

Jussi Jyväsjärvi

Environmental Drivers of Lake
Profundal Macroinvertebrate
Community Variation - Implications
for Bioassessment



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- Implications for Bioassessment

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ABSTRACT

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Yhteenveto: Järvisyvänteiden pohjaeläinyhteisöjä säätelevät ympäristötekijät ja niiden merkitys järvien biologisen tilan arvioinnissa

Diss.

The EU Water Framework Directive (WFD) aims to achieve at least good ecological status for European waterbodies. Ecological assessment is essentially premised on comparison of the observed biota with reference biota representing conditions undisturbed by human. Hence, successful assessment requires basic research into both natural and anthropogenic sources of biological variation. Profundal macroinvertebrates (PMI) are one of the elements required for the ecological assessment of lakes. My study aims were: 1) to determine the extent of natural PMI community variation and its dependence on, and hence predictability from, environmental variation insensitive to human disturbance; 2) to evaluate various modelling approaches in comparison to the operative WFD-compliant lake typology to predict the natural variation (i.e. the reference status of PMI fauna); and 3) to quantify the importance of food in relation to oxygen and temperature in structuring PMI communities. The natural variation of PMI communities was primarily attributable to lake depth. A novel paleolimnological validation procedure showed that a simple linear regression model was superior to typology in the estimation of reference values for a key PMI assessment metric. Development of multivariate models to predict the PMI fauna was more challenging and the models were imprecise, although apparently outperforming the typology approach. Food controlled the PMI communities, particularly in nutrient-poor lakes, but in general, the communities are structured by food, oxygen and temperature in concert. The results imply that comparison of PMI communities among lakes, and hence also the assessment of PMI fauna, should be controlled for lake morphometry, preferably by statistical models rather than categorical typologies. The functional explanation for lake morphometry as a key predictor of PMI fauna is the covariance of the proximate driving factors with depth in particular.

Keywords: Bioassessment; ecological stoichiometry; predictive modelling; profundal macroinvertebrates; stable isotopes; Water Framework Directive.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following four original papers, which will be referred to in the text by their Roman numerals I-IV.

I planned all studies with my supervisor Heikki Hämäläinen. I wrote all four manuscripts and was mainly responsible for collecting and analyzing both the existing national macroinvertebrate data (I-III) and field data (IV). Co-authors contributed to data collecting, laboratory and statistical analyses. All papers were finished together with the co-authors.

- I Jyväsjärvi J., Tolonen K.T. & Hämäläinen H. 2009. Natural variation of profundal macroinvertebrate communities in boreal lakes is related to lake morphometry: implications for bioassessment. *Canadian Journal of Fisheries and Aquatic Sciences* 66: 589-601.
- II Jyväsjärvi J., Nyblom J. & Hämäläinen H. 2010. Palaeolimnological validation of estimated reference values for a lake profundal macroinvertebrate metric (Benthic Quality Index). *Journal of Paleolimnology* 44: 253-264.
- III Jyväsjärvi J., Aroviita J. & Hämäläinen H. 2011. Evaluation of approaches for measuring taxonomic completeness of lake profundal macroinvertebrate assemblages. *Freshwater Biology* DOI: 10.1111/j.1365-2427.2011.02603.x
- IV Jyväsjärvi J., Boros G., Jones R.I. & Hämäläinen H. 2011. The importance of food, relative to oxygen and temperature, in structuring lake profundal macroinvertebrate assemblages. Submitted manuscript.

1 INTRODUCTION

1.1 Profundal macroinvertebrate communities

The bottom of lakes is divisible into three distinct zones: littoral, sublittoral and profundal. The latter, the profundal area, can be characterised as the deeper water area with fine sediments, lacking illumination and thus rooted vegetation (Wetzel 2001). Thermal stratification of dimictic boreal lakes during the summer and winter stagnation periods results in permanently low water temperature and extended periods when the hypolimnetic oxygen consumed by degradation of organic material depositing at the lake bottom is not replenished (Suess 1980). Consequently, low oxygen concentration, or even complete anoxia, are a common situation in profundal areas of boreal lakes (Fulthorpe & Paloheimo 1985). Due to the lack of light, the profundal ecosystem is heterotrophic and fully dependent on poor quality sedimenting organic material originating from the upper water column, littoral areas or terrestrial production (Lopez & Levington 1987, Covich et al. 1999).

Despite the harsh conditions, the profundal zone provides a unique habitat for a characteristic and surprisingly diverse and abundant macroinvertebrate fauna (Jónasson 1996). The core of profundal benthic communities in boreal lakes is typically comprised of larvae of non-biting midges (Diptera: Chironomidae) and of segmented worms (Annelida: Oligochaeta). Amphipod crustaceans (e.g. *Monoporeia affinis*, *Pallasea quadrispinosa*), small mussels (*Pisidium* spp. and *Sphaerium* spp.), water mites (Acari: Hydrachnellae) and non-chironomid dipteran larvae (Chaoboridae and Ceratopogonidae) are usually the additional components.

Profundal macroinvertebrates play a key role in lake ecosystems. Most species are detritivores and, due to high abundances, they are capable of processing considerable amounts of dead and dying organic matter sedimenting from the upper water column. Furthermore, many species are important prey items for predatory invertebrates and benthivorous fish (Lindegaard 1994). The various substances assimilated by profundal invertebrates are thus transferred to higher trophic levels within a lake, or

alternatively transported to adjacent terrestrial ecosystem via aerial life stages of e.g. chironomids and chaoborids (Reinhold et al. 1999, Jones & Grey 2011).

1.2 Profundal macroinvertebrates in lake monitoring

Benthic macroinvertebrates are perhaps the most widely used group of organisms in biological monitoring and assessment of freshwaters. Several factors advocate the utility of benthic assemblages in bioassessment. First, they are long-lived and sedentary and the communities will thus indicate environmental stress at a meaningful scale, both in time and space. Second, macroinvertebrate assemblages comprise diverse species with varying and well known responses to human-induced environmental stress (Rosenberg & Resh 1993). Furthermore, the sampling of macroinvertebrates is relatively cheap, quick and well standardized and their identification has become easier due to revised taxonomy and availability of up-to-date identification guides (e.g. Brooks et al. 2007).

