Comparative biodiversity of aquatic habitats in the European agricultural landscape

Article *in* Agriculture Ecosystems & Environment · May 2008

Impact Factor: 3.4 · DOI: 10.1016/j.agee.2007.10.006

P. Nicolet
Freshwater Habitats Trust

David A Sear
University of Southampton

Stephen J Maund
Syngenta

Available online at www.sciencedirect.com
ScienceDirect
Agriculture, Ecosystems and Environment 125 (2008) 1–8
Agriculture Ecosystems & Environment
www.elsevier.com/locate/agee

Comparative biodiversity of aquatic habitats in the European agricultural landscape

Bella Davies [a,*], Jeremy Biggs [a], Penny Williams [a], Mericia Whitfield [a], Pascale Nicolet [a], David Sear [b], Simon Bray [c], Steve Maund [d]

[a] *Pond Conservation: The Water Habitats Trust, c/o School of Life Sciences, Oxford Brookes University, Gipsy Lane, Headington, Oxford OX3 0BP, UK*

[b] *Shackleton Building, University of Southampton, University Road, Southampton SO17 1BJ, UK*

[c] *Centre for Environmental Sciences, School of Civil Engineering and the Environment, University of Southampton, University Road, Southampton SO17 1BJ, UK*

[d] *Syngenta Crop Protection AG, 4002 Basel, Switzerland*

Received 9 March 2007; received in revised form 22 October 2007; accepted 24 October 2007
Available online 3 December 2007

Abstract

Recent evidence has begun to call into question the assumption that aquatic biodiversity is concentrated exclusively in larger rivers and lakes, instead showing that it is distributed throughout the landscape and that small waterbodies, such as ponds and ditches, make a significant contribution to biodiversity. We compared the physicochemical and aquatic biodiversity characteristics of ditches, lakes, ponds, rivers and streams in five locations in Europe in three biogeographic zones. At the individual site level (alpha diversity), rivers were found to be the most species-rich waterbodies; however, at the regional level (gamma diversity), ponds were the most species-rich aquatic habitat for both wetland plants and macroinvertebrates. In terms of rare species, ponds also had a higher rarity value, measured by a Species Rarity Index, than other habitat types, although data for this analysis were only available from the United Kingdom. The high biodiversity values of ponds suggest that they should be more central to strategies for the protection and management of aquatic biodiversity.

Keywords: Freshwater; Waterbody; Farming; Aquatic biota; Small waterbodies; Pond

1. Introduction

Currently, most attempts to control or mitigate the impacts of agriculture on freshwaters (in particular nutrient and pesticide pollution) are based on the assumption that aquatic biodiversity is mainly found in larger waterbodies, predominantly rivers and lakes. For example, in the Water Framework Directive (2000/60/EC) the word ‘pond’ is not mentioned and almost all Member States have effectively excluded standing waters less than 50 ha in area (i.e. all ponds) from the improvement mechanisms provided by the Directive. This reflects the long-standing tendency of aquatic ecologists to concentrate their work on larger lakes, rivers and streams, overlooking the often numerous smaller waterbodies, both natural and man-made, which are common in agricultural landscapes such as ditches, ponds, headwater streams, springs and flushes (Biggs et al., 2005; Downing et al., 2006).

Recent data have begun to call into question the simplicity of the ‘upstream pollutant source-downstream receiving water’ paradigm upon which mitigation from agricultural impacts is based. In one of the first studies of its kind, Williams et al. (2004) showed that, in a typical agricultural landscape in southern England, small waters distributed throughout the landscape contributed more to regional aquatic biodiversity than larger ‘downstream’ rivers, with the largest proportion of the regional species

* Corresponding author. Tel.: +44 1865 483269; fax: +44 1865 483282.
E-mail address: brdavies@brookes.ac.uk (B. Davies).

0167-8809/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.agee.2007.10.006

pool occurring in the smallest type of waterbody surveyed: ponds. This probably reflects, in part, the fact that 'downstream' locations in catchments are typically the most impacted by human activities, resulting in greater biodiversity impacts in these locations. Although around 71% of the wetland plant and aquatic invertebrate species found in the study area were present in ponds, these ponds had the smallest total surface area of the five waterbody types investigated (Table 7.1 in Davies, 2005). Ditch systems and small streams have also been found to be important reservoirs for aquatic biodiversity (Painter, 1999; Malmqvist and Hoffsten, 2000; Armitage et al., 2003; Heino et al., 2005). Taken together these observations suggest that a new paradigm of aquatic biodiversity in the agricultural landscape is needed, one in which biodiversity is seen as occurring in waterbodies embedded throughout the agricultural landscape.

There is, therefore, an urgent need for comparative data that describe the characteristics of aquatic ecosystems to provide the basis for more refined models of the structure and function of freshwater habitats in agricultural ecosystems. The aim of the present work was to extend earlier studies undertaken in the United Kingdom (Williams et al., 2004; Davies, 2005; Biggs et al., 2007) to explore the biodiversity patterns of a range of waterbody types and investigate whether the patterns observed by Williams et al. (2004) in southern England were repeated in other agricultural landscapes. This involved characterising and comparing the biological, physicochemical and morphological characteristics of the ditch, lake, pond, river and stream habitats of a range of agricultural landscapes. Specifically, the present study assessed the patterns of aquatic biodiversity of the different waterbody types in terms of species richness, and where possible species rarity, in three biogeographic zones of Europe (Atlantic, Continental and Mediterranean), using data from study locations in the United Kingdom (UK), France, Germany and Denmark.

