Pond biodiversity and habitat loss in the UK

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Abstract

Ponds are common landscape features but have been poorly studied compared to other freshwater habitats in the UK, despite their high frequency of occurrence. In the last century, many ponds have been lost and those that remain face increasing pressure due to agricultural land drainage, pollution and urban development. However, ponds provide important habitats for diverse floral and faunal communities including a number of rare taxa of conservation interest. This paper examines the biodiversity and wider environmental value of ponds with particular reference to the aquatic invertebrate and amphibian communities they support, and the adverse impact of anthropogenic activity on their aquatic habitats.

Key Words:- ponds, UK, aquatic invertebrates, biodiversity, conservation, habitat loss.

Introduction

The study of riverine catchments has formed a central role in the development of physical geography and particularly geomorphology, hydrology and more recently biogeography (Calow and Petts 1994). In contrast, the study of standing water bodies (lentic ecosystems) has lagged somewhat behind running water systems, although their use in palaeoenvironmental and palaeoecological research is widely acknowledged (e.g., Berglund 1996; Birks et al 2000). Standing (still) water bodies provide an ideal opportunity to examine biogeographical patterns and relationships since the aquatic organisms that occupy them effectively inhabit aquatic islands in a sea of land. The aquatic organisms that inhabit ponds, small water bodies between 1 m^2 and 2 ha in area which hold water for all or part of the year (Pond Action 1993; Rouen 2001), face similar pressures to terrestrial organisms on oceanic islands. They provide ideal sites to examine island biogeography theory (Bilton et al 2001), including the effect of geographic distance between sites on the colonisation and dispersal of different taxa, and the impact of habitat isolation on pond populations (Boecklen 1997; Griffiths 1997).

Small standing water bodies (including pools, marl and brick pits, dells, bog pools, kettle holes and lagoons – herein collectively termed ponds) have been poorly studied in the UK despite the high density of occurrence in both rural and urban locations and are of considerable cultural, recreational and biological value. Ponds are a natural element of the landscape, although they have been poorly incorporated into traditional landscape studies compared to riverine (e.g., Gardiner 1997) and other terrestrial ecosystems (e.g., Burger 2000; Miles et al 2001). The principal reasons for this deficiency reflects the fact that the effective pond landscape (pondscape) includes the pond and its immediate catchment, but also the terrestrial matrix of land between ponds. As a result, land management activities some distance away from the waterbody may threaten individual ponds or complexes in both rural and urban locations (Boothby 1997). This has considerable importance when considering the dispersal of aquatic organisms (such as aquatic insects and amphibia) from their birth pond and the colonisation of new or adjacent ponds. In the case of amphibians the pondscape matrix also strongly influences foraging activity and the availability of suitable winter hibernation sites (Griffiths 1997).

Ponds account for around 97% of the total number of standing water bodies in the UK but only 14 % of the total surface area (Bailey-Watts et al 2000). They have been created by a variety of natural processes such as glaciation, land subsidence, river action and tree falls, although in the contemporary landscape anthropogenic activities are widely acknowledged as the dominant force influencing their creation and elimination in temperate latitudes (Rackham 1986). Ponds are naturally more common in areas with impervious geologies where surface waters easily collect in depressions. However, this pattern is not always clear since large numbers of irrigation, livestock and dew-ponds have historically been created in areas underlain by highly porous rock (e.g., chalk and limestone) where natural surface waters are uncommon, to ensure reliable water sources for agriculture (Beebee 1997; Stanton 1995).

Ponds occur in almost all landuse types including mountainous uplands, moorlands, woodlands, grasslands, coastal margins and in all agricultural settings. They have considerable aesthetic value and historically medieval fish ponds were an important source of food (Rees 1997). Ponds have been created for a wide variety of functions including mineral extraction (Andrews and Kinsman 1990), watering livestock, irrigation for agriculture (Gee et al 1997), as ornamental features (Williams et al 1997), and even to drive industrial processes (Giles and Goodall 1992). The amenity value of ponds is widely acknowledged and they are commonly incorporated as hazard features on golf courses (Stubbs 1999), and extensively utilised for recreational angling (Williams et al 1998).

