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Mission possible: diatoms can be used to infer past duckweed (lemnoid Araceae) dominance in ponds

Dave Emson · Carl D. Sayer · Helen Bennion · Ian R. Patmore · Patrick Rioual

Abstract Compared to larger lakes, ponds have rarely been the focus of palaeoecological studies. A common feature of ponds, especially those subject to eutrophication, is mass surface coverings of lemnoid Araceae (duckweed) which have severe implications for ecological processes in small waterbodies, in particular lowered oxygen content. To help understand the implications of duckweed dominance for the long-term ecology of ponds, and to determine the potential for palaeoecological studies in ponds more generally, we develop a new diatom-based *Lemna*-indicator metric. Recent studies of diatom host-plant relationships have shown significant associations between duckweed and the epiphytes *Lemnicola hungarica* and *Sellaphora saugerresii* (formally known as *Sellaphora seminulum*). To determine the potential of these species as palaeo-indicators of long-term duckweed dynamics in ponds, we investigated the diatom composition of surface sediment assemblages in sets of duckweed and non-duckweed-dominated ponds in Norfolk, eastern England. In addition, we undertook diatom analysis of two cores from a small farmland pond (Bodham Rail Pit) subject to a known duckweed dominance event (1999–2005). Both *L. hungarica* and *S. saugerresii* were significant predictors of past *Lemna* dominance in the surface sediments. Further, in the core study, both diatom species accurately and closely tracked the documented "on–off" duckweed cycle. Our study suggests huge potential for using ponds in palaeoecological studies and for diatom-based investigations of floating plant histories.

Keywords Floating plants · *Lemnicola hungarica* · Palaeoecology · *Sellaphora saugerresii* · *Sellaphora seminulum* · Surface sediments

Introduction

To date, both ecological and palaeoecological research has focused almost entirely on large, deep and shallow lakes, with minimal attention devoted to the 'poor cousins' of shallow lakes, namely ponds. The definition of a pond is currently fluid (Biggs et al. 2005), but in this study, we use it to refer to waterbodies with a maximum diameter of less than 100 m, where insufficient wind-mixing permits chemical stratification of the water-column (Sayer et al. 2013). In terms of palaeoecology, the lack of studies in ponds is particularly acute (Edwards et al. 2011; Emson 2015). While a number of palaeo-studies have been undertaken in arctic ponds (Douglas and Smol

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1994; Keatley et al. 2011; Bouchard et al. 2012; Stewart et al. 2013), few if any studies have focused on temperate European lowland ponds—as in this study. Nonetheless, in recent years, a number of studies have shown the predominantly agricultural pond resource of lowland Europe to be of major importance in terms of aquatic biodiversity conservation (Ruggiero et al. 2008; Sayer et al. 2012), aquatic—terrestrial energy subsidies (Davies et al. 2016) and carbon sequestration (Downing et al. 2008), among other roles. Given increasing interest in pond conservation, palaeoecology could have an important role in inferring long-term changes in pond ecology and function in response to environmental impacts.

A key impact, particularly in ponds subject to eutrophication and/or enhanced shading (terrestrialisation), is the development of dense mats of lemnoid Araceae (formally Lemnaceae, and hereafter referred to as duckweed) which typically results in severe water-column anoxia (Lewis and Bender 1961; Pokornŷ and Rejmánková 1983; Janes 1998) in turn causing fish kills (Lewis and Bender 1961), diurnal temperature stratification (Dale and Gillespie 1976), reductions in pH (McLay 1976) and loss of submerged macrophytes and macroinvertebrates (Janse and Van Puijenbroek 1998). The invasion of dense mats of free-floating plants is acknowledged as an important threat to the functioning and biodiversity of freshwater systems (Scheffer et al. 2003), with this especially true of ponds (Sayer et al. 2011). In this study, we test the potential for using sedimentary diatoms to indirectly infer the past presence of duckweed dominance in ponds.

For many diatom species, preferences for particular plant structures are generally poorly understood (Bennion et al. 2010). Indeed, despite several studies, potential species-habitat associations between epiphytic diatoms and different macrophyte species have remained relatively elusive, and it is probable that species-specific plant-diatom relationships are rare (Eminson and Moss 1980). There are some studies which do show strong host-plant links, however. For example Reavie and Smol (1997) revealed a close association between *Cocconeis pediculus* Ehrenb., and the filamentous algae *Cladophora* sp. in the St. Lawrence River, Canada. Additionally, Comte and Cazaubon (2002) showed a significant degree of homogeneity of the diatom communities associated with *Chara vulgaris* L., *Groenlandia densa* L. and *Cladophora glomerata* Kütz., in a large Mediterranean river, likely linked to substantial variation in plant surface micro-habitat.

Perhaps the best known example of diatom-habitat specificity is between *Lemnicola hungarica* (Grunow) Round and P.W. Basson (Synonym: *Achnanthes hungarica* (Grunow) Grunow in Cleve and Grunow) and free-floating lemnoid (duckweed) plants (Goldsborough 1993; Round and Basson 1997). Grunow first described *A. hungarica* in 1863 (hereafter referred to as *L. hungarica*), and it was noted that this species was found in lakes where duckweed was present. Hustedt (1930) commented that *L. hungarica* had a predisposition towards *Lemna* spp., and Round (1973) confirmed the observed association between *Lemna* spp. and *L. hungarica*. This habitat association was also used by Round and Basson (1997) to justify the establishment of *Lemnicola* as a new genus distinct from *Achnanthes* sensu lato. Associations between *L. hungarica* and free-floating plants were also observed by Bowker and Denny (1980), Goldsborough and Robinson (1985), and Goldsborough (1993, 1994) from field studies of diatom epiphytes sampled from *Lemna minor* L. Further, Zuberer (1984) identified *L. hungarica* in Scanning Electron Microscopy (SEM) studies of *L. minor*, as did Buczkó (2007) from herbarium specimens of various free-floating plants including *L. minor*, and Desianti (2012) from field collections of diatom epiphytes on free-floating plants. In a host-diatom study of 131 macrophyte samples from 63 sites, covering North and South America, northern Europe, southern Africa, Australia and Asia (Emson 2015), *L. hungarica* showed a significant association with free-floating plants, as did *Sellaphora seminulum* (recently named *Sellaphora saugerresii* (Desm.) C.E. Wetzel et D.G. Mann comb. nov., and hereafter referred to as *S. saugerresii*—Wetzel et al. 2015). Thus, several studies suggest a strong and robust association between *L. hungarica* and duckweed, and potentially *S. saugerresii* also.

