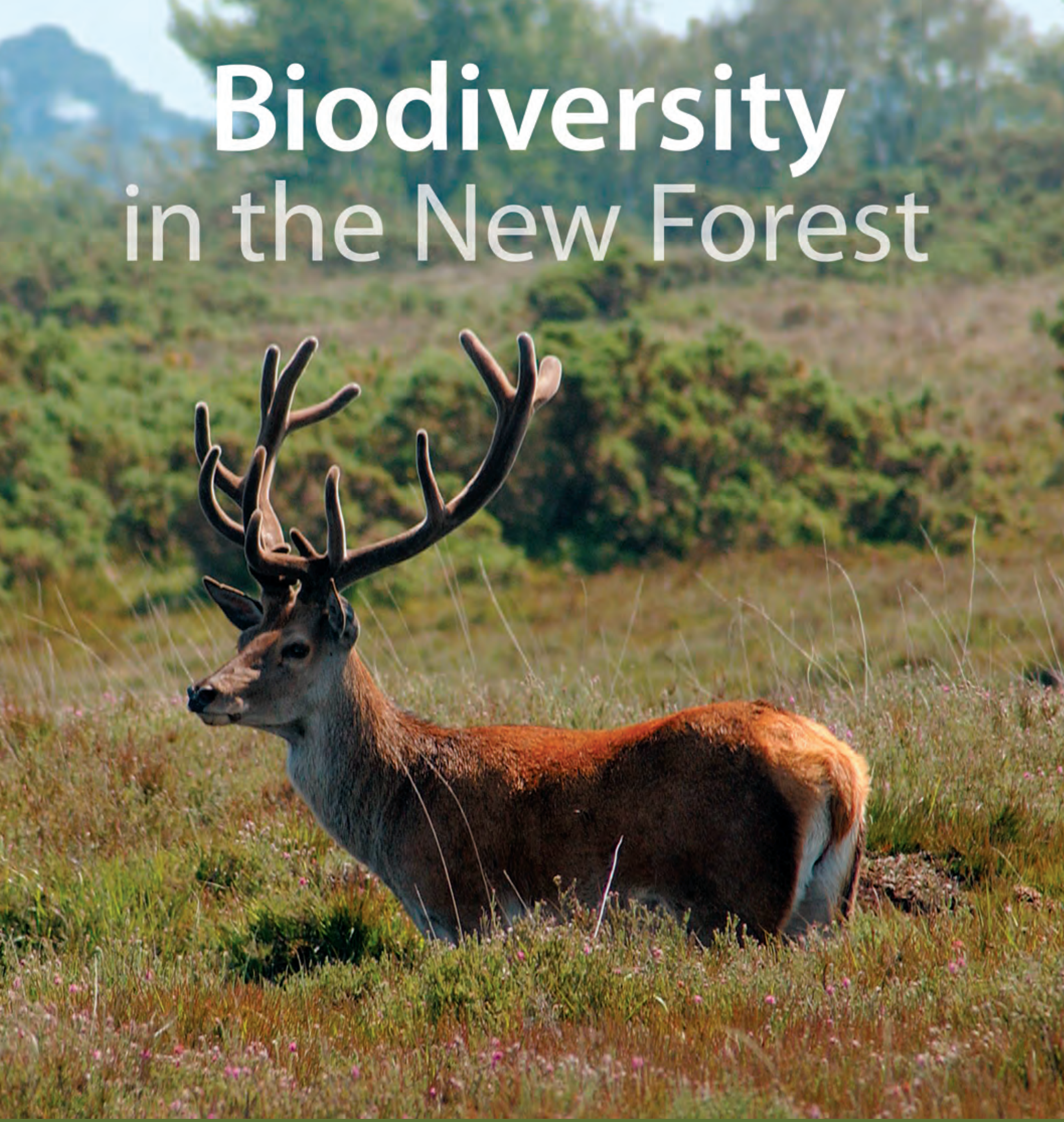
Biodiversity in the New Forest



Edited by Adrian C. Newton

Biodiversity in the New Forest

Edited by
Adrian C. Newton

Centre for Conservation Ecology and Environmental Change,
School of Conservation Sciences,
Bournemouth University,
Poole,
Dorset,
United Kingdom

piscespublications

Newbury, Berkshire

Dedicated to the memory of
Muriel Eliza Newton (1929–2009),
who loved the New Forest,
especially the donkeys.

First published 2010.

British-Library-in-Publication Data
A catalogue record for this book is available from the British Library.

ISBN 978-1-874357-42-1

Designed and published for Bournemouth University by Pisces Publications

Pisces Publications is the imprint of NatureBureau, 36 Kingfisher Court, Hambridge Road,
Newbury, Berkshire RG14 5SJ
www.naturebureau.co.uk

Printed by Information Press, Oxford

Cover photographs
Front cover: Red deer *Cervus elaphus* (Isobel Cameron / Forest Life picture library, Forestry Commission); noble chafer *Gnorimus nobilis* (Matt Smith); Dartford warbler *Sylvia undata* (David Kjaer); wild gladiolus *Gladiolus illyricus* (Adrian Newton)
Back cover: Wood Crates (Adrian Newton)

The maps in this book are for illustrative purposes only, and do not represent the legal definition of National Park boundaries or any other feature

Contents

Contributors

Keith Alexander, 59 Sweetbrier Lane, Heavitree, Exeter, Devon EX1 3AQ.

Patrick D. Armitage, Freshwater Biological Association, Moor House, Field Station, Garrigill, Alston, Cumberland DL12 0HQ.

Andrew J. Barker, 13 Ashdown Close, Chandler's Ford, Eastleigh, Hampshire SO53 5QF.

Ian Barker, New Forest National Park Authority, South Efford House, Milford Road, Everton, Lymington, Hampshire SO41 0JD.

Samantha Broadmeadow, Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH.

Libby Burke, Forestry Commission, The Queen's House, Lyndhurst, Hampshire SO43 7NH.

Elena Cantarello, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Clive Chatters, c/o Hampshire and Isle of Wight Wildlife Trust, Beechcroft, Vicarage Lane, Curdridge, Hampshire SO32 2DP.

Greg Conway, British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU.

John Davy-Bowker, Centre for Ecology and Hydrology, c/o Freshwater Biological Association, East Stoke, Wareham, Dorset BH20 6BB.

Sarah Douglas, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Maxine Elliott, Environment Agency, Solent and South Downs Office, Colvedene Court, Colden Common, Hampshire SO21 1WP.

Naomi C. Ewald, Department of Biology and Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG.

David Green, Butterfly Conservation, The Cottage, West Blagdon, Cranborne, Dorset BH21 5RY.

Rachel Green, Natural England, 1 Southampton Road, Lyndhurst, Hampshire SO43 7BU.

Sue E. Hartley, Department of Biology and Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG.

Timothy Holzer, Environment Agency, Solent and South Downs Office, Colvedene Court, Colden Common, Hampshire SO21 1WP.

John G. Jones, Centre for Environmental Sciences, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton, Hampshire SO17 1BJ.

Terry Langford, Centre for Environmental Sciences, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton, Hampshire SO17 1BJ.

