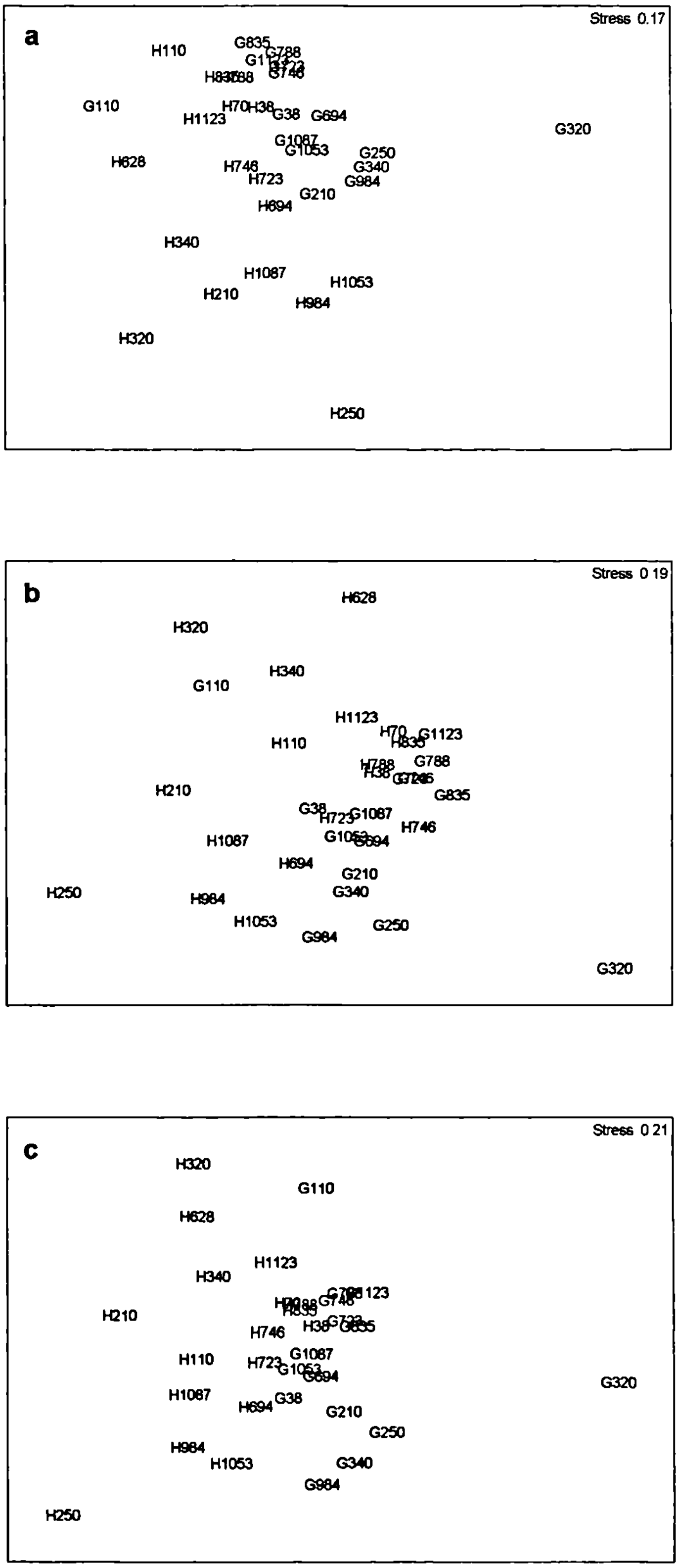
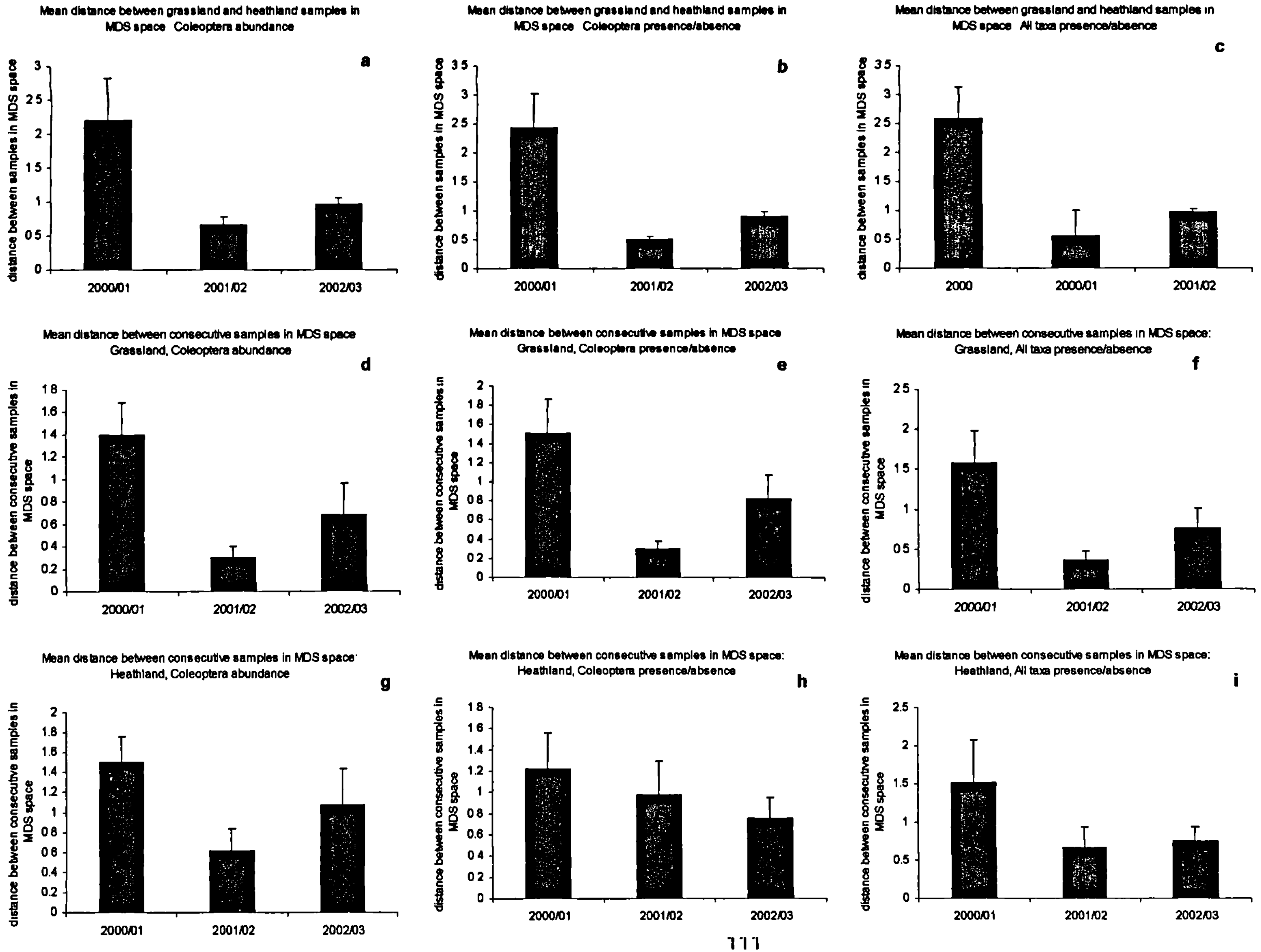


Figure 4.10: MDS plots of Bray-Curtis similarity for mean assemblage composition across replicates through time a) mean beetle abundance (fourth root transformed), b) presence absence of beetles and c) presence absence of all taxa.

Figure 4.11: Within (a-c) and between (d-i) plot variation in heathland and grassland macroinvertebrate assemblage composition for Coleopteran abundance (a, d & g), Coleopteran presence/absence (b, e & h) and presence/absence of all taxa (c, f & i), calculated from the MDS distances between samples



4.4.4 Relationship between macroinvertebrates, plants & physicochemistry

Overall taxon richness in individual ponds was positively correlated with pond permanence but decreased with increasing pond depth, pH and phosphate concentration (Table 4.6).

Correlation with $\log_{10}$ no taxa	r	p
area	0.24	ns
depth	-0.573	<0.05
permanence	0.701	<0.01
pH	-0.677	<0.01
conductivity	-0.063	ns
turbidity	-0.192	ns
temperature	-0.042	ns
nitrate	0.086	ns
phosphate	-0.616	<0.05

Table 4.6: Results of correlations between log overall number of taxa per pond (total number recorded over three years) and transformed and standardised physicochemical parameters.

Ponds with similar plant assemblages tended to also have similar physicochemistry as pond physicochemical *dissimilarity* and plant *similarity* were significantly negatively correlated (standardised Mantel's r = -0.546, p <0.001). Partial mantel tests showed that assemblage similarity, based on Coleoptera abundance, was significantly related to both pond physicochemical and plant assemblage similarity (Table 4.7). However, the occurrence of beetle species was not significantly correlated with either physicochemistry or vegetation composition (Table 4.7). The occurrence of all taxonomic groups was significantly related to plant assemblage similarity, but not physicochemistry (Table 4.7).

Macroinvertebrates and physicochemistry (plant similarity factored out)	Mantel's standardised r	p
(i) Overall Coleoptera abundance (Steinhaus similarity)	-0.352	<0.01
(ii) Overall Coleoptera presence absence (Jaccard similarity)	-0.093	ns
(iii) Overall taxa presence absence. (Jaccard similarity)	-0.019	ns
Macroinvertebrates and plants (physicochemical dissimilarity factored out)		
(i) Overall Coleoptera abundance (Steinhaus similarity)	0.365	<0.01
(ii) Overall Coleoptera presence absence (Jaccard similarity)	0.155	ns
(iii) Overall taxa presence absence. (Jaccard similarity)	0.247	<0.05

Table 4.7: Partial Mantel tests examining the relationship between macroinvertebrate assemblage similarity and physicochemical and plant assemblage (dis)similarity

4.4.5 Comparison with natural pond assemblages

On average small natural ponds (<10m^2; sampled February 2000) contained significantly more taxa than the experimental ponds in February 2001 but there was no significant difference in 2002 and 2003. Larger natural sites (>10m^2) contained significantly more taxa than the experimental ponds in all years sampled ($F_{4,82}$ = 22.93, p <0.001; Fig. 4.12a). Small natural ponds had significantly more taxa than heathland ponds (pooled across years) however they were not significantly richer than grassland ponds ($F_{3,83}$ = 25.72, p <0.001; Fig. 4.12b).

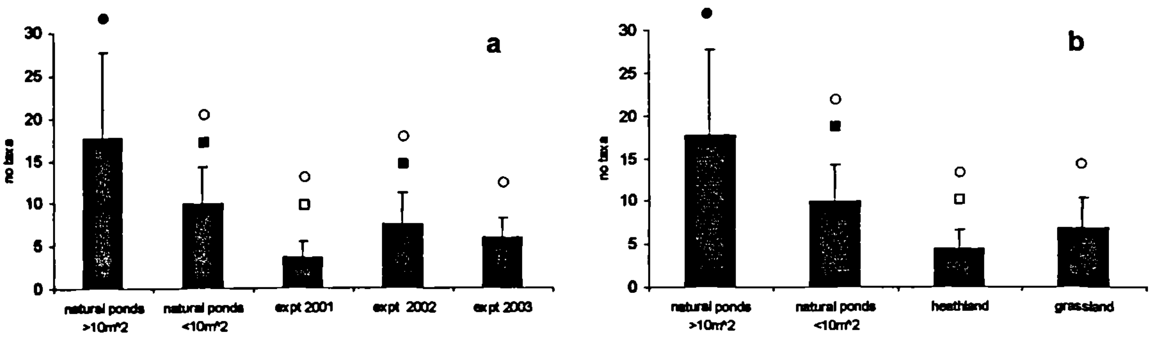


Figure 4.12: Mean number of taxa for natural ponds and experimental pond February samples a) compares experimental ponds between years and b) compares experimental ponds on heathland and grassland. Filled and open symbols indicate significant difference between means

Experimental ponds contained 43 taxa in total, with 29 of these present in February samples (appendix 4.6.6). A substantial number of these species were not found in natural ponds (22 from total and 10 from February data sets). Small natural ponds (<10m^2) supported 28 taxa in February of which 7 were not found in experimental ponds in any month (appendix 4.6.6).

Experimental pond composition was variable having a wide spread in MDS space. Grassland and heathland sites seemed equally variable although, in general, variation in assemblage composition both between and within plots appears to lessen between 2001 and 2003 (Fig. 4.13). Although there were significant between group differences between small natural pond assemblages and heathland and grassland ponds in different years (Table 4.8) when data were pooled across habitat types or across years fewer differences were observed. Small natural sites were not significantly different from heathland and grassland ponds (Table 4.9) or experimental ponds in 2001 or 2002 (Table 4.10).

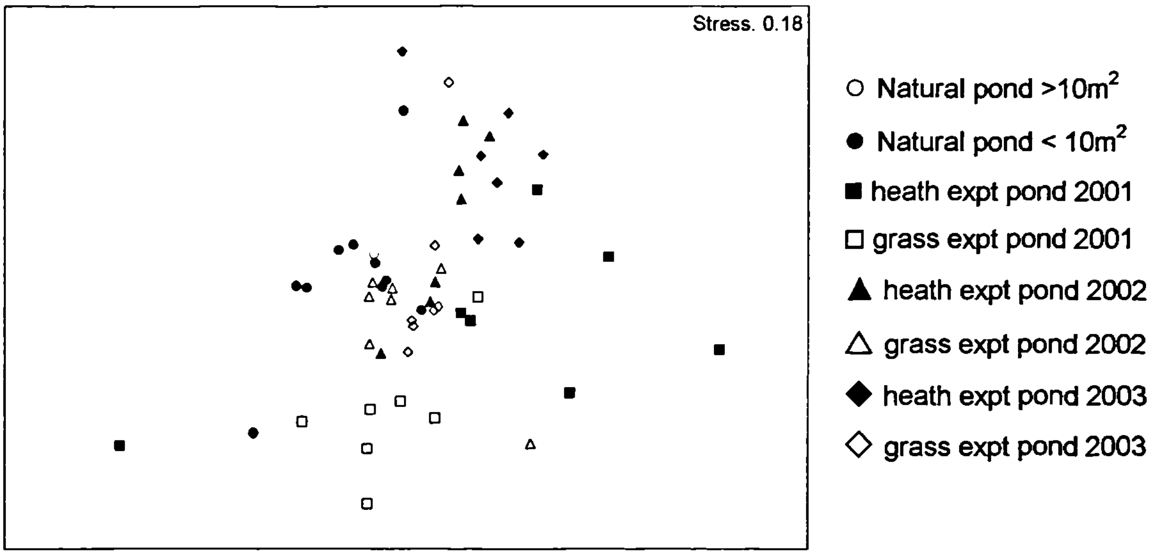


Figure 4.13: MDS plots showing the similarity between natural ponds (sampled February 2000) and experimental pond assemblage composition (February samples) separated by plot and year.

Global 0.334, p <0.001

	Natural >10m^2	Natural <10m^2	Expt heath 01	Expt grass 01	Expt heath 02	Expt grass 02	Expt heath 03
Natural <10m^2	**R = 0.058, ns**						
Expt heath 01	R = 0.666, p <0.001	R = 0.432, p <0.001					
Expt grass 01	R = 0.641, p <0.001	R = 0.503, p <0.01	R = 0.575, p <0.001				
Expt heath 02	R = 0.414, p <0.001	R = 0.227, p <0.05	R = 0.293, p <0.05	R = 0.466, p <0.01			
Expt grass 02	R = 0.195, p <0.05	**R = 0.007, ns**	R = 0.302, p <0.01	R = 0.474, p <0.01	R = 0.249, p <0.01		
Expt heath 03	R = 0.592, p <0.001	R = 0.552, p <0.01	R = 0.317, p <0.01	R = 0.846, p <0.001	**R = 0.162, ns**	R = 0.482, p <0.001	
Expt grass 03	R = 0.292, p <0.01	R = 0.251, p <0.05	R = 0.302, p <0.01	R = 0.404, p <0.01	R = 0.207, p <0.05	**R = 0.132, ns**	R = 0.402, p <0.05

Table 4.8: ANOSIM comparison of and natural ponds assemblage with experimental ponds on heathland and grassland in all years,

Global R = 0.281, p <0.001

	Natural ponds >10m^2	Natural ponds <10m^2	Expt ponds on heath
Natural ponds <10m^2	**R = 0.058, ns**		
Expt ponds on heath	R = 0.486, p <0.001	**R = 0.102, ns**	
Expt ponds on grass	R = 0.402, p <0.001	**R = 0.147, ns**	R = 0.26, p <0.001

Table 4.9: ANOSIM comparison of natural ponds with heathland and grassland assemblages

Global R = 0.311, p <0.001

	Natural ponds >10m^2	Natural ponds <10m^2	Expt ponds 2001	Expt ponds 2002
Natural ponds <10m^2	**R = 0.058, ns**			
Expt ponds 2001	R = 0.584, p <0.001	**R = 0.089, ns**		
Expt ponds 2002	R = 0.307, p <0.01	**R = 0.021, ns**	R = 0.118, p <0.05	
Expt ponds 2003	R = 0.44, p <0.001	R = 0.239, p <0.01	R = 0.204, p <0.01	**R = 0.038, ns**

Table 4.10: ANOSIM comparison of natural pond with experimental pond assemblages in each year.

4.5 Discussion

Small man-made ponds on the Lizard were rapidly colonised by macroinvertebrates and quickly resembled the assemblages in small natural ponds in the region. Rates of colonisation were dependent on within-plot habitat availability and chance colonisation, which were both influenced by variation in pond permanence. The ponds in different plots differed in their physicochemistry and plant assemblage composition, but grassland and heathland macroinvertebrate assemblages became more similar as time progressed.

Despite pond replicates having the same dimensions on construction, grassland and heathland ponds soon differed in their depth, permanence and water chemistry. Grassland ponds tended to be deeper, more turbid and have greater phosphate concentrations, probably due to high levels of cattle poaching. They were also less permanent due most likely to higher soil permeability and reduced groundwater inflow. Heathland ponds had higher conductivity, which was likely to reflect the differences in soil structure and permeability. Throughout physicochemical and biotic analyses pond G1, the most permanent of the grassland pond replicates due to its position in waterlogged soil, resembled heathland sites more than the other grassland sites, indicating that increased permanence affected plant and macroinvertebrate assemblage composition. Although physicochemical parameters were different between grassland and heathland ponds they varied synchronously through time and within-plot temporal variation in physicochemistry was consistently greater than between-plot differences (Fig. 4.5). The effect of seasonal fluctuation in pond physicochemistry, caused by changes in rainfall and insolation/evaporation, therefore had more influence on pond physicochemistry than differences in pond substrate.

Colonisation was governed by both pond permanence and chance, as more permanent ponds were available for colonisation for longer. Overall taxon accumulation was faster on the heathland plot (Fig. 4.6a), as there was a greater availability of wet ponds. However, per pond taxon accumulation was greater in grassland ponds (Fig. 4.6c), as fewer were wet and habitat density was therefore locally reduced. Taxon accrual slowed more gradually in the grassland plot, because the chance of a species reaching a wet grassland site improved as time progressed, whereas in heathland sites rate of colonisation slowed rapidly after an initial phase of rapid colonisation due to greater habitat availability. After ca. 200 days of colonisation the absolute number of species observed in each of the plots converged and varied in synchrony through time, despite continuing seasonal turnover in assemblage composition. The experimental ponds did not reach immigration-extinction equilibrium, as they continued to accrue species throughout the study period (Ward & Blaunstein 1994).

Although the experimental ponds were rapidly colonised only a quarter of the macroinvertebrate taxa occurred at least once in all of the ponds after three years (appendix 4.6.3). The ponds were dominated by a high abundance of these ubiquitous species, many of which were found to be idiosyncratic (chapter 3), having good powers of dispersal and life history stages that tolerate desiccation. However, when the overall occurrence of macroinvertebrate colonists was examined 41% were idiosyncratic although 39% were found to be nested, and 18% were not recorded within the February 2000 samples (appendix 4.6.3, chapter 3). This indicates that pond taxa with a range of life history strategies were found in the ponds over the three years. Nested and idiosyncratic taxa did, however, differ in their level of occurrence as idiosyncratic taxa generally colonised a greater proportion of ponds over three years (one tailed Mann Whitney W = 369.0, p <0.05). However, a subset of nested taxa (*Helophorus granularis, Hydrobius fuscipes, Limnebius truncatellus* and *Ochthebius minimus*) were also widespread amongst the created sites, indicating that they were were probably found to be nested in chapter 3 because there were no gaps in their expected distribution patterns during February 2000 (see section 3.5). It seems that small sites are not solely important for temporary pond specialists, nested taxa, which are typically found in more permanent waters (chapter 3), also colonised some of the ponds. Small sites may therefore have an additional function as 'stepping stone' (Briers & Warren 2000) habitat patches for nested taxa as they disperse between more suitable permanent ponds.

Even if all the ponds were suitable for every colonist chance dictates that every species would not reach all of the ponds (Jeffries 1989, Talling 1951). Chance is likely to more strongly influence the distribution of species with a low number of aerial colonists (either because the species are locally rare, or exhibit life history strategies where dispersal is rare) than species with a high density of colonists. The effect of chance, rather than individual pond characteristics might explain why some species are observed in just one or two sites over the three year period.

The order of succession in grassland and heathland ponds differed subtly. The first colonists in both plots were a suite of Coleoptera species (appendices 4.6.4 & 4.6.5) so assemblage composition of ponds in the two plots was similar at the start of colonisation; however the timing of arrival of other taxonomic groups differed between the plots. These differences in the contingency of colonisation may explain why assemblage composition was most dissimilar between the plots during the first wet phase (Fig. 4.11 a, b & c). Loo *et al.* (2002) suggest that a stochastic rain of colonists would initially produce random assemblage structure, after which assemblages would become more similar, because the chance of a species reaching each habitat patch would increase over time. These data show evidence of this, as pond assemblage composition becomes more similar over three years as seasonal succession also declines (Fig. 4.11). During the first year, between-plot variation in assemblage composition was greater than within-plot seasonal variation, but during years two and three between-plot variation diminished and the effect seasonal succession on assemblage composition was of approximately equal magnitude (Fig 4.11).

Other studies of assemblage succession in systems subjected to periodic dry down have shown assemblage composition to diverge through time (Wilbur 1997, McGradySteed & Morin 1996). This is likely to occur when priority effects structure assemblage membership, so that early colonists exclude later arriving species through biotic interactions. The increase in biotic similarity observed in this system of temporary ponds indicates that differences in contingency of colonisation did not alter assemblage succession. Instead each assemblage accrued new species, at a rate that was determined by mean pond permanence, and the assemblages grew more similar through time as each species colonised more of the ponds. Permanence has previously been shown to be an important determinant of temporary pond assemblage richness and structure (Kiflawi *et al.* 2003, Rundle *et al.* 2002, Schneider & Frost 1996, Wellborn *et al.* 1996).

Aerial colonists of annually drying temporary ponds might be expected to repeat a similar pattern of colonisation and succession after pond wetting each year. This was not observed as the magnitude of seasonal variation in assemblage composition diminished after the first year (Fig 4.11 d-i). Coleoptera were observed to breed successfully in the ponds as larvae and teneral adults were sampled regularly (appendices 4.6.7 & 4.6.8). Many taxa have larvae that can develop rapidly during the wet phase or are semi-terrestrial and some have a life stage that can enter diapause in order to tolerate dry conditions (Wiggins *et al.* 1980). In addition, many adult beetles were observed to bury themselves in crevices in the substrate or under damp vegetation as the pond dried (see Davy-Bowker 2002). The presence of drought tolerant life stages in the ponds meant that colonisation did not have to restart for all taxa each year. The increasing prevalence of resting stages across the plots through time may also have contributed to grassland and heathland ponds becoming more similar.

Colonisation of the ponds appeared to occur irrespective of physicochemical characteristics, as physicochemistry had no effect on taxon occurrence (Table 4.7). Coleopteran abundance, however, was correlated with physicochemistry, perhaps indicating that likelihood of breeding or larval survival differed between ponds with different physicochemical characteristics. Differences in pond productivity may have been at least partially due to between pond differences in nutrient levels. Similar results were gained when the correlation with plant assemblage similarity was examined, although there was a weak correlation between plant assemblage similarity and the colonisation of all taxonomic groups. Velasco *et al.* (1998) found that experimental pond colonists were either generalists, which occurred independently of environmental conditions, or selective species that colonised ponds depending on their vegetation, substrate, salinity and insolation characteristics. Many macroinvertebrates, including Notonectidae, Trichoptera and Simuliidae have also been shown to distinguish between oviposition microhabitats (Reich & Downes 2003, Briers & Warren 2000, Golini & Davis 1975). Detailed information on the influence of vegetation composition on macroinvertebrate colonisation and oviposition are limited, although macrophytes are important for invertebrates as they provide food (Jones *et al.* 2000), shelter (Maurer & Brusven 1983) and oviposition sites (Lawton 1986). Assemblage composition became more similar through time despite continued fluctuation in within and between plot physicochemistry (Fig 4.5).

Unmeasured differences in the proportion of bare substrate and the amount of detrital input between grassland and heathland plots may also have affected colonisation, leading to differences in overall assemblage structure. Corixids, chironomids and hydrophilid beetles have been shown to preferentially colonise habitats with a proportion of bare substrate (Batzer & Resh 1992, de Szalay & Resh 2000) and the rate at which detritus decomposes differs between plant species and in different physicochemical conditions, which has consequences for detritivore palatability (Kok & Vanderveld 1994, Kornijow *et al.* 1995, Barnes 1983).

Monitoring of complexes of small man-made water bodies on the Lizard Peninsula has shown that small water filled depressions in the landscape can be colonised rapidly by large numbers of macroinvertebrate species and individuals within six weeks of creation. Such speed of colonisation may indicate that such habitats are a limited resource within the landscape. Over three years forty eight taxa were represented in the ponds with a total maximum area of $56m^2$. A number of the species were of international or national conservation importance including *Graptodytes flavipes* and *Dryops striatellus,* both vulnerable Red Data Book (RDB) coleopteran species and *Helophorus granularis, Helophorus alternans, Paracymus scutellaris, and Laccobius ytenensis* (all nationally scarce water beetles) later on in the successional process. One grassland site was also colonised by *Ranunculus tripartitus* (three-lobed water crowsfoot; vulnerable RBD & UK Biodiversity Action Plan species) within the first year, although the species was subsequently lost as other semi-terrestrial species encroached throughout the pond. In addition, the sites were utilised for both macroinvertebrate and amphibian reproduction (appendix 4.6.7) and 14 species of teneral (newly metamorphosed) adult Coleoptera were observed during sampling, with most observations occurring in the more permanent ponds (appendix 4.6.8).

Small natural ponds on the Lizard tend to occur on grassland in depressions along the hedgerow or on the ancient track ways that cross the Peninsula. They do not, however, commonly occur on the heathland. These results show that taxa of conservation importance will also colonise small ponds on heathland and that pond permanence has more influence than land use type on the composition of the assemblages that form in man-made ponds. Pond creation could therefore be a used on a variety of land use types. Permanence is governed by soil structure, which was shown to be locally patchy as ponds in this study had very different permanencies despite being dug within 50m of each other. Groups of small ponds should therefore be dug in order to (i) increase the area of habitat locally and (ii) increase the length of time the habitat is wet, which together should increase the chance of successful colonisation and reproduction of macroinvertebrate species.

Although data collected on the assemblage structure of small natural ponds on the Lizard Peninsula were gathered in a different year, it seems that small man-made water bodies mimic natural sites closely. Other studies have used straight sided replicate mesocosms to examine temporary pond colonisation and have found them reasonably similar to natural ponds (e.g. Wilbur 1997), the ponds used in this study have the advantage of natural substrate and sloping sides. Taxon richness of the experimental sites after two or three years was not significantly different to that found in small natural sites (Fig. 4.12a) and the species richness of samples from grassland sites across years were also not different (Fig. 4.12b).

Although there were significant differences between natural and experimental ponds in assemblage structure between plots and years (Fig. 4.13, Table 4.8) experimental pond assemblage composition was not found to be significantly different from natural sites when data were pooled across years (Table 4.10) or habitat type (grassland versus heathland; Table 4.9). Suites of small man-made ponds might therefore be considered a useful, low cost mitigation strategy in landscapes where there is already a high density of ponds, but the number of small sites is declining due to changes in land use.

4.6 Appendices

4.6.1 **Appendix 1:** Dates of sampling occasions with number of days since the ponds were created. Ponds that were wet are coded 1.

Date sampled	Time (days) since dug	H1	H2	H3	H4	H5	H6	H7	G1	G2	G3	G4	G5	G6	G7	No ponds wet
03/03/2000	0															
10/04/2000	38	1	1	1	1	1	1	1	1	1						9
12/05/2000	70				1	1	1	1								4
21/06/2000	110							1	1							2
29/09/2000	210	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
08/11/2000	250	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
18/01/2001	320	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
07/02/2001	340	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
22/11/2001	628	1	1	1				1								4
28/01/2002	694	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
26/02/2002	723	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
21/03/2002	746	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
02/05/2002	788	1	1	1	1		1	1	1	1		1				9
18/06/2002	835	1	1	1	1	1	1	1	1	1		1	1			11
14/11/2002	984	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
23/01/2003	1053	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
26/02/2003	1087	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
03/04/2003	1123	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
No sampling trips pond wet		15	15	15	15	14	15	17	15	14	11	13	12	11	11	193

4.6.2 **Appendix 2**: Summary of mean physicochemistry for each pond replicate

Mean physicochemistry	H1	H2	H3	H4	H5	H6	H7	G1	G2	G3	G4	G5	G6	G7
area (m^2)	2.815	2.871	3.140	3.521	3.474	3.375	2.536	3.416	2.765	2.574	2.409	3.043	3.121	2.891
max depth (m)	0.154	0.167	0.180	0.195	0.183	0.170	0.161	0.194	0.184	0.221	0.175	0.224	0.232	0.216
Permanence ratio	0.882	0.882	0.882	0.882	0.824	0.882	1	0.882	0.824	0.647	0.765	0.706	0.647	0.647
pH	7.221	7.258	7.358	7.424	7.275	7.572	7.407	6.951	7.164	8.349	6.901	8.439	8.219	8.504
conductivity (mS)	380.4	343.7	450.3	438.1	478.3	466.0	372.7	312.292	279.4	392.6	255.9	346.1	253.7	483.1
turbidity (NTU)	37.3	38.1	19.3	13.8	27.0	25.3	66.6	79.8	123.0	87.0	107.3	60.8	71.2	100.0
temperature (°C)	14.1	12.8	12.7	12.6	13.1	13.5	13.8	12.1	11.4	12.9	11.4	13.1	19.1	12.8
nitrate (mg/l)	0.18	0.19	0.09	0.14	0.12	0.11	0.16	0.17	0.18	0.13	0.26	0.13	0.13	0.30
phosphate (mg/l)	0.05	0.04	0.04	0.04	0.04	0.04	0.05	0.04	0.04	0.06	0.06	0.07	0.08	0.07
Copper (mg/l)	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Zinc (mg/l)	0.01	0.02	0.01	0.01	0.03	0.01	0.03	0.01	0.04	0.01	0.02	0.01	0.01	0.01
Iron (mg/l)	1.17	3.18	0.35	0.49	2.16	0.42	1.48	0.43	0.43	0.29	0.65	0.35	1.09	0.45
Cobalt (mg/l)	0.00	0.01	0.00	0.01	0.01	0.00	0.01	0.02	0.02	0.02	0.01	0.01	0.04	0.01
Chromium (mg/l)	0.08	0.08	0.06	0.03	0.07	0.06	0.09	0.03	0.02	0.01	0.03	0.01	0.02	0.03
Nickel (mg/l)	0.03	0.02	0.02	0.01	0.05	0.02	0.02	0.07	0.09	0.06	0.07	0.06	0.07	0.10
Aluminium (mg/l)	0.5	2.5	0.1	0.3	1.9	0.4	1.4	0.5	0.2	0.0	0.4	0.1	0.5	0.0
Magnesium (mg/l)	6.7	4.7	8.4	7.6	14.4	10.5	9.8	12.8	5.1	6.3	4.8	5.7	4.3	9.7
Sodium (mg/l)	24.5	21.9	30.2	25.4	38.9	29.6	30.1	24.4	11.4	9.1	10.8	8.8	8.7	201.8

4.6.3 **Appendix 3**: Overall occurrence of all recorded taxa after three years. Taxa ordered by frequency and ponds by taxon richness. IUCN category is noted for each taxon. Nested taxa are indicated n and idiosyncratic taxa i, species that were not assessed in chapter 3 are noted ?

C - Coleoptera, D - Diptera, H - Hemiptera, M - Mollusca, V - Vertebrate, T - Trichoptera, O - Oliochaeta, Od - Odonata, E – Ephemeroptera

	Taxa	IUCN	nested (n) or idiosyncratic (I)	G1	H1	H7	G2	H2	H4	H5	H3	G6	G7	G4	H6	G5	G3	Ponds/ taxa
Anacaena lutescens	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Helophorus aequalis	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Helophorus brevipalpis	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Helophorus grandis	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Helophorus obscurus	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Helophorus granularis	C	nsB	n	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Hydrobius fuscipes	C	lc	n	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Hydroporus pubescens	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Hydroporus tessellatus	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Ilybius montanus	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Limnebius truncatellus	C	lc	n	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Ochthebius minimus	C	lc	n	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Chironomidae	D	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Oligochaeta	O	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Hydroporus planus	C	lc	i	1	1	1	1	1	1	1	1	1	1	1	1	1		13
Helophorus alternans	C	nsB	?		1	1	1	1	1	1		1	1	1	1	1	1	12
Hydroporus memnonius	C	?lc	?	1	1	1	1	1	1	1	1	1	1	1	1			12
Helophorus minutus	C	lc	i	1	1	1	1	1	1	1	1	1		1	1			11
Ochthebius dilatatus	C	lc	i	1		1	1		1	1	1	1	1	1		1	1	11
Lymnaea truncatula	M	lc	i	1	1	1	1	1	1	1	1	1		1	1			11
Agabus bipustulatus	C	lc	i	1	1	1	1	1	1	1	1		1		1			10
Graptodytes flavipes	C	VU	i	1	1	1		1	1	1	1		1		1	1		10
Paracymus scutellaris	C	nsB	n	1		1	1	1	1		1	1	1	1				9
Dryops luridus	C	lc	n	1	1	1		1	1	1	1							7
Sigara spp	H	-	n		1	1	1	1		1			1		1			7

Appendix 4.6.3 cont.	Taxa	IUCN		G1	H1	H7	G2	H2	H4	H5	H3	G6	G7	G4	H6	G5	G3	Ponds/ taxa
Tipulidae	D	-	-	1			1					1	1	1		1	1	7
Dryops striatellus	C	VU	i	1	1			1	1	1	1							6
Hydroporus nigrita	C	lc	?	1	1	1	1									1	1	6
Hydroporus melanarius	C	lc	i		1			1	1	1	1							5
Triturus helveticus	V	-	?	1		1			1		1			1				5
Colymbetes fuscus	C	lc	n	1	1			1			1							4
Lymnephilus spp	T	-	-	1		1	1			1								4
Rana temporaria	V	-	?	1	1			1	1									4
Hydroporus gyllenhalii	C	lc	i			1			1	1								3
Hygrotus confluens	C	lc	?			1	1											2
Enochrus fuscipennis	C	lc	n												1	1		2
Haliplus lineatocollis	C	lc	i	1			1											2
Notonecta marmorea	H	lc	n			1	1											2
Cloeon dipterum	E	lc	n		1							1						2
Sympetrum spp	Od	-	n		1			1										2
Eristalis spp	D	-	-									1	1					2
Lymnaea palustris	M	lc	?	1	1													2
Agabus nebulosus	C	lc	?			1		1										2
Dytiscus semisulcatus	C	lc	?	1														1
Haliplus ruficollis	C	lc	n		1													1
Laccobius ytenensis	C	nsB	n		1													1
Limnebius nitidus	C	?lc	?	1														1
Gerris spp	H	-	?			1												1
Notonecta maculata	H	lc	n	1														1
Culicidae	D	-	-									1						1
Bufo bufo	V	-	?	1														1
Taxa per pond				36	33	33	29	29	29	28	27	25	24	23	23	21	18	

4.6.4 **Appendix 4**: Order of colonisation for grassland ponds

Grassland Ponds **Days since ponds constructed**	**38**	**110**	**210**	**250**	**320**	**340**	**694**	**723**	**746**	**788**	**835**	**984**	**1053**	**1087**	**1123**
Agabus bipustulatus	●														
Anacaena lutescens			●												
Hygrotus confluens				●											
Colymbetes fuscus									●						
Dytiscus semisulcatus				●											
Dryops striatellus										●					
Dryops luridus	●														
Enochrus fuscipennis															●
Graptodytes flavipes	●														
Haliplus lineatocollis						●									
Helophorus aequalis	●														
Helophorus alternans			●												
Helophorus brevipalpis	●														
Helophorus grandis	●														
Helophorus obscurus	●														
Helophorus granularis			●												
Helophorus minutus								●							
Hydrobius fuscipes							●								
Hydroporus memnonius		●													
Hydroporus nigrita								●							
Hydroporus planus	●														
Hydroporus pubescens	●														
Hydroporus tessellatus	●														
Ilybius montanus	●														
Limnebius nitidus										●					
Limnebius truncatellus	●														
Ochthebius dilatatus	●														
Ochthebius minimus								●							
Paracymus scutellaris							●								
Sigara spp				●											
Notonecta maculata					●										
Cloeon dipterum						●									
Tipulidae				●											
Culicidae						●									
Eristalis spp												●			
Lymnaea palustris						●									
Lymnaea truncatula							●								
Lymnephilidae								●							
Triturus helveticus						●									
Bufo bufo						●									
Rana temporaria									●						
Chironomidae		●													
Oligochaeta			●												
no new taxa	**13**	**2**	**4**	**4**	**1**	**6**	**3**	**4**	**2**	**2**	**0**	**1**	**0**	**0**	**1**
cumulative no taxa	**13**	**15**	**19**	**23**	**24**	**30**	**33**	**37**	**39**	**41**	**41**	**42**	**42**	**42**	**43**

4.6.5 **Appendix 5:** Order of colonisation for heathland ponds

Heathland Ponds **Days since ponds constructed**	**38**	**70**	**110**	**210**	**250**	**320**	**340**	**628**	**694**	**723**	**746**	**788**	**835**	**984**	**1053**	**1087**	**1123**
Agabus bipustulatus	●																
Agabus nebulosus		●															
Anacaena lutescens	●																
Hygrotus confluens		●															
Colymbetes fuscus										●							
Dryops striatellus		●															
Dryops luridus	●																
Enochrus fuscipennis													●				
Graptodytes flavipes	●																
Haliplus ruficollis				●													
Helophorus aequalis	●																
Helophorus alternans	●																
Helophorus brevipalpis	●																
Helophorus grandis	●																
Helophorus obscurus	●																
Helophorus granularis	●																
Helophorus minutus	●																
Hydrobius fuscipes	●																
Hydroporus gyllenhalii			●														
Hydroporus melanarius	●																
Hydroporus memnonius		●															
Hydroporus nigrita		●															
Hydroporus planus	●																
Hydroporus pubescens	●																
Hydroporus tessellatus	●																
Ilybius montanus	●																
Laccobius ytenensis									●								
Limnebius truncatellus	●																
Ochthebius dilatatus	●																
Ochthebius minimus	●																
Paracymus scutellaris	●																
Sigara spp		●															
Gerris spp																	●
Notonecta marmorea																	●
Cloeon dipterum															●		
Sympetrum spp																●	
Lymnaea palustris												●					
Lymnaea truncatula		●															
Lymnephilidae	●																
Triturus helveticus					●												
Rana temporaria				●													
Chironomidae		●															
Oligochaeta	●																
no new taxa	**23**	**8**	**1**	**2**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	**0**	**1**	**1**	**2**
cumulative no taxa	**23**	**31**	**32**	**34**	**35**	**35**	**35**	**35**	**36**	**37**	**37**	**38**	**39**	**39**	**40**	**41**	**43**

4.6.6 **Appendix 6**: Pool of taxa found over three years in experimental ponds compared with taxa found in small natural ponds (<10m^2) and experimental ponds during February.

