

Back to the future: using palaeolimnology to infer long-term changes in shallow lake food webs

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SUMMARY

1. Shallow lakes are often cited as classic examples of systems that exhibit trophic cascades but, whilst they provide good model systems with which to test general ecological theory and to assess long-term community change, their food web linkages have rarely been resolved, so changes associated with the structure and dynamics of the ecological network as a whole are still poorly understood.

2. We sought to redress this, and to demonstrate the potential benefits of integrating palaeolimnological and contemporary data, by constructing highly resolved food webs and stable isotope derived measures of trophic interactions and niche space, for the extant communities of two shallow U.K. lakes from different positions along a gradient of eutrophication. The contemporary surface sediment cladoceran and submerged macrophyte assemblages in the less enriched site, Selbrigg Pond, matched the palaeolimnological assemblages of the more enriched site, Felbrigg Hall Lake, in its more pristine state during the 1920s. Thus, Selbrigg was a temporal analogue for Felbrigg, from which the consequences of long-term eutrophication on food web structure could be inferred. These data represent the first steps towards reconstructing not only past assemblages (i.e. nodes within a food web), but also past interactions (i.e. links within a food web): a significant departure from much of the previous research in palaeolimnology.

3. The more eutrophic food web had far fewer nodes and links, and thus a less reticulate network, than was the case for the more pristine system. In isotopic terms, there was vertical compression in $\delta^{15}\text{N}$ range (NR) and subsequent increased overlap in isotopic niche space, indicating increased trophic redundancy within Felbrigg. This structural change, which was associated with a greater channelling of energy through a smaller number of nodes as alternative feeding pathways disappear, could lead to reduced dynamic stability, pushing the network towards further simplification. These changes reflected a general shift from a benthic-dominated towards a more pelagic system, as the plant-associated subweb eroded.

4. Although these data are among the first of their kind, the palaeo-analogue approach used here demonstrates the huge potential for applying food web theory to understand how and why these ecological networks change during eutrophication. Furthermore, because of the rich biological record preserved in their sediments, shallow lakes represent potentially important models for examining long-term intergenerational dynamics,

thereby providing a means by which models and data can be integrated on meaningful timescales – a goal that has long proved elusive in food web ecology.

Keywords: ecological networks, eutrophication, macrophytes, palaeo-ecology, stable isotope analysis

Introduction

Over the last century, eutrophication has resulted in widespread and marked declines in the biodiversity and ecological status of shallow lake ecosystems (Jeppesen *et al.*, 1998). Although the mechanisms behind the responses to enrichment are still moot, it is generally agreed that submerged macrophytes are eventually displaced by a phytoplankton-dominated community (Brönmark & Hansson, 2005; Jeppesen & Sammalkorpi, 2002). The shift from benthic to pelagic primary production (Vadeboncoeur *et al.*, 2003) and a decline in plant-associated invertebrates (Jeppesen *et al.*, 2000) have been explained in terms of reduced habitat heterogeneity, as macrophytes play a vital structuring role in lakes by providing refugia from predation (Jeppesen *et al.*, 1998), structurally diverse habitats (Lauridsen & Lodge, 1996; Diehl & Kornijów, 1998), and a range of food sources (plant detritus and periphyton) for many taxa (Lodge, 1985).

Much of the research on ecological changes associated with environmental stressors has focussed on the shifts in community composition and the loss of species populations, rather than considering the consequences of losing the interactions between them (but see Petchey, 2004; Brooks *et al.*, 2006; Duffy *et al.*, 2007). However, knowledge of the energy flow and trophic interactions amongst species in an ecosystem is essential for understanding and predicting likely system-level responses to perturbations (McCann, 2000; Montoya, Pimm & Solé, 2006; Ings *et al.*, 2009; Woodward, 2009). For example, palaeolimnology has focussed primarily on sub-fossil assemblage-based reconstructions of past environmental conditions and, although this has yielded invaluable insights into long-term community change (e.g. Anderson & Battarbee, 1994), it has for the most part neglected information on past trophic interactions. The same is true of studies in contemporary systems that involve correlating data across nutrient gradients and space-for-time substitution, as although there are large bodies of data on species population abundances at different 'trophic levels', explicit characterisations of

community food webs are still surprisingly rare (Jeppesen *et al.*, 2000; Jones & Sayer, 2003; Jones & Jeppesen, 2007).

The primary focus of many experimental studies and the palaeo-ecological investigations that have considered species interactions (e.g. Leavitt, Carpenter & Kitchell, 1989; Leavitt *et al.*, 1994; Kerfoot, 1981) has been upon trophic cascades, rather than the full community food web: i.e. a food chain, rather than a food web, perspective. These studies have tended to lump species populations into nodes representing putative guilds or 'trophic levels' (e.g. fishes–herbivores–primary producers), rather than treating them as discrete components within the ecological network (e.g. Jones & Waldron, 2003; Jones & Jeppesen, 2007; Beresford & Jones, 2010). This is important because species are reproductively isolated entities, whose population dynamics are embedded within the wider food web, rather than aggregated 'black boxes' (Ings *et al.*, 2009; Woodward, 2009).

It is becoming increasingly apparent, from both data and theory, that it is not simply the number of links, but their patterning within the trophic network and their strength that is important in determining food web stability (Emmerson, Montoya & Woodward, 2005; Berlow *et al.*, 2009). These newly emerging ideas go beyond the complexity–stability debate that pervaded ecology for decades following May's (1972, 1973) pioneering modelling work (Ings *et al.*, 2009). Thus the concepts of keystone species and complexity–stability relations as drivers of community structure and ecosystem functioning are not necessarily mutually exclusive: keystones are important because they often have strong links and trophic cascades are more likely to arise where there are fewer weak links to stabilise them (McCann, 2000; Ings *et al.*, 2009).