Colleen Mainstone, Hampshire Bat Group, 42 Saxon Way, Halterworth, Romsey, Hampshire SO51 5QY.

Gillian Myers, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Adrian C. Newton, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

Martin Noble, New Forest Ecological Consultants, Keepers Cottage, Holmsley, Burley, Ringwood, Hampshire BH24 4HY.

Andrew Page, Forestry Commission, The Queen's House, Lyndhurst, Hampshire SO43 7NH.

Bryan J. Pinchen, 7 Brookland Close, Pennington, Lymington, Hampshire SO41 8JE.

Rory Putman, Keil House, Ardgour by Fort William, Inverness-shire PH33 7AH.

Martin Rand, South Hampshire Vice-county Recorder, Botanical Society of the British Isles, email: vc11recorder@hantsplants.org.uk.

Neil A. Sanderson, Botanical Survey and Assessment, 3 Green Close, Woodlands, Southampton, Hampshire SO40 7HU.

Peter Shaw, Centre for Environmental Sciences, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton, Hampshire SO17 1BJ.

Jane Smith, Forestry Commission, The Queen's House, Lyndhurst, Hampshire SO43 7NH.

Rod Stern, British Bryological Society, 15 Selham Close, Chichester, West Sussex PO19 5BZ.

Alan J. A. Stewart, Department of Biology & Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG.

Natalia Tejedor, Centre for Conservation Ecology and Environmental Change, School of Conservation Sciences, Bournemouth University, Poole, Dorset BH12 5BB.

David J. Thompson, School of Biological Sciences, University of Liverpool, Crown Street, Liverpool, Lancashire L69 7ZB.

Stephen Trotter, New Forest National Park Authority, South Efford House, Milford Road, Everton, Lymington, Hampshire SO41 0JD.

Lena K. Ward, 53 Miles Avenue, Sandford, Wareham, Dorset BH20 7AS.

Phillip C. Watts, School of Biological Sciences, University of Liverpool, Crown Street, Liverpool, Lancashire L69 7ZB.

Diana Westerhoff, Natural England, 1 Southampton Road, Lyndhurst, Hampshire SO43 7BU.

Simon Wotton, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL

16 A pooled history of temporary pond research in the New Forest

Naomi Ewald, Sue Hartley and Alan Stewart

Introduction

The ponds of the New Forest are as much a part of its landscape as the heathland, woodland, grassland and riverine habitats so often used to describe this area of lowland Britain. In fact ponds are scattered across this entire landscape, occurring in every vegetation community and on every type of geology and yet in spite of this, they are less well studied than other habitats (Williams *et al*. 2001, Wood *et al*. 2003). Temporary ponds are a particularly important part of the mosaic of wetlands, containing many rare species of interest to conservation (Bratton 1990, Bratton 1991, Chatters 1996, Collinson *et al*. 1995, Tubbs 1997). This review brings together information from both published and unpublished sources on the current distribution and status of temporary ponds in the New Forest and information on some of the threatened taxa associated with this habitat type.

Temporary ponds in the New Forest

For the purposes of this review, temporary ponds are defined as bodies of water of man-made or natural origin, between 1 m^2 and 2 ha in area, which usually hold water for at least four months of the year and/or which have a fauna capable of withstanding a recurrent dry phase. This definition is constructed from those given in the National Pond Survey methodology (Pond Action 1998), the DETR Lowland Pond Survey (Williams *et al*. 1998), the National Pond Survey (Pond Action 1998), Williams (1997) and Nicolet *et al*. (2004). The definition takes into account the small scale of many of the temporary ponds in the New Forest and the short hydroperiod that many of them experience, for example Bolton's Bench, which still retains specialist species adapted to a recurrent dry phase, even though it may only hold water for as little as one month per year (Ewald pers. obs.).

Temporary ponds are also characterised by the predictable and recurrent nature of the dry phase (Williams 1987, 1997, 2006; Williams *et al*. 2001). In the New Forest, temporary ponds normally fill in the autumn any time from the beginning of September to the end of October. They remain full throughout the winter, usually peaking in size during the spring and then drying down again in early summer. They can therefore be termed temporary autumnal pools (Wiggins 1973), differentiating them from vernal spring pools that are primarily filled from snow melt. In exceptional years (such as 1954, 1977, 1992 and 2007), they may fill during the summer months, holding water for a few weeks and then drying once more before the autumn fill (Ewald 2008; Hall 1961; Hampshire and Isle of Wight Wildlife Trust unpublished). This pattern of wetting and drying halts wetland succession (Williams *et al*. 2001), so that the pond may remain a feature of the landscape for hundreds or even thousands of years (Fryer 1966, Gray and Taylor 1988).

Species within temporary ponds are specially adapted to withstand a recurrent dry phase (Williams 1997, 2006). Wiggins *et al*. (1980) divided species in vernal pools into four major types depending on the strategy used to survive the dry phase and the timing of their appearance in the pond. The same principles can be used to define species in autumnal pools in the New Forest. The first group can be described as year-round residents of the pond. When the pond first fills, species that have survived as partly developed cysts or eggs (e.g. the tadpole shrimp *Triops cancriformis* (Fox 1949), fairy shrimp *Chirocephalus diaphanus* (Hall 1953), an ostracod *Heterocypris incongruens* (Henderson 1990)), as adults buried in the mud (e.g. the mud snail *Omphiscola glabra* (Boycott 1936)) or by finding refuge in damp leaf litter (e.g. water louse *Asellus spp.* (Wiggins *et al*. 1980)) become active and breed.

The second group includes those mobile species that appear in the pond at some time during the autumn (e.g. the common darter dragonfly *Sympetrum striolatum* and diving beetles *Agabus* spp.; Wiggins *et al*. 1980). They will leave the water before the pond dries down in the summer and spend the dry spell as winged adults, eggs or larvae, either within or away from the pond basin. One specialist species of caddis fly, *Glyphotaelius pellucidus*, is an active airborne adult during the spring, laying eggs in a gelatinous mass on tree leaves above the pond. These are then shed into the pond in the autumn, where rehydration triggers hatching (I. Wallace, pers. comm.).

The third group of species arrives in the spring (e.g. the palmate newt *Lissotriton helveticus* (Buckley 2001), the mayfly *Cloeon dipterum* and true fly species (Wiggins *et al*. 1980)), taking advantage of the warm, nutrient-rich waters found in temporary ponds to complete their development rapidly before the pond dries out. Like the previous group these spring recruits are mobile, but do not require permanent water to survive the dry spell, spending the summer and winter as eggs, larvae or adults, within or away from the pond basin.

The final group is a tranche of mostly predatory species, which take advantage of the fish-free water to breed, rear young and feed (e.g. greater water boatman *Notonecta* spp., whirligig beetles *Gyrinus* spp. and diving beetles *Acilius* spp. (Wiggins *et al*. 1980)). These species are not adapted to withstand a recurrent dry phase and will return to more permanent waters when the pond dries out.