Group		Overall expt ponds	Feb. expt ponds	Feb. natural ponds <10m
Coleoptera	*Agabus bipustulatus*	1	1	1
	Agabus montanus	1	1	1
	Agabus nebulosus	1	1	
	Anacaena globulus			1
	Anacaena lutescens	1	1	1
	Hygrotus confluens	1		
	Colymbetes fuscus	1		
	Dryops luridus	1		
	Dryops striatellus	1	1	1
	Dytiscus semisulcatus	1		
	Enochrus fuscipennis	1		
	Graptodytes flavipes	1	1	
	Haliplus lineatocollis	1	1	1
	Haliplus ruficollis	1		
	Helophorus aequalis	1	1	1
	Helophorus alternans	1		
	Helophorus brevipalpis	1	1	1
	Helophorus grandis	1	1	1
	Helophorus granularis	1	1	
	Helophorus minutus	1	1	1
	Helophorus obscurus	1	1	1
	Hydrobius fuscipes	1	1	1
	Hydroporus gyllenhalii	1		1
	Hydroporus melanarius	1	1	
	Hydroporus memnonius	1	1	
	Hydroporus nigrita	1		
	Hydroporus planus	1	1	1
	Hydroporus pubescens	1	1	1
	Hydroporus tessellatus	1	1	1
	Laccobius ytenensis	1		
	Limnebius nitidus	1		
	Limnebius truncatellus	1	1	
	Ochthebius minimus	1	1	
	Ochthebius dilatatus	1	1	1
	Paracymus scutellaris	1		1
Trichoptera	*Limnephilius auricula*	1	1	1
	Limnephilus vittatus	1	1	1
	Limnephilus lunatus			1
Hemiptera	*Corixa punctata*			1
	Corixa affinis			1
	Sigara spp	1	1	
	Gerris spp	1		
	Notonecta spp	1		
Gastropoda	*Lymnaea palustris*	1	1	1
	Anisus leucostoma			1
	Lymnaea truncatula	1	1	1
Bilvalvia	*Pisidium spp*			1
Isopoda	*Asellus aquaticus*			1
Ephemeroptera	*Cloeon dipterum*	1	1	
Odonata	*Sympetrum spp*	1	1	

4.6.7 **Appendix 7**: Number of grassland and heathland ponds with Coleoptera and anuran larvae

			No ponds containing larvae						
month	days	grass/ heath and	*Hydroporus spp*	*Agabus/Ilybius spp*	*Dytiscus semisulcatus*	*Dryops spp*	*Colymbetes fuscus*	*Hydrobius fuscipes*	Anuran
apr	38	h							
may	70	h	1						
june	110	h							
sept	210	h		3					
nov	250	h		2					
jan	320	h	2	4					2
feb	340	h	4	1					3
nov	628	h							
jan	694	h		7					3
feb	723	h	1	6			1		
mar	746	h	5	4			1		3
may	788	h	1	3				1	3
june	835	h	2						
nov	984	h		7					4
jan	1053	h	2	7					6
feb	1087	h	2	7					7
apr	1123	h		7					1
apr	38	g							
may	70	g							
june	110	g							
sept	210	g							
nov	250	g	4	2	1	1			
jan	320	g	2	4					
feb	340	g	2	4					
nov	628	g							
jan	694	g		4					
feb	723	g	2	3					
mar	746	g	3						
may	788	g	2						
june	835	g							
nov	984	g		3					
jan	1053	g	4	6					
feb	1087	g	4	7					2
apr	1123	g	5	3					

4.6.8 Appendix 8: Records of teneral (newly metamorphosed) Coleoptera species

	H1	H2	H3	H4	H5	H6	H7	G1	G2	G3	G4	G5	G6	G7
Apr-00														
Hydroporus melanarius	3	10	6											
Hydroporus tesselatus								1						
May-00														
Ilybius montanus					3									
Agabus bipustulatus							5							
Jun-00														
Hydroporus gyllenhalii							3							
Jan-01														
Hydroporus melanarius		1												
Feb-01														
Hydroporus melanarius	2													
Jan-02														
Agabus bipustulatus						1								
Hydroporus pubescens											1			
Hydroporus tesselatus							1							
May-02														
Ilybius montanus	4	5	8	12			4	21	3					
Agabus bipustulatus		1				17	1							
Agabus nebulosus							1							
Hydroporus pubescens	5		4	3		4	3							
Hydroporus tesselatus	2	3	3	1		4	2	1	1					
Hydroporus memnonius	3			1		2		2						
Hydroporus melanarius		1												
Hydroporus planus									2					
Jun-02														
Ilybius montanus	2		3	8	7	1	4		2					
Agabus bipustulatus	1		3	2			1	6	1					
Dytiscus semisulcatus								2						
Colymbetes fuscus	1		2											
Hydroporus pubescens			2				2	2	4		1			
Hydroporus tesselatus			1											
Hydroporus melanarius					1									
Hydroporus planus														
Hydrobius fuscipes								1						
Limnebius truncatellus					1									
Feb-03														
Hydroporus melanarius		1												
Apr-03														
Hydroporus melanarius	2													
Hydroporus pubescens	1													
Hydroporus tesselatus	2												1	
Permanence	**0.88**	**0.88**	**0.88**	**0.88**	**0.82**	**0.88**	**1.00**	**0.88**	**0.82**	**0.65**	**0.77**	**0.71**	**0.65**	**0.65**

5 Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions?

5.1 Abstract

Habitat structure is one of the fundamental factors determining the distribution of organisms at all spatial scales. Vegetation is important in shaping the structural environment for invertebrates in many systems. However, invertebrates commonly live within stands of mixed species composition, making estimates of structural complexity difficult to obtain. This study firstly used digital images to quantify the fractal complexity of fifteen plant species. Digital image analysis was rapid and allowed fractal structure to be analysed at finer resolution than has been attained before. Fractal indices were then used for the first time to describe the structural complexity of mixed stands of pond macrophytes, in order to examine the effect of habitat complexity on the structure of invertebrate assemblages that utilise the habitat in three dimensions. Fractal indices were not related to total macrophyte surface area and were found to be significantly related to both invertebrate biomass-body size scaling and overall invertebrate biomass; more complex stands of macrophytes contained a greater number of small animals. Habitat complexity was unrelated to invertebrate taxon richness and macrophyte surface area and species richness were not correlated with any of the invertebrate assemblage parameters. The biomass-body size scaling relationship of lentic macroinvertebrates matched that predicted by a model incorporating fractal dimension of habitat and allometric scaling of resource use, demonstrating that both habitat fractal complexity and allometry use are likely to influence density-body size scaling in lentic macroinvertebrate assemblages.

5.2 Introduction

The structural complexity of habitat is of broad ecological significance as it limits the distribution of species across all scales (Holling 1992). At local scales habitat structure can regulate species diversity, with complex habitats normally being more species rich (Downes *et al.* 1998). This may be due to microhabitat choice (McNett & Rypstra 2000), modification of biotic interactions (Finke & Denno 2002, Bartholomew *et al.* 2000, Mosknes *et al.* 1998) or changes in resource partitioning and niche breadth (McCoy & Bell 1991, May 1972). Complexity can also alter assemblage structure by affecting the frequency of body sizes, as animals of different sizes utilise habitat space differently (Schmid *et al.* 2002, Raffaelli *et al.* 2000, Morse *et al.* 1985). However, the importance of habitat structure has not always been recognised because of taxonomic bias within studies and problems quantifying structural complexity (McCoy & Bell 1991); in addition, habitat complexity and habitat area often co-vary in the field (Johnson *et al.* 2003). These problems need to be resolved in order to facilitate cross-system and cross-scale comparisons of the effect of habitat structural complexity on assemblage composition and structure (McCoy & Bell 1991).

The relationship between vegetation architecture and invertebrate assemblages has been the most widely studied. Authors have used many different measures of plant structure to examine its effect on phytophilous fauna, these include shoot density (Hovel 2003, Kurashov *et al.* 1996), biomass (Wyda *et al.* 2002, Attrill *et al.* 2000) and surface area (Mathooko & Otieno 2002), though such measures examine the amount of available habitat rather than complexity *per se*. Other studies have compared invertebrate assemblages amongst plants with different gross morphologies (Cheruvelil & Soranno 2002, Feldman 2001, Cyr & Downing 1988) or developed complexity indices based on the number and arrangement of stems and leaves (Lillie & Budd 1992). However, in order to study the effects of habitat complexity on assemblage composition and structure it is necessary to quantify complexity in a way that allows comparison at different scales. To this end the most valuable development has been the use of habitat fractal dimensions as an index of structural complexity (e.g. Schmid *et al.* 2002, Attrill *et al.* 2000, Gee & Warwick 1994a/b, Jeffries 1993). Objects that have true fractal structure retain their complexity under successive magnification (Simon & Simon 1995), i.e. they are self–similar at all scales (Sugihara & May 1990, Mandlebrot 1983). However, biological structures are fractal over a limited range of scales, and fractal dimension (level of complexity) can vary with scale of measurement (Morse *et.* *al.* 1985, Bradbury *et al.* 1984). Fractal dimension can be estimated from the perceived rate of increase in a structure's perimeter (or area) as the scale of measurement is decreased; Sugihara and May (1990) and Schmid (2000) have reviewed common techniques used to measure the fractal structure of habitat.

The scale at which organisms perceive and use the environment differ depending on body size (Gee & Warwick 1994a,1994b, Levin 1992) and habitat structure might therefore shape the distribution patterns of species in different ways at different spatial scales. For instance, small animals may live on, or in, parts of a plant's structure that are not utilised by larger animals (Lawton 1986), therefore there is likely to be more perceived space on vegetation for small animals than large, and plants with more complex structure would be expected to support more small animals than simple plants. Habitats of greater complexity might thus be expected to have both increased richness and smaller modal body size, when compared to habitats which are structurally simple (Schmid *et al.* 2002, Raffaelli *et al.* 2000, Morse *et al.* 1985).

Habitat structure is, however, unlikely to be the main factor shaping the form of animal body size distributions, organisms are probably more strongly influenced by the allometric scaling of resource use between individuals, as small-bodied animals utilise less energy per individual than large bodied animals. The relationship between population density and body size generally scales with an exponent of -0.75, (Damuth 1981), where metabolic rate increases as body size$^{0.75}$ (Brown & West 2000, Schmidt-Nielsen 1984). Morse *et al.* (1985) incorporated both this allometric scaling of resource use and the fractal dimension of habitat into a model that predicts the expected increase in density of organisms as body size decreases, the validity of this model has not been widely tested, particularly in aquatic systems.

So far, investigations that *quantify* the structural complexity of plant species and relate it to invertebrate assemblage composition and body-size distribution have been mainly limited to the terrestrial (e.g. Shorrocks *et al.* 1991, Lawton 1986, Morse *et al.* 1985) and marine environments (e.g. Davenport *et al.* 1999, Gee & Warwick 1994a/b). However, vegetation structure and composition also influences the distribution and abundance of macroinvertebrate species in lentic freshwaters (Scheffer *et al.* 1984, Dvorak & Best 1982). Macrophyte stands provide invertebrates with food (Jones *et al.* 2000, Lodge *et al.*. 1998), shelter (Heck & Crowder 1991, Maurer & Brusven 1983), oviposition sites (Lawton 1986, Welch 1935) and modified physicochemical conditions

(Jeffries 1993). Most authors working in lentic systems have compared the invertebrate assemblages associated with aquatic macrophytes of different gross morphologies. Some studies have found invertebrate abundance to be highest on species with dissected leaves (Cheruvelil *et al.* 2002, Dvorak & Best 1982, Krecker 1939), whereas others have found no relationship between the invertebrate assemblages living on plants with different levels of leaf dissection (Cyr & Downing 1988, Rooke 1984). As far as I am aware Jeffries (1993) is the only other lentic freshwater study examining the relationship between fractal habitat complexity and invertebrate assemblage composition and density.

This study is the first to quantify plant density and fractal complexity in mixed stands of vegetation in order to examine the influence of habitat structure on the species diversity, density and biomass-body size distribution of macroinvertebrates living both on and amongst the plants. This is achieved by sampling mixed stands of macrophytes from wetland ponds to gain three complementary measures of vegetation structure: (i) a structural complexity index, derived from fractal measures of each macrophyte species and their proportional density within the stand (ii) density, measured as overall surface area of the stand and (iii) diversity, the number of macrophyte species within the stand. The influence of these habitat complexity measures on macroinvertebrate assemblage species richness, total biomass and the scaling of biomass amongst animal body sizes are then examined. Finally the overall biomass body size distribution is compared with that expected by Morse *et al.*'s (1985) model, the first time this has been attempted for fresh water invertebrate assemblages.

5.3 Methods

5.3.1 Field sampling

In June 2001, fifteen samples were taken from each of two large, semi-permanent ponds on the Lizard Peninsula in Cornwall with similar macrophyte assemblage composition, Kynance Farm Pond (SW 682142) and Croft Pascoe Pool (SW 731197). Samples were taken at a fixed water depth of 15cm using a plastic core of 30cm diameter (area $0.07m^2$, volume 10.6 litres) with a 1mm mesh bag attached. Sampling effort was spread amongst a wide range of vegetation densities and plant species compositions. The core was pushed rapidly down through the water column into the substrate, to prevent the escape of actively swimming macroinvertebrates. The plug of substrate was then dug out and inverted to empty all invertebrates into the mesh bag. The sediment core was transferred to a white plastic tray and all macrophytes were rinsed, removed and sorted by species. The mud core was then carefully discarded to avoid sampling invertebrates not associated with macrophytes, and invertebrates were sieved through the mesh bag. In the laboratory, macrophyte species from the samples were pressed separately and dried for 48 hrs at 60°C. Biomass was then recorded individually for all macrophyte species in each sample. Macroinvertebrates were preserved in 70% alcohol for sorting, identification and enumeration.

Five intact plants of each of the fifteen macrophyte species found in the samples were also collected from the field in order to measure the fractal complexity of each species. Each replicate plant was placed in a separate plastic bag, in order to prevent damage. In the laboratory the plants were floated out in shallow trays to separate the branches and divided leaves, and then pressed carefully and dried for 48hrs at 60°C.

5.3.2 Macrophyte Habitat structure

5.3.2.1 Determining the structural complexity of individual macrophyte species

In order to determine the fractal dimension of each macrophyte species that occurred in the samples replicate pressed plants were photographed at two different magnifications (low magnification pixel width 0.28mm; high magnification pixel width 0.03mm); two scales of magnification were used in order to resolve both fine and coarse structural detail. All photographs were taken using a Nikon Coolpix 995 digital camera and saved as uncompressed TIFF files.

Each digital photograph was transferred to greyscale and thresholded to produce a binary image. ImageJ software (Rasband 1997-2003) was then used to analyse fractal structure of each image at low and high magnifications. ImageJ uses a fractal box count algorithm which is analogous to the general grid method of Sugihara and May (1990) and can quantify the fractal dimension of both perimeter and area. A series of grid sizes ranging from 2 to 64 pixel widths (0.06-1.92mm for high magnification and 0.56-17.92mm for low magnification) were used to estimate both perimeter and area of each photograph at each magnification. By examining fractal structure across a range of measurement scales (resolved distance 0.06-18mm) we made few assumptions about the scale at which macroinvertebrates perceive the available habitat. $\log_{10}$ plots of the perimeter and area estimates against measurement scale (grid size) were then constructed within ImageJ for each photograph, the gradient of which estimated the fractal dimension of the plant. Each of the fifteen macrophyte species had four fractal parameters estimated from five replicate plants: area at high and low magnification and perimeter at high and low magnification. The mean fractal measures for each species were then used to calculate macrophyte complexity indices for the samples (see section 5.3.2.3).

5.3.2.2 Interpreting fractal scores

Differences in the fractal dimension of area (fdarea) and perimeter (fdperim) between macrophyte species emphasise differences in the degree of branching and dissection of the vegetation. Fdarea indicates how two-dimensional space is filled by the plant; high scores (≈2) mean more of the plane is filled. At low magnification (fdareaL) *Potamogeton polygonifolius,* a species with large broad leaves, had fdareaL similar to *Apium inundatum* which has finely divided leaves (Fig. 5.1 a and b), because branches finer than 0.56mm wide were not adequately resolved. Examining fdarea at high magnification (fdareaH) highlights the differences between the plant structures (Fig. 5.1 c and d).

Measuring fdperim augments the description of structural complexity giving an indication of the level of dissection of the plant. High values (≈ 2) indicate a high level of leaf dissection; in contrast a simple-edged plant would give an fdperim value ≈ 1 (the euclidean dimension for a straight line). Differences between *P.polygonifolius* and *A inundatum* are seen at both low and high magnification when considering fdperim (Fig. 5.1). Plant structure is therefore more accurately described by measures of both fdarea and fdperim. In summary, fdarea gives an indication of how available surface area changes with scale, whereas fdperim contains information on how the size and number of gaps in the vegetation changes.

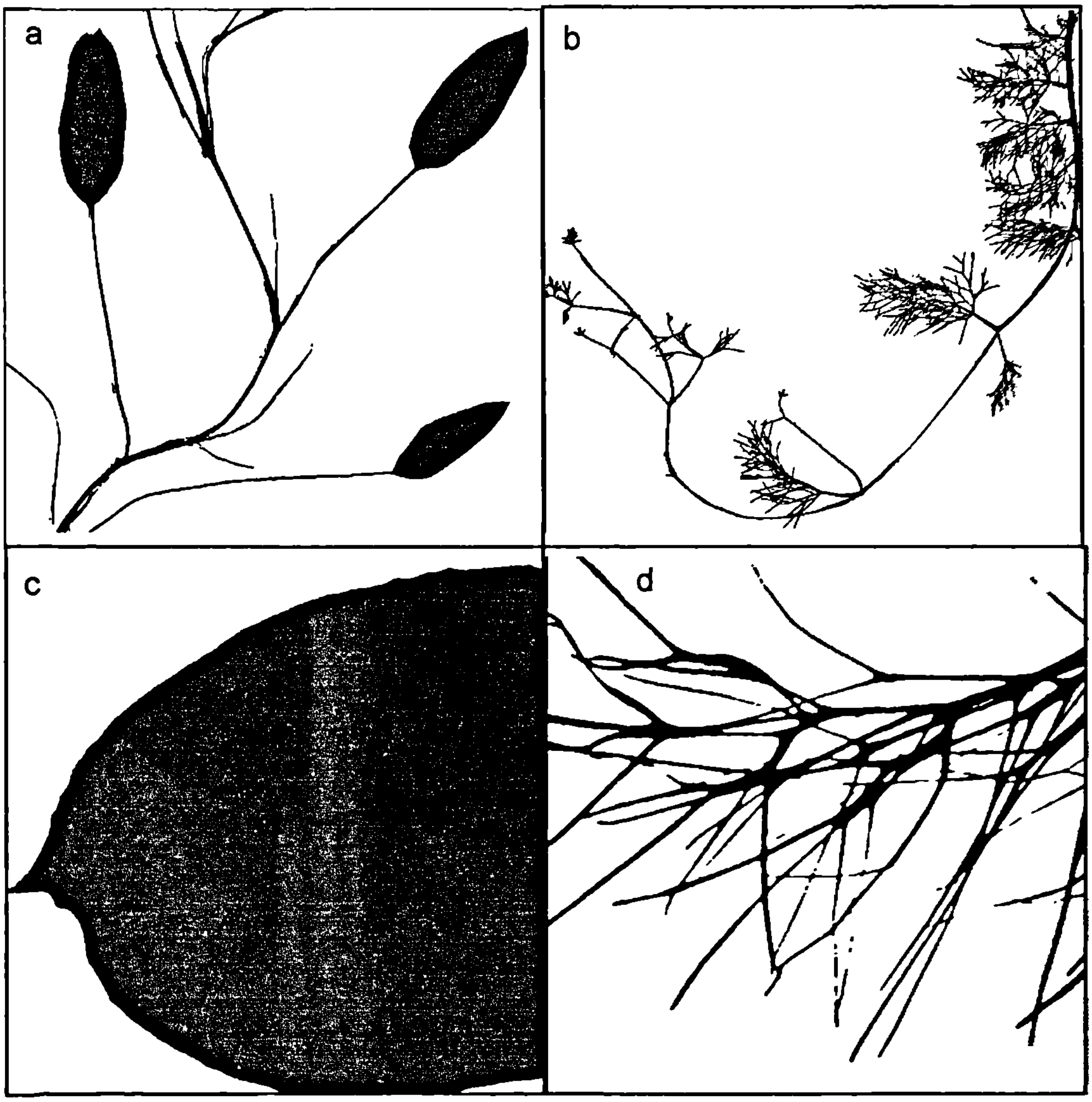


Figure 5.1 Thresholded macrophyte photographs. (a) *Potamageton polygonifolius* at low magnification, fdarea 1.54, fdperim 1.30, (b) *Apium inundatum* at low magnification, fdarea 1.52, fdperim 1.50, (c) *P. polygonifolius* at high magnification, fdarea 1.95, fdperim 1.10 and (d) *A. inundatum* at high magnification, fdarea 1.54, fdperim 1.29.

5.3.2.3 Macrophyte structural complexity indices

In order to describe the overall complexity of macrophytes within a sample, the proportion of total biomass contributed by each macrophyte species was multiplied by the relevant fractal measure for that species and the values were summed for each sample. Four indices of macrophyte fractal complexity were therefore generated for each sample: fractal dimension of area and perimeter at high magnification (fdareaH and fdperimH) and low magnification (fdareaL and fdperimL).

5.3.2.4 Macrophyte surface area

Each of the replicate plants were weighed and surface area was measured from the low power digital photographs using ImageJ. The relationship between macrophyte biomass and surface area were then examined using Ordinary Least Squares (OLS) regression and the linear equations for each macrophyte species were then used to estimate total macrophyte surface area for each sample.

5.3.3 Macroinvertebrate assemblage structure

Macroinvertebrates were sorted and identified to species where possible. Chironomids, some coleopteran larvae and early instar anisopteran larvae were identified to genus, whilst other dipteran larvae and pupae, juvenile corixids, ostracods, cladocerans and Acari were identified to these major taxa. Body length (distance along the dorsal surface of the organism from the anterior of the head capsule to the tip of the abdomen, excluding antennae, anal prolegs and cerci) was measured for each individual using a binocular microscope with an eyepiece graticule. As chironomids were highly abundant, a length-width relationship was constructed using digital photographs and 'Analysis^{TM}' image analysis software. Chironomid width was then measured for a sub sample (25%) of the individuals in each sample.

5.3.3.1 Biomass-body size distributions

Biomass-body size relationships are often presented in a normalised form in aquatic systems (Ramsay *et al.* 1997). The technique, developed by Sheldon *et al.* (1972), plots $\log_2$ biomass against $\log_2$ body size classes, which transforms the relationship into a negative log-linear form when the smallest size class is the mode. The method facilitates comparison of body size-biomass scaling in different systems and is therefore useful for examining general patterns in ecological assemblages. The construction of normalised biomass-body size distributions simplifies between sample comparisons of biomass-body size relationships (Sprules & Munawar 1986), as the gradient of the fitted line gives the scaling exponent of the biomass-body size relationship and the intercept indicates variation in total macroinvertebrate biomass between samples.

Biomass for each macroinvertebrate individual was estimated from family level length-mass power function relationships compiled from the literature; equations were taken from Benke *et al.* (1999)

with the exception of those for dipteran pupae, coleopteran larvae, and microcrustaceans which were taken respectively from Burgherr and Meyer (1997), Meyer (1989), and Manca and Comoli (2000). Where a family level equation was unavailable the order level equation was used, or, in the case of the Coleoptera, the most appropriate alternative family relationship, based on assessment of overall body shape. Animals that were less than 1mm long (the size of the mesh used for sampling) were excluded. Normalised biomass-body size distributions were then constructed for each sample, by plotting $\log_2$ biomass against $\log_2$ body size classes, and gradient and intercept values were recorded from OLS regression, for correlation with macrophyte fractal complexity indices, surface area and species richness parameters. It should be noted that because individual animal biomasses were recorded and summed, the gradient of the normalised biomass-body size graph is equivalent to that gained by plotting log density against log body size.

5.3.3.2 Testing Morse *et al's* model

In order to compare the data with Morse *et al.*'s (1985) model a normalised biomass-body size distribution was firstly constructed for the pooled data from all the samples. Then a 'null' biomass body size distribution was superimposed over the observed distribution, which was generated based on the habitat having a fractal dimension of 1. This was achieved by calculating the expected biomass per body size category based on density scaling as body mass$^{-0.75}$, constrained by the total number of macroinvertebrate individuals observed (median biomass per size class was used in calculations). The resulting normalised biomass–body size distribution therefore had a gradient of -0.75, which is consistent with the theory that the animals in each body size category utilise the same amount of energy, the 'energy equivalence' hypothesis (Damuth 1981).

Mean fractal complexity indices fdperimH and fdareaL were then calculated across all samples, and the expected fold increase in density for an order of magnitude reduction in body length (equivalent to 1000 fold reduction in biomass) were calculated for each index from equation 1 (Box 5.1).

Box 5.1

fold increase in density = $([L^3]^{0.75})(L^{FD-1})$ (eqn 1)

where FD is the fractal dimension of the habitat and L is the fold decrease in body length

The expected gradient of the normalised biomass-body size distribution when habitat fractal complexity was incorporated could then be calculated from equation 2 (Box 5.2 below) and compared with the observed gradient.

Box 5.2:

$$\frac{\mathrm{Ln}1/y}{\mathrm{Ln}1000} = x \qquad \text{(eqn 2)}$$

where y is the fold increase in density for a 1000 fold decrease in biomass, and x is the gradient of the resulting normalised density-body size distribution

5.3.4 Data analysis

Initial correlations between macrophyte structural complexity parameters showed that fdareaH and fdperimL co-varied with macrophyte surface area and the number of macrophyte species, these complexity indices were therefore exclude from further analyses. There was no significant between pond difference in any of the remaining macrophyte habitat parameters (t test $p > 0.05$) so subsequent analyses pooled samples from both ponds. Six of the twenty nine samples (one sample was excluded due to damage) had normalised biomass-body size distribution gradients which were statistically insignificant, ($p > 0.05$) however data from all the samples were included in the analyses.

All the parameters were checked for normality ($p > 0.05$, Anderson-Darling test) and heteroscedasticity of residuals before product moment correlations were performed between the three macroinvertebrate assemblage parameters (species richness, biomass-body size gradient and biomass body size intercept) and the four macrophyte structure variables (species richness, total surface area, fdareaL and fdperimH).

Where correlations between macroinvertebrate assemblage parameters and macrophyte structure were significant Reduced Major Axis (Model II) regression was used to further examine the relationships, as both response and explanatory variables were subject to measurement error (Sokal & Rohlf 1995). RMA software for Reduced Major Axis Regression v1.14b (Bohonak 2002) was used with 10,000 bootstraps for each calculation.

5.4 Results

5.4.1 The structural complexity of individual macrophyte species

Constant fractal dimension across the scales examined (statistical self similarity) shows that a macrophyte species is likely to be perceived similarly by both large and small invertebrates. The only macrophyte species which was statistically self similar for both fdarea and fdperim was *Myriophyllum alterniflorum* which lies close to the origin of Fig. 5.2. There was considerable variation in the fractal measures between macrophyte species (Table 5.1) and four main groups were identified, based on visual assessment of plant morphology (Fig. 5.2). Finely dissected macrophytes, with radially symmetrical leaves such as *Apium inundatum* and *Chara fragifera* (group 1 Fig. 5.2) showed relatively unchanging fdarea across the magnifications but fdperim varied. In contrast species with finely dissected flat leaves (*Eleogiton fluitans, Juncus bulbosus* and *Galium palustris*, group 2) had constant fdperim but fdarea was greater at high magnification. Species in group three (*Ranunculus flammula, Carex* spp, *Potamogeton polygonifolius, Glyceria fluitans, Eleocharis palustris, Juncus articulatus, Littorella uniflora* and *Hydrocotyle vulgaris*) are of simpler structure, fdarea was greater at high magnification whereas fdperim was greater at low magnification. Bryophyte specimens (group 4) gave both fdarea and fdperim that were greatest at high magnification.

species	**FdareaL**	FdareaH	FdperimL	**FdperimH**
Myriophyllum alterniflorum	**1.58 ± 0.027***	1.56 ± 0.034	1.51 ± 0.053*	**1.52 ± 0.027**
Glyceria fluitans	**1.41 ± 0.017**	1.83 ± 0.0057	1.23 ± 0.012	**1.08 ± 0.054**
Carex spp	**1.39 ± 0.029**	1.72 ± 0.043	1.27 ± 0.005	**1.13 ± 0.017**
Eleocharis spp	**1.36 ± 0.013**	1.79 ± 0.019	1.22 ± 0.026	**1.09 ± 0.005**
Juncus articulatus	**1.30 ± 0.018**	1.71 ± 0.029	1.24 ± 0.010	**1.16 ± 0.014**
Juncus bulbosus	**1.28 ± 0.051**	1.50 ± 0.015	1.26 ± 0.042	**1.25 ± 0.024**
Chara spp	**1.48 ± 0.026**	1.52 ± 0.036	1.14 ± 0.033	**1.42 ± 0.017**
Littorella uniflora	**1.44 ± 0.035**	1.81 ± 0.024	1.20 ± 0.022	**1.14 ± 0.006**
Potamogeton polygonifolius	**1.54 ± 0.024**	1.89 ± 0.023**	1.27 ± 0.009	**1.12 ± 0.014****
Apium inundatum	**1.50 ± 0.038**	1.54 ± 0.013***	1.46 ± 0.050	**1.34 ± 0.037*****
Eleogiton fluitans	**1.38 ± 0.036**	1.51 ± 0.021	1.38 ± 0.039	**1.33 ± 0.033**
Hydrocotyle vulgaris	**1.32 ± 0.036**	1.90 ± 0.024	1.18 ± 0.010	**1.10 ± 0.006**
Bryophyte spp	**1.49 ± 0.026**	1.67 ± 0.011	1.25 ± 0.018	**1.34 ± 0.009**
Galium palustris	**1.27 ± 0.026**	1.68 ± 0.022	1.18 ± 0.017	**1.19 ± 0.005**
Ranunculus flammula	**1.46 ± 0.012**	1.75 ± 0.033	1.27 ± 0.001	**1.15 ± 0.018**

Table 5.1: Mean fractal dimension (± s.e.m) for each macrophyte species at high and low magnification. (n=5, except * n =4 **n=8 and ***n=10).

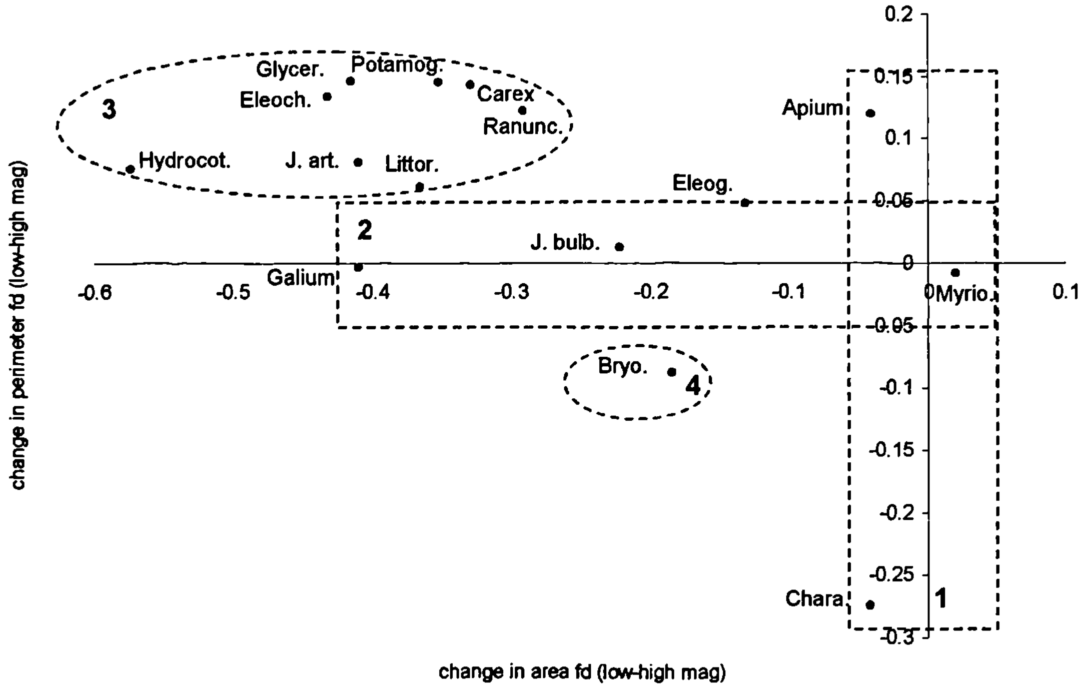


Figure 5.2: Difference between fractal dimension at high an low magnifications for each macrophyte species Difference in fdperim plotted against the difference in fdarea. Species lying nearest the origin are most self similar across the range of scales observed

5.4.2 Relationship between macrophyte structure parameters and macroinvertebrates

Macrophyte structural complexity (fdareaL and fdperimH) was significantly negatively related to macroinvertebrate biomass-body size scaling (Table 5.2). This indicates that macrophyte stands with more complex vegetation (higher fractal dimension) supported a greater number of small macroinvertebrates. Reduced major axis regression showed fdareaL, to explain more variation in the biomass-body size gradient (R^2 = 20.6%, Fig. 5.3a) than fdperimH (R^2 = 11.1%, Fig. 5.3b). Macrophyte stands with more complex vegetation also supported greater overall macroinvertebrate biomass (Table 5.2; fdareaL R^2 = 17.9%, Fig. 5.3c and fdperimH R^2 = 15.1%, Fig. 5.3d). Removing data points with high leverage values and standardised residuals did not alter the significance of any of the correlations or make a significant difference to the R^2 values.

There was no relationship between structural complexity and macroinvertebrate species richness and macrophyte surface area and species richness were unrelated to macroinvertebrate assemblage richness, biomass body size scaling or overall biomass (Table 5.2).

		Macrophyte structure			
		complexity		diversity	density
		fdareaL	fdperimH	no species	total surface area
Macroinvertebrate assemblages	Biomass-body size scaling biomass-body size gradient	**r = -0.466, p < 0.05**	**r = -0.367, p < 0.05**	r = 0.267 ns	r = -0.026 ns
	biomass biomass-body size intercept	**r = 0.449, p < 0.05**	**r = 0.412, p < 0.05**	r = 0.076 ns	r = 0.292 ns
	Taxon richness	r = 0.259 ns	r = 0.202 ns	r = 0.330 ns	r = 0.354 ns

Table 5.2: Correlations between macroinvertebrate scaling, biomass and taxon richness with macrophyte fractal complexity, surface area and species richness.

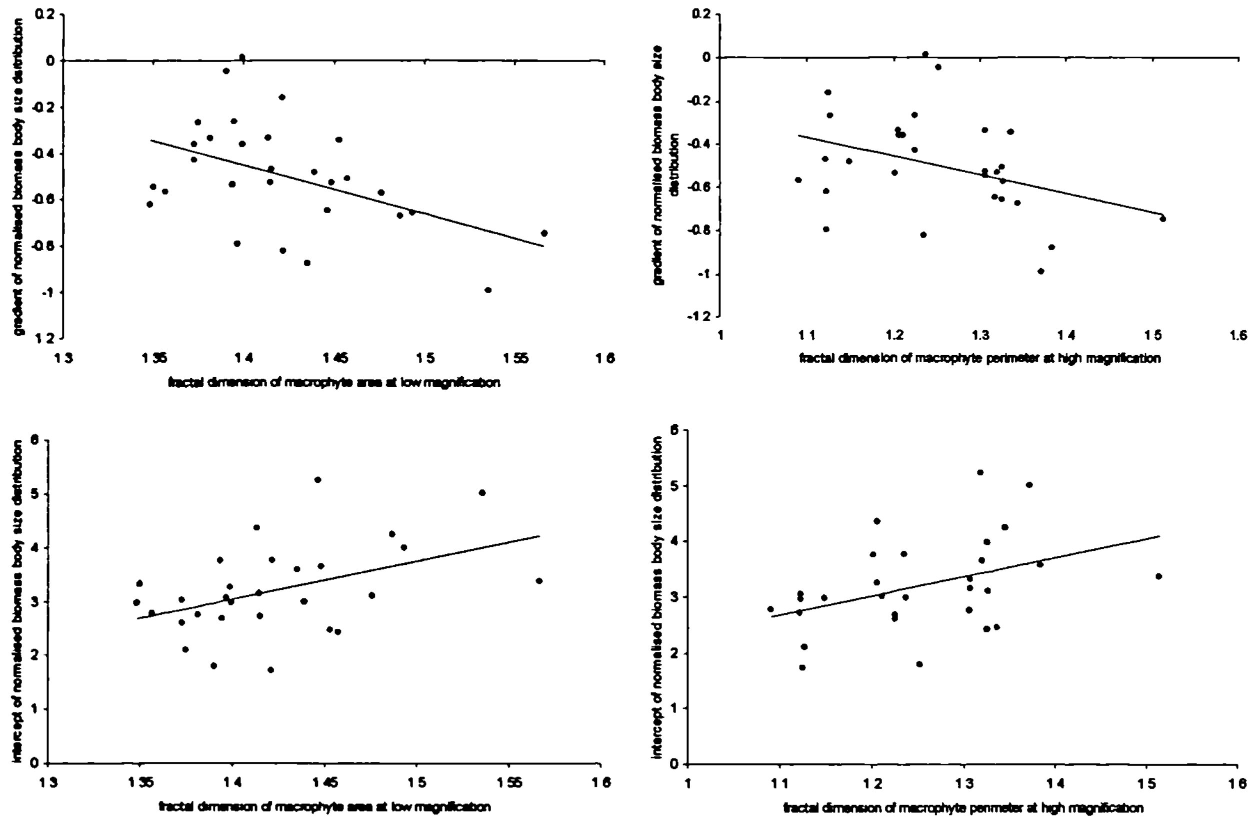


Figure 5.3: Reduced major axis regression relationships (a) biomass-body size gradient and fdareaL (b) biomass scaling across body sizes and fdperimH (c) biomass-body size intercept and fdareaL (d) biomass-body size intercept fdperimH.

5.4.2.1 Testing Morse *et al*'s model

The overall biomass-body size spectrum had a gradient of -0.8276 (R^2= 95.9%, $p<0.001$), and an intercept of 8.56 (Fig. 5.4). The observed gradient shows that scaling of biomass across body sizes is steeper than the -0.75 expected, indicating that proportionally more small animals were observed than expected if density scaled with resource use alone.

Mean fdperimH across all samples was 1.240 and mean fdareaL was 1.423. Placing mean fdperimH in equation 1 (Box 5.1) gave an expected increase in density of 309 fold, whereas fdareaL predicted a 471 fold increase. These figures correspond to an expected normalised biomass-body size gradient of between -0.83 and -0.89 (equation 2), which is in accordance with the observed gradient of -0.8276, which gives a 304 fold increase ($1/1000^{-0.8276}$) in density.

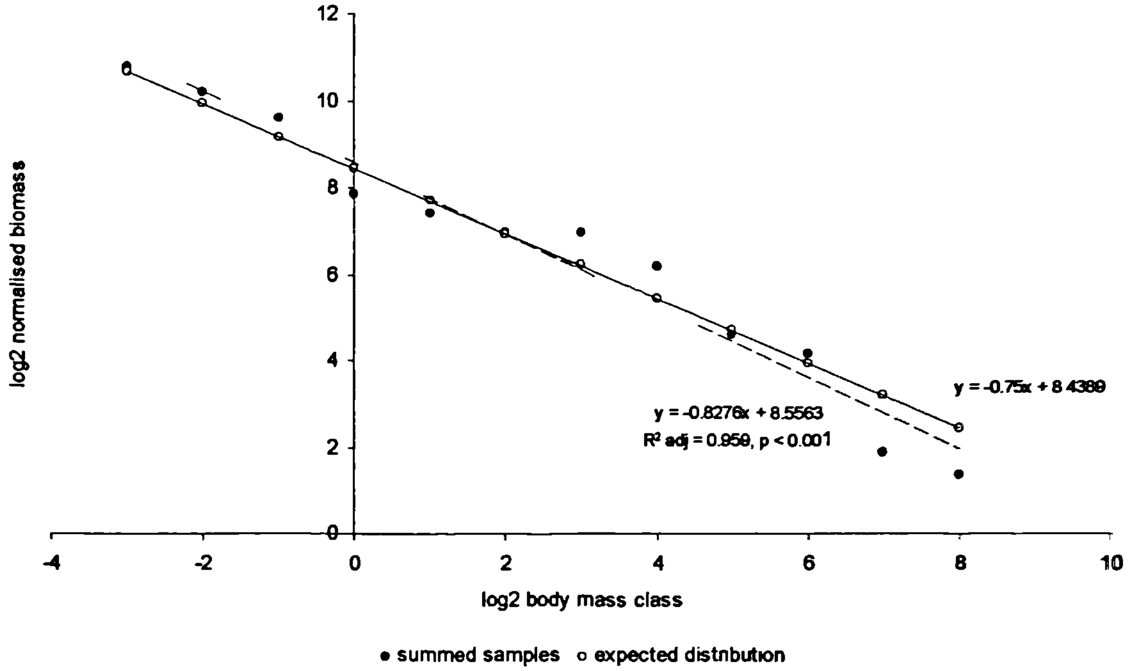


Figure 5.4: Overall normalised biomass-body size distribution summed across all samples. The expected gradient of -0.75 is overlain.

