

Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD)

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Abstract With the implementation of the EU Water Framework Directive (WFD), the member states have to classify the ecological status of surface waters following standardised procedures. It was a matter of some surprise to lake ecologists that zooplankton were not included as a biological quality element (BQE) despite their being considered to be an important and integrated component of the pelagic food web. To the best of our knowledge, the decision of omitting zooplankton is not wise, and it has resulted in the withdrawal of zooplankton from many so-far-solid monitoring programmes. Using examples from particularly Danish, Estonian, and the UK lakes,

we show that zooplankton (sampled from the water and the sediment) have a strong indicator value, which cannot be covered by sampling fish and phytoplankton without a very comprehensive and costly effort. When selecting the right metrics, zooplankton are cost-efficient indicators of the trophic state and ecological quality of lakes. Moreover, they are important indicators of the success/failure of measures taken to bring the lakes to at least good ecological status. Therefore, we strongly recommend the EU to include zooplankton as a central BQE in the WFD assessments, and undertake similar regional calibration exercises to obtain relevant and robust metrics also for zooplankton as is being done at present in the cases of fish, phytoplankton, macrophytes and benthic invertebrates.

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Introduction

With the implementation of the EU Water Framework Directive (WFD), the member states have to classify the ecological status of surface waters following standardised procedures. Ecological status is defined as an expression of the quality of the structure and functioning of aquatic ecosystems based on the assessment of a series of biological quality elements (BQEs—macroinvertebrates, fish, phytoplankton, macrophytes and phytobenthos) and supported by a set of chemical and hydromorphological quality data (Annex V, 2000/60/EC), and efforts are demanded to restore (if needed) the natural waterbodies to at least good ecological status within a limited time period.

As a matter of surprise, to many lake ecologists, zooplankton were not included as a BQE, despite the latter being considered a key component of the pelagic food web. The reason for this omission remains unclear (see discussion in Caroni & Irvine, 2010). Zooplankton are mentioned in the WFD CIS Monitoring guidance (CIS, 2003) as a ‘supportive/interpretative parameter’ of fish ‘often/typically measured or sampled at the same time’. During the 1950–1970s monitoring of West European lakes mainly focussed on a number of chemical variables, chlorophyll *a* (as an indicator of phytoplankton) and sometimes phytoplankton biomass, phytoplankton production and benthic invertebrates (Premazzi & Chiaudiani, 1992). Such programmes were based on the view that lake ecosystems are driven from the ‘bottom-up’, i.e. the view that nutrients fuel phytoplankton that are harvested by consumers up through the food web to the top predators. Another issue of concern was oxygen depletion in the bottom water (mainly deep stratified lakes were monitored), and benthic invertebrate communities were deemed to be suitable indicators. However, following the discovery that ‘top-down’ regulation in lakes can be profound (Hrbacek et al., 1961; Brooks & Dodson, 1965; Gliwicz, 2003), i.e. that changes at the top of the food web can have cascading effects through zooplankton to phytoplankton (Carpenter et al., 2001), and even to nutrient concentrations (Jeppesen et al., 1998) and carbon

emission (Cole et al., 2000), zooplankton and sometimes fish were added to several national monitoring programmes in, for example, Austria, Denmark, Finland, the Netherlands and Norway (EEA, 1996). In Eastern Europe, zooplankton have been routinely sampled since the 1950s, and in Estonia, for example, zooplankton have been monitored regularly since the 1960s in large Lake Peipsi and Lake Võrtsjärv. Zooplankton have traditionally also had a prominent position in lake status assessment in Russia (Andronikova, 1996), Hungary (Pärpalä et al., 2003), Poland (Karabin, 1985; Radwan & Popiołek, 1989), and several other East European countries.

The value of zooplankton as an indicator of ecological conditions stems from their position in the food web, sandwiched between the top-down regulators (fish) and bottom-up factors (phytoplankton), thus providing information about the relative importance of top-down and bottom-up control and their impact on water clarity. It could be argued that since fish and phytoplankton are included, zooplankton would be redundant. Clearly, phytoplankton and fish monitoring cannot be replaced by zooplankton. However, an extremely costly fish monitoring programme is needed to gain the same insight into trophic dynamics that zooplankton can provide in a more cost-effective manner. Such a programme would need to include detailed monitoring of young-of-the-year fish and invertebrate predators that have, hitherto, been only rarely considered.

An unfortunate corollary of the WFD not including zooplankton as an indicator of lake condition has been a general decrease in their use as an indicator of lake status. In Denmark, where scientists have repeatedly shown the usefulness of zooplankton as an indicator of changes in trophic dynamics and the ecological state of lakes related to changes in nutrient loading and climate (e.g. Jeppesen et al., 2000, 2005, 2009; Søndergaard et al., 2005), national authorities have recently decided to either reduce substantially or completely exclude zooplankton sampling from future key national monitoring programmes with reference to the WFD assessment programmes: this despite recommendations of not excluding zooplankton from scientists responsible for developing and running the programmes. In Estonia, zooplankton were omitted from small lake programmes after the implementation of the WFD. Zooplankton monitoring in the UK is ad hoc and under pressure, even in the Norfolk Broads where

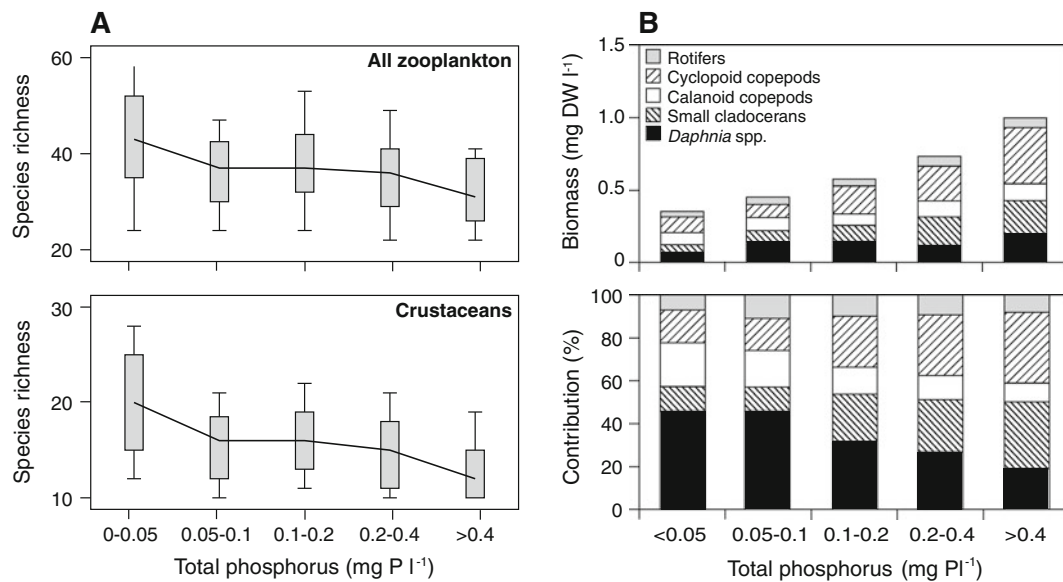


Fig. 1 **A** Box-plot showing the species richness of total zooplankton and cladocerans in five different TP classes. The full line represents median values. Also shown are 10, 25, 75 and 90% percentiles of the variables. **B** Time-weighted

summer mean biomass and percentage contribution of zooplankton to total biomass in five different TP classes (from Jeppesen et al., 2000)

many decades of research and monitoring have been conducted (e.g. Gurney, 1929; Timms & Moss, 1984).

Not only are the contemporary lake water zooplankton useful indicators of ecological status, but also their sedimentary remains provide information on ecosystem state and change through time. The top centimetre of sediment may give an integrated picture of not only the pelagic community, but also of the role of benthic- and plant-associated species, as sediment samples typically include more species and exhibit higher species diversity than contemporary samples (Davidson et al., 2007; Nevalainen, 2010) as they integrate spatially (sediment focusing) and temporarily (all seasons and a few years) gathered samples (Battarbee et al., 2005; Vandekerckhove et al., 2005). Benthic zooplankton taxa are well represented among sedimentary remains and when methods are adapted to include analysis of ephippia remains the keystone species *Daphnia* will be better represented (Jeppesen et al., 2001a, b; Davidson et al., 2007). Thus, sedimentary remains are useful as an indicator of ecological conditions as they reflect not only the ‘sandwich’ between top-down and bottom-up forces, but also represent both benthic and pelagic taxa and can track changes in the relative importance of the respective habitats.

In this article, we demonstrate mainly with examples from Denmark, Estonia and UK that zooplankton are important indicators of ecological state and discuss simple metrics that with further development could be useful indicators of the structure and function of lake ecosystems and their ecological status. We finally appeal to the EU to include zooplankton as a BQE as soon as possible.