2. Methods

2.1. Study locations

Data for the present study were collected from five locations across Europe centred on Avignon (France), Braunschweig (Germany), Funen (Denmark), Coleshill (UK) and Whitchurch (UK). Study locations in Denmark, Germany and France were approximately 60 km × 60 km in area, whereas those in the UK were about 10 km × 10 km in area. The UK sites and Funen were located in the Atlantic biogeographic region of Europe, with Braunschweig in the Central region, and Avignon in the Mediterranean biogeographic region (EEA, 1995). To ensure that the study results would be broadly typical of European agricultural regimes, the study locations were selected to represent the agricultural scenarios developed under the EU FOCUS programme for pesticide risk assessment (FOCUS, 2001). These scenarios are based on combinations of soils, climate and cropping for 10 landscape types representative of European agriculture.

Table 1
The number of survey sites at each study location by waterbody type

	Ditches	Lakes	Ponds	Rivers	Streams	Total
Avignon	30	9	21	9	21	90
Braunschweig	30	1	29	4	26	90
Funen	30	1	29	8	22	90
Coleshill	20	1	19	11	9	60
Whitchurch	13	n/a	13	0	13	39

Waterbodies in the study locations were first categorised as either ditches, lakes, ponds, rivers or streams according to the definitions in Williams et al. (2004). For sites in France, Germany and Denmark, existing national GIS datasets on ditches were also used. In Whitchurch no waterbodies were wide enough to be categorised as rivers and, therefore, only streams were surveyed. Sample sizes were not always the same between study locations (Table 1), for example, resource limitations meant that the sample size at Whitchurch was smaller. In Funen and Braunschweig lakes were rare features so most of the standing waters surveyed were ponds (29 ponds + 1 lake). In Avignon there were fewer ponds and it was necessary to survey 8 lakes to obtain a sample of 30 ponds and lakes. In the remainder of the paper the ponds + lakes category, which predominantly comprised ponds, is referred to as 'ponds'.

2.2. Survey techniques

Surveys were undertaken from 1997 to 2002 (surveys at Whitchurch were carried out from April to May 1997 and March to May 1998, at Coleshill April to May and October to November 2000, at Funen in July 2001, at Braunschweig in August 2001 and at Avignon in July 2002). Sampling was undertaken on an area-limited basis to eliminate species-area effects from the study. In the UK, a 75 m^2 sampling area was used for all waterbodies, while in Denmark, Germany and France, a 50 m^2 sampling area was used. Thus, for a 1 m wide ditch in a UK site, a 75 m length was surveyed. For ponds and lakes, a wedge-shaped area was surveyed with the apex at the centre of the waterbody and the base following the margin. The sampling area within the waterbody was selected (visually) to be representative of the waterbody as a whole, e.g. if the waterbody included both shaded and open mesohabitats a sampling area was selected which included both these types of mesohabitat. Although this area-based survey method enabled waterbodies with widely differing dimensions and characteristics to be compared, it had the disadvantage that small waterbodies less than 75 or 50 m^2 (depending on the study location) could not be included in the survey.

Physicochemical data were collected from each of the sites. pH and conductivity were measured at all sites while additional more detailed chemical data describing nutrient, suspended sediment and dissolved oxygen concentrations were collected at UK sites. pH, conductivity and dissolved oxygen concentrations were measured in the field; for all other chemical parameters, water samples were collected in the field and returned to the laboratory for analysis using standard methods. All wetland macrophytes present in each sample area were recorded either by walking and wading shallow regions and the margins of waterbodies, or in deeper water using a grapnel thrown from the bank or a boat. In the UK, 'wetland macrophytes' were defined as those plants listed as wetland plants in the National Pond Survey methods guide (Biggs et al., 1998), whilst in other locations, wetland macrophytes were those species listed as being associated with wetlands in Flora Europaea (Tutin et al., 1980). This included aquatic marginal, emergent, floating-leaved and submerged plants.

Data on macroinvertebrates were collected from sites in the Coleshill, Whitchurch and Avignon areas only. A 1 mm mesh hand-net was used to sample for a total of 3 minutes, with the total sampling time being divided equally between the major mesohabitats present in the survey area, e.g. riffles, pools, bank, open water and stands of vegetation with differing structure. Samples were live-sorted in the laboratory to remove all individual macroinvertebrates, with the exception of very abundant taxa (>100 individuals), which were sub-sampled. In the UK, where reliable distribution data and Red Data Book information were available, macroinvertebrates were identified to species level except for *Pisidium* species, Diptera larvae and Oligochaeta, which were noted at family or genus level and were not included in the analysis of species richness. In Avignon, macroinvertebrates were identified to family level.

2.3. Data analysis

The richness and, where possible, national status ('rarity') of macrophyte and macroinvertebrate taxa were used to assess the biodiversity value of each waterbody type. A summary of the biodiversity patterns at the European level was made by grouping macrophyte data from the five sites.