Given the poor preservation of *Lemna* spp. fronds in sediments, and because species in the lemnoid Araceae rarely produce flowers, pollen or seeds (Hillman 1961; Landolt 1986), it is likely infeasible to reconstruct past duckweed dominance directly. Hence, this study will investigate the potential for using diatoms, specifically *L. hungarica* and *S. saugerresii*, as indirect indicators of duckweed in ponds. Firstly, we conducted a study of surface

sediment diatom assemblages from *Lemna*-covered ponds and from ponds with no *Lemna* surface coverage to establish contemporary diatom-duckweed relationships and thereby assess the potential for inferring changes in free-floating macrophyte cover, in small waterbodies. Secondly, we tested the ability of diatoms to track a documented duckweed "on–off" cycle in a small pond (Bodham Rail Pit) through diatom analysis of a sediment core.

Study sites

The surface sediment study focuses on a set of small ponds in Norfolk, eastern England. For the most part, the ponds are situated in arable agricultural land and have their origins as 'marl pits' being formed by marl extraction largely in the eighteenth–nineteenth centuries (Prince 1964). Other ponds have their origins as pingos formed at the end of the Last Glaciation 12.7–11.5 cal kyr BP (Flemel 1976). The ponds were all small (< 40 m max. diameter), shallow (generally < 1 m) and, in the case of the farmland ponds, largely alkaline and eutrophic (Table 1). Further details on the history, geography and ecology of ponds in the study area are given in Sayer et al. (2012).

Some 12 *Lemna*-dominated ponds were selected for study based on local knowledge of duckweed occurrence. In these ponds *L. minor* and/or *Lemna minuta* Kunth., was known to have been prevalent over at least 2–3 years at between 25 and 100% of water-surface cover. At the time of sampling (2012) 1, 3 and 8 sites were dominated by *L. minor*, *L. minuta* and co-dominated by *L. minor* and *L. minuta* respectively. For comparison 14 non-*Lemna* ponds were selected at random from a comparable study area. In all cases, it was known that these sites had not experienced duckweed domination in the recent (about the last 5 years) past.

The focus of the palaeoecological investigation was the Bodham Rail Pit (52° 54′20. 62″N; 1°09′21. 23″E), hereafter referred to as Rail Pit, a typical small (350 m^2), shallow (mean depth 103 cm) pond located in Bodham, North Norfolk (Fig. 1). The Rail Pit is located in arable farmland and surrounded by a 10 m rough grassland buffer zone. The pond is primarily ground-water fed but also receives surface runoff via a small road. Water levels in the pond fluctuate seasonally by about 1 m but it never completely dries out. The age of the pond is unknown, but it is shown on a tithe map dating to 1841, suggesting that it is at least 150–200 years old. Importantly, the pond underwent a major duckweed dominance event over 1999–2005, before and after which it is known to have been largely duckweed free. Over the period 1994–1998, prior to high duckweed coverage, the Rail Pit had abundant stands of *Potamogeton natans* L., but more recently (2008-present) it has been dominated by *Ceratophyllum submersum* L (Fig. 2).

Materials and methods

Historical plant records: Rail Pit

A recent history of aquatic macrophyte abundance for the Rail Pit is available from 1994 to 2016 (Sayer and Emson, unpublished data). In each year, plants were recorded on the DAFOR scale (Dominant—5, Abundant—4, Frequent—3, Occasional—2, Rare—1) based on visual observations assisted by plant collections made with a double–headed rake.

Surface sediment and core sampling

Surface sediments (upper 0–1 cm) were collected from the *Lemna*-covered (n = 12) and non-*Lemna* ponds (n = 14) variously using a Glew gravity corer (Glew 1991) and an improvised ladle attached to a long metal rod ("Pond Putter").

A 118-cm sediment core (RAIL1) was collected from the Rail Pit using a 'Big Ben' wide-bore piston corer (Patmore et al. 2014) from a southern central location at a depth of 108 cm (Fig. 1). The core was sliced on site at 1-cm intervals. On extrusion the core length was reduced to 75 cm, likely due to compaction of the very soft upper sediments which were very flocculent. Given the fluid upper section of RAIL1, and as the key aim was to track recent duckweed coverage, a short (22 cm) Glew core was also collected from an adjacent location. This core (RAIL2) was sliced at 0.5-cm intervals throughout.

All sediment samples were placed in sealed plastic bags and subsequently stored at 4 °C prior to analysis.