An alternative, yet complementary, approach to using high resolution gut content analysis to characterise these complex trophic networks is the use of community-wide metrics derived from stable isotope analyses of food web components (*sensu* Layman *et al.*, 2007a,b). Although taxonomic resolution is

inevitably sacrificed, these metrics represent a summation of all energy pathways routed through a food web and, most importantly, depict species' niche space as an integration of temporal and spatial data. Despite the acknowledged caveats affecting the application of such metrics (see arguments in Layman *et al.*, 2007a,b), one feature of this approach is that potential biases introduced at the single species level are unlikely to affect the metrics derived from multiple species in a web significantly, especially when comparing across a perturbation gradient that is expected to alter food web architecture and fluxes.

Our principal intention in this proof-of-concept paper is to demonstrate how palaeo and contemporary approaches can be integrated to infer 'palaeo food webs', via the use of space-for-time substitution (e.g. Flower, Juggins & Battarbee, 1997), for a shallow, eutrophic lake. High resolution contemporary food webs and complementary stable isotopic bi-plots were constructed for this and another less enriched shallow lake, to assess the impact of eutrophication on the architecture of their respective ecological networks. The contemporary community of the less enriched site (Selbrigg Pond) was identified by palaeolimnological analysis to be an analogue of an older 'palaeo' community (c. 1920s) within the more eutrophic site (Felbrigg Hall Lake), thus providing an extant dataset from which to infer past trophic interactions. As well as yielding potentially important new insights into the long-term dynamics of eutrophication, this addition of a temporal dimension offers great potential for reconstructing food webs over intergenerational timescales that reflect community responses to other long-term perturbations, including acidification and climate change (e.g. Battarbee *et al.*, 2005; Meerhoff *et al.*, 2007).

Methods

Study sites

Two lakes, Felbrigg Hall Lake and Selbrigg Pond, which have experienced different degrees of eutrophication were selected for food web characterisation from an extensive dataset of 29 shallow lakes in Norfolk, U.K. (described in Sayer, Davidson & Jones, 2010a). Both lakes are small, shallow (Table 1) and artificially created (Felbrigg in the late 1700s and Selbrigg in the early 1800s). Felbrigg is fed by two

Table 1 Physicochemical characteristics of Felbrigg Hall Lake and Selbrigg Pond

Physicochemical variable	Felbrigg Hall Lake	Selbrigg Pond
Location	52°54.10'N, 1°15.19'E	52°54.27'N, 1°08.01'E
Maximum depth (m)	1.6	1.1
Average depth (m)	0.9	0.8
Area (ha)	2.7	1.0
TP ($\mu\text{g L}^{-1}$)	107 (40–229)	35 (20–50)
NO ₃ ⁻ -N (mg L^{-1})	1.3 (0.2–3.5)	0.1 (0.0–0.3)
Chlorophyll-a ($\mu\text{g L}^{-1}$)	14.9 (0.7–52.6)	5.3 (1.0–17.4)
PVI (%) June	48	37
PVI (%) August	0	24

Chemical data are mean annual concentrations attained from an intensive survey carried out in 1999–2000 (Sayer *et al.*, 2010a). TP, total phosphorous; NO₃⁻-N, nitrate nitrogen and PVI (%), macrophyte percentage volume infested score (see text). The range of TP, NO₃⁻-N and chlorophyll-a are given in brackets.

small streams that drain a predominantly agricultural catchment of pasture, arable land and parkland. It is consequently more eutrophic than Selbrigg, which receives its water via seepage from a small, wet woodland-dominated catchment (Sayer *et al.*, 2010a). As a result of its low nutrient status (Table 1), Selbrigg is a clear-water lake with nine species of submerged macrophyte that provide extensive plant coverage, both temporally (May–September) and spatially (c. 80% of the lake area). By contrast, Felbrigg supports just four macrophyte species within a smaller area (c. 60%) and over a shorter plant-covered period (May to early July), sandwiched between spring and late summer peaks of phytoplankton (Sayer *et al.*, 2010a). A mid-summer macrophyte 'collapse' at Felbrigg, has been linked to its species-poor plant community, which is dominated by *Potamogeton pectinatus* L., *Potamogeton pusillus* L. and *Zannichellia palustris* L. and is a recurrent phenomenon (C.D. Sayer, unpublished data): e.g. in 1999–2000 macrophyte density measured with the percentage volume infested (PVI) system (Canfield *et al.*, 1984) scores fell from 48% to 0% between June and August, whereas the plant coverage in Selbrigg was reduced only from 37% to 24% over the same period.

Palaeolimnological data from Felbrigg (see Sayer *et al.*, 2010b; Davidson *et al.*, 2010b) show at least a century of ecological change as a consequence of eutrophication. Macrofossil remains of macrophytes suggest an abundant and diverse (10+ species)

submerged vegetation for the 150 years prior to c. 1900, followed by a decline in species richness. The predominant plant assemblage has shifted in terms of dominance from *Myriophyllum spicatum* L. (c. pre-1900), to *Ceratophyllum demersum* L. and *Chara* sp. (c. 1900–1960) to the current impoverished community (post-1960s) (Sayer *et al.*, 2010b). Following this trajectory, the contemporary submerged vegetation of Selbrigg is analogous to that of Felbrigg in the 1920s, when it supported a mixed community dominated by *Chara* spp., *C. demersum* and *Potamogeton crispus* L., with some *Ranunculus* sect. *Batrachium*, *Z. palustris* and fine-leaved *Potamogeton* species.