Alpha diversity (i.e. average site diversity) was the mean number of taxa or their rarity at a site, whilst gamma diversity (i.e. total diversity for a waterbody type) was the total richness or rarity of taxa across all sites for three categories of waterbody: ditches, ponds + lakes and rivers + streams. Amalgamation of pond and lake sites and of river and stream sites was necessary to attain equal sample sizes. True regional gamma diversity was estimated for each waterbody type at each study location using the program EstimateS with 500 randomisations (Version 7.5; Colwell, 2005). The non-parametric Incidence-Based Coverage Estimator (ICE) was always used to estimate likely species richness unless the incidence distribution exceeded a value of 0.5, in which case Chao2 was used, as instructed by Colwell (2005). These techniques use information about the occurrence of rare species to take account of the species present but not observed to predict the likely species richness of an area. Where an asymptote was not reached in this process the value given was the minimum number of species likely to be present. An asymptote was considered to have been reached when the last two values were identical or within 1% of each other and the last 20% of the values were within 2% of the final value (Foggo et al., 2003). The similarity of species between sites (beta diversity) was investigated for both macrophytes and macroinvertebrates using Jaccard's similarity coefficient, calculated using EstimateS.

Species rarity data were available for the UK and a Species Rarity Index (SRI) was used to assess rarity for the UK sites. This index was calculated in three steps: (i) each species was assigned a score based on its national rarity status (Table 2); (ii) the score was summed for each site to give a Species Rarity Score (SRS); (iii) the SRS was divided by the number of species at that site. Thus, the resulting SRI value enabled rarity to be compared without being biased towards species-rich sites or penalising inherently species poor sites and habitats.

3. Results

UK waterbodies were surrounded by the highest proportions of intensive landuses and, as might be expected, ditches were associated with the highest proportions of intensive landuse in all locations. Ranges of physicochem-

Table 2
Species Rarity Score for UK species (after Foster et al., 1990)

Rarity status	Score	Description of occurrence
Common	1	Species generally regarded as common
Local	2	Plants: local species recorded between 101 and 700, 10 km × 10 km grid squares in Britain (Preston et al., 2002). Macroinvertebrates: species either confined to limited geographical areas where populations may be common or with widespread distribution but relatively low population
Nationally scarce	4	Recorded from 15 to 100, 10 km × 10 km grid squares in Britain
Red Data Book	8	Conservation dependent or near threatened
Red Data Book	16	Endangered or vulnerable
Red Data Book	32	Critically endangered

Table 3
Summary of physicochemical characteristics of waterbodies in the five study areas: (a) Avignon, (b) Braunschweig, (c) Funen, (d) Coleshill and (e) Whitchurch

