

# Limnological deterioration forces community and phenotypic changes in Cladocera: Tracking eutrophication of Mallusjärvi, a lake in southern Finland

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A 300-year sediment record was used to investigate cladoceran community and phenotypic responses under extreme eutrophication process in the clay-turbid Mallusjärvi, a lake in southern Finland. The aims were to identify reference and disturbed communities, and to assess species and functional diversity and phenotypic characteristics as indices for lake ecological quality. The results showed that the oligomesotrophic reference status is characterized by rich planktonic and littoral-benthic assemblages with high species and functional diversity. Nutrient-enrichment, caused by increased agricultural activities in the catchment, was enhanced during the 19th century, inducing gradual responses in cladoceran community composition (decreasing benthic and increasing planktonic taxa) and functioning (decreasing invertebrate and increasing fish predation, decreasing species and functional diversity), and changes in phenotypic properties (decreasing body size of *Bosmina longirostris* and relative ephippial production). The disturbed state was characterized by eutrophic-hypereutrophic conditions and subsequent high abundance of planktonic cladocerans and deteriorated littoral-benthic conditions. Our results suggest that cladoceran communities, and their functional and phenotypic indices, are sensitive indicators of long-term limnological deterioration and ecosystem equilibrium.

## Introduction

Since anthropogenic nutrient enrichment can be identified as the single most serious threat to freshwater lakes across agricultural landscapes (Brönmark and Hansson 2002, Carpenter 2005), lake management, restoration, and conservation have become increasingly relevant for regional environmental politics and legislation, as well

as for local inhabitants living in the proximity of polluted waters (Lindenmayer *et al.* 2008). In Europe, legislation in the form of the EU Water Framework Directive (WFD) has set future targets for lake management, since its central agenda is to restore and conserve surface waters (Kallis and Butler 2001) with the aim of 'good' and 'nondeteriorating' ecological status. Accordingly, knowledge of pristine lake ecosystem

status prior to any anthropogenic disturbances (reference conditions) is necessary for implementation of the WFD, albeit the assessment of reference status may be problematic, due to natural ecosystem variability (Bennion *et al.* 2011). Furthermore, the changing climate regimes in temperature and effective moisture are likely to increase the challenge of nutrient enrichment in lakes (Jeppesen *et al.* 2009).

In the WFD, ecological status is defined as ‘the quality of the structure and functioning of aquatic ecosystems’ and it can be assessed by measuring the ecological resource of interest and using a reference state to determine whether the conditions measured differ from those expected or previously occurring (Hawkins *et al.* 2010). In determining reference conditions in lakes, the paleolimnological approach, relying on the physical, chemical, and biological information archived in the lake sediment record is very useful (Smol 2008), since usually even the longest environmental monitoring does not extend back in time to the preanthropogenic period (Bennion *et al.* 2011). Since phytoplankton and macrobenthic communities are included in the WFD as ‘biological quality elements’, i.e. measures of ecological quality, and are partially (e.g. diatoms and midge larvae) preserved as subfossil assemblages in lake sediments, they have been used successfully in paleolimnology as indicators for reference conditions (Quinlan and Smol 2002, Bennion *et al.* 2004, Räsänen *et al.* 2006, Luoto and Salonen 2010).

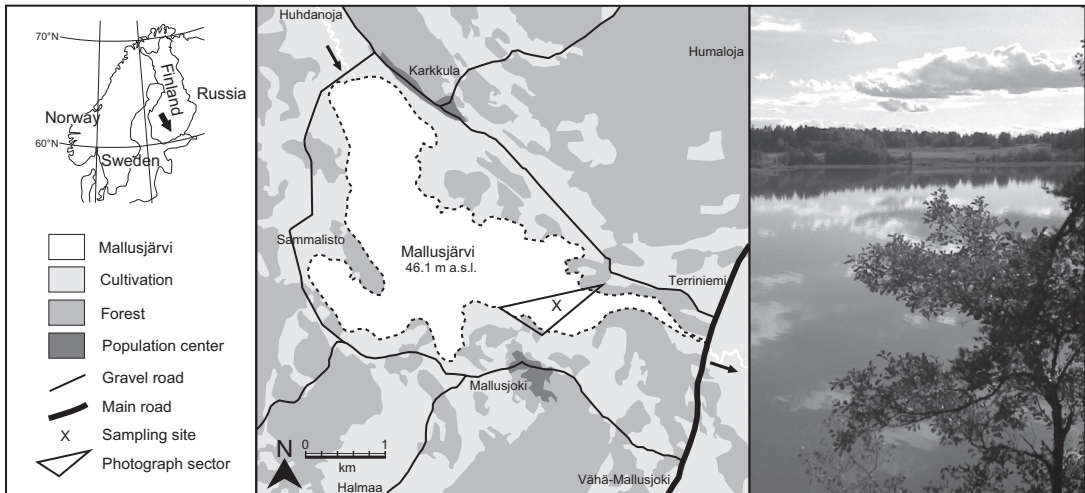
Despite the keystone position of zooplankton in aquatic food webs, they have not been included as a measure in ecological quality assessments of the WFD. Crustacean zooplankters and cladoceran microbenthos are important links between bottom-up (phytoplankton) and top-down (invertebrate predators, fish) biotic forces and, thus, are good indicators of ecosystem functioning. Furthermore, cladocerans are applicable in the paleolimnological approach for determining reference conditions because most taxa are preserved as subfossils in lake sediments. Moss *et al.* (2003) and de Eyto *et al.* (2003) already argued for recognizing zooplankton and cladoceran microbenthos in the classification of lake ecological status and, recently, Jeppesen *et al.* (2011) set up a scientifically-

based plea for including zooplankton in ecological quality assessment. Consequently, the objective of the present study was to use subfossil cladoceran assemblages in assessing changes in ecological quality of a severely eutrophicated lake. We aimed to identify reference and disturbed cladoceran communities and indicator species and to assess species and functional diversity, and specific phenotypic characters (i.e. body size, ephippial production) as indices for ecological quality attributable to eutrophication succession. The hypothesis behind the study was that top-down (fish predation) and bottom-up (algal production) driven cladoceran responses to deteriorated ecological conditions can be detected as changes in community composition and functioning, species diversity, and phenotypic properties and, accordingly, used in assessing the ecological quality and reference conditions.

