Combining contemporary ecology and palaeolimnology to understand shallow lake ecosystem change

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SUMMARY

1. Palaeolimnology and contemporary ecology are complementary disciplines but are rarely combined. By reviewing the literature and using a case study, we show how linking the timescales of these approaches affords a powerful means of understanding ecological change in shallow lakes.

2. Recently, palaeolimnology has largely been pre-occupied with developing transfer functions which use surface sediment-lake environment datasets to reconstruct a single environmental variable. Such models ignore complex controls over biological structure and can be prone to considerable error in prediction. Furthermore, by reducing species assemblage data to a series of numbers, transfer functions neglect valuable ecological information on species' seasonality, habitat structure and food web interactions. These elements can be readily extracted from palaeolimnological data with the interpretive assistance of contemporary experiments and surveys. For example, for one shallow lake, we show how it is possible to infer long-term seasonality change from plant macrofossil and fossil diatom data with the assistance of seasonal datasets on macrophyte and algal dynamics.

3. On the other hand, theories on shallow lake functioning have generally been developed from short-term (<1–15 years) studies as opposed to palaeo-data that cover the actual timescales (decades–centuries) of shallow lake response to stressors such as eutrophication and climate change. Palaeolimnological techniques can track long-term dynamics in lakes whilst smoothing out short-term variability and thus provide a unique and important means of not only developing ecological theories, but of testing them.

4. By combining contemporary ecology and palaeolimnology, it should be possible to gain a fuller understanding of changing ecological patterns and processes in shallow lakes on multiple timescales.

Keywords: aquatic ecology, eutrophication, palaeolimnology, shallow lakes, temporal scale, transfer functions

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Introduction

In the late 1980s–early 1990s, a number of articles were published in predominately palaeolimnological publications calling for greater collaboration between palaeolimnology and aquatic ecology (e.g. Davis &

Smol, 1986; Smol, 1990). Furthermore, a recent review (Battarbee *et al.*, 2005) advocated such an approach to help understand long-term lake responses to nutrient reduction. However, with notable exceptions (e.g. Bradshaw & Anderson, 2003; Brodersen *et al.*, 2004; Manca *et al.*, 2007; Sayer *et al.*, 2010a), few studies have linked contemporary experiments and surveys with palaeolimnology, and thus different timescales of investigation.

Contemporary ecological studies on shallow lakes include experiments; laboratory (Jones *et al.*, 1999; Burks, Jeppesen & Lodge, 2001), mesocosm (Jeppesen *et al.*, 2002; Jones *et al.*, 2002; Liboriussen *et al.*, 2005) and whole-lake (Hansson & Bergman, 1999; Schindler *et al.*, 2008) studies, multi-lake comparisons along environmental gradients (e.g. Jeppesen *et al.*, 1990, 2000, 2003; Jones & Sayer, 2003) and monitoring/repeat survey studies (Blindow *et al.*, 1993; Phillips *et al.*, 2005). Such investigations have much enhanced our knowledge of lake ecology (e.g. Brooks & Dodson, 1965; Carpenter, Kitchell & Hodgson, 1985; Schriver *et al.*, 1995; Jeppesen *et al.*, 2000; Vadeboncoeur *et al.*, 2003) and have been used to build theories (e.g. Moss, 1990; Scheffer *et al.*, 1993). However, contemporary studies seldom extend beyond 10 years and thus rarely show how lake ecosystems change over the longer (decadal-centennial) timescales that are relevant to stressors such as eutrophication, acidification and climate change. To truly understand change on longer timescales requires a different approach. This is where palaeolimnology comes in.

Palaeolimnological studies have greatly improved our understanding of long-term lake ecosystem responses to eutrophication and other forcing factors (Anderson & Battarbee, 1994; Rasmussen & Anderson, 2005; Davidson *et al.*, 2005; Bradshaw *et al.*, 2005a; Bradshaw, Rasmussen & Odgaard, 2005b; Ayres *et al.*, 2008). Despite this, it is our opinion that palaeolimnology is yet to achieve its full potential, due largely to a disconnection from aquatic ecology and a tendency to use species assemblages as 'proxies' for environmental variables, rather than considering what species data may tell us about past ecological patterns and processes *per se*. Many organisms leave remains in the sediments of shallow lakes (i.e. algae, macrophytes, zooplankton, benthic invertebrates, fish – Jeppesen *et al.*, 2001; Brodersen *et al.*, 2001; Davidson *et al.*, 2003, 2005; McGowan *et al.*, 2005; Sayer *et al.*,