	Ditches	Ponds	Rivers	Streams
(a) Avignon				
Width (m) or area (m^2)	2.0 (0.7–4.4)	2597.2 (36.0–7500.0)	18.4 (3.0–50.0)	2.9 (0.9–9.0)
Average total depth (m)	0.26 (0–0.9)	0.86 (0–1.51)	0.28 (0.4–0.85)	0.18 (0–0.77)
Permanence	2.4 (1.0–4.0)	2.0 (1.0–4.0)	1.4 (1.0–3.0)	2.1 (1.0–4.0)
Shade (%)	14.7 (0.0–100.0)	11.5 (0.0–60.0)	24.7 (0.0–100.0)	29.9 (0.0–100.0)
Macrophyte cover (%)	7.9 (0.0–50.0)	14.6 (0.0–76.0)	3.4 (0.0–15.0)	7.2 (0.0–90.0)
Intensive landuse in 100 m (%)	75.2 (2.0–100.0)	41.0 (0.0–100.0)	55.3 (0.0–92.0)	61.1 (0.0–100.0)
Overall pollution risk	2.9 (0.0–5.5)	2.7 (0.0–10.0)	2.8 (0.0–5.5)	3.0 (0.0–9.0)
pH	7.6 (4.7–8.3)	7.8 (7.1–9.3)	7.9 (7.2–8.1)	7.6 (7.0–8.3)
Conductivity ($\mu S\ cm^{-1}$)	790 (515–1653)	525 (280–1046)	588 (417–861)	917 (533–1643)
Dissolved oxygen (%)	6.9 (3.4–9.9)	8.0 (1.0–19.0)	8.1 (3.0–10.6)	5.8 (0.9–12.9)
(b) Braunschweig				
Width (m) or area (m^2)	1.3 (0.5–3.6)	2924.5 (110.0–13000.0)	12.0 (6.0–24.5)	2.3 (0.9–9.0)
Average total depth (m)	0.13 (0–0.54)	0.95 (0–1.71)	0.58 (0.39–0.91)	0.22 (0–0.59)
Permanence	2.9 (1.0–4.0)	1.4 (1.0–4.0)	1.0 (1.0–1.0)	2.0 (1.0–4.0)
Shade (%)	14.0 (0.0–100.0)	11.0 (0.0–50.0)	15.0 (0.0–50.0)	38.3 (0.0–100.0)
Macrophyte cover (%)	42.0 (0.3–95.0)	45.9 (20.–100.0)	8.8 (5.0–16.0)	44.8 (0.1–95.0)
Intensive landuse in 100 m (%)	82.9 (0.0–99.0)	43.4 (0.0–95.0)	51.0 (10.0–90.0)	66.9 (5.0–99.0)
Overall pollution risk	4.1 (0.0–6.0)	3.6 (0.0–12.0)	4.8 (2.0–8.0)	3.6 (1.0–6.0)
pH	7.3 (6.4–7.8)	7.3 (5.3–9.2)	7.4 (7.0–7.7)	7.3 (6.0–8.2)
Conductivity ($\mu S\ cm^{-1}$)	800 (297–2320)	469 (97–1714)	1243 (781–2080)	946 (174–2460)
(c) Funen				
Width (m) or area (m^2)	1.7 (0.7–3.4)	1757.4 (70.0–6500.0)	8.4 (4.0–18.0)	3.4 (1.8–6.3)
Average total depth (m)	0.21 (0.02–0.77)	0.74 (0.30–1.55)	0.63 (0.32–0.96)	0.30 (0.04–0.93)
Permanence	2.2 (1.0–4.0)	1.2 (1.0–3.0)	1.0 (1.0–1.0)	1.1 (1.0–2.5)
Shade (%)	37.6 (0.0–100.0)	19.1 (0.0–100.0)	10.8 (0.0–60.0)	46.5 (0.0–100.0)
Macrophyte cover (%)	19.6 (0.1–70.0)	39.9 (0.0–99.0)	42.8 (15.0–80.0)	34.8 (0.1–95.0)
Intensive landuse in 100 m (%)	72.8 (6.0–100.0)	70.3 (16.0–98.0)	46.7 (0.0–77.5)	66.4 (25.0–100.0)
Overall pollution risk	3.8 (0.0–9.5)	3.6 (2.0–8.5)	1.8 (1.0–4.0)	3.6 (1.0–7.5)
pH	7.7 (5.1–8.3)	7.8 (6.3–9.2)	8.1 (7.9–8.4)	8.0 (6.3–8.4)
Conductivity ($\mu S\ cm^{-1}$)	713 (330–2668)	597 (140–1240)	655 (600–770)	581 (340–780)
(d) Coleshill				
Width (m) or area (m^2)	1.2 (0.3–3.5)	614.9 (75.0–3236.0)	7.4 (5.5–10.0)	2.3 (1.0–4.0)
Average total depth (m)	0.23 (0.06–0.62)	0.89 (0.24–1.65)	1.11(0.21–2.00)	0.56 (0.18–1.57)
Permanence	3.2 (1.0–4.0)	1.8 (1.0–4.0)	1.0 (1.0–1.0)	1.4 (1.0–3.0)
Shade (%)	41.7 (0.0–95.0)	32.0 (0.0–95.0)	16.5 (0.0–70.0)	30.3 (0.0–85.0)
Macrophyte cover (%)	26.4 (0.1–98.0)	30.7 (0.2–96.0)	32.0 (2.0–70.0)	25.5 (1.0–85.0)
Intensive landuse in 100 m (%)	87.5 (45.0–100.0)	64.5 (0–99.0)	84.5 (49.0–99.0)	74.4 (44.0–100.0)
Overall pollution risk	4.9 (3.5–7.0)	3.8 (0–7.0)	3.8 (3.5–4.5)	4.8 (2.0–7.0)
pH	8.0 (7.3–9.2)	8.5 (7.5–8.9)	8.2 (7.9–8.4)	8.1 (8.0–8.2)
Conductivity ($\mu S\ cm^{-1}$)	791 (564–1402)	664 (322–1265)	673 (601–705)	781 (575–1059)
Dissolved oxygen (%)	117 (55–222)	134 (63–256)	142 (117–158)	113 (94–140)
Nitrate nitrogen ($mg\ l^{-1}$)	5.6 (0.4–17.7)	3.9 (0.1–38.3)	5.8 (3.2–9.7)	8.4 (2.3–18.5)
Total phosphorus ($mg\ l^{-1}$)	0.14 (0.002–0.880)	0.28 (0.002–2.490)	0.184 (0.064–0.252)	0.313 (0.005–1.340)
Suspended solids ($mg\ l^{-1}$)	35 (1–150)	76 (1–794)	23 (7–101)	19 (10–38)
(e) Whitchurch				
Width (m) or area (m^2)	1.9 (1.1–3.2)	757.3 (75.0–2350.0)	–	2.3 (1.1–4.5)
Average total depth (m)	0.34 (0.05–1.50)	0.91 (0.31–1.36)	–	0.22 (0.07–0.61)
Permanence	2.5 (1.0–4.0)	1.3 (1.0–2.5)	–	1.8 (1.0–4.0)
Shade (%)	34.2 (0–100.0)	32.4 (0.0–100.0)	–	64.8 (2.0–100.0)
Macrophyte cover (%)	34.0 (0.1–80.0)	53.9 (0.1–95.0)	–	8.5 (0.0–23.0)
Intensive landuse in 100 m (%)	78.1 (0–97.0)	88.2 (23.0–100.0)	–	62.9 (0.0–93.0)
Overall pollution risk	–	–	–	–
pH	7.3 (5.2–9.2)	7.6 (6.8–9.4)	–	7.9 (7.1–8.7)
Conductivity ($\mu S\ cm^{-1}$)	738 (289–2190)	378 (120–540)	–	648 (250–936)
Dissolved oxygen (%)	69.3 (11.5–100.4)	74 (13–150)	–	84 (38–114)
Nitrate nitrogen ($mg\ l^{-1}$)	5.3 (0.2–23.3)	0.4 (0.2–1.1)	–	5.4 (1.4–11.7)
Total phosphorus ($mg\ l^{-1}$)	1.06 (0.016–9.02)	0.657 (0.013–5.420)	–	0.357 (0.033–1.680)
Suspended solids ($mg\ l^{-1}$)	102 (15–595)	105 (5–615)	–	18 (7–58)

Values shown are mean with range in parentheses.