5.5 Discussion

Mixed stand structural complexity was found to affect the overall biomass and biomass-body size scaling of macroinvertebrates in ponds. As many of the invertebrates primarily utilise the inter-vegetation gaps, fractal indices might be viewed as a simplified way of describing gap structure within stands, more complex vegetation having a greater number of gaps with smaller mean size than simple vegetation, promoting utilisation by smaller individuals. Differences in the rigidity of macrophyte species are not accounted for; however, so larger individuals may still be able to move through complex habitat by pushing aside finer stems and leaves.

The use of digital image analysis greatly sped and simplified the analysis of habitat fractal complexity and this technique could prove useful for quantifying and separating the effects of habitat structural complexity from habitat density and species richness in any system where mixed vegetation stands are the norm. The wide range of grid sizes (0.06mm-18mm) used to analyse fractal structure meant few assumptions were made about the scale of perception of invertebrates or the 'grain' at which they utilise space. Measuring the fractal dimension of both macrophyte area (fdarea) and perimeter (fdperim) added useful detail to the description of macrophyte branching structure, because if only fdperimL (minimum resolved distance 0.56mm) had been measured, as in previous studies of plant structure, (e.g. Davenport *et al.* 1999, Gee & Warwick 1994, Morse *et al.* 1985) the significant relationships between fdareaL and fdperimH and macroinvertebrate biomass-body size scaling and overall biomass (Fig. 5.3) would not have been detected. FdperimL co-varied with both macrophyte surface area and species richness, so if this commonly used measurement of fractal structure had been relied upon the individual effects of all three measures of habitat structure on macroinvertebrate assemblages would have remained confounded. There have been similar problems in earlier studies, for instance Hills *et al.* (1999) found barnacle settlement density to be related to both euclidean and fractal substrate complexity measures which co-varied.

The marked changes in fractal dimension at different scales seen for most species in this study (Fig. 5 2, Table 5.1) have been noted by other authors. Lawton (1986), Morse *et al.* (1985) and Gee and Warwick (1994) all found a change in plant fractal dimension between two levels of magnification, indicating that most plants are not self similar across the scales of observation but exhibit non-uniform fractal structure (Mandlebrot 1983). Bradbury *et al.* (1984) also found this to be true at larger scales for a coral reef, where fractal dimension changed across scales of centimetres, metres and hundreds of metres. As a consequence of non-uniform fractal structure, macroinvertebrates of different body sizes would be expected to perceive the same macrophyte stand as having different levels of structural complexity. These differences might alter patterns in habitat utilisation for animals of different body sizes, resulting in the observed patterns in changing biomass between macrophyte stands.

Gaston and Blackburn (2000) stated that if the environment is fractal and there is a functional response to the space available, the smallest body size class should be the mode. This was true for the majority of samples (23/29) as they had significant negative normalised biomass-body size gradients. FdareaL and fdperimH had a significant negative effect on gradient and a positive effect on intercept so two-dimensional measures of macrophyte complexity were shown to have a significant effect on the body size distribution and overall biomass of invertebrates within three-dimensional space. Fractal measures may give an indication of how the habitat volume is partitioned, samples of high complexity being more highly divided and having a smaller mean 'gap' size in the vegetation (Bartholomew *et al.* 2000). High fdareaL scores indicate that the plant material effectively forms planes through the water column at scales greater than 0.56mm, which might be of consequence to larger invertebrates, perhaps reducing the ease with which they can move within the stand. In contrast, fdperimH scores indicate the degree of convolution of leaf perimeter which might further divide three-dimensional space at smaller scales (0.06-2mm). Where the habitat is most divided, and mean gap size is smallest, more utilisable space is available for a high density of small invertebrates, which leads to patterns in both increasing biomass and density of small invertebrates (Fig. 5.3).

A limited number of studies in other systems have found similar relationships between habitat fractal complexity and the body size distributions of invertebrates. Williamson and Lawton (1991) compared the distribution of arthropod body sizes with the complexity of birch trees, their data indicate a linear trend between body size gradient and complexity; although no test statistics were reported. Schmid *et al.* (2002) also found that fractal scaling of stream sediment particles was related to macroinvertebrate biomass scaling, finding that more complex habitat had a greater number of small species. The density and number of macroinvertebrate species were shown by Jeffries (1993) to increase with the fractal dimension of artificial pond weeds and Schmid (2000) and Schmid *et al.* (2002) also show that habitat fractal dimension has a positive effect on the density and number of macroinvertebrate species. However, no evidence can be presented, at the scale of this study, to support the hypothesis that habitat structure regulates species diversity at local scales (Downes *et al.* 1998) or that habitat complexity determines the number of fundamental niches that could be maintained in the environment (May 1972), as fractal complexity was unrelated to macroinvertebrate species richness.

Macrophyte surface area and species richness, measures of habitat structure that have received the most attention in freshwater studies, were not significantly related to macroinvertebrate richness, biomass scaling or density. Other studies of the effects of these two parameters have given mixed results (e.g. Cheruvelil *et al.* 2002, Cattaneo *et al.* 1998, Brown *et al.* 1988, Cyr & Downing 1988, Rooke 1986, Scheffer *et al.* 1984, Rooke 1984, Dvorak & Best 1982). Attrill *et al.* (2000) found that seagrass surface area positively affected species richness and density of macroinvertebrates, whereas an index of complexity incorporating fractal dimension had no significant effect. It would, however, have been surprising if macrophyte surface area had been of the same importance for temporary pond macroinvertebrate assemblages where few species are epifaunal.

The overall biomass body size distribution gradient of -0.83 fitted Morse *et al.*'s (1985) model. Slopes greater than -0.75, which is predicted under the energy equivalence hypothesis (Damuth 1981), might occur if: (i) the mean metabolic rate of macroinvertebrates does not scale as body mass$^{0.75}$; (ii) the metabolic rates of invertebrates of different body sizes scale differently so large and small animals use different proportions of available energy; or (iii) if there is disproportionately more available habitat space for small invertebrates due to the fractal nature of habitat structure. Morse *et al.*'s (1985) model examines (iii) although accordance with the model cannot to discount the possible influence of (i) and (ii) on biomass-body size scaling.

Morse *et al.* (1985) showed that five data sets for invertebrates on terrestrial vegetation approximately fitted the model and Shorrocks *et al.* (1991) found similar accordance at small scale when examining the fractal dimension of lichen thalli and the body size distribution of arthropods. Both authors attributed slopes steeper than -0.75 to the fractal complexity of habitat structure. In contrast, the only aquatic study that examines this tentative relationship (Gee & Warwick 1994) found the gradient of density-body size distribution for invertebrates on marine macroalgae to be too shallow to be in accordance to Morse *et al.*'s model. These data show accordance with the Morse *et al.*'s (1985) model for the first time in an aquatic system, where invertebrates use habitat space in a three-dimensional way. In addition the statistical significance of the relationship between fractal structure and biomass body size scaling is demonstrated for the first time (Fig. 5.3 a and b) providing support for the notion that habitat fractal complexity may influence the overall biomass-body size relationship.

6 Discussion

The preceding chapters have used various approaches to examine physicochemical and spatial patterns in pond assemblage composition across two regions of the UK, the colonisation dynamics of small sites and the effect of habitat architecture on macroinvertebrate assemblage structure. Biotic and abiotic data were collected from a wide range of temporary and fluctuating water bodies from each region so that macroinvertebrate and plant assemblages could be objectively classified in order to define and describe Mediterranean Temporary Pond habitat within a UK context. In this chapter I firstly move on from the original aims of the chapters to synthesise the ecological findings of the thesis by examining: (i) the relative importance of regional and local processes in shaping pond assemblages; (ii) the role of ponds as habitat islands in the landscape; and (iii) the influence of plant assemblage composition, diversity and structural complexity on macroinvertebrate assemblages The findings are then placed into an applied context by: (i) re-defining Mediterranean Temporary Ponds in the UK; and (ii) outlining the conservation and management implications of the study.

6.1 Local and regional patterns and processes

6.1.1 Regional patterns in occurrence

The overall occurrence patterns of plant and macroinvertebrate taxa were similar in both the New Forest and on the Lizard (Fig 6.1). Over half the plant and macroinvertebrate taxa found in each region were infrequent, occurring in less than 10% of ponds sampled, whereas less than 10% of taxa occurred in more than half of the sites. Widespread macroinvertebrate taxa on the Lizard comprised Coleoptera, Trichoptera and Mollusca typical of temporary waters. Common plant taxa included *Agrostis* spp and *Ranunculus flammula*, which are routinely found in wet heathland, unimproved grasslands and meadows (Table 6.1). In contrast, widespread New Forest taxa were taxonomically more diverse comprising Chironomidae, Coleoptera, Trichoptera, Odonata and Ephemeroptera, probably because, on average, New Forest ponds seemed more permanent and had greater mean plant diversity. This is further supported by the fact that the most common plant taxa in the New Forest included species that are typical of the fluctuating margins of larger ponds i.e. *Juncus* spp, *Glyceria fluitans, Eleogiton fluitans* and *Hydrocotyle vulgaris* (Table 6.1).

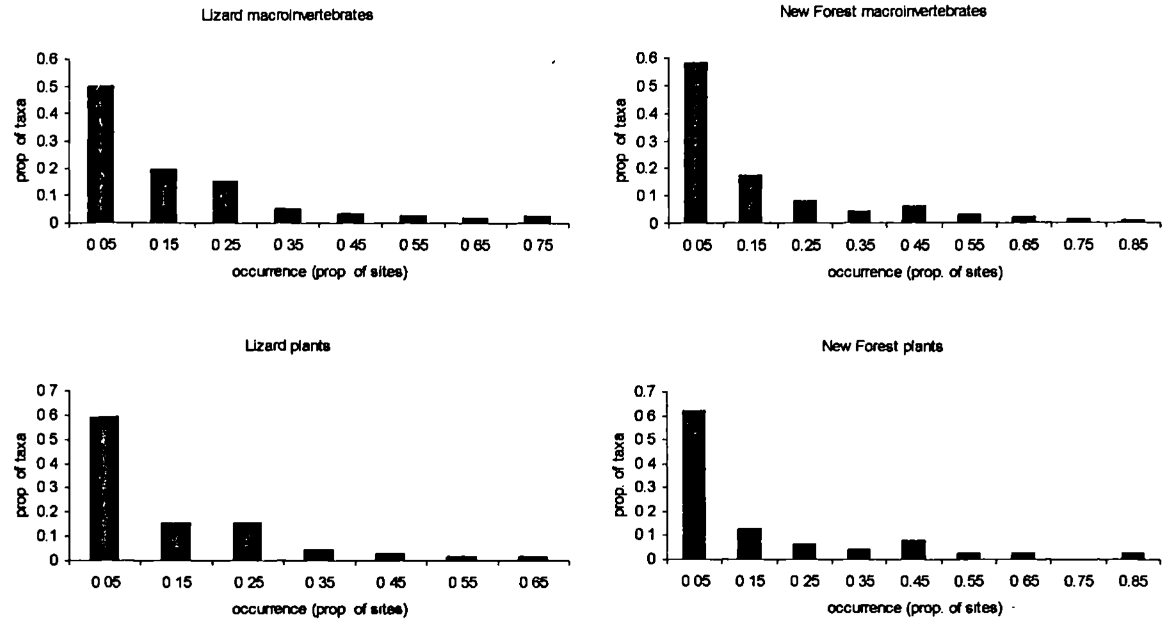


Figure 6.1: Occurrence of New Forest and Lizard plant and macroinvertebrate taxa

	Lizard Peninsula	**New Forest**
macroinvertebrates	*Hydrobius fuscipes* (C)	*Hydroporus pubescens* (C)
	Hydroporus pubescens (C)	*Anacaena lutescens* (C)
	Helophorus grandis (C)	*Limnephilus vittatus* (T)
	Helophorus obscurus (C)	*Psectrocladius* (Ch)
	Helophorus minutus (C)	*Macropelopia* (Ch)
	Limnephilus vittatus (T)	*Procladius* (Ch)
	Limnephilius auricula (T)	*Microspectra* (Ch)
	Anisus leucostoma (M)	*Cloeon dipterum* (E)
		Sympetrum spp (O)
		Asellus aquaticus (I)
plants	*Agrostis* spp	*Juncus bulbosus*
	Ranunculus flammula	*Ranunculus flammula*
		Glyceria fluitans
		Hydrocotyle vulgaris
		Eleogiton fluitans
		Juncus articulatus

Table 6.1: Taxa that occurred in >50% of ponds sampled in each region. C- Coleoptera, Ch – Chironomidae, T –Trichoptera, E – Ephemeroptera, I - Isopoda and M – Mollusca.

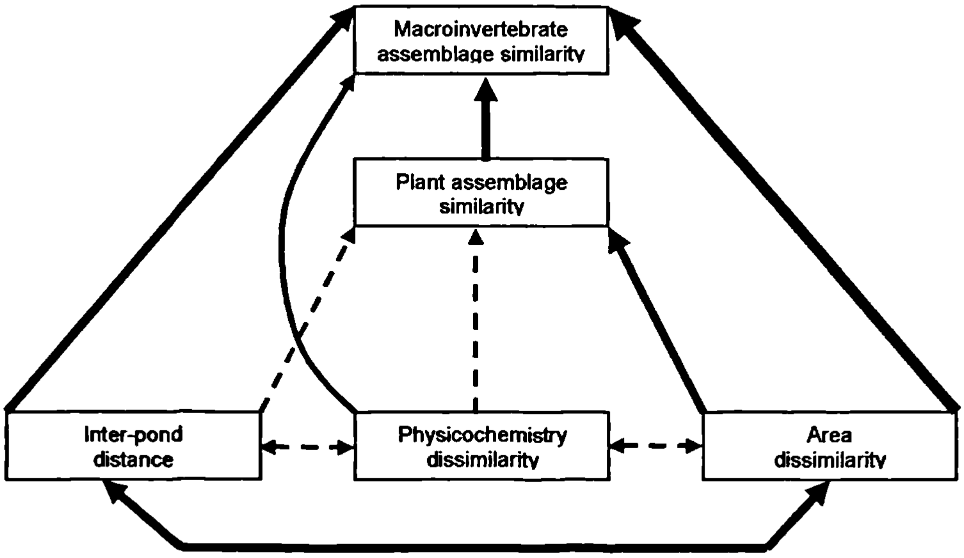
The large proportion of infrequent taxa in both regions led to high within and between region differences in the assemblage composition of individual ponds (chapters 2 and 3). The distributions of taxa were limited due to a combination of regional processes, such as dispersal constraints and pond drying, and local processes such as environmental constraint, biotic interactions and stochastic colonisation.

6.1.2 Relative importance of local and regional processes: large scale

The potential influence of local and regional processes in shaping pond assemblage composition is a recurrent theme of this thesis. Firstly, environmental and spatial pattern in plant and macroinvertebrate assemblage composition were examined independently in the two regions using partial Mantel tests (see chapter 2 & Fig 6.2 below). Local measures of pond environment included area and depth, (which, on the Lizard, appeared correlated with pond permanence), water chemistry and, for macroinvertebrates, plant species composition. Spatial pattern in assemblage composition was likely to be generated by a combination of residual local and regional processes, such as biotic interactions and dispersal limitation respectively, as well as chance.

The strength of environmental and spatial pattern in assemblage composition was found to differ between the New Forest and the Lizard (Fig 6.2), indicating that the relative importance of the local environment in the establishment of plant and invertebrate taxa was not constant across regions. Lizard ponds which were close together and were of similar size, physicochemistry and vegetation composition had similar macroinvertebrate assemblage composition. In contrast, no obvious spatial or environmental patterns were observed in the New Forest, indicating that local pond physicochemistry and inter-pond distance were not as important in limiting macroinvertebrate assemblage composition as for the Lizard. There was, however, a correlation between plant and invertebrate assemblage similarity, which suggests that local macrophyte composition was important in shaping invertebrate assemblages in both regions.

a) Lizard



b) New Forest

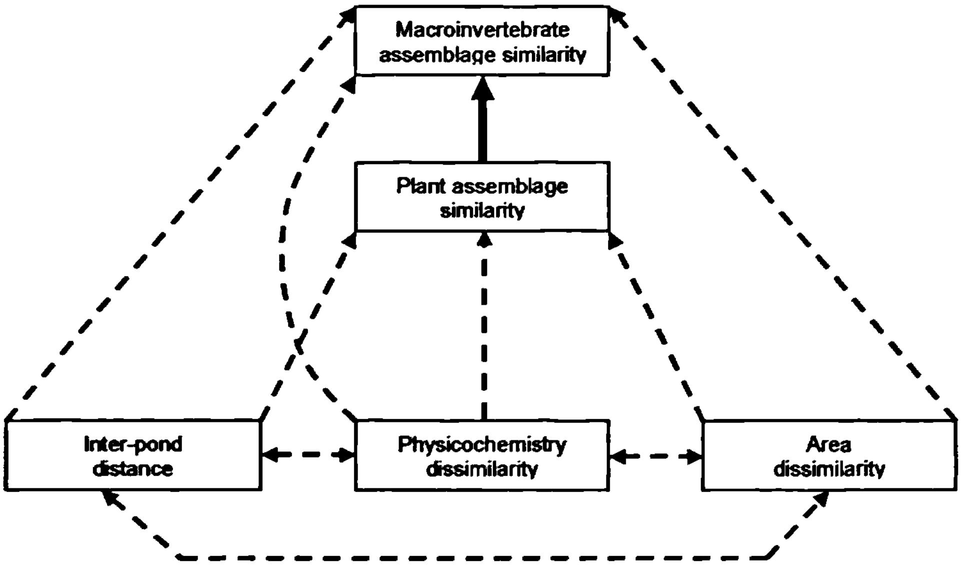


Figure 6.2: Summary of partial Mantel results detailing relationships between assemblage composition and physicochemical and spatial factors. Thickness of arrows indicates magnitude of the partial Mantel correlation coefficients between the similarity matrices (see Fig. 2.9 for statistics) dotted arrows indicate that correlations were not significant.

No strong spatial or environmental pattern in plant assemblage composition was observed for either region (Fig 6.2), which suggests that temporary pond plants do not respond strongly to any of the measured water chemistry parameters, and that other factors may drive their distribution. Therefore, contrary to Bonis *et al.* (1996; 1995), local wet phase parameters appear to have little effect on the assembly of temporary pond plant assemblages at the scale of this study. It is possible instead that frequency, length and timing of dry phase and area of drawdown zone (Bliss & Zedler 1998, Maitland & Morgan 1997) are important in structuring assemblage composition. In addition, dispersal limitation and competition (Honnay *et al.* 2001) may be important as aquatic vegetation is closely coupled to the seedbank (Grillas *et al.* 1993).

Regional differences in the relative strength of environmental and spatial pattern in macroinvertebrate assemblage similarity may have been due to disparities in the scale and resolution of sampling (see section 2.5). Shurin *et al.* (2000) and Loreau (2000) demonstrate that differences in the scale of a study region can affect the perceived magnitude of local and regional processes. However, failure to detect environmental or spatial pattern in New Forest pond assemblage composition might reflect real differences between the regions in the relative strengths of dispersal limitation, environmental constraints and biotic interactions.

The spatial distributions of many macroinvertebrate species across Lizard ponds were found to be governed primarily by pond area (and, therefore, permanence), but other local habitat factors (e.g. depth, water chemistry and plant diversity) also had some effect (Figs 3.1 & 3.2). Such species showed patterns of over dispersion in the landscape, appearing to avoid unsuitable sites. The combined responses of individual taxa to pond area, isolation and local habitat factors resulted in pond assemblages exhibiting a significant pattern of nestedness across the landscape, where species-poor sites tended to comprise subsets of the taxa found in rich sites (see sections 1.4.2 & 3.2). About a quarter of species, however, were found to be habitat generalists, which were apparently less restricted by pond area, local habitat factors or dispersal constraints (Figs 3.1 & 3.2), as they were frequently found to be completely randomly distributed throughout the landscape (Table 3.6). These taxa were idiosyncratic (deviating from the nestedness pattern) and often found in both small species-poor sites and large more permanent ponds. New Forest macroinvertebrates also showed significant but weaker nesting, with around 40% of taxa being idiosyncratic; indicating that there was greater spatial turnover in the assemblage composition of ponds. The majority of New Forest idiosyncratic taxa also have good powers of dispersal and many also have desiccation resistant life stages so can tolerate the most ephemeral sites (see appendix 6.2.3.1).

Many authors have recognised that the predictability and timing of pond dry phase are critical in shaping assemblage composition and structure (e.g. Wilbur 1997, Williams 1996 &1987, Wiggins *et al.* 1980). Permanence mediates the relative strength of local and regional processes (Kiflawi *et al.* 2003, section 1.3.1), but might itself be regarded as having both local and regional influences on assemblage composition. Successful establishment after colonisation, the frequency of extinction and strength of biotic interactions (Schneider 1997, Schneider & Frost 1996, Wellborn *et al.* 1996) all depend locally upon pond permanence. However, at a regional level synchronous summer drying decreases pond availability in the landscape and may also reduce the ability of dispersing taxa to detect ponds visually (Schwind 1995 & 1991). Such regional effects of permanence limit the distribution of vagile (actively dispersing) taxa which exploit the most ephemeral habitat patches.

Idiosyncratic species distributions are regulated by regional fluctuations in pond availability, i.e. the regional effect of drought (Bohonak & Jenkins 2003), as many of the idiosyncratic taxa are known to track available habitat throughout the year (Osborne *et al.* 2002, Svensson 1998; 1999, Landin & Stark 1973, Pajunen & Jansson 1969). In contrast, the establishment of nested taxa is likely to be limited locally by pond permanence, vegetation diversity, water chemistry and perhaps biotic interactions as there is much evidence of increased effects of competition and predation in more permanent and species rich systems (Foggo *et al.* in prep., Schneider & Frost 1996, Wellborn *et al.* 1996). Nestedness analysis may be a useful method for objectively dividing taxa occurring in any insular system into two distinct groups (nested vs idiosyncratic, see section 3.5) based on their occurrence patterns; this may illuminate commonalities between species in their life history strategies and/or aid inferences regarding the influence of local and regional factors on their distribution.

Differences in the relative strength of local and regional processes in shaping the distribution of organisms with different life history strategies have previously been noted (Cáceres & Soluk 2002), as local processes are expected to play a more dominant role when populations rarely undergo local extinction (Cohen & Shurin 2003), either because the habitat is stable or because the population is maintained by a drought resistant egg or seed bank. In this study, nested taxa are those that are less frequently subjected to local extinction because they preferentially occur in large ponds that rarely dry completely, local processes therefore primarily govern the occurrence of nested taxa. As the ponds occupied are relatively stable some nested species also show reduced ability and tendency to fly (Johnson 1969, Brown 1951), which is likely to be a locally advantageous strategy as the risks of dispersal are commonly greater than the benefits of colonising new habitat, so energy is more profitably directed to reproducing in the current habitat. When large ponds do dry, nested taxa might be secondarily subject to the regional process of dispersal limitation, although some species avoid this by being plastic. For example, long winged individuals (e.g. *Helophorus granularis;* Bilton *et al.* 2001b), or diapausing eggs, (e.g. Chironomidae; Chou *et al.* 1999, McLachlan & Cantrell 1980) may be produced in response to changing environmental cues related to pond drying. In contrast, idiosyncratic taxa include species that are more likely to undergo regular local extinction due to pond drying and therefore disperse throughout the landscape to find new sites for oviposition/mating.

6.1.3 Relative importance of local and regional processes: small scale

The small-scale effects of differences in pond permanence are shown by the colonisation patterns of the experimental ponds (chapter 4), which dried regularly but often asynchronously due to patchy soil structure in the plots. The most ephemeral ponds accrued fewer species (Table 4.6) including larval and teneral (newly metamorphosed) Coleoptera (chapter 4, appendices 4.6.7 & 4.6.8), indicating that less species became established in the most temporary sites, which had hydroperiods that were approximately two to four weeks shorter. Other local environmental constraints, such as water chemistry and vegetation composition were also shown to be important in governing the abundance of species in small man-made ponds, perhaps because they limited successful recruitment (Table 4.7).

In addition to the life history restrictions imposed by short hydroperiod, the most temporary of ponds are only available for colonisation for a brief time frame, which reduces the probability that dispersing individuals will reach them. The distribution of taxa, that can colonise such ephemeral habitat might be expected to be stochastic; some evidence for this is seen in the random spatial distribution of many idiosyncratic taxa (Table 3.6) and in the bimodal occurrence of taxa which colonised the experimental ponds (Fig. 6.3), which shows that a third of the taxa reached less than 20% of the ponds, despite their close proximity, over the three year period.

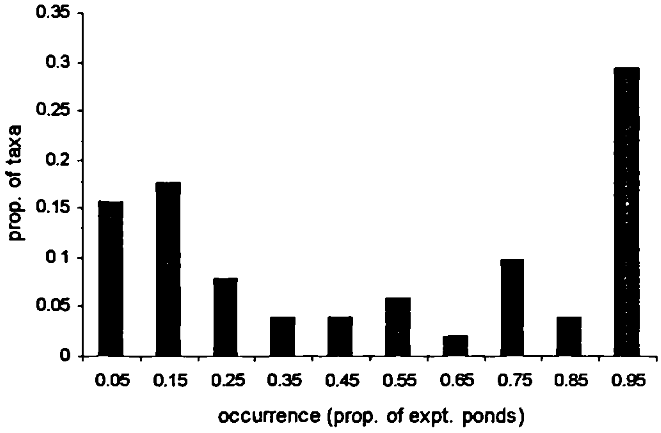


Figure 6.3: Occurrence of experimental pond taxa over three years

Although pond permanence, is believed to mediate the relative strength of biotic interactions, as it determines the frequency of local extinction (Kiflawi *et al.* 2003, Schneider & Frost 1996), the intensity of such local interactions are also likely to be affected by the regional effect of seasonal drying as it changes habitat availability in the landscape. Levels of coleopteran co-occurrence have been shown to decrease, in more permanent Lizard ponds during the dry season (Foggo *et al.* in prep.), potentially indicating increased competitive exclusion during summer months. However, inter and intra-specific interactions are less likely to result in competitive exclusion within assemblages in small ephemeral ponds as there is little time available for such local processes to occur (Shorrocks & Rosewell 1987, Lockwood *et al.* 1997).

In summary, the relative strength of local and regional processes on temporary pond assemblage composition are affected by the (i) scale of the study, (ii) permanence regime of the focal pond(s) and (iii) the life history strategies of the constituent taxa. Patterns in macroinvertebrate assemblage similarity and the distribution of individual taxa appear to be governed by a combination of local environmental constraints and regional habitat availability, along with chance. The relative influence of these factors differs between taxa with different life history characteristics (nested vs idiosyncratic) and between ponds. In contrast, the assemblage composition and distribution of plants is more likely to be governed by dry phase characteristics, biotic interactions and/or dispersal constraints.

6.1.4 Temporary ponds as habitat islands

The theory of island biogeography (MacArthur & Wilson 1967) makes a number of predictions about the outcome of colonisation and extinction processes in insular habitats:

(i) that there will be a positive correlation between number of species and island area,

(ii) that there will be a dynamic equilibrium between colonisation and extinction, where species turnover occurs but richness remains constant through time and

(iii) that extinction rates will be greatest on smaller islands.

However, as mentioned in the introduction (section 1.3.2), a model based upon constant rates of colonisation and extinction across habitat islands of varying size and isolation is likely to be a simplistic way of viewing pond assembly processes as it assumes that: (i) islands are constant throughout time; (ii) species do not interact; and (iii) that islands of the same size are equally favourable habitats. All of these assumptions are violated in a proportion of ponds within each region. This thesis provides mixed support for MacArthur and Wilson's (1967) above predictions. Prediction (i): Lizard macroinvertebrates and plants both showed a significant species-area relationship (Table 2.6). In addition, macroinvertebrate and Lizard plant assemblage composition were also related to pond size (Table 2.8). Although pond isolation was not found to affect species richness on the Lizard, when differences in pond area and habitat were accounted for (Table 3.4), assemblage composition was influenced by proximity to neighbouring ponds (Fig 2.10a).

Prediction (ii): seasonal turnover in macroinvertebrates has been shown to occur in both temporary and permanent ponds (Jeffries 1994) and was observed in the small experimental ponds (Fig. 4.9). However, these small sites did not reach dynamic immigration-extinction equilibrium, as they continued to accrue species throughout the study period. Large ponds, although more likely to be at equilibrium due to reduced frequency of drying, may exhibit seasonal fluctuations in species richness, as habitat availability varies in the landscape and temporary pond specialists leave large sites to breed in the winter/spring but return during summer months. In contrast, temporary pond plants are less likely to show turnover, unless seasonal die back of species promotes colonisation or germination from the seed bank. Lastly prediction (iii): small habitat patches generally confer increased risk of extinction for macroinvertebrates, because they dry more quickly and frequently, but drying is unlikely to cause the same degree of local extinction for plant taxa in small sites, as many are semi-terrestrial species that do not rely on a permanent standing water body for survival.

Other studies have also had limited success in fitting temporary pond data into an island biogeography framework. Ward and Blaunstein (1994) found that although there was a significant relationship between species richness and pond area, turnover of species was not at equilibrium, so the slope of the species area relationship decreased through time. Barnes (1983) also found MacArthur and Wilson's model to have limited applicability, as species' extinction probability changed through time. Overall it appears that simple models of island biogeography are of limited use for predicting patterns of species richness in temporary ponds. Recently, however, Kiflawi *et al.* (2003) developed a colonisation-extinction model which incorporated both pond area and permanence finding that it accounted for 62% of the variation in pond species richness, although the process of turnover was ignored and ponds were assumed to be at equilibrium. Measurement of dynamic equilibria is empirically difficult as repeated samplings are necessary, which themselves interfere with the processes being investigated. Techniques such as nestedness analysis (chapter 3) present an easier and perhaps more informative method for exploring species distribution patterns as they retain information on species' identities so that patterns in assemblage composition rather than species richness can be examined.

Levins' (1969) classic metapopulation model expanded island biogeographic theory by considering a number of demographically identical islands or patches that were all linked by dispersal and subject to stochastic extinction. Few species have been found to exhibit classic metapopulation structure, however (Bohonak & Jenkins 2003), so the metapopulation concept has been broadened to incorporate any set of local populations that are linked by dispersal (Hanski 1999). The level of dispersal between fragmented subpopulations in a landscape is now thought to form a continuum (see Fig 6.4, adapted from Bullock *et al.* 2002). Species with high levels of inter-site dispersal form patchy populations, whereas when inter-site dispersal tends towards zero species have isolated or remnant populations. Dispersal can be approximately equal between patches, as is the case for classic metapopulations, or unequal, where patches differ in their size, suitability or productivity so that some act as 'sources' and others 'sinks' of dispersing individuals (Okamura & Freeland 2002).

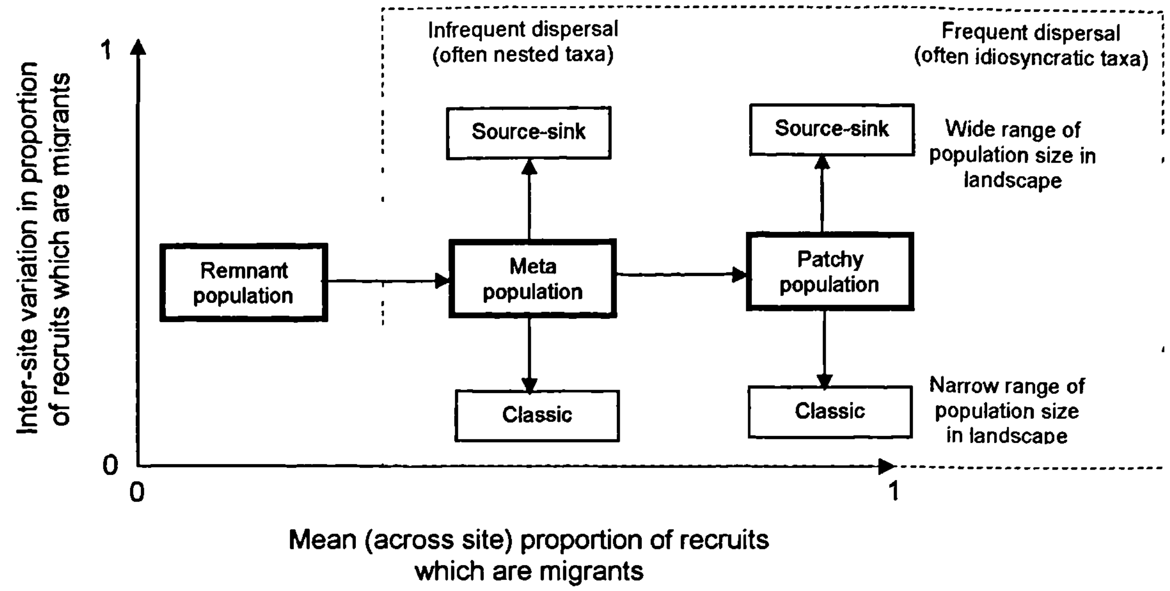


Figure 6.4: Continuum of dispersal frequency linking subpopulations. Variation in the mean level of inter-site dispersal forms a continuum in population structure, from remnant populations which are isolated in the landscape to patchy populations which frequently exchange individuals between sites. Where the level of dispersal is approximately equal between patches classic metapopulation/patchy populations exist, however, rates of dispersal are often unequal between patches giving rise to source-sink populations. Adapted from Bullock *et al.* (2002).

Populations of pond species do not always fit the strict assumptions of classic metapopulation models (Briers & Warren 2000) as ponds are frequently not at equilibrium because they dry regularly and pond habitats vary in their suitability both spatially and temporally with local dynamics and hydroperiod often being spatially autocorrelated (Bohonak & Jenkins 2003). However, some studies (e.g. Caudill 2003, Briers & Warren 2000, Jeffries 1994) have found that metapopulation approaches are useful for describing and understanding the population dynamics of pond species.

Temporary pond species having distributions that are restricted by pond hydroperiod may be less likely to disperse than taxa which have broad ecological tolerance, as the chances of reaching an equally suitable site are lowered. (These taxa were frequently found to have nested distributions in this study, chapter 3). Such taxa probably disperse relatively slowly amongst large similar sites on the Lizard and might therefore hypothetically be species most likely to exhibit classic metapopulation structure (Fig 6.4, Table 6.2). In contrast, idiosyncratic taxa may more regularly disperse between ponds, although the net direction of dispersal is likely to be from small to large ponds, so they might be expected to have source-sink patchy populations (Fig 6.4, Table 6.2).

	Infrequent dispersal (Nested taxa)	**Frequent dispersal (Idiosyncratic taxa)**
Wide range of population sizes in landscape	***Source-sink metapopulation*** Species that disperse rarely and occur in a range of sites so may have unequal across site density Large ponds are source patches Literature: *Calibaetis ferrugineus* (Ephemeroptera, Caudill 2003) *Chaoborus flaviscens* (Berendonk & Bonsall 2002)	***Source-sink patchy population*** Active dispersers that breed in small temporary waters so may exhibit a range of population densities across occupied sites Small ponds are source patches *e.g. Agabus bipustulatus, Ilybius montanus, Graptodytes flavipes* (VU), *Hydroporus pubescens, Hydroporus planus, Hydroporus tessellatus* & many *Helophorus* spp
Narrow range of population sizes in landscape	***Classic metapopulation*** Species that disperse rarely and have relatively even population sizes across occupied patches e.g. *Haliplus variegatus* (EN), Literature: *Hydroporus memnonius* (Jeffries 1994), Some *Gyrinus* spp (Svensson 1992), *Chaoborus crystallinus* (Berendonk & Bonsall 2002)	***Classic patchy population*** Active dispersers which are restricted to the most temporary ponds. Species that breed in small sites and remain in pond basin during summer i.e. don't utilise large sites e.g. *Ranunculus tripartitus* (VU), *Cicendia fililformis* (ns), *Juncus pygmaeus* (VU), *Dryops striatellus* (VU)

Table 6.2: Types of metapopulation model that might be relevant to populations of pond species with examples from the literature and from observations within the thesis.

There is still relatively little known about the probability, rate and dispersal distances of freshwater invertebrates (Bohonak & Jenkins 2003), so further work is required to characterise the dispersal curve and behaviour of such taxa (Williamson 2002). Such studies are empirically demanding and laborious in pond systems where it is often difficult to accurately census species occurrence (see Svensson 1992 for an example of one approach). However, the construction of metapopulation models for individual species relies upon these parameters, and until this information is gained there can be no tests of my unsubstantiated predictions in Table 6.2. Knowledge of the rates of exchange of individuals between subpopulations would further our understanding of the landscape ecology of pond assemblages, giving greater insight into the spatial and temporal scales at which different macroinvertebrate and plant species utilise their environment. This would allow more informed decision making about the location and timing of habitat creation and could also indicate, if spatially explicit models were used (e.g. Hanski 2001), which ponds are critical in the landscape for the long-term persistence of focal species (also see section 6.2.2.8 below).

6.1.5 Effect of plant assemblages on macroinvertebrates

The significant correlations between plant and macroinvertebrate species richness (Table 2.6) and assemblage similarities (Fig. 2.9) were the only relationships common to both regions. In addition, macrophyte richness played a part in structuring the nested subset structure of macroinvertebrates (Tables 3.1 & 3.4). Macrophyte richness and composition are therefore likely to be of general importance in shaping macroinvertebrate assemblages. Previous studies have examined macroinvertebrates and plants within the same pond, stream or lake (e.g. Cattaneo *et al.* 1998, Rooke 1984) and comparison of studies gives mixed conclusions about the effects of macrophyte composition, diversity and surface area on macroinvertebrate abundance and diversity (section 5.5). This thesis shows, at a larger scale than has been studied before, that macrophyte richness and composition affect macroinvertebrate assemblages between ponds across regions.

At a smaller scale, fractal measures of macrophyte structural complexity were shown to influence both body size scaling and overall biomass of macroinvertebrates in mixed macrophyte stands (Table 5.2). In addition, the species composition of plants that colonised the experimental ponds appeared to affect the colonisation and, potentially, subsequent survival of macroinvertebrate colonists (section 4.5 & Table 4.7). Examination of macrophyte stands within ponds, however, showed that neither macrophyte diversity nor surface area was related to invertebrate diversity (Table 5.2). The non-significant relationship with plant surface area is unsurprising considering that the macroinvertebrates assemblages were not predominantly epiphytic and individuals were therefore more likely to utilise the plants as oviposition substrates, shelter from predation or to trap particulate organic matter. The lack of a plant–invertebrate diversity relationship in chapter 5 may have been a result of small sample size, which limited the diversity of macrophytes within each sample.

The results from this thesis illustrate that pond plants structure invertebrate assemblages in different ways at different spatial scales. Such scale dependent results may explain why conflicting results regarding invertebrate-plant diversity and abundance relationships have been gained by previous studies. Further work is needed to mesh findings at different scales together. For instance, the effect of experimental changes in vegetation might be examined, in order to understand how succession/seasonal changes in macrophyte structure affect invertebrate assemblages. The effect of different levels of vegetation complexity on biotic interactions between macroinvertebrates might also be explored, in order to detect whether vegetation changes could have knock on consequences for trophic interactions within macrophyte stands, which might cause larger scale changes in pond functioning.

6.2 Conservation and Management

The importance and fragility of freshwater biodiversity is often underestimated, largely because less is known about the ecology and distribution of the fauna compared with that of terrestrial systems (Maitland & Morgan 1997). The importance of freshwater conservation efforts is highlighted by Ricciardi and Ramussen (1999) who showed that faunal extinction rates in North American freshwaters are five times as high as those in the terrestrial realm and are comparable to those of tropical rain forests. Temporary ponds, although small and comparably cryptic, are now considered an important biodiversity resource throughout Europe and the UK (Nicolet 2002, Collinson 1995, European Commission 2003), however they are still often overlooked (e.g. Maitland & Morgan 1997) and are under increasing threat in the two study regions (see Table 6.6 below).