Radiometric analysis

Dried sediment samples from cores RAIL1 and RAIL2 were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by

Table 1 The site characteristics of duckweed and non-duckweed ponds in the surface sediment dataset

Site name	Site number	Location (latitude–longitude)
Duckweed Sites		
Pingo 19	1	55.209 N, − 4.678 W
Roadside Pingo	2	55.225 N, − 4.370 W
Ramsgate Horse Pond	3	55.373 N, − 3.048 W
Pond Farm Pond 1	4	55.408 N, − 2.970 W
Old Church Barn Pond 1	5	55.383 N, − 3.000 W
Bullock Shed Plantation Pond 2	6	55.388 N, − 3.133 W
Aldersbrook Pond	7	54.734 N, − 5.320 W
Lower Farm Pond	8	55.414 N, − 2.945 W
Priory Pond 1	9	55.441 N, − 2.904 W
Saxlingham Road Pond	10	55.311 N, − 2.953 W
Manor Farm Pond 29	11	55.353 N, − 3.058 W
College Farm Pingo	12	55.216 N, − 4050 W
Non-Duckweed Sites		
Pingo 37	13	55.200 N, − 4.993 W
Henry's Pit	14	55.351 N, − 3.066 W
Pond Farm Pond 2	15	55.408 N, − 2.971 W
Bodham Marl Pit	16	55.404 N, − 2.969 W
Salle Patch Pond	17	55.387 N, − 3.194 W
Bodham Rail Pit	18	55.401 N, − 2.966 W
Pond Hills Pond	19	55.385 N, − 2.560 W
Bodham Mystery Pit	20	55.403 N, − 2.957 W
Sayer's Black Pit	21	55.404 N, − 2.955 W
Bullock Shed Plantation Pond 1	22	55.390 N, − 3.133 W
Kiosk Pit	23	55.373 N, − 3.131 W
Cinders Hill Pond	24	55.386 N, − 3.125 W
Hempstead Rookery Pond	25	55.381 N, − 2.988 W
Otom Pit	26	55.371 N, − 3.145 W

direct gamma assay at the Bloomsbury Environmental Isotope Facility (BEIF), University College London, using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. ^{210}Pb was determined via its gamma emissions at 46.5 keV, and ^{226}Ra using the 295 keV and 352 keV gamma rays emitted by its daughter isotope ^{214}Pb following three weeks storage in sealed containers to allow radioactive equilibrium. ^{137}Cs and ^{241}Am were measured by their emissions at 662 keV and 59.5 keV respectively (Appleby et al. 1986). The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self-absorption of low energy gamma rays within each sample (Appleby et al. 1992).

Chronologies and sediment accumulation rates for both of cores RAIL1 and RAIL2 were calculated using the constant rate of ^{210}Pb supply (CRS) model (Appleby and Oldfield 1978). Use of the constant initial ^{210}Pb concentration (CIC) model was precluded because of irregular declines in unsupported ^{210}Pb activities resulting in non-monotonic features in the ^{210}Pb profiles of both cores (Fig. 3).

Diatom analysis

A total of 48 sediment samples were analysed for diatoms from core RAIL1. The uppermost 10–20 cm of the core was analysed at contiguous 1-cm intervals and below this samples were analysed at 2-cm intervals. A total of 44 contiguous samples were
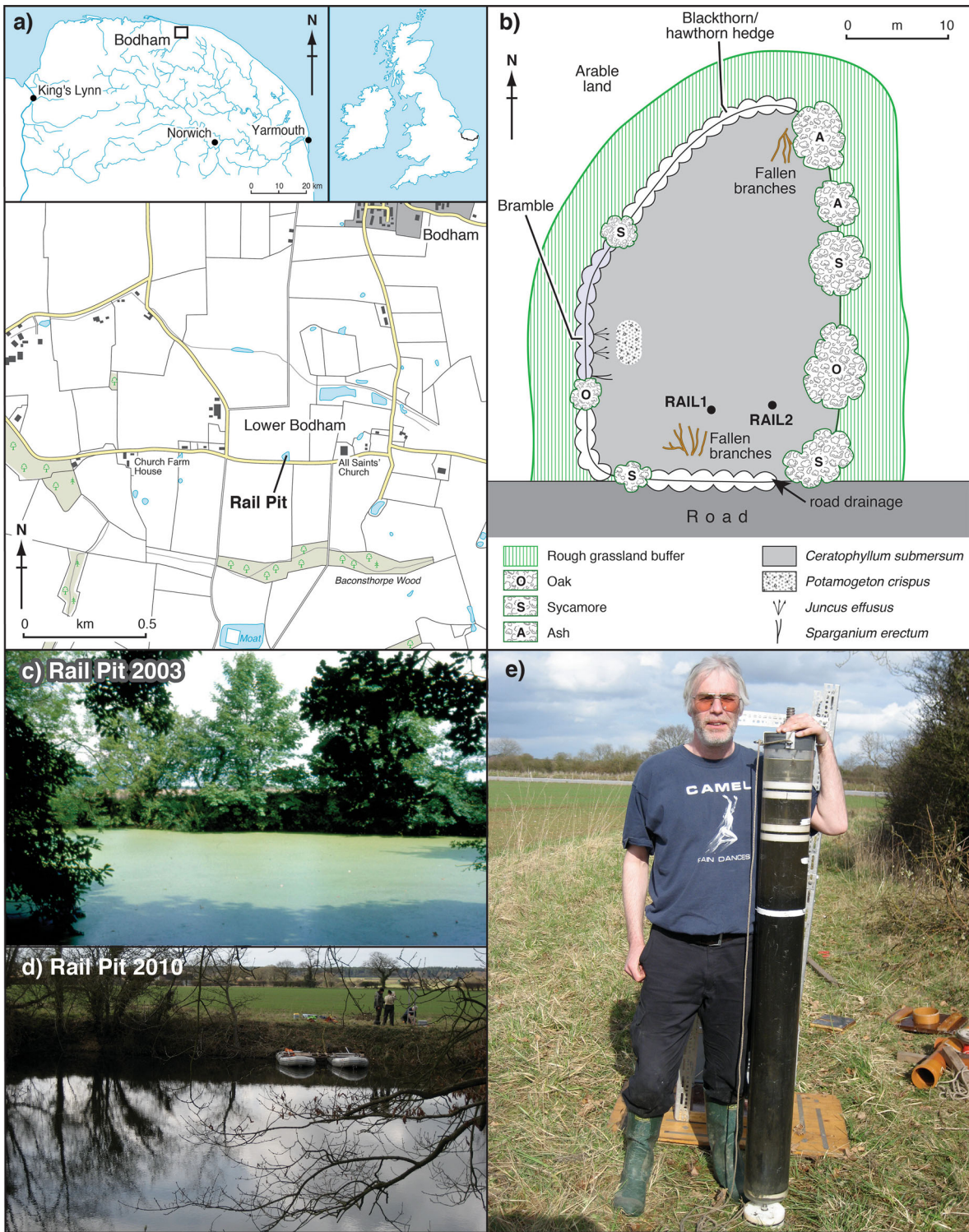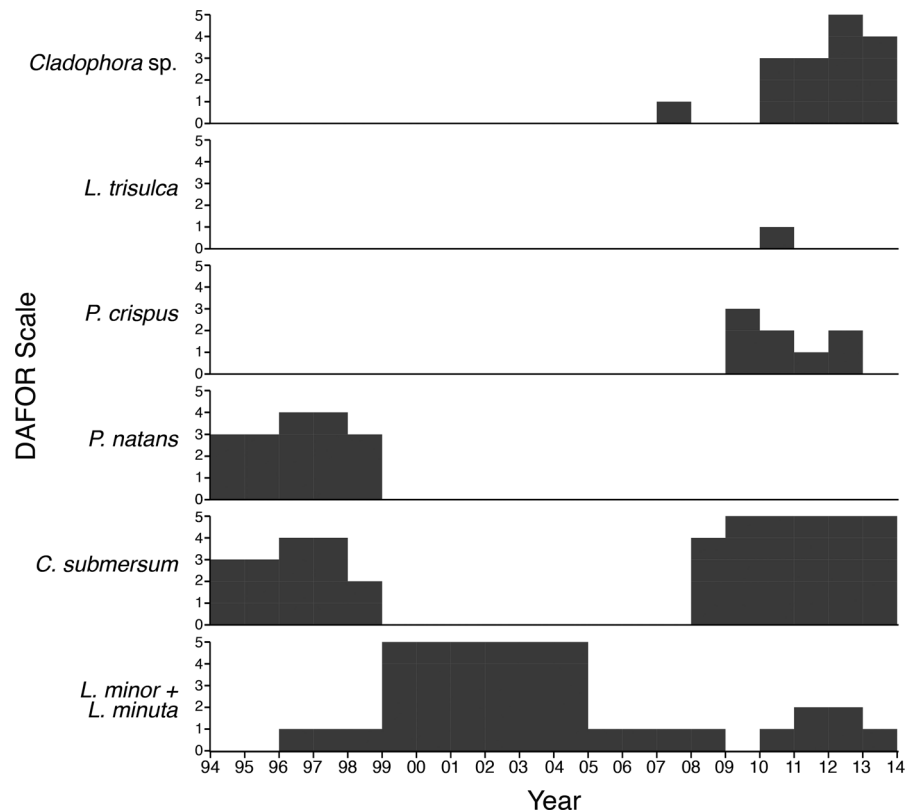
Fig. 1 Bodham Rail Pit, Norfolk, eastern England (**a**), and site map showing distribution of contemporary aquatic, emergent and riparian vegetation (**b**). Bodham Rail Pit showing *Lemna* dominance in 2003 (**c**) and *Lemna* absence in 2010 (**d**). Core RAIL1 (**e**). Note the dark organic silt above lighter grey marl at the base of the core (Photographs: CD Sayer)