The total number of ponds in the UK is not known, although Rackham (1986) estimated that around 800,000 ponds existed in England and Wales in 1880, based on detailed analysis of Ordnance Survey Maps and applying a correction factor for ponds less than 6 m in diameter that would have not been surveyed. A similar survey for the 1920's estimated that around 340,000 ponds existed although there was considerable spatial variability across England and Wales (Figure 1). The lowest density of ponds occurred in upland areas and the highest in areas of ancient woodland and agricultural land in Norfolk, Suffolk and Cheshire. The *Lowland Pond Survey 1996* estimated the number of lowland ponds in Great Britain to be around 228,900 (Williams et al 1998). However, almost all attempts to determine the number of ponds in an area will be an underestimate. Four main sources of error exist:- i) analysis of historical maps only identifies larger ponds that have been surveyed; ii) even the most extensive field survey will not capture all sites and there is a bias towards larger ponds; iii) a large proportion of naturally ephemeral ponds that hold water for a few months or even weeks each year have been overlooked historically; and iv) the total number of ornamental garden ponds in the urban environment has never been estimated.

Ponds are essentially ephemeral, sedimentation and hydroseral succession gradually leading to the terrestrialisation of a pond through loss of open water and a reduction in depth until the basin is largely indistinguishable from the surrounding land. Due to the naturally ephemeral nature of ponds it has been argued that even anthropogenically created sites provide habitat for flora and fauna that is indistinguishable from that of a natural pond (Biggs et al 1994).

Most ponds do not have any statutory protection in the UK (Mackay 1997) and little routine scientific monitoring of their biological resources has been undertaken. There is increasing concern that many ponds have been lost due to changes in agricultural practices, land drainage and urban development. This paper considers the ecological value of ponds in terms of the biological diversity they support (biodiversity – the number of species in a particular area or community (Allaby, 2000)) and the threats that ponds and the organisms that inhabit them face, due to habitat loss and management in the UK.

Pond Biodiversity

Until recently, the ecology of ponds in the UK has been poorly studied. Their relatively small size and high frequency of occurrence led to the widely held belief that they were ecologically unimportant. However, it has now been acknowledged that this common misconception may have inadvertently allowed many ponds to be drained with little or no regard to aquatic habitat loss or biodiversity (Everard et al 1999).

Ponds provide a significant biological resource. Data collected as part of the *Lowland Pond Survey 1996* clearly demonstrates that they support a greater number of aquatic macroinvertebrate species (animals without a backbone greater than 0.5 mm in size), and particularly uncommon species with specific conservation interest, than riverine systems (Table I) (Williams et al 1998). In addition, the wide variety of ponds occurring in the UK comprise an important habitat for around 400 species of aquatic plants and approximately 150 of the 280 wetland invertebrates listed for conservation value in the UK Red Data

Book (Duigan and Jones 1997). This includes 23 of the 38 fresh and brackish water organisms given specific protection under Schedules 5 and 8 of the Wildlife and Countryside Act, more than any other freshwater habitat (Table II). The significance of ponds as habitats and refugia for 'rare' species is clear although common and ubiquitous organisms are most frequently encountered, even in the most degraded urban and industrial locations (Wood and Barker, 2000).

The following case study illustrates the high conservation value of the beetle (Coleoptera) community within a single brackish water pond and the wider value of this geographically limited resource. Coastal ponds may support populations of freshwater, marine and specialist brackish water organisms (Sherwood et al 2000). Brackish water ponds depend on a regular input of freshwater, largely derived from rainfall or inflowing streams, and groundwater, which dilutes the seawater. However, during the summer months evaporation processes may concentrate marine salts within the pond creating hypersaline conditions, excluding most faunal species. Coastal brackish water ponds are predominantly located close to or above the spring tide high water line and may only receive marine water input in the form of sea-spray. In some locations individual sites may support nationally significant communities and populations of organisms. A number of nationally rare aquatic beetles (Coleoptera) with restricted distributions utilise these uncommon and relatively hostile habitats (Foster 2000, Sage 1996).