Assessment: contemporary samples

Zooplankton community as indicator of eutrophication

An analysis of data from Danish lakes has shown clear changes in zooplankton community structure and richness along a eutrophication gradient (Jeppesen et al., 2000; Fig. 1). Zooplankton species richness declined considerably with increasing total phosphorus (TP) concentrations (Fig. 1A). The decline was particularly noticeable for the number of cladoceran species, although a pronounced decline was also observed in the species (taxon) number of copepods and rotifers. The zooplankton biomass increased with TP for all major groups (Fig. 1B). However, the

contribution of *Daphnia* spp. to the total biomass of cladocerans decreased and the contribution of cyclopoids to the total abundance and biomass of copepods increased. Multiple regressions revealed that CPUE of plankti-benthivorous fish by numbers contributed positively and significantly to the variation in the percentage of *Daphnia* spp. to mean specimen biomass of cladocerans and to the biomass percentage of calanoids to total copepods.

Results from Estonian lakes concur with these findings. Long-term investigations of the moderately eutrophic and large Lake Peipsi and the very eutrophic Lake Võrtsjärv have shown that both abundance and biomass of zooplankton increase with eutrophication (Haberman, 1996, 1998). Moreover, the number, biomass and proportion by number and biomass of rotifers increased with trophic state, the proportion of *Daphnia* of total crustacean biomass decreased, while, in contrast to Danish lakes, copepod biomass decreased (Haberman et al., 2007). In the Estonian lakes, the proportion of rotifers by number and biomass and the biomass of zooplankton are most closely linked with trophic state, while others—as in the Danish lakes—are better indicators of top-down regulating factors.

As most zooplankton species are found in a wide variety of lake types, the indicator value of individual species is somewhat limited to extreme oligotrophic or eutrophic conditions. In some instances, certain zooplankton species, especially rotifers, have an apparent indicator value for lakes (Gannon & Stemberger, 1978). However, indices based on species may be valuable indicators. Mäemets (1980) demonstrated a clear relationship between zooplankton community composition, lake type and trophic state, and developed the trophic state index E :

$$E = \frac{K(x+1)}{(A+Y)(y+1)},$$

where K , A and Y are the number of the species of rotifers, copepods and cladocerans, respectively; and x and y are the numbers as indicators of meso-eutrophy and oligo-mesotrophy. Mäemets (1980) further demonstrated that E is below 0.2 in the pelagial of oligotrophic lakes, and that it ranges between 0.2 and 1 in mesotrophic lakes, between 1 and 4 in eutrophic lakes, and is above 4 in hypertrophic lakes. This system has yet to be tested on other comparable lake systems.

Zooplankton size as indicator of eutrophication and predation

Zooplankton size also changes markedly with eutrophication and the related increase in fish predation. In a study of Danish lakes (Jeppesen et al., 2000), the mean individual body weight of cladocerans decreased substantially with increasing TP (Fig. 2). This reduction reflected not only the low relative

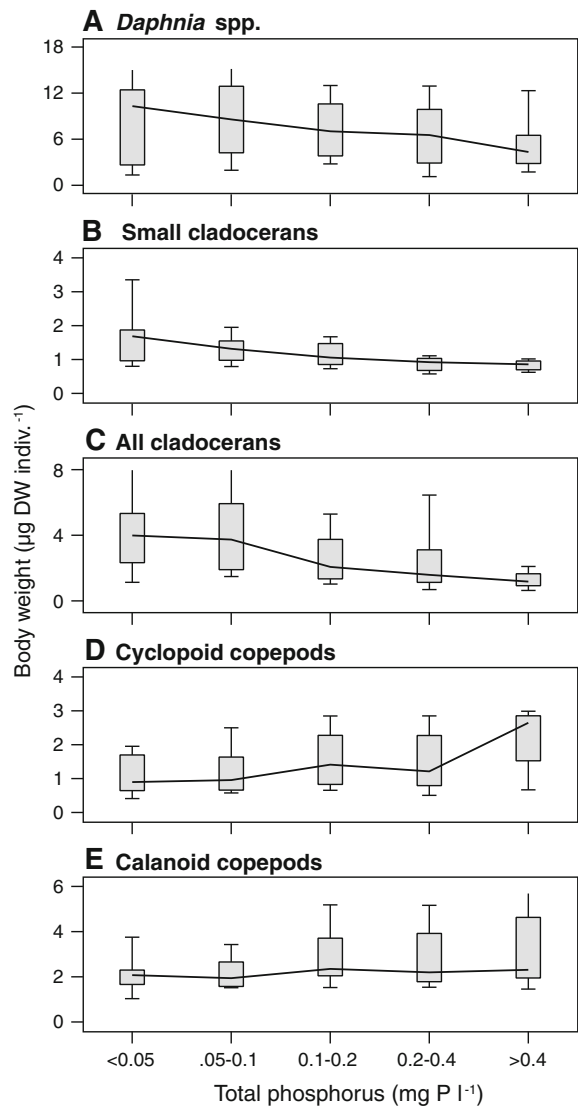


Fig. 2 Box-plot (see also legend of Fig. 1) showing summer average specimen weight of various genera and groups of zooplankton in five different TP classes (from Jeppesen et al., 2000)

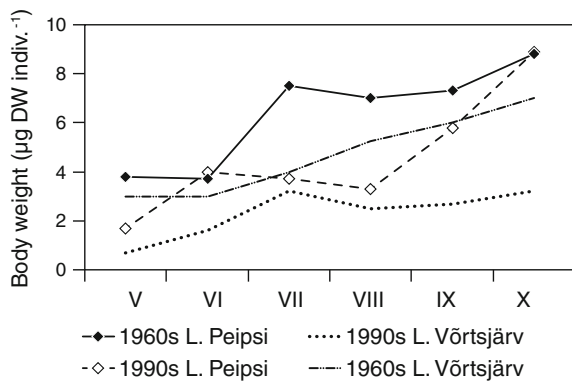


Fig. 3 Change in seasonal dynamics in body weight of zooplankton with increasing eutrophication in large mesotrophic Lake Peipsi and very eutrophic Lake Võrtsjärv, Estonia (from Haberman & Laugaste, 2003)

abundance of large *Daphnia* spp., but also a reduction in the body weight of the remaining *Daphnia* spp. and of small cladocerans.

The body weight of zooplankton was also strongly affected by trophic state in the two Estonian lakes (Haberman & Künnap, 2002; Haberman & Laugaste, 2003). Thus, mean zooplankton body weight was 4.4 µg (average for 1997–2000) in moderately eutrophic Lake Peipsi, but only 2.7 µg in the more eutrophic Lake Võrtsjärv. This difference could be followed for all zooplankton groups; moreover, concurrently with increasing eutrophication, there was a marked decrease in zooplankton body weight (during the 1960–1990s) in both lakes (Fig. 3).

Zooplankton:phytoplankton ratio as indicator of zooplankton grazing

The changes in the zooplankton appear to cascade to the phytoplankton. We used the zooplankton:phytoplankton biomass ratio (Zoo:Phyto ratio) as an indicator of the cascading effects on phytoplankton. In the Danish lakes, the mean Zoo:Phyto ratio during summer decreased significantly with increasing TP, from an average of 0.46 at low TP to 0.08–0.15 at high TP groups 3–5 (Fig. 4A) (Jeppesen et al., 2000). In a study of 466 lakes spanning an even larger TP gradient, Jeppesen et al. (2003a) also found a decreasing Zoo:Phyto ratio with increasing TP in both shallow and deep lakes (Fig. 4B). Further evidence has come from Estonian lakes. Blank

et al. (2010) recorded the Zoo:Phyto ratio during 1997–2008 in different parts of Lake Peipsi: the northern eutrophic Peipsi, the southern hypertrophic Lake Pihkva, and Lake Lämmijärv connecting the two parts. The average ratio for the period differed substantially among the lake parts, showing a marked decline with increasing eutrophication (Fig. 5A), and the change with time was also clear (Fig. 5A, B). The ratio was inversely related to TP and positively to lake transparency (expressed as the Secchi depth) (Fig. 5C, D).

Zooplankton as indicator of change in climate

Based on data from 81 shallow European lakes (North Sweden to Spain) sampled with standardised methods, Gyllström et al. (2005) showed that zooplankton biomass was related to TP in all climate zones following the same relationship in all the regions. Importantly, however, fish biomass and the fish:zooplankton biomass ratio increased from cold to warm lakes, while the zooplankton:Chl *a* ratio decreased substantially (Fig. 6). These effects may be interpreted as an increase in fish predation in warmer relative to colder lakes, resulting in cascading effects on the potential of zooplankton to control the phytoplankton community. The data suggested that bottom-up forces, such as nutrient concentration, are the most important predictors of zooplankton biomass. However, climate contributes significantly—possibly by affecting top-down regulation by fish—and may interact with productivity in determining the zooplankton standing biomass and community composition (Gyllström et al., 2005). Hence, the study suggested that food web dynamics are closely linked with climatic features.