These inferred changes in the macrophyte community were also mirrored by changes in the cladoceran stratigraphy (Davidson *et al.*, 2010a). Over this trajectory Felbrigg gradually changed from a lake with abundant macrophytes and a dominance of benthic primary production (pre-1900) to the more recent (post-1960s) situation whereby macrophytes are less abundant and phytoplankton production is much more prominent (see Doc. S1 and Davidson *et al.*, 2010b for a detailed description of these temporal changes). Further, the surface sediment cladoceran assemblage in Selbrigg is very similar to the sub-fossil cladoceran assemblage of Felbrigg in c. 1927 (i.e. at 31 cm depth in the Felbrigg core; Fig. S1). Given the similarities between contemporary Selbrigg and 1920s Felbrigg, based on multiple biological proxies, coupled with the lakes' similar origins, physical characteristics and proximity, substituting space-for-time should provide a robust analogue that enables us to infer changes in the food web over many decades of eutrophication.

Sample collection

Selbrigg and Felbrigg were visited between the 4th June and 5th July, 2007. During this period, potential carbon sources and taxa representative of the major (i.e. most abundant) trophic elements (i.e. representatives of the basal resources, primary consumers, fish and invertebrate secondary consumers) were collected for food web characterisation and processed for gut contents or stable isotope analyses. The taxa collected in our survey were similar to those found in an earlier study (Beresford & Jones, 2010) and provided adequate representation of the fauna and flora. Seston was collected by filtering 10 L of water from each lake and

freeze-drying the residue on return to the laboratory. Macrophytes were harvested at three randomly chosen locations and frozen until subsequent processing. Periphyton was sampled in the laboratory by taking scrapings from the dominant submerged macrophyte species, with any contamination removed following inspection with an inverted microscope. Detritus, predominantly consisting of decomposing leaves and plant material of allochthonous origin, was collected from the lake bed and frozen. Zooplankton was collected by horizontal net trawls (mesh size 75 µm) and macroinvertebrates by sweeping amongst submerged and emergent plant stands with a standard ISI pond net (mesh size 330 µm). All specimens for gut content analyses were immediately preserved in industrial methylated spirit (70%). Invertebrates for stable isotope analysis were sorted on the bank into different taxa and stored alive in regularly changed algal-free water for 24 h to empty their guts (Feuchtmayr & Grey, 2003). Fishes were selected in accordance to species coverage and size class (after Zambrano *et al.*, 2006) and were sampled by a combination of point abundance sampling by electro-fishing (600 Hz pulsed DC electrofisher powered by a 1.1 kV generator), depletion sampling in stop-netted areas by electro-fishing, and rod and line sampling where necessary. Fin clips were taken from larger specimens, especially eel (*Anguilla anguilla* L.) and tench (*Tinca tinca* L.), which enabled a larger sample size to be attained without further detriment to the fish community. All fish were killed humanely and frozen immediately.

Stable isotope analyses

On return to the laboratory all samples (except seston) for stable isotope analyses were oven-dried at 60 °C for 48 h and homogenised with a pestle and mortar. The macrophytes were vigorously shaken in algal-free water to remove any attached algae before drying. Samples preferentially corresponded to individuals, with a minimum of three per species, although this was dependent on body mass: for the smaller invertebrates, 10–30 individuals were processed together to provide sufficient mass for isotopic analysis and a minimum of three subsamples were run. Snails were removed from their shells because CaCO₃ is derived from dissolved inorganic carbon (DIC) that is typically ¹³C-enriched relative to the diet. White muscle

tissue was removed from the fishes and, for individuals from which only fin clips were taken, an estimation of the isotope value for white muscle tissue was derived from calibration curves (R. Rawcliffe, unpublished data).

Fish tissue (0.50 ± 0.01 mg), invertebrates (0.60 ± 0.01 mg) and plant matter (1.00 ± 0.01 mg) were loaded into tin capsules and combusted in a ThermoFinnigan FlashEA 1112 elemental analyser coupled to a ThermoFinnigan Delta^{Plus} CF-IRMS. (ThermoFinnigan, Bremen, Germany). Correct functioning was monitored by initially running a set of six urea standards (ranging from 0 to 600 μg dry wt) and interspersing 0.60 ± 0.01 mg standards of cyclohexanone 2,4 dinitrophenylhydrazone every eight samples. Repeat analyses of the internal standards gave a precision of $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$. Lipid content of tissues was assessed from the C : N ratios and fish tissues were lipid-normalised mathematically, according to Kiljunen *et al.* (2006).

Gut content analysis

Consumer guts were removed from up to 10 individuals of each common species, by dissection. For scarcer taxa (e.g. odonates), where fewer than 10 individuals were caught, all specimens were used (minimum two) and our direct observations (i.e. via gut contents analysis) were supplemented with dietary information extracted from the literature using the large dietary datasets in Brose *et al.* (2005) and Woodward *et al.* (2008); if a feeding link was reported between taxa, we assumed it would also be present in both the Felbrigg and Selbrigg webs wherever the same protagonists co-occurred (e.g. after Martinez, 1992). In total, 141 and 216 guts from Felbrigg and Selbrigg were analysed, respectively, with 76% of the feeding links in Felbrigg and 66% in Selbrigg derived from direct observations of dissected gut contents.

Gut contents were examined under 200 \times magnification for invertebrate prey and 1000 \times magnification for algae. As animal prey was generally ingested whole, or in large fragments, most items could be identified to species (except caddis and chironomid larvae, which were identified to genus). Algae were also identified to genus because of limited optical resolution, as the gut contents of primary consumers were mounted directly onto the slides. This had the

benefit of conserving filamentous algae and organic matter, which would have otherwise decomposed during the H_2O_2 digestion procedure used in standard diatom slide preparations (Battarbee *et al.*, 2001). Five random transects, consisting of a minimum of 300 diatom valves, were counted per slide for each primary consumer gut.