Pond conservation guidelines, in the past, have often treated ponds in isolation, giving guidance about best practice for managing and maintaining pond water quality and habitat heterogeneity in order to maximise species diversity within individual ponds (e.g. Drake 1999, Hine 1994). Gradually, the advantages of landscape-level conservation approaches, developed within terrestrial and lotic freshwaters (e.g. Seelbach *et al.* 2002), have become more widely appreciated and the limitations of such individual pond approaches for conserving invertebrate, plant and amphibian metapopulations are beginning to be more widely realised. Conserving ponds based on rare species composition, although critical, is insufficient, especially when the pond is isolated within a landscape which is under intensive agricultural use. Future pond management in regions which still have a high density of ponds should consider greater spatial scales in order to conserve landscapes (or 'pondscapes', Boothby 1997) which preserve both connectivity between ponds and the matrix within which the ponds lie, since such an approach better reflects the manner in which many organisms utilise pond habitat. Perhaps as a consequence of the paucity of information regarding the population and dispersal dynamics of pond invertebrates there are virtually no existing management guidelines for the conservation of rare invertebrate species within the aquatic management literature (Richardson & Jackson 2002).

The lack of knowledge about the rarity and distribution of freshwater invertebrates has caused difficulty within national and international conservation planning. For instance, the designation of freshwater Special Sites of Scientific Interest (SSSI) is often solely based on the classification and conservation status of aquatic flora and, in some cases, Odonata. Despite the SSSI guidelines being published by the Nature Conservancy Council (NCC; 1989) there seems to have been little progress to incorporate other invertebrate groups in the designation procedure, despite studies which evaluate the conservation value of freshwater invertebrate assemblages (e.g. Nicolet 2002, Collinson *et al.* 1995, Foster *et al.* 1990). Annex I of the EU Habitats Directive (92/43/EEC; see section 1.5) similarly protects freshwater vegetation types with restricted distributions in Europe with little mention of the associated invertebrate assemblages, although there is some attempt to incorporate basic descriptions of habitat physicochemistry. This thesis addresses these issues by examining the conservation importance and ecology of plant and macroinvertebrate assemblages of temporary ponds across two regions of the UK, with special reference to Mediterranean Temporary Ponds (92/43/EEC) a European priority habitat, which until now has been incompletely studied in the UK.

Based on the analyses within the thesis, this section aims to: (i) redefine Mediterranean Temporary Ponds in the UK, based on both plant and macroinvertebrate assemblage composition; (ii) evaluate the conservation importance of MTPs and examine whether small man-made ponds might be used to augment MTP density; (iii) investigate whether the same conservation strategies are applicable to temporary pond plant and macroinvertebrate assemblages; and (iv) examine more general pond conservation strategies and the potential implications of further habitat loss in the regions.

6.2.1 Mediterranean Temporary Ponds

The conservation importance of ponds in both regions has been shown to be high, as the mean number of RDB plant and invertebrate species recorded was significantly greater in the New Forest and on the Lizard than for other UK temporary ponds (Fig. 2.2g). The most ephemeral of the sites in both regions have been assigned MTP status based solely upon the occurrence of one or more characteristic rare plant taxa (see section 1.5.1).

Until now the definition of MTP habitat has lacked clarity due to disparities and inconsistencies between the various methods used to describe vegetation within the UK and Europe. This ambiguity has caused confusion over the status and extent of MTP habitat in the UK. Table 6.3 (below) attempts to summarise and compare sections of the four schemes (Habitats Directive, Corine, NVC and phytosociological) that are commonly used to describe the vegetation of lentic systems, including MTPs, with particular reference to shallow ephemeral waters.

Habitats Directive	Hard oligo-mesotrophic waters with benthic vegetation of *Chara* **3140**	Oligotrophic waters containing very few minerals of the sandy plains (base poor) **3110**	Oligotrophic to mesotrophic standing waters (base poor) **3130**		Oligotrophic waters containing very few minerals generally on sandy soils of the West Mediterranean **3120**	Mediterranean Temporary Ponds (sub type of 3120) **3170**
Corine Biotope	22.12 x 22.44 Mesotrophic waterbodies x submerged algal carpets	22.11 x 22.31 Lime-deficient oligotrophic waterbodies x Northern perennial amphibious community	22.12 x 22.31 Mesotrophic waterbodies x Northern perennial amphibious community	22.12 x 22.32 Mesotrophic waterbodies x Northern Dwarf annual amphibious swards	22.11 x 22.34 Lime-deficient oligotrophic waterbodies x Mediterraneo-Atlantic amphibious communities	22.34 Mediterraneo-Atlantic amphibious communities
National Vegetation Classification (NVC)	Characeae associations not covered by the NVC	A22 *Littorella uniflora -Lobelia dortmanna,* A23 *Isoetes lacustris /setacea*, S19 *Eleocharis palustris-Littorella uniflora,* M29 Hypericum elodes-Potamogeton polygonifolius or M30 Hydrocoto-Baldellion communities	A22, A23, S19, M29, M30	OV31 *Rorippa palustris-Filaginella uliginosa*, OV35 *Lythrum portula-Raunuculus flammula, or* OV36 *Lythrum hyssopifolia-Juncus bufonius communities*		OV34 *Allium schoenoprasm-Plantago maritima* community (in eroded serpentine pans) *Cicendietum filiformis* no NVC equivalent (Rodwell pers. comm.)
Phytosociological	*Littorelletea uniflorae* with *Chara/Nitella spp*	*Littorelletea uniflorae*	*Littorelletea uniflorae*	*Isoëto-Nanojuncetea*		Sub associations of *Isoëto-Nanojuncetea* *Nanocyperion flavescentis*

Table 6.3: Habitats Directive Categories with approximately equivalent NVC communities and phytosociological associations relevant to the UK (compiled from EU 2003, Rodwell 2000, 1995 & 1994, Hill 1993)

6.2.1.1 Current definition of MTPs

According to the Habitats Directive MTP habitat is a subtype of a wider class of vegetation which includes the short grasslands of temporary ponds with *Isoetes* spp (Habitats Directive code 3120 *Isoeto-nanojuncetea*, Table 6.3). MTP habitat is distinguished by the presence of a number of phytosociological alliances (see p15), including *Nanocyperion flavecentis* ('short rush' vegetation; Rodwell 1994) which is the only MTP alliance that occurs in the UK. *Nanocyperion flavecentis* vegetation has been described in the Netherlands and France (e.g. Weeda 1994, de Bruijn *et al.* 1994) where a number of associations have been recognised, the most relevant of which is *Cicendietum filiformis* which incorporates *Cicendia filiformis, Juncus pygmaeus, Juncus capitatus, Radiola linoides* and *Anagallis minima.*

Two *Nanocyperion flavecentis* alliances occur on the Lizard. Firstly, the *Allium schoenoprasm-Plantago maritima* community (Hopkins 1983) occurs in eroded serpentine pans, with *Juncus capitatus* and *Isoetes histrix.* This type of MTP was not sampled within this study, as it is associated with ephemeral seepages rather than a standing body of water. Small ponds on track ways, however, support *Cicendietum filiformis* assemblages comprising *Cicendia filiformis* (nationally scarce), *Juncus pygmaeus* (vulnerable), *Radiola linoides* and *Anagallis minima.* It therefore appears that the Lizard sites are rather similar to the ponds in cart ruts, paths and wet ditches around Lake Lacanau in south west France (de Bruijn *et al.* 1994).

Individual countries have some freedom to interpret and modify the Habitats Directive categories in order to make them directly relevant to biogeographical location of the country. The JNCC therefore also recognise ponds with *Ranunculus tripartitus as* MTPs (McLeod *et al.* 2002), as *R. tripartitus,* like species within the *Cicendietum,* is an annual that is at the most northerly extreme of its range and is restricted to such ephemeral habitats.

All four of the classification schemes (Table 6.3) indicate that MTPs are shallow winter flooded ephemeral water bodies with vegetation dominated by rushes, grasses and annuals (see section 1.5.1 for a list of these). However, all these habitat classification schemes are subjective and none describe MTP habitat in a way that is directly relevant and useful in the UK, where MTP habitat reaches its northerly limit and is consequentially species-poor. In addition, there is no proper characterisation of the habitat's physicochemistry or associated fauna. The current description of MTPs is both overly complex, meshing together disparate vegetation classification schemes, which add little to our ecological understanding of such systems, and restrictive, as it relies on the occurrence of annual rarities with no proper descriptions of the type of ecological assemblage that these focal species occur within in the UK. Based on the current definition it seems that the UK does support MTP habitat as rare plant species of the *Nanocyperion flavescentis* occur in some sites. However, at present habitats which are not even ponds are categorised as MTPs (e.g. the *Allium* pans on eroded serpentine) as they contain the focal plant species. This study has objectively classified the ecological assemblages within which the rare MTP plant species occur and describes the habitat in a more holistic and systematic way, by incorporating physicochemical parameters and characterising typical MTP macroinvertebrate assemblage composition.

6.2.1.2 Redefining MTPs in the UK

6.2.1.2.1 MTP Vegetation

Classification of pond vegetation (section 2.4.2.1) showed that vegetation types followed a gradient in species richness, pond size and permanence. The depauperate vegetation assemblages of small Lizard ponds in TWINSPAN end groups 4, 5 and 6 (Fig. 2.3) are dominated by rushes, grasses and wet ground annuals, and frequently contain *Ranunculus tripartitus*. Such sites would therefore best equate to the UK definition of MTPs (McLeod *et al.* 2002). Characterised in this way MTP vegetation lies at one end of a continuum in temporary pond vegetation (Fig. 6.5 below).

MTP indicator species include *Ranunculus tripartitus, Agrostis stolonifera, Juncus articulatus, Juncus bufonius, Potentilla anserina, Ranunculus repens* and *Chamaemelum nobile*. Other species with high constancy include *Ranunculus flammula, Glyceria fluitans* and *Holcus lanatus* (Fig. 2.3). MTP sites were the most ephemeral ponds in the landscape and were found in grassy depressions along hedgerows and on sections of flooded track way on the Lizard Peninsula, these sites were separated from New Forest and other Lizard ponds at the first division of the vegetation classification (Fig. 2.3), showing that they are unique.

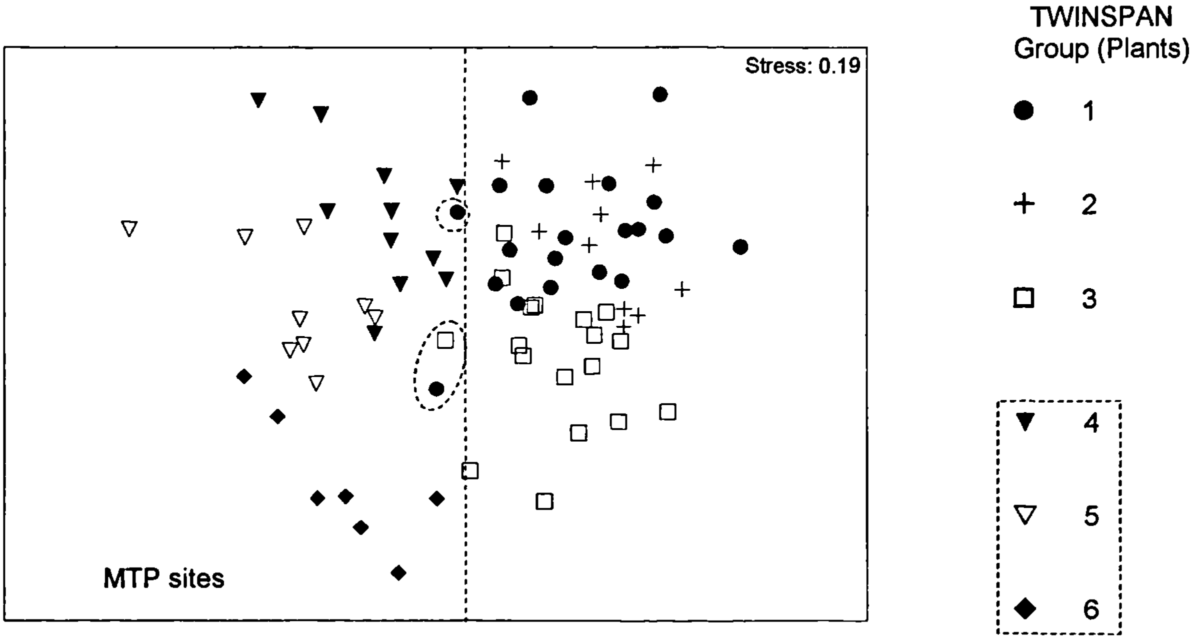


Figure 6.5: Non metric multi-dimensional scaling plot (MDS, adapted from Fig 2.5a) with TWINSPAN vegetation end groups shown. Ponds with similar assemblage composition are drawn close together. Dotted line separates MTP vegetation assemblages.

A subset of MTP sites (17/26 of sites in groups 4, 5 & 6) contained *Ranunculus tripartitus,* so could be considered to be the only ponds fitting the JNCC definition of an MTP. However, the spatial distribution of rare annual species, (including *Cicendia filiformis, Juncus pygmaeus)* varies between years, as germination depends upon the levels of competition within the pond, levels of disturbance and length and timing of inundation (Bliss & Zedler 1998). Rare annual plants, therefore, form temporally and spatially discontinuous populations that are maintained by the seed bank (Grillas *et al.* 1993) and less frequently dispersal. As a consequence it is difficult to predict the likely distribution of a species amongst the ponds in TWINSPAN groups 4, 5 and 6 in any given year and the conservation importance of a given pond's flora is likely to be dynamic. Conservation effort should be invested in maintaining the density of small sites, with vegetation comprising the key MTP indicator species, across the Lizard with the view that they are all *potential* sites for MTP rarities (see section 6.2.1.3).

As vegetation characteristics form a continuum, some species highlighted as MTP taxa (EU 2003) occur within a wide range of assemblage types, where their habitat requirements are met. For instance, a small sub-set of New Forest sites, which were not in groups 4-6 of the classification, contained *Illecebrum verticillatum* (coral necklace) a *Nanocyperion* and MTP species (EU 2003, Lemaire &Weeda 1994). Hence, although MTP assemblages do not occur in the New Forest individual taxa found within MTPs do occur in some sites. This highlights the importance of having an assemblage-level definition of MTP habitat type, rather than focusing on key rare taxa.

6.2.1.2.2 MTP Physicochemistry

As already mentioned MTP sites as defined here were highly ephemeral ponds formed in grassy depressions and on track ways. Ponds in TWINSPAN vegetation groups 4, 5 and 6 have been shown to be significantly smaller and to have greater conductivity than other sites (Table 2.3). In addition, MTP sites tend to be relatively shallow, have low pH and high concentrations of total organic nitrate (Table 6.4). Although levels of disturbance in the sites was not directly measured in this study most areas of MTP habitat were subject to regular trampling and/or vehicle disturbance, which maintains areas of bare ground which are important for the germination of annual species (also see section 6.2.1.3).

	MTP ponds mean	MTP ponds sem	Non MTP ponds mean	Non MTP ponds sem
Area m^2	32.5	8.65	2438.212	886.748
pH	5.91	0.14	6.43	0.13
Conductivity mS	745.12	43.7	455.3	56.9
Turbidity NTU	12.6	1.72	14.1	3.33
Depth cm	16.9	1.24	29.5	3.32
Cu mgL^{-1}	0.003	0.000	0.003	0.001
Zn mgL^{-1}	0.070	0.040	0.031	0.014
Fe mgL^{-1}	0.404	0.073	0.934	0.607
Co mgL^{-1}	0.007	0.002	0.003	0.001
Cr mgL^{-1}	0.009	0.002	0.004	0.001
Ni mgL^{-1}	0.056	0.007	0.020	0.0034
Al mgL^{-1}	0.127	0.026	0.165	0.026
Mg mgL^{-1}	20.02	2.30	14.06	1.67
Ca mgL^{-1}	7.02	0.60	3.62	0.43
Total Organic Nitrate mgL^{-1}	0.889	0.335	0.223	0.040
Soluble Reactive Phosphorus mgL^{-1}	0.010	0.001	0.007	0.002

Table 6.4: Mean physicochemistry of MTP and non MTP sites (Lizard sites vegetation TWINSPAN groups 4, 5 & 6 versus 1, 2 & 3)

6.2.1.2.3 MTP Macroinvertebrates

Classification of the macroinvertebrates showed that 26/27 of the Lizard MTP sites (based on vegetation) had assemblages that fell into groups 4, 5 and 6 of the macroinvertebrate classification (Fig. 2.4). These end groups were dominated by Coleoptera, Trichoptera and Chironomidae (Table 6.5).

Coleoptera	Trichoptera	Chironomidae	Mollusca
Hydrobius fuscipes	*Limnephilius auricula*	*Macropelopia*	*Anisus leucostoma*
Ilybius montanus	*Limnephilus vittatus*	*Micropsectra*	
Hydroporus pubescens		*Chaetocladius*	
Hydroporus planus			
Hydroporus tessellatus			
Helophorus grandis			
Helophorus obscurus			
Helophorus brevipalpis			
Helophorus minutus			
Graptodytes flavipes *			
Dryops striatellus *			

Table 6.5: Typical macroinvertebrate taxa of MTPs, * indicates RDB vulnerable species that are typically found in small sites.

The macroinvertebrate assemblages of three New Forest ponds (NF4, 26 & 34) were also found in these TWINSPAN groups, indicating that such macroinvertebrate assemblages are not exclusive to the Lizard Peninsula, but were rarer in the New Forest region. In addition, the macroinvertebrate assemblages of a number of more permanent sites in the Kynance region of the Lizard Peninsula fell in groups 4, 5 and 6. These sites lie in close proximity to a high density of MTP habitat, so it is unsurprising that their fauna is similar, although their plant assemblages fall in groups 1 -3 of the vegetation classification because they are dominated by fully aquatic taxa. Macroinvertebrate assemblage composition again forms a continuum (Fig 6.6), but the communities that assemble in MTPs are similar to one another, as the majority of sites form a distinct clump in MDS space (see Fig. 6.6).

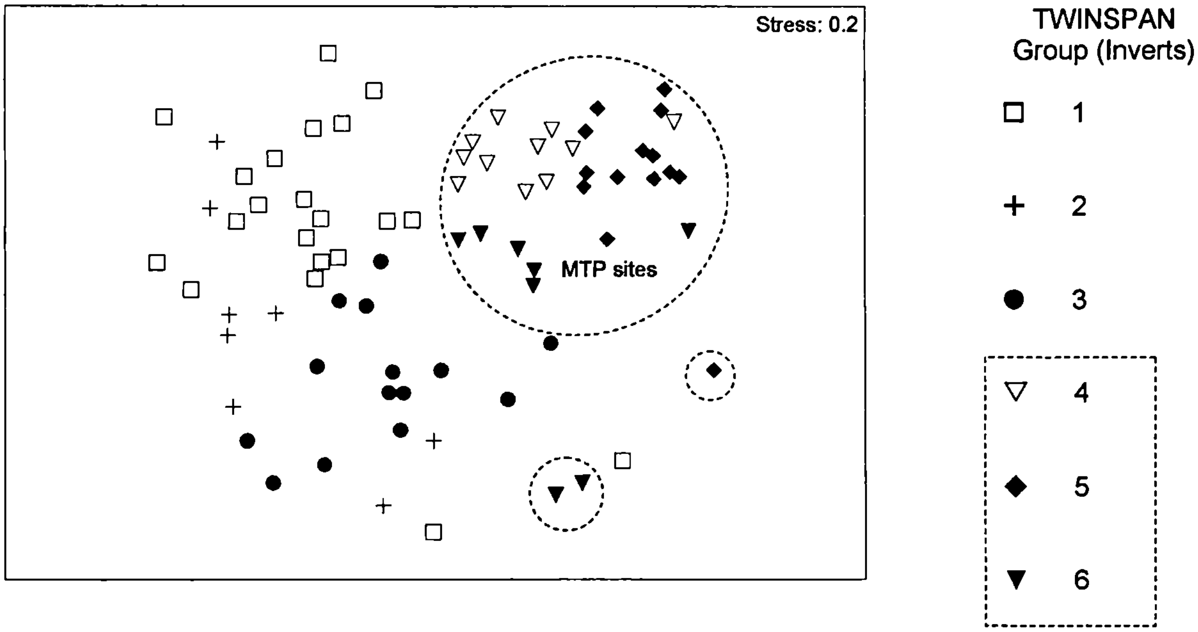


Figure 6.6: Non metric multi-dimensional scaling (MDS) plot (adapted from Fig 2.5b) with TWINSPAN macroinvertebrate end groups shown. Ponds with similar assemblage composition are drawn close together. Dotted lines indicate MTP macroinvertebrate assemblages.

Both macroinvertebrate and plant assemblages form a continuum across temporary ponds in the landscape (Figs 6.5 & 6.6), so it is unsurprising some sites have mixed plant and invertebrate MTP characteristics. For example, one Lizard site (L37) had MTP type vegetation but had macroinvertebrate assemblage composition typical of more permanent sites as it was larger than other MTP sites. In contrast several sites (L3, 22, 25, 38 & 39) had macroinvertebrate assemblages typical of highly ephemeral pools but had vegetation comprising floating, emergent or submerged aquatic taxa. Three of these sites were more permanent (L3, 22 & 25), so may be important summer refugia for taxa that colonise MTP sites during the winter and spring months. Contrastingly two sites were ephemeral (L38 & 39) and had invertebrate assemblages and physicochemistry that was typical of MTPs, however, the presence of *Chara fragifera*, *Juncus bulbosus* and *Eleogiton fluitans* amongst typical MTP flora meant that the vegetation was classified in group 1. Such sites with mixed characteristics are also important for the persistence of MTP taxa in the landscape.

In summary, MTPs in the UK can be equated to highly ephemeral winter flooded temporary ponds that occur in shallow grassy depressions and on track ways subject to high levels of disturbance. They are apparently restricted to the Lizard Peninsula, although some sites in other southern and western regions (e.g. New Forest) show affinities with these floras. MTPs are dominated by a range of low growing grasses and rushes along with rare annual species of the *Nanocyperion* alliance; typical plant species include *Ranunculus tripartitus, Cicendia filiformis, Juncus pygmaeus, Ranunculus flammula, Agrostis stolonifera, Juncus bufonius, Juncus articulatus, Potentilla anserina* and *Chamaemelum nobile*. The sites are typically of moderately acidic pH (mean 5.91) with high conductivity (mean 745µS) and high levels of total organic nitrate (mean 0.9 mgL^{-1}) compared with other ponds in the landscape. MTPs also have characteristic and relatively depauperate macroinvertebrate assemblages comprising Coleoptera (predominantly *Helophorus* and *Hydroporus* spp), Trichoptera (*Limnephilus vittatus* & *L. auricula*) and Chironomidae (*Macropelopia, Chaetocladius* & *Micropsectra*) along with the rare coleopterans *Graptodytes flavipes* (VU) and *Dryops striatellus* (VU). MTPs in the UK have some floristic similarities with sites in South West France (Moubayed 1998, de Bruijn *et al.* 1994) and Wales (section 2.5; Nicolet 2002), potentially indicating that such assemblages may form a continuum along the western Atlantic fringe.

6.2.1.3 Conservation of MTPs

Marginal and ephemeral habitats, such as MTPs, are of conservation importance as species that are rare often have limited distributions or ranges because they have poor competitive ability and so do well in such habitats as they have low species richness and/or population density. Marginal habitats are, therefore, more commonly becoming the focus of conservation effort e.g. woodland rides, river shingle etc. Biodiversity legislation at the European level classifies important habitats by creating lists of typical species. Whilst such an approach does highlight the importance of particular habitats, and allows changes in range size of important rare species to be monitored, it also often leads to countries in different biogeographic provinces with different species complements performing an exercise in 'shoe-horning' in order to ensure that a suite of species or a habitat type of national importance gains protection at the European level. Many marginal habitats, like temporary ponds, do not fit easily and parsimoniously into existing habitat classification schemes, such as Corine, due to their ill defined (due to being species poor) or spatially and temporally variable species composition. Such habitats might be more profitably described by physicochemical measures, including disturbance regime and landscape context, combined with examples of typical flora and fauna with notes about their dominant life history characteristics, so that land mangers in different regions can evaluate local habitats and assemblages more easily by looking for overall ecological similarities within a European context.

MTPs are of conservation importance because they support a suite of rare invertebrates and plants which often utilise species-poor sites, perhaps because they are poor competitors. A high density of small ponds, flooded track ways, grassy depressions and eroded serpentine pans should be maintained in the landscape to maintain high densities of the rare annual species, which indicate favourable MTP status. In addition the connectivity between them should be maximised, by creating more small ponds (see below) to encourage the transfer of seeds via floodwaters or the trampling of grazing animals. Work in the Netherlands has shown that the creation of bare ground by sod cutting successfully increased local densities of *Cicendietum filiformis* vegetation (Eysink & de Bruijn1994). Such measures should maximise the success of the rare annual species with temporally and spatially disjunct populations and also increase the density of breeding ponds for rare macroinvertebrate taxa which are dependent on small ponds for reproduction e.g. *Graptodytes flavipes* and *Dryops striatellus.*

The importance and unique nature of the most ephemeral ponds in both regions is highlighted by nestedness analysis (chapter 3 & appendices 6.2.3.1 & 6.2.3.2). Significant nestedness has been used in the past to infer that the preservation of a single large site will conserve more species than the preservation of several small sites of equivalent area (the Single Large Or Several Small SLOSS debate). However, a high proportion of idiosyncratic taxa, as seen for plants and macroinvertebrates in both regions (appendices 6.2.3.1 & 6.2.3.2), indicates that protecting the most species rich sites would not adequately conserve all species. Idiosyncratic taxa tend to occur in species-poor ponds, which are those that are least permanent, as only a restricted proportion of species with suitable life history characteristics utilise them. Idiosyncratic macroinvertebrate taxa that occur in these sites therefore tend to be temporary pond specialists that disperse throughout their life cycle in order to utilise such sites for reproduction. A number of the idiosyncratic plant and invertebrate species in the New Forest and on the Lizard are nationally or internationally threatened (appendices 6.2.3.1 & 6.2.3.2), which further highlights the importance of maintaining these ephemeral sites in the landscape.

The plant and macroinvertebrate communities that assemble in small man-made sites have been shown to rapidly resemble those in similar sized natural ponds in the landscape (see chapter 4). Focal macroinvertebrate MTP taxa were quick to colonise the experimental ponds and fourteen Coleoptera taxa successfully bred in the sites. *Ranunculus tripartitus* also colonised one of the grassland sites from a neighbouring ditch ca.50m away, although it was subsequently competitively excluded, highlighting the need for continued disturbance, especially within grassland sites. The experimental sites were used by a wide range of taxa throughout the year, including taxa which tend to breed in more permanent sites (chapter 4). This finding suggests that small temporary ponds are doubly important, as they not only provide breeding habitat for many rare coleopteran and annual plant species but also play a vital role in maintaining the connectivity of the landscape for other pond dwelling organisms by being 'stepping stones' habitat patches (chapter 4; Briers & Warren 2000). Creation of small sites might therefore be a useful way of (i) augmenting the density of MTPs in the landscape and (ii) increasing landscape connectivity for pond organisms. Chapter 4 showed that a cluster of seven 4m^2 ponds within a plot of 2500m^2 (approximately 1% of the area) provided adequate habitat density for successfully colonisation and reproduction by a wide range of temporary pond macroinvertebrate and plant species.

The macroinvertebrate assemblages that developed in ponds created on grassland and heathland became more similar through time, indicating that the type of land the ponds are created on was not of primary importance for invertebrates. Instead pond permanence was shown to influence the rate and suite of species which colonised the sites. Permanence of the experimental ponds varied due to the patchy nature of soil characteristics, even though the ponds were of identical profile and closely spaced (section 4.3.1). The unpredictability of soil structure highlights the need to create a number of ponds in one location in order to ensure development of a range of vegetation assemblages, and that some remain wet long enough for successful macroinvertebrate reproduction and development.

The rapid colonisation and high abundance of macroinvertebrates observed in the ponds may indicate that such ephemeral sites are a limited resource in the landscape, highlighting the need for increased density of such habitat in the landscape. Man-made complexes of ponds could be used to restore the density of small sites in areas where tourist pressure and changes in land use have caused habitat loss. Suites of ponds could be created quickly and cheaply as each pond in this study was just $4m^2$ and 30cm deep and was dug by hand within one to four hours, depending on substrate conditions. The relative position of existing water bodies, with a source of colonists, in the landscape should guide the decision on where to locate new pond habitat. On the Lizard assemblage composition of ponds less than 675m apart has been shown to be similar (Fig. 2.9) so a rough guideline for the maximum distance between new and existing water bodies might be around 500m.

Although it may be possible to successfully augment the number of small ephemeral ponds on the Lizard it is essential to conserve remaining density of natural MTP habitat (i.e. track and pinch point ponds) across the Peninsula, as seed banks of rare annuals (*Juncus pygmaeus, Cicendia filiformis, Ranunculus tripartitus* etc) will have developed within them (Grillas & Roché 1997). Creation of new sites close to existing habitat might expand the extent of MTP habitat if new and established ponds are connected via floodwater and/or animal trampling (Kirchner *et al.* 2003). This strategy might be pioneered in the Kynance region of the Lizard Peninsula where a high density of *Ranunculus tripartitus* is already known to exist. If results were favourable, i.e. *Ranunculus tripartitus* colonised the newly created ponds, more sites could be created in other regions of the Peninsula which (i) have a reasonable density of small ponds preferably with populations of rare plant species and (ii) are in reasonable proximity ca. 500m from large ponds. Suitable regions might include areas of track south-east of Lower Predannack Wollas, where there are past records of *Juncus pygmaeus* (Hopkins pers comm.), near Grochall track which supports *Cicendia filiformis* (pers. obs.) and on Lizard Downs where the condition and density of small sites has been in decline in recent years (pers. obs).

6.2.2 General pond conservation in the regions

This section explores general conservation strategies that might be applied to temporary pond plant and macroinvertebrate assemblages in both regions. At the end of each section a number of management recommendations are highlighted.

6.2.2.1 Threats to ponds in the regions

Although ponds on the Lizard and in the New Forest frequently lie within Sites of Special Scientific Interest or National Nature Reserves they may in the future be subjected to anthropogenic factors such as the introduction of exotic species or regional scale water abstraction as the landscape becomes increasingly urbanised. In addition some important sites are privately owned so may be subjected to a broader range of risks including pollution and drainage for agricultural purposes The likely impacts of such effects are listed in Table 6.6 along with potential mitigation strategies.

Threat	Source	Likely impacts	Mitigation / Management Recommendations
Habitat loss	Loss small track way ponds due to pressure of tourism & increases in agricultural intensity Intensification agriculture (e.g. L37) & drainage Succession of sites due to changes in disturbance regime	Loss of MTP habitat as paths and tracks are surfaced for tourist access Gradual loss of species with restricted habitat distribution from the landscape. Reduced between pond connectivity	Creation of small sites Is viable and rapid (2-3 yr) this may partially compensate for loss of smallest sites Not viable to create larger sites that are critical for maintaining regional diversity Liaison with local land owners in order to raise awareness of importance of 'puddle' habitat Ensure adequate disturbance of sites to limit unwanted succession
Lowering of the water table	Global climate change Abstraction Intensification agriculture & drainage	Loss of large ground water charged sites. Changes in water table may also result in loss of ponds which lie above perched water tables e.g. Ruan Pool (L36)	Liaison with local government re abstraction licences in the region and local land owners
Degradation of water quality	Eutrophication from stock & run off from agricultural land Acidification Chemical pollution (e.g. Preddannack Airfield) run off/ wind blown/ point source	Changes in trophic status of pond reduced light penetration and O_2 levels change vegetation species composition and structure knock on consequences for macroinvertebrates Acidification more likely to affect New Forest ponds, as soft water has poor buffering capacity. Lower pH reduces calcium availability which affects mollusc species and increases metal toxicity which can interfere with invertebrate respiratory epithelia. Some plant species are not acid tolerant Ongoing research into impacts of wind blown chemical pollution Environment Agency (Lizard)	Careful selection of grazing animal and monitoring of stocking levels. Rotation to different areas if dunging on trackways becomes problematic. Variation in location of winter feeding stations to encourage movement of livestock through track way habitats
Invasive species	*Myriophyllum aquaticum* *Crassula helmsii, Elodea canadensis* etc introduced via aquaculture trade	Out compete native vegetation reducing local and potentially regional species diversity. Changes in vegetation diversity and structure have knock on consequences for invertebrate fauna. *E. canadensis* present in L29 and *C. helmsii* present in NF1	During regular monitoring of temporary pond habitat note invasive species so that spread is documented. Any invertebrate monitoring studies should be informed to minimise spread on sampling equipment e.g. nets. Removal work should aim to minimise spread of propagules. Success of removal process should be closely monitored in subsequent years

Table 6.6: Potential future threats to temporary pond habitat, with suggestions for monitoring and mitigation

6.2.2.2 Monitoring pond assemblages

Plant and macroinvertebrates assemblages across regions showed disparate responses to physicochemical and spatial variables (Fig 2.9), and TWINSPAN groups only weakly corresponded to physicochemical variables (Tables 2.3 & 2.5). National monitoring of freshwaters often uses models based on physicochemical parameters to prediction the likely occurrence of plant and invertebrate taxa e.g. the River InVertebrate Prediction And Classification System (RIVPACS; Wright *et al.* 1997) and, for ponds, the Predictive System for Multimetrics (PSYM method; Williams *et al.* 1996, Nicolet 2002). Given the results of this study (see chapter 2 & Fig 6.2), it seems that when studying a large number of ponds within a region, physicochemical measurements are unlikely to give consistently accurate information on likely invertebrate and plant composition, rendering such approaches inadequate.

Macrophyte and invertebrate species richness, assemblage composition and structure were related throughout the thesis (section 6.1.5, Tables 2.6, 4.7 & 5.2 and Fig. 6.2). Hence, macrophyte assemblage richness and composition may play an important role in driving macroinvertebrate assemblage composition and structure across regions and scales. Monitoring of vegetation may, therefore, assist in the indirect assessment of macroinvertebrate assemblages within temporary ponds. This thesis also demonstrated, however, that plant assemblages are not always an accurate guide to invertebrates present within a pond, particularly in the case of rare taxa. For this reason, any monitoring of pond assemblages and their condition should combine botanical and zoological data, and not view these aspects in isolation. Physicochemical data alone would not allow an accurate prediction of a pond's ecological or conservation status.

Recommendation

1. Temporary pond monitoring schedules should assess changes in semi-terrestrial and macrophyte species composition and macroinvertebrate assemblages in combination.

6.2.2.3 Assessing pond conservation status

The overall conservation importance of individual ponds might be underestimated if assessment is based solely on plant species composition, as ponds with common and widespread plant taxa, may support rare invertebrate taxa, (correlations between plant and macroinvertebrate species rarity indices are insignificant in both regions). This is especially true of large ponds on the Lizard, which tend to support invertebrate assemblages with greater mean rarity (Table 6.7). Rare plants and invertebrates, in the New Forest, occur across ponds of all sizes, so the full spectrum of pond sizes and permanencies in each region should be maintained (Table 6.7). Although large Lizard sites tended to be more species rich and support more rare invertebrate species, small sites often supported important populations of *Graptodytes flavipes* and *Dryops striatellus* both vulnerable (RDB2) coleopteran species. Larger sites supporting beds of *Littorella uniflora* and *Pilularia globulifera,* some of which are highlighted in the Habitats Directive (92/43/EEC) are also important for rare invertebrate taxa such as *Haliplus variegatus.* So both highly ephemeral and more permanent fluctuating water bodies are important for plants and invertebrates in both regions.

	New Forest Plant SRI	New Forest invertebrate SRI	Lizard Plant SRI	Lizard invertebrate SRI
Pond area	$r_s = 0.31$, ns	$r_s = -0.16$, ns	$r_s = 0.14$, ns	$r_s = 0.46$, $p < 0.001$
Species richness	$r_s = 0.39$, $p < 0.05$	$r_s = 0.22$, ns	$r_s = -0.15$, ns	$r_s = 0.34$, $p < 0.05$

Table 6.7: Spearman rank correlations between plant and macroinvertebrate species rarity indices (SRI) and pond area for each region.

Monitoring of plant assemblage composition and physicochemistry, or a snap-shot examination of macroinvertebrate assemblage composition, overlooks temporal variation in assemblage composition due to seasonal turnover in ponds. Many macroinvertebrate temporary pond specialists utilise more than one pond each year as small sites are colonised for reproduction in the winter and large sites are used as refugia during summer months (see chapters 3 & 4). Frequent between pond dispersal by rare species that form patchy populations throughout the landscape (chapter 4, Table 6.2) mean that the conservation importance of ponds (especially small highly ephemeral ones) is dynamic. A similar scenario is likely to occur for annual plants, such as *Ranunculus tripartitus* (VU), as species germinate at different times of year and conditions for germination vary annually between sites due to timing of inundation, temperature and/or disturbance levels, e.g. cattle trampling, which may alter the local level of interspecific competition. Such temporal and spatial variation in species occurrence further reinforces the need to maintain a diverse range of pond habitats across the regions.

Recommendations

1. Plant assemblage composition gives a broad indication of macroinvertebrate richness and composition.
2. Overall pond conservation status cannot be inferred from surveys of plant species as species occurrence may be dynamic and ponds with common plant species may support rare invertebrate taxa.
3. The best strategy for conserving rare pond species is to maintain a range of ponds sizes, permanencies and habitat types throughout the landscape.

6.2.2.4 Management of vegetation

Within ponds, complex stands of vegetation (i.e. those with a high proportion of *Myriophyllum alterniflorum*, *Chara* spp, *Apium inundatum, Eleogiton fluitans* and bryophytes; Table 5.1 & Fig. 5.2) have greater invertebrate biomass and more small individuals than simple vegetation comprised of species such as *Glyceria fluitans*, *Carex* spp and *Juncus* spp (Table 5.2). Changes in vegetation complexity, due to alterations in the relative abundance and species composition of macrophyte beds, are therefore likely to result in changes in the structure of invertebrate assemblages due to differences in the partitioning of habitat space (section 5.5). Such changes in complexity could have knock on consequences for trophic interactions within macrophyte stands, as rates of predation (Finke & Denno 2002, Bartholomew *et al.* 2000), detritus gathering and grazing of epiphyton, also might be altered. Further work is needed to examine whether such changes in vegetation complexity cause larger scale changes in pond functioning and whether annual and seasonal changes in invertebrate biomass are affected by fluctuations in vegetation complexity.

Vegetation management (i.e. removal) has been shown to have an important influence on the conservation importance of coleopteran assemblages in arable fenland (Foster *et al.* 1990). Where management of overgrown vegetation is deemed necessary in larger ponds, either to encourage a more heterogeneous and patchy macrophyte flora or to create open pond sediment to encourage rare species of lesser competitive ability, the impacts on the invertebrate (and amphibian) fauna should be carefully considered as even careful removal of vegetation can also remove invertebrate eggs and pupae (Foster *et al.* 1990). Some ponds are formed above perched water tables (Williams 1992) and, where this is the case it is imperative that additional care is taken when undertaking management of any kind, as disturbance of the pond sediment and the underlying soil structure could result in permanent pond drainage. This highlights the importance of detailed hydrological surveying of groundwater charged temporary water bodies with high conservation value.

In smaller sites, management for rare plant species is often accomplished via disturbance by grazing livestock or vehicles (Edwards *et al.* 2000, Stewart *et al.* 2000), which increase the proportion of bare ground, encouraging germination from the seed bank. In addition, seeds may be transported short distances along wet tracks and across grassland; (the benefits of such increases in habitat connectivity are discussed in below). Rare plant taxa supported in such sites (e.g. *Ranunculus tripartitus*, *Juncus pygmaeus* and *Cicendia filiformis*) benefit from such disturbance in winter or early spring, the time of year when the habitat is wet and being utilised for reproduction by high densities of macroinvertebrates and amphibians. No evidence was gained in this study that such management efforts are detrimental to macroinvertebrate recruitment. However, grazing and disturbance during the spring and summer months, when rare annual species are in flower, might reduce seed production effecting recruitment in subsequent years (Maitland & Morgan 1997).