Similar results were obtained by Havens & Beaver (2011) who compared the Zoo:Phyto ratio in subtropical Florida lakes with a number of north European lakes exhibiting a similar range of chlorophyll *a* and TP concentrations (Fig. 7). They found very low ratios in the Florida lakes compared with shallow mesotrophic to hyper-eutrophic lakes from Denmark and Germany. The highest ratios in Florida consistently occurred in the turbid pelagic region of Lake Okeechobee, where perhaps the suspended sediment particles reduce the reaction distance for visual planktivorous fishes; yet, the ratio still was four-fold lower than in the shallow temperate lakes

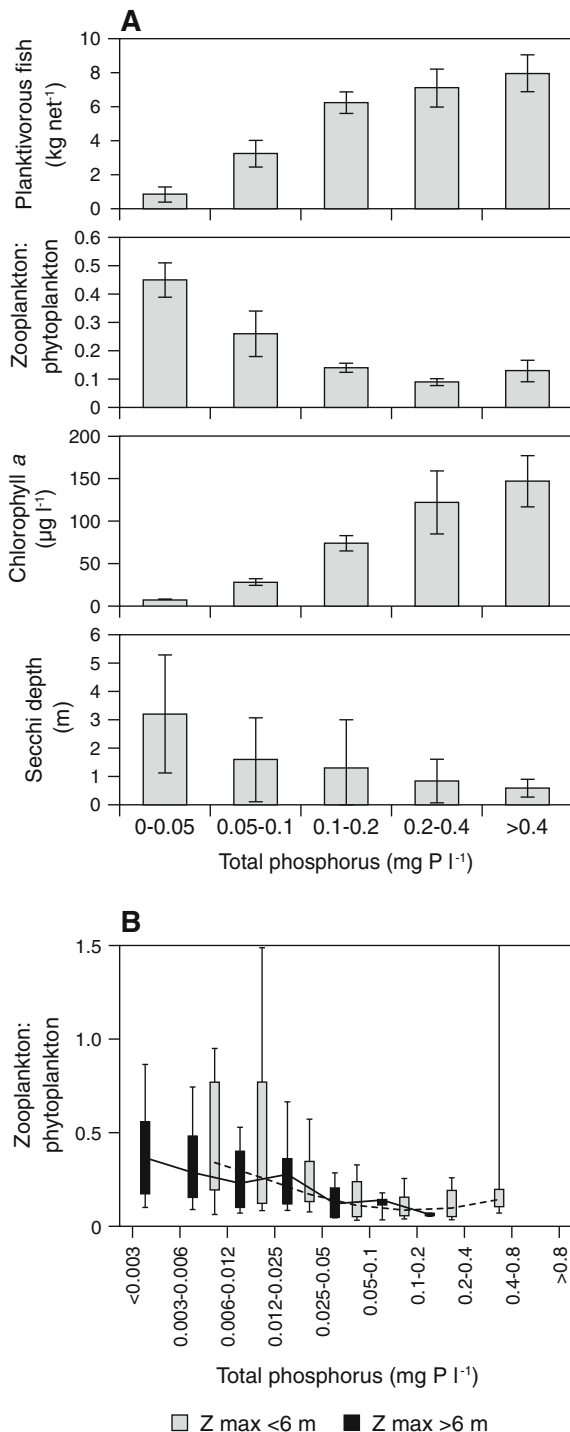


Fig. 4 **A** August biomass of zooplanktivorous fish (CPUE, catch in multiple mesh-size gill nets, 14 different mesh sizes 6.25–75 mm in late summer) versus summer mean lake water concentrations of TP. Also shown are summer mean (1 May–1 Oct) of the zooplankton:phytoplankton biomass ratio, the epilimnion chlorophyll *a* concentration and Secchi depth versus TP. Mean \pm SD of the five TP groups is shown (from Jeppesen et al., 2000). **B** Box-plots showing the biomass ratio of zooplankton to phytoplankton (means for July–August) in 466 deep (>6 m) and shallow (<6 m) Danish and Norwegian lakes (from Jeppesen et al., 2003a)

Assessment: palaeoecological samples

Cladoceran remains as indicators of structure and function

The response of cladocerans to anthropogenically induced changes has enabled pseudofossils of cladocerans, in particular chydorids, to be used widely in palaeolimnological studies to reconstruct trophic or acid conditions (Harmsworth & Whiteside, 1968; Whiteside, 1970; Brodersen et al., 1998; Jeppesen et al., 2001a), infer changes in macrophyte and fish communities (Jeppesen et al., 2001b; Davidson et al., 2010a, b) and to trace temperature changes (Duigan & Birks, 2000). The fact that cladocerans have been used to track changes in such a variety of parameters is an indication of their sensitivity to the many anthropogenic stresses currently at play as discussed above. This sensitivity stems from their central position in the food web and the good representation of both benthic and pelagic taxa, meaning that the assemblage responds to variations in predation pressure, resource provision and habitat availability. This is a great benefit for the use of cladocerans as indicators of ecological state, but also represents a challenge to palaeoecological modelling and interpretation of past changes in assemblage. Thus, it bears reiteration (Smol, 1991; Battarbee et al., 2005; Sayer et al., 2010a) that it is vital that an understanding of modern cladoceran ecology is well integrated into palaeoecological investigations, particularly when the aim is the assessment of ecological conditions.

The use of sub-fossils as indicators of change in contemporary communities is well founded (Jeppesen et al., 2001a, 2003b). Davidson et al. (2007) analysed the contemporary zooplankton populations and their sub-fossil remains in 39 shallow lakes in the UK and Denmark. Contemporary zooplankton populations

(Havens & Beaver, 2011). These authors also argued that higher fish predation in the Florida lakes was of key importance.

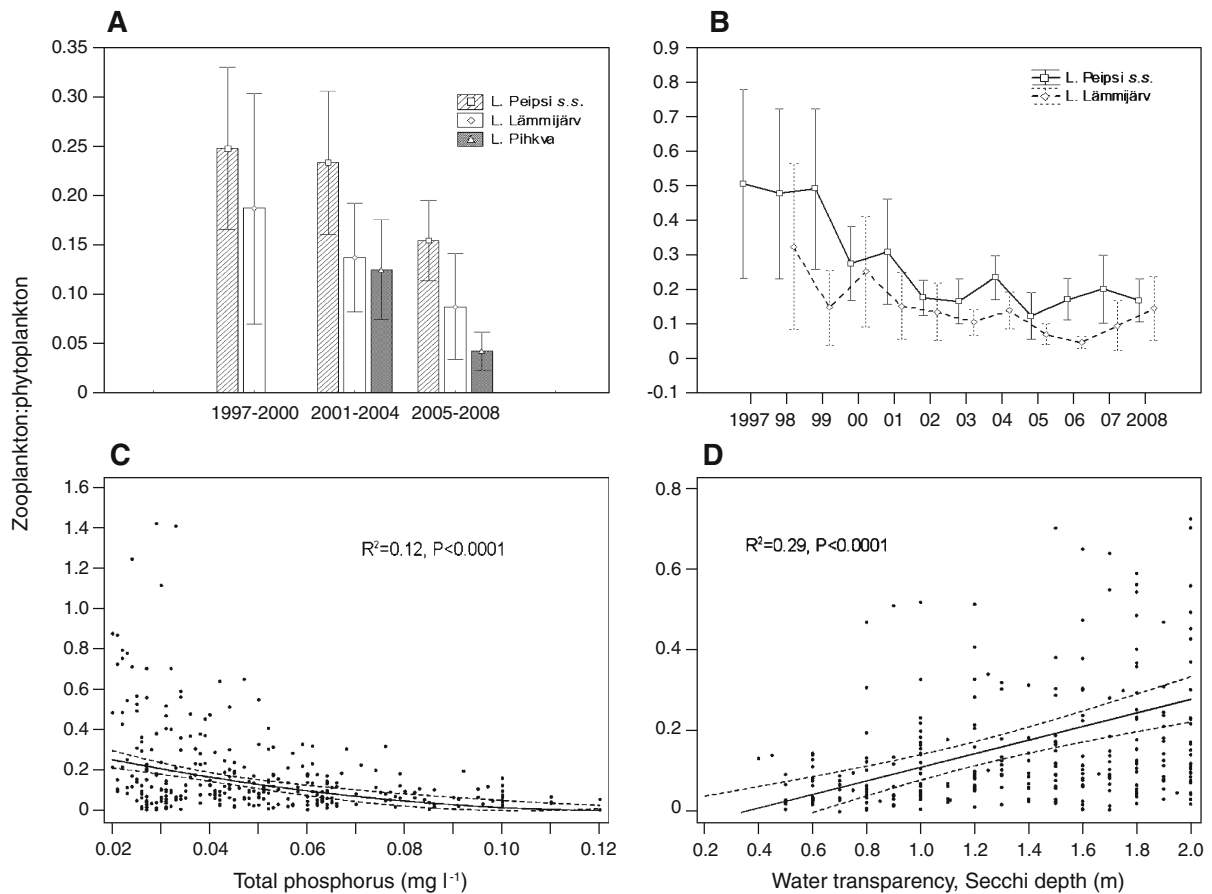


Fig. 5 **A** The zooplankton:phytoplankton biomass ratio (Zoo:Phyto) in three parts of Lake Peipsi with different trophic state (mean values for August 1997–2008). **B** Changes in the Zoo:Phyto ratio during 1997–2008 in two of the basins (mean values of samples from May to October). **C** Relationships between the Zoo:Phyto ratio and TP in Lake Peipsi s.s. *Lines*