2006; Langdon *et al.*, 2006, 2010) and consequently may provide information on whole-ecosystem responses and even changes to food webs (Birks & Birks, 2006; Rawcliffe *et al.*, 2010). Nevertheless, over the last two decades, quantitative palaeo-studies of eutrophication have tended to neglect ecological changes in favour of the reconstruction of chemical variables [e.g. total phosphorus (TP), chlorophyll-*a*] using transfer functions (Birks & Birks, 2006 and see later). Moreover, where a multi-proxy approach has been pursued, studies have focused on comparisons of transfer function reconstructions derived from different fossil groups (Brooks, Bennion & Birks, 2001), the timing and/or rates of changes to biological structure (Birks, Battarbee & Birks, 2000; Birks & Birks, 2001; Bradshaw *et al.*, 2005b) and changes in biodiversity (Sayer *et al.*, 1999). Only occasionally have they sought to elucidate ecological processes or test ecological theories (see McGowan *et al.*, 2005; Rasmussen & Anderson, 2005; Anderson *et al.*, 2008; Sayer *et al.*, 2010a).

It is our thesis that palaeolimnology would much benefit from a fuller consideration of contemporary aquatic ecology, particularly species' environment/habitat preferences, seasonality and interactions. Equally, we believe that palaeo-data can greatly enhance our understanding of lake ecosystems by posing and testing ecological theories within a long-term framework. In this article, we show how combining contemporary ecological and palaeolimnological approaches afford a powerful means to assess change in shallow lake ecosystems. To do this, first, we demonstrate the frailty of the standard transfer function approach and explore the advantages of carefully constructed contemporary studies for informing palaeo-reconstructions. Second, we emphasise how a palaeolimnological perspective can provide a unique and continuous long-term dimension to our understanding of shallow lake responses to eutrophication and other human impacts.

Problems with transfer functions from an ecological perspective

Transfer functions have become a standard tool in palaeolimnology, and, over the last two decades, hundreds of models have been constructed for a variety of biological groups-environmental variables in shallow lakes, among others; diatoms-TP (Anderson,

1997), ostracods-conductivity (Mezquita *et al.*, 2005), cladocerans-planktivorous fish density (Jeppesen *et al.*, 1996) and cladocerans-macrophyte coverage (Johansson *et al.*, 2005). Reconstruction of past conditions via transfer functions involves two stages: the surface sediment assemblages of usually 30+ sites are calibrated against contemporary environmental data, and the optima and tolerances of different taxa are determined for the variable of interest. These derived relationships are then used to reconstruct change in that variable over time from fossil assemblages in a sediment core. On their entry to the palaeolimnological scene, transfer functions were hailed as a major ecological advance, because the objective methods they employ [canonical correspondence analysis (CCA) and weighted averaging (WA) calibration and regression] assume unimodal responses of species to the environment as are thought to occur in nature (ter Braak & Prentice, 1988; Stevenson *et al.*, 1989). However, despite a number of promising 'validation' studies (e.g. Bennion, Wunsam & Schmidt, 1995; Bradshaw & Anderson, 2001), the values predicted by transfer functions have increasingly been called into question (Fritz, Kingston & Engstrom, 1993; Brodersen *et al.*, 2004; Battarbee *et al.*, 2005; Davidson *et al.*, 2010a), especially for diatom–TP reconstructions in shallow lakes (Sayer, 2001).

The problems associated with the development and application of transfer functions relate to the complex ways via which species are connected to each other and the environment (Brodersen *et al.*, 2004, 2008; Birks & Birks, 2006). Although it is acknowledged that the controls over species assemblages are multivariate, because transfer functions model the most important *measured* structuring influence, it is generally assumed that they remain ecologically relevant and robust. A key problem with this notion is that transfer functions have often been developed for palaeolimnology from data sets that exclude variables known to exert a significant influence over community composition. For example, despite the known importance of submerged plants as habitat and food resources for macroinvertebrates (Jeppesen *et al.*, 1998), chironomid calibration sets for shallow lakes (e.g. Brodersen & Lindegaard, 1999; Brooks *et al.*, 2001; Langdon *et al.*, 2006) have focused on an array of predominately physico-chemical variables (including chlorophyll-*a* and dissolved oxygen) but have neglected measures of macrophyte abundance. Clearly, logistical and financial constraints are at play here, but, where incorporated, a key structuring role of macrophyte parameters (abundance, species richness) on chironomid communities has been revealed (Langdon *et al.*, 2010). The same issues undoubtedly apply to other biological groups, including diatoms, for which training sets have also excluded macrophytes, although some studies have acknowledged an important plant effect linked to variations in water depth (Bennion, 1994; Werner & Smol, 2005). By not measuring important biological and/or habitat variables (such as macrophytes), transfer functions inevitably lack realism and relevance, and thus the actual factors that drive historical changes in species composition may not be revealed (Fritz *et al.*, 1993).