Fig. 2 Recent history of aquatic macrophytes recorded from the Bodham Rail Pit. Macrophyte abundances are presented using the DAFOR scale (*D* Dominant-5, *A* Abundant-4, *F* Frequent-3, *O* Occasional-2, *R* Rare-1). Note that *Lemna minor* was generally co-dominant with *Lemna minuta*

analysed for diatoms in core RAIL2 at 0.5-cm intervals covering the full length of the 22-cm core. Samples were prepared for diatom analysis using standard methods (Battarbee 1986; Battarbee et al. 2001). Given that eutrophication can potentially swamp rare species by abundance increases of meso-eutraphentic and hyper-eutraphentic species (Van Dam and Mertens 1993), and as the aim was to determine how well the diatom stratigraphy tracked past duckweed dominance using two indicator species, large diatom counts (range 500–4700 valves per sample) were undertaken to reduce the dominance of common diatom species, whilst allowing responses of rarer taxa to be more accurately captured. All samples were mounted on microscope slides using Naphrax™ and absolute numbers of diatoms present in 0.1 g of sediment were counted at 1000× magnification with oil immersion under phase-contrast illumination using a Leitz 'Laborlux S' light microscope. Diatoms were identified to species level and diatom data for both cores were presented as percentage relative abundances. Images of the two indicator species used in the study are given in Fig. 4.