show the linear fit with \ln TP and the 95% confidence band. **D** Relationships between the Zoo:Phyto ratio and Secchi depth in summer in all lake parts during 1997–2008. *Lines* show the linear fit and the 95% confidence band (all from Blank et al., 2010)

sampled from both the lake edge and the open water in August were compared with surficial sediment assemblages. The same two factors, zooplanktivorous fish density and submerged macrophyte abundance, were not only the main structuring forces for both datasets, but also explained very similar amounts of the variation in the different assemblages. Procrustes analysis (Jackson, 1995), a technique which compares ordination results and tests the significance of these results, demonstrated that, despite inevitable differences in the fossil assemblage and the live community that formed them, living communities and their sedimentary remains reflect the environment by which they are shaped in broadly similar ways.

Daphnia proportion of resting eggs

A study of surface sediment from lakes around the globe by Jeppesen et al. (2003b) showed that the contribution of *Daphnia* to the total pool of *Bosmina* spp. and *Daphnia* spp. ephippia in the surface sediment was zero (with one exception) when the abundance of fish CPUE (catch per gillnet per night) exceeded 0.3 fish net⁻¹ in low-TP Greenland lakes and 3–10 fish net⁻¹ in New Zealand lakes in which TP was somewhat higher. In contrast, *Daphnia* percentage contribution remained high in some nutrient-rich Danish lakes until 70 fish net⁻¹ (Fig. 8). This is in good agreement with data from the UK (Davidson et al., 2007). Accordingly, a

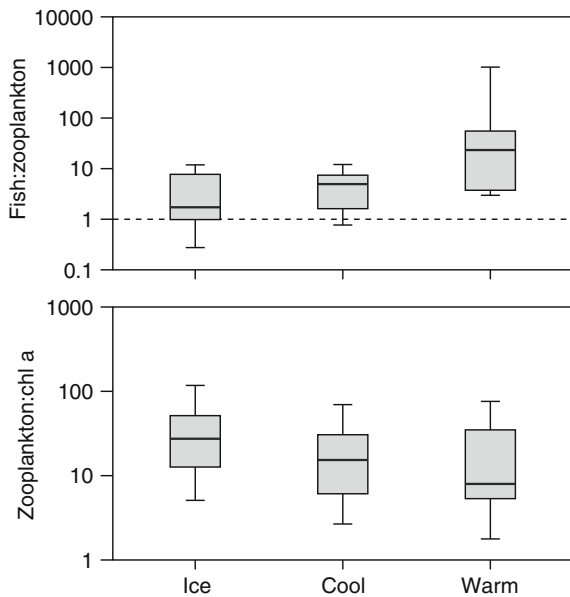


Fig. 6 The relationship with climate of the planktivorous and benthivorous fish:zooplankton ratio and the zooplankton:Chl *a* ratio. Box-plots show the 10, 25, 50, 75, and 90% percentiles for the three climate zones (from Gyllström et al., 2005)

multiple regression revealed that the proportion of *Daphnia* ephippia (*Daphnia* ephippia/(*Daphnia* ephippia + *Bosmina* ephippia) %, DAPsed (%)) was strongly inversely related to CPUE and positively related to TP (mg P l^{-1}):

$$\begin{aligned} \text{DAPsed (\%)} &= 136 \pm 17 - 19 \pm 2 \log_e(\text{CPUE} + 1) \\ &\quad + 16 \pm 4 \log_e(\text{TP}), \\ r^2 &= 0.45, P < 0.0001. \end{aligned}$$

The above findings demonstrate that the occurrence of *Daphnia* in sediments is a reflection of the abundance of fish and also of the trophic state of the lakes, illustrating the ‘sandwich’ indicator role of zooplankton.

Shifts in cladoceran assemblages reflecting ecosystem change

Under oligotrophic conditions the on/off nature of the relationship between *Daphnia* and fish presence makes it a powerful indicator of changes in the predation pressure over time. The challenge in systems with higher trophic status has been to develop methods that are capable of separating the impact of changes in the fish population from those of nutrient enrichment

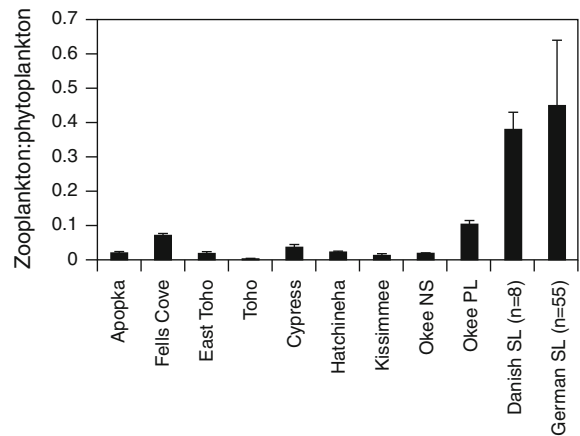


Fig. 7 Ratio of zooplankton to phytoplankton biomass (Zoo:Phyto) at the nine Florida study sites compared with ratios determined in the same manner for eight shallow Danish lakes (Jeppesen et al., 2005) and 55 shallow German lakes (Auer et al., 2004) (from Havens & Beaver, 2011)

and changes in macrophyte abundance. Previous inference models have reconstructed a single variable in isolation, such as fish density (Jeppesen et al., 1996) or macrophyte PVI (Johansson et al., 2005). Recently, regression tree-based models have highlighted the potential of this technique to be used to separate changes in fish community from the impacts of changing macrophyte abundance (Davidson et al., 2010b). The application of the model, in combination with plant macrofossil, diatom and chironomid analyses, to sediment cores from a shallow lake (Davidson et al., 2010a; Sayer et al., 2010b) provided a detailed picture of eutrophication driven change in the ecology of the lake over time.

The comparison of assemblage change through time, summarised by PCA axis scores, demonstrates that cladocerans and chironomids were the most sensitive to the effects of eutrophication (Fig. 9). The initial change in macrophyte flora, dating to around 1850s between 45 and 50 cm, occurred in concert with the first shifts in the cladoceran assemblage community (see Davidson et al., this volume) and preceded the response of the diatom assemblage the change in which was only detectable in the 1930s coinciding with the later stages of eutrophication (Fig. 8). The chironomid assemblage also changed relatively early in the record (Davidson et al., 2010a), indicating that benthic fauna are the most sensitive indicators of the ecological changes associated with the early stages of nutrient enrichment. The