Multi-lake field studies show that species almost always respond to several interacting forces; *inter alia* chironomids to TP, macrophyte abundance and macrophyte species richness (Langdon *et al.*, 2010) and cladocerans to fish, macrophyte abundance and food availability (Brooks & Dodson, 1965; Luecke *et al.*, 1990; Schriver *et al.*, 1995; Blumenshine, Lodge & Hodgson, 2000; Jeppesen *et al.*, 2001). As recognised by Brodersen & Anderson (2002) and Davidson *et al.* (2010a) using a transfer function under these circumstances to model a single variable is problematic. However, where contemporary ecological studies are conducted in parallel with the development of training sets, some of these complexities can be revealed (see Brodersen *et al.*, 2004). For example, by sampling both contemporary zooplankton populations and surface sediment in 39 shallow lakes, Davidson *et al.* (2007) revealed a strong coinfluence of macrophyte and zooplanktivorous fish densities on cladoceran communities, both extant and fossil. There were also complexities concerning the coinfluence of structuring forces as the effect of plants on the strength of predation pressure exerted by zooplanktivorous fish was non-uniform along the gradient of macrophyte density (Davidson *et al.*, 2010a). Consequently, a fundamental assumption of the transfer function approach, that environmental variables other than the one of interest have little influence on community composition, or are linearly related to the modelled variable (Birks *et al.*, 1990), was not met (Davidson *et al.*, 2010a).

A further problem is that modelled species–environment relationships are often indirect, while the physiological/ecological mechanisms that underlie them may be poorly understood. A classic example

here is the often-used relationship between diatoms and TP in shallow lakes (Bennion, Juggins & Anderson, 1996; Anderson, 1997; Werner & Smol, 2005). Clearly, diatoms need nutrients, including phosphorus, to survive, and we know that nutrient resource ratios (including Si : P and N : P) influence community structure (Tilman, 1977). However, the influence of TP on diatoms is probably both direct and indirect via other correlated variables. Diatom assemblages in lake sediments are derived from a number of habitats; open water, macrophyte stands, sediments etc. Combinations of water depth, lake size and in particular light climate will affect the relative productivity of these habitats, and in turn light will be influenced by phytoplankton biomass and nutrients (Liboriussen & Jeppesen, 2003). Thus, both light availability and macrophyte abundance may vary in a semi-order manner with increasing phosphorus (Jeppesen *et al.*, 1990), and in part this probably explains the relatively strong diatom–TP relationship in training sets from shallow lakes. However, ultimately a large portion of the diatom–TP relationship is indirect, and in this situation, a transfer function will be prone to considerable error (Sayer, 2001). Notwithstanding the clear advantages of quantitative reconstructions in terms of communicating information to lake managers (Bennion, Fluin & Simpson, 2004; Bjerring *et al.*, 2008), by reconstructing one environmental/biological variable in isolation from others, transfer functions neglect the more complex pathways of ecological change that may occur (see Fritz *et al.*, 1993; Brodersen *et al.*, 2004, 2008; Davidson *et al.*, 2010a,b).

Alternative approaches to palaeo-reconstruction

Regression trees and semi-quantitative techniques

An alternative palaeolimnological method that accommodates the problem of multiple structuring forces on biological communities is the regression tree approach as pioneered by Davidson (2006) and Davidson *et al.* (2010a,b). Regression trees employ binary recursive partitioning to model species–environment relationships (De'ath, 2002). In contrast to transfer functions which determine the optima and tolerances for individual species in relation to a single environmental variable, a regression tree considers the whole assemblage and can model the impact of a number of variables simultaneously. Further explanation of the

approach, including its statistical nuances, is given in Davidson *et al.* (2010a,b) who used a 39 shallow lake dataset to develop a model for inferring varying combinations of zooplanktivorous fish and macrophyte densities from subfossil assemblages of cladocerans. Currently, the regression tree approach is semi-quantitative, although further refinement (such as multivariate adaptive regression splines) may allow for more quantitative predictions (Leathwick *et al.*, 2005). Nonetheless, such a procedure allows for variation in factors, such as the strength of the trophic cascade, along the productivity gradient (Chase, 2003), and in the case of Davidson *et al.* (2010a), variation in the impact of zooplanktivorous fish density on the cladoceran community along a gradient of macrophyte abundance. A model with a single predictor (as in a transfer function) cannot do this and is thus largely inappropriate when controlling variables are multiple. We expect that regression trees and techniques based on similar principles to gain favour in palaeolimnology over the coming decade.