Enochrus bicolor (Hydrophilidae) is a nationally notable water beetle in the UK (Foster 2000). Throughout the UK and Ireland, *E. bicolor* is confined to brackish water and has been recorded in coastal ponds, slow-flowing ditches and the Cheshire meres (Figure 2). A four-year study of a population of *E. bicolor* from a saltmarsh pond created in 1850 to provide access to an oyster processing plant, Brightlingsea, Essex, identified a dynamic community of organisms of national significance (Greenwood and Wood 2003). The salinity of the pond was variable but attained almost twice the salinity of seawater during the summer of 1997. Of the 31 aquatic organisms identified at the Flag Creek site, 11 Red Data Book Coleoptera were recorded, 10 being nationally scarce and 1 being nationally endangered, *Paracymus aeneus* (Table III).

Examination of historic distribution records indicated that *P. aeneus* is currently confined to two 10 km grid squares in England, having only ever been recorded from a total of six 10 km grid squares. *P. aeneus* lives in saline pools above the high-water mark, usually in association with vegetation at the edge of ponds. In the UK this species is classified as endangered and has been given full protection under Schedule 5 of the Wildlife and Countryside Act 1981 (Table II). A Biodiversity Action Plan has been developed for *P. aeneus* with an emphasis on the protection of existing populations from damaging activities and the creation of additional habitats (shallow ponds with marginal vegetation) around the high-water mark (Foster 1999).

Essex provides an important centre for brackish water habitats along a narrow coastal corridor, containing 20% of the national saltmarsh habitat (Mason et al 1991). A large proportion of this habitat is under threat from rising sea level, pollution, construction of sea defences and land drainage (Barnes 1989). In addition, overall pond loss within the county between 1870 and 1989 was estimated to be 55 – 69% based on map and field surveys of selected areas, with around a 20% loss since 1960 (Heath and Whitehead 1992).

Habitat Loss

The destruction of pond habitats has three component, straightforward loss of habitat, increased fragmentation of the remaining habitat, and reduced habitat quality. Fragmentation can be defined as the remaining habitat of fixed total area that is located within increasingly smaller and more isolated discrete fragments (patches) (Hanski 1999). Habitat loss and fragmentation usually occur together and have undoubtedly lead to greater pressure on a number of pond species due to a reduction in dispersal and colonisation opportunities (Godreau et al 1999; Müller 2003).

Attempts to quantify pond loss are difficult since the total number of ponds in the UK is unknown. It is widely acknowledged that natural succession, agricultural land drainage and developments for urban housing, industry or transport infrastructure have significantly reduced the number of ponds over the last 150 years (Boothby and Hull 1997). Regional estimates of loss vary widely from 90% for parts of London (Langton 1985) to 6% for urban ponds in Edinburgh (Jeffries and Mills 1990) (Table IV). However, direct comparison between studies is not always possible since many only provide an estimate of pond number, or rates of pond loss, rather than definitive figures. Pond loss appears to have been greater in the last two decades than during any other period (Boothby et al 1995). Data from the *Lowland Pond Survey 1996* (Williams et al, 1998) indicate that most ponds lost between 1990 and 1996 were from arable land while there was a net increase on pastural land.

The importance of both perennial and temporary ponds for amphibian populations is widely recognised, since all seven British species utilise ponds for breeding and larval development (Griffiths, 1997). The decline of great crested newt (*Triturus cristatus)* populations is largely due to the destruction or pollution of their habitat. Elimination of even a limited number of great crested newt breeding sites may have far reaching consequences since adult newts have a tendency to migrate towards their traditional breeding sites and individuals are unable to travel more than 900 m (Oldham and Humphries 2000). To compound the problems of habitat loss, newt larvae require open water and as a result are particularly vulnerable to predation by fish (Buckley 2001).

Many ponds support fish populations that have been artificially stocked with either coarse or salmonid fish. In some instances recreational angling has lead to the protection of individual ponds, particularly in urban locations (Wood et al 2001a); although due to the predatory nature of many fish there is increasing evidence that reduced amphibian and invertebrate biodiversity occurs in angling ponds (Müller et al 2003). However, evidence from other studies indicates that aquatic plant (macrophyte) diversity may be increased by the management activities associated with angling (Linton and Goulder 2000).