Research into profundal macroinvertebrate communities has a long-standing tradition in limnology. The early lake classifications schemes were based on profundal chironomid fauna and their empirical relationships to lake trophicity (see Brinkhurst 1974 for a review). Three subsequent studies were particularly seminal and formed the cornerstones of profundal bioassessment. Brundin (1949, 1951) was among the first to show empirically that hypolimnetic oxygen is pivotal in structuring profundal communities and this has since remained a central tenet of profundal macroinvertebrate ecology (Int Panis et al. 1996, Real et al. 2000, Verneaux et al. 2004). Later, Saether (1979) characterized the trophic preferences of 57 Palearctic and Nearctic profundal chironomid taxa and developed a classification system in which the occurrence of particular taxa indicated the varying nutrient status of a lake, corresponding to one of 15 lake types (α - o). Wiederholm (1980) quantified the indicator values of profundal macroinvertebrates by developing the Benthic Quality Index (BQI), which uses the relative abundances of seven chironomid taxa or five oligochaete species to indicate anthropogenic nutrient enrichment.

The demonstrations by Saether (1979) and Wiederholm (1980) of the correspondence between occurrence of profundal indicator species and lake nutrient status enabled a more comprehensive understanding of pelagic-benthic coupling: anthropogenic nutrient enrichment accelerates algal primary production, and the diversity, abundance and community composition of profundal fauna respond to the consequent alteration of nutrient and oxygen regimes prevailing in the profundal zone (Hanson & Peters 1984, Rasmussen & Kalff 1987, Graf 1989, Johnson & Wiederholm 1992, Goedkoop & Johnson 1996, Blumenshine et al. 1997). After the works of Saether (1979) and Wiederholm (1980), profundal assemblages rapidly became widely applied in the monitoring of either water quality or biota *per se* (e.g. Edmonds & Ward 1979, Kansanen et

al. 1984, Aagaard 1986, Gerstmeier 1989, Johnson & Wiederholm 1989, Johnson et al. 1992, Int Panis et al. 1996, Dinsmore et al. 1999, Real et al. 2000, Milbrink et al. 2002, Verneaux et al. 2004).

Lake sediments in profundal areas are a burial ground for organic and inorganic material, pollutants and many dead aquatic and terrestrial organisms such as fish, aquatic insects, algae and plants. Hard body parts (e.g. diatom [Bacillariophyceae] valves, chitinized exoskeleton of insects, fish scales) are usually well preserved in the bottom sediments and thus provide a unique paleolimnological archive of various physico-chemical and biological changes at a site during its ontogeny (Smol 2008).

Chironomids are one of the most frequently used groups in palaeolimnological studies as the heavily chitinized subfossil head capsules of chironomid larvae shed during ecdysis can be identified usually to genus level or in some cases, even to species (e.g. Davies & Jackson 2006, Smol 2008). Due to their ubiquitousness, high abundance in lake sediments and well established ecological preferences of the majority of taxa, lentic chironomids have been successfully applied to infer past nutrient status (Lotter et al. 1998, Brodersen & Lindegaard 1999), oxygen availability (Quinlan & Smol 2002), acidification (Schnell & Willasen 1996) and climatic oscillations (e.g. Larocque et al. 2001, Heiri et al. 2003, Larocque & Hall 2003).

Finnish paleolimnologists have contributed to paleolimnological research by many excellent case studies demonstrating the long-term succession of profundal chironomid assemblages during the heavy pollution periods in the 20th century. The studies have indisputably authenticated and quantified the degradation of chironomid communities during the pollution period and reversibility of this process following the gradual recovery. Indeed, these studies have demonstrated that profundal chironomid communities respond 'ideally' to stress (see Rapport 1992), as they show marked and consistent *i*) reduction of species richness, *ii*) predominance of pollutant-tolerant species and *iii*) alteration of species abundance within and among taxa due to anthropogenic disturbance (e.g. Kansanen 1985, Meriläinen et al. 2000, 2003, Hynynen et al. 2004).

1.3 Bioassessment of freshwaters

1.3.1 Towards a global emphasis on the natural status of biota

Global concern of perpetual degradation of freshwater and marine ecosystems has engendered legislative mandates, such as the Clean Water Act in the United States (Anon. 1972), the National River Health Program in Australia (Norris & Norris 1995) and the Water Framework Directive in Europe (WFD; Anon. 2000), for protection and management of surface waters. These programs are fundamentally altering the conventional water quality-centred monitoring of

freshwaters by emphasising ecosystem integrity as a primary management objective. More specifically, the assessment in these programs is based on the Reference Condition Approach (RCA), in which the current status of an evaluated site is compared to the reference conditions representing the presumed natural status of the site (Hughes et al. 1995, Reynoldson et al. 1997, Bailey et al. 2004, Stoddard et al. 2006).

The Water Framework Directive (Anon. 2000) was formed to promote the sustainable use of aquatic resources and to harmonise and consolidate the ecological assessment among the EU Member States. The Directive necessitates the assessment of biological and hydro-morphological conditions as well as evaluation of water quality and harmful substances of coastal areas, rivers and lakes. The ecological assessment of lakes is based predominantly on the composition and abundance of phytoplankton, fish, macrophytes and macroinvertebrates. The deviation from the natural conditions is quantified by comparing the observed (O) biological parameter to the expected (E) reference value (Ecological Quality Ratio; EQR). The evaluated site is classified into one of the five ecological classes (high [EQR ~ 1], good, moderate, poor and bad [EQR ~ 0]) on the basis of EQR values, and all surface water bodies should achieve at least good ecological status or good ecological potential (heavily modified water bodies) by 2015 (Anon. 2000) or later (see Hering et al. 2010).

1.3.2 Controlling for natural biological variation

Establishing the reference conditions is the most challenging and critical stage of ecological assessment (Irvine 2004). Inaccuracy in assessment of the biological condition due to poorly estimated reference status might impede detection of severe ecological impacts or, alternatively, cause economic waste because of unnecessary remedial actions.