Qualitative approaches informed by contemporary ecological data

Given the aforementioned problems with transfer functions, Birks & Birks (2006) suggest that palaeolimnologists need to get 'back to basics' and to consider more fully the niche dimensions and ecology of species found as fossils. We echo this view and urge palaeolimnologists not to ignore qualitative approaches that are carefully informed by contemporary data regarding species' habitat preferences, seasonality, feeding strategies and interactions. Indeed, an early tradition in diatom and cladoceran-based palaeolimnology used species' affinities for different physical habitats (associations with plants and/or sediment and/or open water) to reconstruct changes in habitat structure (e.g. macrophyte loss) associated with eutrophication (Whiteside, 1970; Moss, 1977, 1979). In addition, a limited number of diatom-based studies have used contemporary plankton data to help interpret sediment core profiles in terms of changed diatom seasonality (Sayer & Roberts, 2001) and environmental conditions (Bradshaw & Anderson, 2003). Nonetheless, in general, such studies have been few.

A tremendous challenge to palaeolimnology that might be usefully addressed by carefully linked contemporary ecological studies is that of reconstruct-

ing past trophic interactions (Anderson & Battarbee, 1994). In shallow lakes, enormous quantities of species information can be derived from sediment cores that cross all areas of the food web. If large volumes of sediment can be collected, several often-neglected invertebrate groups (e.g. Trichoptera, Ephemeroptera, Coleoptera), and even large-bodied organisms such as fish can be included (Davidson *et al.*, 2003; Greenwood, Wood & Monk, 2006; Sayer *et al.*, 2006; Whitehouse *et al.*, 2008). While multiple species groups are often enumerated in cores, few palaeo-projects have inferred the connections between species. Some studies have used sediment core data to infer trophic cascade responses to changes such as fish manipulations (e.g. Leavitt, Carpenter & Kitchell, 1989; Leavitt *et al.*, 1994), but small numbers of species have been considered, and a food-chain (fish → herbivore → primary producer) approach has been employed as opposed to one which considers all species as important and discrete entities in a trophic network. The latter requires data on the linkages between species that can be usefully derived from contemporary field studies employing gut contents and stable isotope analysis (Woodward, 2009). Indeed, where these data exist for contemporary lakes, it is possible to substitute space-for-time and to use modern analogue food webs to infer long-term food web change (Rawcliffe *et al.*, 2010). In the past, it has generally been assumed that it is not possible to study the development of food webs even more directly by inferring the linkages between species' fossil remains because of the palaeolimnological record being a 'fragmentary record' of extant communities. However, given the incredible richness of the palaeolimnological record in shallow lakes (Bradshaw *et al.*, 2005b), this notion should be questioned, and in the future, sediments will hopefully be exploited much more fully in this way.

Case study – linking seasonal and centennial timescales for diatom plankton

The value of the combined ecological–palaeolimnological approach can be illustrated by a case study of two shallow (<1.5 m average depth) English lakes; Selbrigg Pond and Felbrigg Hall Lake. Details regarding the geographical settings, water chemistry and ecology of these lakes are given in Rawcliffe *et al.* (2010). Both lakes are small (<3 ha), but Selbrigg is less

nutrient rich (annual TP – 35 μg L^{-1}) than Felbrigg (annual TP – 107 μg L^{-1}). A link between the lakes has been made in time: palaeolimnological evidence (close matches in cladoceran and plant macro-remains) suggests that Selbrigg is a good analogue for a less-eutrophic Felbrigg in the early decades of the 20th century (Rawcliffe *et al.*, 2010). In Fig. 1, seasonal changes in the diatom plankton are compared with surface sediment (0–1 cm sample) diatom assemblages for the lakes. The surficial assemblages in Selbrigg (Fig. 1a) is dominated (100%) by epi-benthic species probably associated with plant and mud surfaces, in particular small, colonial *Staurosira/Staurosirella/Pseudostaurosira* species (formerly *Fragilaria* spp. and termed so hereafter). Similar to Selbrigg, the surficial assemblage in Felbrigg (Fig. 1b) is dominated by epi-benthic taxa, including small 'Fragilaria' species, *Gomphonema minutum* Agardh and *Cocconeis pediculus* Ehrenb., but small centric planktonic species (particularly *Cyclotella meneghiniana* Kütz., *Cyclostephanos invisitatus* Theriot, Stoermer & Håkansson and *Cyclostephanos tholiformis* Stoermer, Håkansson & Theriot) also contribute significantly (*c.* 15%) to the assemblage. Contemporary diatom plankton data help to explain these differences. In Selbrigg, the plankton is consistently dominated by small 'Fragilaria' spp., while planktonic taxa are sparse throughout the year (<1.5 × 10^5 cells L^{-1}). By contrast, whilst 'Fragilaria' spp. are abundant in the plankton of Felbrigg, there are two distinct peaks of planktonic diatoms (<7 × 10^5 cells L^{-1}) in March (*C. tholiformis* and other centrics) and August–September (*C. tholiformis* and *C. meneghiniana* in particular).