Table 4
Mean site richness (alpha diversity) for (a) macrophyte species, (b) macroinvertebrate species and (c) macroinvertebrate families, with range in parentheses

	Ditches	Ponds	Rivers	Streams
(a) Macrophyte species				
Avignon[a]	6.0 (0–16)	8.1 (2–18)	9.8 (2–17)	7.1 (2–16)
Braunschweig	5.8 (2–14)	7.8 (2–22)	6.3 (5–8)	6.3 (2–11)
Funen	6.5 (1–11)	9.4 (0–20)	12.0 (8–17)	8.9 (0–14)
Coleshill	6.1 (1–14)	10.2 (2–17)	10.7 (6–19)	7.3 (1–17)
Whitchurch	9.5 (1–20)	15.3 (1–41)	–	7.2 (0–15)
(b) Macroinvertebrate species				
Coleshill	12.9 (2–35)	32.7 (5–67)	45.3 (18–66)	18.7 (3–50)
Whitchurch	17.3 (1–30)	29.7 (3–62)	–	18.5 (9–29)
(c) Macroinvertebrate families				
Avignon[a]	16.9 (10–24)	13.5 (2–21)	23.7 (15–29)	15.8 (3–28)
Coleshill	9.0 (2–15)	16.3 (2–32)	29.4 (16–36)	13.9 (3–31)
Whitchurch	9.8 (1–18)	14.5 (3–27)	–	12.5 (6–16)

[a] Excluding dry sites.

ical values tended to be greater in smaller waterbodies, with sites in larger waterbodies having more homogenous physicochemical characteristics (Table 3). In most locations, rivers had the highest mean macrophyte diversity and ditches the lowest, although the difference between all waterbody types was not significant (Kruskal–Wallis test) (Table 4a). However, ponds generally supported the greatest number of macrophyte species recorded at an individual site. Similar alpha diversity patterns were observed for macroinvertebrates at both the species (Table 4b) and family level (Table 4c). The SRI calculated for UK sites showed that ponds usually had the highest mean values for both macrophytes and macroinvertebrates, they also had the highest recorded SRI value and the greatest range of values. For macrophytes, ditches and streams had low SRI values, while for macroinvertebrates, ditches had relatively high SRI values and streams had relatively low values.

In terms of regional species richness, ponds collectively supported the highest values for both macrophytes (Fig. 1) and macroinvertebrates (Fig. 2), a pattern that was clearly reinforced by the predicted species richness values. At the regional scale macroinvertebrate family richness was greatest in rivers and streams (Fig. 3). Regional patterns of species rarity showed that ponds generally had the highest SRI scores for both macrophyte and macroinvertebrate species, with ditches also scoring highly for macroinvertebrate rarity. Relatively low SRI values were observed for ditch macrophytes and river + stream macroinvertebrates. In terms of beta diversity, the Jaccard's similarity coefficients showed river and stream sites to support the most uniform assemblages while pond sites had the most dissimilar macrophyte communities and ditches the most dissimilar macroinvertebrate communities. All waterbody types supported unique species, i.e. species that were not observed in any other waterbody type, with the greatest number clearly occurring in ponds (Table 5).

By way of summarising patterns with all locations combined, mean alpha macrophyte diversity was greatest for rivers (10.3, range 2–19) followed by ponds (9.5, range 0–41), lakes (7.6, range 2–15), streams (7.5, range 0–17) and lastly ditches (6.6, range 0–20). Macrophyte gamma

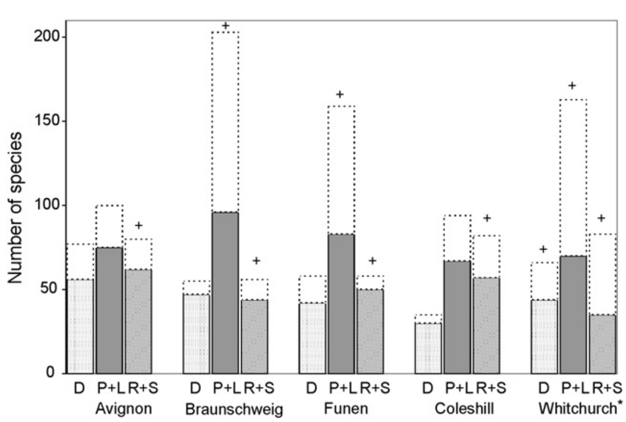

Fig. 1. Surveyed (shaded) and predicted (dashed line) macrophyte gamma diversity (regional species richness) across each study location by waterbody type. "+" indicates a minimum predicted richness value; D = ditches; P + L = ponds + lakes; R + S = rivers + streams. *No rivers or lakes present.