Temporary ponds, standing water bodies that experience a recurrent dry phase (Williams et al 2001) are probably at greater threat in the UK than any other small water body. A major reason for this is a lack of public awareness and scientific research. Even within recognised conservation areas, temporary ponds have been ignored when compared to permanent water bodies – lakes, streams and rivers and perennial ponds. However, temporary ponds are some of the most long-lived, with some ephemeral pingos (ancient periglacial ponds) in Britain more than 8,000 years old. Temporary ponds are typically shallow and are more vulnerable to soil drainage in agricultural and urban areas than permanent waterbodies. To compound this problem, their low water volume combined with a small catchment, makes them highly susceptible to pollution (Williams et al 1998).

The periodic desiccation of habitat within temporary waterbodies means that there is usually relatively little overlap in the species composition compared to that of perennial ponds (Collinson et al 1995). However, temporary ponds frequently have high floral and faunal biodiversity (Nicolet 2001). Some invertebrate taxa have life cycles that enable them to utilise ephmeral aquatic habitats and some adults and eggs may even be able to withstand partial or complete desiccation (Bratton and Fryer 1990, Drake 2001). In addition, the recurrent dry phase allows a number of semi-aquatic, terrestrial and riparian taxa to utilise the pond basin even when it is dry (Lott 2001).

All amphibian species have been impacted by temporary pond habitat loss to varying degrees; although natterjack toad (*Bufo calamita*) populations have experienced the most significant reductions over the last century (Denton et al, 1997, Oldham and Humphries 2000). The natterjack toad (*Bufo calamita*) relies on ephemeral ponds in open early sucessional habitats for reproduction. They require unshaded, shallow ponds (less than 10 cm deep) with gently sloping banks for tadpoles and toadlets to develop successfully. Today, temporary freshwater ponds in the coastal dune systems of the west and east coast of England provide the species' only stronghold. Historically, temporary ponds in pastoral fields and on heathland supported viable populations in several parts of the UK. However, land drainage and changes in the management of heathland have eliminated almost all inland populations (Buckley 2001).

Future Prospects

Ponds support considerable biodiversity reflecting the many different types of pond and habitats they contain. Detailed medium to long-term studies of pond ecology, hydrology and water chemistry are required to provide information on natural hydrological variability and population dynamics to facilitate management and ultimately allow modelling of the pond resource under scenarios of environmental change (Bailey-Watts et al 2000). Long-term datasets are widely available for lakes (e.g. Savage 2000) and riverine systems (Speirs et al 2000), and the data has been widely incorporated into hydro-climatological and eco-hydrological models (Bradley and Ormerod 2001, Wood et al 2001b). Until a greater understanding and appreciation of ponds is achieved this type of modelling will not be possible for ponds. New guidelines for sampling and a network of sites across the UK have been established to address some of these issues (Williams et al 2000), although it will be some time before long-term baseline data are available.

The management of existing ponds and creation of new sites to provide habitat for taxa of specific conservation interest, wildlife in general or for recreation and public appreciation may all be desirable, but should be undertaken with care (Williams et al, 2000). In the past, lack of information regarding ponds has lead to the development of some widely held misconceptions concerning the management of ponds for nature conservation. Some of the most damaging misconceptions include the belief that maintaining open water by the physical removal of aquatic vegetation, silt, and trees shading the water surface is vitally important for all ponds (Biggs et al 1994). Since almost all ponds are utilised by aquatic organisms irrespective of size, age, naturalness or degree of permanence, it is important that habitat diversity is maintained rather than creating a pond ‘stereotype’. Dredging a temporary pond to create a more permanent water body will almost certainly eliminate aquatic flora or fauna adapted to ephemeral habitats (Biggs et al 2001). In most instances, the physical alteration of an existing pond is unnecessary and the most important factor is to ensure that water quality is maintained by the protection of the surrounding catchment.

Ponds have considerable amenity value in the urban and rural environment. Increasingly, ponds are being created for specific anthropogenic purposes, for example, to provide flood water storage in urban areas and to provide settling and storage basins for fine sediments and pollutants. Public awareness of ponds has improved due to the increasing number that are located within nature reserves and Pond Warden Schemes established to develop and encourage local interest in pond preservation and conservation (Boothby et al 1995). The British Trust for Conservation Volunteers (BTCV) actively involves local communities in the management and conservation of ponds. The BTCV promotes 'Pond Weeks' to encourage the general public to become involved in the monitoring and management of ponds and to place them at the centre of the community (King 1999). These are all valuable exercises in raising public awareness and the understanding of pond habitats and the organisms they support.