Table 43
Variation in environmental variables between New Forest temporary ponds

Variable		Examples of pond locations
Pond depth	Min 6 cm Max 100 cm	Temporary pools near Rush Bush Bignell Wood
Pond area	Min 12 m^2 Max 1,500 m^2	Ponds along the B3078 road Fletchers Green
pH	Min 3.6 Max 7.8	Pools within valley mires Gorley
Conductivity	Min 19 µS Max 465 µS	Pools near Star Pole Pond Spur Lake Lawn

There are an estimated 570 ponds within the New Forest SSSI boundary (Ewald 2008). Over 75% of these are temporary, putting the New Forest well above the national average of 40% of ponds in the wider countryside being temporary (Biggs *et al*. 2005, Nicolet *et al*. 2004). This is despite extensive drainage in the New Forest during the 1920s (Tubbs 1986). Pond creation has been via natural and man-made processes, including digging for minerals (clays, sands and gravels), stock ponds, floodplain ponds, oxbow lakes, uprooted trees, depressions created by grazing animals and those created during war and forestry operations. Over 170 species of macro-invertebrate have been recoded from temporary ponds in the New Forest to date (Ewald 2008, McAbendroth 2004, Nicolet 2002), with one in three ponds surveyed containing one or more Red Data Book species (Ewald 2008). Again this is higher than the national average (one in four) determined by Nicolet *et al*. (2004).

The temporary ponds across the New Forest vary considerably in terms of environmental variables. Khalaf and MacDonald (1975) found marked variation between five temporary ponds, over a period of 24 months, in terms of water volume, pH, conductivity and dissolved oxygen levels. A survey (2004) of 72 New Forest temporary ponds (Ewald 2008) also found extremes, between the maximum and minimum values for a range of environmental variables (examples of which are given in Table 43). Despite this variation, it is possible to identify groups of ponds that have similar environmental conditions and therefore contain similar macro-invertebrate and floral assemblages, which may be helpful for developing conservation strategies.

Classification of temporary ponds

Attempts have been made to classify temporary ponds in the New Forest into general types. Sanderson (2001) made a provisional classification based on wetland plants and their corresponding NVC communities (Table 44).

Ewald (2008) classified 72 New Forest ponds into 11 types according to their macro-invertebrate composition using TWINSPAN. This procedure split ponds into subgroups based on the abundance of species on a semi-quantative scale. Indicator species identified at each division can help in the description of the pond group. Thus, ponds in Group 4 contained fairy shrimp *Chirocephalus diaphanus* (a characteristic temporary pond species; Bratton 1991), those in groups 2 and 3 a New Forest specialist water beetle *Graptodytes flavipes* (Friday 1988) and those in group 9 and 10 *Omphiscola glabra,* a snail capable of withstanding desiccation that is rare elsewhere in the UK (Bratton 1991).

Shade, turbidity, pH and the amount of poaching explained 23.4% of the variation in the macro-invertebrate community composition of ponds (constrained ordination; $F = 1.636$, $P = 0.002$) (Ewald 2008). Ponds on the base rich clays of the Headon beds had the highest species richness and diversity, compared to the base poor clays and sands found elsewhere in the Forest. The grazed lawns and heaths also had high species richness and diversity. One of the reasons for this diversity, compared to other grassland

Table 44
Floral assemblages of New Forest temporary ponds (Sanderson 2001).

Pond Group	Community	NVC Equivalent
1	*Eleocharis multicaulis-Molinia caerulea* community	Covered by the M30: *Hydrocotylo-baldellion* of seasonally-inundated habitats
2	*Apium inundatum-Eleogiton fluitans-Pilularia globulifera* community	M30 above, but where less acidic; OV35: *Lythrum portula-Ranunculus flammula*, and where some water movement exists; M29 *Hypericum elodes- Potamogeton polygonifolius* soakaway
3	*Agrostis stolonifera-Alopecurus geniculatus-Persicaria* spp. community	Near neutral pH in neutral lawns (MG6b), or in depressions in parched acid grassland (U1), comparable to OV31: *Rorippa palustris- Gnaphalium uliginosa* community, with variation through to, OV30: *Bidens tripartita-Persicaria hydropiper*
4	*Glyceria fluitans* community	S22: *Glyceria fluitans* Water Margin Vegetation
5	Pool edge assemblages: a number of specialist species in a zone with *Juncus bufonius*, including the nationally scarce species *Illecebrum verticillatum*, and *Cicendia filiformis*, often in association with *Radiola linoides* and *Anagallis minima*	–

and heathland sites, is the input of nutrients to these ponds from dung (as highlighted by Bratton (1990), Chatters (1996) and Tubbs (1997)).

These analyses confirmed that ponds with a similar set of environmental variables shared a similar macro-invertebrate community. The composition of the wetland plant community from these 72 ponds was analysed using the same classification procedure. A greater number of distinct pond types could be identified using invertebrate, rather than the floral communities, suggesting that macro-invertebrates are responding to more subtle differences in environmental conditions between ponds (Pond Conservation and Environment Agency 2002). Therefore, whilst macrophytes may enable a coarse classification of temporary pond habitats, macro-invertebrate community composition offers a more detailed description upon which to base management decisions.

The National Pond Survey methodology and the Predictive Score for Multimetrics (PSYM) developed by Ponds Conservation, provide a standardised detailed methodology upon which to assess both the flora and macro-invertebrate composition of temporary pond communities. However, a provisional classification, such as given in Table 45, may provide enough

Table 45
Provisional classification of temporary ponds in the New Forest based on macro-invertebrate composition (Ewald 2008).

Pond Group	Habitat / Geology	pH	Shade/ Conductivity/ Turbidity	Area/ Depth/ Isolation	Hydroperiod	Grazing	Characteristic species
1	Grassland habitats on gravels.	Neutral	Open habitat. High due to nutrient input from dung.	Very small surface area, very shallow. Isolated.	Very short, less than 5 months of the year.	Heavily grazed but not heavily poached.	Lowest species diversity. Ponds in this group may contain *Chirocephalus diaphanus*, but the occurrence of this species in any one year will be variable
2	Heathland sites on clays.	Low	Open habitat.	Relatively large and often in a complex with other ponds.	Relatively short hydroperiod.	–	Higher invertebrate diversity than group 1. *Hydroporus gyllenhalii*, a species tolerant of low pH[1]. *Graptodytes flavipes*, a New Forest specialist water beetle[2]. *Agabus nebulosus*, a species tolerant of temporary pond conditions[3]. *Limnephilus auricula*, a widespread and common caddis of temporary pools[4].
3	Heathland sites on sands.	Low	Open habitat. Low in conductivity.	Small in area and isolated.	–	Lightly grazed.	Sanderson's type 1 floral assemblage. Macro-invertebrate species diversity is low with a similar assemblage to pond type 2; *Hydroporus gyllenhalii* and *Graptodytes flavipes* still present, but joined by few other species, and only those which are mobile e.g. *Sigara nigrolineata*[5].
4	Pre-dominantly grassland but some heathland overlaying base-poor clays, sands and gravels.	–	Open habitat.	Relatively large but not very deep.	Moderate, neither very long nor very short.	Heavily grazed but not heavily poached.	Sanderson's type 2 floral assemblage. Highest macro-invertebrate species diversity; characterised by temporary pond species when the pond first fills, e.g. *Chirocephalus diaphanus* and in suitable years *Triops cancriformis*[6]. Colonised by more mobile species as the hydroperiod continues into the spring e.g. *Hesperocorixa sahlbergi*[5].
5	Heathland and grassland, overlaying a mixture of base-rich clays and gravels.	Near neutral	Open habitat. Turbid	Largest surface area.	Relatively long hydroperiod.	Heavily grazed and poached.	Relatively low macro-invertebrate species diversity. Species present require a long hydroperiod e.g. *Cloeon dipterum*[7], *Planorbis leucostoma*[8] and *Sigara striolatum*[5].
6	Grasslands on gravels and sands	Neutral	Open habitat.	–	Very ephemeral. They may not hold water every year.	Heavily grazed but not heavily poached.	A subset of the type 3 ponds identified by Sanderson. They have the potential to contain important temporary pond species e.g. *Chirocephalus diaphanus* and *Triops cancriformis*[9], but due to the brevity of the hydroperiod coinciding with suitable conditions for these species, they are often overlooked.