## Material and methods

### Study site

Mallusjärvi (60°44′N, 25°38′E) is a lake located in southern Finland, near the city of Orimattila (Fig. 1), about 80 km north of Helsinki and 30 km south of Lahti. The bedrock in the catchment consists of microcline granite, gabbro and diorite, mica schist and mica gneiss, and granodiorite, tonalite, and quartz diorite. The soils are characterized by clay, moraine, and bedrock outcrops. The adjacent landscape of the shoreline of Mallusjärvi is dominated by cultivated fields and pastures (Fig. 1). The lake is shallow (maximum and average depths are 8.83 and 4.07 m, respectively) and naturally clay-turbid, with a surface area of 5.4 km<sup>2</sup> and catchment area of approximately 88 km<sup>2</sup>. The lake is currently judged by the Finnish Environment Institute as having ‘poor status’ based on the measured limnological parameters (epilimnetic values in September 2008 and August 2010, respectively: chlorophyll  $\alpha$  8.5 and 13.0  $\mu\text{g l}^{-1}$ , total phosphorus ( $P_{\text{tot}}$ ) 103 and 93  $\mu\text{g l}^{-1}$ , total nitrogen 960 and 570  $\mu\text{g l}^{-1}$ , pH 7.3 and 7.6, and electrical conductivity 8.8 and 9.4 mS cm<sup>-2</sup>; source: Hertta database, Finnish Environment Institute).



**Fig. 1.** Location and catchment characteristics of Mallusjärvi, a lake in southern Finland.

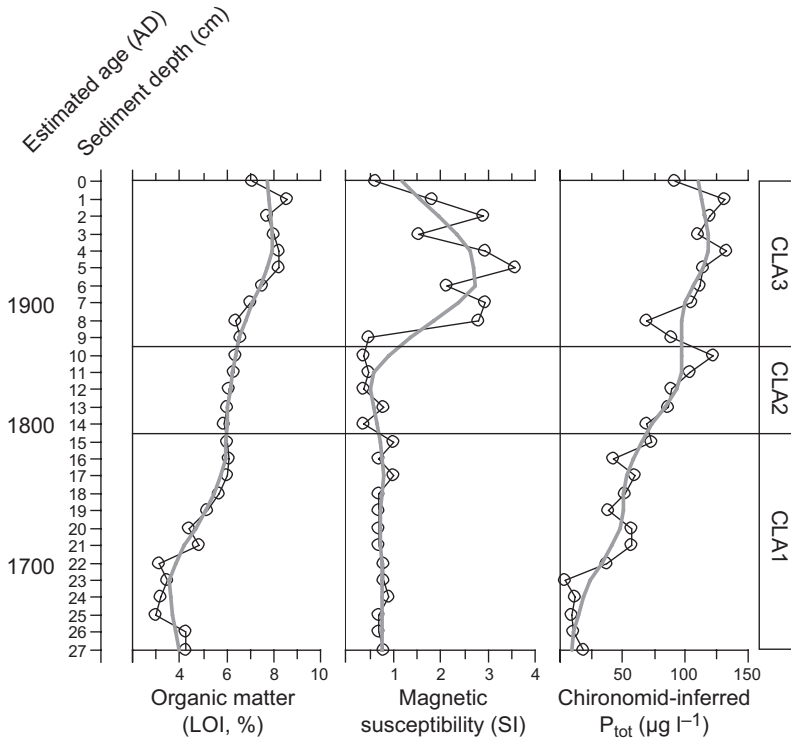
The Development Project of Mallusjärvi (2001–2004) was launched by the city of Orimattila and some local actors with the aim of improving the quality of the lake for ecological and recreational purposes. The project included general environmental planning, controlling of catchment erosion, aeration of the anoxic lake bottom, biomanipulation (33 510 kg of fish were removed), and monitoring the water quality. In addition, a municipal water and sewage system was built to reduce the external load of phosphorus entering the lake from the scattered settlements (Liukkonen 2004). Despite the lake management activities, Mallusjärvi has not entered a true phase of recovery, since algal blooms still occur during most summers and the nutrient levels remain very high (Hertta database).

The cultural landscape of Mallusjärvi and its catchment are listed as an important cultural heritage by the Finnish National Board of Antiquities. There are two small population centers, or villages, around the lake (Mallusjoki and Karkkula, *see* Fig. 1). They constitute the cultural landscape of Mallusjoki. Mallusjoki is situated along the river valley of the Porvoonjoki, which is heavily cultivated and has been inhabited since the Stone Age (10 000–4000 BP). The first villages were formed in the area of the Porvoonjoki river valley during the Iron Age (2500–850 BP), but the catchment of Mallusjärvi (villages Mallusjoki and Karkkula, Fig. 1) was inhabited during the 14th–16th centuries. By the

late 18th century, the number of inhabitants and agricultural activities in the area increased considerably (Penttilä *et al.* 1987, Lahelma 2002, Taipale-Heikkilä 2002). Currently, there are about 700 inhabitants in the area, which is used mostly in agriculture for cultivation and cattle pastures.