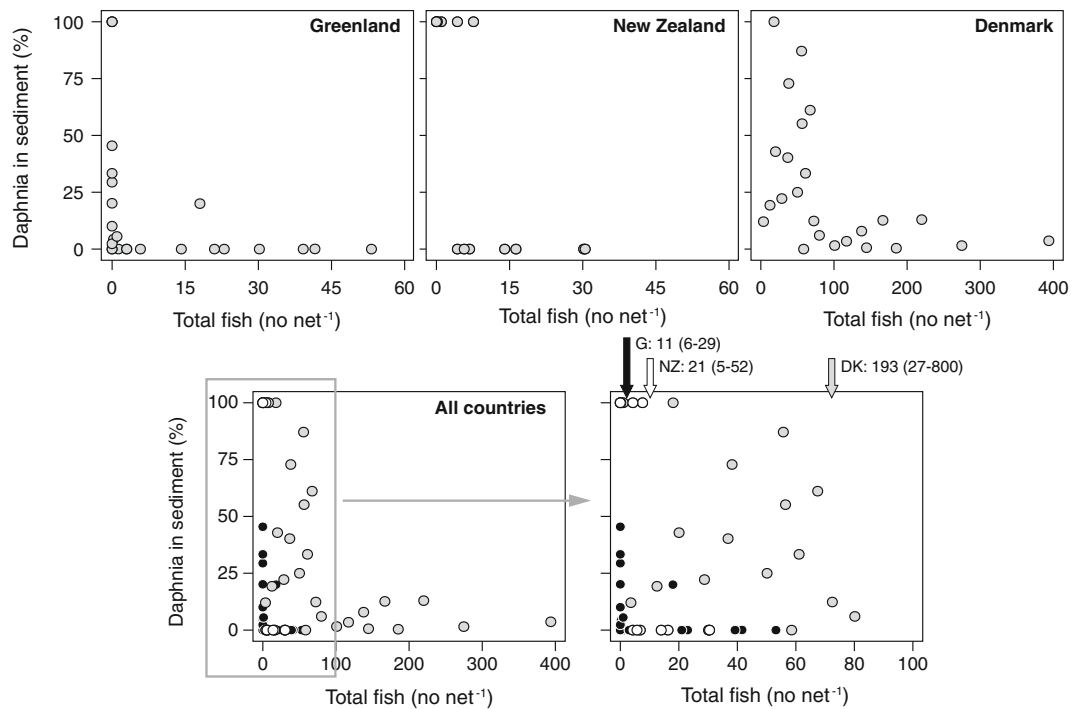


Fig. 8 Above Contribution of *Daphnia* to the sum of *Daphnia* and *Bosmina* ephippia in the top 1 cm of the sediment sampled at a mid-lake station in Greenland (G), New Zealand (NZ) and Denmark (DK) versus catch net⁻¹ night⁻¹ (CPUE) of fish in gill nets with 14 different mesh sizes (6.25–75 mm). Below

The data for the three countries now merged (left) and parts of the figure are upscaled to the right. Also shown are the mean TP ($\mu\text{g l}^{-1}$) concentrations for all the sampling dates and ranges (in parentheses) among lakes in the three countries (from Jeppesen et al., 2003b)

cladoceran PCA axis 1 scores summarise the shift from an evenly distributed assemblage dominated by benthic taxa to a less even community where a few pelagic taxa had the highest relative and absolute abundance, reflecting change from the bottom up. The change in *Daphnia* abundance in the 1970s reflects the loss of the dominant zooplanktivore and a sharp decline in total fish abundance (Davidson et al., 2010a). This change in fish predation pressure was reflected neither by the diatom nor the chironomid record (Davidson et al., 2010a). The fact that cladocerans can be both benthic and pelagic makes them not only sensitive to environmental change, it also means alteration of the composition of the taxa may elucidate changes in ecosystem function (Davidson et al., 2010a, b). In this case, the eutrophication-associated increase in pelagic over benthic taxa (Fig. 8) is in good agreement with a broad spatial scale response to eutrophication, namely, a shift from benthic to pelagic primary production (Vadeboncoeur et al., 2003).

Egg size versus fish abundance

The size of *Daphnia* resting eggs has been shown to be a valuable indicator. Jeppesen et al. (2002) found a significant linear relationship between the size of the ephippia-bearing *Daphnia* females, as measured from the centre of the eye to the base of the tail spine, versus dorsal length of ephippia (Fig. 10): length (mm) = $0.33 \pm 0.02 + 1.55 \pm 0.03$ ephippia size (mm), $r^2 = 0.91$, $P < 0.001$, $n = 230$.

The combination of these different palaeoecological approaches based on *Daphnia* size and the application of assemblage-based models capable of dealing with multiple structuring forces has opened up the possibility, particularly in combination with analysis of other biological groups, such as plant macrofossils (Birks, 1980; Davidson et al., 2005), of tracking change in the ecological status of lakes over timescales outside the range of most monitoring studies. Currently, the missing step has been the integration of the modern assessment of ecological conditions and

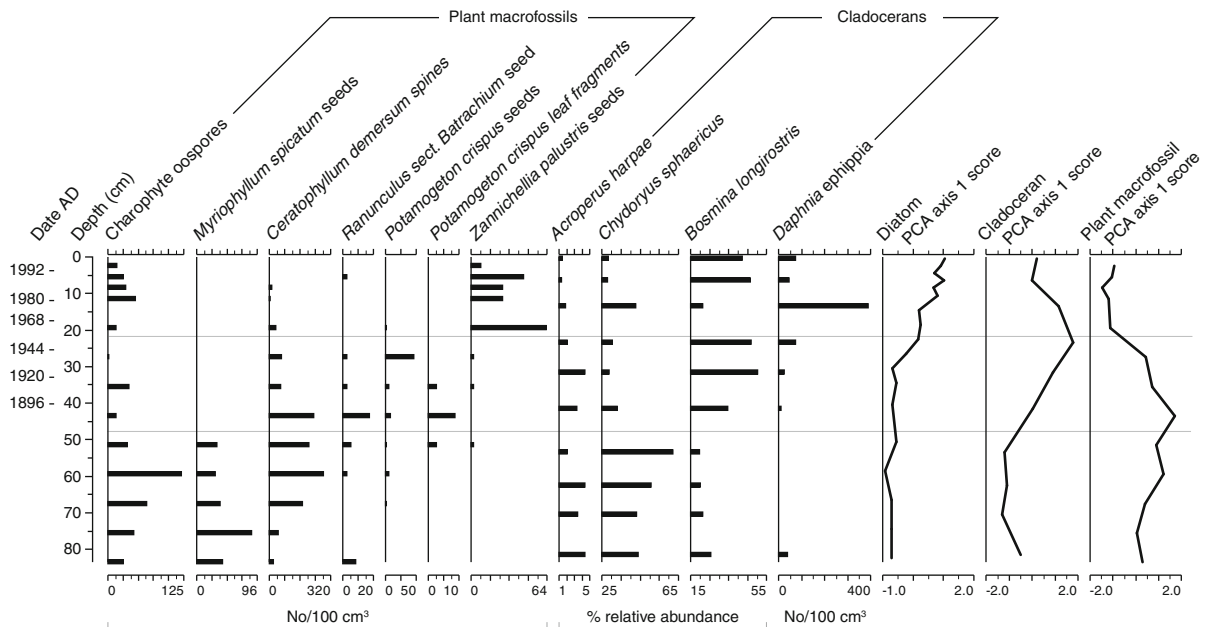


Fig. 9 Plant macrofossil and cladoceran profiles from core FELB1 (Felbrigg Lake) showing key taxa (see text and Davidson et al., 2010a; Sayer et al., 2010b). The zones are defined by the macrofossil assemblage: 1 = *Myriophyllum*–*Chara*–*Ceratophyllum*–*Potamogeton*, 2 = *Chara*–*Ceratophyllum*–*Potamogeton*,

3 = *Potamogeton*–*Zannichellia*. PCA axis 1 scores which summarise change in community on the principal axis of variation in each respective data set are given for diatoms (see Sayer et al., 2010b), cladoceran and plant macrofossils

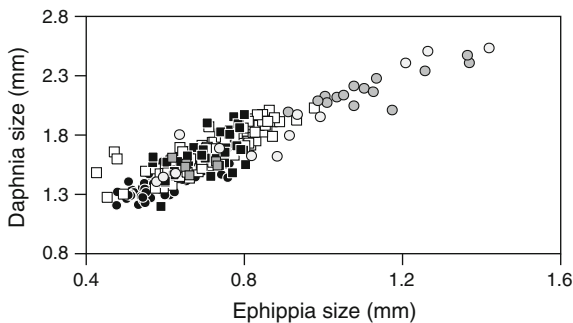


Fig. 10 Relationship between dorsal length of ephippia and size of adult female *Daphnia*, measured from the base of the tail spine to the centre of the eye. The species included were *D. magna*, *D. pulex*, *D. cucullata*, *D. galeata*, *D. hyalina*, *D. longispina* and hybrids. The different symbols represent different species and hybrids (from Jeppesen et al., 2002)

metric development with palaeoecological methods to develop a model capable of inferring past change in some metrics of ecological conditions. This would allow the current status of an individual lake to be placed in the context of its past condition and also to classify a lake's deviation from the undisturbed (reference) conditions as required in the WFD. There are few other potential BQEs that have this potential

for providing a long-term perspective on both patterns and processes of ecological change.