Food web construction, isotope metrics and statistics

The nodes (i.e. trophic elements) within the food webs were identified using published taxonomic keys. Taxonomic resolution was high throughout both webs, with the majority of nodes being resolved to species (53%) or genus (88%) and similar sampling effort in both lakes. This enabled us to compare structural properties of the two food webs, including the absolute numbers of nodes (S) and links (L), linkage density (L/S), and directed connectance ($C = L/S^2$) for the entire network. The latter measure represents a measure of the fraction of all the possible trophic links within a food web that are realised, including cannibalistic loops (e.g. Woodward & Hildrew, 2001). Complexity was calculated by $S [L/S (S - 1)/2]$ (after Montoya *et al.*, 2006). Binary (i.e. presence/absence) food webs were constructed using the PAJEK 1.20 software package (V. Batagelj & A. Mrvar, Ljubljana, Slovenia), which enabled both graphical visualisation and numerical analysis of the networks. Community-wide metrics of trophic diversity were derived from stable isotope data, after Layman *et al.*, 2007a,b. In brief, four metrics were derived from the spacing of species within $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot space [$\delta^{13}\text{C}$ range (CR), NR, total area (TA) measured from convex hulls, and mean distance to centroid]. A further two metrics were calculated to describe the relative position of species to each other within isotope niche space (nearest neighbour distance and the standard deviation of nearest neighbour distance) and to give estimates of the extent of trophic redundancy.

Results

Stable nitrogen and carbon isotope bi-plots of the Selbrigg and Felbrigg food webs are illustrated in Fig. 1. Primary producers were omitted and some invertebrate species data have been condensed to aid visualisation, but the full species list with isotope

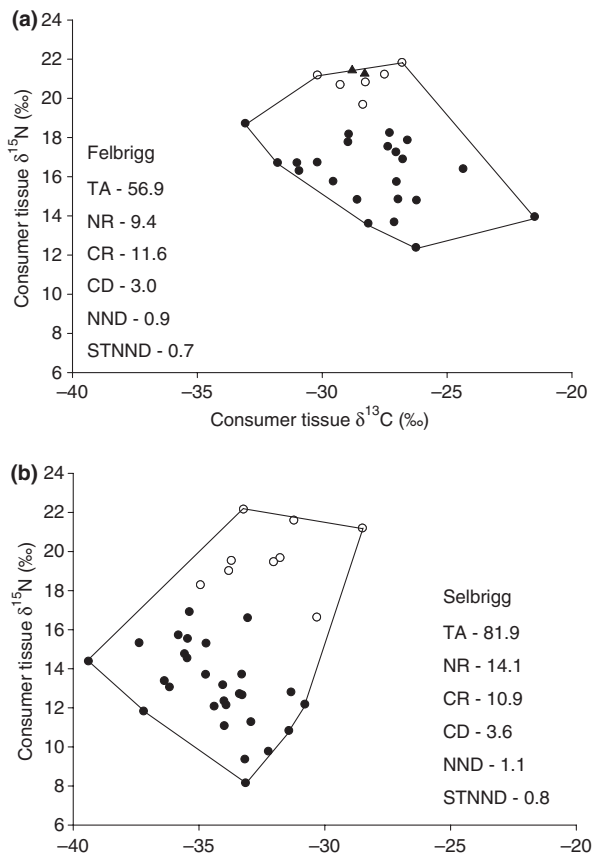


Fig. 1 Stable isotope bi-plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for fish (open circles) and invertebrates (closed circles) from (a) Felbrigg Hall Lake and (b) Selbrigg Pond. Note fish parasites, *Argulus* and *Piscicola* (closed triangles) from Felbrigg Hall Lake. Lines represent convex hull areas defining isotopic niche space from which various community wide metrics were calculated according to Layman *et al.*, 2007a,b: TA, total area; NR, $\delta^{15}\text{N}$ range; CR, $\delta^{13}\text{C}$ range; CD, mean distance to centroid; NND, nearest neighbour distance; STNND, standard deviation around NND. Each datapoint represents a single trophic element (approximately species population) within the food web. Values for individual taxa are presented in the Doc. S1.

values is listed in Table S1. In general, the food web of Selbrigg was ^{13}C -depleted by *c.* 6‰ compared with that of Felbrigg although the relative position of species varied between 2‰ and 12‰. Primary consumers (and primary producers) in Felbrigg were more ^{15}N -enriched, reflecting a higher isotopic baseline. The $\delta^{15}\text{N}$ values placed fish at the top of the food webs in both lakes, a position also shared by the fish parasites *Argulus foliaceus* L. and *Piscicola geometra* L. Pike (*Esox lucius* L.) were piscivorous in both lakes, as were 2+ perch (*Perca fluviatilis* L.; Fork length = 140–180 mm) and eel in Selbrigg, and these species were