### Sampling and sample analyses

A 27-cm sediment core was sampled from the ice in winter 2009 with a Limnos gravity corer (Kansanen *et al.* 1991) from a point in which the water depth was 3.5 m (Fig. 1). This sampling point was located away from areas of lake management activities (e.g. hypolimnetic aeration), which could have affected sedimentation and caused sediment mixing. The sediment core was subsampled at 1-cm intervals and stored in plastic bags in a cold room at +4 °C. The sediment lithology, based on loss-on-ignition (LOI, Dean 1974), was clay gyttja between 27 and 18 cm (< 6% organic matter, OM), and gyttja clay between 17 and 0 cm (> 6% OM). The physical properties of the sediment (OM and magnetic susceptibility MS) were determined (Fig. 2) and subfossil midges (Chironomidae and Chaoboridae) were analyzed for their community assemblages. Additionally, the chironomid assemblages were used to reconstruct the past variability of the lake's epilimnetic  $P_{\text{tot}}$  (*see* Fig. 2).



**Fig. 2.** Organic matter (OM), magnetic susceptibility (MS), and chironomid-inferred epilimnetic total phosphorus ( $P_{\text{tot}}$ ) in the Mallusjärvi sediment core [OM and MS from Luoto Nevalainen (2011), and  $P_{\text{tot}}$  from Luoto and Raunio (2011)]. The gray lines indicate general trends and were generated with locally-weighted scatterplot smoothing (span 0.35). The local faunal zones (CLA1–CLA3) are based on the cluster analysis of subfossil cladoceran assemblages.

The chironomid-based inference model used in the  $P_{\text{tot}}$  reconstruction of Mallusjärvi is that of Luoto (2011): it was constructed from 51 lakes in Finland with  $P_{\text{tot}}$  gradients of 2–105  $\mu\text{g l}^{-1}$  and is based on the weighted averaging partial least squares regression technique with favorable performance ( $r^2_{\text{jack}} = 0.92$  and root-mean-squared error of prediction 6.68  $\mu\text{g l}^{-1}$ ). The age estimations of the sediment core were based on an accelerator mass spectrometry (AMS)  $^{14}\text{C}$  chronology previously published by Luoto and Nevalainen (2011).

The sediment subsamples were further analyzed for their subfossil cladoceran species composition and ephippia. For determining subfossil cladoceran community assemblages from the sediment subsamples, 3 g wet weight (WW) was processed with the methods described in Szeroczyńska and Sarmaja-Korjonen (2007). Here, slight modifications were used, since no KOH treatment was performed due to the low organic content of the sediment. The samples were washed carefully under running tap water and sieved through a 51- $\mu\text{m}$  mesh, centrifuged to concentrate the cladoceran remains, and

known volumes were mounted in glycerine jelly stained with safranin on microscope slides. The subfossil specimens were identified and enumerated under a light microscope (magnifications 100–400 $\times$ ), using the identification key by Szeroczyńska and Sarmaja-Korjonen (2007). The most frequent body parts (e.g. carapaces, headshields, ephippia, postabdomens) were used to assess the number of individuals of each species encountered. The samples were analyzed for species composition until > 0.5 g WW and > 50 individuals were encountered. The body sizes of *Bosmina* spp. were measured during the analysis from the anterior to the posterior margin from all or a maximum of about 30 individuals (cf. Korosi *et al.* 2008, Liu *et al.* 2009, Nykänen *et al.* 2010). The sizes were not evaluated if fewer than 15 carapaces were measured. In addition, *Chaoborus* mandibles were enumerated during the cladoceran analysis (cf. Nevalainen *et al.* 2012), and the remains were identified according to the Finnish specimens illustrated by Luoto and Nevalainen (2009). To determine the abundance of cladoceran ephippia, additional sediment subsamples (8 g WW) were washed under running

tap water and sieved through a 100- $\mu$ m mesh. The residues were examined with an inverted microscope (magnifications 100–400 $\times$ ) and all ephippia encountered were enumerated.

## Data analysis and indices

To characterize the temporal succession of cladoceran communities in the sediment core for local faunal zones (sample groups), a constrained cluster analysis (unweighted pair-group method with arithmetic mean, UPGMA) with the Bray-Curtis similarity measure (cutoff value 0.7) was applied to the cladoceran relative abundances. Furthermore, among the local faunal zones defined by the cluster analysis, a similarity percentage (SIMPER) analysis with a Bray-Curtis measure was carried out to assess which taxa were primarily responsible for the differences observed among the zones. UPGMA and SIMPER were performed with the Paleontological Statistics (PAST) program (Hammer *et al.* 2001). The rarefaction approach was applied to the cladoceran incidence data to characterize  $\alpha$ -diversity (species richness and Shannon's diversity index,  $H'$ ) of cladoceran communities. Here, the null model software EcoSim (Gotelli and Entsminger 2004) was used for individual-based rarefaction and 50 individuals were set as a minimum to allow comparison of diversity between the subsamples.