As data representing the pristine status of a lake or a river are virtually never available, various alternative approaches have been proposed for the estimation of the natural biological status of water bodies (Stoddard et al. 2006). The simplest approach, and the default in the WFD, is classification, or more precisely termed *a priori* typology of sites on the basis of their natural environmental characteristics (Anon. 2000, 2003). Even though typology is easy to understand and use, there is growing awareness that such a rough categorical classification may be over-simplistic and thus inadequate in accounting for continuous variation of environment and biological communities. A number of studies now suggest that considerably more accurate estimates of site-specific reference status and thus more credible assessment results can be obtained by statistical modelling approaches (Davy-Bowker et al. 2006, Mazor et al. 2006, Aroviita et al. 2009).

1.3.3 Measuring ecological status

Univariate biotic indices are traditionally used for summarising the macroinvertebrate community patterns and assessing the status of assemblages

in relation to various environmental stresses (e.g. eutrophication, acidification; see Cairns & Pratt 1993, Johnson et al. 1993). Many indices have a long history in aquatic research, their calculation is simple and they are thus easy to use in practical bioassessment. Nevertheless, the use of indices may have some shortcomings. In most cases, univariate biotic indices are stressor-specific and calibrated for certain locally pivotal environmental gradients and taxa. However, aquatic ecosystems are rarely disturbed by a single stressor and therefore the utility of unidimensional, stressor-specific metrics might ignore the complex interactions of multiple coexisting environmental stressors (Johnson et al. 1993, Aroviita 2009). In addition, the use of often over-adjusted biotic indices potentially hinders the harmonization of ecological classification among different ecoregions and countries (Hering et al. 2010). Thus, there has been widespread interest to develop more general measures of biological integrity.

Predictive multivariate models provide a variety of approaches to estimate the occurrence of native taxa (i.e. those expected to occur at a site in the absence of human disturbance). The expected number of taxa in reference conditions (E) is derived by summing the predicted probabilities of occurrence, estimated by the model, and the faunal deviation of an evaluated site from the reference conditions is quantified by the relative difference between observed (O) and expected taxonomic composition (E) - the O/E (hereafter O/E_{TAXA}) index, or 'taxonomic completeness' (Hawkins 2006). Given that O is always a subset of E, the O/E_{TAXA} quantifies the integrity of native biota and is thus a globally consistent, ecologically meaningful and easily interpreted measure of biotic condition (Hawkins 2006).

The pioneer of predictive modelling for bioassessment needs was the River InVertebrate Prediction And Classification System (RIVPACS; Moss et al. 1987, Wright et al. 2000, Clarke et al. 2003) which was originally developed for stream macroinvertebrates. RIVPACS-type models have since been adapted to lotic fishes (Joy & Death 2002, Kennard et al. 2006, Meador & Carlisle 2009), macrophytes (Mykrä et al. 2008), and diatoms (Feio et al. 2007), and also to lake littoral macroinvertebrates (Johnson 2003, Neale & Rippey 2007). The example of RIVPACS models led to emergence of alternative modelling approaches based either on a similar philosophy (Linke et al. 2005, Chessman et al. 2008) or different statistical approaches (Oberdorff et al. 2001, Olden 2003, Joy & Death 2004). Hitherto, such approaches have not been developed for profundal fauna and there is a clear need for an evaluation of the potential of these approaches to measure taxonomic completeness of profundal communities.

1.3.4 Validation of the assessments

Whatever index or metric will be used in biological assessment, it is essential to validate the approaches used. This fundamental stage often remains unsatisfactory as we are lacking data prior to disturbance, and hence documentation of the actual biological impairment and its magnitude. Cao & Hawkins (2005) and Hawkins et al. (2009) tried to overcome this problem by

comparing the assessed against simulated impairment of stream macroinvertebrate community composition. In lakes, paleolimnological records offer a more valid alternative. The biological records representing the pre-industrial period (Smol 2008) can be used either to authenticate the detected anthropogenic impairment or to validate alternative approaches for establishment of reference conditions for those groups leaving remains in sediments (e.g. lentic chironomids or diatoms). Recent studies have utilized paleolimnological methods for ascertaining the present pristine environmental (Kauppila et al. 2002, Andersen et al. 2004, Miettinen et al. 2005) or biological (Bennion et al. 2004, Leira et al. 2006) conditions of individual reference sites. To my knowledge, only few studies have applied palaeolimnological data to directly assess the ecological status of a site (Meriläinen et al. 2003, Kauppila et al. 2011), while none have validated approaches for estimation of reference conditions or assessments of biological impairment by palaeolimnological data; for these uses there are obvious opportunities and needs.

1.4 Study aims

Understanding the extent of natural biological variation and causal relationships between biological responses and anthropogenic disturbance requires in-depth studies of species and community level patterns and their relationships with environmental variation. This will help to recognise the factors structuring biological communities in space and time in both near pristine and disturbed sites and will enable discrimination of the human induced community changes from those driven by natural temporal and spatial variation. Profundal communities are considered to be governed by multiple inter-related environmental factors (i.e. bottom temperature, oxygen and food) that covary along with both natural (lake morphometry) and anthropogenic (nutrient enrichment) environmental variation. However, their actual contribution in structuring profundal fauna, food in particular, is still poorly known, thus impeding the interpretation of causes of natural community variation and anthropogenic degradation.