Generally speaking, higher nutrient availability in Felbrigg (Fig. 1b) probably explains its more substantial plankton peaks. In addition, as discussed by Sayer, Davidson & Jones (2010b), the late season plankton peak may be linked to an 'opening up' of the water column following a mid-summer senescence of macrophytes. By contrast, in Selbrigg, lower nutrient concentrations probably favoured benthic as opposed to planktonic primary production, while a longer period of macrophyte occupancy (*c.* May–September) may have reduced plankton development by direct competition and enhanced grazing by plant-associated Cladocera (Fig. 1b). Thus, although nutrients are undoubtedly a key force behind the different sedimentary diatom communities of the two lakes, the assemblages are probably connected to nutrients via
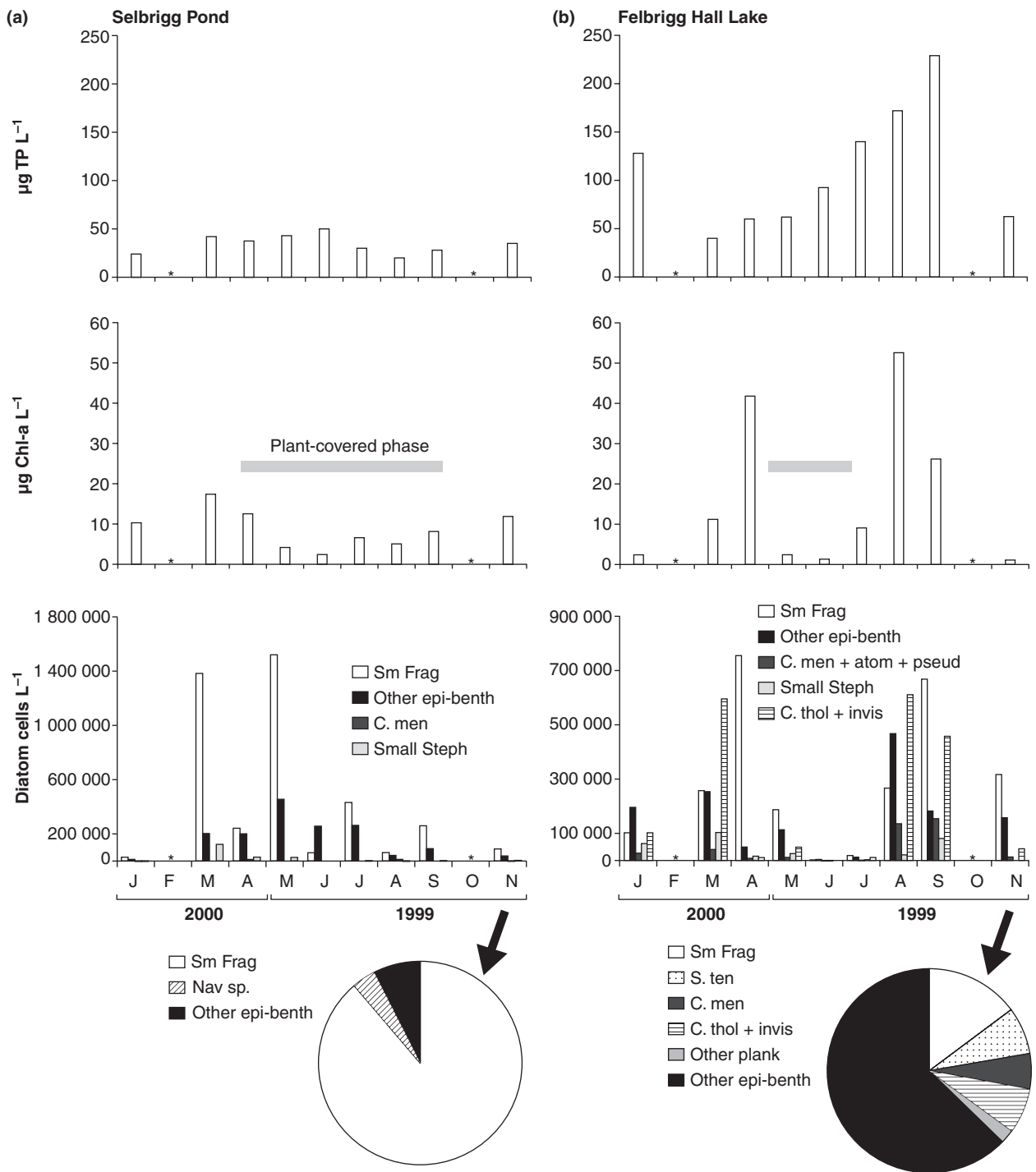
Fig. 1 Seasonal changes in total phosphorus (TP), chlorophyll-*a*, numbers of dominant diatoms in the plankton and the composition of surface sediment diatom assemblages in two shallow lakes, Selbrigg Pond (a) and Felbrigg Hall Lake (b). The duration of plant dominance in each lake (''plant-covered period'') is shown as a grey bar. The years 1999 and 2000 are reversed to show more clearly an annual sequence of