Ornamental and garden ponds have been excluded from most historic studies due to difficulties in obtaining access, and their inclusion in future studies is essential. Garden ponds provide a haven for amphibians, plants and invertebrate fauna in the urban environment. However, many of these ponds contain high densities of ornamental fish (e.g., goldfish, Koi carp) that may feed on aquatic vegetation and invertebrate taxa, and thereby reduce the overall biodiversity of the pond. Due to the current popularity of ponds as garden features the number of non-native plant species introduced is likely to be substantial. The *Lowland Pond Survey 1996* indicated that 14% of the ponds surveyed supported one or more exotic plant species and the figure for garden ponds is likely to be substantially higher (Williams et al 1998). In addition, it is possible that exotic invertebrate fauna will be introduced into ponds with plants, and may ultimately disperse into the wider environment.

Ponds remain an important landscape feature in the UK even though the traditional function of ponds in agriculture and industry may have changed. Management and conservation of individual ponds and pondscapes may be required to ensure the protection of habitat, the survival of individual species and overall pond biodiversity. It is also essential to maintain the diversity of pond types within the landscape. Further research is required to increase our understanding of pond habitats and ecology, and the importance of maintaining connectivity within pondscapes. However, greater public awareness and participation may ultimately be required to ensure the continued survival of ponds and pondscapes.

Acknowledgements

We gratefully acknowledge the helpful and constructive comments of colleagues following a lunchtime research seminar presentation given in the Department of Geography, Loughborough University. Thanks to Mark Szegner for the production of the figures for this paper and Professor G.N. Foster for permission to reproduce Figure 2. Thanks to Dr E. Brown for helpful comments on a draft of this manuscript and the constructive comments of two referees.

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List of Tables and Figures

Table I. Comparison of macroinvertebrate biodiversity in ponds and rivers in the United Kingdom indicating species richness, nationally scarce and rare Red Data Book species.

Invertebrate Group		Species Richness		Nationally Scarce Species		Red Data Book Species	
	Common Name	Ponds	Rivers	Ponds	Rivers	Ponds	Rivers
Planariidae	Flatworms	8	9	1	0	0	0
Mollusca	Snails & orb mussels	34	33	1	2	4	2
Hirudinea	Leeches	10	14	1	0	0	0
Crustacea	Shrimps, slaters & crayfish	6	10	0	0	0	0
Ephemeroptera	Mayflies	19	37	0	1	1	3
Plecoptera	Stoneflies	7	27	0	1	0	0
Odonata	Dragonflies	26	13	4	2	1	0
Hemiptera	Water Bugs	45	27	2	0	1	0
Coleoptera	Water Beetles	170	100	60	27	13	4
Megaloptera	Alderflies & spongeflies	2	3	0	1	0	0
Trichoptera	Caddis flies	71	95	3	7	1	4
Total number of species		**398**	**368**	**72**	**41**	**21**	**13**

Modified from Williams et al, (1998) and Bailey-Watts et al, (2000). Comparison is based on data from 156 sites in the National Pond Survey (Williams et al, 1998) and 614 sites from the RIVPACS programme (Wright et al, 1996). The comparison is based on all invertebrate groups sampled in both surveys for which reliable published national distribution and status data are available.

Note:- Numbers of taxa given by Wright et al, (1996) in Table 1 were modified to enable simple comparisons to be made see Williams et al, (1998) for details.

Table II. Freshwater animals and plants given full protection under Schedules 5 and 8 of the Wildlife and Countryside Act 1981 (Adapted from Williams et al, 1998).