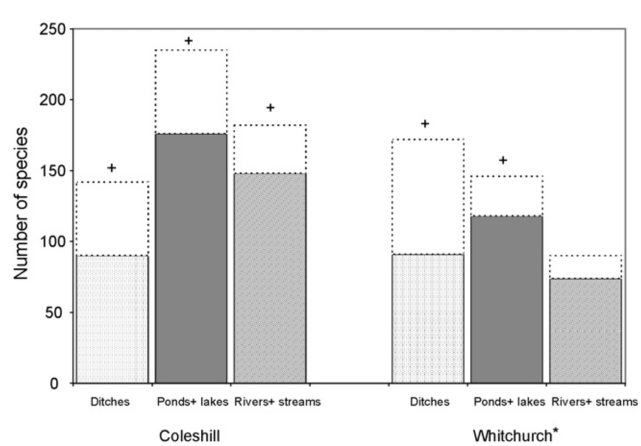

Fig. 2. Surveyed (shaded) and predicted (dashed line) macroinvertebrate gamma diversity (regional species richness) across locations in the UK. "+" indicates a minimum predicted richness value. *No rivers or lakes present.

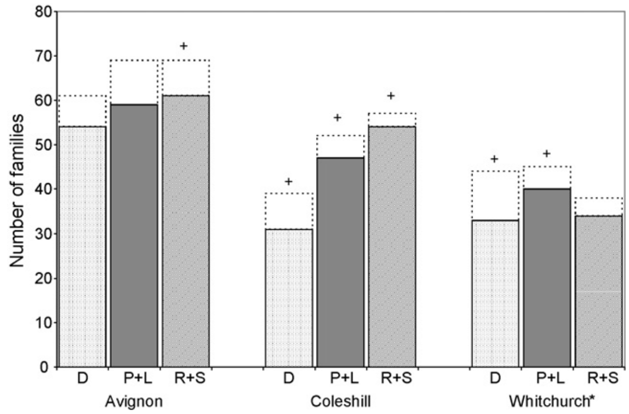

Fig. 3. Surveyed (shaded) and predicted (dashed line) macroinvertebrate family richness (gamma diversity). "+" indicates a minimum predicted richness value; D = ditches; P + L = ponds + lakes; R + S = rivers + streams. *No rivers or lakes present.

Table 5
Unique species contributed by each waterbody type

	Ditches	Lakes	Ponds	Rivers	Streams
Macrophytes					
Avignon	6	1	10	3	3
Braunschweig	5	1	45	1	2
Funen	5	1	42	7	2
Coleshill	3	0	22	10	3
Whitchurch	10	–	36	–	8
Total	29	3	155	20	18
Macroinvertebrates					
Coleshill	11	0	55	24	1
Whitchurch	14	–	50	–	27
Total	22	0	96	25	32

diversity was greatest for ponds for both surveyed (171) and predicted (>204) species richness and similar between the ditch and rivers + streams categories (109 and 113 species surveyed, respectively), although predicted species numbers (131 and >130, respectively) indicated that more species may occur in rivers + streams than in ditches at the European level. The most similar macrophyte communities occurred within the ditch sites (Sj = 0.14, S.D. = 0.11), the stream sites (Sj = 0.14, S.D. = 0.11) and the river sites (Sj = 0.13, S.D. = 0.09), whilst the lake sites (Sj = 0.09, S.D. = 0.08) and pond sites (Sj = 0.11, S.D. = 0.08) supported the most dissimilar communities. Ponds clearly supported the highest overall number of unique macrophyte species (49), followed by ditches (11), rivers and streams (3 each) and lastly lakes (1 unique species).

4. Discussion

There was an overall trend for smaller and more lentic waterbodies to have more variable physicochemical characteristics and larger, more lotic waterbodies to be more similar. Such variability amongst the physicochemical characteristics of small waterbodies has been noted previously (e.g. Biggs et al., 2005; De Meester et al., 2005; Søndergaard et al., 2005) and is likely to have resulted from a combination of the small size of ponds and ditches and the relative ease with which they are created. These characteristics enable them to exist over a wide variety of geographic and environmental gradients (e.g. altitude, geology, aspect, land cover types) and so they are subject to a multiplicity of influences on a variety of scales. In contrast the location within the landscape of rivers, and to some extent streams, tends to be less diverse. For example, rivers naturally occupy the lowest topographic point and tend to drain relatively large catchment areas causing any environmental variation across a catchment to be integrated, leading to comparatively uniform physicochemical environments (Biggs et al., 2005). Conversely, ponds have relatively small catchment areas (Davies et al., 2008) enabling different ponds in close proximity to have quite different catchment characteristics.

In all study locations, alpha diversity patterns replicated the results of Williams et al. (2004) working only at Coleshill, with rivers tending to have the highest alpha diversity for both plants and macroinvertebrates. The least species-rich habitats were ditches, probably reflecting their small size and physically simple structure as well as their temporary nature and close proximity to agricultural land: for example, the use of herbicides is likely to reduce the number of plant species (Armitage et al., 2003; Williams et al., 2004). However, previous studies have found ditches to be diverse and sometimes exceptionally so for both plants (Verdonschot, 1990; Milsom et al., 2004; Biggs et al., 2007) and macroinvertebrates (Painter, 1999). These species-rich ditches typically occur in low-lying fen landscapes, which are generally deeper and more permanent than the ditches of the current study and often have considerable historic continuity with ancient natural wetlands and comparatively clean unpolluted water (Drake, 2004; Watson and Ormerod, 2004).