Recommendations

1. Vegetation monitoring may highlight when and where management intervention is necessary e.g. increased grazing pressure/disturbance or removal of invasive species and cutting back of encroaching scrub.
2. Removal of aquatic macrophytes should only be carried out if absolutely necessary, e.g. due to the invasion of exotic species, as it may adversely effect invertebrate and amphibian populations. Where possible a time of year when few species are breeding should be chosen in order to minimise the removal of macroinvertebrate larvae and pupae. The underlying soil should be minimally disturbed by the management actions.
3. If vegetation management is deemed necessary in larger temporary ponds, heterogeneity of stand composition and complexity should be maintained by removing patches of vegetation to thin local density, or a 'wedge' that bisects a range of different vegetation compositions, rather than removing all vegetation at a certain depth or of a certain species composition.
4. Some small ponds should be disturbed during the winter/early spring months before early germinating species, such as *Ranunculus tripartitus*, are in flower as disturbance at this time may reduce seed production.

6.2.2.5 Pond connectivity

Historically, the New Forest had a lower density of ponds than the Lizard Peninsula (Rackham 1986) and this has been exacerbated in recent years by the surfacing of ancient track ways that crossed the heathlands and ran between inclosures. As well as reducing the local densities of small ephemeral sites, the spatial arrangement of ponds in the landscape has been altered by the loss of small ponds in the New Forest, so that sites have become more isolated. Although only a subset of species reproduce in the most ephemeral sites (often those that have idiosyncratic distributions, see chapter 3) it seems that other invertebrate species may use small ponds as stepping stone habitats, which facilitate dispersal between more suitable sites (see chapter 4), this function of small sites will have been reduced in the New Forest. Habitat loss is therefore likely to have reduced the connectivity of the landscape in the New Forest for most pond dwelling invertebrates and plants.

Spatial pattern in assemblage composition is seen for Lizard invertebrates, (ponds closer than ca.700m tend to haves similar faunas) whereas such a pattern is not observed for New Forest invertebrates (Figs 2.9). This may be a consequence of lowered connectivity in the New Forest, perhaps not only due to lower pond density, but also differences in landscape topography and the vegetation matrix which surrounds ponds. The Lizard is flat and dominated by low growing heath and grassland, whereas the New Forest has a more heterogeneous topography and a vegetation matrix of heathland and woodland, which may form barriers for short distance invertebrate dispersal (Delettre & Morvan 2000). No spatial pattern in plant assemblage composition was observed, which may indicate that between pond connectivity is low for plants in both regions or that short distance dispersal events are unsuccessful, perhaps due to competitive interactions with the existing vegetation.

Recommendation

1. Preventing loss of small temporary ponds is likely to maintain landscape connectivity which benefits all freshwater taxa, not just those that rely on ephemeral waters to breed, as they provide ‘stepping stone’ habitat for taxa that are typical of more permanent waters.

6.2.2.6 The potential effect of habitat loss

The location and type of habitat lost within the regions is likely to affect species differently. More permanent sites are inhabited by a greater number of species, and are preferred by nested taxa (chapter 3). In contrast, temporary pond specialist invertebrate taxa are found in all pond types, as their distribution patterns are frequently spatially random amongst ponds (Table 3.6); however such taxa often breed in small sites. The loss of the most permanent ponds from the landscape would be likely to cause the greatest loss in plant and invertebrate diversity but the loss of small sites would reduce the reproductive success of temporary pond invertebrate taxa and cause regional extinction of rare temporary pond plant taxa which are restricted to such sites.

Reduction in density and changes in its spatial arrangement of habitat in the landscape may reduce the chance of successful colonisation in the short term, leading to increased mortality during dispersal. In the longer term, Olivieri *et al.* (2001) have shown that local plant populations adapt so that the number of dispersing individuals within a population is lowered. Lowered dispersal rates caused by increased habitat isolation may lead to increased chance of local extinction, due to stochastic and deterministic processes. Sub-populations in large ponds which were once connected by infrequent dispersal across the landscape might become non-equilibrium metapopulations (Harrison 1991) where rates of extinction exceed rates of colonisation; such species are most vulnerable to habitat loss at the landscape level.

Recommendations

1. Loss of more permanent ponds would cause the greatest loss of biodiversity. However, loss of small sites would reduce the reproductive success of invertebrates that breed in ephemeral waters and might cause regional extinction of rare temporary pond plant taxa which are restricted to small water bodies.
2. Habitat loss may also indirectly cause local extinction by reducing the number of successful dispersal events and isolating local sub-populations making them vulnerable to stochastic or deterministic extinction.

6.2.2.7 Increasing connectivity

Kirchner *et al.* (2003) examined the influence of flooded corridors on *Ranunculus nodiflorus* a threatened temporary pond species in France with similar ecology to *Ranunculus tripartitus* (i.e. it cannot reproduce vegetatively and is a poor competitor that inhabits small oligotrophic and acidic temporary ponds in flooded depressions and along the edges of ditches). They found that connectivity between small ponds via flood waters increased its persistence in the landscape by facilitating seed dispersal between habitat patches. Connectivity via flooding is likely to be important for *R. tripartitus* metapopulation persistence too, as ponds in which it occurs are closely spaced within the Kynance region of the Lizard Peninsula. Such connectivity might be increased by the creation of new small ponds (see chapter 4 & section 6.2.1.3) which may also be of benefit to some of the other rare annual species.

Recommendations

1. Creation of complexes of small ponds near existing pond habitat with important rare taxa (see section 6.2.1.3) might augment population size and increase connectivity for invertebrate species. Creation of closely spaced sites may encourage dispersal by flood waters.
2. Ensure grazing regimes help to connect ponds through stock movements/trampling.
3. Create bare ground during winter (see section 6.2.2.4) in neighbouring sites to encourage annual plants to germinate.
4. Provide corridors through terrestrial vegetation matrix for amphibian dispersal.

6.2.2.8 Predicting the consequences of habitat loss and the use of indicator species

At present the effect of habitat loss on the population dynamics of pond species within a region can only be hypothesised. Metapopulation approaches have been useful in constructing conservation strategies for terrestrial species such as butterflies (Wilson & Thomas 2002). However, the data from metapopulation models is inherently species specific and therefore conservation strategies at the assemblage-level would need to be based around the combined results of a number of representative target species (Breininger et al. 2002). Such an approach, if deemed necessary for the successful conservation of systems of freshwater ponds, might logically follow more general assemblage level studies, such as this, which identify key target taxa.

Further work is needed to examine the dispersal ability and metapopulation dynamics of representative temporary pond species which have (i) low dispersal frequency and specific habitat requirements (*i.e.* nested taxa, that are limited to large ponds e.g. *Colymbetes fuscus*) and (ii) patchy populations that rely on regular dispersal to small ponds for successful reproduction (*i.e.* idiosyncratic taxa e.g. *Ilybius montanus*), as these species might be thought of as indicator species that are susceptible to landscape scale changes in pond density and may provide information about broader scale changes in overall assemblage dynamics (Noon & Dale 2002, Lambreck 1997). Such indicator species should also ideally be (i) relatively common in the region and (ii) readily identifiable by eye. Collecting metapopulation data would be time consuming and difficult to gain as it relies on capture-recapture studies, the detection of rare long range dispersal events and computer modelling in order to properly characterise the frequency and scale at which dispersal occurs. However, such data are essential for (i) accurate prediction of the effect of habitat loss on species dynamics, (ii) an understanding of the spatial scale at which connectivity (i.e. inter-pond distance) should be maintained and (iii) prediction of the minimum amount and spatial arrangement of suitable habitat which is needed for species persistence.

Recommendations

1. The spatial arrangement and density of habitat is likely to have an important influence on the dynamics of most pond species. More work is therefore needed to measure dispersal limitation and metapopulation dynamics of temporary pond species in order to fully understand the implications of habitat loss.
2. In the mean time habitat loss and change should be prevented by monitoring and liaison with landowners and conservation managers to raise awareness of the importance of maintaining small water bodies in the landscape.

6.2.3 Summary

- The occurrence pattern of taxa was similar in both regions. Most species were rare, (over half the species observed occurred in less than 10% of ponds), whereas less than 10% of taxa were common (occurring in over half of the ponds sampled).
- The strength of physicochemical and spatial pattern in assemblage composition varied between the regions. The relative strength of local and regional processes on temporary pond assemblage composition were affected by the (i) scale of the study, (ii) permanence regime of

the focal pond(s) and (iii) the life history strategies of the constituent taxa. Lizard macroinvertebrate assemblage similarity was spatially autocorrelated and related to water chemistry and pond area whereas New Forest macroinvertebrate similarity was not related to any of the measured physicochemical parameters.

- Plant assemblage composition was only weakly related to wet phase physicochemistry and spatial factors. Pond vegetation may therefore be more strongly influenced by the frequency, timing and length of dry phase, biotic interactions and dispersal limitation. Pond vegetation structured macroinvertebrate assemblages in different ways at different spatial scales. At large-scales, macrophyte richness and composition affected macroinvertebrate assemblage composition in both regions, whereas, at smaller scales, macrophyte structural complexity (measured using fractals) influenced body size scaling and overall biomass of macroinvertebrates.
- Freshwater macroinvertebrate life history strategies form a continuum. Nestedness analysis objectively split species into (i) idiosyncratic taxa which were opportunistic species that often occurred completely spatially randomly across sites, regardless of species richness or habitat characteristics; such species tended to retain dispersal ability throughout life history and/or have a drought resistant or semi-terrestrial life history stage and (ii) nested taxa which tended to be limited to more permanent waters. Species poor sites tended to be subsets of species rich sites, however, a high proportion of idiosyncratic taxa showed that there was a degree of spatial turnover in assemblage composition between ponds in both regions. A range of temporary pond habitats should be actively maintained in the landscape, as rare invertebrate and plant taxa did not always occur in the most species rich sites, as many were idiosyncratic in their distributions.
- As defined here MTPs in the UK are ephemeral winter flooded temporary ponds that occur in shallow depressions that are subject to high levels of disturbance. They are dominated by low growing grasses, rushes and rare annual species of the *Nanocyperion* alliance along with a depauperate macroinvertebrate assemblage comprising Coleoptera (including characteristic rare taxa), Trichoptera and Chironomidae. MTPs are typically of moderately acidic pH, with high conductivity and total organic nitrate. Such ponds have some floristic similarities with other western Atlantic fringe sites. Suites of small temporary ponds can be created quickly and cheaply in suitable sites, the assemblage composition of which quickly resembles existing

MTPs. Augmentation of current MTP habitat could therefore be achieved by creating new sites in close proximity to current habitat.

- Spatial proximity of neighbouring ponds i.e. connectivity is likely to be important for many species, as this influences the rates of exchange of individuals between subpopulations. More work is needed to measure dispersal limitation and metapopulation dynamics of key temporary pond species in order to fully understand the future implications of habitat loss. In the meantime a landscape-level approach to temporary pond conservation should be taken as many macroinvertebrate species utilise more than one pond during their life cycles and rare annual plant populations would benefit if landscape connectivity was actively maintained and the density of small temporary ponds was increased via habitat creation.

6.2.4 Appendices

6.2.4.1 Appendix 1:

Results of Lizard and New Forest macroinvertebrate nestedness analysis with idiosyncratic taxa that occur preferentially in species-poor sites listed. Analyses used the Nestedness temperature calculator (Atmar & Patterson 1995) with the default null model, where both row and column totals vary (see chapter 3). A number of idiosyncratic species are rare: * nationally scarce list A or B, *** vulnerable

Lizard Macroinvertebrates	**New Forest Macroinvertebrates**
15.5°, p <0.001 mean 56.1°, sd 1.9°	**24.7°, p <0.001** mean 51.5°, sd 2.1°
Coleoptera	
Agabus bipustulatus	*Agabus bipustulatus*
Ilybius montanus	*Ilybius montanus*
Graptodytes flavipes ***	*Graptodytes flavipes* ***
Helophorus brevipalpis	*Helophorus brevipalpis*
Helophorus grandis	*Helophorus grandis*
Helophorus minutes	*Helophorus minutus*
Helophorus obscurus	*Helophorus obscurus*
Hydroporus planus	*Hydroporus planus*
Anacaena lutescens	*Helophorus flavipes*
Dryops striatellus ***	Helophorus granularis *
Gyrinus substriatus	*Hydroporus nigrita*
Haliplus lineatocollis	*Hydroporus gyllenhalii*
Haliplus fulvus	*Berosus signiaticollis* *
Helophorus aequalis	*Berosus affinis* *
Helophorus obscurus	*Hyphydrus ovatus*
Hydroporus melanarius	*Plasicuris phellandrii*
Hydroporus pubescens	*Enochrus ochropterus* *
Hydroporus tessellatus	*Limnebius truncatellus*
Ochthebius dilatatus	*Helochares punctatus* *
Chironomidae	
Micropsectra	*Micropsectra*
Chironomus	*Chironomus*
Paratanytarsus	*Paratanytarsus*
Macropelopia	*Psectrocladius*
Chaetocladius	*Zalutschia*
Limnophyes	*Psectrotanytarsus*
Metriocnemus	*Tanytarsus*
	Demicryptochironomus
	Natarsia
Trichoptera	
Limnephilus vittatus	*Limnephilus vittatus*
	Limnephilus centralis
	Limnephilus marmoratus
	Limnephilus auricula
	Berea pullata
	Berea maurus
Hemiptera	
Corixa punctata	*Corixa punctata*
Corixa affinis	*Sigara nigrolineata*
	Sigara lateralis
	Sigara concinna

Lizard Macroinvertebrates	New Forest Macroinvertebrates
Hemiptera cont.	
	Notonecta glauca
	Notonecta obliqua
	Plea leachii
	Geris lacustris
	Geris gibbifer
	Ilyocoris cimicoides
	Hesperocorixa castanea
Mollusca	
Lymnaea truncatula	*Lymnaea truncatula*
	Lymnaea peregra
	Pisidium spp
	Physa fontinalis
	Potamapergus antipodarum
	Acroloxus lacustris
	Anisus leucostoma
Crustacea	
Crangonyx pseudogracilis	*Crangonyx pseudogracilis*
	Asellus aquaticus
Odonata	
Enallagma cyanthigerum	*Libellula* spp
	Coenagrion puella/pulchellum
Ephemeroptera	
	Cloeon dipterum

6.2.4.2 Appendix 2:

Results of Lizard and New Forest plant nestedness analysis with idiosyncratic taxa that preferentially occur in species-poor sites listed. Analyses as appendix 1 (& see chapter 3).

* nationally scarce list A or B, ** near threatened or conservation dependent *** vulnerable

Lizard plants	**New Forest plants**
16.5°, $p < 0.001$ mean 42.2°, sd 2.4°	**20.4°, $p < 0.001$** mean 51.9°, sd 2.8°
Semi terrestrial species	
Glyceria fluitans	*Glyceria fluitans*
Alopercurus geniculatus	*Alopercurus geniculatus*
Molinea caerulea	*Molinea caerulea*
Glyceria declinata	*Glyceria declinata*
Carex panicea	*Carex panicea*
Ranunuculus repens	*Ranunuculus repens*
Salix repens	*Salix repens*
Chamaemelum nobile *	*Chamaemelum nobile* *
Holcus lanatus	Agrostis spp
Poa spp	*Erica tetralix*
Catabrosa aquatica	Carex flacca
Bromus erectus	*Polygonum aviculare*
Dactylis glomeratus	
Carex rostrata	
Ranunculus tripartitus ***	
Ranunculus acris	
Potentilla anseria	
Rumex spp	
Trifolium repens	
Sagina procumbens	
Anagalis arvensis	
Lithospermum officinale	
Submerged, floating and emergent aquatic species	
Juncus effusus	*Juncus articulatus*
Canadensis elodea	*Eleocharis palustris*
Nuphar spp	*Eleocharis multicaulis*
	Eleogiton fluitans
	Apium inundatum
	Hypericum elodes
	Potamogeton polgonifolius
	Ludwigia palustris **
	Mentha aquatica
	Lythrum portula
	Alisma plantago-aquatica
	Eriophorium augustifolium
	Chara virgata
	Drosera rotundifolia
	Pulicaria dysenterica
	Limosella aquatica *
	Veronica beccabunga
	Lythrum salicaria
	Iris pseudacorus
	Filupendia spp

7 Appendices

7.1 Appendix 1: Lizard macroinvertebrates presence absence and conservation status (CS)

Site		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Coleoptera	**CS**																																													
Agabus bipustulatus	LRlc	1	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1
Ilybius montanus	LRlc	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Anacaena globulus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1
Anacaena lutescens	LRlc	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1
Bagous limosus	LRns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Berosus signaticollis	LRnsB	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Colymbetes fuscus	LRlc	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copelatus haemorrhoidalis	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0
Dryops auriculatus	LRnt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Dryops luridus	LRlc	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0
Dryops striatellus	VU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Enochrus coarctatus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0
Enochrus affinis	LRnsB	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus fuscipennis	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Enochrus melanocephalus	LRnsB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Graptodytes flavipes	VU	1	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
Gyrinus substriatus	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Haliplus confinis	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus fulvus	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus lineatocollis	LRlc	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Haliplus ruficollis	LRlc	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	1	1	0	1	0
Haliplus variegatus	EN	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0
Helochares punctatus	LRnsB	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0
Helophorus aequalis	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helophorus brevipalpis	LRlc	0	0	1	0	0	0	1	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1
Helophorus grandis	LRlc	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
Helophorus granularis	LRnsB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helophorus minutus	LRlc	1	0	1	1	1	1	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	0	1	1
Helophorus obscurus	LRlc	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1
Hydrobius fuscipes	LRlc	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0	0	1	0	1	0	1	1	0	1	0	0	1	0	1	1
Hydrochus angustatus	LRnsB	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0

7.1 Lizard macroinvertebrates cont.

Site		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Coleoptera	CS																																													
Hydroporus erythrocephalus	LRlc	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0
Hydroporus gyllenhalii	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1
Hydroporus melanarius	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus obscurus	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hydroporus palustris	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Hydroporus planus	LRlc	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus pubescens	LRlc	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	1	1	1	1	1	0	0	0	1	1
Hydroporus tessellatus	LRlc	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	1
Hydrovatus clypealis	LRnt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hygrotus inaequalis	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Hyphydrus ovatus	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laccobius bipunctatus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Laccobius ytenensis	LRnsB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Laccophilus minutus	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnebius truncatellus	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	1
Noterus clavicornis	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	0
Ochthebius dilatatus	LRlc	0	0	1	0	0	1	1	1	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
Ochthebius minimus	LRlc	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0
Paracymus scutellaris	LRnsB	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	1
Plateumaris sericea	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Chironomidae	LRlc																																													
Ablabesmyia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Arctopelopia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Conchapelopia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Krenopelopia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Macropelopia	LRlc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	1	0	1	1	1	0	1
Natarsia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Psectrotanypus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1
Procladius	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	1	1
Xenopelopia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	1	1	1	0	0
Zavrelimyia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0
Acricotopus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0

7.1 Lizard macroinvertebrates cont.

Site		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Chironomidae	CS																																													
Chaetocladius	LRlc	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	1	0	0	0	0	1
Cricotopus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Corynoneura	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	1	0
Diplocladius	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnophyes	LRlc	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
Metriocnemus	LRlc	0	0	1	0	1	1	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Paraphaenocladius	LRlc	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Psectrocladius	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	1	1	0
Zalutschia	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0
Chironomus	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	1	0
Kiefferulus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Microspectra	LRlc	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	1	0	0	0	1	0	1
Microtendipes	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0
Paratanytarsus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Polypedilum	LRlc	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0
Stempellinella	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	1	0	0	0
Trichoptera	LRlc																																													
Limnephilus auricula	LRlc	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	0	1	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1
Limnephilus vittatus	LRlc	1	1	1	1	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	1
Limnephilus lunatus	LRlc	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1
Limnephilus stigma	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Limnephilus rhombicus	LRlc	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0
Limnephilus marmoratus	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1	1	0
Limnephilus flavicornis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus luridus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Limnephius affinis/incisus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Limnephilus bipunctatus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Glyphotaelius pellucidus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Holocentropis picicornis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Agrypnia obsoleta	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Hemiptera	LRlc																																													
Plea leachii	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0

7.1 Lizard macroinvertebrates cont.

Site		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Hemiptera	CS																																													
Notonecta glauca	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Notonecta obliqua	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Corixa punctata	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Corixa affinis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sigara nigrolineata	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hesperocorixa castanea	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0
Nepa cinerea	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Arctocorisa germari	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odonata	LRlc																																													
Anax imperitor	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Libellula spp	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	1	0
Sympetrum spp	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1
Pyrrhosoma nymphula	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Ishnura elegans	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0
Enallegma cyanthigerum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Coenagrion puella/pulchellum	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0
Mollusca	LRlc																																													
Lymnaea peregra	LRlc	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0	1	1	1	1	0
Lymnaea truncatula	LRlc	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1
Anisus leucostoma	LRlc	1	1	1	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	0	0
Physa fontinalis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Potamopyrgus antipodarum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0
Pisidium spp	LRlc	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0
Isopoda	LRlc																																													
Asellus aquaticus	LRlc	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0	0
Amphipoda	LRlc																																													
Crangonyx pseudogracilis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	LRlc																																													
Cloeon dipterum	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	1	1	1	1	1
Plecoptera	LRlc																																													
Nemoura cinerea	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1	0
Hirudinea	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

7.2 Appendix 2: New Forest macroinvertebrates presence absence and conservation status (CS)

Sites		1	2	4	5	6	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	33	34	35
Coleoptera	CS																															
Agabus bipustulatus	LRlc	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0
Agabus labiatus	LRnt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ilybius montanus	LRlc	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0
Agabus nebulosus	LRlc	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anacaena globulus	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Anacaena lutescens	LRlc	0	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	1	0	0
Aphodius niger	EN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Bagous limosus	LRns	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Berosus affinis	LRnsB	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Berosus signaticollis	LRnsB	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Coelambus confluens	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelambus impressopunctatus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Colymbetes fuscus	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copelatus haemorrhoidalis	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0
Dryops lundus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Dryops striatellus	VU	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
Enochrus coarctatus	LRlc	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochorus affinis	LRnsB	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochrus nigritus	VU	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Enochorus ochropterus	LRnsB	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Graptodytes flavipes	VU	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Graptodytes granulans	LRnsB	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Haliplus fulvus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus heydeni	LRnsB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliplus ruficollis	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helochares punctatus	LRnsB	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	0	0	0	0
Helophorus brevipalpis	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Helophorus discretus	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helophorus flavipes	LRlc	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	1
Helophorus grandis	LRlc	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1
Helophorus granulans	LRnsB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Helophorus griseus	LRnsB	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0

7.2 New Forest macroinvertebrates cont

Sites		1	2	4	5	6	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	33	34	35
Coleoptera	CS																															
Helophorus minutus	LRlc	0	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Helophorus obscurus	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Hydraena riparia	LRlc	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrobius fuscipes	LRlc	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0
Hydrochus angustatus	LRnsB	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hydroglyphus pusillus	LRnsB	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydroporus erythrocephalus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydroporus gyllenhalii	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0
Hydroporus melanarius	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Hydroporus nigrita	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0
Hydroporus planus	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Hydroporus pubescens	LRlc	0	1	1	0	1	0	1	1	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	1
Hydroporus tristis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hygrotus inaequalis	LRlc	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hyphydrus ovatus	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laccobius ytenensis	LRlc	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnebius truncatellus	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Noterus clavicornis	LRlc	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ochthebius minimus	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracymus scutellaris	LRnsB	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0
Plasicuris phellandrii	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhantus suturalis	LRnsB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chironomidae																																
Ablabesmyia	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clinotanypus	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conchapelopia	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Krenopelopia	LRlc	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Macropelopia	LRlc	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1
Natarsia	LRlc	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psectrotanypus	LRlc	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Procladius	LRlc	0	1	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0	1	0	1	0	1
Telmatopelopia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0

7.2 New Forest macroinvertebrates cont

Sites		1	2	4	5	6	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	33	34	35
Chironomidae	**CS**																															
Xenopelopia	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0
Zavrelimyia	LRlc	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	0	1	1	1	0	1
Acricotopus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Chaetocladius	LRlc	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0	0	0	0
Cricotopus	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterotanytarsus	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnophyes	LRlc	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Metriocnemus	LRlc	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthocladius	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psectrocladius	LRlc	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	1
Zalutschia	LRlc	0	0	0	1	1	1	0	1	0	0	1	0	1	1	0	0	1	0	1	1	0	0	0	1	0	1	1	0	0	0	0
Chironomus	LRlc	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1
Demicryptochironomus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicrotendipes	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kiefferulus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Microspectra	LRlc	0	1	1	1	0	1	0	1	0	0	1	1	1	0	1	0	0	1	1	1	1	0	0	1	0	0	1	1	1	1	1
Neozavrelia	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parachironomus	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paratanytarsus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Paratendipes	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Phaenospectra	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polypedilum	LRlc	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
Stempellinella	LRlc	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tanytarsus	LRlc	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Trichoptera																																
Limnephilius auricula	LRlc	1	1	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	0	1	0	0
Limnephilus vittatus	LRlc	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0	1	1	1
Limnephilus lunatus	LRlc	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Limnephilus stigma	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus marmoratus	LRlc	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus centralis	LRlc	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	1	1	1	1	0	0
Limnephius affinis/incisus	LRlc	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

7.2 New Forest macroinvertebrates cont

Sites		1	2	4	5	6	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	33	34	35
Trichoptera	**CS**																															
Limnephilus politus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus binotatus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnephilus sparsus	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichostegia minor	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0
Triaenodes bicolor	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyphotaelius pellucidus	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Berea pullata	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Berea maurus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Agrypnia varia	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemiptera																																
Plea leachii	LRlc	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notonecta glauca	LRlc	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notonecta obliqua	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Corixa punctata	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corixa affinis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corixa panzeri	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sigara nigrolineata	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Sigara lateralis	LRlc	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Sigara semistriata	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sigara concinna	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocorixa castanea	LRlc	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hesperocorxa linnaei	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocorixa sahlbergi	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocoris cimicoides	LRlc	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gerris lacustris	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gerris thoracicus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Gerris gibbifer	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Odonata																																
Libellula spp	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Orthetrum spp	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympetrum spp	LRlc	1	1	0	1	1	0	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0
Pyrrhosoma nymphula	LRlc	1	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

7.2 New Forest macroinvertebrates cont

Sites		1	2	4	5	6	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	33	34	35
Odonata	CS																															
Coenagrion puella/pulchellum	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca																																
Lymnaea peregra	LRlc	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Lymnaea truncatula	LRlc	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Anisus leucostoma	LRlc	1	1	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	1	0	0	0	1	1	1	0	0	1	1	1	0	0
Physa fontinalis	LRlc	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Potamapergus antipodarum	LRlc	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stagnicola fuscus	LRlc	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1
Omphiscola glabra	VU	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0
Acroloxus lacustris	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Armiger crista	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pisidium spp	LRlc	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	1	1	0	0
Isopoda																																
Asellus aquaticus	LRlc	1	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	1	1	0	1	0	1	1	1	0	1	1	1	0	0
Amphipoda																																
Crangonyx pseudogracilis	LRlc	1	1	1	0	0	0	0	1	1	1	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Ephemeroptera																																
Cloeon dipterum	LRlc	0	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	1	1	1
Plecoptera																																
Nemoura cinerea	LRlc	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0
Hirudinea	LRlc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0

7.3 Appendix 3: Lizard plants presence absence with conservation status (CS)

Sites	CS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Agrostis spp	LRlc	1	1	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	1	1	0	1	1	0	0	1	0	0	1	1	1	0	1	1	0	0	0	1
Alopercurus geniculatus	LRlc	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Anagalis arvensis	LRlc	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apium inundatum	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Baldellia ranunculoides	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Bromus erectus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callitriche spp	LRlc	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0
Cardamine pratensis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Carex flacca	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex nigra	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
Carex panicea	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex rostrata	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex viridula	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	0
Catabrosa aquatica	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cerastium holosteoides	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Chamaemelum nobile	LRns	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chara fragifera	LRnt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	1	1	0
Cynosurus cristatus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dactylis glomeratus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eleocharis multicaulis	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Eleocharis palustris	LRlc	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	1	1	0	0	0	1	1	1	0	0
Eleogiton fluitans	LRlc	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	1	1	0	1	0
Elodea canadensis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium palustre	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	1	0	0	0
Glyceria declinata	LRlc	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyceria fluitans	LRlc	1	0	1	1	1	1	0	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1
Holcus lanatus	LRlc	0	0	0	0	1	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Hydrocotyle vulgaris	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	1	1	1	0	0
Hypericum elodes	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Juncus articulatus	LRlc	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	0	0	1	1	0	1	1
Juncus bufonius	LRlc	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
Juncus bulbosus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	0	0	0	1	1	1	1	1	0	1	1	1	1	0	1	0	0

7.3 Lizard plants cont

Sites	CS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Juncus conglomeratus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Juncus effusus	LRlc	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0
Leontodon spp	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Lithospermum officinale	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Littorella uniflora	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	0
Lychnis flos-cuculi	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Medicago lupulina	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mentha spp	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Molinia caerulea	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0
Myriophyllum alterniflorum	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nitella opaca	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Nitella translucens	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Nympha spp	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lythrum portula	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Pilularia globulifera	VU	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Plantago lanceolata	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Poa spp	LRlc	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla anserina	LRlc	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Potentilla reptans	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Potamogeton polygonifolius	LRlc	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0
Ranunculus acris	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Ranunculus aquatilis agg.	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ranunculus flammula	LRlc	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0
Ranunculus repens	LRlc	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Ranunculus tripartitus	VU	1	1	0	1	1	0	1	0	0	0	1	0	0	1	0	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Rubus spp	LRlc	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex spp	LRlc	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sagina procumbens	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Salix repens	LRlc	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
Schoenus nigricans	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
Trifolium dubium	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Trifolium glomeratum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium pratensis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

7.3 Lizard plants cont

Sites	**CS**	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Trifolium repens	LRlc	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Bryophyte records	LRlc																																													
Calliergonella cuspidata	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	1
Warnstorfia exannulata	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0
Scorpidium scorpioides	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudodephemerum nitidum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocladus aduncus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Cratoneuron filicinum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

7.4 Appendix 4: New Forest plants presence absence with conservation status (CS)

Sites	CS	1	2	4	5	6	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	33	34	35
Agrostis sp	LRlc	0	1	1	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	1
Alisma plantago-aquatica	LRlc	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alopercurus geniculatus	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Anagalis arvensis	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Anagalis tenella	LRlc	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
Apium inundatum	LRlc	1	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	0
Apium nodiflorum	LRlc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baldellia ranunculoides	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0
Callitriche	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1
Cannabiaceae spp	LRlc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardamine pratensis	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex flacca	LRlc	0	0	1	0	1	1	1	1	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0
Carex nigra	LRlc	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Carex panicea	LRlc	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Carex viridula	LRlc	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Catabrosa aquatica	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Chamaemelum nobile	LRns	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Chara virgata	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crassula helmsii	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drosera intermedia	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drosera rotundifolia	LRlc	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eleocharis multicaulis	LRlc	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	0	1
Eleocharis palustris	LRlc	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Eleogiton fluitans	LRlc	0	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	1	0	1
Equisetum spp	LRlc	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Erica cinerea	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Erica tetralix	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eriophorium augustifolium	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Filupendia spp	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium palustre	LRlc	1	0	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	0	1
Glyceria declinata	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Glyceria fluitans	LRlc	1	1	1	1	0	1	1	0	1	1	0	1	0	0	1	1	0	1	0	1	1	1	1	1	1	0	1	0	1	0	0
Hydrocotyle vulgaris	LRlc	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	0	0	1	0	1	1	0	0	0	1	1	0	0

7.4 New Forest plants cont

Sites	CS	1	2	4	5	6	7	8	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	33	34	35
Hypericum elodes	LRlc	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1	0	0	0
Illecebrum verticillatum	LRns	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iris pseudacorus	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus articulatus	LRlc	1	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	1	1	1	0	0	1
Juncus bufonius	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus bulbosus	LRlc	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Juncus conglomeratus	LRlc	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus effusus	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lemna minor	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lemna trisulca	LRlc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limosella aquatica	LRns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Littorella uniflora	LRlc	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ludwigia palustris	LRnt	1	0	0	1	0	0	0	1	1	0	1	0	1	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0
Lythrum salicaria	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mentha sp	LRlc	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Menyanthes trifoliata	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Molinia caerulea	LRlc	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Myosotis scorpiodes	LRlc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myriophyllum alterniflorum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Narthecium ossifragum	LRlc	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphar spp	LRlc	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pedicularis palustris	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lythrum portula	LRlc	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	1
Pilularia globulifera	VU	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum aviculare	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Potentilla anserina	LRlc	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla erecta	LRlc	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla reptans	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Potamogeton polygonifolius	LRlc	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0
Prunella vulgaris	LRlc	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
Pulicaria sp	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus aquatillis agg.	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus flammula	LRlc	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1

7.4 New Forest plants cont

Sites	**CS**	**1**	**2**	**4**	**5**	**6**	**7**	**8**	**10**	**11**	**12**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**32**	**33**	**34**	**35**
Ranunculus repens	LRlc	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Rorippa nasturtium-aquaticum	LRlc	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex spp	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Salix repens	LRlc	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
Schoenus nigricans	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scilla spp	LRlc	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Senecio jacobea	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Sparganium erectum	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Trifolium repens	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Typha latifolia	LRlc	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Utricularia minor	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veronica beccabunga	LRlc	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryophyte records																																
Calliergonella cuspidata	LRlc	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Warnstorfia exannulata	LRlc	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Calliergonella stramineum	LRlc	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum compactum	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum inundatum	LRlc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum denticulatum	LRlc	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Sphagnum cuspidatum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphagnum papillosum	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campylium stellatum	LRlc	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Scorpidium scorpioides	LRlc	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drepanocladus revolvens	LRlc	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Campylopus introflexus	LRlc	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pellia epiphylla	LRlc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

7.5 Appendix 5: Lentic freshwater Habitats Directive categories (92/43/EEC) reported present in the New Forest and Lizard regions

Habitats Directive code	Corine code	JNCC definition	Key species	Lizard Vegetation	New Forest Vegetation	Lizard Inverts	New Forest Inverts
3110	22.11 x 22.31	**Oligotrophic waters containing very few minerals of the sandy plains (*Littorelletalia uniflorarae*)** Restricted to sandy plains that are acidic and low in nutrients. Water clear and moderately acid – acid moorland. Vegetation forms zones in which species form monospecific lawns **Present New Forest – Hatchett pond**	Zones dominated by. *Lobelia dortmanna, Littorella uniflora, Isoetes lacustris,* **Only one the above species needs to be present to conform with the definition of this habitat type** *Juncus bulbosus, Pilularia globulifera, Luronium natans, Potamogeton polygonifolius, Myriophyllum alteriflorum*		No sites fit criteria		none
3130	22.12 x (22.31 and 22.32)	**Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or *Isoëto-Nanojuncetea* (OML)** Clear **soft** water with low to moderate plant nutrients. Vegetation community dominated by amphibious short perennial species *Littorella uniflora* is defining, *Nanocyperetalia*. Margins of the shore can be exposed in summer **Present throughout New Forest**	*Littorella uniflora, Potamogeton polygonifolius, Juncus bulbosus, Eleocharis sciculans, Myriophyllum alterniflorum, Sparganium angustifolium, Nuphar lutea, Persicaria amphibian, Chara* spp, *Sparganium natans, Potamogeton* spp, *Luronium natans, Pilularia globulifera*		Subset of TWINSPAN groups 2 & 3 NF11, NF 16 & NF 18 have *L. uniflora* NF 6, 7 & 8 have *Illecebrum verticillatum*		Subset of TWINSPAN groups 1, 2 & 3
3140	22.11 or 22.41 x 22.44	**Hard oligo-mesotrophic waters with benthic vegetation of *Chara* (HOM)** Water has **high base content** usually calcium but rarely magnesium therefore confined to limestone and other base rich substrates. Clear water and low nutrient status therefore catchment unaffected by intensive land-use **Present on Lizard Peninsula**	*Chara* spp and *Nitella* spp	Subset of TWINSPAN group 1 L32, L33, L34, L35, L41, L43, L44 Plus L6 in group 3		Subset of TWINSPAN group 1	
3170	22.34	**Mediterranean Temporary Ponds** Winter flooded area dry out to give vegetation rich in annuals many of which are nationally rare species with southern European distribution which are principally confined to this habitat **Present on Lizard Peninsula**	In acidic pools: *Juncus pygmaeus, Mentha pulegium, Cicendia filiformis, Ranunculus tripartitus,* In eroded serpentine pans: *Allium schoenoprasum, Juncus capitatus, Isoetes histrix*	TWINSPAN groups 4,5 & 6 all potential MTP habitat		Subset of TWINSPAN groups 4,5 & 6	

7.6 Appendix 6: Lizard physicochemistry and grid references (TON total organic nitrate, SRP soluble reactive phosphorus)

Site	grid ref	area m2	pH	cond mS	turbidity NTU	depth cm	Cu mg/L	Zn mg/L	Fe mg/L	Co mg/L	Cr mg/L	Ni mg/L	Al mg/L	Mg mg/L	Ca mg/L	TON mg/L	SRP mg/L
1	SW684138	37.9	5.44	445	12.6	19.4	0.000	0.014	0.190	0.002	0.015	0.018	0.061	6.125	3.371	0.009	0.016
2	SW684138	23.6	5.79	462.3	9.7	15.4	0.000	0.008	0.313	0.002	0.009	0.025	0.063	6.510	3.321	0.000	0.007
3	SW684138	501	5.77	522.5	8.8	40.2	0.002	0.016	0.272	0.002	0.000	0.035	0.071	9.345	3.904	0.006	0.003
4	SW683140	112	6.63	959.8	6.1	17.6	0.002	0.010	0.271	0.009	0.000	0.073	0.051	32.975	8.610	0.031	0.007
5	SW683142	42.1	6.61	585.4	20.4	16	0.001	0.016	0.508	0.000	0.005	0.054	0.078	13.785	6.489	0.004	0.012
6	SW683143	3480	6.38	454.7	56.3	36.67	0.001	0.007	1.050	0.013	0.000	0.042	0.447	9.380	4.081	0.006	0.004
7	SW682140	4.3	6.29	857.5	5.6	24	0.007	0.021	0.155	0.015	0.000	0.060	0.080	19.105	8.705	0.228	0.029
8	SW682141	3.6	5.9	1070.1	5.8	20.2	0.003	0.001	0.068	0.006	0.006	0.034	0.205	26.590	10.415	0.722	0.008
9	SW682142	3.5	6.48	889.6	5	18.2	0.005	0.007	0.149	0.010	0.000	0.025	0.132	27.525	7.900	0.117	0.005
10	SW682142	11.3	6.09	803.2	4.2	14.6	0.002	0.010	0.139	0.019	0.000	0.027	0.056	21.945	10.245	0.003	0.000
11	SW683142	12.9	6.74	989.9	21.9	9.4	0.001	0.168	0.277	0.013	0.015	0.052	0.116	31.915	9.265	7.494	0.000
12	SW682142	10.3	5.64	467.7	18.1	10.2	0.003	0.022	0.333	0.003	0.009	0.029	0.085	7.580	5.573	0.017	0.000
13	SW682142	13.4	5.51	539.1	5.5	11.5	0.003	0.156	0.203	0.016	0.014	0.046	0.057	9.565	8.662	2.720	0.012
14	SW682142	5.3	5.99	789.1	2.8	18.6	0.002	0.037	0.114	0.008	0.012	0.059	0.062	14.600	8.061	0.346	0.007
15	SW681142	11.5	6.35	985.8	9.6	24.2	0.007	0.020	0.192	0.010	0.015	0.079	0.047	31.440	16.985	0.428	0.013
16	SW682141	23.8	5.56	776	7.6	25.2	0.006	0.020	1.436	0.000	0.036	0.204	0.125	21.965	8.559	0.062	0.029
17	SW682140	10	6.4	956.4	22.9	10	0.005	1.054	0.928	0.001	0.009	0.054	0.103	28.275	8.680	3.715	0.015
18	SW685138	7	5.89	530.4	8.6	15.6	0.002	0.018	0.057	0.004	0.019	0.039	0.048	10.685	3.694	0.161	0.002
19	SW684138	13.5	5.63	378.1	14.7	18.2	0.000	0.021	0.089	0.003	0.010	0.017	0.097	5.560	3.117	0.232	0.002
20	SW683138	41.9	5.85	1027.8	13.2	6.2	0.001	0.006	0.040	0.000	0.000	0.063	0.101	60.190	3.955	1.005	0.013
21	SW682138	2.1	5.74	873.9	8.4	11.8	0.006	0.011	0.494	0.000	0.007	0.076	0.247	15.995	7.180	0.369	0.021
22	SW676140	903	5.33	1113.2	12.2	19.6	0.002	0.019	0.045	0.004	0.005	0.042	0.149	24.260	6.255	0.507	0.011
23	SW679141	37.9	4.62	785.6	17.6	6.8	0.002	0.014	0.893	0.041	0.014	0.058	0.626	18.225	5.748	0.035	0.007
24	SW680140	131	4.47	478.3	28.3	21.8	0.003	0.089	0.255	0.001	0.000	0.030	0.248	7.750	4.099	3.632	0.007
25	SW681140	167	4.62	875.5	7.5	17.8	0.003	0.020	0.509	0.007	0.000	0.053	0.431	20.380	7.706	0.434	0.006
26	SW681140	14.9	4.98	819.3	11.5	17	0.002	0.006	0.997	0.007	0.013	0.090	0.072	20.625	8.401	0.430	0.010
27	SW682140	4.6	6.93	940.5	21	24.2	0.004	0.008	1.000	0.004	0.008	0.073	0.058	19.155	5.333	0.304	0.014
28	SW690138	138	6.64	474.4	1.4	14.6	0.002	0.016	0.111	0.006	0.004	0.013	0.132	13.535	2.965	0.093	0.004
29	SW691132	81	6.74	694.1	2.4	50	0.000	0.011	0.127	0.013	0.000	0.017	0.018	16.725	3.881	0.228	0.001
30	SW691132	1.9	6.68	747.1	1.9	33.6	0.006	0.014	0.768	0.006	0.004	0.045	0.023	17.240	4.009	0.318	0.008
31	SW691132	106	6.76	731.7	1.4	50	0.004	0.069	0.092	0.000	0.000	0.013	0.237	16.465	3.677	0.542	0.019
32	SW693172	1311	6.61	273.2	17.4	21.7	0.006	0.026	0.589	0.002	0.001	0.018	0.161	7.445	2.547	0.138	0.012
33	SW694172	759	6.63	266.7	13.9	18.2	0.003	0.022	0.297	0.000	0.004	0.020	0.101	7.565	2.321	0.081	0.002