This thesis focuses on profundal macroinvertebrate communities in boreal lakes and the relationships between community and environmental variation. One of the primary objectives was, on the basis of a large national data set, to evaluate the extent and origin of natural variation of lake profundal communities and, furthermore, to address the implications of this natural variation for the status assessment of profundal fauna (I). The second objective was, based on the patterns uncovered by the first study, to develop predictive models for estimation of the reference status of profundal assemblages and to evaluate their potential in lake bioassessment. For this purpose, a simple regression model (II) and also a selection of more complex multivariate predictive models (III) were developed to estimate values of chironomid Benthic Quality Index (BQI) and the occurrence of taxa, respectively, in the

absence of human disturbance and to serve as reference conditions for status assessment. The BQI model (II) was validated using a novel approach based on paleolimnological archives representing the pristine status of a site, whereas multivariate predictive models (III) were validated with independent contemporary data. In both cases the performance of modelling approach was evaluated in comparison to a WFD-compliant *a priori* typology. These approaches for predicting and controlling for the natural biotic variation need to use easily measured predictors, which are not affected by humans. These correlates do not necessarily reveal any causality. Therefore, the third aim was to evaluate the relative importance of environmental variables (oxygen, temperature and food) generally considered more proximally structuring profundal macroinvertebrate fauna (IV). Particular emphasis was put on analysis of quantity, quality and origin of sedimenting organic material (food resource) in order to evaluate its previously poorly known contribution to regulation of profundal community composition.

2 MATERIAL AND METHODS

2.1 National profundal macroinvertebrate data (I-III)

2.1.1 Site selection and environmental data

The studies I-III were based on an extensive national macroinvertebrate and environmental data set compiled for this thesis and also for the development of ecological classification of profundal macroinvertebrate communities of Finnish lakes. The data were repeatedly updated as more data became available, and therefore the studies I-III differ in the number of reference sites (Table 1). Presently, the data set contains 179 mainly central and eastern Finnish lake basins (Fig. 1A), and has been compiled from various sources, including the archives of the Finnish environmental authorities, monitoring reports, theses and my own observations. The sites were divided into two *a priori* groups: sites with minimal anthropogenic disturbance (hereafter REF sites, $n = 107$) and sites with varying human impact (IMP sites, $n = 72$). REF site selection followed the criteria suggested by the EU REFCOND guidance document (Anon. 2003) and was based on suggestions of authorities from the Finnish Environment Institute (FEI) using all available information on anthropogenic pressures.

TABLE 1 Data sources and number of study basins for the studies I – IV. REF and IMP denote minimally disturbed reference sites and variously impacted sites due to human actions, respectively.

Data	Status	Study I	Study II	Study III	Study IV
National macroinvertebrate data	REF	55	73	74	-
	REF (Validation)	-	-	33	-
	IMP	-	-	72	-
Paleolimnological literature data	REF & IMP	-	24	-	-
Sediment trap data	REF & IMP	-	-	-	26

Site-specific environmental data were acquired from the HERTTA-database maintained by FEI (Table 2). The data cover a range of environmental characteristics including geographic, water quality and morphometric variables. The water quality measurements are accordant to the Finnish standards and are from the macroinvertebrate sampling sites and from the summer stagnation period (August) of the year of macroinvertebrate sampling. In those few cases, when these data were not available, water quality information from the preceding year was used. Landscape position of the 55 REF sites used in the first study (I) was characterized by lake order. This is analogous to Strahler's stream order (Strahler 1952) and provides a proxy for numerous physical, chemical and biological features essential for lake functioning (see Riera et al. 2001, Quinlan et al. 2003). Lake order was determined following Riera et al. (2001) using 1:15 000 scale electronic maps.

TABLE 2 Summary of geographic, morphometric and water chemistry variables for 107 REF sites and 72 IMP sites. Variables considered as independent of human actions and thus used as community predictors in studies I-III are denoted with symbol *.

	REF sites (n=107)			IMP sites (n=72)		
	Mean	Min	Max	Mean	Min	Max
Altitude (m.a.s.l.)*	114	47	254	104	71	222
Latitude (N°)*	62.4	60.2	69.1	62.4	61.1	64.6
Longitude (E°)*	27.4	23.6	31.2	27.3	23.5	31.0
Area (km ²)*	123.5	1.2	1378.0	147.6	1.4	1378.0
Volume (km ³)*	1.32	0.001	14.88	1.95	0.002	14.87
Mean depth (m)*	7.9	2.3	21.0	7.6	2.7	16.5
Sampling depth (m)*	26.7	3.7	91.0	23.9	3.9	71.0
Depth ratio*	0.36	0.14	0.87	0.35	0.15	0.80
Relative depth*	0.71	0.10	2.31	0.51	0.10	2.70
Temperature (°C)*	10.26	4.97	19.8	11.9	4.1	19.6
Distance to shore (m)*	379	31	3001	442	41	1651
Total phosphorus (µg l ⁻¹)	11.1	4.3	37.2	20.4	6.0	61.7
Total nitrogen (µg l ⁻¹)	379.1	177.8	1288.3	570.5	208.9	1288.3
Conductivity (mS m ⁻¹)	5.2	1.5	15.9	6.5	2.7	14.5
Chlorophyll <i>a</i> (µg l ⁻¹)	6.7	1.8	42.7	11.3	2.0	58.9
Dissolved oxygen (mg l ⁻¹)	6.1	1.0	12.7	5.2	1.0	11.5
Colour (mg Pt l ⁻¹)*	48.9	5.5	161.0	65.3	11.0	161.0

2.1.2 Macroinvertebrate data

Macroinvertebrate samples for the studies I-III were collected and species identified by various people and agencies. However, the sampling procedure in all cases was in accord with the Finnish standard (SFS 5076). The quantitative macroinvertebrate samples were taken from the deepest part of each basin in September-November using an Ekman grab or a similar sampling device (surface area 250-300 cm²). Sampling effort ranged from 2 to 8 replicates per site. In cases of more intensive sampling, five replicates were randomly resampled to produce a balanced data set. The collected material was passed in most cases

through a 500 μm sieve in the field and the retained material was preserved in 70 % ethanol. In the laboratory, all animals were screened from other material on a well illuminated white dish. If necessary, head capsules of chironomid larvae, whole oligochaetes and chaoborid larvae were mounted on microscope slides for identification and the animals were identified to the lowest possible taxonomic level and counted. In order to achieve taxonomic consistency, the species data were harmonised as necessary, e.g. some species identifications reduced to genus. At the final stage, the data comprised 112 taxa, which were identified to 83 species/species-group, 23 genera, one sub-family, three families, one sub-order and one class.