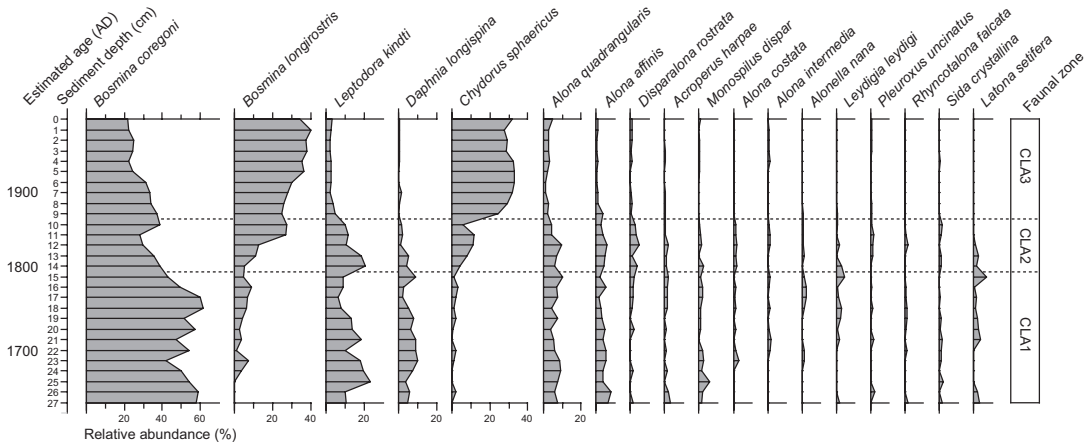
Based on the cladoceran and ephippium analyses, several indices and ratios were used in characterizing cladoceran community structure and functioning. Total cladoceran abundance and total resting egg production as numbers of individuals and ephippia per gram of dry weight (DW) sediment were calculated for each sample. Body size development of *Bosmina* spp. was estimated with body size measurements from carapaces. Rarefied species richness, as actual number of species, and Shannon's diversity index were used in determining  $\alpha$ -diversity. Benthic production was assessed with a ratio of encountered benthic (*Latona setifera*, *Sida crystallina* and Chydoridae without the *Chydorus sphaericus* type) to planktonic cladocerans (*Bosmina* spp., *Daphnia longispina*-type, *Leptodora kindti*, *Limnosida frontosa* and *Chydorus*

*sphaericus* type). The pressure of invertebrate predation on planktonic herbivorous cladocerans was estimated with a ratio of planktonic predators *Chaoborus flavicans* (Diptera: Chaoboridae) and *Leptodora kindti* to herbivorous cladocerans (*Bosmina* spp., *Daphnia longispina* type, *Limnosida frontosa* and *Chydorus sphaericus* type). The contribution of sexual reproduction throughout the community was calculated with a ratio of total ephippia to individuals (cf. Sarmaja-Korjonen 2004, Bjerring *et al.* 2009). Abundance of fish was estimated with a ratio of *Daphnia* ephippia to the sum of *Daphnia* + *Bosmina* ephippia calculated during the cladocera analysis (Jeppesen *et al.* 2003a, Nykänen *et al.* 2010).

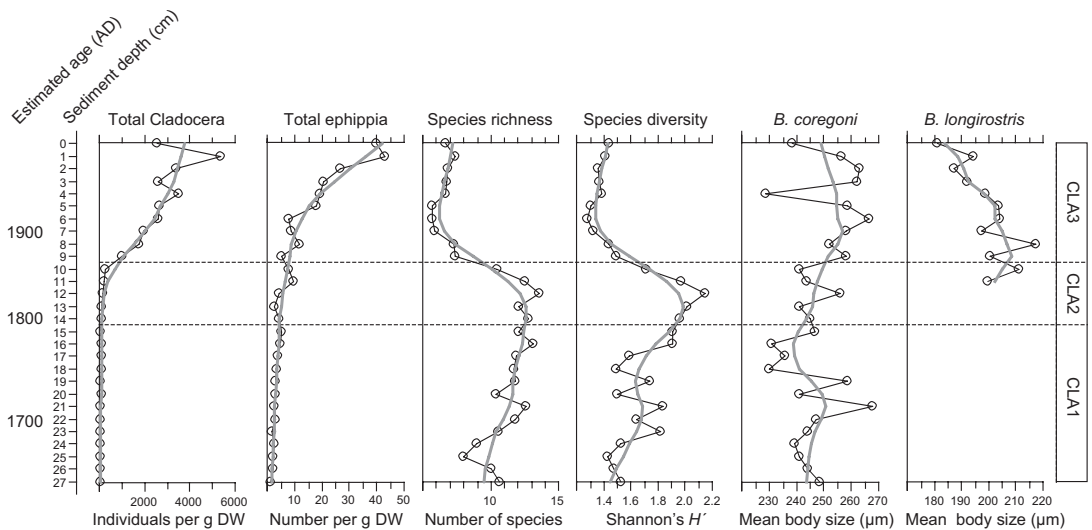
## Results and discussion

### Reference state of Mallusjärvi (pre-1800 AD)

The cluster analysis divided the cladoceran assemblages into three separate sample groups (local faunal zones CLA1–CLA3) that were clearly distinct from each other (Fig. 3). Historical records showed that the human impact on the lake's catchment began to accelerate by the late 18th century and, therefore, zone CLA1 (until ca. 1800 AD) probably represents the predisturbance period and reference conditions of Mallusjärvi with only slight human impact. The proportion of OM and the amount of magnetic minerals in the sediment were stable and low suggesting relatively low production and input of allochthonous material from the catchment (Thompson *et al.* 1975, Nesje and Dahl 2001, Shuman 2003), as indicated by LOI and MS measurements of the sediment (Fig. 2, see also Luoto and Nevalainen 2011). Further evidence of the low productivity during the reference state is provided by the very low abundance of cladocerans in the sediment, which resulted in a generally lower counting sum (51–66 indiv. per 3 g WW) in the lowest sediment samples. The total number of cladocerans did not exceed 100 indiv. per g DW (Fig. 4), indicating very low secondary production, which is directly linked with primary production. The chironomid-inferred  $P_{\text{tot}}$  level prior to 1700 AD had been generally low (5–20  $\mu\text{g l}^{-1}$ ), indicat-



**Fig. 3.** Subfossil cladoceran assemblages (taxa with > 1% maximum abundance and > 5 occurrences) in the Mallusjärvi sediment core since ca. 1700 AD. The local faunal zones (CLA1–CLA3) are based on the cluster analysis.