Changes in water level, salinity and climate

Major changes in the ecological state of lakes can be expected in the future because of climate change (Blenckner et al., 2007; Jeppesen et al., 2009) that in arid areas is accompanied by changes in water level and salinity (Beklioglu et al. 2007). Cladocerans may also be useful proxies for direct and indirect effects of climate change. Changes in temperature may also be tracked by changes in the proportion of the resting egg to carapace ratio of *Bosmina*, which decreases several order of magnitudes from Greenland to Spain (Jeppesen et al. 2003a, b), or by changes in this ratio among chydorids (Sarmaja-Korjonen, 2003). The cladoceran community composition is affected by salinity (Bos et al., 1996, 1999; Amsinck et al., 2005a, b; Brucet et al., 2009) because of variations in physiological tolerance of the species, and by changes in water level (Korhola et al., 2000; Amsinck et al., 2006; Kattel et al., 2007; Nevalainen et al., 2011; Nevalainen, 2011) as the proportion of benthic

and pelagic forms is dependent on lake depth. There are, however, other factors, in particular changes in fish predation which also shape the cladoceran assemblage and thus, quantitative models must be applied with caution (Davidson et al., under review). Cladocerans may prove to be useful indicators of past climate change, as demonstrated for several tropical lake studies by Verschuren et al. (1999a, b, 2000).

Do zooplankton respond to changes in the short term?

If a BQE and the associated metrics are good indicators of the ecological status of lakes, then they should respond to changes in pressures. In this article, we provide examples showing that zooplankton metrics respond to nutrient loading reduction, sudden shifts in ecological state related to fish kills or lake restoration attempts. Furthermore, we give an example of gradual change in ecological conditions and a changing cladoceran community in response to fish stocking, and an example of long-term effects of eutrophication on the ecological structure and function of a shallow lake.

Response to nutrient loading reduction

In a comprehensive study of lakes in recovery from eutrophication, Jeppesen et al. (2005) analysed changes in the seasonal dynamics of zooplankton in eight shallow Danish lakes studied during 13 years (Fig. 11). They found no changes in zooplankton biomass, except for an increase in November and December. However, the biomass of small cladocerans declined during summer and autumn, and the proportion of *Daphnia* to cladoceran biomass increased. Average body weight of *Daphnia* and that of all cladocerans increased. The proportion of calanoids among copepods decreased in summer, and the average body weight of cyclopoids and calanoids decreased during summer and autumn/early winter. Moreover, the Zoo:Phyto ratio during summer increased, indicating reduced top-down control on zooplankton and enhanced grazing on phytoplankton. Except for the lack in response of the zooplankton biomass, all these changes follow the pattern expected when the nutrient level is reduced from the multi-lake analysis described above, an indication that zooplankton are a sensitive BQE (Fig. 11).

Response to changes in fish abundance

Natural fish kills may substantially influence the phytoplankton abundance, composition and biomass and, with it, the water clarity too. For example, changes in duration of ice cover may influence summer plankton because of changes in the proportion of fish that survives the winter. In shallow eutrophic lakes covered by ice for up to 5 months a year, fish abundance is typically low due to frequent intense fish kills. Comparative studies of Danish coastal lakes and continental Canadian lakes with similar summer temperatures, but major temperature differences during winter, have shown fourfold lower chl *a*:TP ratios and higher Zoo:Phyto ratios in the winter-cold Canadian lakes, perhaps because of a lower winter survival of zooplanktivorous fish under ice in the latter (Jackson et al., 2007). Monitoring data from Danish lakes show indications of reduced fish predation in 1996 after the only cold winter with prolonged ice cover (ca. 60–90 days) during the monitoring period, 1989–2006. The size structure of the main cladoceran species in the Danish lakes was displaced towards larger size classes in the summer following the cold winter, resulting in a greater grazing capacity on phytoplankton. At the community level, zooplankton constituted a larger proportion of larger-bodied taxa during the following summer. Accordingly, phytoplankton biomass (as chl *a*) was lower, and grazing (identified as a chl *a*:TP ratio) was higher (Balayla et al., 2010).

Likewise, Ruuhijärvi et al. (2010) showed marked increases in the size of *Daphnia* after recorded fish kills under ice in the winter 2002–2003 (Fig. 12). They also showed major concurrent changes in phytoplankton abundance and water clarity, and even more noteworthy also in the composition of phytoplankton, with much less harmful cyanobacteria in the 2 years following the fish kills. Although not included, the Zoo:Phyto ratio was also higher in the years after fish kills, demonstrating the value, as for the Danish lakes, of using cladoceran size and Zoo:Phyto ratios as indicators of changes in trophic dynamics related to changes in fish stocks. Only very comprehensive fish programmes, unrealistic in a WFD context, would have illustrated correctly the important changes in cyanobacteria abundance in, for instance, the Finnish lake.

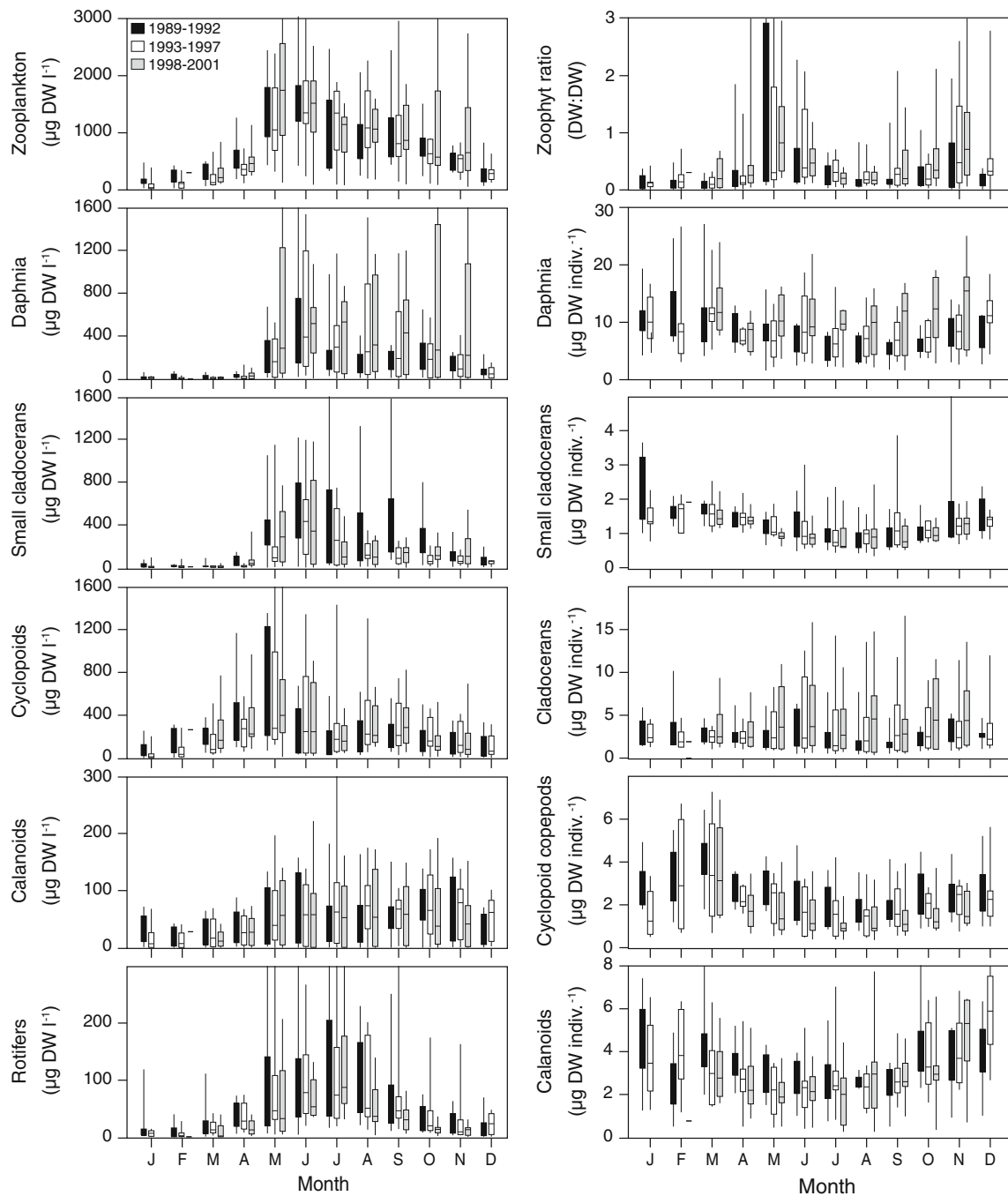


Fig. 11 Box-plot (minimum, 25%; median, 75%; maximum) of seasonal variation in the biomass of various zooplankton taxa, the zooplankton-to-phytoplankton biomass ratio, and the

mean body weight of various zooplankton taxa in eight shallow lakes during three periods. Maximum values are occasionally outside the range of the panels (from Jeppesen et al., 2005)

Response to restoration by biomanipulation

When nutrient loading is reduced, lakes often exhibit a slow response (Jeppesen et al., 2005). In order to

reinforce recovery, various methods, among which removal of planktivorous fish (termed biomanipulation, Shapiro et al., 1975; Benndorf, 1995) has been particularly popular, have been used. Biomanipulation