Table 45 ... continued

Pond Group	Habitat / Geology	pH	Shade/ Conductivity/ Turbidity	Area/ Depth/ Isolation	Hydroperiod	Grazing	Characteristic species
7	Woodland ponds on base-poor clays and sands	–	Least shaded wooded sites. Low conductivity. Low turbidity.	Isolated.	Very long hydroperiod.	Not heavily poached.	High invertebrate diversity. Species that require a long period of inundation are able to colonise, e.g. *Planorbis leucostoma*[8], *Cloeon dipterum*[7] and *Limnephilus centralis*[4].
8	Woodland sites on base-poor clays and sands	Low	Shaded. Turbid.	Deep	Long hydroperiod.	–	Sanderson's type 5 floral assemblage. Macro-invertebrate diversity relatively high. Characterised by species tolerant of low pH; *Hydroporus gyllenhalii*[1] and *Limnephilus vittatus*[4].
9	Woodland ponds on a mixture of base-rich clays and sands	Near neutral	At least 50% open water.	Within a complex of other ponds. Convoluted shallow margins.	Relatively short hydroperiod.	Poached.	Sanderson's type 2 floral assemblage. Species invertebrate richness relatively low, but heterogeneity of habitat allows shade and open water species to co-exist. *Omphiscola glabra*, *Lymnaea truncatula*[8], *Anacaena globulosus*[1], *Glyphotaelius pellucidus*[4] and *Hirudo medicinalis*[10].
10	Woodland ponds on a mixture of base-rich clays and sands	Low	Shaded. Turbid.	–	–	–	Ponds would share a similar macro-invertebrate community to ponds in Group 9 and presumably at one point did so, but the surrounding habitat has been planted with conifers. Species richness is less and no species were identified as characteristic of this habitat type. Ponds in this group have the potential for restoration.
11	Woodland sites on gravels and clays.	Low	Heavily shaded.	–	–	–	Few wetland plant species, clumps of *Sphagnum* spp. in the drawdown zone. They are species poor, but the species present are tolerant of anaerobic conditions, for example *Trichostegia minor*[4] or low pH e.g. *Hydroporus gyllenhalii* [1]

– Environmental variable is not useful in the categorisation of this pond type.
1 Friday (1988); 2 Bratton (1990); 3 Balfour-Browne (1950); 4 Wallace et al. (1990); 5 Savage (1989); 6 Williams (1987); 7 Elliott et al. (1988); 8 Macan (1977); 9 Hall (1976); 10 Ausden and Dawes (2000).

information upon which to base management strategies and as a tool to prioritise ponds for future survey.

Species research

Other than a handful of studies already mentioned, little investigation has been made of temporary pond communities in the New Forest; most work has concentrated on individual species. The following section reviews research on two flagship species, the tadpole shrimp *Triops cancriformis* and the fairy shrimp *Chirocephalus diaphanus*, associated with temporary ponds in the New Forest.

Triops cancriformis (tadpole shrimp)

Triops cancriformis is the best known temporary pond species in the UK, often described as one of the true 'living fossils' (Futuyma 1990 in Zierold *et al*. 2007) as it appears to be morphologically unchanged since the Devonian Period (Tasch 1963). It is a rare species in Britain and classed as RDB endangered (Bratton 1991). It has been recorded from a single site in the UK, in the New Forest, since 1935 (Ewald 2001, 2008; Fox 1949, Hampshire and Isle of Wight Wildlife Trust unpublished, Hobson and Omer-Cooper 1935), but records as early as 1816 may refer to this site (Leach 1816 unpublished, records kept by Hampshire and Isle of Wight Wildlife Trust). Other sites in the UK appear to have lost their populations, probably as a result of cessation in grazing (Maitland 1995), and one in Scotland that was lost to the sea (Balfour-Browne 1909). However, *T. cancriformis* has since been rediscovered in the same locality in Scotland by a site ranger, whilst he was conducting a Natterjack toad survey (BBC 2004). This highlights the fact that populations may not develop in a pond for several years, waiting for ideal conditions, and that populations at low densities can easily be overlooked.

Laboratory studies have identified that this species requires a hatching temperature of between 15°C and

20°C (Hempel-Zawitkowska 1967). Field studies in the New Forest supported these results. In 1999, the pond where *Triops cancriformis* occurs in the New Forest first filled in mid-September. Temperatures were between the required hatching temperatures and *T. cancriformis* were present in the pond a few weeks later. The following year the pond filled later in the year (by 10 October), by which time the temperature was below the minimum required for hatching and *T. cancriformis* did not appear that year (Ewald 2001).

It is not understood why this species is apparently restricted to a single site in the New Forest when other seemingly suitable ponds are located nearby. Translocations, funded by WWF, were undertaken in 1975 to two new sites in the New Forest (Hall 1976), one of which appears to have been successful (Hall 1977). However, no adults have been seen laying eggs in this pond (which has a very short hydroperiod) so its viability as a population is unknown (Ewald, pers. obs.).

Chirocephalus diaphanus (fairy shrimp)

The second archetypal temporary pond species for which research work exists is the fairy shrimp *Chirocephalus diaphanus*. It is listed as RDB vulnerable (Bratton 1991) and is known from 72 10-km squares nationally (Bratton and Fryer 1990). In the New Forest it has been recorded from seven 10-km squares and is present in 10 to 15 ponds each year depending on weather conditions (Ewald 2008). The national breeding programme population was established with stock from a New Forest pond (P. Wisniewski, pers. comm.).

The species is confined to temporary ponds because it is apparently defenceless against predators (Bratton and Fryer 1990) and has the potential to reach maturity within three weeks (Hall 1953). Studies have looked at different aspects of their environment and the life history traits of *C. diaphanus,* many of which have been based on the New Forest populations (Ewald 2008, Hall 1953, 1959a,b,c, 1961, Khalaf and Hall 1975, Lake 1969, Taylor 1965). In summary, *C. diaphanus* is tolerant of a wide range of temperatures (5°C–26°C, Nourisson 1964) and has been known to survive at temperatures above 30°C (Mura 1991) and at low temperatures (e.g. Hall (1961) observed the species under ice), although their survival and reproductive ability is affected at these extremes (Lake 1969). Water depth has also been identified as a significant factor limiting egg hatching (Hall 1959c). However, the impact of predation on this species has not been investigated, until now (Ewald 2008).