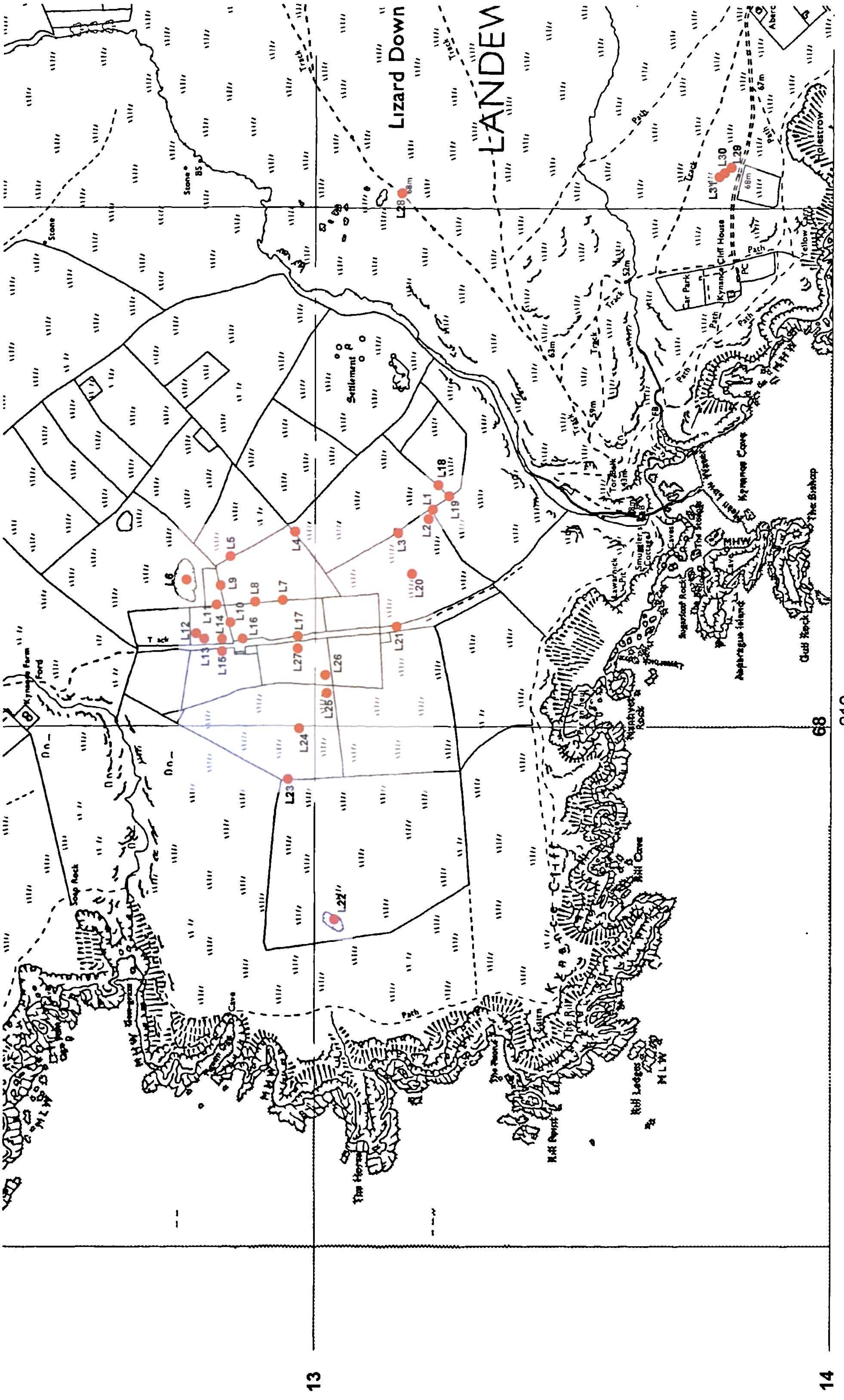
7.6 Lizard physicochemistry and grid references cont

Site	grid ref	area m2	pH	cond mS	turbidity NTU	depth cm	Cu mg/L	Zn mg/L	Fe mg/L	Co mg/L	Cr mg/L	Ni mg/L	Al mg/L	Mg mg/L	Ca mg/L	TON mg/L	SRP mg/L
34	SW694171	4377	6.63	293.7	12.4	25 4	0.003	0.016	0.483	0.002	0.007	0.028	0.154	8.165	3.514	0.052	0.002
35	SW695170	15005	6.6	325	46	30	0.004	0.010	0.559	0.006	0.003	0.005	0.072	11.675	3.850	0.235	0.003
36	SW696159	5766	6.58	256.3	8.3	22 5	0.006	0.019	0.294	0.000	0.011	0.028	0.141	6.595	2.806	0.400	0.002
37	SW702146	151	6.69	353.75	71.6	22 8	0.002	0.010	0.565	0.004	0.000	0.026	0.185	5.570	7 889	0.722	0.002
38	SW699144	9	6.68	401.7	12.4	12	0.002	0.004	0.365	0.006	0.010	0.007	0.210	19.830	7.350	0.120	0.001
39	SW699144	15	6.63	428.1	26.6	9	0.001	0.006	0.499	0.002	0.006	0.013	0.182	22.140	5.047	0.201	0.001
40	SW700137	682	6.69	553.7	6.6	34.9	0.013	0.283	11.813	0.000	0.006	0.001	0.250	10.375	3.135	0.133	0.006
41	SW731198	8827	6.75	162.3	8.8	29.1	0.001	0.018	0.391	0.000	0.002	0.025	0.095	6.365	0.842	0.155	0.027
42	SW734214	3000	6.71	269.8	1.5	28.8	0.004	0.016	0.111	0.000	0.006	0.000	0.112	15.720	1.677	0.200	0.014
43	SW735205	1180	6.76	202.1	11.1	35	0.001	0.012	0.069	0.001	0.005	0.014	0.149	8.135	1.206	0.518	0.008
44	SW727182	18.5	6.74	351.8	13.75	65	0.000	0.010	0.077	0.000	0.003	0.012	0.027	33.040	2.077	0.194	0.020
45	SW728180	97	6.75	341.4	38.2	13	0.001	0.005	0.139	0.002	0.008	0.069	0.032	24.780	4.526	0.312	0.011

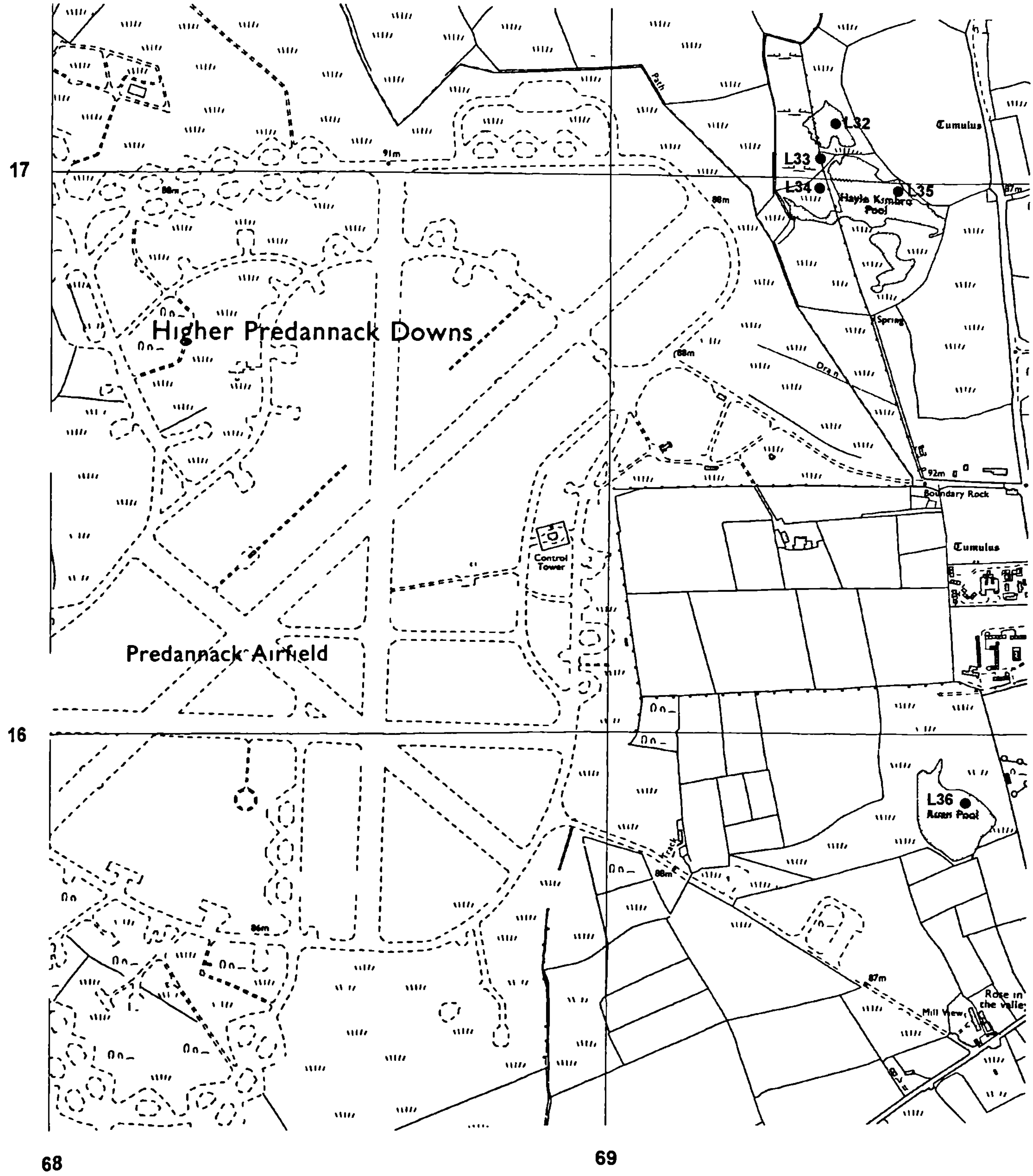
7.7 Appendix 7: New Forest physicochemistry and grid references (TON total organic nitrate, SRP soluble reactive phosphorus)

Site	grid ref	area m2	pH	cond mS	turbidity NTU	depth cm	Cu mg/L	Zn mg/L	Fe mg/L	Co mg/L	Cr mg/L	Ni mg/L	Al mg/L	Mg mg/L	Ca mg/L	TON mg/L	SRP mg/L
1	SZ364977	354.2	7.49	356.5	1.5	25.3	0.003	0.022	0.046	0.018	0.009	0.070	0.000	0.001	0.002	0.000	0.015
2	SZ364976	33.75	7.07	515.5	6.4	16	0.003	0.023	0.048	0.054	0.089	0.109	0.000	0.001	0.004	0.000	0.047
4	SZ365976	20.25	6.11	139.2	0.6	7.7	0.001	0.043	0.090	1.826	0.940	0.290	0.000	0.000	0.002	0.030	0.040
5	SZ366977	2550	6	155.2	1.3	13.2	0.000	0.038	0.053	0.032	0.072	0.139	0.000	0.000	0.000	0.002	0.003
6	SZ367977	14.14	7.72	142.6	6	10.2	0.005	0.062	0.082	0.497	0.323	0.180	0.002	0.001	0.000	0.020	0.007
7	SZ367977	22	7.32	128.2	0.1	15.4	0.003	0.035	0.076	0.191	0.097	0.062	0.000	0.000	0.000	0.005	0.019
8	SZ367977	4.7	6.71	144.4	1.9	7	0.012	0.040	0.074	0.119	0.099	0.073	0.000	0.000	0.000	0.010	0.088
10	SZ366980	4.2	6.53	191.4	4.1	9.6	0.001	0.012	0.030	0.014	0.066	0.046	0.000	0.000	0.000	0.007	0.005
11	SZ351989	49.5	7.05	544.2	6.3	10	0.004	0.026	0.057	0.176	0.088	0.069	0.000	0.001	0.001	0.000	0.000
12	SZ351989	60	6.94	406.8	36	12.5	0.000	0.010	0.026	0.180	0.090	0.115	0.000	0.002	0.001	0.000	0.001
14	SU367017	121.5	7	214	8.1	8.3	0.000	0.015	0.041	0.032	0.016	0.043	0.000	0.000	0.000	0.015	0.071
15	SU368017	7.1	5.61	139.3	12.7	9.6	0.001	0.055	0.173	1.599	0.800	0.200	0.000	0.000	0.000	0.018	0.009
16	SU368013	1251.7	8.09	143.4	0.5	37	0.003	0.016	0.033	0.020	0.010	0.027	0.000	0.003	0.002	0.022	0.000
17	SZ353995	66	7.25	509.6	1.8	35.4	0.000	0.035	0.070	1.105	0.553	0.000	0.000	0.000	0.000	0.001	0.000
18	SZ353993	60	7.88	795.6	4.2	34.2	0.003	0.014	0.026	0.052	0.026	0.000	0.000	0.002	0.004	0.002	0.000
19	SZ368976	368.1	5.03	163.4	95.1	16	0.011	0.052	0.092	0.485	0.243	0.000	0.000	0.000	0.000	0.038	0.002
20	SU384051	5301	4.18	117.6	47.8	15	0.001	0.053	0.101	0.230	0.115	0.029	0.000	0.000	0.000	0.019	0.000
21	SU385076	28.3	6.06	382.1	36.8	14	0.004	0.212	0.199	0.136	0.098	0.086	0.005	0.010	0.010	0.064	0.000
22	SU363043	16.75	3.68	242.9	12.8	9.4	0.009	0.054	0.099	0.131	0.106	0.081	0.000	0.002	0.004	0.034	0.000
23	SU364042	12	3.9	265.2	103.1	5.6	0.011	0.081	0.151	0.814	0.423	0.033	0.000	0.004	0.007	0.022	0.005
24	SU306035	2945	5.29	110.3	120	13.2	0.006	0.045	0.076	4.000	2.067	0.550	0.000	0.003	0.002	0.302	0.038
25	SU304030	736.25	6.42	295.1	39.1	20	0.010	0.036	0.056	1.371	0.686	0.171	0.011	0.015	0.011	0.028	0.030
26	SZ286997	141.4	5.4	159.2	18.5	13.2	0.003	0.033	0.085	0.205	0.132	0.048	0.000	0.004	0.003	0.036	0.007
27	SZ286997	7.1	5.64	248	67.4	19	0.007	0.036	0.080	0.063	0.046	0.020	0.000	0.000	0.000	0.007	0.007
28	SZ286997	72	5.67	170.1	18.2	17	0.006	0.038	0.067	0.122	0.097	0.042	0.001	0.002	0.002	0.024	0.003
29	SZ286997	11	4.2	148.1	4.8	16.4	0.006	0.054	0.130	0.565	0.306	0.088	0.000	0.001	0.001	0.038	0.003
30	SZ286998	24	5.45	143.5	30.4	18.6	0.001	0.019	0.059	0.067	0.034	0.008	0.000	0.001	0.001	0.032	0.005
32	SZ222986	42	6.17	353.7	2.2	20	0.001	0.018	0.035	0.428	0.285	0.142	0.000	0.001	0.002	0.000	0.001
33	SZ225986	120	6.49	335	6.9	13.8	0.006	0.020	0.035	0.133	0.140	0.072	0.006	0.006	0.006	0.000	0.000
34	SU229167	15.1	6.19	243.9	15.5	8.2	0.011	0.023	0.042	0.021	0.024	0.012	0.001	0.001	0.001	0.075	0.001
35	SU177149	60	5.4	113.5	4.7	10.2	0.015	0.036	0.062	0.288	0.198	0.076	0.007	0.004	0.001	0.019	0.021

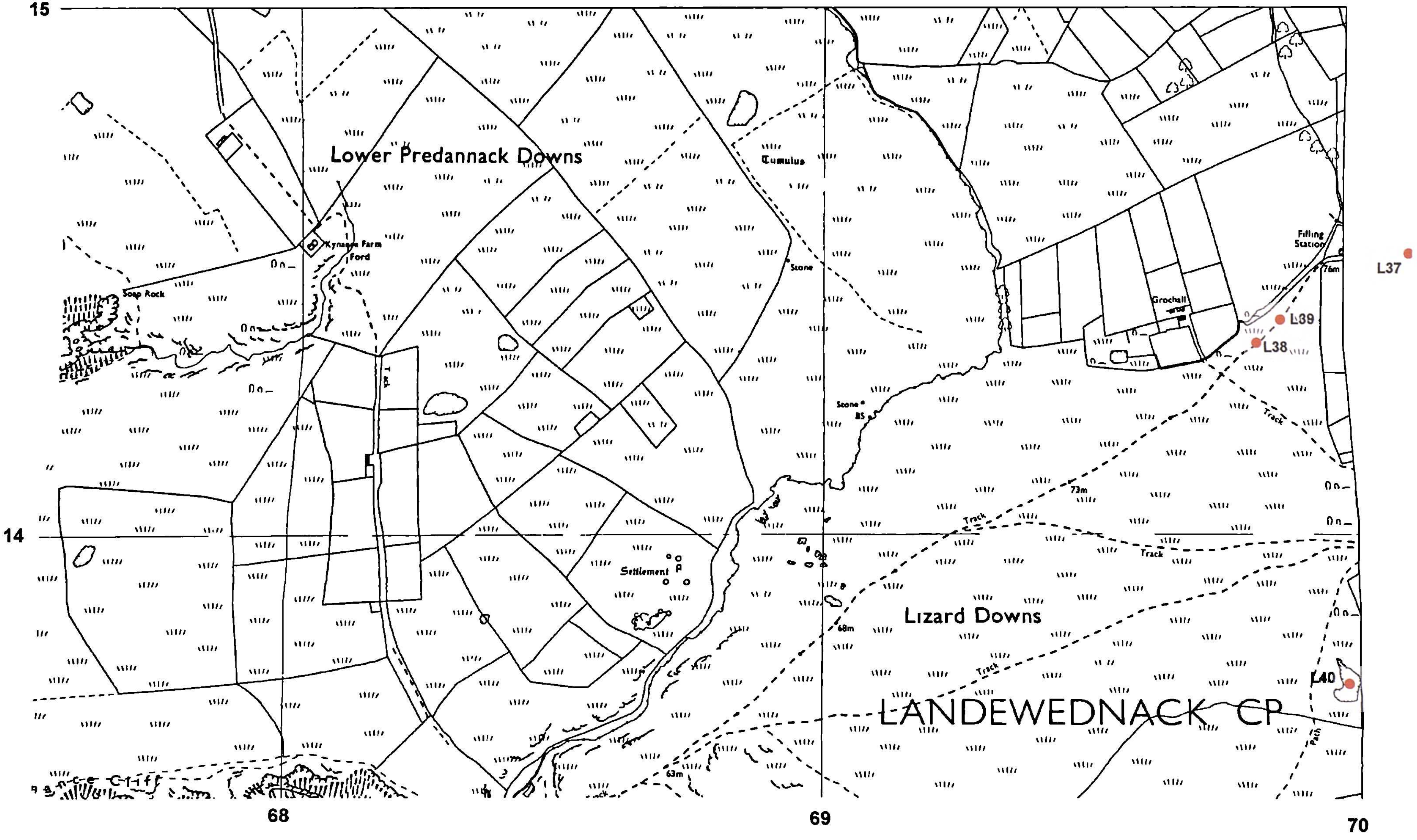
7.8: Map A, Lizard Peninsula, ponds L1-31



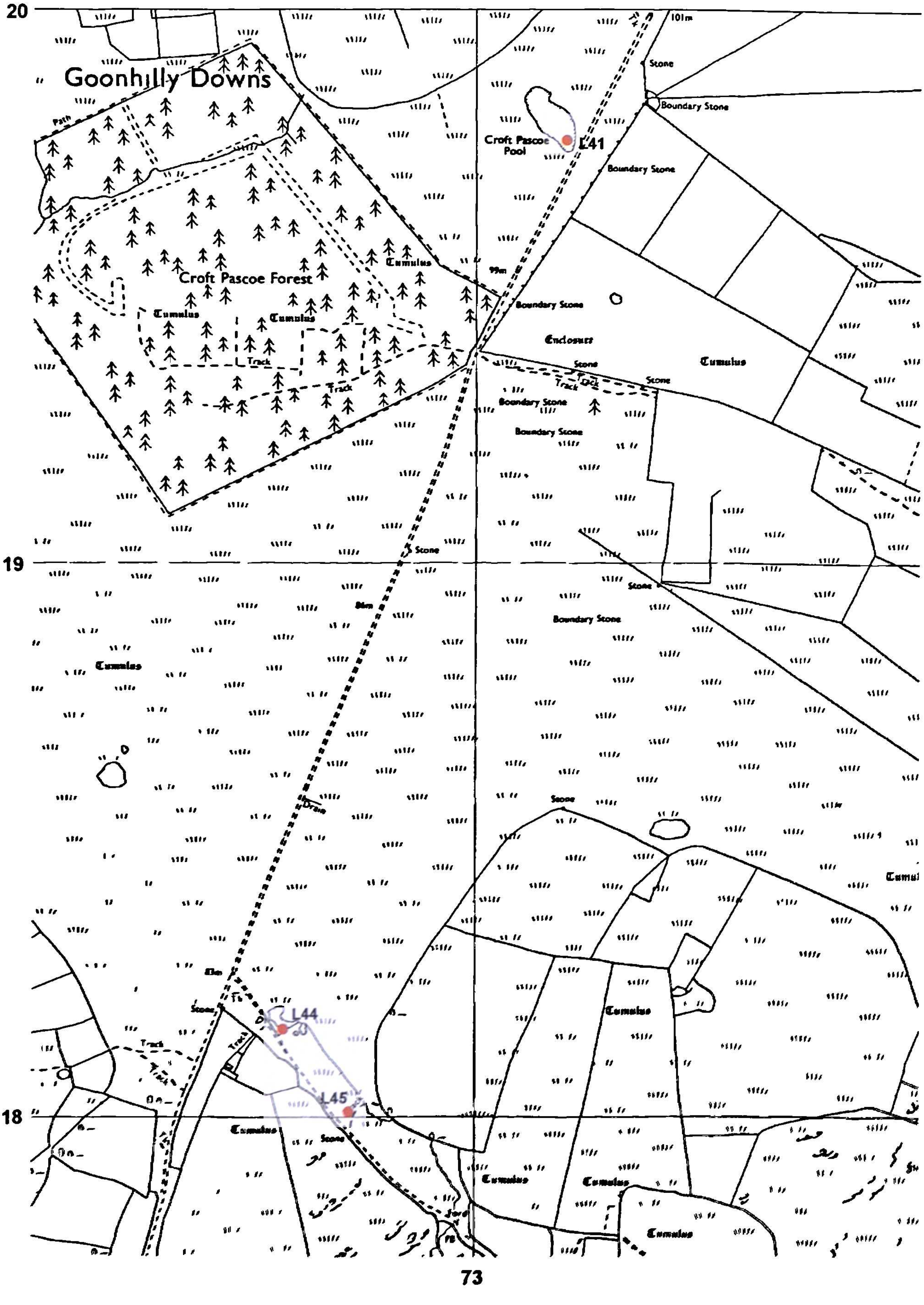
7.9: Map B, Lizard Peninsula, ponds L32-36



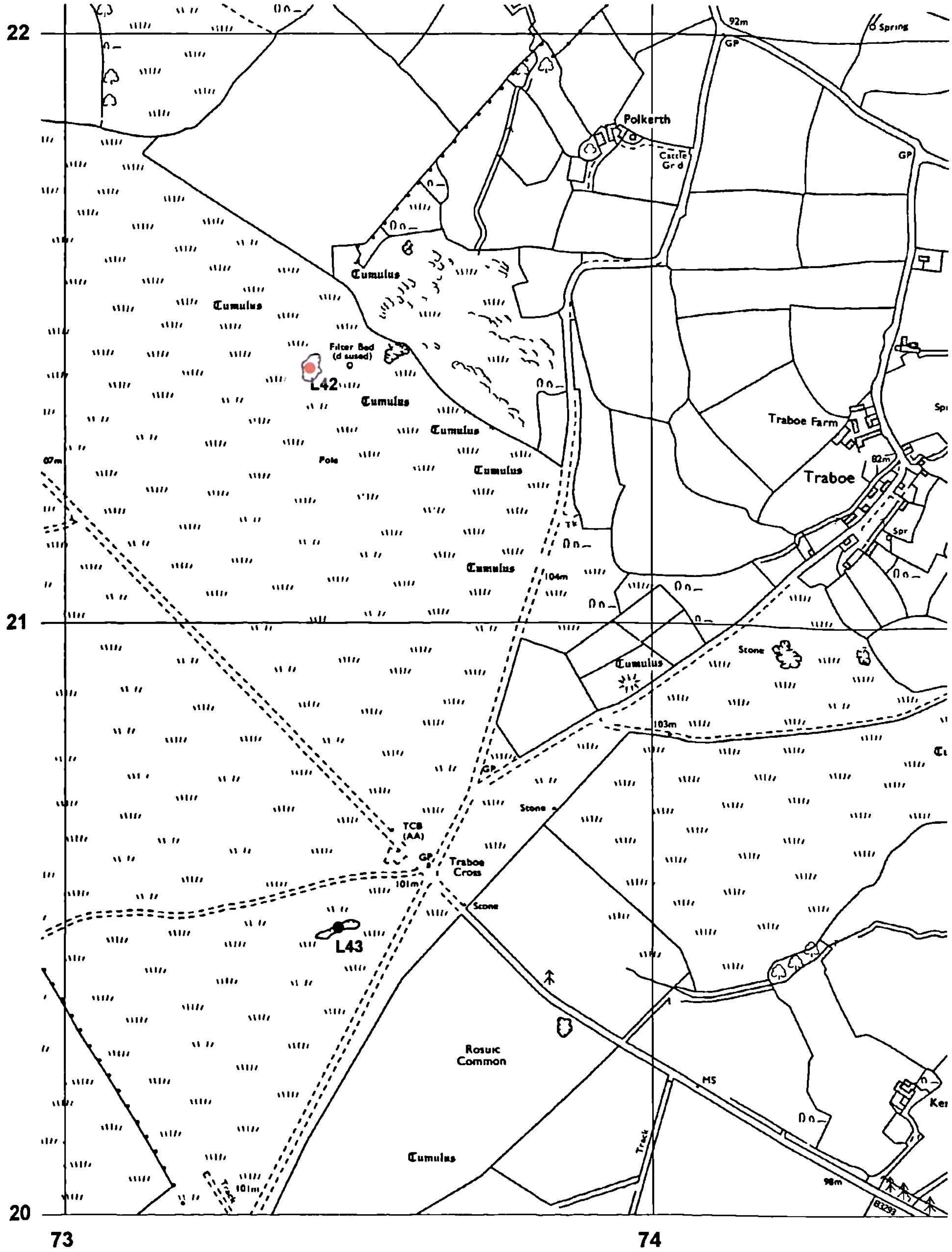
7.10: Map C, Lizard Peninsula, ponds L37-40. L37 is at grid reference 702146



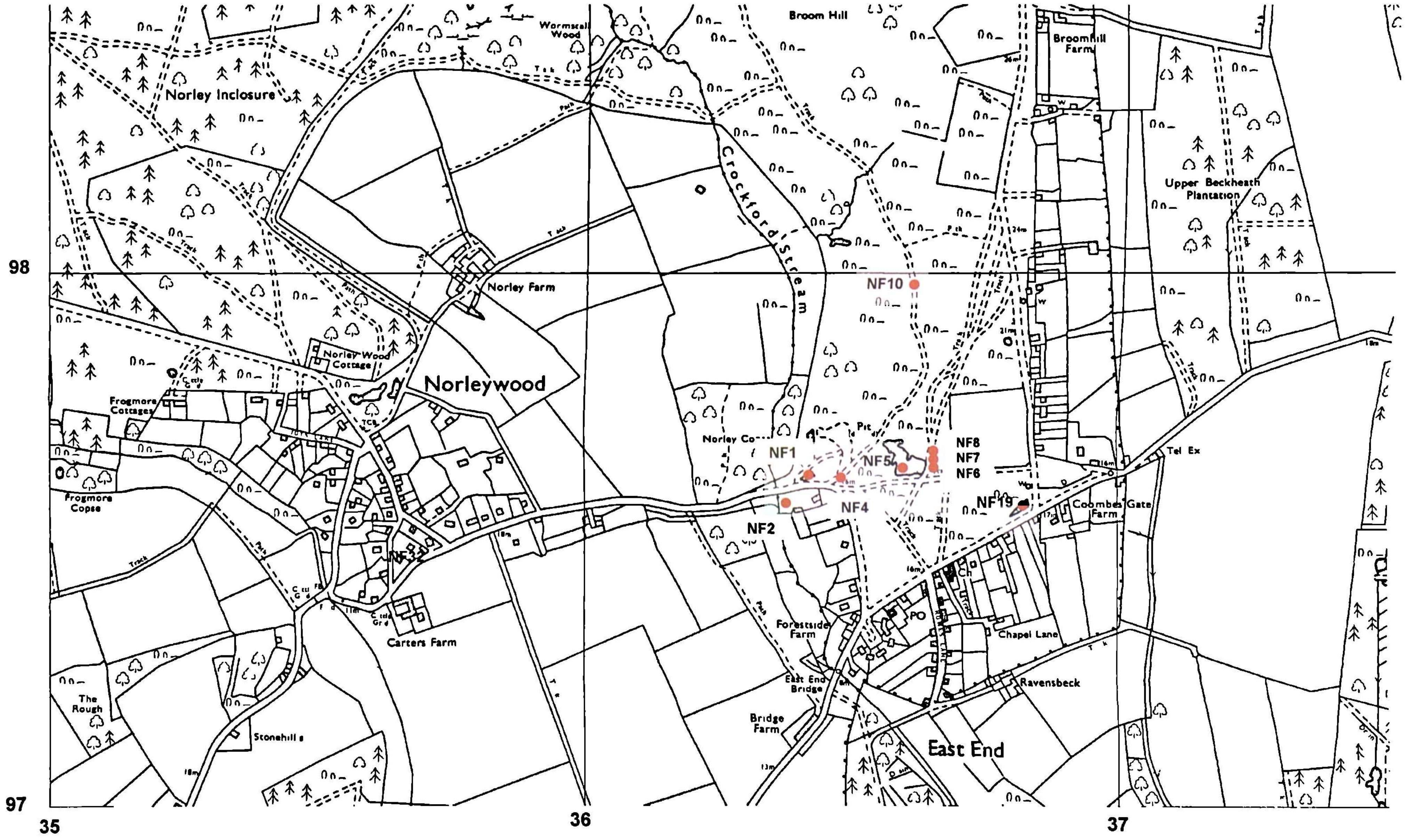
7.11: Map D, Lizard Peninsula, ponds L41, L44 and L45



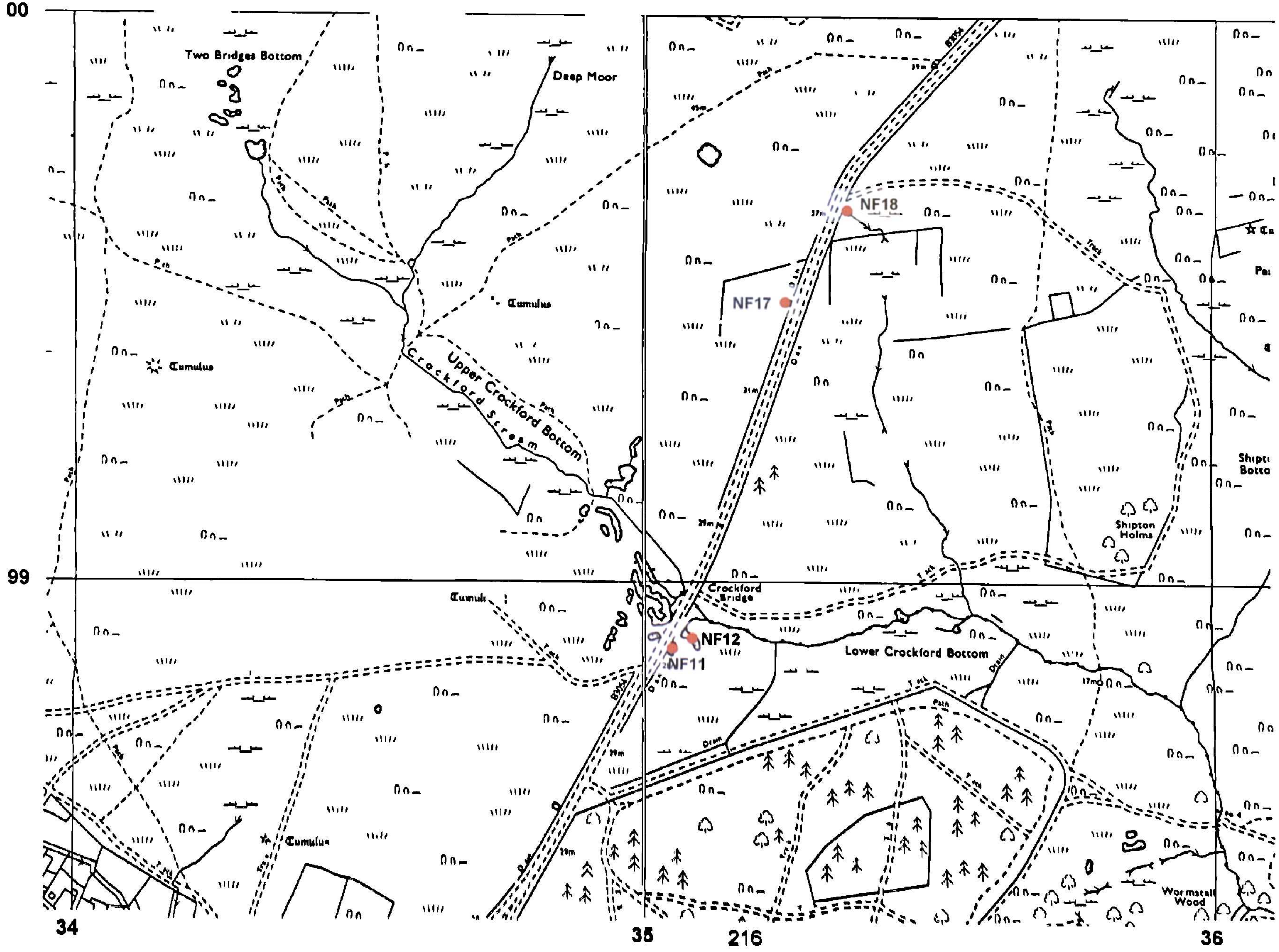
7.12: Map E, Lizard Peninsula, ponds L42 and L43



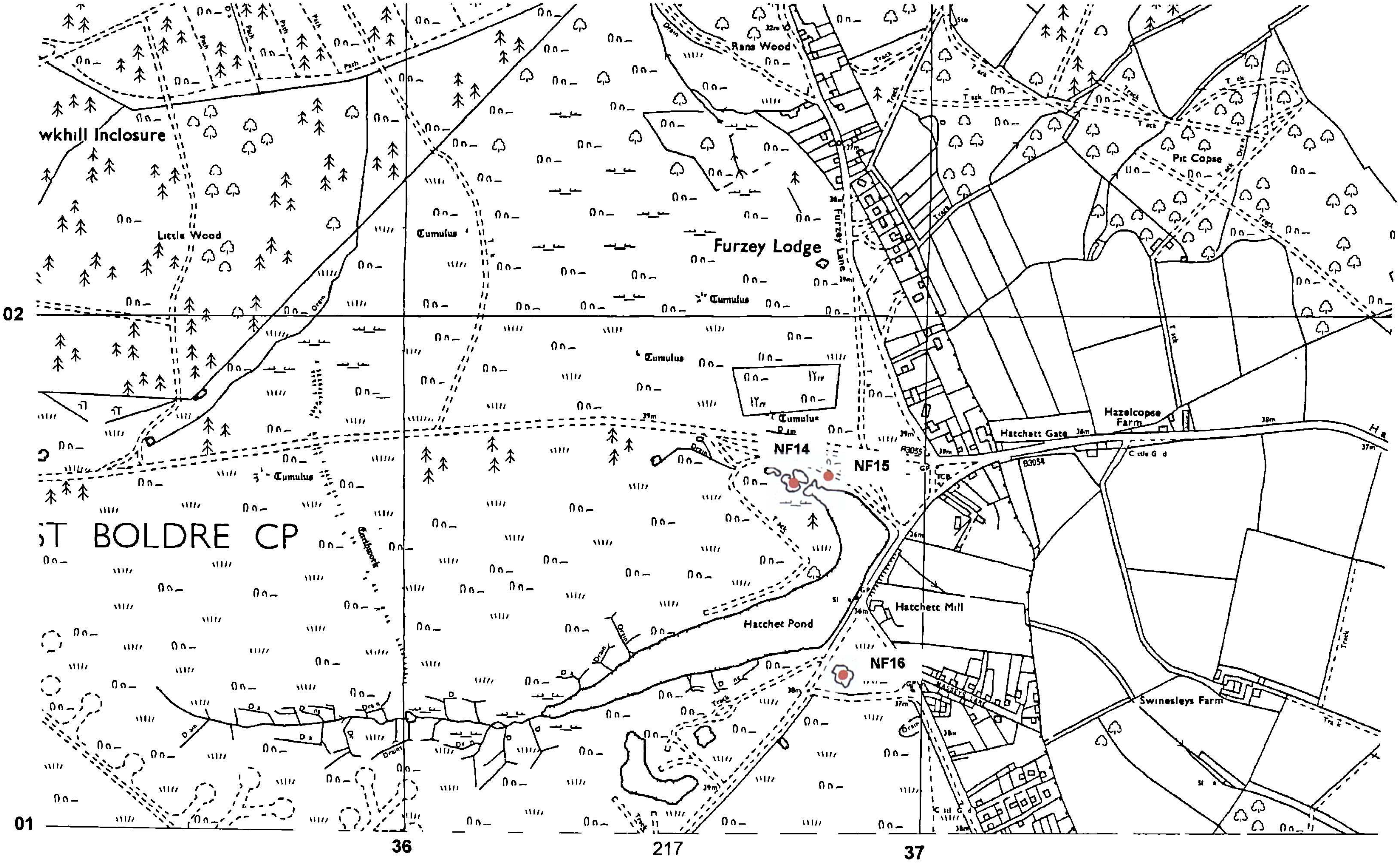
7.13 Map F, New Forest ponds NF1 to NF10 and NF19