Data manipulation and analysis

Binomial logistic regression was performed using SPSS version 22 (2013) to determine whether *L. hungarica* and *S. saugerresii* could faithfully predict *Lemna* dominance in the ponds.
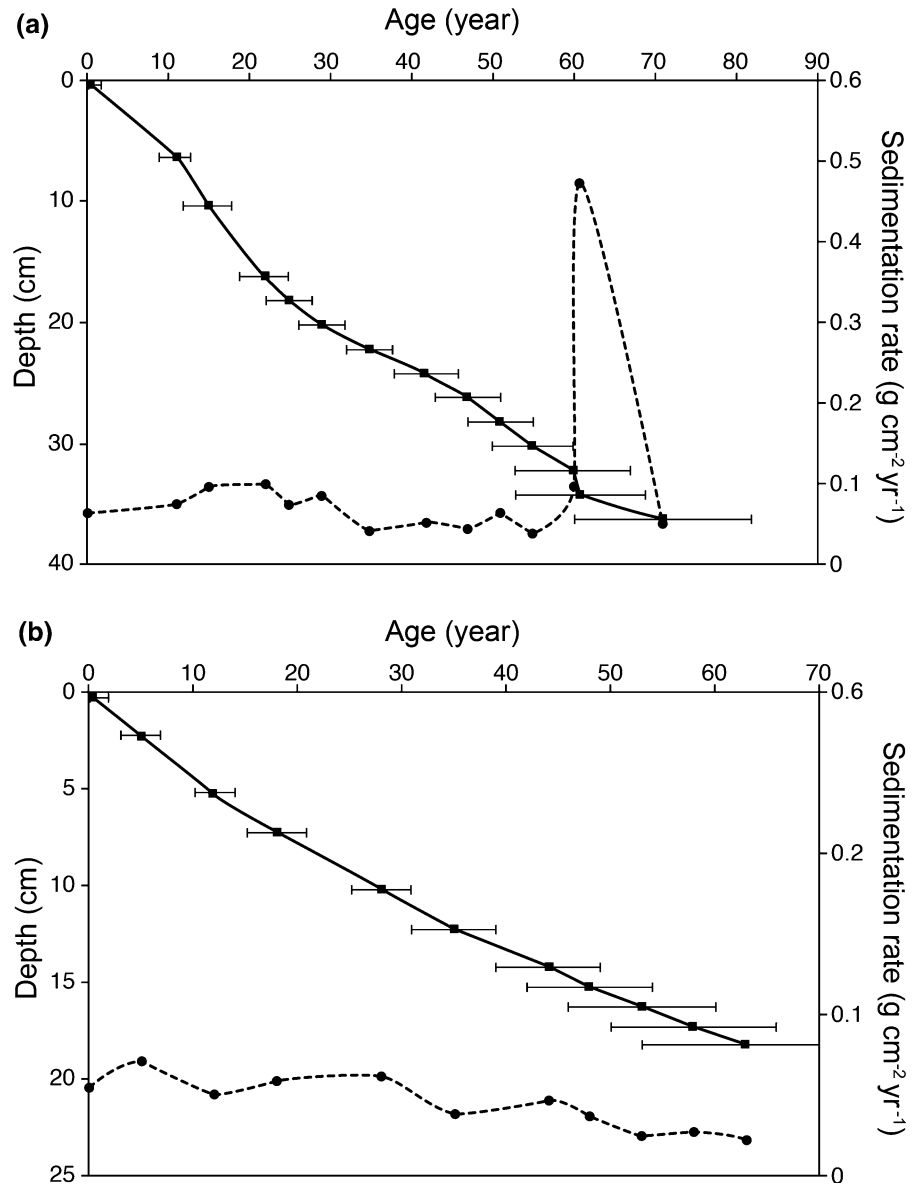
Pearson's correlation analysis was applied to *L. hungarica* and *S. saugerresii* relative abundances to determine the strength of their bivariate relationship in both of cores RAIL1 and RAIL2. Diatom core stratigraphic data were plotted using C2 software (Juggins 2007).

Results

Recent macrophyte history

The Rail Pit macrophyte data show a cyclical shift between submerged macrophytes and lemnid dominance (Fig. 2). The submerged *C. submersum* and *P. natans* were abundant in the early 1990s during years of low *Lemna* abundance (1994–1998), but rapidly

Fig. 3 Chronologies of cores RAIL1 (**a**) and RAIL2 (**b**) showing CRS model-inferred ^{210}Pb dates and sedimentation rates. Solid lines show chronological age with depth, and dashed lines show sedimentation rates

declined and disappeared in the late 1990s (1999–2005) with the onset of a *Lemna*-dominance phase (typically > 90% surface cover). This *Lemna* phase ended relatively abruptly in 2005 leaving the Rail Pit resembling a 'bacterial soup' (C.D. Sayer pers. observ.) until 2008 when *C. submersum* reappeared as abundant (DAFOR = 4 in 2008) together with *P. crispus* (DAFOR = 3 in 2009). During this second phase of submerged plant dominance, *P. natans* was absent, *Lemna trisulca* L. was recorded for the first time as a rare species (DAFOR = 1), and *Cladophora* sp. became more prevalent (DAFOR = 3). At the time

of core collection (April 2010) the only macrophytes present were *C. submersum* (DAFOR = 4), *L. minor* (DAFOR = 1) and *L. minuta* (DAFOR = 1) the latter both found in marginal areas (Fig. 2).

Surface sediments

L. hungarica and *S. saugerresii* were significantly more abundant in the *Lemna* sites (Fig. 5). Both *L. hungarica* (max. = 54%, min. = 5%, mean = 16%) and *S. saugerresii* (max. = 8%, min. = 1%, mean = 3%) were recorded from the surface
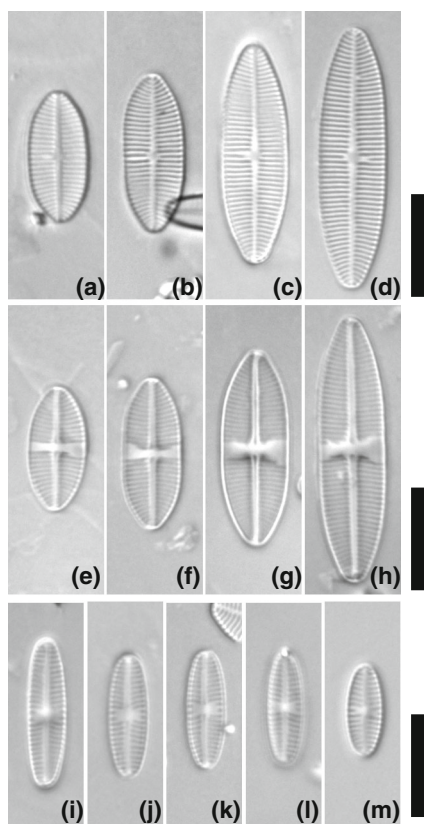
Fig. 4 Light microscopic images of the two *Lemna*-indicator diatom species: *Lemnicola hungarica* (**a–h**) and *Sellaphora saugerresii* (**i–m**). *Lemnicola hungarica* rapheless valves (**a–d**) and raphe valves (**e–h**). Scale bars = 10 μm (Photographs: P Rioual)