Protection and conservation status

Temporary ponds in the New Forest fall short of the Habitats Directive definition of Mediterranean temporary ponds (European Commission 1992), although the statement for the New Forest SAC acknowledges that they support elements of the floral assemblage associated with that habitat (JNCC 2008). In fact, Macabendroth (2004) has found that the New Forest ponds contain slightly fewer invertebrate species than the Mediterranean temporary ponds (as defined in the SAC) on the Lizard Peninsula, but that the New Forest ponds show greater heterogeneity. Several sites within the New Forest are included within the 'Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or of the *Isoëto-Nanojuncetea*' definition (European Commission 1992), although this is only a small percentage of the total number of ponds (Ewald, pers. obs.).

Despite the lack of Annex 1 status, the importance of the temporary ponds has been acknowledged in the New Forest SAC management plan (Wright and Westerhoff 2001), which highlights the conservation importance of both the plant and animal species that they support. The citation for the New Forest SSSI also includes temporary ponds as a reason for notification because of the nationally important assemblages of rare and scarce invertebrates (Natural England 1996). In addition the Hampshire Biodiversity Action Plan (Hampshire Biodiversity Partnership 1998) requires an individual habitat action plan to be written because of the importance of ephemeral pools and their conservation value in maintaining the county's biodiversity. However, few documented management prescriptions exist for these ponds, and it is worth considering here some of their requirements and the key threats that they currently face.

Habitat management

In most cases, the management prescription for temporary ponds will be non-intervention (Biggs *et al.* 2001), the ideal being numerous ponds across a range of environmental conditions. The New Forest is unique in the UK because it provides this pond heterogeneity within a mosaic of habitats. Data collected on Coleoptera occurring within the New Forest marl pits (number of sites surveyed =14, total beetle species = 87) showed that pond complexes contained the highest number of species. Isolated marl pit ponds contained an average of 18 beetle species, whilst those within a complex of ponds, as for example at Crockford Bridge, had on average of 26 species per pond (Ewald 2008).

As already mentioned, continuity of grazing is important for the temporary ponds on the New Forest lawns. It ensures that at least 25–75% of the habitat will remain open at the end of the summer (Wright and Westerhoff 2001). It also provides both areas of bare, poached mud, important for specialist plant and animal species (Chatters 1996), and a supply of dung, whose nutrients form the basis of the temporary pond food chain (Kuller and Gasith 1996, Tubbs 1997, Williams 1987).

Grazing is also important for other temporary ponds, including the base-rich marl sites. *Bidessus unistriatus* is one of the rarest beetles in Britain, currently known from only three sites, one of which is in the New Forest (Foster 2006). The shallow, neutral poached pools on the edge of this pond are thought to be important for its survival. In fact it was lost from a second site in the New Forest because the site became very heavily overgrown with scrub (Foster 2006). A survey (2007) for Coleoptera in New Forest marl pits, showed that sites which had been cleared of scrub for a number of years (greater than 5), or those which appeared to have always maintained at least one pond that was open within a complex of ponds, had the greatest number of beetle species. Within one complex, ponds that were open contained 20% more species than those that were shaded (Ewald 2008).

It is important, though, to consider heterogeneity within individual ponds and not just between sites. One temporary pond in the New Forest is a site for both *Hirudo medicinalis* (medicinal leech) and *Omphiscola glabra* (the mud snail). As this is one of only six ponds in the New Forest known to hold *H. medicinalis* (Reeves 1998), a species that requires high temperatures (Ausden and Dawes 2000), the decision was made to clear willow scrub from half of the pond (M. Noble, pers. comm.). Two years later, the number of juvenile leech in the pond had doubled and continues to be high (Ewald, pers. obs.). However, the pond is also a site for *Omphiscola glabra*, which in many of the New Forest sites appears to prefer ponds with a layer of leaf litter sediment (M. Willing, pers. comm.; Ewald 2008). This species is also rare in the UK, with a scattering of sites in the New Forest. Thus, the fact that the site remains partly shaded provides heterogeneity, benefiting both species.

Invasive species: New Zealand pigmyweed *Crassula helmsii*

Invasion by alien species is recognised as a significant global threat to the diversity of native flora and fauna (Glowka *et al*. 1994, Hobbs and Huenneke 1992, Vitousek *et al*. 1997). The threat is also recognised in the UK, at both national (Clement and Foster 1994, DEFRA 2003, Williamson 1999) and local scales (Hampshire Biodiversity Partnership 1998, Wright and Westerhoff 2001). One such invasive alien weed, New Zealand pigmyweed *Crassula helmsii* has been identified as a major threat to UK freshwaters (Dawson and Warman 1987, Huckle 2007, Leach and Dawson 1999). It is a perennial plant with both aquatic and terrestrial growth forms and is tolerant of a wide range of environmental conditions (Leach and Newman 2000). It was first recorded as 'naturalised' in a pond in Essex in 1956 (Dawson and Warman 1987) and in the New Forest in 1976 (Crutchley and Wicks 2001).

In a survey by Hampshire and Isle of Wight Wildlife Trust (HWT) in 1999, it was found that 39% of water bodies surveyed within or adjacent to the New Forest SAC contained *Crassula helmsii* (Crutchley and Wicks 2001). A fourfold increase in its distribution was recorded in 10 years, from 21 sites in 1990 to 76 sites in 1999 (Crutchley and Wicks 2001). It is easily spread as tiny fragments of stem and in some circumstances it forms extremely dense stands of vegetation (Stone 2002), which can lead to severe oxygen depletion (Newman 2004).

Despite concerns, few experiments have been conducted to investigate what impact *Crassula helmsii* has on native flora and fauna. There are anecdotal accounts of its impact on notable flora in the New Forest (Crutchley and Wicks 2001). At Hatchet Pond Triangle in 1986, *C. helmsii* was recorded along with pillwort *Pilularia globulifera*, but the latter had disappeared by the 1999 survey. Both Hampshire-purslane *Ludwigia palustris* and slender marsh-bedstraw *Galium constrictum* were recorded from Hill Top Pond in 1976, but by 1986 *C. helmsii* was abundant and only *L. palustris* remained. By 1999, only *C. helmsii* was present (Crutchley and Wicks 2001). Langdon *et al.* (2004) have shown that *C. helmsii* can suppress the germination of native plants by up to 83%; however, there is no significant loss of plant species. They also found that the developmental stage of great crested newts *Triturus cristatus* at hatching was unaffected whether eggs were laid on *C. helmsii* or on another plant. Whilst smooth newt *Lissotriton vulgaris* eggs were at a later developmental stage on hatching when they were laid on *C. helmsii*, this may have had no effect on overall population numbers.