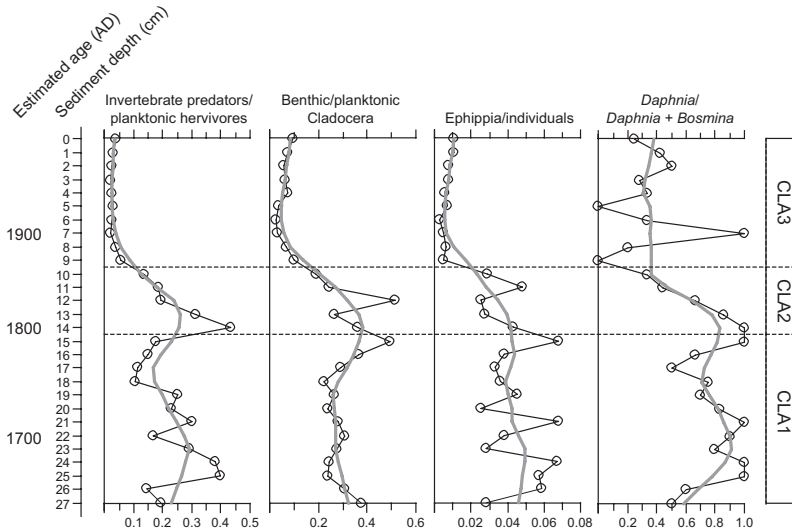


**Fig. 4.** Total Cladocera and ephippia,  $\alpha$ -diversity, and *Bosmina* body size development in the Mallusjärvi sediment core since ca. 1700 AD. The gray lines indicate general trends and were generated with locally weighted scatterplot smoothing (span 0.35). The local faunal zones (CLA1–CLA3) are based on the cluster analysis of subfossil cladoceran assemblages.

ing oligomesotrophic conditions, but started to increase and leveled off at approx.  $50 \mu\text{g l}^{-1}$  during the 18th century (Fig. 2). However, prior to 1700 AD Mallusjärvi probably was not truly oligotrophic due to clay turbidity, but rather naturally mesotrophic, and that the extremely low  $P_{\text{tot}}$  values inferred were probably caused by decreased productivity during the Little Ice Age (Luoto and Nevalainen 2011).

During the reference state, the cladoceran community (Fig. 3) was dominated by the planktonic *Bosmina* (*Eubosmina*) *coregoni* (approx.

50%), which thrives under mesotrophic conditions (Hofmann 1987, 1996). In addition, a predatory cladoceran *Leptodora kindtii* (10%), a keystone grazer *Daphnia longispina* type (approx. 5%–10%), and the benthic *Alona quadrangularis* and *Alona affinis* (both approx. 5%–10%) were abundant in the lake. Additionally, the lake was inhabited by rich littoral and benthic communities including mostly species from the family Chydoridae (Fig. 3). For example, the chydorids *Disparalona rostrata*, *Acroperus harpae*, *Monospilus dispar*, *Leydigia leydigi* and



**Fig. 5.** Ratios of planktonic invertebrate predators (*Chaoborus flavicans* and *Leptodora kindti*) to planktonic herbivorous cladocerans, benthic to planktonic cladocerans, total ephippia to total individuals, and *Daphnia* ephippia to sum of *Daphnia* + *Bosmina* ephippia in the Mallusjärvi sediment core since ca. 1700 AD. The gray lines indicate general trends and were generated with locally-weighted scatterplot smoothing (span 0.35). The local faunal zones (CLA1–CLA3) are based on the cluster analysis of subfossil cladoceran assemblages.

the large littoral *Sida crystallina* of the family Sididae, species associated with diverse bottom substrata and aquatic vegetation (Røen 1995, Flössner 2000), were present, suggesting the prevalence of diverse benthic habitats with variation in substrata and aquatic macrophytes. Due to the diverse chydorid fauna, the species richness of the cladoceran assemblages during the predisturbance period was high (generally > 10) and the number of taxa encountered increased to 12 species toward the top of the zone (Fig. 4). Species diversity, measured with Shannon's diversity index ( $H'$ ), exhibited a clear increase toward 1800 AD of from 1.5 to 1.9 (Fig. 4), in correlation with the increased productivity (Fig. 2). This was likely driven by occasionally occurring chydorid species (e.g. *Alona intermedia*, *Alonella nana*, *Pleuroxus uncinatus*) and partly by the appearance of a planktonic grazer *Bosmina longirostris* at 24 cm, along with the slightly increased  $P_{tot}$  and OM (Figs. 2 and 3), affecting species richness and evenness of the cladoceran assemblages (Fig. 4). Fitting well with the observed trend toward the increase in productivity (Fig. 2), *B. longirostris* is known to be an indicator of eutrophication, as shown in many paleolimnological studies (Szeroczyńska

1991, 1998, Luoto *et al.* 2008, Liu *et al.* 2009, Chen *et al.* 2010, Perga *et al.* 2010, Richard Albert *et al.* 2010). Furthermore, the slight increase in *Daphnia* around 1700 AD (and the increase in the ratio of *Daphnia* ephippia to *Daphnia* + *Bosmina* ephippia; see Fig. 5) may actually be a reflection of the slightly increased productivity (Fig. 2). The relatively abundant *Daphnia* populations are associated with intermediate nutrient enrichment, since they maintain stability and buffer against high phytoplankton productivity (Jeppesen *et al.* 2003b, Davidson *et al.* 2011).