sediments of all *Lemna*-dominated sites, with the exception of both *L. hungarica* and *S. saugerresii* in Priory Pond 1 and *S. saugerresii* alone in Old Church Barn Pond 1 (Table 1). Only one non-*Lemna* site, Sayer's Black Pit (Site 21), contained *L. hungarica* in its surface sediments but at a very low percentage abundance (0.003%). There were three non-*Lemna* sites namely, Pond Farm Pond 2, Sayer's Black Pit and Otom Pit (Sites 15, 21 and 26 respectively) which recorded *S. saugerresii*, again at very low percentage abundances (0.002, 0.01 and 0.006% respectively). Logistic regression analysis indicated that duckweed-covered sites successfully predicted the presence of both *L. hungarica* ($p = 0.0001$, $r^2 = 0.903$) and *S. saugerresii* ($p = 0.002$, $r^2 = 0.758$) confirming their potential as indicator species. The predictive model was equally accurate for both the duckweed (93% correct) and non-duckweed sites (92% correct).

Radiometric dating of cores RAIL1 and RAIL2

The simple CRS model places the 1963 maximum nuclear weapons fallout layer (^{137}Cs peak) at 23.5 cm, slightly above the ^{137}Cs peak (26.5 cm) in core RAIL1. There is a sudden and dramatic increase in sedimentation rate at 34.5 cm (1940s) to 0.47 g cm^{-2} year^{-1} which may be due to a sediment slumping event (Fig. 3a). This is followed by a relatively uniform period covering the 1950s to the 1970s of 0.04–0.07 g cm^{-2} year^{-1} and an increased relatively uniform sedimentation rate of 0.08–0.1 g cm^{-2} year^{-1} for the last 30 years. For core RAIL2 the CRS dating model places 1963 at 12.5 cm, just above that suggested by the ^{137}Cs and ^{241}Am records at 15.5 cm. This may be due to non-continuous sedimentation before 1963. The CRS calculated chronology indicates that sediment accumulation rates gradually increased from 0.02 g cm^{-2} year^{-1} in the 1940s to 0.06 g cm^{-2} -year^{-1} since the 1980s (Fig. 3b).

RAIL1 and RAIL2 diatom stratigraphies and correlation

There was high temporal concordance between relative abundance peaks of *L. hungarica* and *S. saugerresii* and the observed *Lemna*-covered period for 1999–2005 in both the RAIL1 (7–3 cm; 1999–2005) and RAIL2 (6–3 cm; 1999–2005) cores (Phase 4 in Fig. 6). Similarly, peaks of both diatoms occurred for the 1950s (Phase 3 in Fig. 6), with this better defined in RAIL1 (32–27 cm) with increases in *L. hungarica* (2.5%) and *S. saugerresii* (3.5%), and increases of *L. hungarica* (11%) and *S. saugerresii* (7%) for RAIL2 (19–17 cm).