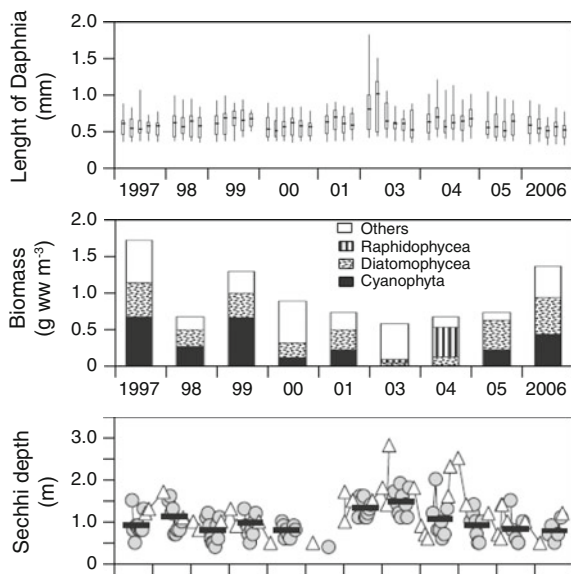


Fig. 12 Change in size of cladocerans, biovolume of various classes of phytoplankton and water transparency (Secchi depth) before and after a major winter fish kill under ice during the cold winter of 2002–2003 in shallow Lake Äimäjärvi, Finland (modified from Ruuhijärvi et al., 2010)

studies of Danish lakes (Søndergaard et al., 2007, 2008) show the profound effect that fish have on trophic state and WFD selected ecological state indicators, and the importance of including zooplankton as ecological indicator. Initially, removal of plankti-benthivorous fish resulted in substantial reductions in chlorophyll and suspended matter and increases in water clarity. As in the examples of fish kills, major changes also occurred in the phytoplankton composition, and especially the biomass of the harmful cyanobacteria was markedly reduced. While the zooplankton biomass was not affected, both size of *Daphnia* (+) and other (small) cladocerans (–), and not the least the zooplankton:chlorophyll *a* ratio (+), were affected in many of the lakes (Fig. 13). After the return of fish after some years to most of the lakes, this tendency was reversed and cyanobacteria returned. Again, size of cladocerans and the Zoo:Phyto ratio appeared to be good indicators of the changes.

Response to fish stocking

The opposite scenario to biomanipulation is fish introduction. A palaeoecological study at Kenfig Pool, a shallow (max depth = 2.6 m) moderately large (24 ha) lake in an extensive sand dune system in

South Wales provides evidence of the utility of cladocerans in tracking change in ecosystem structure and function associated with fish stocking. The investigation was conducted to support the fish management strategy at the site (Davidson & Appleby, 2003). The cladoceran record and the application of the MRT model (Davidson et al., 2010b) highlighted two main periods of change: the first around 1850s (45-cm depth) was abrupt; and the second, initiated in the 1950s (around 25 cm), was a more gradual change from that point continuing to the present (Fig. 13A, B). Plant macrofossils' remains, which have been shown to accurately reflect changes in the dominant components of submerged vegetation (Davidson et al., 2005), were also analysed.

The change around the 1850s consisted of a sharp increase in the abundance of charophyte oospores and a pronounced increase in the relative abundance of pelagic cladoceran taxa (in particular *Daphnia* spp.) (Fig. 14). The reason for these changes is unclear, but a likely candidate is a step change in water depth, caused by human management around the 1850s, and a large increase in the area of the pelagic habitat. The second point of change starting around the 1950s was a shift in from the dominance of *Daphnia* to *Bosmina*, concurrent with the gradual decline the relative abundance of *Chydorus sphaericus*. The MRT model infers this post 1950s change as an increase in the abundance of zooplanktivorous fish, which agrees well with documentary evidence of fish stocking events (Davidson & Appleby, 2003). Before the 1950s, the lake had a fish community consisting of eel and sticklebacks. In 1957, 3,000 mixed coarse fish were stocked into the lake, and stocking with a variety of species (*Salmo trutta* L., *Perca fluviatilis* L., *Scardinus erythrophthalmus* L. and even *Cyprinus carpio* L.) has continued at regular intervals since that year. The MRT model suggests that there has been a gradual increase in predation pressure, as reflected by the cladoceran community over the last 50 years. The final two changes in MRT group membership from group C at 10 cm to group D at 5 cm and then B at the surface suggest that chlorophyll *a* has increased during the last 10 years, as the average value for group C was $10 \mu\text{g l}^{-1}$, and the mean value for both group D and B is $20 \mu\text{g l}^{-1}$. These recent changes from MRT group B to C suggest a shift, in agreement with the plant macrofossils, from dominance of several charophyte species to the site where finely leaved

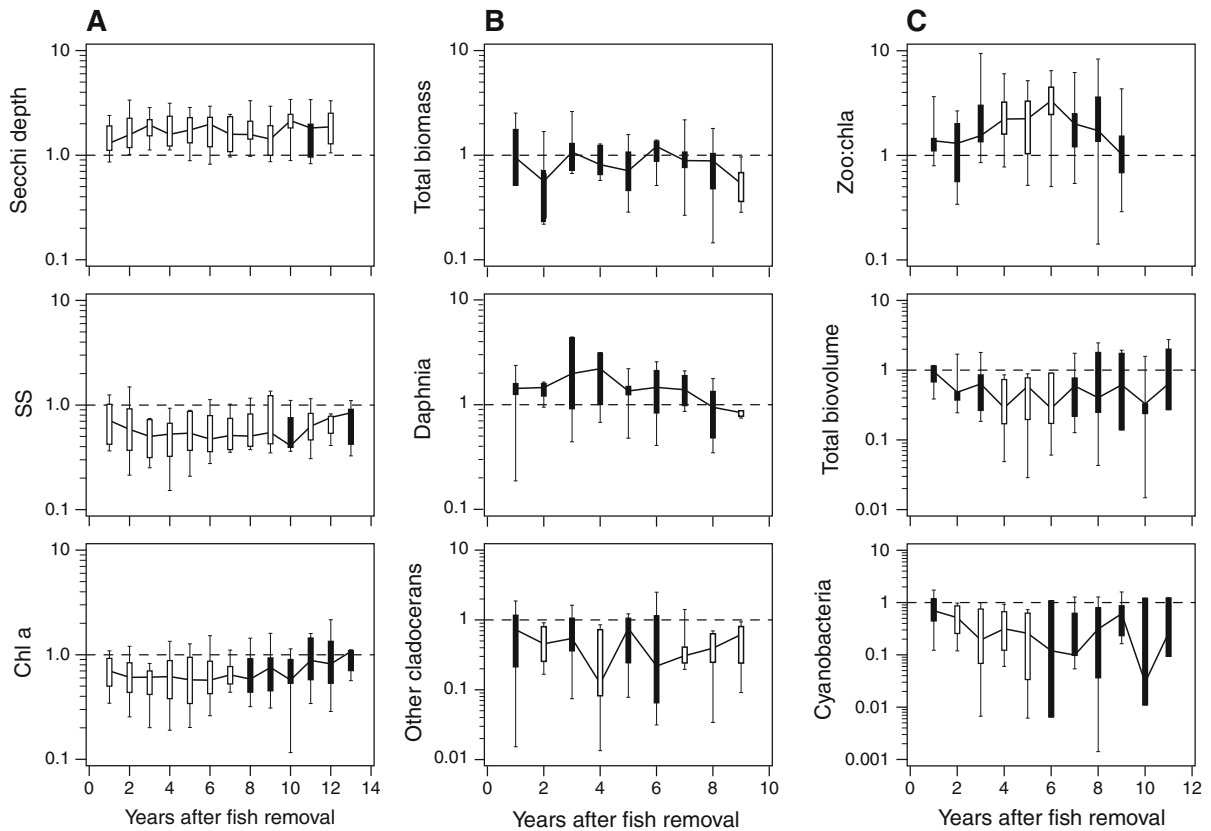


Fig. 13 **A** The effect of removal of >200 kg fish ha^{-1} relative to the levels during <3 years before intervention on Secchi depth SS, chl-*a*, TP, and TN in 27 lakes (time-weighted summer means). *Light boxes* show significant differences from the pre-removal situation. The *boxes* show 10 and 90% fractiles (outer lines), 25 and 75% fractiles (boxes). **B** Biomass of total

zooplankton and of *Daphnia* and other cladocerans (dry weight) relative to the pre-removal situation (number of lakes = 10). **C** Zooplankton:chl *a* ratio, phytoplankton biomass and the relative share of cyanobacteria (number of lakes = 10) (modified from Søndergaard et al., 2008)

Potamogeton taxa are the most abundant group, which accurately reflects the modern submerged flora of the site (Goldsmith et al., unpublished data).