The stability of several indices (Figs. 4 and 5) during the reference state in Mallusjärvi suggests that the functioning of the aquatic food web did not experience significant changes but remained in a state of equilibrium. The body size of *B. coregoni* varied from 230 to > 260  $\mu\text{m}$  in zone CLA1 but generally remained at approx. 250  $\mu\text{m}$  (Fig. 4), suggesting that the assemblage of its predators (fish) remained unchanged as well (Salo *et al.* 1989, Nykänen *et al.* 2010) and the species was not under heavy predation pressure from fish. Additionally, the ratio of *Daphnia* ephippia to *Daphnia* + *Bosmina* ephippia (Fig. 5), inversely indicating fish abundance,

remained high and stable suggesting a low abundance of zooplanktivorous fish (Jeppesen *et al.* 2003a). The stable and relatively high ratio of the large invertebrate planktonic predators *Lepidodora kindti* and *Chaoborus flavicans* to their planktonic cladoceran prey (mostly *Bosmina* and *Daphnia*) give further evidence for the balance of the food web (Fig. 5) and low fish abundance, since these large free-swimming predatory invertebrates are vulnerable to fish predation (Stenson 1978, Uusitalo *et al.* 2003). However, the nutrient increase as evidenced by increased OM and  $P_{\text{tot}}$  (Fig. 2) strongly influenced cladoceran community structure and functioning; e.g. since the *B. longirostris* population was established (Fig. 3), some benthic species appeared in the record and, consequently,  $\alpha$ -diversity increased (Fig. 4).

### Accelerated eutrophication ca. 1800 AD

More pronounced shifts in species composition of Cladocera occurred in Mallusjärvi ca. 1800–1850 AD, and the cluster analysis showed that samples at depths of 14–10 cm (zone CLA2, Fig. 3) differed from previous assemblages. The LOI and chironomid-inferred nutrient reconstruction showed that both OM (approx. 6%) and  $P_{\text{tot}}$  ( $> 75 \mu\text{g l}^{-1}$ ) continued to increase, suggesting the onset of nutrient-enrichment in Mallusjärvi from 1800 AD onward (Fig. 2). Cladoceran remains became more frequent in zone CLA2 (counting sum 110–285 indiv. per 3 g WW) and, consequently, there was a slight rise in cladoceran (up to 280 indiv. per g DW) and ephippial production (Fig. 4), supporting the increased production (Binford 1986, Liu *et al.* 2009, Richard Albert *et al.* 2010). The onset of eutrophication was clearly driven by increased agricultural activities in the catchment. This is supported by historical documentations indicating an increase in the human population in the vicinity of the lake by the late 18th century (Penttilä *et al.* 1987, Taipale-Heikkilä 2002), the period generally characterized by enhanced clearing of new land areas for agricultural use in southern Finland (Luoto *et al.* 2008). Here, the relative abundance of *B. coregoni* (30%) and *Daphnia* ( $< 5\%$ ) decreased, while *Bosmina longirostris* and *Chydorus sphaeri-*

*cus* type increased to  $> 20\%$  and approx. 10%, respectively (Fig. 3). The replacement of *Eubosmina* (*B. coregoni*) by *B. longirostris* and an increase in *C. sphaericus*, a chydorid taxon able to utilize pelagic habitats, are typical signs of eutrophication processes (Boucherle and Züllig 1983, Hofmann 1987, Szeroczyńska 1991, 1998, Luoto *et al.* 2008, Liu *et al.* 2009). Accordingly, SIMPER showed that the decrease in *B. coregoni* and the increase in *B. longirostris* were mostly responsible for the change in the community composition between zones CLA1 and CLA2, giving further support to the assumption that the succession of *B. coregoni* and *B. longirostris* can be used in tracking eutrophication processes.

The period of zone CLA2 (ca. 1800–1850 AD) was characterized by striking changes in most indices (Figs. 4 and 5). Species richness and diversity peaked around 1800 AD (Fig. 4), which were likely driven by rich littoral-benthic species assemblages (Fig. 3). However,  $\alpha$ -diversity began to decline toward the top, which was likely associated with changes in evenness of the species composition, because *B. longirostris* and *C. sphaericus* started to predominate and the benthic and vegetation-associated species declined and disappeared. The abundance and diversity of littoral aquatic vegetation are extremely important in maintaining diverse habitats for benthic cladocerans (Whiteside and Harmsworth 1967). High chydorid diversity is clearly related to water transparency (presence of aquatic macrophytes) and low nutrient status (Nevalainen 2010, Richard Albert *et al.* 2010). Thus, higher levels of  $P_{\text{tot}}$  (Fig. 2) probably increased phytoplankton production and decreased macrophyte growth via higher turbidity of the lake water and eventually caused the decline in  $\alpha$ -diversity (Fig. 4).

In addition, the early 19th century in Mallusjärvi was characterized by changes in food-web functioning, which was indicated by reduced values between invertebrate predators and herbivorous cladocerans, benthic and planktonic cladocerans, and the ratio of *Daphnia* to *Daphnia* + *Bosmina* ephippia (Fig. 5). These reduced ratios indicate that planktonic herbivorous cladocerans succeeded over benthic species and invertebrate predators under higher levels of nutrients. Zooplankton species usually benefit from nutrient increase because food availability