A further *Lemna*-dominance phase was evident in core RAIL1 with *L. hungarica* and *S. saugerresii* peaks over 48–40 cm (Phase 2 in Fig. 6a). Finally, a potential earlier *Lemna* phase was evidenced by increases in *S. saugerresii* (2–4%) and to a lesser extent *L. hungarica* (< 1%) at around 68 cm (Phase 1 in Fig. 6a). Despite some scatter and a lesser degree of agreement, especially in the lower sections of RAIL1, a positive linear relationship was found between percentages of *L. hungarica* and *S. saugerresii* in both of cores RAIL1 (r = 0.57, $p < 0.01$, Fig. 7a) and RAIL2 (r = 0.72, $p < 0.01$, Fig. 7b).
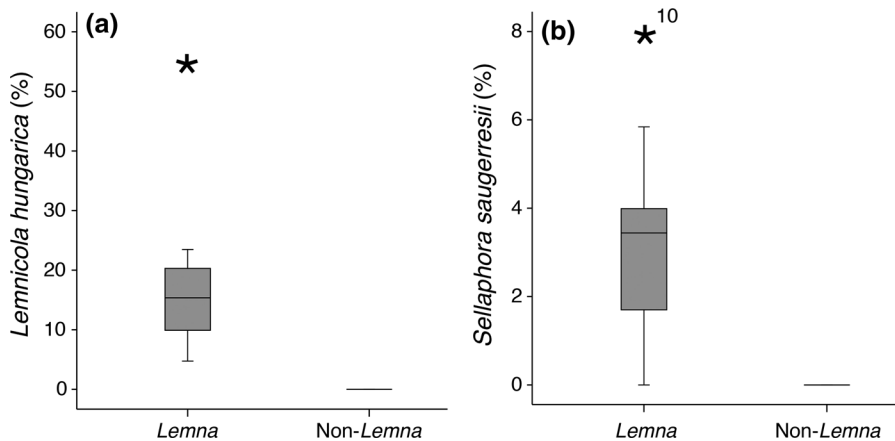
Fig. 5 Percentage relative abundances of *Lemnicola hungarica* (**a**) and *Sellaphora saugerresii* (**b**) in surface sediment samples from *Lemna*-covered (n = 12) and non-*Lemna* covered (n = 14) ponds. 25–75 percent quartiles (excluding outliers) are shown using a box, median is the horizontal line, whiskers represent the highest/lowest data points, and outliers are shown as stars
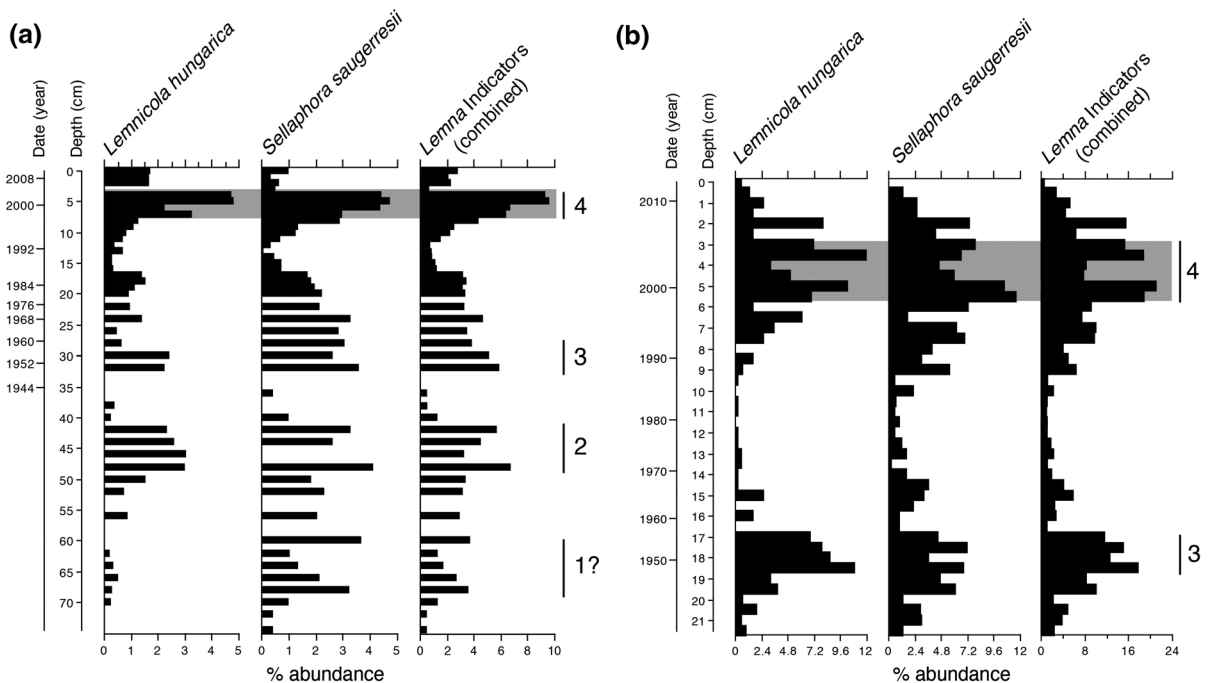

Fig. 6 Percentage abundance stratigraphies of *Lemnicola hungarica*, *Sellaphora saugerresii* and both species combined, for cores RAIL1 (**a**) and RAIL2 (**b**). Grey shading denotes the 1999–2005 observed *Lemna* dominance period

Discussion

The first formal documented record of a diatom was in 1703 (thought to be *Tabellaria flocculosa*) sampled from the roots of *Lemna* (Round et al. 1990), but on Christmas day in 1702 Van Leeuwenhoek looked at the roots of *Lemna* and also probably saw diatoms, although he described his findings as 'animalcula' in the Philosophical Transactions of the Royal Society (Van Leeuwenhoek 1703). Since these early days, many workers have investigated potential host-macrophyte relationships for diatoms (Prowse
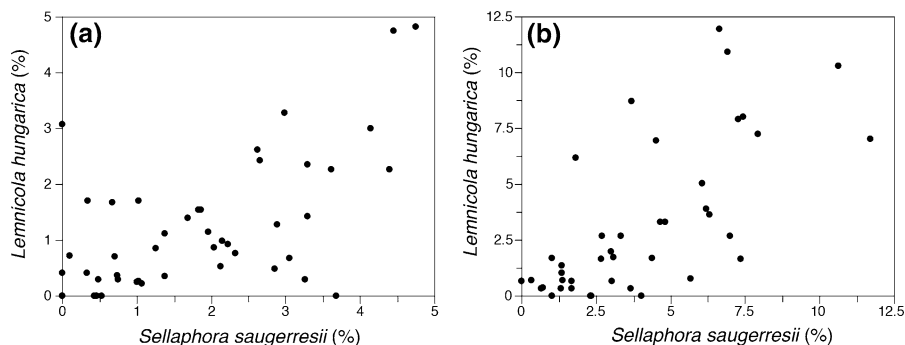
Fig. 7 Relationships between *Lemnicola hungarica* and *Sellaphora saugerresii* percentage relative abundances for cores RAIL1 (**a**) and RAIL2 (**b**)

1959; Siver 1977; Eminson and Moss 1980; Millie and Lowe 1983). Round (1973), Bowker and Denny (1980), Goldsborough and Robinson (1985) and Goldsborough (1993, 1994) were amongst the first researchers to acknowledge the association between *L. minor* and *L. hungarica*. Following these pioneering studies other workers have investigated the consistency and robustness of diatom-duckweed relationships. Buczkó (2007) found *L. hungarica* dominated diatom assemblages attached to *L. minor*, *Lemna gibba* L., *Spirodela polyrhiza* L. Schleid., and *Wolffia arhiza* L. Horkel ex Wimm., in marked contrast to assemblages found on *L. trisulca* which were dominated by *Cocconeis placentula* Ehrenb. Buczkó (2007) concluded that *L. hungarica* was tightly attached to well definable taxa of the lemnoid Araceae. Desianti (2012) also reported *L. hungarica* for *L. minor*, *S. polyrhiza* and *Wolffia* spp.