Thus, in summary, and similar to the example of Felbrigg Lake (Davidson et al., 2010a), the changes in sub-fossil cladoceran assemblage through time at Kenfig Pool, reflect variation in the physical and biological elements, such as water depth and the species composition/abundance of macrophytes (Davidson et al., this issue), and also change in the top down factor predation. Establishing relationships between cladoceran assemblages and their environmental controls from contemporary data has opened up the possibility of disentangling these two drivers of change. Several other studies have also sought to elucidate the effect of fish stocking on lake ecosystems using cladoceran remains in the sediment as

proxies (e.g. Verschuren & Marnell, 1997; Buchaca et al., 2011).

Most sensitive metrics

Further exercises are needed to develop metrics at the regional level through Europe as in the cases of the other BQEs. Size structures (zooplankton, resting eggs) proportion of large zooplankton, zooplankton size, cladoceran size and the Zoo:Phyto ratio can indicate ‘top-down’ processes. Important indicators of ‘bottom-up’ processes could be zooplankton biomass, the proportion of rotifers by numbers and the proportion of calanoid copepods. Perhaps also zooplankton fecundity would be worth exploring as a ‘bottom-up’ metric as suggested by Caroni & Irvine

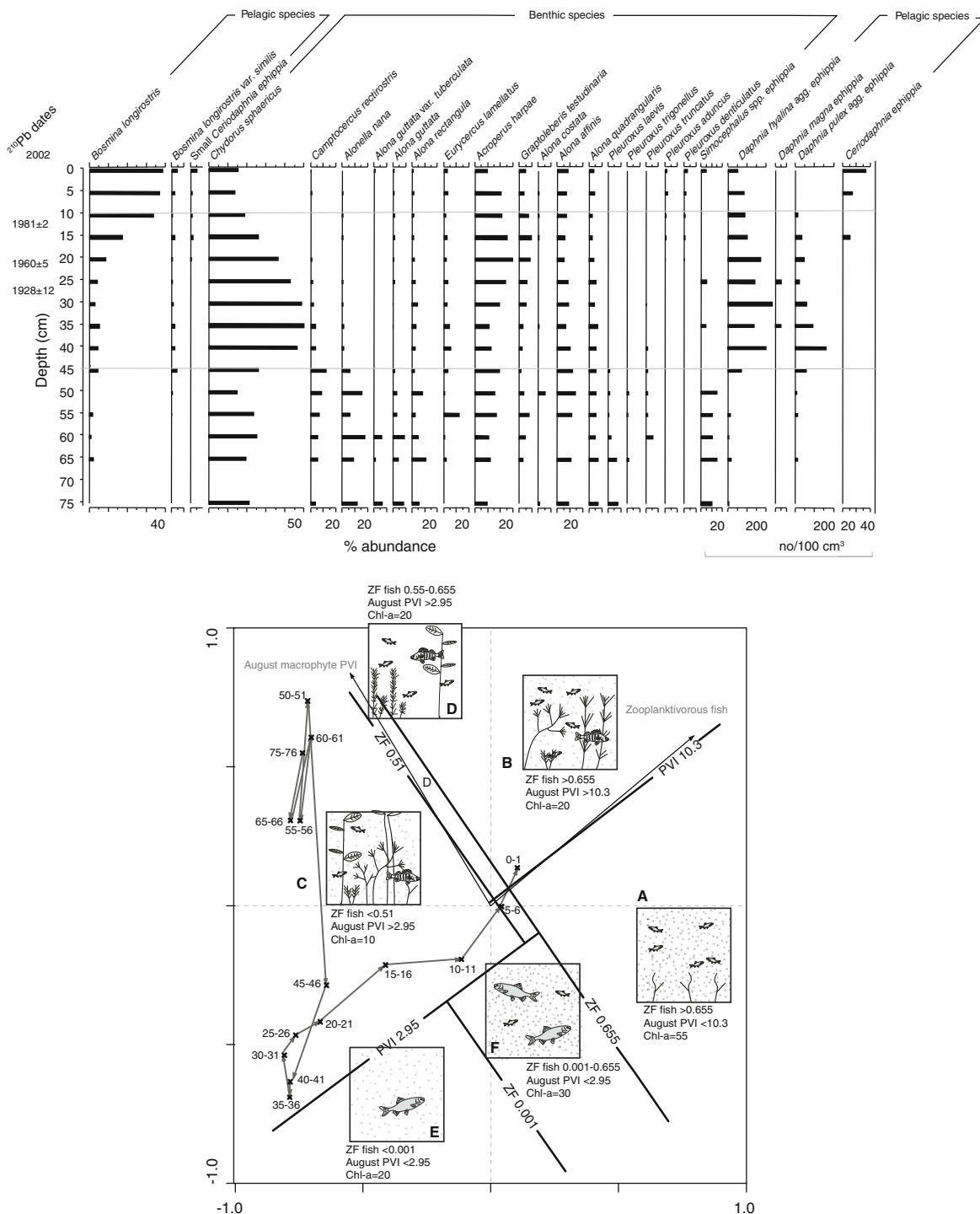


Fig. 14 Above Cladoceran stratigraphy from Core KENF2 (Kenfig Pool), chitinous remains are expressed as % relative abundance and ephippial remains are expressed as number per 100 cm³ of sediment. Zones were determined by constrained cluster analysis of both chitinous and ephippial remains. Below

Multivariate regression tree groups superimposed on RDA of surface sediment assemblages from 39 sites with the cladoceran assemblage from core KENF2 passively placed to track changes in macrophyte and fish density (from Davidson, 2006; Davidson & Appleby, 2003)

(2010). With better feeding, zooplankton produce more eggs. This indicator of food availability provides a more reliable estimate of trophic dynamics than chlorophyll *a* concentrations, because the former is dependent on food ingested rather than potential food present, which can be reduced through dietary unsuitability or unavailability of some phytoplankton (Caroni & Irvine, 2010). Combination of ‘top-down’ and ‘bottom-up’ indicator metrics might yield a solid assessment of trophic conditions in the pelagic of lakes.

In palaeoecological terms, the absence of zooplankton from the WFD means that there has been little support for the development of appropriate metrics. However, the palaeoecological data presented here suggest that sedimentary cladoceran assemblages are sensitive to ecological change and a relatively simple metric summarising a combination of the benthic/pelagic balance of taxa, and the size of the remains as a measure of fish predation pressure could be a useful predictor of ecological quality.

Conclusions and epilogue

The above described examples in this study illustrate that zooplankton are important indicators of the structure and function of freshwater lake ecosystems and their ecological status. Further exercises are certainly needed to develop metrics at the regional level throughout Europe as in the cases of other BQEs. So far, the most promising metrics based on *contemporary samples* are zooplankton biomass, the proportion of rotifers by numbers, the proportion of large zooplankton, zooplankton size, cladoceran size, the proportion of calanoid copepods, and zooplankton:phytoplankton biomass ratio; for *surface sediment*: size and the proportion of large forms of resting eggs and the proportion of pelagic cladoceran remains.

We strongly support the epilogue of the article by Caroni & Irvine (2010) stating that: ‘The freshwater zooplankters occupy an important and strategic position within the trophic web of a lake ecosystem and are sensitive to anthropogenic impacts. Sampling zooplankton is generally straightforward, and no more complex or expensive than many other forms of sampling. While their absence from monitoring recommended under the European Water Framework

Directive (2000/60/EC) seems a curious omission, there is no well argued scientific explanation why zooplankton should not be part of national monitoring designed to support the protection of (Irish) lakes. Meeting the minimum requirement of international policy is not necessarily synonymous with environmental protection’.

It is important to emphasise, though, that zooplankton monitoring can be included in schemes of *operational monitoring* (for waterbodies identified as being at risk of failing to meet their environmental objectives, and for those into which priority list substances are discharged), and *investigative monitoring* (if the reason for deviations is unknown, to ascertain the causes of a waterbody or waterbodies failing to achieve the environmental objectives, or to ascertain the magnitude and impacts of accidental pollution). Zooplankton can be included into these monitoring schemes if it can be proven to be the quality element most sensitive to the pressures to which the waterbodies are subjected. However, based on the experience from Denmark, it is clear that the risk is very high (maybe close to 100%) that the policy makers and managers follow the minimum requirement policy. We, therefore, strongly appeal to the relevant EU authorities to consider (and include) zooplankton as a BQE during the first revision of the programme. We also see the omission of zooplankton as a loss of opportunity for transitional waters and large rivers. As highlighted by Moss et al. (2003), Moss (2008) and Caroni & Irvine (2010), the focus mainly on ecosystem structure and less on function in the WFD must be reconsidered, and we have shown that zooplankton are a key element here for understanding lake ecosystem function—and perhaps also for large rivers and transitional waters.

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