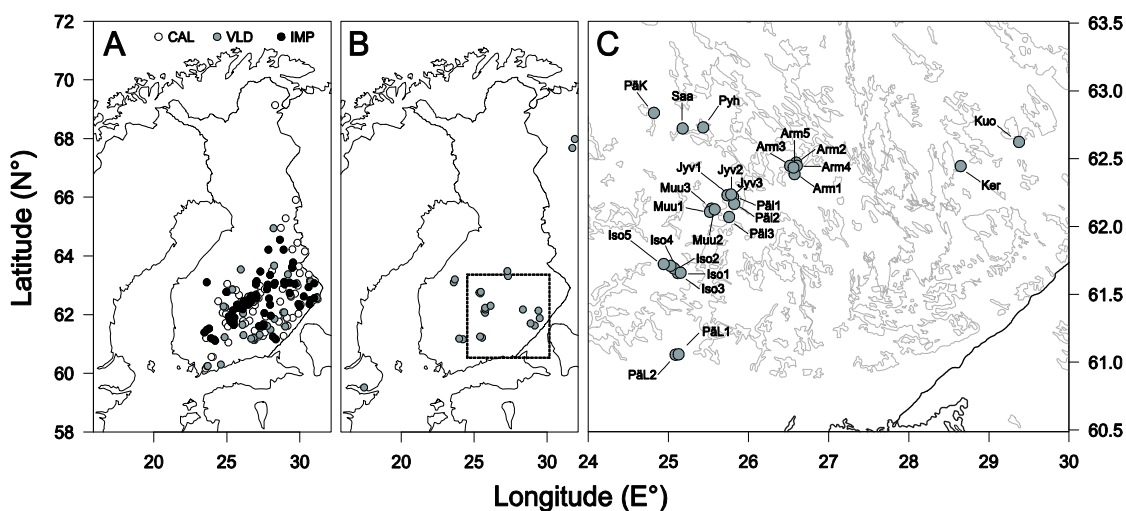


FIGURE 1 The geographical locations of A) 179 lake basins with national macroinvertebrate data (I, II and III), B) 24 paleolimnological validation sites (II) and C) 26 sediment trap sites (IV). The area delineated in panel B with dashed line denotes the region represented in panel C.

2.1.3 Lake typology

The establishment of type-specific biological, hydromorphological and physico-chemical reference conditions for Finnish lakes is based by default on lake typology “System B” (Anon. 2000). Lake surface area and water colour (indicative of geology) are the primary typology descriptors, and altitude, morphometry (mean depth as a binary factor, threshold 3.0 m), hydrology (short vs. long retention time), and catchment geology are used as additional variables to differentiate special lake types from the main categories (Vuori et al. 2006). Using this typology, the 179 (I, II, III) sites of the national macroinvertebrate data were first divided into three categories based on water colour. Oligohumic lakes (OHL, $n=63$) were further divided into types of medium-sized (MOHL, $n=29$), large (LOHL, $n=30$) and shallow (ShOHL, $n=4$) lakes. Mesohumic lakes (MHL, $n=90$) were assigned to four lake types according to surface area (SMHL, $n=41$; MMHL, $n=18$; LMHL, $n=22$) and mean depth (ShMHL, $n=9$). Polyhumic lakes (PHL, $n=22$), were divided into two lake types based on mean depth (DPHL, $n=11$; ShPHL, $n=11$). Two sites were

assigned to the type of short retention time lakes (SRT) and naturally nutrient-rich (NNR) lakes. High altitude lakes (HAL) was the only lake type not represented in the present data (Fig. 2).

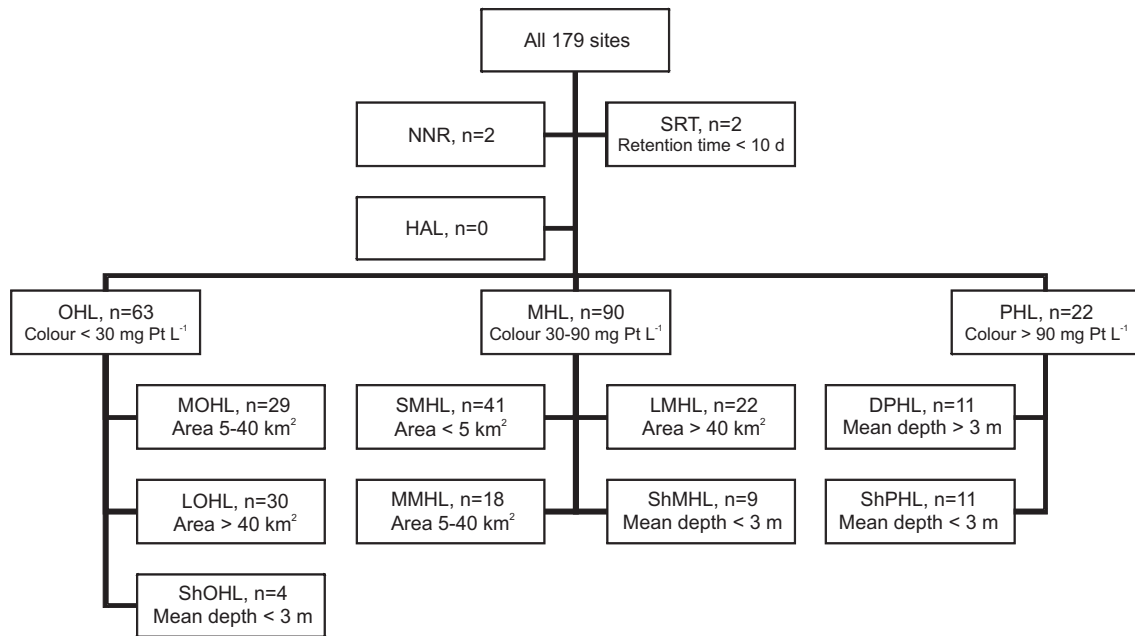


FIGURE 2 The operational Finnish lake typology showing the division criteria and number of study sites assigned to each lake type.