In a supplementary study, *Crassula helmsii* had no significant effect on macro-invertebrate species richness, species diversity or community composition when comparing four ponds with and four ponds without heavy infestations (>75% cover). However, there was a significant increase in the diversity of molluscs in ponds with *C. helmsii*, possibly because of the greater surface area provided by *C. helmsii* from which they could graze algae. There was no significant decline or increase in any other taxonomic group between the ponds. It is worth noting that it was difficult to find enough ponds with which to perform a comparative study. This was because, although the number of ponds with *C. helmsii* has increased since the HWT survey, presumably spreading outward from areas of infestation by the action of grazing ponies, the density of *C. helmsii* at many sites had declined, kept in check it would seem by the grazing animals (Ewald 2008).

In the light of these results, more investigation is needed on the impact of *Crassula helmsii* on the conservation value of temporary ponds in the New Forest SAC and on how grazing may suppress *C. helmsii* (Dawson and Warman 1987).

What effect will climate change have on New Forest temporary ponds?

In the UK, human-induced climate change is likely to result in increases in average annual temperature, with greatest warming in summer and autumn. The onset of temperature rise in spring is expected to be one to three weeks earlier and the onset of winter temperature declines one to three weeks later (Hulme *et al.* 2002). Annual rainfall may decrease, but seasonal differences are likely to lead to less rainfall in the summer months and a greater risk of storm events in the winter (Fowler *et al*. 2005; Hulme *et al*. 2002). Cloud cover and relative humidity are expected to decrease, with a corresponding increase in solar radiation (Hulme *et al*. 2002). The New Forest falls within the UK South East region, where average daily temperatures are expected to increase by between 3 °C and 5 °C by 2080. Summer precipitation is predicted to decrease by 15–60% and winter precipitation to increase by 15–30% (Hulme *et al*. 2002).

Temporary ponds have a delicately balanced hydrological regime and may therefore be under increased threat from climate change (Bailey-Watts *et al*. 2000, Graham 1997). Temporary ponds are subject to predictable changes on a seasonal and annual basis, i.e. in any one year, there will be a dry phase, followed by an autumnal through to spring wet phase. Species within temporary ponds are adapted to respond to these changes (Wiggins *et al*. 1980, Williams 1997, Williams 2006). However, in some years temperatures may be below or above the physiological tolerances of species normally found within temporary pools, or there may be no rainfall at times when these temperatures persist. In these unsuitable years, species may not be reproductively successful but they have bet-hedging strategies to allow them to recover and replenish the population in the next suitable year (Cohen 1966). Climate change is likely to increase both within- and between-year variation in precipitation and temperature and hence alter the hydrological regimes permanently beyond the tolerances of specialist species and perhaps beyond the abilities of species to recover (Williams and Biggs 1998).

The impact of changing climatic conditions on pond communities and the sensitivity of temporary pond species to change was illustrated by field observations of New Forest temporary ponds, both within and between years. In year one of an investigation (2004/2005) in the month when the pond filled, mean temperatures were 11.3 °C, sunshine hours were 107.0 hours and rainfall was 129.6 mm. In the second year (2005/2006) temperatures were higher, 17.1 °C, but sunshine hours were similar (105.6 hours) and rainfall was less, 98.0 mm (Met Office 2004/2005), affecting when the pond filled: at the end of September in year 1 and the end of October in year 2 (Ewald 2008). Temporary ponds in the New Forest experienced a reduction in water levels between years one and two, as a result of a reduction in rainfall and an increase in temperature which increased evaporation rates (Hulme *et al*. 2002).

Investigation showed that the communities from different pond types (Table 45) responded differently to changes in climatic conditions. Woodland ponds (groups 7–11) remained stable between years; retaining the same macro-invertebrate community composition despite changes in climatic conditions. Ponds in open habitats (groups 1–6) such as those on the New Forest lawns, including species such as *Chirocephalus diaphanus,* were less stable and changed in community composition between years. Species diversity in these ponds was also significantly less in year 2 compared with year 1. The results would suggest that the open exposed ponds, which have the highest biodiversity value, may be most at risk from changes in climate.

Changes in community composition may result from the environmental tolerance limits of individual species being exceeded or disruption of the complex interactions between species. Laboratory experiments investigated the impacts of temperature on the life history traits of two species characteristic of the grassland pools in the New Forest: *Chirocephalus diaphanus* and one of its predators, *Heterocypris incongruens.* Reared in the absence of the predator, hatching success and fecundity for *C. diaphanus* were greatest at 20 °C, followed by 10 °C. Despite hatching early and growing quickly initially, most individuals were killed by temperatures of 25 °C. Therefore, modest temperature increases beyond those currently experienced would benefit *C. diaphanus,* but a marked increase would have a negative impact on their performance (Ewald 2008). However, the hatching success of the predator *H. incongruens* was greatest at 25 °C and rates of predation were significantly higher at 20 °C compared with 10°C. The predator benefited more from an increase in temperature than the prey, such that the optimal temperature for *C. diaphanus* survival, in the presence of *H. incongruens,* is only 10 °C. This is at the lower limit of the temperature range currently experienced by *C. diaphanus* in the field.

Predicting the impacts of climate change on invertebrate communities in temporary ponds will clearly be complex, but the results from this study suggest that large increases in temperature will have adverse effects on prey, whilst even small increases in temperature will be very detrimental where such changes increase the rate of predation and/or increase predator growth rates, to a greater extent than those of the prey.

Management recommendations

The temporary ponds of the New Forest are an important habitat type, both in terms of the species they contain and the contribution they make to the biodiversity of the New Forest. They also provide important study systems to assess the impact of environmental change. Although there is no immediate need for management intervention, a long-term management plan for these ponds would ensure that heterogeneity is maintained and that overall numbers of temporary ponds do not decline further.

There are currently gaps in our knowledge, particularly with regard to species distributions, of both rare and common taxa. Even when the distribution and status of rare species are known, it is often difficult to determine management prescriptions because of a lack of knowledge about species requirements. More work is required to assess the impact of potential threats, for example invasive alien species and climate change, in order to implement effective conservation strategies. Continued survey and a programme of monitoring would help to answer these questions. Although single species surveys are obviously extremely important, a community level approach will ultimately provide more useful insights into the condition and status of temporary pond communities.

References

Ausden, M. and Dawes, S. (2000). *Medicinal leech progress report June 1999 to December 1999.* UK Medicinal Leech BAP Steering Group.

Bailey-Watts, T., Lyle, A., Battarbee, R., Harriman, R. and Biggs. J. (2000). Lakes and ponds, In Acerman, M. (ed.) *The hydrology of the UK: a study of change,* pp. 180–203. Routledge, London.

Balfour-Browne, F. (1909). Notes on the rediscovery of *Apus cancriformis* in Britain. *Annales of Scottish Natural History,* 118.

Balfour-Browne, F. (1950). *British water beetle species*, volume II. The Ray Society, London.

BBC. (2004). Ancient creatures found in firth. http://news.bbc.co.uk/1/hi/scotland/3714524.stm

Biggs, J., Fox, G., Nicolet, P., Whitfield M. and Williams, P. (2001). Dangers and opportunities in managing temporary ponds. In Sutcliffe, D. and Rouen, K. (eds.) *European Temporary Ponds: a threatened habitat. Freshwater Forum*, 17, 71–80.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P. and Weatherby, A. (2005). 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. *Aquatic Conservation – Marine and Freshwater Ecosystems*, 15, 693–714.