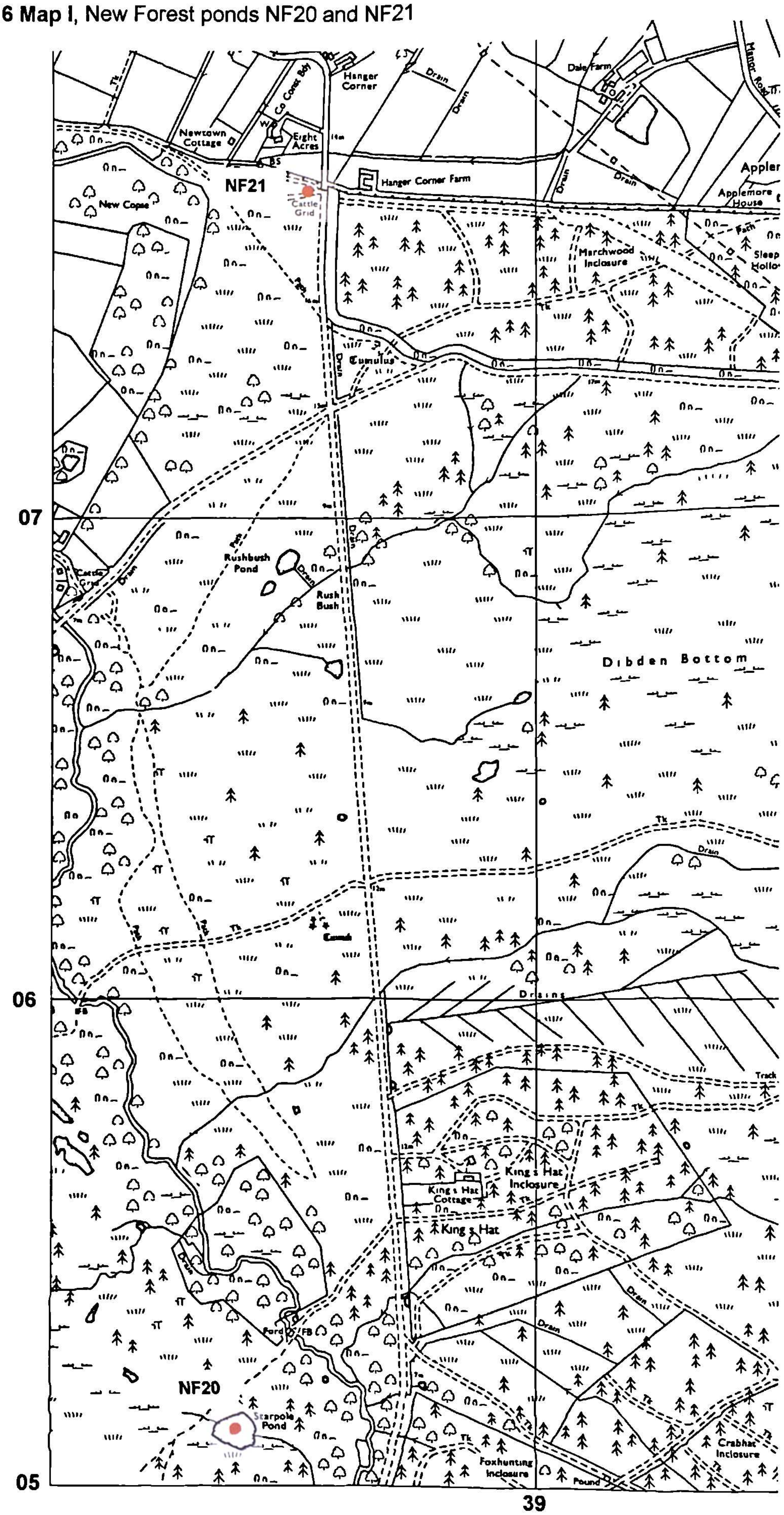
7.14 Map G, New Forest ponds NF11, NF12, NF17 and NF 18



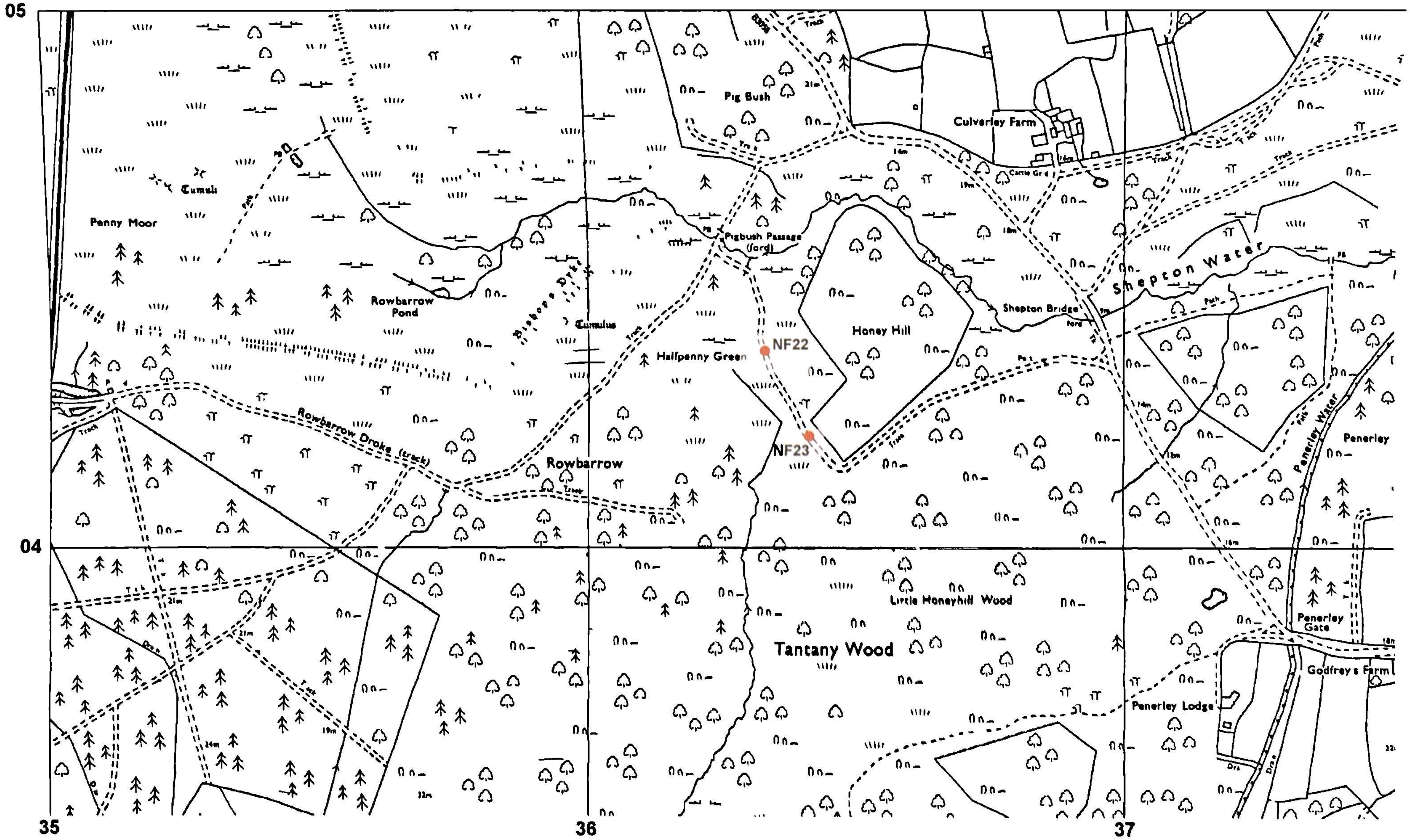
7.15 Map H, *New Forest ponds NF14 to NF16*



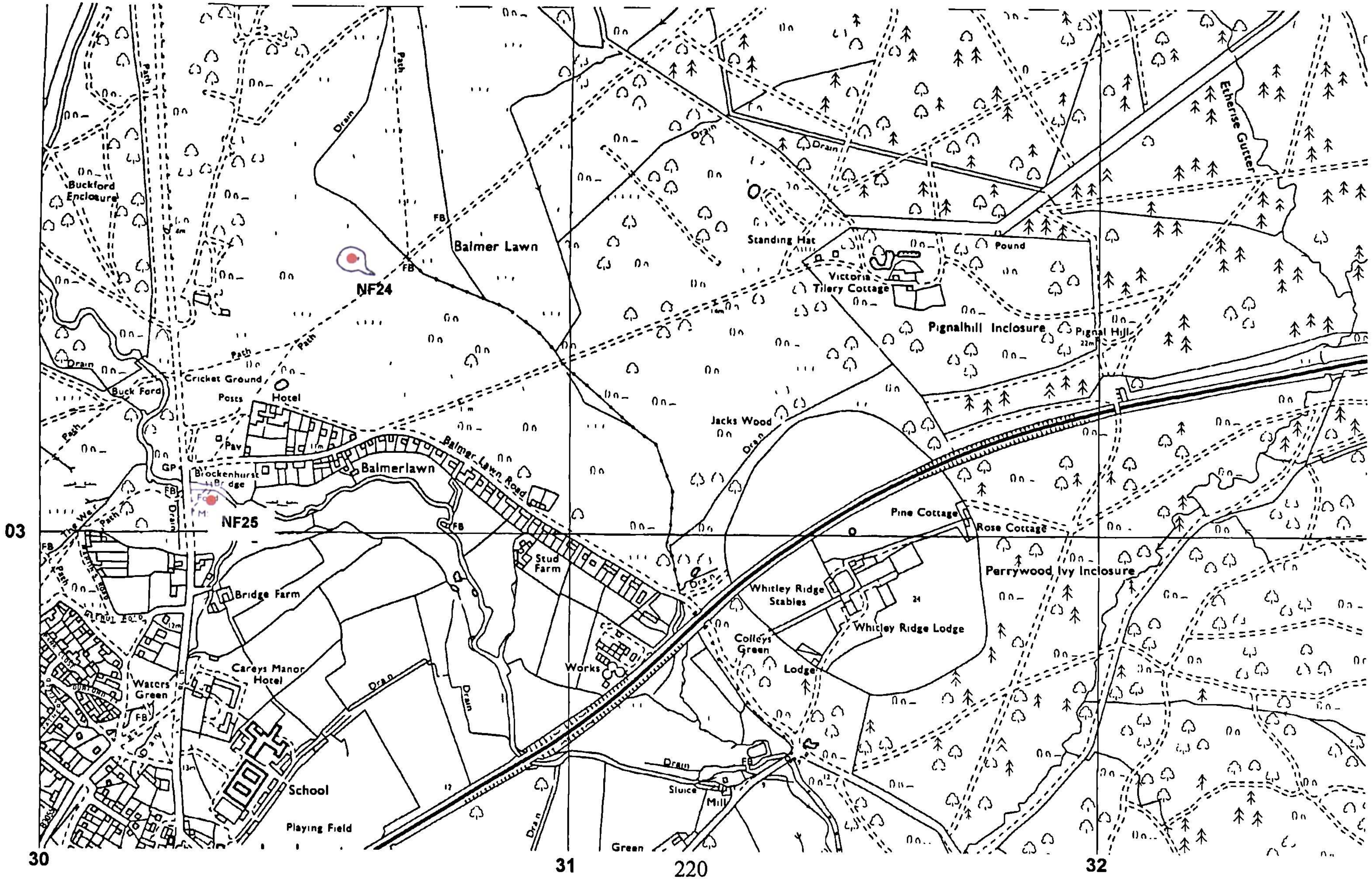
7.16 Map I, New Forest ponds NF20 and NF21



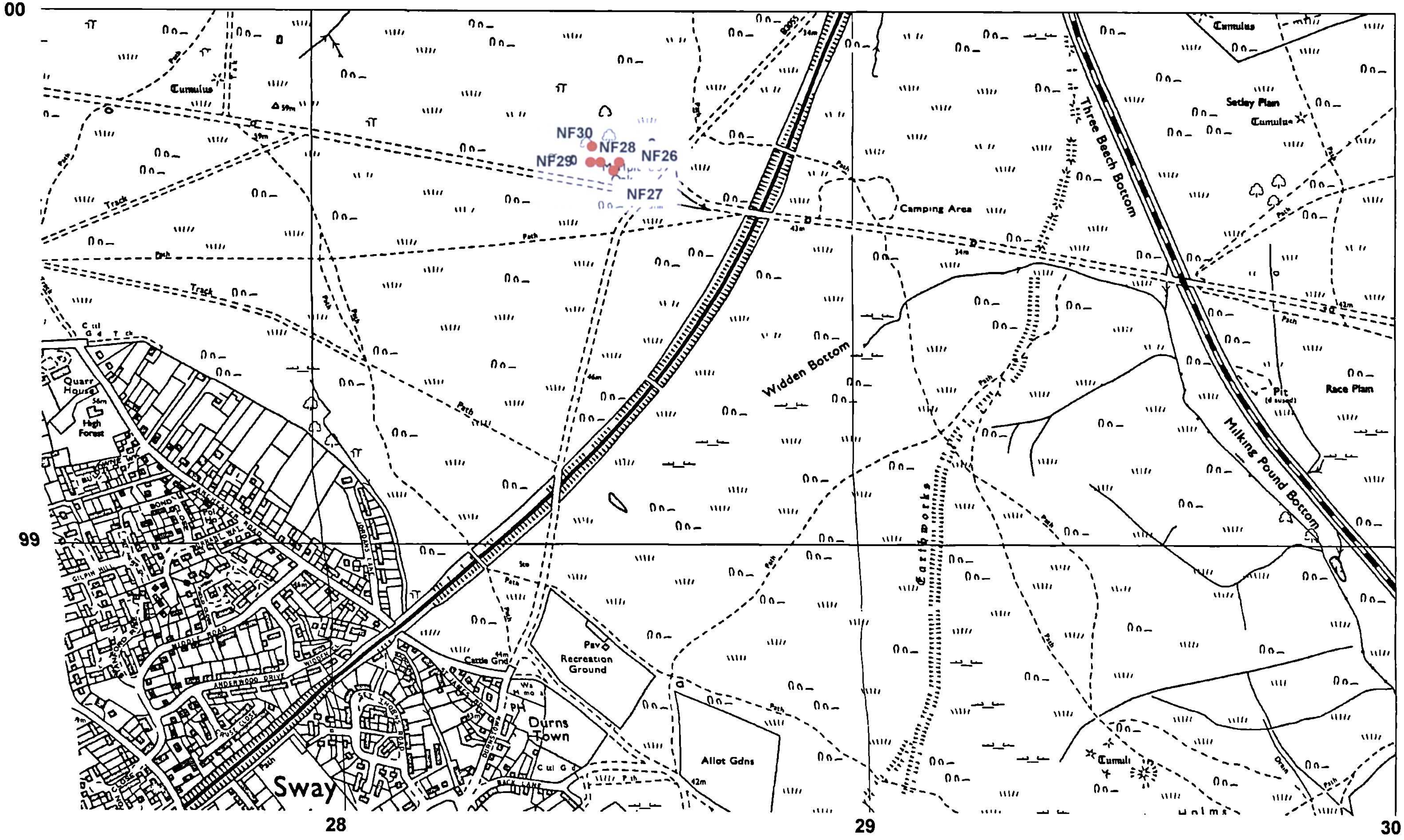
7.17 Map J, New Forest ponds NF22 and NF23



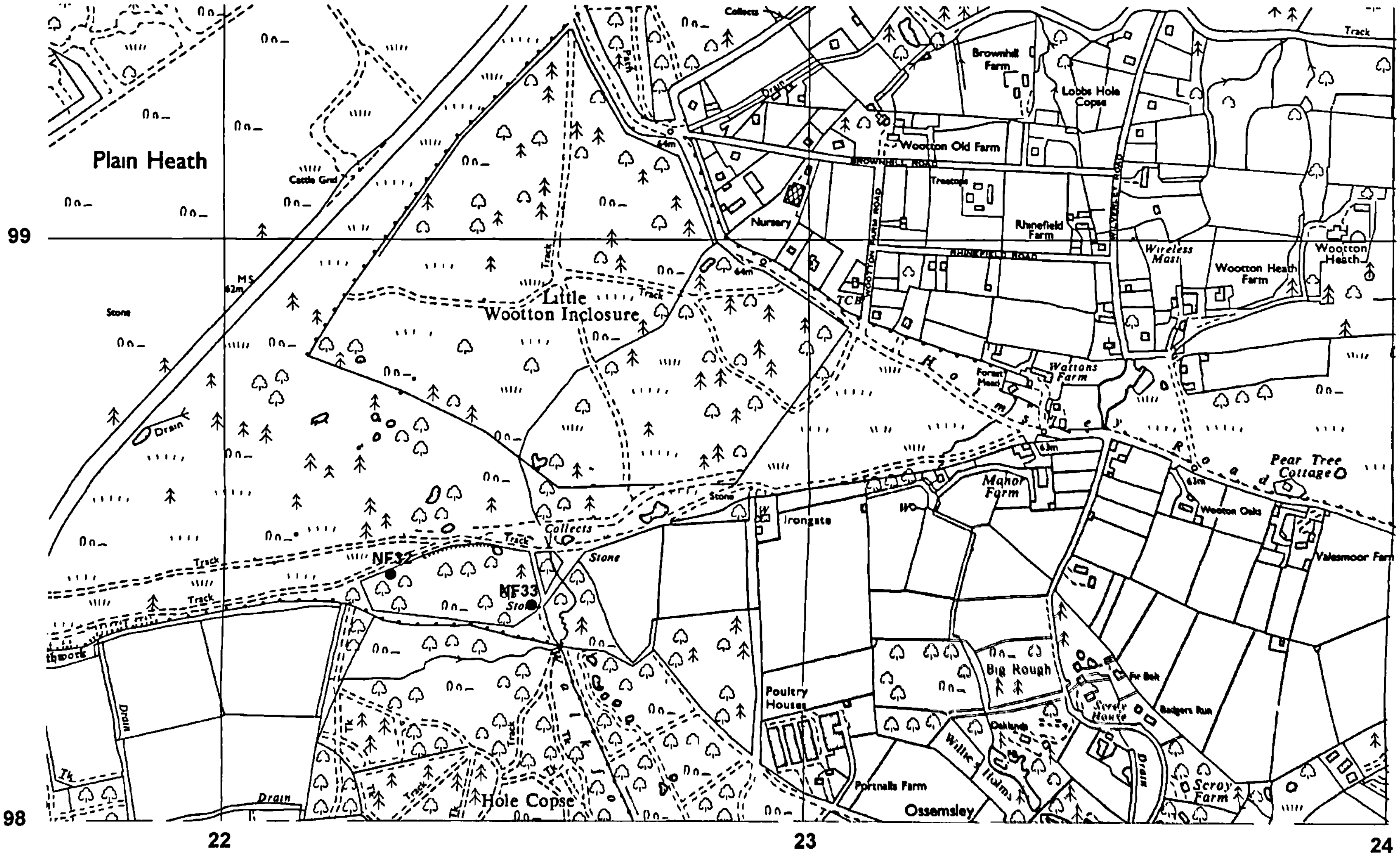
7.18 Map K, New Forest ponds NF24 and NF25



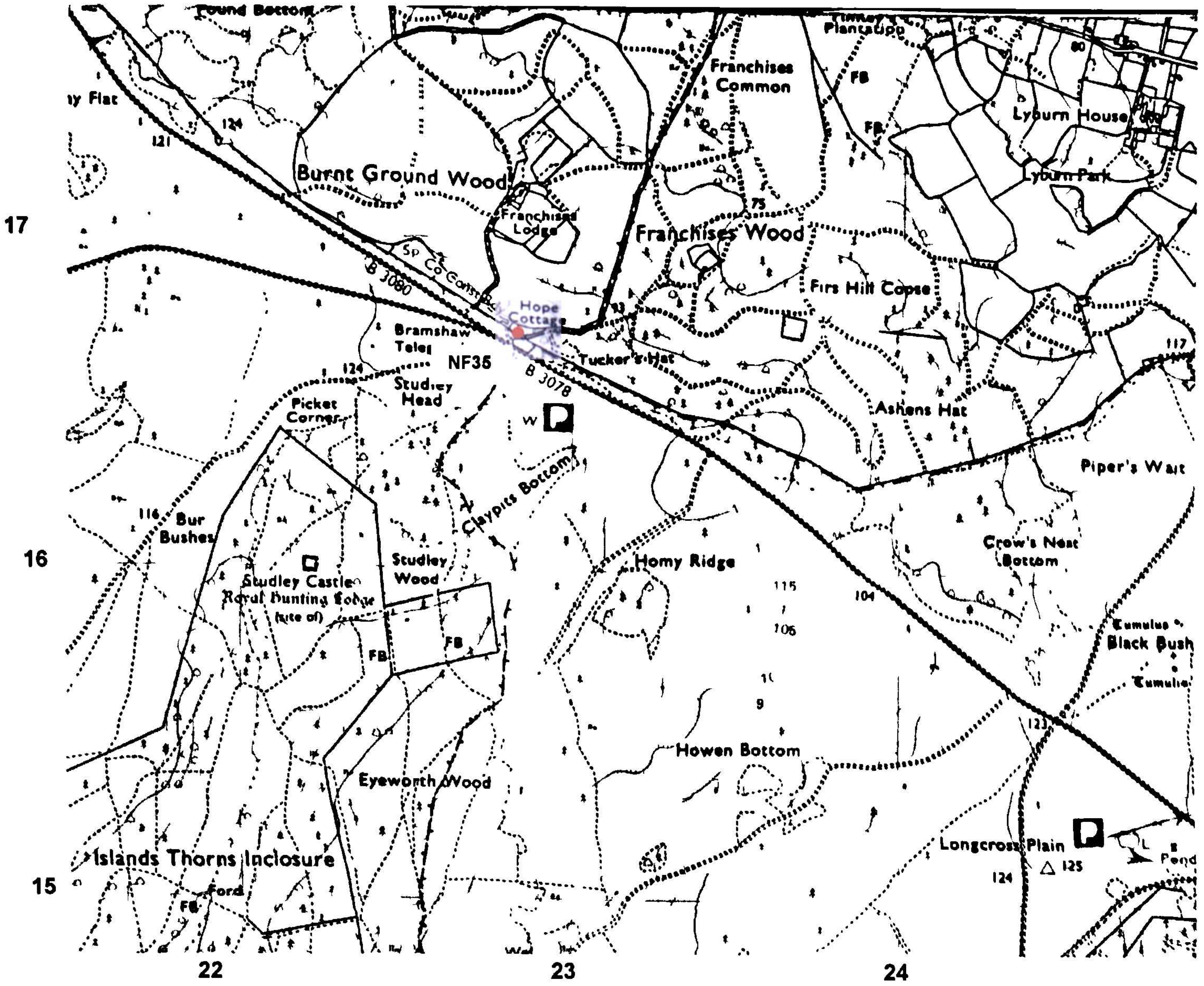
7.19 Map L, New Forest ponds NF26 to NF30



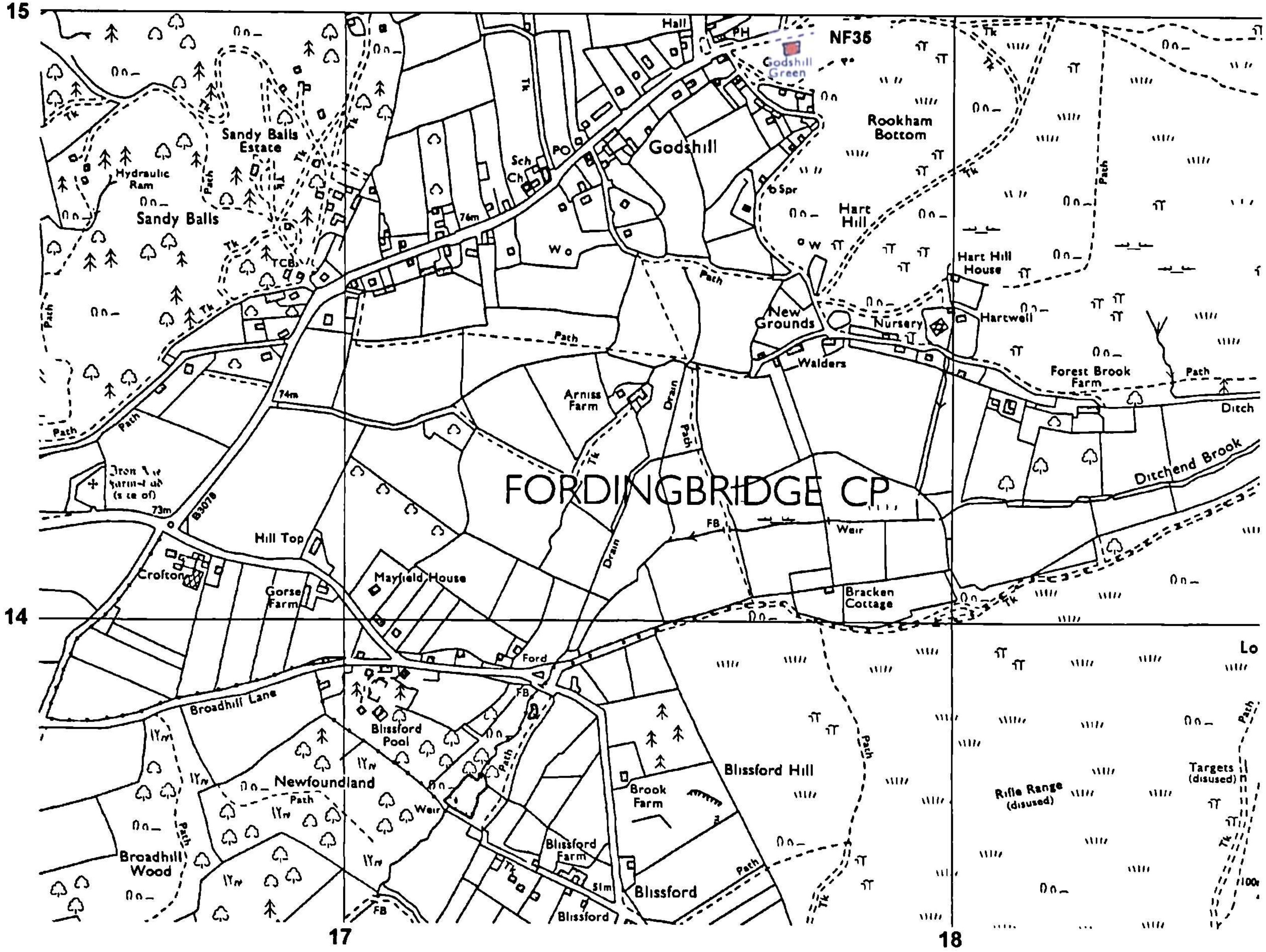
7.20 Map M, New Forest ponds NF32 and NF33



7.21 Map N, New Forest pond NF34



7.22 Map O, New Forest pond NF35



8 References

Angold, P.G. 1997. The impact of a road upon adjacent heathland vegetation: effects on plant species composition. Journal of Applied Ecology, 34: 409-417.

Atkinson, T. 1984. The plant communities of valley mires in the New Forest, Hampshire. Journal of Biogeography, 11: 289-317.

Atmar, W. & Patterson, B.D. 1995. The nestedness temperature calculator: a visual basic program, including 294 presences-absence matrices. AIC Research Inc., University Park, NM and the Field Museum Chicago, IL. <www.aics-research.com/nestedness/tempcalc.html>

Atmar, W. & Patterson, B.D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia, 96: 373-382.

Attrill, M.J., Strong, J.A. & Rowden, A.A. 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? Ecography, 23: 114-121.

Barnes L.E. 1983. The colonization of ball-clay ponds by macroinvertebrates and macrophytes. Freshwater Biology, 13: 561-578.

Barr C.J., Howard D.C. & Benefield C.B. 1994. *Inland Water Bodies*, Countryside 1990 Series Volume 6. Department of the Environment, London.

Bartholomew, A., Diaz, R.J. & Cicchetti, G. 2000. New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. Marine Ecology Progress Series, 206: 45-58.

Batzer, D.P. & Resh, V.H. 1992. Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. Wetlands, 12(1): 1-7.

Batzer, D.P. & Wissinger, S.A. 1996. Ecology of insect communities in non-tidal wetlands. Annual Review of Entomology, 41: 75-100.

Bazzanti, M., Della Bella, V. & Seminara, M. 2003. Factors affecting macroinvertebrate communities in astatic ponds in central Italy. Journal of Freshwater Ecology, 18(4): 537-548.

Bechara J.A. 1996. The relative importance of water quality, sediment composition and floating vegetation in explaining the macrobenthic community structure of floodplain lakes (Parana river, Argentina). Hydrobiologia, 333: 95-109.

Beebee, T.J.C. 1997. Changes in dewpond numbers and amphibian diversity over 20 years on chalk downlands in Sussex, England. Biological Conservation, 81: 215-219.

Beja, P. & Alcazar, R. 2003. Conservation of Mediterranean temporary ponds under agricultural intensification: an evaluation using amphibia. Biological Conservation, 114(3): 317-326.

Bellemakers M.J.S. & van Dam, H. 1992. Improvement of breeding success of the moor frog (*Rana arvalis*) by liming of acid moorland pools and the consequences of liming for water chemistry and diatoms. Environmental Pollution, 78: 165-171.

Belyea L.R. & Lancaster J. 1999. Assembly rules within a contingent ecology. Oikos, 86: 402-416.

Benke, A.C., Huryn, A.D., Smock, L.A. & Wallace, J.B. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society, 18(3): 308-343.

Berglund, H. & Jonsson, B.G. 2003. Nested plant and fungal communities; the importance of area and habitat quality in maximising species capture in boreal old-growth forests. Biological Conservation, 112: 319-328.

Biggs, J., Fox, G., Nicolet, P., Whitfield, M. & Williams, P. 2001. Dangers and opportunities in managing temporary ponds. In *European temporary ponds: a threatened habitat.* Freshwater Forum, 17: 71-80.

Bilton D.T., Foggo A. & Rundle S.D. 2001a. Size, permanence and the proportion of predators in ponds. Archiv fur Hydrobiologie. 792: 1-8.

Bilton, D.T., Freeland, J.R. & Okamura, B. 2001b. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics, 32: 159-181.

Blaunstein, L., Friedman, J. & Fahima, T. 1996. Larval Salamandra drive temporary pool community dynamics: evidence from an artificial pool experiment. Oikos, 76: 392-402.

Blaunstein, L., Garb, J.E., Shebitz, D. & Nevo, E. 1999. Microclimate, development plasticity and community structure in artificial temporary pools. Hydrobiologia, 392: 187-196.

Bliss, S.A. & Zedler, P.H. 1998. The germination process in vernal pools: sensitivity to environmental conditions and effects on community structure. Oecologia, 113: 67-73.

Boecklen, W.J. 1997. Nestedness, biogeographic theory, and the design of nature reserves. Oecologia, 112: 123-142.

Bohonak, A.J. 2002. RMA software for Reduced Major Axis Regression v1.14b http://www.bio.sdsu.edu/pub/andy/RMAmanual.pdf

Bohonak, A.J. & Jenkins, D.G. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecology Letters, 6: 783-796.

Bonis, A., Lepart, J. & Laloe, F. 1996. Effect of temperature on the instalment and growth of annuals in Mediterranean temporary marshes. Canadian Journal of Botany, 74(7): 1088-1094.

Bonis, A., Lepart, J. & Grillas, P. 1995. Seed bank dynamics and co-existence of annual macrophytes in a temporary and variable habitat. Oikos, 74(1): 81-92.

Boothby, J. 1997. Pond conservation: towards a delineation of pondscape. Aquatic Conservation: Marine and Freshwater Ecosystems, 7: 127-132.

Bradbury, R.H., Reichelt, R.E. & Green, D.G. 1984. Fractals in ecology: methods and interpretation. Marine Ecology Progress Series, 14: 295-296.

Bratton J.H. 1990. Seasonal pools – an overlooked invertebrate habitat. British Wildlife, 2(1): 22-29.

Bray, J. R. & J. T. Curtis. 1957. An ordination of upland forest communities of southern Wisconsin. Ecological Monographs, 27: 325-349.

Breininger, D.R., Burgman, M.A., Akçakaya, H.R. & O'Connell, M.A. 2002. Use of metapopulation models in conservation planning. In *Applying landscape ecology in biological conservation*, pp 405-427, ed Gutzwiller, K.J. Springer-Verlag, New York.

Brewis, A., Bowman, P. & Rose, F. 1996. *The flora of Hampshire.* Harley Books, Colchester.

Briers, R.A. & Biggs, J. 2003. Indicator taxa for the conservation of pond invertebrate diversity. Aquatic Conservation: Marine and Freshwater Ecosystems, 13(4): 323-330.

Briers, R.A. & Warren, P.H. 2000. Population turnover and habitat dynamics in *Notonecta* (Hemiptera: Notonectidae) metapopulations. Oecologia, 123: 216-222.

Brown, C.A., Thomas, P., Poe, J., French, R.P. & Schloesser, D.W. 1988. Relationships of phytomacrofauna to surface area in naturally occurring macrophyte stands. Journal of the North American Benthological Society, 7: 129-139.

Brown, E.S. 1951. The relation between migration rate and type of habitat in aquatic insects, with special reference to certain species of Corixidae. Proceedings of the Zoological Society, 121: 539-545.

Brown, J.H. 1995. *Macroecology.* University of Chicago Press.

Brown, J.H. & West, 2000, G.B. 2000. *Scaling in biology.* Oxford University Press.

Brualdi, R.A. & Sanderson, J.G. 1999. Nested species subsets, gaps and discrepancy. Oecologia, 119: 256-264.

Buchwalter, D.B., Jenkins, J.J. & Curtis, L.R. 2003. Temperature influences on water permeability and chlorpyrifos uptake in aquatic insects with differing respiratory strategies. Environmental Toxicology and Chemistry, 22(11): 2806-2812.

Bullock, J.M, Moy, I.L., Pywell, R.F., Coulson, S.J., Nolan, A.M. & Caswell, H. 2002. In *Dispersal ecology*, pp 279-302, eds Bullock, J.M., Kenward, R.E. & Hails, R.S. Blackwell Science Ltd, Oxford.

Burgherr, P. & Meyer, E.I. 1997. Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. Archiv fur Hydrobiologie, 139(1): 101-112.

Cáceres, C.E. & Soluk, D.A. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia, 131: 402-408.

Campbell P.G.C. & Stokes P.M. 1985. Acidification and toxicity of metals to aquatic biota. Canadian Journal of Fisheries and Aquatic Science, 42: 2034-2049.

Cao, Y. & Larsen, D.P. 2001. Rare species in multivariate analysis for bioassessment: some consideration. Journal of the North American Benthological Society, 20(1): 144-153.

Cao, Y., Williams, D.D. & Williams, N.E. 1998. How important are rare species in aquatic community ecology and bioassessment? Limnology and Oceanography, 43(7): 1403-1409.

Carr, R. & Nilsson, A.N. 1988. Larval morphology and phenology of the two cryptic species *Agabus chalconatus* and *A. melanocornis* (Coleoptera: Dytiscidae) with notes on other species. Entomologist's Gazette, 39: 313-325.

Casgrain, P. & Legendre, P. 2001. The R package for multidimensional and spatial analysis, version 4.0d5 User's manual. Département biologiques, Université de Montréal. <http://www.fas.umontreal.ca/BIOL/legendre/>

Cattaneo, A., Galanti, G., Gentinetta, S. & Romo, S. 1998. Epiphytic algae and macroinvertebrates on submerged and floating-leaved macrophytes in an Italian lake. Freshwater Biology, 39: 725-740.

Caudill, C.C. 2003. Empirical evidence for nonselective recruitment and a source-sink metapopulation in a mayfly population. Ecology, 84(8): 2119-2132.

Cheruvelil, K.S., Soranno, P.A., Madsen, J.D. & Roberson, M.J. 2002. Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. Journal of the North American Benthological Society, 21(2): 261-277.

Chou, R.Y.M., Ferrington, L.C., Hayford, B.L. & Smith, H.M. 1999. Composition and phenology of Chironomidae (Diptera) from an intermittent stream in Kansas. Archiv fur Hydrobiologie, 147(1): 35-64.

Clarke, M.J. & Barber, K.E. 1987. Mire development from the Devensian Lateglacial to the present at Church Moor, Hampshire. In *Wessex and the Isle of Wight field guide*, pp 22-32, eds Clarke, M.J. & Barber, K.E. Quarternary Research Association, Cambridge.

Clarke, K. R. 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology, 18: 117-143.

Clarke K.R. & Gorley R.N. 2001. PRIMER v5: User manual/tutorial. PRIMER-E, Plymouth, UK.

Clarke, K.R. & Warwick, R.M. 2001. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E Ltd.

Cohen, G.M. & Shurin, J.B. 2003. Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos, 103(3): 603-617.

Collinge, S.K. 2001. Spatial ecology and biological conservation – Introduction. Biological Conservation, 100 (1): 1-2.

Collinson, N.H., Biggs, J., Corfield, A., Hodson, M.J., Walker, D., Whitfield, M. & Williams, P.J. 1995. Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. Biological Conservation, 74: 125-133.

Connor E.F. & McCoy E.D. 1979. The statistics and biology of the species-area relationship. The American Naturalist, 113(6): 791-833.

Coombe, D.E. & Frost, L.C. 1956. The heaths of the Cornish serpentine. Journal of Ecology, 44:226-256.

Cornell, H.V. & Lawton, J.H. 1992. Species interactions local and regional processes, and the limits to the richness of ecological communities: a theoretical perspective. Journal of Animal Ecology, 61:1-12.

Cyr, H. & Downing, J.A. 1988. The abundance of phytophilous invertebrates on different species of submerged macrophytes. Freshwater Biology, 20: 365-374.

Dale, M.R.T., Dixon, P., Fortin, M.J., Legendre, P. Myers, D.E. & Rosenberg, S. 2002. Conceptual and mathematical relationships among methods for spatial analysis. Ecography, 25: 558-577.

Damuth, J. 1981. Population density and body size in mammals. Nature, 290: 699-700.

Davenport, J. Butler, A. & Cheshire, A. 1999. Epifaunal composition and fractal dimension of marine plants in relation to emersion. Journal of the Marine Biological Association, U.K. 79: 351-355.

Davidar, P., Yogananad, K., Ganesh, T. & Devy, S. 2002. Distribution of forest birds and butterflies in the Andaman islands, Bay of Bengal: nested patterns and processes. Ecography, 25: 5-16.

Davy-Bowker, J. 2002. A mark and recapture study of water beetles (Coleoptera: Dytiscidae) in a group of semi-permanent and temporary ponds. Aquatic Ecology, 11: 327-336.

de Bruijn, O., Eysink, A.Th.W. & Hofstra, J. 1994. De Dwergbiezen van Mistre (ZW-Frankrijk). Plantensociologische Kring Nederland. Stratiotes, 9: 52-61.

Delettre, Y.R. & Morvan, N. 2000. Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. Freshwater Biology, 44(3): 399-411.

de Szalay, F.A. & Resh, V.H. 2000. Factors influencing macroinvertebrate colonization of seasonal wetlands: responses to emergent plant cover. Freshwater Biology, 45(3): 295-308.

Diaz-Paniagua, C. 1990. Temporary ponds as breeding sites for amphibians at a locality in southwestern Spain. Herpetological Journal, 1: 447-453.

Downes, B.J., Lake, P.S., Schreiber, E.S.G. & Glaister, A. 1998. Habitat structure and regulation of local species diversity in a stony upland stream. Ecological Monographs, 68(2): 237-257.

Drake, M. Ed. 1999. *Managing ponds for wildlife*. English Nature.

Dvorak, J. & Best, E.P.H. 1982. Macro-invertebrate communities associated with the macrophytes of Lake Vechten: structural and functional relationships. Hydrobiologia, 95: 115-126.

Edwards, B., Duckworth, J. & FitzGerald, R. 2000. Conservation of plant biodiversity on the Lizard: report on the 2nd insitu meeting. Report no. 157, Plantlife.

Edwards, P.J. & Hollis, S. 1982. The distribution of excreta on New Forest grasslands used by cattle, ponies and deer. Journal of Applied Ecology, 19: 953-964.

European Commission. 2003. *Interpretation manual of European Union habitats*, Version EUR25. European Commission DG Environment.