Clearly, several studies have concluded that *L. hungarica* has a strong habitat preference for duckweed, while Emson (2015) showed a similar association for *S. saugerresii* (Synonym: *Sellaphora seminulum* (Grunow) D.G. Mann). This good understanding of diatom ecology begs the question: is it possible to employ these diatoms as palaeo-indicators of past *Lemna* dominance? To this end, our study clearly shows both *L. hungarica* and *S. saugerresii* to be successfully transferred from duckweed mats to the sediment strongly suggesting a positive answer to this question. Further, this study shows that, even at low percentages (< 5%), these diatoms can indicate high duckweed coverage (Fig. 6). Importantly, this indicator status for *L. hungarica* and *S. saugerresii* applies not only to the lemnoid Araceae (with the exception of

L. trisulca) but can also be applied to other free-floating plants such as *Azolla* spp. and *Riccia* spp. (Emson 2015).

Confirmation of a strong *Lemna*-diatom association comes from comparing the RAIL1 and RAIL2 diatom stratigraphies with historical observations in the Rail Pit. In both cores the documented arrival and termination of high *Lemna* coverage over 1999–2005 is clearly tracked by peaks of both *L. hungarica* and *S. saugerresii* (Phase 4 in Fig. 6). Thus, even despite highly flocculated upper sediments for RAIL1 after collection, the *Lemna* signal remained intact. Core RAIL1, which extended to the beginning of sedimentation in the Rail Pit, showed some degree of bloom versus low-abundance (boom-bust) cyclicity for both *L. hungarica* and *S. saugerresii*, with three further potential *Lemna*-covered phases (Fig. 6a). For the penultimate peak (Phase 3 in Fig. 6) reasonable temporal accordance was evident between cores RAIL1 (32–27 cm = 1950–1960) and RAIL2 (19–17 cm = 1948–1958) giving faith in the reconstruction. The two earlier inferred duckweed peaks in RAIL1 (Phase 2—48–40 cm; Phase 1—68–60 cm) were less well defined for *S. saugerresii* compared to *L. hungarica*, however, potentially suggesting that *L. hungarica* is the most reliable *Lemna* indicator. On this basis low percentages of *L. hungarica* for Phase 1 make an inference of duckweed-dominance more questionable. Indeed, despite a significant positive correlation between *L. hungarica* and *S. saugerresii* in both cores, differences in their responses in RAIL1 suggest that these species may have slightly different ecological preferences and further studies in this respect could be fruitful. Given this, the merit of

combining *L. hungarica* and *S. saugerresii* to provide a *Lemna*-indicator metric (Fig. 6) is open to debate.

The ability to infer periods of free-floating plant dominance through time is of particular relevance to small waterbodies where duckweed proliferation, often symptomatic of high-nutrient loading, results in extensive surface coverings of duckweed (Portielje and Roijackers 1995). These dense mats physically prevent oxygen from being dissolved from the atmosphere and increase carbon dioxide levels (Janes 1998) causing a reduction in pH (McLay 1976; Janes 1998) and increased conductivity (Greaves et al. unpublished data). In addition, lemnid dominance can attenuate photosynthetic active radiation (PAR) by up to 99% with associated temperature fluctuations which can lead to diurnal temperature stratification (Dale and Gillespie 1976; Goldsborough 1993). Dense duckweed mats can cause significant species losses in submerged macrophyte and invertebrate communities (Janse and Van Puijenbroek 1998), and associated cold, anoxic conditions can cause fish kills (Lewis and Bender 1961). Thus, a diatom-*Lemna* inference tool has much utility in terms of reconstructing the past ecology of ponds, with the same potentially true of shallow lakes and indeed larger lakes under certain circumstances across the globe (Duarte and Kalff 1990) where high *Lemna*-coverage occurs. For example, dominance of free-floating mats of lemnids have also occurred in Lake Maracaibo, Venezuela and Lake Titicaca, Peru due to increased nutrient inputs (Cruz et al. 2006), and seasonal blooms of duckweeds have also been observed in cut-off meanders in large rivers (Beauger et al. 2015). Significant relationships between *L. hungarica* and duckweed have been demonstrated for a variety of climatic conditions and waterbody types in many parts of the world including Canada (Goldsborough 1993, 1994), USA (Zuberer 1984; Desianti 2012), Brazil (Garcia and Fonseca de Souza 2006) and substantial tracts of Europe (Buczkó 2007; Emson 2015). Consequently, with the caveat that more work on habitat preferences is needed for *S. saugerresii*, compared to *L. hungarica*, we strongly suggest that both diatoms might be reliably used to infer past free-floating plant dominance much more widely. Will it be "mission possible" in other waterbodies in the world? Certainly, we urge other workers to go out and test this idea.

Conclusions

This study suggests that ponds in lowland European agricultural landscapes have considerable palaeolimnological potential. Indeed, the close agreement of diatom-*Lemna* signals in two cores from the Rail Pit strongly suggest that palaeo-techniques can be confidently applied to these often over-looked waterbodies, at least where ponds are permanent.

The study also shows the huge advantage of incorporating 'rare' species in diatom analysis and of undertaking large (> 500 valves per slide) counts to better characterize diatom signals in cores. In this case the two *Lemna*-indicator diatoms occurred at relatively low percentages (< 5%) in both stratigraphic sequences and in the surface sediments, even where duckweed was entirely dominant. This is particularly pertinent given that conventional diatom studies, based on counts of 300 or at best 500 diatom valves, tend to delete species at < 5% relative abundance from summary plots. Thus, as a 'rule of thumb', the duckweed-covered signal afforded by *L. hungarica* and *S. saugerresii* would typically be missed.

Finally, in developing two diatom-indicators of free-floating plants, our research highlights the huge value of understanding diatom species ecologies for interpreting palaeo-data. In this respect, similar to previous studies (Bennion et al. 2010; Sayer et al. 2010), we suggest that a greater understanding of diatom responses to habitat and chemical variation across and between different littoral zone structures in lakes and ponds would greatly improve the interpretation of sediment records dominated by non-planktonic diatoms.

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