2.2 Sediment trap data (IV)

2.2.1 Collection of sedimenting organic material

Sedimenting organic material (SOM) and profundal macroinvertebrates were collected from 26 basins of 11 lakes in central and eastern Finland (Fig. 1C) in 2005 (13 basins) and 2008 (13 basins). The data set comprises sites with varying human disturbance, and encompasses the faunal and environmental variation among Finnish lakes. SOM was collected using a sediment trap technique (Bloesch & Burns 1980, Blomqvist & Håkanson 1981). The traps were deployed 1.5 m above the lake bottom in the deepest point of each study basin in late August, and removed after 26-30 days. The samples were stored in preweighed plastic vials (50 ml), freeze-dried for 72 h and reweighed to determine the areal rate of dry weight accumulation ($\text{g m}^{-2} \text{day}^{-1}$) of the collected material.

The proportion of organic matter (loss on ignition; % LOI) was determined by weighing a subsample of material before and after combustion at 550 °C for 3 h. The proportions of carbon (C %) and nitrogen (N %) and their stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were determined using a FlashEA 1112 elemental

analyzer coupled to a Thermo Finnigan DELTAplus Advantage isotope ratio mass spectrometer. Total phosphorus content was measured from the preweighed subsamples of sediment trap material using a spectrophotometric determination of PO₄ after hot-acid hydrolysis with K₂S₂O₈ (Grasshoff et al. 1983). The stoichiometric ratios of carbon, nitrogen and phosphorus (C:N:P) were calculated based on their molar units. The sedimentation rates (g m⁻² day⁻¹) of organic matter, C, N and P were calculated from their proportional contributions to the total sedimentation.

2.2.2 Macroinvertebrate data

Quantitative profundal macroinvertebrate samples were taken from the sediment collection sites using standardised methods (SFS 5076) described above. All animals were identified to the lowest possible taxonomic level, counted and wet weights (g) of macroinvertebrate groups (Chironomidae, Oligochaeta, Chaoboridae, Bivalvia, Acari, Crustacea and Ceratopogonidae) were weighed according to Finnish standard (SFS 5076) with an accuracy of 0.1 mg. Supplementary chironomid samples were taken to evaluate the variation of stable isotope signatures and stoichiometric ratios within and among chironomid taxa with contrasting trophic preferences (Saether 1979, Wiederholm 1980). Head capsules of the larvae were mounted on microscope slides for later identification and the abdomens were dried at 62 °C and after homogenisation, the samples were analysed for C:N:P stoichiometry and δ¹³C and δ¹⁵N.

2.3 Macroinvertebrate indices (I-IV)

Community variation and status of profundal macroinvertebrate fauna was evaluated with four univariate indices which have been widely used in profundal studies: Shannon diversity index (I, IV), Oligochaeta/Chironomidae -index (I), Benthic Quality Index (I, II, IV), total biomass (IV). In addition, the utility of multivariate measures of taxonomic completeness (i.e. O/E_{TAXA}) in assessment of profundal fauna were tested (III).

Shannon diversity index (H'; Shannon & Weaver 1949) is a classical ecological metric and is frequently used to measure the diversity of profundal invertebrate assemblages (Bazzanti & Seminara 1985, Johnsson & Wiederholm 1989, Veijola et al. 1996, Dinsmore et al. 1999). It is estimated using the formula

$$H' = -\sum_{i=1}^S \left(\frac{n_i}{n} \right) \left(\log \frac{n_i}{n} \right),$$

where S is the number of taxa, n_i is the number of individuals belonging to the taxon i out of the S species and n is the total number of individuals in a sample.

The ratio of Oligochaeta and Chironomidae (O/C; Wiederholm 1980) was calculated as the percentage of oligochaete individuals in the total of oligochaete and sedentary (non-Tanytopodinae) chironomids. The O/C index is based on the assumption that the abundances of generally more tolerant oligochaete species will increase with nutrient enrichment in relation to more intolerant chironomid fauna and has been widely applied in profundal assessment studies (Särkkä 1982, Zinchenko 1992, Johnson 1996, Johnson 1998).

The chironomid Benthic Quality Index (BQI, Wiederholm 1980) was used to assess the composition and ecological status of the chironomid assemblages (Johnson & Wiederholm 1989, Johnson 1998, Hämäläinen et al. 2003, Meriläinen et al. 2003, Rask et al. 2011, Verbruggen et al. 2011). BQI is based on the relative abundances of seven chironomid species or genera, which are scored by integers from 1 (eutrophic species) to 5 (oligotrophic) according to their perceived preference along a lake trophy gradient. BQI was calculated for each site from the pooled macroinvertebrate samples as the abundance weighted average of taxon scores k_i :

$$\text{BQI} = \sum_{i=0}^7 \frac{n_i \times k_i}{N},$$

where k_i is the score for each indicator taxon i , n_i is the numerical abundance of taxon i and N is the sum of n_i . The included indicator taxa with their corresponding scores are: *Chironomus plumosus* (Cp , $k = 1$), *Chironomus anthracinus* (Ca , 2), *Sergentia coracina* (Sc , 3), *Stictochironomus rosenschoeldi* (Sr , 3), *Micropsectra* spp. (Msp , 4), *Paracladopelma* spp. (Psp , 4) and *Heterotrissocladius subpilosus* (Hs , 5). According to Wiederholm (1980), the absence of indicator species gives a BQI value of zero, which indicates the worst or most stressful conditions. However, these observations were systematically ignored because *i*) they may stem from sampling error, *ii*) the index in these cases is formally undefined and *iii*) inclusion of zero values would make the BQI scale non-continuous.

The secondary production of the profundal fauna was indirectly quantified by the total biomass (TB; Rasmussen & Kalff 1987, Dinsmore et al. 1999), which is simply a sum of wet weights (g) of all taxonomic groups (see above) in an aggregated sample per unit area (m^2).