Eyre, M.D., Carr, R., McBlane, R.P. & Foster, G.N. 1992. The effects of varying site-water duration on the distribution of water beetle assemblages, adults and larvae (Coleoptera: Haliplidae, Dytiscidae, Hydrophilidae). Archiv fur Hydrobiologie, 124(3):281-291.

Eysink, A.Th.W & de Bruijn O. 1994. Kruipnieuws van de gradiënt... de Wijdbloeiende rus (*Juncus tenageia*) floreert weer in Twente. Plantensociologische Kring Nederland. Stratiotes, 9:62-103.

Fairbairn, D. & Desranleau, L. 1987. Flight threshold, wing muscle histolysis, and alary polymorphism - correlated traits for dispersal tendency in the Gerridae. Ecological Entomology, 12(1): 13-24.

Feldman, R.S. 2001. Taxonomic and size structures of phytophilous macroinvertebrate communities in Vallisneria and Trapa beds of the Hudson River, New York. Hydrobiologia, 452(1-3): 233-245.

Fernando, C.H. 1958. The colonization of small freshwater habitats by aquatic insects. 1 General discussion, methods and colonization in the aquatic Coleoptera. Ceylon Journal of Science, 1(2): 117-154.

Finke, D.L., & Denno, R.F. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology, 83(3): 643-652.

Fischer, J. & Lindenmayer, D.B. 2002. Treating the nestedness temperature calculator as a "black-box" can lead to false conclusions. Oikos, 99(1): 193-199.

Fitzgerald R., Holyoak D. & James P. 1999. Conservation of plant biodiversity on the Lizard: report on the in-situ meeting held 10-12 May 1999. Report number 132.

Fleishman, E., Betrus, C.J., Blair, R.B., MacNally, R. & Murphy, D.D. 2002. Nestedness analysis and conservation planning: the importance of place, environment and life history across taxonomic groups. Oecologia, 133: 78-89.

Fleishman, E. & MacNally, R. 2002. Topographic determinants of faunal nestedness in Great Basin butterfly assemblages: applications to conservation planning. Conservation Biology, 16(2): 422-429.

Flett, J.S. 1946. *Geology of the Lizard and meneage.* Her Majesty's Stationery Office, London.

Foggo, A., Rundle, S.D. & Bilton, D.T. in prep. Making and breaking the rules? Fluctuating habitat availability drives co-occurrence patterns in coleopteran assemblages.

Foggo, A., Rundle, S.D. & Bilton, D.T. 2003. The net result: evaluating species richness extrapolation techniques for littoral pond invertebrates. Freshwater Biology, 48: 1756-1764.

Foster, G.N. 1996. Wetscore revisited – the value of values and scores of scores. In *Environmental monitoring, surveillance and conservation using invertebrates*, pp 93-96, ed Eyre, M.D. EMS Publications, Newcastle upon Tyne.

Foster, G.N., Foster, A.P., Eyre, M.D. & Bilton, D.T. 1990. Classification of water beetle assemblages in arable fenland and ranking of sites in relation to conservation value. Freshwater Biology, 22: 343-354.

Friday, L.E. 1988. *A key to the adults of British water beetles.* Field Studies Council 7.

Friday L.E. 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. Freshwater Biology. 18: 87-104.

Gamito, S. & Raffaelli, D. 1992. The sensitivity of several ordination methods to sample replication in benthic survey. Journal of Experimental Marine Biology and Ecology, 164: 221-232.

Gaston, K.J. & Blackburn, T.M. 2000. *Pattern and process in macroecology.* Blackwell Science Ltd, Oxford.

Gaston, K.J. & Spicer J.I. 1998. *Biodiversity: an introduction.* Blackwell Science Ltd, Oxford.

Gee, J.H.R., Smith, B.D., Lee, K.M. & Griffiths, S.W. 1997. The ecological basis of freshwater pond management for biodiversity. Aquatic Conservation: Marine and Freshwater Systems, 7: 91-104.

Gee, J.M. & Warwick, R.M. 1994a. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. Marine Ecology Progress Series, 103: 141-150.

Gee, J.M. & Warwick, R.M. 1994b. Body-size distribution in a marine metazoan community and the fractal dimensions of macroalgae. Journal of Experimental Marine Biology and Ecology, 178: 247-259.

Gilbert, J.J. 2002. Endogenous regulation of environmentally induced sexuality in a rotifer: a multigenerational parental effect induced by fertilisation. Freshwater Biology, 47(9): 1633-1641.

Gilbert, J.J. & Schreiber, D.K. 1998. Asexual diapause induced by food limitation in the rotifer *Synchaeta pectinata.* Ecology, 79(4): 1371-1381.

Golini, V.I. & Davies, D.M. 1975. Relative response to colored substrates by ovipositioning blackflies (Diptera: Simuliidae) 1. Oviposition by *Simulium* (*Simulium verecundum*) Stone and Jamnback. Canadian Journal of Zoology, 53: 521-35.

Gotelli, N.J. & Graves, G.R. 1996. *Null models in ecology.* Smithsonian Institution Press, Washington.

Gotelli, N.J. & McCabe, D.J. 2002. Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. Ecology, 83(8): 2091-2096.

Gower, A.M., Myers, G., Kent, M. & Foulkes, M.E. 1994. Relationships between macroinvertebrate communities and environmental variables in metal-contaminated streams in south-west England. Freshwater Biology, 32:199-221.

Grillas, P., Garcia-Murillo, P., Geertz-~Hansen, O., Marbá, N., Montes, C., Duarte, C.M., Ham, L.T. & Grossmann, A. 1993. Submerged macrophyte seed bank in a Mediterranean temporary marsh: abundance and relationship with established vegetation. Oecologia, 94: 1-6.

Grillas, P. & Roché, J. 1997. *Vegetation of temporary marshes, ecology and management.* Conservation of Mediterranean Wetlands – number 8. Tour du Valat, Arles, France.

Hadley, E.A. & Maurer, B.A. 2001. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. Evolutionary Ecology Research, 3: 477-486.

Hairston, N.G., Hansen, A.M. & Schaffner, W.R. 2000. The effect of diapause emergence on the seasonal dynamics of a zooplankton assemblage. Freshwater Biology, 45(2): 133-145.

Hanski, I. 2001. Spatially realistic models of metapopulation dynamics and their implications for ecological, genetic and evolutionary processes. In *Intergrating ecology and evolution in a spatial context*, pp 139-156, eds Silvertown, J. & Antonovics, J. Blackwell Science Ltd, Oxford.

Hanski, I. 1999. *Metapopulation ecology.* Oxford University Press.

Harper, D., Mekotova, J., Hulme, S., White, J. & Hall, J. 1997. Habitat heterogeneity and aquatic invertebrate diversity in floodplain forests. Global Ecology and Biogeography Letters, 6: 275-285.

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

Harte J. & Kinzig A.P. 1997. On the implications of species-area relationships for endemism, spatial turnover and food web patterns. Oikos, 80:417-427.

Hausdorf, B. & Hennig, C. 2003. Nestedness of north-west European land snail ranges as a consequence of differential immigration from Pleistocene glacial refuges. Oecologia, 135: 102-109.

Havel, J.E. & Shurin, J.B. 2004. Mechanisms, effects and scales of dispersal in freshwater zooplankton. Limnology and Oceanography, *in press.*

Heath, D.J. & Whitehead, A. 1992. A survey of pond loss in Essex, South-east England. Aquatic Conservation: Marine and Freshwater Ecosystems, 2: 267-273.

Heck, K.L. & Crowder, L.B. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. In *Habitat structure: the physical arrangement of objects in space*, eds Bell, S.S., McCoy, E.D. & Mushinsky, H.R. Chapman and Hall, London.

Hecnar, S.J. & MCloskey, R.T. 1997. Patterns of nestedness and species association in a pond-dwelling amphibian fauna. Oikos, 80(2): 371-381.

Heegaard, E., Birks, H.H., Gibson, E., Smith, S.J. & Wolfe-Murphy, S. 2001. Species-environmental relationships of aquatic macrophytes in Northern Ireland. Aquatic Botany, 70(3): 175-223.

Hildrew, A.G. 1985. A quantitative study of the life-history of a fairy shrimp (Branchiopoda, Anostraca) in relation to the temporary nature of its habitat, a Kenyan rainpool. Journal of Animal Ecology, 54(1): 99-110.

Hill, M. O. 1993. *TABLEFIT version 0.0, for identification of vegetation types.* Institute of Terrestrial Ecology, Huntingdon.

Hill, M.O. 1979a. TWINSPAN – A FORTRAN Program for Arranging Multivariate Data in an Ordered Two Way Table by Classification of the Individuals and the Attributes. Department of Ecology and Systematics, Cornell University, Ithaca, N.Y.

Hill, M O. 1979b. DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Department of Ecology and Systematics. Cornell University Ithaca, N.Y.

Hills, J.M., Thomason, J.C. & Muhl, J. 1999. Settlement of barnacle larvae is governed by Euclidean and not fractal surface characteristics. Functional Ecology, 13: 868-875.

Hine, A. Ed. 1994. *Woodland pond management*, Proceedings of the annual meeting hosted by the corporation of London. Richmond Publishing, London.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs, 63(4): 447-502.

Honnay, O., Hermy, M. & Coppin, P. 1999. Nested plant communities in deciduous forest fragments: species relaxation or nested habitats? Oikos, 84(1): 119-129.

Honnay, O., Verhaeghe, W. & Hermy, M. 2001. Plant community assembly along dendritic networks of small forest streams. Ecology, 82(6): 1691-1702.

Hopkins, J.J. 1983. *Historical ecology, vegetation and flora of the Lizard District, Cornwall, with particular reference to heathland.* Ph.D. Thesis, University of Bristol.

Hopkins, J.J. 1978. The conservation status of the inland heathlands and other vegetational types and their associated rare and uncommon species at the Lizard District, Cornwall. Report to the Nature Conservancy Council.

Hopkins, J.J. & Buck, A.L. 1995. The Habitats Directive Atlantic biogeographic region. JNCC Report no. 247. <http://www.jncc.gov.uk/Publications/JNCC247/default.htm>

Hovel, K.A. 2003. Habitat fragmentation in marine landscapes: relative effects of habitat cover and configuration on juvenile crab survival in California and North Carolina seagrass beds. Biological Conservation, 110(3): 401-412.

Hughes, M. 1988. *Experimental management of heathland in the Lizard District, Cornwall.* PhD thesis, University of Bristol.

Jackson, D.J. 1950. *Noterus clavicornis* Deeger and *N. capricornis* Herbst (Col. Dytiscidae) in Fife. Entomologists monthly magazine, 86: 39-43.

Jeffries, M.J. 2003. Idiosyncratic relationships between pond invertebrates and environmental, temporal and patch-specific predictors of incidence. Ecography, 26: 311-324.

Jeffries, M.J. 1998. Pond macrophyte assemblages, biodisparity and spatial distribution in the Northumberland coastal plain, UK. Aquatic Conservation: Marine and Freshwater Ecosystems, 8(5): 657-667.

Jeffries, M. 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology, 32: 603-612

Jeffries, M. 1993. Invertebrate colonization of artificial pond weeds of differing fractal dimension. Oikos, 67: 142-148.

Jeffries, M.J. 1989. Measuring Talling's 'element of chance' in pond populations. Freshwater Biology, 21:383-393.

Jenkins, D. G. 1995. Dispersal-limited zooplankton distribution and community composition in new ponds. Hydrobiologia, 313/314: 15-20.

Jenkins, D.G. & Buikema, A.L. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. Ecological Monographs. 68(3): 421-443.

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

Johnson, M.P., Frost, N.J., Mosley, M.W.J., Roberts, M.F. & Hawkins, S.J. 2003. The area-independent effects of habitat complexity on biodiversity vary between regions. Ecology Letters, 6(2): 126-132.

Joint Nature Conservation Committee. 1997. The Habitats Directive: selection of Special Areas of Conservation in the UK, JNCC report no. 270. Eds Brown, A.E., Burn, A.J., Hopkins, J.J. & Way, S.F. Peterborough, UK.

Jones, J.I., Moss, B., Eaton, J.W. & Young, J.O. 2000. Do submerged aquatic plants influence periphyton community composition for the benefit of invertebrate mutualists? Freshwater Biology, 43: 591-604.

Jonsson, B.G. 2001. A null model for randomization tests of nestedness in species assemblages. Oecologia, 127: 309-313.

Keddy, P. & Weiher, E. (1999) The scope and goals of research on assembly rules. In *Ecological assembly rules perspectives, advances, retreats,* pp 130-164, eds Weiher E. & Keddy P. Cambridge University Press, Cambridge.

Keitt, T.H., Bjørnstad, O.N., Dixon, P.M. & Citron-Pousty, S. 2002. Accounting for spatial pattern when modelling organism-environment interactions. Ecography, 25(5): 616-625.

Kholin, S.K. & Nilsson, A.N. 1998. Regional enrichment of predacious water beetles in temporary ponds at opposite east-west ends of the Palearctic. Journal of Biogeography, 25(1): 47-55.

Kiflawi, M., Eitam, A. & Blaustein, L. 2003. The relative impact of local and regional processes on macro-invertebrate species richness in temporary ponds. Journal of Animal Ecology, 72: 447-452.

King, J.L., Simovich, M.A. & Brusca, R.C. 1996. Species richness, endemism and ecology of Crustacea assemblages in North California vernal pools. Hydrobiologia, 328(2): 85-116.

Kirchner, F., Ferdy, J.B., Andalo, C., Colas, B. & Moret, J. 2003. Role of corridors in plant dispersal: an example with the endangered *Ranunculus nodiflorus.* Conservation Biology, 17(2): 401-410.

Kok, C.J. & Vanderveld, D.G. 1994. Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf litter material in alkaline and acid still water. Freshwater Biology, 31(1): 65-75.

Kolasa, J. 1996. Nestedness and discontinuities in species range-size distributions. Trends in Ecology and Evolution, 11(10): 433.

Kornijow, R. Gulati, R.D. & Ozimek, T. 1995. Food preference of freshwater invertebrates - comparing fresh and decomposed angiosperm and filamentous alga. Freshwater Biology, 33(2): 205-212.

Krecker, F.H. 1939. A comparative study of the animal populations of certain submerged plants. Ecology, 20: 553-562.

Kubiëna W. L. 1953. *The soils of Europe.* Thos. Murby, London.

Kurashov, E.A., Telesh, I.V., Panov, V.E., Usenko, N.V. & Rychkova, M.A. 1996. Invertebrate communities associated with macrophytes in Lake Ladoga: effects of environmental factors. Hydrobiologia, 322(1-3): 49-55.

Lahr, J. 1999. Ecotoxicology of organisms adapted to life in temporary freshwater ponds in arid and semi-arid regions. Archives of Environmental Contamination and Toxicology, 32: 50-57.

Lambreck, R.J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology, 11: 849-856.

Landin, J. 1980. Habitats, life histories, migration and dispersal by flight of two water-beetles, *Helophorus brevipalpis* and *H. strigifrons* (Hydrophilidae). Holarctic Ecology, 3: 190-201.

Landin, J. & Stark, E. 1973. On flight thresholds for temperature and wind velocity, 24-hour flight periodicity and migration of the water beetle *Helophorus brevipalpis* Bedel (Col. Hydrophilidae). Zoon, 1: 105-114.

Lang, J.D. 2003. Factors effecting immatures of *Ochlerotatus taeniorhynchus* (Diptera: Culicidae) in San Diego County, California. Journal of Medical Entomology, 40(4): 387-394.

Lawton, J.H. 1986. Surface availability and insect community structure: the effects of architecture and fractal dimension of plants. In *Insects and the plant surface,* pp. 317-332, eds Juniper, B. & Southwood, R. Edward Arnold, London.

Layton, R.J. & Voshell, J.R. 1991. Colonisation of new experimental ponds by benthic macroinvertebrates. Environmental Entomology, 20: 110-117.

Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography, 25: 601-615.

Legendre, P. & Legendre, L. 1998. *Numerical ecology developments in environmental modelling* no. 20. Elsevier, Amsterdam.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology, 73(6): 1943-1967.

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

Lichko, L.E. & Calhoun, A.J.K. 2003. An evaluation of vernal pool creation projects in New England: project documentation from 1991-2000. Environmental Management, 32(1): 141-151.

Lillie, R.A. & Budd, J. 1992. Habitat architecture of *Myriophyllum spicatum* L as an index to habitat quality for fish and macroinvertebrates. Journal of Freshwater Ecology, 7(2): 113-125.

Lockwood, J.L., Powell, R.D., Nott, M.P. & Pimm, S.L. 1997. Assembling ecological communities in time and space. Oikos. 80: 549-553.

Lodge, D.M., Cronin, G., van Donk, E. & Froelich, A.J. 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. In *The structuring role of submerged macrophytes in lakes,* pp. 149-174, eds Jeppesen, E. Søndergaard, M., Søndergaard, M. and Christofferen, K. Springer-Verlag, New York,

Lomolino, M.V. 1996. Investigating causality of nestedness of insular communities: selective immigrations or extinctions? Journal of Biogeography, 23: 699-703.

Loo, S., MacNally, R. & Quinn, G.P. 2002. An experimental examination of colonization as a generator of biotic nestedness. Oecologia, 132: 118-124.

Loreau, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. Ecology Letters, 3: 73-76.

MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography.* Princeton University Press. Princeton.

Maier, G., Hössler, J. & Tessenow,U. 1998. Succession of physical and chemical conditions and of crustacean communities in some small, man made water bodies. International Review of Hydrobiology, 83(5-6): 405-418.

Maitland, P.S. & Morgan, N.C. 1997. *Conservation management of freshwater habitats.* Chapman & Hall, London.

Malloch, A.J.C. 1971. Vegetation of the maritime cliff-tops of the Lizard and Lands End Peninsulas, West Cornwall. New Phytologist, 70:1155-1197.

Malmqvist, B. 1999. Lotic stoneflies (Plecoptera) in northern Sweden: patterns in species richness and assemblage structure. In *Biodiversity in benthic ecology, Proceedings from Nordic benthological meeting, Silkeborg, Denmark 1997*, pp 63-72, eds Friberg, N. & Carl, J.D. National Environmental Research Institute Technical Report No. 266, Silkeborg, Denmark.

Malmqvist, B. & Eriksson, A. 1995. Benthic insects in Swedish lake-outlet streams: patterns of species richness and assemblage structure. Freshwater Biology, 34: 285-296.

Malmqvist, B. & Hoffsten, P. 2000. Macroinvertebrate taxonomic richness, community structure and nestedness in Swedish streams. Archiv fur Hydrobiologie, 737:1-25.

Malmqvist, B., Meisch, C. & Nilsson, A.N. 1997. Distribution patterns of freshwater Ostracoda (Crustacea) in the Canary Islands with regards to habitat use and biogeography. Hydrobiologia, 347: 159-170.

Malmqvist, B., Zhang, Y. & Adler, P.H. 1999. Diversity, distribution and larval habitats of North Swedish blackflies (Diptera: Simuliidae). Freshwater Biology, 42:301-314.

Maltby, L., Calow, P., Cosgrove, M. & Pindar, L. 1987. Adaptation to acidification in aquatic invertebrates; speculation and preliminary observations. Annales de la Societe Royale Zoologique, de Belgique, 117: 105-115.

Manca, M. & Comoli, P. 2000. Biomass estimates of freshwater zooplankton from length-carbon regression equations. Journal of Limnology, 59(1): 15-18.

Mandlebrot, B.B. 1983. *The fractal geometry of nature.* Freeman and co., New York.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research, 27: 209-220.

Marrs, R.H. & Proctor, J. 1978. Chemical and ecological studies of heath plants and soils of the Lizard Peninsula, Cornwall. Journal of Animal Ecology. 66: 417-432.

Mathooko, J.M. & Otieno, C.O. 2002. Does surface textural complexity of woody debris in lotic ecosystems influence their colonization by aquatic invertebrates? Hydrobiologia, 489(1-3): 11-20.

Maurer, M.A. & Brusven, M.A. 1983. Invertebrate abundance and colonization rate in *Fontinalis neo-mexicana* (Bryophyta) in and Idaho Batholith stream, U.S.A. Hydrobiologia, 98: 9-15.

May, R.M. 1972. Will large complex systems be stable? Nature, 238: 413-414.

McCoy, E.D. & Bell, S.S. 1991. Habitat structure: the evolution and diversification of a complex topic. In *Habitat structure: the physical arrangement of objects in space,* eds Bell, S.S., McCoy, E.D. & Mushinsky, H.R. Chapman and Hall, London.

McCune, B. & Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data, Version 4.0. MjM Software Design, Gleneden Beach, Oregon.

McGradySteed, J. & Morin, P.J. 1996. Disturbance and the composition of rain pool microbial communities. Oikos, 76(1): 93-102.

McKee, D., Atkinson, D., Collings, S.E., Eaton, J.W., Gill, A.B., Harvey, I., Hatton, K., Heyes, T., Wilson, D. & Moss, D. 2003. Response of freshwater microcosm communities to nutrients, fish and elevated temperature during winter and summer. Limnology and Oceanography, 48(2): 707-722.

McLachlan, A.J. & Cantrell, M.A. 1980. Survival strategies in tropical rain pools. Oecologia, 47: 344-351.

McLeod, C.R., Yeo, M., Brown, A.E., Burn, A.J., Hopkins, J.J. & Way, S.F. (eds.). 2002. *The Habitats Directive: selection of Special Areas of Conservation in the UK.* 2nd edn. Joint Nature Conservation Committee, Peterborough. <www.jncc.gov.uk/SACselection>

McNett, B.J. & Rypstra, A.L. 2000. Habitat selection in a large orb-weaving spider: vegetation complexity determines site selection and distribution. Ecological Entomology, 25(4): 423-432.

Medland, V.L. & Taylor, B.E. 2001. Strategies of emergence from diapause for cyclopoid copepods in a temporary pond. Archiv fur Hydrobiologie, 150(2): 329-349.

Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. Archiv fur Hydrobiologie, 117(2): 191-203.

Millien-Parra, V. & Loreau, M. 2000. Community composition and size structure of murid rodents in relation to the biogeography of the Japanese archipelago. Ecography, 23: 413-423.

Moksnes, P.O., Pihl, L. & Van Montfrans, J. 1998. Predation on postlarvae and juvenile of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. Marine Ecology Progress Series, 166: 211-225.

Morgan, R.K. 1987. An evaluation of the impact of anthropogenic pressures on woodland regeneration in the New Forest, Hampshire. Journal of Biogeography, 14: 439-450.

Morse, D.R., Lawton, J.H., Dodson, M.M. & Williamson, M.H. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. Nature, 314: 731-733.

Moss, B. 1998. *Ecology of freshwater, man and medium, past and future.* Blackwell Scientific, Oxford.

Moubayed, J. 1998. Le plateau basaltique de Roque-Haute (Hérault, France): principales caractéristiques et qualité globale de la zone humide. Ecologia Mediterranea, 24(2): 185-206.

Nature Conservancy Council. 1989. Guidelines for the selection of biological SSSIs. <http://www.jncc.gov.uk/Publications/sssi/sssi_content.htm>

Nicolet, P. 2002. *The classification and conservation value of wetland plant and macroinvertebrate assemblages in temporary ponds in England and Wales.* PhD thesis, Oxford Brookes University.

Nicolet, P. 2001. Temporary ponds in the UK: a critical biodiversity resource for freshwater plants and animals. In *European temporary ponds: a threatened habitat.* Freshwater Forum, 17: 16-25.

Nilsson, A.N. & Svensson, B.W. 1994. Dytiscid predators and culcid prey in two boreal snowmelt pools differing in temperature and duration. Annales Zoologici Fennici, 31:365-376.

Noon, B.R. & Dale, V.H. 2002. Broad-scale ecological science and its application. In *Applying landscape ecology in biological conservation*, pp 34-52, ed Gutzwiller, K.J. Springer-Verlag, New York.

Oertli, B., Joye, A.J., Castella, E., Juge, R., Cambin, D. & Lachavanne, J. 2002. Does size matter? The relationship between pond area and biodiversity. Biological Conservation, 104: 59-70.

Okamura, B. & Freeland, J.R. 2002. Gene flow and the evolutionary ecology of passively dispersing aquatic invertebrates. In *Dispersal ecology,* pp 194-218, eds Bullock, J.M., Kenward, R.E. & Hails, R.S. Blackwell Science Ltd, Oxford.

Oksanen, J. & P. R. Minchin. 1997. Instability of ordination results under changes in input data order: explanations and remedies. Journal of Vegetation Science, 8: 447-454.

Olivieri, I. 2001. The evolution of seed heteromorphism in a metapopulation: interactions between dispersal and dormancy. In *Intergrating ecology and evolution in a spatial context*, pp 245-270, eds Silvertown, J & Antonovics J. Blackwell Science Ltd, Oxford.

Osborne, J.L., Loxdale, H.D. & Woiwod, I.P. 2002. Monitoring insect dispersal: methods and approaches. In *Dispersal ecology*, pp 24-49, eds Bullock, J.M., Kenward, R.E. & Hails, R.S. Blackwell Science, Oxford.

Pajunen, V.I. & Jansson, A. 1969. Dispersal of the rock pool corixids *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.) (Heteroptera, Corixidae). Annuals Zoologica Fennici, 6: 391-427.

Palmer, M.A., Allan, D.J. & Butman, C.A. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. Trends in Ecology and Evolution, 11(8): 322-326.

Patterson, B.D. & Atmar, W. 2000. Analysing species composition in fragments. In *Isolated vertebrate communities in the tropics,* pp 93-108, ed. Rheinwald G. Bonner Zoologische Monographen 46, Bonn, Germany.

Patterson, B.D. & Atmar. W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. In *Island biogeography of mammals,* pp 65-82, eds Heaney L.R. & Patterson B.D. Academic Press, London.

Plantlife. 2001. Proceedings of the BAP wetland plant species meeting 2001: *Ranunculus tripartitus, Pilularia globulifera, Lycopodiella inundata.* Unpublished Report.

Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society, 16(2): 391-409.

Pond Action. 1994. *The Oxfordshire pond survey vol. 1 and 2.* Pond Action, Oxford.

Powell, A. 2001. Introduction. In *European temporary ponds: a threatened habitat.* Freshwater Forum 17: 5-7.

Preston, F.W. 1960. Time and space and the variation of species. Ecology, 29: 611-627.

Proctor, J. 1971. The plant ecology of serpentine II. Plant responses to serpentine soils. Journal of Ecology, 59: 397-410.

Putman, R.J., Pratt, R.M., Erkins, J.R. & Edwards, P.J. 1987. Food and feeding behaviour of cattle and ponies in the New Forest, Hampshire. Journal of Applied Ecology, 24: 369-380.

Rackham, O. 1986. *The history of the countryside.* Weidenfeld and Nicholson

Raffaelli, D., Hall, S., Emes, C. & Manly, B. 2000. Constraints on body size distributions: an experimental approach using a small-scale system. Oecologia, 122: 389-398.

Ramsay, P.M., Rundle, S.D., Attrill, M.J., Uttley, M.G., Williams, P.S. & Abada, A. 1997. A rapid method for estimating biomass size spectra of benthic metazoan communities. Canadian Journal of Fisheries and Aquatic Sciences, 54: 1716-1724.

Rasband, W.S. 1997-2003. ImageJ, National Institutes of Health, Bethesda, Maryland. <http://rsb.info.nih.gov/ij/>

Ratcliffe, D. ed 1977. *A nature conservation review.* Cambridge University Press.

Reich, P. & Downes, B.J. 2003. Experimental evidence for physical cues involved in oviposition site selection of lotic hydrobiosid caddis flies. Oecologia, 136(3): 465-475.

Richardson, J.S. & Jackson, M.J. 2002. Aquatic Invertebrates. In *Handbook of ecological restoration, Volume 1: principles of restoration,* pp 300-410, eds Perrow, M.R. & Davy, A.J. Cambridge University Press.

Ricciardi, A. & Ramussen, J.B. 1999. Extinction rates of North American freshwater fauna. Conservation Biology, 13:1220-1222.

Ricklefs, R.E. & Schluter, D. 1993. Species diversity: regional and historical influences. In *Species diversity in ecological communities*, eds Ricklefs, R.E. & Schluter, D. University of Chicago Press.

Rodwell, J.S. 2000. *British plant communities*. Volume 5. *Maritime communities and vegetation of open habitats*. Cambridge University Press.

Rodwell, J.S. 1995. *British plant communities*. Volume 4. *Aquatic communities, swamps and tall-herb fens*. Cambridge University Press.

Rodwell, J.S. 1994. A short rush through the British Nanocyperion. Plantensociologische Kring Nederland. Stratiotes. 9: 107-107.

Rooke, J.B. 1986. Macroinvertebrates associated with macrophytes and plastic imitations in the Eramosa River, Ontario, Canada. Archiv fur Hydrobiologie. 106(3): 307-325.

Rooke, J.B. 1984. The invertebrate fauna of four macrophytes in a lotic system. Freshwater Biology, 14: 507-513.

Rundle, S.D., Bilton, D.T., Foggo, A. & Choisel, V. 2002. Are distribution patterns linked to dispersal mechanism? An investigation using pond invertebrate assemblages. Freshwater Biology, 47(9): 1571-1581.

Rundle S.D., Spicer J.I., Coleman R.A., Vosper J. & Soane J. 2004. Environmental calcium modifies induced defences in snails. Proceedings of the Royal Society of London Series B Biological Sciences, 271: 67-70, supplement 3.

Sanderson, N. 1998. *Description and evaluation of New Forest grasslands and mires.* Consultancy report for English Nature.

Scheffer, M., Achterberg, A.A. & Beltman, B. 1984. Distribution of macro-invertebrates in a ditch in relation to the vegetation. Freshwater Biology, 14: 367-370.

Schmid, P.E. 2000. Fractal properties of habitat and patch structure in benthic ecosystems. Advances in Ecological Research, 30: 339-401.

Schmid, P.E., Tokeshi, M. & Schmid-Araya, J.M. 2002. Scaling in stream communities. Proceedings of the. Royal Society London Series B, 269: 2587-2594.

Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important?* Cambridge University Press.

Schneider, D.W. 1997. Predation and food web structure along a habitat gradient. Oecologia, 110: 567-575.

Schneider, D.W. & Frost, T.M. 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society, 15(1):64-86.

Schwind, R. 1995. Spectral regions in which aquatic insects see reflected polarised light. Journal of Comparative Physiology, 177A: 439.

Schwind, R. 1991. Polarized vision in water insects and insects living on moist substrate. Journal of Comparative Physiology, 169A: 531.

Seelbach, P.W., Wiley, M.J., Soranno, P.A. & Bremigan, M.T. 2002. Aquatic conservation planning: using landscape maps to predict ecological reference conditions for specific waters. In *Applying landscape ecology in biological conservation*, pp 454-478, ed. Gutzwiller, K.J. Springer-Verlag, New York.

Semlitsch, R.D. 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management, 64(3): 615-631.

Serrano, L. & Toja, J. 1995. Limnological description of four temporary ponds in the Donana national Park (SW, Spain). Archiv fur Hydrobiologie, 133(4): 497-516.

Sheldon, A.L. 1984. Colonization dynamics of aquatic insects. In *Ecology of aquatic insects,* pp 401-429, eds Rosenberg, D.M. & Resh V.H. Praeger, New York.

Sheldon, R.W., Prakash, A. & Sutcliffe, W.H. 1972. The size distribution of particles in the ocean. Limnology and Oceanography, 17: 327-340.

Shorrocks, B., Marsters, J., Ward, I. & Evenett, P.J. 1991. The fractal dimensions of lichens and the distribution of arthropod body lengths. Functional Ecology, 5(4): 457-460.

Shorrocks, B. & Rosewell, J. 1987. Spatial patchiness and community structure: coexistance and guild size in drosophilids on ephemeral resources. In *Organisation of communities past and present,* eds Gee J.H.R. & Giller P.S. Blackwell Science Ltd, Oxford.

Shurin, J.B. 2001. Interactive effects of predation and dispersal on zooplankton communities. Ecology, 82(12): 3404-3416.

Shurin, J.B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology, 81(11): 3074-3086.

Shurin, J.B. & Allen, E.G. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. The American Naturalist, 158(6): 624-637.

Shurin, J.B., Havel, J.E., Leibold, M.A. & Pinel-Alloul, B. 2000. Local and regional zooplankton species richness: a scale-independent test for saturation. Ecology, 81(11): 3062-3073.

Simon, R.H. & Simon, R.M. 1995. Mid Atlantic salt march shorelines: mathematical commonalities. Estuaries, 18: 199-206.

Simovia, M.A. & Hathaway, S.A. 1997. Diversified bet-hedging as a reproductive strategy of some ephemeral pool anostracans (Branchiopoda). Journal of Crustacean Biology, 17(1): 38-44.

Sokal, R.R. & Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research.* Freeman & co., New York.

Somerfield, P.J., Clarke, K.R. & Olsgard, F. 2002. A comparison of the power of categorical and correlational tests applied to community ecology data from gradient studies. Journal of Animal Ecology, 71(4): 581-593.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology, 46: 337-365.

Spencer, M., Blaunstein, L., Schwartz, S.S. & Cohen, J. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. Ecology Letters, 2: 157-166.

Spencer, M., Schwartz, S.S. & Blaunstein, L. 2002. Are there fine-scale spatial patterns in communitiy similarity among temporary freshwater pools? Global Ecology and Biogeography, 11: 71-78.

Sprules, W.G. & Munawar, M. 1986. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. Canadian Journal of Fisheries and Aquatic Science, 43: 1789-1794.

Stace, C. 1997. *New flora of the British Isles.* 2nd Ed. Cambridge University Press.

Staines, S.J. 1984. *Soils in Cornwall II* (Sheets SW61, 62, 71 & 72; The Lizard). Lawes Agricultural Trust (Soil Survey of England and Wales), Harpenden.

Stewart, N.F., FitzGerald, R., Lansdown, R.V. & Jermy, A.C. 2000. The conservation of pillwort *Pilularia globulifera* in England, Interim report no. 2. Report number 151, Plantlife.

Stewart, A.J.A. & Hutchings, M.J. 1996. Conservation of populations. In *Conservation biology*, pp 122-140, ed. Spellerberg, I.F. Longman Group Ltd, Harlow.

Sugihara, G. & May, R.M. 1990. Applications of fractals in ecology. Trends in Ecology and Evolution, 5(3): 70-86.

Summerville, K.S., Veech, J.A. & Crist, T.O. 2002. Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? Oikos, 97: 195-204.

Svensson, B.W. 1999. Environmental heterogeneity in space and time: patch use, recruitment and dynamics of a rock pool population of a gyrinid beetle. Oikos, 84: 227-238.

Svensson, B.W. 1998. Local dispersal and its life-history consequences in a rock pool population of a gyrinid beetle. Oikos, 82: 111-122.

Svensson, B.W. 1992. Changes in occupancy, niche breadth and abundance of three *Gyrinus* species as their respective range limits are approached. Oikos, 63: 147-156.

Swan, M.J.S. & Oldham, R.S. 1989. *Amphibian communities, final report.* Nature Conservancy Council, Peterborough.

Talling, J.F. 1951. The element of chance in pond populations. The Naturalist 157-171.

Tausch, R. J., Charlet, D. A., Weixelman, D.A. &. Zamudio, D.C. 1995. Patterns of ordination and classification instability resulting from changes in input data order. Journal of Vegetation Science, 6: 897-902.

ter Braak, C.J.F. & Šmilauer, P. 1998. CANOCO reference manual and user's guide to CANOCO Windows, software for Canonical Community Ordination version 4. Microcomputer Power, Ithaca.

Tokesi, M. 1999. *Species co-existence: ecological and evolutionary perspectives.* Blackwell Science Ltd, Oxford.

Townsend, C.R., Begon, M. & Harper, J.L. 2000. *Essentials of ecology.* Blackwell Science Ltd, Oxford.

Underwood, A.J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance.* Cambridge University Press.

Velasco, M.L., Suárez, M.L. & Vidal-Abarca, M.R. 1998. Factores que determinan la colonización de insectos acuáticos en pequeños estanques. Oecologia Aquatica, 11: 87-99.

Vepsäläinen, K. 1978. Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In *Evolution of Insect Migration and Diapause,* pp 218-253, ed. Dingle, H. Springer-Verlag, New York.

Wallace, I.D. Wallace, B. &. Philipson, G.N. 2003. *Key to the case-bearing caddis larvae of Britain and Ireland.* Freshwater Biological Association, Scientific Publication 61, Ambleside, UK.

Ward, D. & Blaunstein, L. 1994. The overriding influence of flash floods on species-area curves in ephemeral Negev Desert pools: a consideration of the value of island biogeography theory. Journal of Biogeography, 21: 595-603.

Weeda, E.J. 1994. Plantensociologie 'avant la lettre'. Plantensociologische Kring Nederland. Stratiotes. 9: 3-21.

Weiher, E. & Boylen, C.W. 1994. Patterns and predictions of α and β diversity of aquatic plants in Adirondack (New York) lakes. Canadian Journal of Botany, 72: 1797-1804.

Welch, P.S. 1935. *Limnology.* McGraw-Hill, New York.

Wellborn, G.A., Skelly, D.K. & Werner, E.E. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecological Systematics, 27: 337-363.

Whitten, A.J. 1990. *Recovery.* A proposed programme for Britain's protected species. Nature Conservancy Council CSD report no. 1089.

Wiggins, G.B., MacKay, R.J. & Smith, I.M. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv fur Hydrobiologie 58: 97-206.

Wilbur, H.M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology, 78(8): 2279-2302.

Williams, A. 1992. *A preliminary investigation and collation of background information on the hydrology of the Lizard Peninsula.* Report for English Nature.

Williams, C.B. 1943. Area and number of species. Nature, 152: 264-267.

Williams, D.D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of the American Benthological Society, 15(4): 634-650.

Williams, D.D. 1987. *The ecology of temporary waters.* Chapman & Hall, London.

Williams, P., Biggs, J., Fox, G., Nicolet, P. & Whitfield, M. 2001. History, origins and importance of temporary ponds. In *European temporary ponds: a threatened habitat.* Freshwater Forum, 17: 7-15.

Williams, P., Biggs, J., Dodds, L., Whitfield, M., Corfield, A. & Fox, G. 1996. Biological techniques of still water quality assessment, Phase 1: scoping study. Environment Agency R & D report.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P. & Sear, D. 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape. Biological Conservation, 115(2): 329-341.

Willamson, M. 2002. Overview and synthesis: the tale of the tail. In *Dispersal ecology,* pp 431-443, eds Bullock, J.M., Kenward, R.E. & Hails, R.S. Blackwell Science Ltd, Oxford.

Williamson, M.H. & Lawton, J.H. 1991. Fractal geometry of ecological habitats. In *Habitat structure: the physical arrangement of objects in space,* eds Bell, S.S., McCoy, E.D. & Mushinsky, H.R. Chapman and Hall, London.

Wilson, J.B. 1999. Assembly rules in plant communities. In *Ecological assembly rules perspectives, advances, retreats,* pp 130-164, eds Weiher E. & Keddy P. Cambridge University Press, Cambridge.

Wilson, R.J. & Thomas, C.D. 2002. Dispersal and the spatial dynamics of butterfly populations. In *Dispersal ecology,* pp 257-278, eds Bullock, J.M., Kenward, R.E. & Hails, R.S. Blackwell Science Ltd, Oxford.

Wissinger, S.A., Brown, W.S. & Jannot, J.E. 2003. *Ochlerotatus taeniorhynchus*, factors affecting immatures, San Diego County. Freshwater Biology, 48(2): 255-270.

Wood, P.J., Greenwood, M.T. & Agnew M.D. 2003. Pond biodiversity and habitat loss in the UK. Area, 35(2): 206-216.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. & Atmar, W. 1998. A comparative analysis of nested subset patterns of species composition. Oecologia, 113: 1-20.

Wright, J.F., Moss, D., Clarke, R.T. & Furse, M.T. 1997. Biological assessment of river quality using the new version of RIVPACS (RIVPACS III). In *Freshwater quality: defining the indefinable?* pp102-107, eds Boon, P.J. & Howell, D.L. Edinburgh: Scottish Natural Heritage Press.

Wyda, J.C., Deegan, L.A., Hughes, J.E. & Weaver, M.J. 2002. The response of fishes to submerged aquatic vegetation complexity in two ecoregions of the mid-Atlantic bight: Buzzards Bay and Chesapeake Bay. Estuaries, 25(1): 86-100.

Young, E.C. 1965. Flight muscle polymorphism in British Corixidae: ecological observations. Journal of Animal Ecology, 34: 353-390.