change in the two lakes. * = no data collected. Sm Frag = small '*Fragilaria*' spp. (see text), Nav sp. = *Navicula* spp., Other epi-benth = other epiphytic and benthic taxa, Small Steph = *Stephanodiscus parvus* and *Stephanodiscus hantzschii*, S. ten = *Synedra tenera*, C. men = *Cyclotella meneghiniana*, C. men+atom+pseud = *C. meneghiniana, Cyclotella atomus* and *Cyclotella pseudostelligera*, C. thol+invis = *Cyclostephanos tholiformis* and *Cyclostephanos invisitatus*, Other plank = other planktonic taxa.
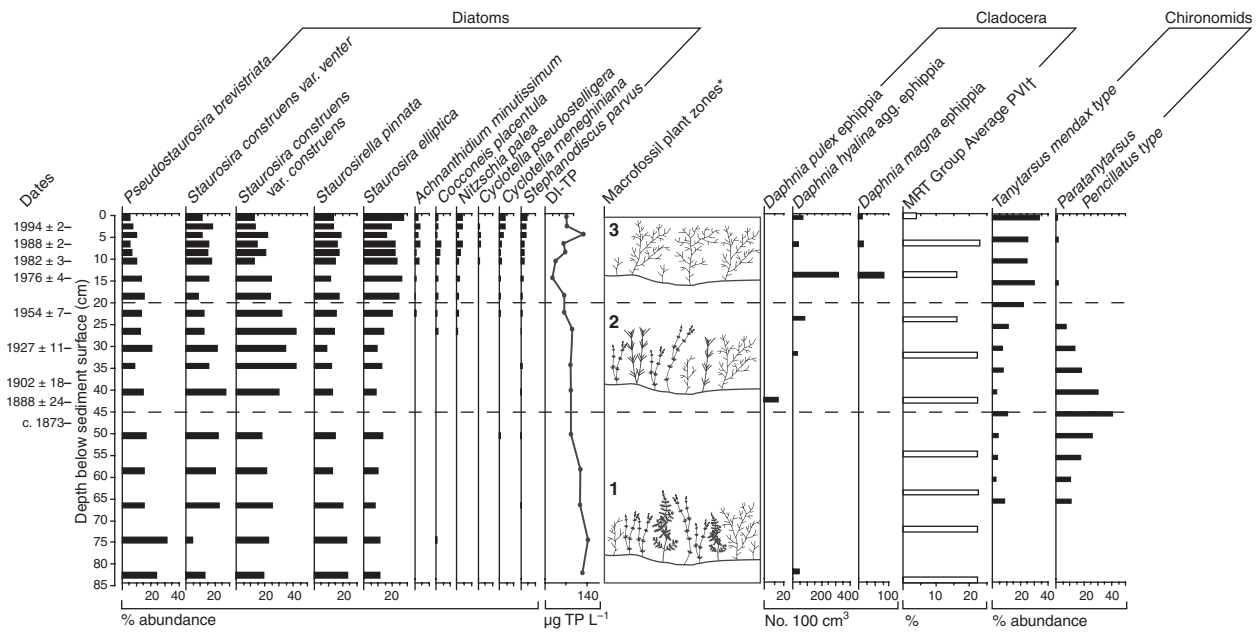
Fig. 2 Multi-proxy palaeolimnological diagram for core FELB1 (Felbrigg Hall Lake) showing summary diatom stratigraphy, a diatom-inferred total phosphorus (DI-TP) reconstruction, macrophyte community changes inferred from macrofossils (see text and Sayer *et al.*, 2010a for further details), profiles of key cladoceran and chironomid taxa and a cladoceran-based multivariate regression tree (MRT) reconstruction of changing macrophyte abundance (see text and Davidson *et al.* (2010b) for further details on the cladoceran and chironomid data). * Macrofossil-defined plant zones as follows: 1 = *Myriophyllum-Chara-Ceratophyllum-Potamogeton*, 2 = *Ceratophyllum-Chara-Potamogeton*, 3 = *Potamogeton-Zannichellia*.