Taxonomic completeness, or the O/E_{TAXA} , was calculated as the ratio of number of observed taxa (O) predicted to be captured ($P_{\text{TAXON}} \geq \text{threshold probability, } P_t$) to the expected number of these taxa (E) estimated by the evaluated approaches (IV, see below). E will be given by

$$E = \sum P_{\text{TAXON}} | P_{\text{TAXON}} \geq P_t.$$

Taxa with small capture probabilities are commonly excluded from O/E_{TAXA} calculations (e.g. Hawkins et al. 2000, Aroviita 2009) and $P_t = 0.5$ is a commonly

used threshold for stream macroinvertebrates. According to initial trials, O/E_{TAXA} obtained by $P_t = 0.25$ were generally the most accurate and precise for the profundal fauna and thus the results are presented for $P_t = 0+$ and $P_t = 0.25$ (IV).

2.4 Multivariate ordination analyses (I, IV)

Profundal macroinvertebrate community patterns were demonstrated, and their relationships with environmental variation were quantified (I, IV) using two multivariate ordination techniques. Detrended Correspondence Analysis (DCA; I, IV) was used to summarize the principal patterns of community composition. DCA is an ordination technique based on reciprocal averaging and it ordines both the species and samples simultaneously (Hill & Gauch 1980).

DCA suggested a unimodal model for both species data (I, IV) (first axis gradient length > 3.0 standard deviation units; see ter Braak & Prentice 1988) and, therefore, Canonical Correspondence Analysis (CCA) with a randomized Monte Carlo permutation test was used to reveal relationships between the studied environmental variables and the species data. CCA is a direct gradient analysis in which the ordination axes are constrained to be linear combinations of the environmental variables so as to maximize the species–environment relationships (ter Braak 1986). To meet the requirements of normal distributions, environmental variables with skewed distributions were either \log_{10} -, arcsine(SQRT)- or $X^{0.1}$ -transformed.

Partial CCA (pCCA) (Borcard et al. 1992, Økland & Eilertsen 1994) was used to evaluate the relative contribution of environmental variables insensitive to human activities, geographical position and variables sensitive to anthropogenic disturbance (I), and of oxygen, temperature and food (IV). More specifically, the first variable group in study I consisted of a suite of morphological variables, altitude, hypolimnetic water temperature, and colour – a soil-dependent surrogate for humic content (Jones & Arvola 1984, Jones 1992, Kortelainen 1993). Group 2 included the geographical coordinates of the study sites (X, latitude, and Y, longitude) and their quadratic and cubic terms plus their interactions (Borcard et al. 1992). Group 3 included total phosphorus and dissolved oxygen, which are assumed to affect the biota more directly than the variables in groups 1 and 2 but are also strongly influenced by human disturbances (Simola & Arvola 2005) and are therefore usually the main concern in lake monitoring and assessment. In study IV, principal component analysis was applied (see below) to summarise the quality and quantity of food (Group 1). Hypolimnetic dissolved oxygen and temperature based on single end-of-summer measurements represented oxygen (Group 2) and thermal (Group 3) conditions, respectively.

A series of separate CCAs were run in which the variables of each group were included step-wise as explanatory variables to assess the extent of total

variation attributable to these variables. Then the total explained inertia was determined, including all the selected variables of the three variable groups in the analysis. The total variation was partitioned among the three variable groups using one group at a time as constraining variables and the two other groups as covariables, one at a time and simultaneously. From the results of these runs, the fractions of community variance (unexplained, shared with the predictor groups, and unique to each group) were calculated according to Økland & Eilertsen (1994). Variance inflation factors (VIF) were applied to control for the possible multicollinearity of the explanatory variables.

Multiple autocorrelated measures of SOM were summarised using principal component analysis (PCA). Principal component analysis uses an orthogonal transformation to convert a set of observations on correlated variables into a set of values of uncorrelated latent variables i.e. principal components (PC) (McCune & Grace 2002). A broken-stick model (Jackson 1993) was here applied to choose the appropriate number of components. Multivariate analyses were performed using CANOCO software (I) (version 4.0; ter Braak & Smilauer 1998), PC-Ord software (I) (version 4.39; McCune & Mefford 1999) and vegan-package (IV) (Oksanen et al. 2008) designed for the R-program (Anon. 2008).

2.5 Estimation of reference conditions for profundal fauna (II, III)

2.5.1 Development and validation of BQI regression model (II)

A multiple linear least squares regression model was developed to predict the natural Benthic Quality Index values corresponding to undisturbed conditions. Using the calibration data from 73 REF sites (Table 1), forward selection with the stepwise method was applied to select significant ($\alpha = 0.05$) predictors of BQI variation from the candidate environmental variables insensitive to anthropogenic disturbance (Table 2). Variables were transformed (\log_{10} -, SQRT- or arcsine(SQRT)) if necessary to meet statistical assumptions of the analysis.

The performances of the regression model and WFD-compliant typology were evaluated by two validation procedures. First, an internal 'leave-one-out' cross-validation technique (e.g. Stone 1974, Efron & Gong 1983, Fielding & Bell 1997) was applied. For the modelling approach, each site in turn was excluded from the data and the BQI for this site was predicted by the regression model fitted to the remaining $n-1$ sites. For the typology approach, each site in turn was removed from the data and the reference value was estimated for the excluded site using the remaining sites of the corresponding lake type (see Aroviita et al. 2009). The predicted (cross-validated) BQI was compared with the observed BQI and linear regression (R^2) and Root Mean Squared Error of the Prediction (RMSEP) (Wallach & Goffinet 1989) was used to assess the predictive performance of the approaches.

Historical values for BQI calculated from subfossil chironomid head capsules using paleolimnological literature data were used for external validation of the model. Data for 24 sites (Fig. 1B, Table 1) were obtained from 12 Finnish (21 sites), Swedish (two sites) and Russian (one site) case studies (II). For each site the average BQI of the period considered to represent pristine status (number of sediment strata 1-10, from the period of ca. 1800-1900), was used as an estimator of the reference value (E_{BQI}). For these sites with paleolimnological data an environmental data was also compiled for predicting the reference values of BQI by the developed regression model and by typology. The predictive performance of the two approaches was assessed as described above, considering the paleolimnological E as the true site-specific reference value.