Species	Aquatic Habitats	Species	Aquatic Habitats
Mammals		**Invertebrates** (Continued)	
Lutra lutra (Otter)	R, L, **P**	*Paracymus aeneus* (a water beetle)	**BP**
Arvicola terrestris (Water Vole)	**P**, R	*Hydrochara caraboides* (Lesser silver diving beetle)	**P**
		Dolomedes platarius (Fen Raft Spider)	**P**
Fish			
Accipenser sturio (Sturgeon)	R	**Plants**	**P**
Alosa alosa (Allis Shad)	R	*Ranunculus ophioglossifolius* (Adder's-tongue Spearwort)	**P**
Coregonus albula (Vendace)	L	*Cyperus fuscus* (Brown Galingale)	WG
Coregonus laveratus (Powan)	L	*Apium repens* (Creeping Marshwort)	**P**
Lota lota (Burbot)	R	*Liparius loeselii* (Fen Orchid)	**P**
		Luronium natans (Floating water-plantain)	**P**
Amphibians [1]		*Lythrum hyssopifolia* (Grass-poly)	L
Bufo calamita (Natterjack toad)	**P**	*Najas flexilis* (Slender Naiad)	L
Triturus cristatus (Great crested newt)	**P**	*Najas marina* (Holly-leaved Naiad)	**P**
Rana lessonae (Pool frog)	**P**	*Mentha pulegium* (Pennyroyal)	**P**
		Crassula aquatica (Pigmyweed)	**P**
Invertebrates		*Alisma graminuem* (Ribbon-leaved Water-plantain)	**P**
Hirudo medicinalis (Medicinal leech)	**P**	*Damasonium alisma* (Starfruit)	**P**
Myax glutinosa (Glutinous snail)	**P**	*Corigiola littoralis* (Strapwort)	**P**
Margaritifera margaritifera (a pearl mussel)	R	*Limosella ausralis* (Welsh Mudwort)	**P**
Triops cancriformis (a tadpole shrimp)	**P**	*Cryphaea lamyana* (Multi-fruited River-moss)	R
Chirocepalus diaphanus (a fairy shrimp)	**P**	*Chara canescens* (Bearded Stonewort)	**P**
Austropotamobius pallipes (Atlantic stream crayfish)	R	*Colemma dichotomum* (River Jelly Lichen)	R
Grapoderus zonatus (spangled water beetle)	**P**		

Key:- R = River; L = Lake; P = Pond; BP = Brackish Pond and WG = Wet Grassland.
Note:- [1] The Common Toad (*Bufo bufo*), Smooth Newt (*Triturus vulgaris*) and Palmate Newt (*Triturus helvetica*) are not given complete protection and have been excluded from the table.

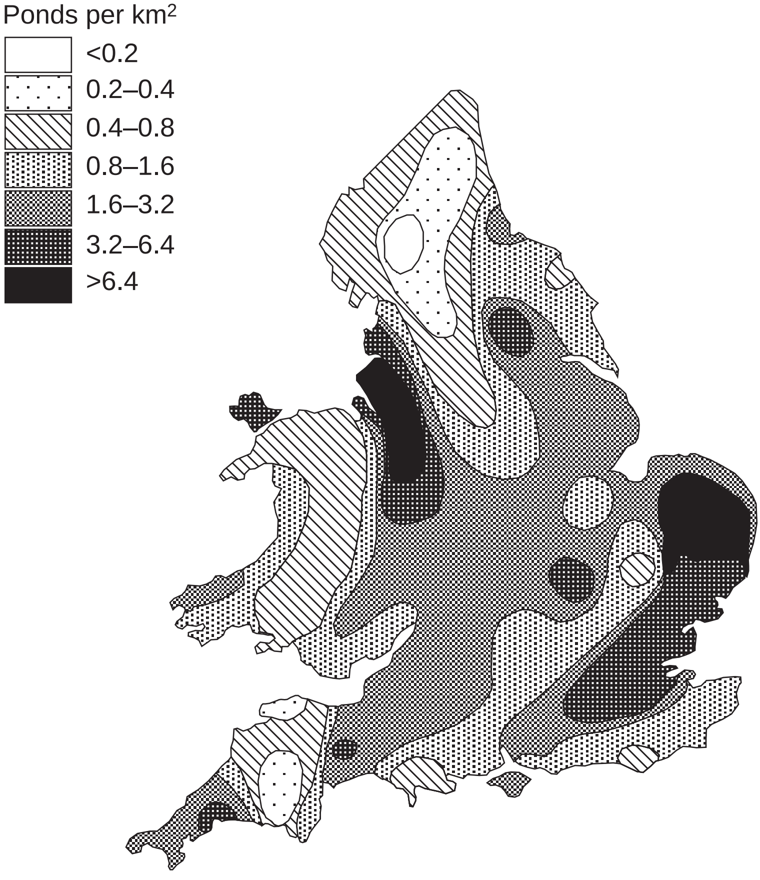
Table III. Aquatic Coleoptera of conservation interest recorded at the Flag Creek brackish water pond, Brightlingsea, Essex (Adapted from Greenwood and Wood 2003)