Regional species richness showed strikingly different patterns to those seen for alpha diversity, with ponds (or ponds + lakes) clearly supporting the largest number of plant and macroinvertebrate species. These patterns are alluded to by national species datasets, for example, Biggs et al. (2005) compared UK national datasets for pond and river macroinvertebrates and for pond and lake microphytes. Despite the river database including three times as many sample sites, the ponds supported approximately 10% more macroinvertebrate species and twice as many rare species as the rivers. The lake database contained over five times as many sites as the pond database but the ponds supported only a few less macrophyte species, an equal number of which were rare. In the present study, the patterns of gamma richness were most pronounced at the locations in continental Europe, strongly supporting the initial results of Williams et al. (2004) in the UK and two smaller-scale studies by Verdonschot (1990) and Usseglio-Polatera (1994). It is, therefore, clear that smaller waterbodies are not simply inferior versions of their larger counterparts in terms of species richness as has often been assumed.

Ponds also had high rarity index values at both site and regional scales and at Whitchurch, ditches had high macroinvertebrate SRI values. The importance of ponds and ditches for rare species has been observed in a number of studies (e.g. Nicolet et al., 2004; Watson and Ormerod, 2004; Della Bella et al., 2005) but, as in other aspects of landscape biodiversity, the causes of their high species rarity are not well understood. However, the overall high gamma species richness observed for ponds is likely to be related to their relatively high beta diversity and attributable to two main factors. Firstly, the relatively large ranges in their physicochemical conditions provide a variety of habitats which cumulatively result in greater species richness across the region. Secondly, stochastic events tend to have greater influence over the biotic assemblages of small waters, resulting in high beta diversity (Scheffer et al., 2006). It is important to note that the clear and consistent biodiversity patterns observed for macrophyte species and for macroinvertebrate species differed when looking at regional family level macroinvertebrate data, demonstrating the need for species level data to assess true patterns of biodiversity at the landscape scale (e.g. Furse et al., 1984; Hawkins and Vinson, 2000; Schmidt-Kloiber and Nijboer, 2004).

Although the pond and lake data had to be amalgamated to obtain equal sample sizes for gamma diversity comparisons, the high richness of the standing waters was not likely to be the result of including large lakes in the analysis. In all study locations except Avignon, standing waters included a maximum of one lake, which always had lower species richness than the ponds. The classic species–area relationship has not always been observed in lentic waterbodies (e.g. Oertli et al., 2002), with higher levels of biodiversity often being found in smaller waterbodies (van Geest et al., 2003; Søndergaard et al., 2005; Biggs et al., 2007), possibly because of the reduced presence of fish (e.g. Schinder et al., 2001; Søndergaard et al., 2005; Scheffer et al., 2006). In addition, a recent extension to the Coleshill dataset to include 20 lake sites (Davies, 2005) showed ponds to remain the most species-rich habitat type across the study area (with 238 species) followed by rivers (201 species), lakes (186 species), streams (163 species) and lastly ditches (120 species) (Davies et al., 2008).

The present study has a number of implications for the protection and management of freshwater ecosystems in agricultural landscapes. It is first important to note that agricultural landscapes are not 'deserts' for aquatic biota: a range of aquatic species were supported in each landscape and all of the surveyed waterbody types contributed to this biodiversity, with each supporting unique species. However, it was clear from the results that aquatic biodiversity is not spread evenly across an agricultural landscape, implying that resources allocated for the protection of aquatic biota in farmed areas may be used most effectively if they are focussed towards waterbody types supporting high biodiversity, such as ponds. Current options for the widespread protection of ponds offered under European agri-environment initiatives tend to involve passive mitigation, e.g. protection using buffer strips, rather than proactive management and creation. Encouraging the more extensive protection and creation of ponds throughout agricultural landscapes, so that a variety of successional stages are maintained, is likely to enhance the aquatic biodiversity of agricultural areas at the landscape scale.

Acknowledgements

The authors would like to thank Syngenta for funding the collection of data in Denmark, France and Germany, Defra for funding the collection of data at Whitchurch and NERC at Coleshill. The authors would also like to thank the Jonathan and Polly Wood Family Trust for funding part of the reporting of this research.

References

Armitage, P.D., Szoszkiewicz, Blackburn, J.H., Nesbitt, I., 2003. Ditch communities: a major contributor to floodplain biodiversity. Aquat. Conserv.: Mar. Freshwater Ecosyst. 13, 165–185.

Biggs, J., Fox, G., Nicolet, P., Walker, D., Whitfield, M., Williams, P., 1998. A Guide to the Methods of the National Pond Survey. Pond Action, Oxford.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Weatherby, A., 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. Aquat. Conserv.: Mar. Freshwater Ecosyst. 15, 693–714.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Brown, C., Hollis, J., Arnold, D., Pepper, T., 2007. The freshwater biota of British agricultural landscapes and their sensitivity to pesticides. Agric. Ecosyst. Environ. 122, 137–148.

Colwell, R.K., 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application published at: http://purl.oclc.org/estimates.

Davies, B.R., 2005. Developing a strategic approach to the protection of aquatic biodiversity. Unpublished Ph.D. Thesis. Oxford Brookes University.