the indirect influence of macrophyte coverage (in space and time), light and grazing, all of which affect the seasonal productivity of different diatom habitat groups (epipelic versus epiphytic versus planktonic).

The limnological data summarised in Fig. 1 can be used to interpret the diatom stratigraphy of a sediment core (FELB1) from Felbrigg (Fig. 2) and in the section that follows a qualitative approach informed by contemporary survey data is compared with the standard transfer function approach. Details regarding core collection, radiometric dating and all other core analyses are given in Sayer *et al.* (2010a) and Davidson *et al.* (2010b). For the qualitative reconstruction, an array of palaeolimnological data are available in addition to the diatoms; plant macro-remains (Sayer *et al.*, 2010a), cladocerans, chironomids and Mollusca (Davidson *et al.*, 2010b) a summary of which is given in Fig. 2. A TP reconstruction was performed on the core data using the NW European transfer function model of Bennion *et al.* (1996). To reconstruct TP, weighted averaging partial least squares regression (WAPLS) calibrations were applied to pre-harmonised diatom data using the programme C2 (Juggins, 2003).

The transfer function reconstruction (Fig. 2), if taken on its own, indicates high TP (*c.* 99–139 μg L^{-1}) over the last 200 years with a suggestion of declining TP for the 1960s–1970s (<100 μg TP L^{-1}) and slightly higher TP thereafter (>110 μg TP L^{-1}). Thus, overall, a trend of oligotrophication is suggested. On the other hand, a qualitative interpretation of assemblage data reveals a more complex ecological story linked to progressive eutrophication. Macro-remains of aquatic plants (Sayer *et al.*, 2010a and summarised in Fig. 2) suggest dynamic changes to Felbrigg's submerged vegetation over the last two centuries:– *Myriophyllum-Chara-Potamogeton* (*c.* pre-1900) → *Ceratophyllum-Chara-Potamogeton* (*c.* 1900–60) → *Potamogeton-Zannichellia* (*c.* post-1960). Based on macrophyte seasonality studies of 39 shallow lakes in the region (including Felbrigg), the later stage is thought to be associated with a truncated seasonal period of plant dominance (Sayer *et al.*, 2010b). Cladoceran and chironomid data for the core (Fig. 2 and Davidson *et al.*, 2010b) indicate a clear-water lake with a structurally diverse macrophyte community *c.* pre-1900, followed by increased macrophyte abundance *c.* 1900–60. Increases in pelagic cladocerans (e.g. *Daphnia*) and declines in plant-associated cladoceran and chironomid

(e.g. *Paratanytarsus pencillatus* type – Fig. 2) taxa *c.* post-1960 suggest an increase in phytoplankton and a reduced abundance of plants (Davidson *et al.*, 2010b), with the latter also indicated by a cladoceran-based multivariate regression tree (MRT) model (Fig. 2 and see Davidson *et al.*, 2010b). At the same time, increased representation of small, centric diatoms since the mid-1900s suggests that a shortened period of macrophyte dominance was probably 'sandwiched' between peaks of planktonic algae, as in the present day (Fig. 1b and see Sayer *et al.*, 2010b). Thus, our qualitative interpretation is that macrophyte abundance has been reduced in both space (coverage of the lake) and time (seasonally) since the mid-twentieth century, while phytoplankton production has increased. Such changes indicate progressive eutrophication (Vadeboncouer *et al.*, 2003).