Taxa	Conservation Status [a]	
	Red Data Book (GB)	IUCN proposed status (GB)
Enochrus bicolor Fabricius	Nb	LRnsB
Ochthebius marinus (Payk.)	Nb	LRnsB
Ochthebius viridis Peyrhiff	Nb	LRnsB
Ochthebius punctatus Steph.	Nb	LRnsB
Hygrotus parallelogrammus (Ahrens)	Nb	LRnsB
Berosus affinis Brulle	Nb	LRnsB
Agabus conspersus (Marsham)	Nb	LRnsB
Rhantus frontalis (Marsham)	Nb	
Rhantus suturalis (MacLeay)	Nb	LRnsB
Paracymus aeneus Fabricus	RDB1	EN
Haliplus apicalis Thomson	Nb	LRnsB

Note:- [a] Conservation status based on Foster (2000); IUCN = The World Conservation Union; Nb = Nationally Notable List B; RDB1 = Red Data Book category 1; LRnsB = IUCN Red List category – Lower Risk, nationally scarce, list B and EN = IUCN Red List category – endangered.

Table IV. Estimates of pond loss from different parts of the UK.

Area	Period	Loss (%)	Annual Loss (%)	Change in number of Ponds (n)	Landuse	Source
Huddersfield	1985 - 1997	31	2.60	60 – 42	Urban / Industrial	Wood et al 2001a
North Leicestershire	1934 - 1979	60	1.33	958 - 370	Mostly pasture	Beresford and Wade 1982
Bedfordshire	1910 - 1981	82	1.15	Not quoted	Intensive arable	Beresford and Wade 1982
Sussex	1977 - 1996	21	1.10	33 – 26	Pasture (Dewponds)	Beebee 1997
London region	1870 - 1984	Up to 90	0.79	up to 16000 – 1600	Mixed	Langton 1984
Huntingdonshire (Cambs.)	1890 - 1980	56	0.68	Not quoted	Mixed	Beresford and Wade 1982
Cheshire	1870 - 1993	61	0.50	41564 – 16728	Rural and urban	Boothby and Hull 1997
Essex (selected areas)	1870 – 1989	55 – 69	0.46 – 0.58	1366 to between 616 and 423	Mixed	Heath and Whitehead 1992
Cambridgeshire	1840/90 - 1990	68	0.45 - 0.68	Not quoted	Intensive arable	Jeffries and Mills 1990
Leicestershire	1840/90 - 1990	60	0.40 - 0.60	Not quoted	Intensive arable	Jeffries and Mills 1990
Durham	1840/90 - 1990	41	0.27 - 0.41	Not quoted	Arable and pasture	Jeffries and Mills 1990
Clwyd	1840/90 - 1990	32	0.21 – 0.32	Not quoted	Arable and pasture	Jeffries and Mills 1990
Midlothian	1840/90 - 1990	23	0.15 – 0.23	Not quoted	Arable and pasture	Jeffries and Mills 1990
Edinburgh	1840/90 - 1990	6	0.04 – 0.06	Not quoted	Urban	Jeffries and Mills 1990
England and Wales	1880 - 1920	57.5	1.41	800000 – 340000	Mixed	Rackham 1986
Britain	1990 - 1996	7.4	1.23	230600 - 228900	Mixed – lowland ponds	Williams et al 1998
Great Britain	1900 - 1990	75	0.78	1189200- 297300	Mixed	Bailey-Watts et al 2000



Ponds per km2
<0.2
0.2–0.4
0.4–0.8
0.8–1.6
1.6–3.2
3.2–6.4
>6.4