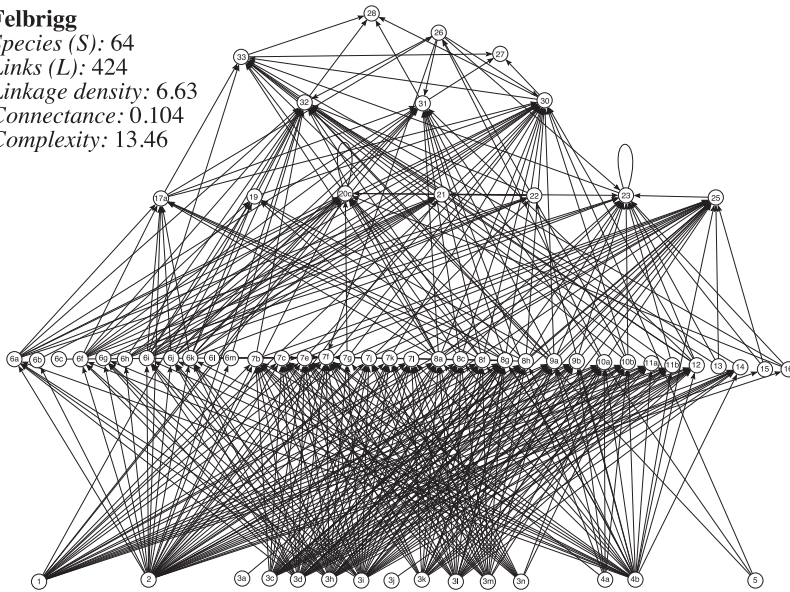
consequently the most ^{15}N -enriched. Despite the difference in isotopic baseline between the two lakes, the top predators exhibited similar $\delta^{15}\text{N}$ values, resulting in a NR of 14.1 in Selbrigg (excluding primary producers) and a NR value of 9.4 in Felbrigg. The CR of both lakes were similar (10.9 and 11.6 for Selbrigg and Felbrigg respectively). The convex hull area occupied by species in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ niche space resulted in TA estimates of 81.9 and 56.9 for Selbrigg and Felbrigg, respectively, and all other metrics values were higher in Selbrigg than Felbrigg (see Fig. 1).

The fish assemblage in Felbrigg consisted of tench, perch, rudd (*Scardinius erythrophthalmus* L.) and pike, while in Selbrigg the same species were present in addition to roach (*Rutilus rutilus* L.) and eel. The composition in both lakes was similar to surveys in 1999–2000 (cf. Jones & Sayer, 2003; Zambrano *et al.*, 2006). Fishes in both lakes were highly omnivorous based upon gut content analyses, with most species feeding at many different positions within and among food chains, a finding supported by similar studies of other eutrophic shallow lakes in the region (Jones & Waldron, 2003). However, both gut content and stable isotope data revealed more marked dietary ontogenetic shifts in fishes from Selbrigg relative to those from Felbrigg, and this was highlighted in the increased NR and CR values for the fish assemblage Selbrigg (NR: 5.5 versus 2.1; CR: 6.4 versus 3.4). The primary consumer assemblage in both lakes was composed largely of detritivorous and phytophagous chironomids and chydorids, whose gut contents were composed mainly of FPOM and periphyton. Basal resources included fine particulate organic matter (FPOM), coarse particulate organic matter (CPOM), filamentous algae (e.g. *Spirogyra* spp.), diatoms and other algae (e.g. *Closterium* spp.), and terrestrial invertebrates.

Selbrigg had a more diverse invertebrate assemblage than did Felbrigg, with 20% more species of primary consumer and more than twice as many predatory invertebrate species (Fig. 2). The most numerically abundant predatory invertebrates found in both lakes were larvae of tanypodine midges and of the caddis *Holocentropus dubius* Rambur, with cannibalism and mutual predation evident among these taxa. The common darter *Sympetrum striolatum* Charpentier and *Ischnura elegans* Vander Linden were found only in Selbrigg, and only one of the five

Felbrigg

Species (*S*): 64
 Links (*L*): 424
 Linkage density: 6.63
 Connectance: 0.104
 Complexity: 13.46

**Selbrigg**

Species (*S*): 81
 Links (*L*): 837
 Linkage density: 10.33
 Connectance: 0.127
 Complexity: 20.93

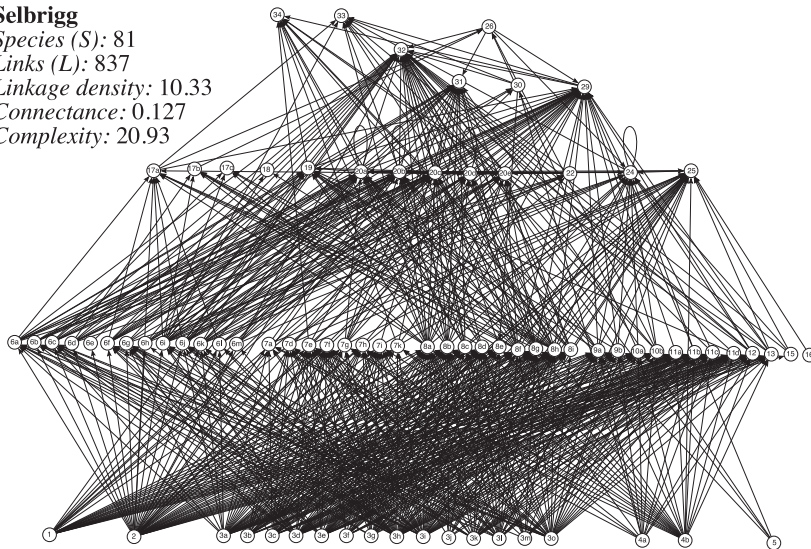


Fig. 2 Connectance food webs for Felbrigg Hall Lake and Selbrigg Pond. The food web is structured vertically with the arrows representing the direction of energy flux, such that the basal resources are in the lowest tier, with primary invertebrate consumers in the trophic level above them. Secondary invertebrate predators are grouped in the third tier from the base, beneath the fishes. Piscivores (and fish parasites) are placed above the non-piscivorous fishes. Loops imply cannibalism. Nodes (circles) correspond to trophic elements and can be identified from the key in Table 2.

Selbrigg genera of tanypod midges was found in Felbrigg (Fig. 2). The Selbrigg web contained 81 trophic elements and 839 links, with a relatively high linkage density, connectance and complexity (Fig. 2; species key provided in Table 2). In contrast, the Felbrigg web was smaller and simpler, with a lower linkage density, connectance and complexity. The loss of species was skewed in terms of their trophic position: basal resources were 1.2 times more diverse in Selbrigg than in Felbrigg, whereas the intermediate invertebrate consumers, with the greatest number of links (both upwards and downwards), and the fish assemblage were both 1.5 times more species-rich in the more pristine food web.