Boycott, A. E. (1936). The habitats of fresh-water mollusca in Britain. *Journal of Animal Ecology*, 5,116–186.

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

Bratton, J. H. (1991). *Invertebrates: Red Data Books*, vol. 3. JNCC, Peterborough.

Bratton, J. H., and Fryer, G. (1990). The distribution and ecology of *Chirocephalus diaphanus* Prevost (Branchiopoda, Anostraca) in Britain. *Journal of Natural History*, 24, 955–964.

Buckley, J. (2001). The conservation and management of amphibians in UK temporary ponds, with particular reference to natterjack toads. In Sutcliffe, D. and Rouen, K. (eds.) *European Temporary Ponds: a threatened habitat. Freshwater Forum*, 17, 54–62.

Chatters, C. (1996). Conserving rare plants in muddy places. *British Wildlife*, 7(5), 281–286.

Clement, E. J. and Foster, M. C. (1994). *Alien plants of the British Isles: a provisional catalogue of vascular plants (excluding grasses)*. Botanical Society of the British Isles, London.

Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology,* 12, 119–129.

Collinson, N. H., Biggs, J., Corfield, A., Hodson, M. J., Walker, D., Whitfield, M., and 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.

Crutchley, S. and Wicks, D. (2001). *Australian swamp stonecrop (Crassula helmsii) in the New Forest: an assessment of current distribution and potential for eradication*. Hampshire and Isle of Wight Wildlife Trust, Curdridge, Hampshire.

Dawson, F. H. and Warman, E. A. (1987). Crassula helmsii (T-Kirk) Cockayne – is it an aggressive alien aquatic plant in Britain? *Biological Conservation*, 42, 247–272.

DEFRA. (2003). Review of non-native species policy: Report of the working group. Department for Environment, Food and Rural affairs, London.

Elliott, J. M., Humpesch, U. H. and Macan, T. T. (1988). *Larvae of the British Ephemeroptera: a key with ecological notes.* Freshwater Biological Association, Ambleside, Cumbria.

European Commission. (1992). *On the conservation of natural habitats and of wild fauna and flora.* Council Directive 92/43/EEC 21 May 1992.

Ewald, N. C. (2001). *Report to identify and study the biotic and abiotic factors which affect the presence of Triops cancriformis in temporary ponds in the New Forest, Hampshire.* Bsc(Hons) thesis, Farnborough College of Technology, Farnborough.

Ewald, N. C. (2008). *The impact of climate change on temporary pond macroinvertebrate communities*. DPhil thesis, University of Sussex, Brighton, Sussex.

Foster, G. N. (2006). *The status of the one-grooved diving beetle Bidessus unistriatus (Goeze, 1777) (Coleoptera, Dytiscidae) in Britain – an update*. Report to the Environment Agency, The Aquatic Coleoptera Conservation Trust.

Fowler, H. J., Ekstrom, M., Kilsby, C. G. and Jones, J. I. (2005). New estimates of future changes in extreme rainfall across the UK using regional climate model integrations. 1. Assessment of control climate. *Journal of Hydrology*, 300, 212–233.

Fox, H. M. (1949). On *Apus* – its rediscovery in Britain, nomenclature and habits. *Proceedings of the Zoological Society of London*, 119, 693–702.

Friday, L. (1988). A key to the adults of British water beetles. *Field Studies,* 7, 1–151.

Fryer, G. (1966). *Branchinecta gigas* Lynch, a non-filter-feeding raptory anostracan, with notes on the feeding habits of certain other anostracans. *Proceedings of the Linnean Society of London,* 177, 19–34.

Glowka, L., Burhenne-Guilmin, F. and Synge, H. (1994). *A guide to the Convention on Biological Diversity*. IUCN, Cambridge and Gland.

Graham, T. B. (1997). Climate change and ephemeral pool ecosystems: potholes and vernal pools as potential indicator systems. In *Impacts of Climate Change and Land Use in the Southwestern United States*. World Wide Web poster session. http://geochange.er.usgs.gov/sw/

Gray, J. and Taylor, D. W. (1988). Evolution of the fresh-water ecosystem – the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62, 1–214.

Hall, R. E. (1953). Observations on the hatching of eggs of *Chirocephalus diaphanus* Prevost. *Proceedings of the Zoological Society of London,* 123, 95–109.

Hall, R. (1976). *Conservation of the Notostracan crustacean Triops cancriformis. Report on the year October 1975 – October 1976*. World Wildlife Fund, Godalming.

Hall, R. (1977). *Conservation of the Notostracan crustacean Triops cancriformis. Report on the year December 1976 – December 1977*. World Wildlife Fund, Godalming.

Hall, R. E. (1959a). Delayed development of eggs of *Chirocephalus diaphanus* Prevost. *Hydrobiologia*, 13, 160–169.

Hall, R. E. (1959b). The development of eggs of *Chirocephalus diaphanus* Prevost at a low temperature. *Hydrobiologia*, 13, 156–159.

Hall, R. E. (1959c). The development of eggs of *Chirocephalus diaphanus* Prevost in relation to depth of water. Hydrobiologia 13:79–84.

Hall, R. E. (1961). On some aspects of the natural occurrence of *Chirocephalus diaphanus* Prevost. *Hydrobiologia*, 17, 205–217.

Hampshire and Isle of Wight Wildlife Trust. unpublished. *Notes on the wetting and drying patterns of a temporary pond in the New Forest*. Paper notes by various authors. Hampshire and Isle of Wight Wildlife Trust, Curdridge, Hampshire.

Hampshire Biodiversity Partnership. (1998). *Biodiversity Action Plan for Hampshire. Volume 1*. Hampshire County Council.

Hempel-Zawitkowska, J. (1967). Natural history of *Triops cancriformis* (Bosc.). *Zoologica Poloniae*, 17, 173–239.

Henderson, P. A. (1990). *Freshwater ostracods: synopsis of the British fauna (New Series)*. vol. 42. Universal Book Services, Oegstgeest, Netherlands.

Hobbs, R. J. and Huenneke, L. F. (1992). Disturbance, diversity and invasion – implications for conservation. *Conservation Biology*, 6, 324–337.

Hobson, A. D. and Omer-Cooper, J. (1935). *Apus cancriformis* in Great Britain. *Nature*, 135, 972.

Huckle, J. (2007). *The Invasive Alien Species Project: Crassula helmsii*. Fact Sheet 1. English Nature and University of Liverpool.

Hulme, M., Jenkins, G. J., Lu, X., Turnpenny, J. R., Mitchell, T. D., Jones, R. G., Lowe, J., Murphy, J. M., Hassell, D., Boorman, P., McDonald, R. and Hill, S. (2002). *Climate change scenarios for the United Kingdom*. The UKCIP02 Scientific Report. Norwich, Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia.

JNCC. (2008). Special Areas of Conservation: Habitats Accounts. Freshwater Habitats: 3170 Mediterranean temporary ponds. http://www.jncc.gov.uk/

Khalaf, A. N. and Hall, R. E. (1975). Embryonic development and hatching of *Chirocephalus diaphanus* Prevost (Crustacea-Anostraca) in Nature. *Hydrobiologia*, 47,1–11.