Davies, B.R., Biggs, J., Williams, P.J., Lee, J.T., Thompson, S., 2008. A comparison of the catchment sizes of rivers, streams, ponds, ditches and lakes: implications for protecting aquatic biodiversity in an agricultural landscape. Hydrobiologia 597, 7–17.

Della Bella, V., Bazzanti, M., Chiarotti, F., 2005. Macroinvertebrate diversity and conservation status of Mediterranean ponds in Italy: water, permanence and mesohabitat influence. Aquat. Conserv.: Mar. Freshwater Ecosyst. 15, 583–600.

De Meester, L., Declerck, S., Stoks, R., Louette, G., Van de Meutter, F., De Bie, T., Michels, E., Brendonck, L., 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. Aquat. Conserv.: Mar. Freshwater Ecosyst. 15, 715–725.

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M., Middleburg, J.J., 2006. The global abundance and size distribution of lakes, ponds and impoundments. Limnol. Oceanogr. 51, 2388–2397.

Drake, C.M., 2004. Grazing marsh assemblages and site classification using macroinvertebrates. English Nature Research Report 579. English Nature, Peterborough.

European Environment Agency (EEA), 1995. Europe's environment: second assessment. A report on the changes in the Pan-European environment as a follow-up to Europe's environment: The Dobris Assessment. EEA, Copenhagen.

FOCUS, 2001. FOCUS surface water scenarios in the EU evaluation process under 91/414/EEC. Report of the FOCUS working group on surface water scenarios, EC Document Reference SANCO/4802/2001-rev.1.

Foggo, A., Rundle, S.D., Bilton, D., 2003. The net results: evaluating species richness extrapolation techniques for littoral pond invertebrates. Freshwater Biol. 48, 1756–1764.

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

Furse, M.T., Moss, D., Wright, J.F., Armitage, P.D., 1984. The influence of seasonal and taxonomic factors on ordination and classification of running-water sites in Great Britain and on the prediction of their macroinvertebrate communities. Freshwater Biol. 14, 257–280.

Hawkins, C.P., Vinson, M.P., 2000. Weak correspondence between landscape classifications and stream invertebrate assemblages: implications for bioassessment. J. North Am. Benthol. Soc. 19, 501–517.

Heino, J., Parviainen, J., Paavola, R., Jehle, M., Louhi, P., Muotka, T., 2005. Characterizing macroinvertebrate assemblage structure in relation to stream size and tributary position. Hydrobiologia 539, 121–130.

Malmqvist, B., Hoffsten, P.O., 2000. Macroinvertebrate taxonomic richness, community structure and nestedness in Swedish streams. Arch. Hydrobiol. 150, 29–54.

Milsom, T.P., Sherwood, A.J., Rose, S.C., Town, S.J., Runham, S.R., 2004. Dynamics and management of plant communities in ditches bordering arable fenland in eastern England. Agric. Ecosyst. Environ. 103, 85–99.

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

Oertli, B., Joyce, D.A., Castella, E., Juge, R., Cambin, D., Lachavanne, J.-B., 2002. Does size matter? The relationship between ponds area and biodiversity. Biol. Conserv. 104, 59–70.

Painter, D., 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken Fen, UK. J. Appl. Ecol. 36, 33–48.

Preston, C.D., Pearman, D.A., Dines, T.D., 2002. New Atlas of the British and Irish Flora. Oxford University Press, Oxford.

Scheffer, M., van Geest, G.J., Zimmer, K., Jeppesen, E., Sondergaard, M., Butler, M.G., Hanson, M.A., Declerck, S., De Meester, L., 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. Oikos 112, 227–231.

Schinder, D.E., Knapp, R.A., Leavitt, P.R., 2001. Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. Ecosystems 4, 308–321.

Schmidt-Kloiber, A., Nijboer, R.C., 2004. The effect of taxonomic resolution on the assessment of ecological water quality classes. Hydrobiologia 516, 269–283.

Søndergaard, M., Jeppesen, E., Jensen, H.P., 2005. Pond or lake: does it make any difference? Arch. Hydrobiol. 162, 143–165.

Tutin, T.G., Heywood, V.H., Burgess, N.A., Valentine, D.H., Walters, S.M., Webb, D.A., 1980. Flora Europaea. Cambridge University Press, Cambridge.

Usseglio-Polatera, P., 1994. Theoretical habitat templets, species traits and species richness: aquatic insects in the Upper Rhône River and its floodplain. Freshwater Biol. 31, 417–437.

van Geest, G.J., Roozen, F.C.J.M., Coops, H., Roijackers, R.M.M., Buijse, A.D., Peeters, E.T.H.M., Scheffer, M., 2003. Vegetation abundance in lowland flood plain lakes determined by surface area, age and connectivity. Freshwater Biol. 48, 440–454.

Verdonschot, P.F.M., 1990. Ecological characterisation of surface waters in the province of OverIjssel (The Netherlands). Unpublished Ph.D. Thesis. University of Wageningen.

Watson, A.M., Ormerod, S.J., 2004. The distribution of three uncommon freshwater gastropods in the drainage ditches of British grazing marshes. Biol. Conserv. 118, 455–466.

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 in Southern England. Biol. Conserv. 115, 329–341.