The qualitative reconstruction of progressive ecological change associated with eutrophication clearly contradicts the diatom–TP reconstruction. Aside from the doubted accuracy of transfer functions, our critique is levelled at the reductionist approach to handling species data. For example, if the reconstruction of Felbrigg's environmental history had been limited to the diatom–TP profile, it could have been assumed that the lake was little changed, and any concerns of a lake manager might have stopped there. Alternatively, an interpretation of multiple species profiles informed by contemporary seasonal data (see also Davidson *et al.*, 2010b; Sayer *et al.*, 2010a) shows dynamic eutrophication-induced changes to the lake ecosystem over at least the last century. In addition, from a management perspective, the lake can be shown to be highly degraded and vulnerable to the complete disappearance of submerged plants in the near future. Clearly, the multi-proxy palaeolimnological approach affords tremendous potential for improving our understanding of past ecological changes in shallow lakes, but as discussed by Birks & Birks (2006), the challenge is how to interpret the data. An improved understanding of species' and community ecology are the key means of advancing palaeolimnology in this respect.

Importance of the long-term perspective

While the palaeolimnological literature has seen periodic calls for the integration of ecological and experimental studies into palaeo-models (Saros, 2009),

there has been less reciprocation in this respect by contemporary limnologists. It is our thesis that contemporary limnologists would much benefit from greater collaboration with palaeolimnologists. Contemporary studies generally cover short snapshots of time (<1–2 years), whereas processes such as eutrophication and/or climate change probably act on much longer timescales (decades–centuries), and the mismatch of temporal scales could lead to spurious findings. This may be particularly true of shallow lakes where functioning is closely linked to slow changes in the benthic zone. For example, bottom sediments not only take years to respond to eutrophication through changes in physical structure (Schutten, Dainty & Davy, 2005), but also have a 'memory of conditions past' as a result of the propagule bank in the case of plants (de Winton, Clayton & Champion, 2000; Bonis & Grillas, 2002) and diapausing bodies for some invertebrates (Hairston & Kearns, 2002; Vandekerkhove *et al.*, 2005). Thus, plant and invertebrate populations may take decades to change as appropriate sediment conditions (cohesion, propagule stores) are unlikely to be lost in all parts of a lake over a few years. In addition, delays in ecosystem responses to eutrophication may result from lags in the onset of internal nutrient-release, slower (i.e. decadal) responses in some longer-lived and resilient biological groups (e.g. fish) and gradual changes in the species pool and hence food web structure. Such changes are unlikely to be detected in short-term research projects, but with careful analysis, they can be revealed in palaeo-studies.

To further frustrate our understanding of change in shallow lake ecosystems, most contemporary ecological experiments are conducted at relatively small spatial and temporal scales (e.g. within-lake enclosures) that exclude population level effects and over-emphasise simple, immediate interactions (e.g. predation) compared with more complex feedback mechanisms that are slower to respond (Beresford & Jones, 2010). Thus, our ability to interpret long-term change is often compromised by a lack of understanding of long-term/large-scale mechanisms. Long-term whole-lake experiments do help to bridge this gap, but they are infrequently undertaken (e.g. Schindler *et al.*, 2008) and often have a management rather than a scientific goal (Hansson & Bergman, 1999). If we are able to progress from individual case studies to a comprehensive understanding of lake

responses to pressures such as eutrophication and climate change, we must embrace all the lines of evidence available, particularly those covering the long temporal scales offered by palaeolimnology.

Conclusions

Over recent decades, palaeolimnology has been pre-occupied with the transfer function approach, and much effort has been placed either in tinkering with existing models to improve their performance, or in the development and application of new models in different regions (Birks & Birks, 2006; Saros, 2009). Given the emerging limitations and problems associated with transfer function reconstructions, we call for palaeolimnologists to take a step back to consider more fully the mechanisms via which species (and thus fossils) are connected to other species and in turn influenced by the environment. In this respect, we advocate the integration of contemporary surveys and experiments with palaeolimnology, so that sediment cores can be better interpreted in terms of changing ecological patterns and processes. Such an approach may lead to a new breed of palaeolimnological approaches, semi-quantitative (e.g. regression trees) and qualitative, that can be used to address key debates in contemporary ecology and to develop and test theory.

It is equally clear that contemporary ecologists need to be more fully aware of the enormous potential of palaeolimnology for reconstructing past lake ecology and of the limitations of solely using short-term data for speculating on population/community level change. Without the long-term view, even large-scale lake experiments and field surveys may fail when it comes to identifying long-term change as seasonality, inter-annual variation and noisy multiple structuring forces may obscure underlying patterns. To more fully understand change in lake ecosystems, integration of palaeolimnology with contemporary studies should provide a promising way forward. As elegantly pointed out by Smol (1990), seeing a lake in the current day is like taking an accurate photograph of a train during its journey, but the journey itself remains unknown. We argue that the journey is of crucial importance to our ecological understanding of shallow lakes and call for greater collaboration between palaeolimnologists and aquatic ecologists in the future.

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