The food web statistics for both systems were within the ranges of metrics calculated for 29 recent, highly resolved freshwater food webs (Fig. 3), indicating that our web characterisations captured comparable amounts of the trophic complexity of Felbrigg and Selbrigg. The scaling exponent ($\beta = 1.72$) of species richness (*S*) versus the number of links (*L*) of these freshwater food webs (from the catalogue listed in Woodward *et al.*, 2008) was lower than that predicted by the constant connectance hypothesis ($\beta = 2$), suggesting that larger webs tended to have more specialist species and compartmentalisation than smaller, more generalist webs: however, in the particular case of the Felbrigg and Selbrigg webs, this

Table 2 Key to web components for the Felbrigg Hall Lake [Fig. 2(i)] and Selbrigg Pond [Fig. 2(ii)] connectance food webs

Key	TL	Trophic element	Key	TL	Trophic element
1	0	CPOM	8a		<i>Chironomus</i> spp.
2		FPOM	8b		<i>Cladopelma</i> spp.
3a		<i>Achnanthes</i> spp.	8c		<i>Dicrotendipes</i> spp.
3b		<i>Amphora</i> spp.	8d		<i>Einfeldia</i> spp.
3c		<i>Cocconeis</i> spp.	8e		<i>Endochironomus</i> spp.
3d		<i>Cymbella</i> spp.	8f		<i>Glyptotendipes</i> spp.
3e		<i>Diatoma</i> spp.	8g		Orthoclaadiinae
3f		<i>Epithemia</i> spp.	8h		<i>Polypedilum</i> spp.
3g		<i>Eunotia</i> spp.	8i		Tanytarsini
3h		<i>Fragilaria</i> spp.	9a		<i>Caenis robusta</i> Eaton
3i		<i>Gomphonema</i> spp.	9b		<i>Cloeon dipterum</i> L.
3j		<i>Gyrosigma</i> spp.	10a		<i>Micronecta minutissima</i> L.
3k		<i>Navicula</i> spp.	10b		<i>Sigara falleni</i> Faeber
3l		<i>Nitzschia</i> spp.	11a		<i>Limnophilus</i> spp.
3m		<i>Rhoicosphenia</i> spp.	11b		<i>Mystacides longicornis</i> L.
3n		<i>Stephanodiscus</i> spp.	11c		<i>Oxyethira</i> spp.
3o		<i>Synedra</i> spp.	11d		<i>Tinodes waeneri</i> L.
4a		Filamentous algae	12		<i>Asellus aquaticus</i> L.
4b		Other algae	13		<i>Gammarus pulex</i> L.
5		Terrestrial adult insect	14		Oligochaeta
6a	1°	<i>Alona affinis</i> Leydig	15	2°	<i>Dugesia</i> spp.
6b		<i>Alona quadrangularis</i> Müller	16		Ceratopogonidae
6c		<i>Alonella nana</i> Baird	17a		<i>Coenagrion puella</i> L.
6d		<i>Bosmina longirostris</i> Müller	17b		<i>Coenagrion pulchellum</i> Vander Linden
6e		<i>Ceriodaphnia</i> spp.	17c		<i>Ischnura elegans</i> Vander Linden
6f		<i>Chydorus sphaericus</i> Müller	18		<i>Sympetrum striolatum</i> Charpentier
6g		Copepoda Calanoida	19		<i>Holocentropus dubius</i> Rambur
6h		<i>Daphnia hyalina/longispina</i>	20a		<i>Ablabesmyia</i> spp.
6i		<i>Eurycercus lamellatus</i> Müller	20b		<i>Guttipelopia</i> spp.
6j		<i>Leydigia leydigii</i> Leydig	20c		<i>Procladius</i> spp.
6k		<i>Pleuroxus aduncus</i> Jurine	20d		<i>Psectrotanypus</i> spp.
6l		<i>Pleuroxus uncinatus</i> Baird	20e		<i>Tanypus</i> spp.
6m		<i>Scapholeberis mucronata</i> Schoedler	21		<i>Chaoborus</i> spp.
6n		<i>Simocephalus vetulus</i> Müller	22		Copepoda Cyclopoida
7a		<i>Bithynia tentaculata</i> L.	23		<i>Agabus didymus</i> Olivier
7b		<i>Gyraulus albus</i> Müller	24		Dysticidae
7c		<i>Gyraulus crista</i> L.	25		<i>Helobdella stagnalis</i> L.
7d		<i>Hippeutis complanatus</i> L.	26		Acari spp.*
7e		<i>Radix balthica</i> L.	27		<i>Argulus foliaceus</i> *
7f		<i>Lymnaea stagnalis</i> L.	28		<i>Piscicola geometra</i> L.*
7g		Ostracoda	29		<u><i>Rutilus rutilus</i> L.</u>
7h		<i>Planorbis contortus</i> Calow	30		<u><i>Scardinius erythrophthalmus</i> L.</u>
7i		<i>Planorbis planorbis</i> L.	31		<u><i>Tinca tinca</i> L.</u>
7j		<i>Pisidium</i> spp.	32		<u><i>Perca fluviatilis</i> L.</u>
7k		<i>Sphaerium lacustre</i> Müller	33		<u><i>Esox lucius</i> L.</u>
7l		<i>Valvata piscinalis</i> Müller	34		<u><i>Anguilla anguilla</i> L.</u>

TL, the 'trophic position', with zero corresponding to basal resources, 1° to primary invertebrate consumers and 2° to secondary and higher consumers [predatory invertebrates, parasitic invertebrates (*) and fishes (underlined)].

CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter.

scaling coefficient was 2.89, far higher than the general relationship. This reflected the lower absolute (i.e. *S* and *L*) and relative metrics (e.g. connectance, *C*) of food web complexity within the more eutrophicated system.

Discussion

Palaeolimnological data have revealed that Felbrigg Hall Lake has experienced progressive nutrient enrichment over at least the last 100 years (Sayer

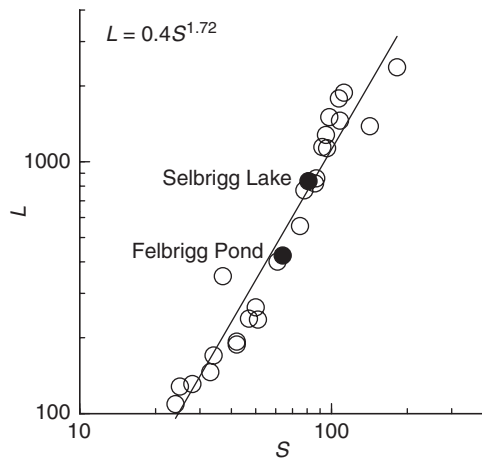


Fig. 3 Species richness (S) versus the number of links (L) in 29 freshwater food webs (from the catalogue listed in Woodward *et al.*, 2008), with the Felbrigg and Selbrigg webs highlighted. The scaling exponent ($\beta = 1.72$) is less than that predicted by the constant connectance hypothesis ($\beta = 2$), suggesting that larger webs have more specialist species and compartmentalisation than the smaller, more generalist webs. We would therefore expect shallow lake food webs to move down this trajectory of the regression line as species are lost during eutrophication.

et al., 2010b; Davidson *et al.*, 2010b), such that its biological communities are currently typical of other highly eutrophic lakes in the region (Sayer *et al.*, 2010a; Beresford & Jones, 2010). With Selbrigg Pond acting as an analogue for Felbrigg in the 1920s, we can infer that the latter had a more diverse, species-rich macrophyte and invertebrate community and more reticulate complex food web (assuming that the fundamental dietary niche of each species has not altered significantly) in the early twentieth century than is presently the case. Felbrigg's contemporary food web is comparatively simple, in terms of absolute numbers of nodes and links, the proportion of links that are realised, food chain length, and the degree of isotopic compaction. This widespread loss of nodes from the food web will impose constraints on the realised diet width of the consumer assemblage, and the associated structural changes in the network are also likely to have profound implications for its dynamics and, by extension, its stability (Woodward, 2009).

Shallow lakes with abundant submerged macrophytes typically support an increased biomass and diversity of invertebrates (Diehl & Kornijów, 1998; Jones & Sayer, 2003) as plants provide an important food resource for grazers, whilst also reducing the

strength of predator–prey interactions through the provision of structurally complex habitats and physical refugia (Lodge, 1985; Diehl, 1992). By contrast, lakes where plants are sparse or absent often exhibit enhanced phytoplankton growth, with the open water providing few opportunities for prey to avoid predation (Wright & Shapiro, 1990). Thus, the reduced spatial area and shorter growing season for plants observed in Felbrigg would not only limit the availability of food, but, because of the loss of vegetative habitat, could leave plant-associated invertebrates more vulnerable to predation (Kornijów, 1989; Van den Berg *et al.*, 1997). This loss of plants (both seasonally and spatially) clearly has ramifications for the entire ecosystem, and can be coupled to a loss of invertebrates that specialise on periphyton or macrophyte-associated food chains (Jones & Sayer, 2003). In turn a decline of associated periphyton and macroinvertebrates diminishes the benthic compartment of the food web, with increasing energy being directed through pelagic food chains (Vadeboncoeur *et al.*, 2003). Compartmentalisation between rapid turnover plankton-based pelagic pathways and slow turnover benthic pathways is believed to stabilise the dynamics of food webs (Krause *et al.*, 2003; Rooney *et al.*, 2006), so the loss of the macrophyte-associated sub-web might increase the vulnerability of the network to further simplification. Future long-term monitoring of Felbrigg, combined with contemporary sampling of other analogue lakes towards this end of the eutrophication gradient will enable more detailed hind-casting and forecasting of the trajectory of change within the food web.

Differences between the connectance food webs of the two lakes were manifested in terms of both network size and complexity: this was further reflected in the isotope-derived metrics. Directed connectance in Felbrigg was *c.* 0.1, the mean value reported for other similarly highly resolved food webs (Dunne, Williams & Martinez, 2002; Montoya & Solé, 2003). The higher connectance in Selbrigg revealed that, on average, there were more alternative pathways through a given node. This might serve to increase stability, as destabilising interactions could be buffered by a diverse suite of species that are capable of differential responses to perturbations (Pimm, Lawton & Cohen, 1991). Selbrigg, for instance, had 27% more species and nearly twice as many links as Felbrigg. Complexity was 35% lower in Felbrigg

than in Selbrigg and when combined with the absence of some of the larger species higher in the food web this resulted in the food web contracting both vertically and horizontally. There were more species of parasite in Felbrigg (three spp.) than in Selbrigg (one sp.), suggesting that the already depauperate fish assemblages (four and six spp. respectively) might be suffering from additional biotic stressors in the more eutrophic system. The increased number of specialist parasites and the loss of generalist fish species (i.e. roach and eel) accounted for much of the difference in connectance between the two webs at the higher trophic levels, and the intermediate invertebrate species, which acted as highly-connected 'hubs' that linked the basal resources to the fish assemblage, were 1.5 times more diverse in Selbrigg than in Felbrigg. The increase in both S and C means that the 'additional' species were contributing many more links (L) to the food web, and the scaling coefficient of L to S was far steeper than that described by a general relationship from a range of systems not exposed to excessive eutrophication.