improves (Sweetman and Finney 2003) and, therefore, the community change in Mallusjärvi may have been controlled by enhanced primary production. However, the decreasing ratio of *Daphnia* to *Daphnia* + *Bosmina* ephippia indicates that fish abundance apparently began to increase along with nutrient enrichment (Jeppesen *et al.* 2003a), emphasizing also the role of top-down control. However, this was not reflected in a decrease in *B. coregoni* body size (Fig. 4), because the mean size between zones CLA1 (244  $\mu\text{m}$ ) and CLA2 (245  $\mu\text{m}$ ) did not differ. This is in contrast with previous results showing that *Eubosmina* body size tends to decrease under heavy fish predation (Salo *et al.* 1989, Nykänen *et al.* 2010), because fish prey on the largest individuals. In addition to body size, size and shape of *Bosmina* appendages may vary as a defense mechanism under high fish or invertebrate predation (Sanford 1993, Hellsten *et al.* 1999, Sakamoto and Hanazato 2008) that may further indicate high levels of planktivory. However, the appendage morphology of *B. coregoni* in Mallusjärvi was not evaluated and thus further morphological alteration in addition to changes in body size cannot be verified. As a result of eutrophication in northern European lakes, the abundance of roach *Rutilus rutilus* generally increases (Persson *et al.* 1991) and roach may retain high levels of algal productivity via bioturbation of the sediment and recycling of nutrients (Horppila and Kairesalo 1990). Evidently, cyprinids were the dominant species in Mallusjärvi prior to the management activities in the early 21st century when masses of fish were removed from the lake, and it is likely that the high cyprinid abundance was partly responsible for maintaining and enhancing eutrophication in the lake (Fig. 2).

The ratio of cladoceran ephippia to individuals was low but variable (approx. 0.02–0.06) during the reference state in Mallusjärvi (CLA1), and varied widely in zone CLA2. However, there was a clear trend toward lower values, beginning around 1800 AD (Fig. 5). This ratio is representative of sexually reproducing individuals in the prevalently asexually reproducing cladoceran community, since ephippia are generated via sexual reproduction under environmental control (Frey 1982). The ratio of ephippia to individu-

als in Mallusjärvi suggested that a very small fraction of reproduction in the cladoceran community was sexual, mirroring well the patterns observed in southern Finland (Kultti *et al.* 2011), where asexual reproduction predominates during the long open-water season and sexual reproduction takes place mostly in autumn, resulting in low frequencies of ephippia in lake sediments. In the Mallusjärvi record, the deteriorating ecological quality was reflected in this ratio as generally lowering values (Fig. 5), which is attributable to increased abundance of total cladocerans (Fig. 4). A very high production of (asexual) cladocerans during the summer may effectively dilute the relative share of ephippia found from sediments even though sexual reproduction *per se* would be very intensive (Nevalainen 2008a, 2008b). In Mallusjärvi, mostly the ephippia of *Daphnia* were recovered, *Bosmina* and chydorid ephippia contributing only slightly to the total abundance and this also affect the interpretation of the ephippia ratio, because *Daphnia* remains are preserved selectively. Usually, only the ephippia and postabdominal claws can be found in sediments (Szeroczyńska and Sarmaja-Korjonen 2007), giving no reliable indication of *Daphnia* (asexual) abundance.

### Deteriorated ecological quality since 1850 AD

The trends in cladoceran community composition and functioning that started ca. 1800 AD continued in zone CLA3, which represents the period of deteriorated ecological quality and eutrophic or even hypereutrophic conditions, with  $P_{\text{tot}} \approx 100 \mu\text{g l}^{-1}$  (Fig. 2). Eutrophication was apparently due to increased agricultural land use in the catchment (Fig. 1), which consequently led to influx of nutrients from the clay soils through accelerated erosion. Indeed, input of inorganic allochthonous material increased considerably during early zone CLA3, as indicated by MS (Fig. 2, Thompson *et al.* 1975). *Bosmina longirostris* (40%) and *Chydorus sphaericus* type (30%) dramatically increased while other planktonic taxa (*B. coregoni*, *Leptodora*, and *Daphnia*) decreased (Fig. 3). SIMPER showed that *B. longirostris* and *C. sphaericus* drove the change

and, accordingly, these taxa can be identified as indicators of eutrophication and deteriorated ecological quality in Mallusjärvi. The increase in these taxa was used previously (e.g. Boucherle and Züllig 1983, Szeroczyńska 1991, Liu *et al.* 2009, Richard Albert *et al.* 2010) to represent the classical community response to nutrient enrichment, since they are known to inhabit meso-eutrophic lakes. Many chydorid species, e.g. *Alona costata*, *Alonella nana*, *Leydigia leydigi*, and *Rhynchotalona falcata* and other littoral-benthic species such as *Sida crystallina* and *Latona setifera* disappeared from the stratigraphy (Fig. 3) and, accordingly,  $\alpha$ -diversity (Fig. 4) and the benthic/planktonic ratio collapsed (Fig. 5). These changes likely indicate a state of turbid water with high algal production and decreased production of submerged aquatic vegetation together with weakening conditions in littoral and benthic habitats. There is usually a clearly negative relationship between littoral and benthic cladoceran diversity and nutrient status (Nevalainen 2010, Richard Albert *et al.* 2010). The shift from benthic to pelagic production observed in Mallusjärvi was similar to the broad-scale impacts of eutrophication in shallow lakes previously observed in sedimentary cladoceran records (Davidson *et al.* 2011).

Furthermore, the total number of cladocerans increased exponentially up to 3000–5000 indiv. per g DW (counting sum in CLA3: 178–463 indiv. per 0.5 g WW) which, together with the ephippia, followed the trend of  $P_{\text{tot}}$  (Figs. 2 and 4). We expected that the ratio of ephippia to individuals (Fig. 5) would increase under pronounced environmental stress, such as eutrophication, but the proportion of sexual reproduction decreased and the number of ephippia was diluted by the high level of production of asexual individuals (Fig. 4). However, since the *Daphnia* ephippia were the most frequently observed and the chydorid ephippia extremely scarce, there was no possibility to track taxon-specific patterns in sexual and asexual production that could unravel species responses to eutrophication in Mallusjärvi. The results (Fig. 5) nevertheless suggest that stability and abrupt changes in the ratio of ephippia to individuals can apparently act as indicators of both environmental stability and limnological deterioration related to eutrophication.