Khalaf, A. N. and Macdonald, L. J. (1975). Physicochemical conditions in temporary ponds in the New Forest. *Hydrobiologia*, 47, 301–318.

Kuller, Z. and Gasith, A. (1996). Comparison of the hatching process of the tadpole shrimps *Triops cancriformis* and *Lepidurus apus* Lubbocki (Notostraca) and its relation to their distribution in rain-pools in Israel. *Hydrobiologia*, 335,147–157.

Lake, P. S. (1969). The effect of temperature on growth, longevity and egg production in *Chirocephalus diaphanus* Prévost (Crustacea: Anostraca). *Hydrobiologia*, 33, 342–351.

Langdon, S. J., Marrs R. H., Hosie C. A., McAllister H. A., Norris K. M. and Potter J. A.. (2004). *Crassula helmsii* in UK ponds: Effects on plant biodiversity and implications for newt conservation. *Weed Technology*, 8, 1349–1352.

Leach, J. and Dawson, F. H. (1999). *Crassula helmsii*: an unwelcome invader. *British Wildlife*, 10, 234–239.

Leach, J. and Newman, J. R. (2000). *Myriophyllum aquaticum*, *Crassula helmsii*, *Hydrocotyle ranunculoides* and *Azolla filiculoides*. In P. Bradley (ed.) *Exotic and invasive species: should we be concerned?* Proceedings 11th Conference of the Institute of Ecology and Environmental Management, 6 April 2000, pp. 62–71. Institute of Ecology and Environmental Management.

Macan, T. T. (1977). *A key to the fresh and brackish-water Gastropods*. Vol. 13, Freshwater Biological Association, Ambleside, Cumbria.

Maitland, P. S. (1995). *Species Action Plan: tadpole shrimp Triops cancriformis (Bosc 1801) (Crustacea, Notostraca)*. Triops Conservation Group, London.

McAbendroth, L. (2004). *The ecology and conservation value of Mediterranean temporary ponds*. DPhil thesis, University of Plymouth, Plymouth.

Met Office. (2004/2005). *Monthly summaries*. http://www.metoffice.gov.uk/

Mura, G. (1991). Life-history and interspecies relationships of *Chirocephalus diaphanus* Prevost and *Tanymastix stagnalis* (L.), (Crustacea, Anostraca) inhabiting a group of mountain ponds in Latium, Italy. *Hydrobiologia*, 212, 45–59.

Natural England. (1996). *New Forest SSSI notification*. http://www.naturalengland.org.uk/

Newman, J. R. (2004). *Information Sheet 11: Australian Swamp Stonecrop*. Centre for Ecology and Hydrology, Wallingford, Oxon.

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

Nicolet, P., Biggs, J., Fox, G., Hodson, M. J., Reynolds, C., Whitfield, M. and Williams, P. (2004). The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. *Biological Conservation*, 120, 261–278.

Nourisson, M. (1964). Existence d'un intervalle de température favorable an développement des öeufs asséchés de *Chirocephalus stagnalis* Shaw. *Comptes rendus l'Académie des sciences de Paris,* 253,1994–1996.

Pond Action. (1998). *A guide to the methods of the National Pond Survey*. Pond Conservation, Oxford.

Pond Conservation, and Environment Agency. (2002). *A guide to monitoring the ecological quality of ponds and canals using PSYM*. Environment Agency Midlands Region.

Reeves, R. (1998). *New Forest medicinal leech survey 1998 interim report*. Hampshire and Isle of Wight Wildlife Trust, Curdridge, Hampshire.

Sanderson, N. (2001). A provisional classification of the flora of New Forest temporary ponds. In Westerhoff, D. and Wright, R. (eds.) *New Forest SAC management plan*. English Nature, Lyndhurst.

Savage, A. A. (1989). *Adults of the British aquatic Hemiptera Heteroptera: a key with ecological notes*. Freshwater Biological Association, Ambleside, Cumbria.

Stone, I. (2002). War against *Crassula helmsii* – one year on. *Enact*, English Nature, 10, 9–10.

Tasch, P. (1963). Evolution of the Branchiopoda. In: *Phylogeny and evolution of Crustacea* (eds. Whittington, H. B. and Rolfe, W. D. I.) , pp. 145–162. Museum of Comparative Zoology, Cambridge.

Taylor, E. W. (1965). *An investigation of the physicochemical adaptations fitting Chirocephalus diaphanus for life in temporary ponds*. DPhil thesis, University of Southampton, Southampton.

Tubbs, C. R. (1986). *The New Forest*. New Naturalist Series. Collins, London.

Tubbs, C. R. (1997). The ecology of pastoralism in the New Forest. *British Wildlife*, 9, 7–16.

Vitousek, P. M., Dantonio, C. M., Loope, L. L., Rejmanek, M. and Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, 21, 1–16.

Wallace, I. D., Wallace B. and Philipson, G. N. (1990). *A key to the case-bearing caddis larvae of Britain and Ireland*. Vol. 51. Freshwater Biological Association, Ambleside, Cumbria.

Wiggins, G. B. (1973). A contribution to the biology of caddisflies (Trichoptera) in temporary pools. *Royal Ontario Museum Life Science Contributions*, 88, 1–28.

Wiggins, G. B., Mackay R. J. and Smith, I. M. (1980). Evolutionary and ecological strategies of animals in annual temporary pools. *Archiv für Hydrobiologie,* 58, 97–206.

Williams, D. D. (1987). *The ecology of temporary waters*. Croom Helm Ltd., Beckenham, Kent.

Williams, D. D. (1997). Temporary ponds and their invertebrate communities. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 7, 105–117.

Williams, D. D. (2006). *The biology of temporary waters.* Oxford University Press, Oxford.

Williams, P. and Biggs, J. (1998). *Seasonal ponds: indicators of climate change*. Pond Conservation, Oxford

Williams, P., Biggs, J., Fox, G., Nicolet, P. and Whitfield, M. (2001). History, origins and importance of temporary ponds. In Sutcliffe, D. and Rouen, K. (eds.) *European Temporary Ponds: a threatened habitat. Freshwater Forum*, 17, 7–15.

Williams P.J., Briggs, J., Barr, C. J., Cummins, C. P., Gillespie, M. K., Rich, T. C. G., Baker, A., Beaseley, J., Corfield, A., Dobson, D., Collin, A. S., Fox, G., Howard, D. C., Luursema, K., Rich, M. M., Samson, D., Scott, W. A., White, R. and Whitfield, M. (1998). *Lowland Pond Survey 1996: Final Report*. Department of the Environment, Transport and the Regions, London.

Williamson, M. (1999). Invasions. *Ecography*, 22, 5–12.

Wood, P. J., Greenwood, M. T. and Agnew, M. D. (2003). Pond biodiversity and habitat loss in the UK. *Area*, 35, 206–216.

Wright, R. and Westerhoff, D. (2001). *New Forest SAC management plan.* English Nature, Lyndhurst.

Zierold, T., Hanfling, B. and Gomez, A. (2007). Recent evolution of alternative reproductive modes in the 'living fossil' *Triops cancriformis. BMC Evolutionary Biology*, 7, 161–173.