The ideas of Elton (1927) and other early ecologists that complexity is positively related to dynamic stability have regained popularity in recent years, although it is not simply the number of links but their strength and patterning that are important (McCann, 2000; Emmerson *et al.*, 2005; Neutel *et al.*, 2007; Ings *et al.*, 2009; Berlow *et al.*, 2009). Recent applications of network theory to ecological systems have demonstrated that complexity can be stabilised by the presence of many 'weak links', which appear to dampen the effects of perturbations (Polis, 1998; McCann, 2000; Ings *et al.*, 2009). Future food web research in shallow lakes is likely to be especially productive if directed towards both increasing the sample size of binary networks and also quantifying the strength of these links across the eutrophication gradient. Recent work based on allometric scaling relations suggests that estimates of interaction strengths could be obtained by combining the binary feeding matrix with information on mean individual body mass for the nodes within the web, and this could then be used to parameterise mathematical models and simulations of dynamic stability (after Emmerson *et al.*, 2005; Berlow *et al.*, 2009).

From an isotopic perspective, the fish and invertebrate species in the Felbrigg web were constrained to a tighter $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ niche space, with the relatively

compacted NR in Felbrigg symptomatic of a compressed web and indicative of reduced trophic height (Layman *et al.*, 2007a,b): this provided independent verification of the general patterns seen in the more highly resolved food web data. There was no apparent difference in CR between the two lakes, indicating that niche diversification at the base of the food web was similar. However, the food web of Felbrigg was markedly ^{13}C -enriched by *c.* 6‰, suggesting considerable differences in DIC dynamics in the two lakes. Primary producers from Felbrigg were highly ^{13}C -enriched (up to 16.5‰; see Doc. S1), which is suggestive of increased productivity and influxes of isotopically heavy atmospheric CO_2 to compensate for the DIC fixed by phytoplankton photosynthesis (Schindler *et al.*, 1997). The $\delta^{13}\text{C}$ values reported from Selbrigg were more typical of a 'balanced' small lake with inputs from pelagic autotrophic primary producers, as well as benthic-derived DIC and allochthonous inputs (Jonsson, Karlsson & Jansson, 2003). Thus, the CR of Felbrigg was biased by the isotopically heavy primary producers, and resulted in an elevated TA because of the highly ^{13}C -enriched *Radix balthica*. In a comparable study, Layman *et al.* (2007a,b) advocated the use of mean distance to centroid (CD) as a better measure of overall trophic diversity within the food web: nearest neighbour distance and CD were lower in Felbrigg than in Selbrigg, indicating reduced trophic diversity and increased redundancy.

The long-term changes in macrophyte abundance and a general shift from the dominance of benthic to pelagic production appear to be associated with a general simplification of the Felbrigg food web. At this point it is possible to make some tentative associations between the stability of the network, the temporal dynamics of the macrophyte assemblage and their associated fauna, and the system's potential vulnerability to future perturbations. Studies of surface sediment cladoceran assemblages from 39 shallow lakes (including Felbrigg and Selbrigg) have shown that the current community of Felbrigg is more akin to sites without plants than to those with diverse submerged macrophyte assemblages and low phytoplankton production (Davidson *et al.*, 2010a). The current macrophyte assemblage of Felbrigg contains just four species (cf. nine in Selbrigg) and any continuation of the progressive loss of species that has occurred over the past century seems likely to result in the seemingly inevitable extirpation of plants and

their associated fauna (Sayer *et al.*, 2010b). If this were to happen, as has been the case for many other eutrophic shallow lakes (Körner, 2002; Scheffer & Carpenter, 2003), the Felbrigg food web is likely undergo further simplification, as pelagic species become dominant. Consequently, the Felbrigg ecosystem appears to be in an extremely vulnerable position in terms of its resilience to further perturbations.

In conclusion, the 'palaeo-analogue' approach used in this study offers a potentially novel way of assessing long-term changes in lake food webs. For the most part food web studies represent snapshots in time, creating a mismatch between the temporal scale of a study and the intergenerational scale changes that are likely to occur as the web is affected by gradual, press perturbations, such as eutrophication, acidification and climate change (Woodward, 2009; Ings *et al.*, 2009). By constructing food webs for contemporary lakes that are analogues for different points along a sediment core sequence of a lake experiencing nutrient enrichment, it should be possible to make inferences about the temporal dynamics of food web structure and stability. Furthermore, shallow lakes preserve exceptionally rich fossil records of their former biological structure, including assemblages of algae (e.g. diatoms and chrysophytes), macrophytes (macro-remains and pollen), zooplankton (particularly Cladocera), invertebrates (Chironomidae, Ostracoda, Mollusca, Trichoptera and Coleoptera amongst other groups) and even fishes (scales and bones). By combining these multiple sources of data from dated cores and by inferring species interactions from contemporary data, trajectories of food web assembly and collapse could be reconstructed over extensive time series. Such a novel approach offers potentially far deeper insights into long-term food web dynamics than has been the case to date. Palaeolimnology has long been focused on studying historical patterns in species nodes: we are now poised to exploit the full potential of the sediment record by characterising the links between them and to consider these ecosystems from a new, holistic and integrated perspective.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Sub-fossil cladoceran assemblages at defined depths from the Felbrigg Hall Lake core passively overlain within a redundancy analysis (RDA) of surface sediment cladoceran assemblages from a 39 shallow lake dataset detailed in Davidson *et al.* (2010a).

Table S1. Stable Isotope values for component members of the Felbrigg food web.

Doc. S1. Integrating palaeo and contemporary community data to reconstruct trajectories of ecosystem change.

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