The invertebrate predators decreased considerably and this was likely due to increased numbers of planktonic herbivorous cladocerans along with increased productivity (Figs. 2 and 5). However, it may also be indicative of higher abundance of fish (cyprinids), which was further supported by the decreased ratio of *Daphnia* to *Daphnia* + *Bosmina* ephippia (Fig. 5, Jeppesen *et al.* 2003a) and eutrophication (Persson *et al.* 1991). As stated above, cyprinids (mainly roach) are the dominant species in eutrophicated lakes, and our results suggest that fish became more abundant in Mallusjärvi in comparison to the reference state (Fig. 5). If so, the community response of cladocerans was likely mediated through top-down effects by roach, and the results show that the larger taxa (*B. coregoni*, *Daphnia* and *Leptodora*) decreased, while the small-bodied *B. longirostris* and *C. sphaericus* type succeeded (Fig. 3). All of the zooplankton taxa mentioned are desirable prey items for roach (Stenson 1976, Hessen 1985, Gliwicz *et al.* 2000, Uusitalo *et al.* 2003). Had the decrease in *B. coregoni* been partly regulated by fish predation and not merely by success and an increase in *B. longirostris*, it would have presumably been seen as a decrease in its body size (cf. Salo *et al.* 1989, Nykänen *et al.* 2010). This, however, was not the case, although a minor decreasing trend in the body size of *B. coregoni* was found (Fig. 4). *Bosmina longirostris* becomes relatively more important in lakes with higher predation pressure from fish, because it is less vulnerable to size-selective predation (Brooks and Dodson 1965, Åhlén *et al.* 2011).

There was a clear trend toward decrease in *B. longirostris* body size since 1900 AD (from approx. 200 to 180  $\mu\text{m}$ ) that would suggest that it was heavily preyed on by fish (Fig. 4). Young roach can prey heavily on the small-sized *B. longirostris* (Townsend *et al.* 1986) and thus it is likely that body size reduction in this species was partly caused by fish predation. Accordingly, the current results suggest that cyprinids first preyed on the larger cladoceran taxa when they were abundant and switched principally to consuming *B. longirostris* when it increased markedly. Apparently, predation resulted in a clear decrease in *B. longirostris* body size, which agrees well with the previously observed pat-

terns of *Bosmina* carapace length being negatively related to fish predation pressure (Liu *et al.* 2009, Åhlén *et al.* 2011). Body size of *B. longirostris* was impacted by fish predation, while that of *B. coregoni* remained mostly unaffected, probably because these taxa utilize different habitats (Hofmann 1998). The truly pelagic *B. coregoni* may have been able to escape predators, whereas *B. longirostris*, which inhabits both open-water and inshore areas, would have been more vulnerable to high predation pressure in near-shore habitats. Furthermore, together with the increasing nutrient status bottom-up forces may have also contributed to the community and body size changes (Figs. 3 and 4), because smaller individuals of planktonic *Daphnia* and *Bosmina* prevail in higher nutrient-level lakes (Korosi *et al.* 2008). This type of cladoceran size structure can be mediated through the competitive advantage of larger cladocerans grazing more efficiently at low nutrient levels, but at higher nutrient levels such competition pressure does not exist and smaller taxa and individuals can proliferate.

The Development Project of Mallusjärvi was launched in the early 21st century to manage the poor ecological status of the lake on behalf of national and local authorities. The project included, among others, control of erosion and influx of material from the catchment and biomanipulation via removal of tons of fish. The project lasted four years and resulted in a moderate decrease in  $P_{\text{tot}}$  (from approx. 150 to 100  $\mu\text{g l}^{-1}$ ). In accordance with the results of the project, the chironomid-inferred  $P_{\text{tot}}$  decreased in the topmost sample (from  $> 125$  to  $< 100$   $\mu\text{g l}^{-1}$ ) along with OM and MS (Fig. 2), representing slightly improved ecological quality of the lake via erosion control. A similar, decreasing trend was also observed in the abundance of total cladocerans (Fig. 4), but community structure and the other functional and phenotypic indices did not change significantly in the topmost sample (Figs. 3 and 5).

## Conclusions

Based on the sedimentary record of Mallusjärvi, during the eutrophication process there was a

profound shift from one equilibrium state to another (*sensu* Scheffer *et al.* 1993). The results indicate that during the reference state, prior to anthropogenic pressure of agricultural land use, Mallusjärvi was oligomesotrophic and contained rich planktonic and littoral-benthic cladoceran assemblages with high species and functional diversity. The onset of severe eutrophication, caused by increased agricultural activities in the catchment, occurred during the 19th century and became enhanced toward the present. The nutrient enrichment evidently caused gradual responses in cladoceran community composition and functioning, and changes in phenotypic properties and shifted the lake ecosystem into another state of equilibrium. The disturbed state of Mallusjärvi was characterized by eutrophic-hypereutrophic conditions and subsequent shift toward the dominance of planktonic cladocerans, deterioration of littoral-benthic conditions, and low  $\alpha$ -diversity. The impacts of eutrophication on cladoceran communities and phenotypic properties were probably further emphasized via top-down effects of increased abundance of cyprinids. Despite the abrupt shift in ecological quality between 1800 and 1900 AD, the reference status and the period of deteriorated limnological conditions were both characterized by stable communities and functioning, and thus, the resilience of ecosystem structure and functions can also be attributed to ecological quality and tracked from sedimentary records.

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