The paleolimnological literature data were also applied to validate the compared approaches in the actual assessment of faunal change. The topmost (corresponding to ca. 2 cm of sediment) BQI values from the sediment cores were used as estimates of the present observed BQI (O) to calculate the O/E_{BQI} ratio, using historical BQI as the reference value. From 19 of these sites standardised contemporary macroinvertebrate data were available (II) to obtain the present BQI (O). Site-specific O/E_{BQI} ratios were calculated using E_{BQI} estimated by both the typology approach and the modelling approach. These O/E_{BQI} ratios were compared to those derived from paleolimnological data, which were assumed to show the actual change in BQI, using coefficient of determination (R^2) and RMSEP as measures of success.

2.5.2 Estimation of expected taxa (III)

All available 179 sites (Table 1) were used in this study and from all available 107 REF sites 33 were randomly separated for model validation (hereafter VLD sites) and the rest were used for calibration of the typology and modelling approaches (hereafter CAL sites) (Fig. 1A). To have appropriate data for the taxon-specific modelling approach (see below), the rarest 73 taxa occurring in less than three calibration sites were omitted from the analyses.

Four statistical modelling approaches and *a priori* lake typology were used to estimate the P_{TAXON} in the absence of human disturbance. Typology (Fig. 2) is the simplest approach suggested by the European Union WFD (Anon. 2000), and therefore also the basis of the national lake assessment (Vuori et al. 2006). The following selected statistical models represented a variety of approaches differing in principle. Multivariate regression tree (MRT; De'ath 2002) is a categorical approach and the output is grouping, which is analogous to typology. However, whereas typology classifies the sites *a priori*, based on their environmental variables only, MRT groups the sites based on their biological similarities, so as to enable the groups to be categorically differentiated by environmental variables. The output of MRT is equally user-friendly as is the typology (see Aroviita et al. 2009).

Limiting Environmental Differences (LED) is a recently introduced method where the selection of reference data is based on similarity matrices

(Chessman et al. 2008). The original, and to my knowledge still the only, published LED-model by Chessman et al. (2008) showed a great potential for prediction of species-poor stream fish fauna and it performed considerably better than the RIVPACS modelling (see below). Therefore this method was selected as a candidate for prediction of the also species-poor profundal fauna.

As the other approaches are based on modelling patterns of the whole communities, Non-Parametric Multiplicative Regression (NPMR; McCune 2006) was selected to represent taxon-specific modelling. Taxon-specificity was assumed to be a potential advantage as it allows different environmental predictors for different taxa. Finally, RIVPACS (Moss et al. 1987) is the most widely used, 'standard' approach to model freshwater faunas and provides a good baseline for the alternatives. The probability of taxa capture (P_{TAXON}) was estimated according to Clarke et al. (2003) and Aroviita et al. (2008).

A baseline for model performance in measuring taxonomic completeness was set by developing a null model (Van Sickle et al. 2005) in which all sites are allocated to one group yielding a single E for all sites. Mean O/E_{TAXA} -ratios derived by different approaches were calculated for CAL, VLD and IMP -sites and standard deviations (SD) of O/E_{TAXA} for CAL and VLD sites. For a successful model, mean O/E_{TAXA} in reference sites should be close to unity (high accuracy relative to the theoretical reference $O/E_{\text{TAXA}} = 1.0$) and standard deviation low (high precision). The sensitivity of the approaches to detect anthropogenic impairment of the fauna was assessed by the proportion of IMP sites with an O/E_{TAXA} -value deviating from natural variation (% IMP sites with an O/E_{TAXA} ratio smaller than the 10th percentile of VLD-site O/E_{TAXA} distribution; e.g. Ostermiller & Hawkins 2004, Van Sickle et al. 2005, Aroviita et al. 2010).

3 RESULTS AND DISCUSSION

3.1 Natural variation of profundal macroinvertebrate communities (I)

After exclusion of taxa occurring only at one site ($n = 30$), 46 taxa remained in the data set. DCA suggested a considerably large community variation among the 55 REF sites as the gradient lengths for the first three axes were 3.633, 2.052, and 1.862 SD units. Such long gradients also suggest unimodal species responses along the first two axes. The first DCA axis represented the depth gradient as the site-specific first DCA axis scores were very strongly correlated with mean (Fig. 3A) and sampling (Fig. 3B) depth of a site.

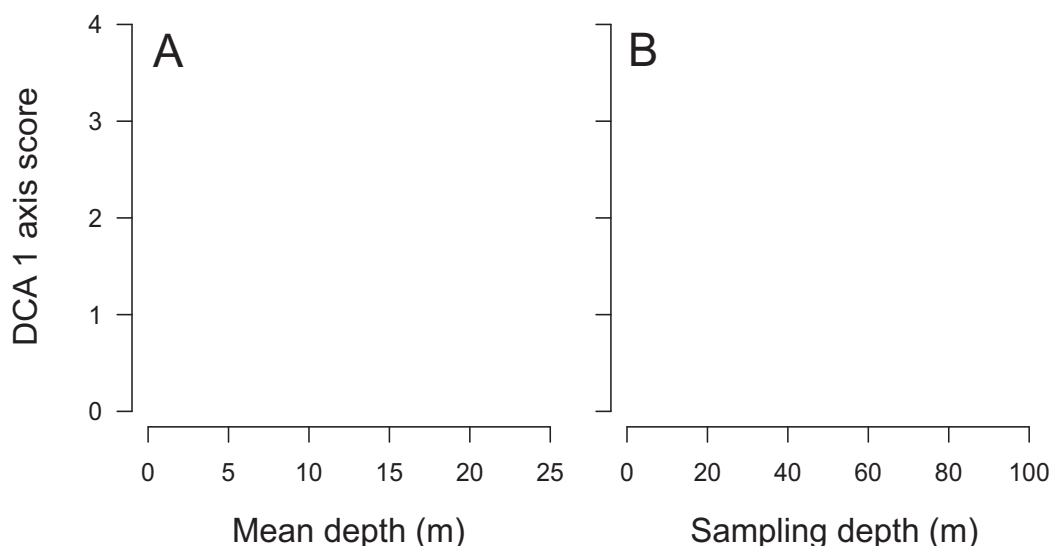


FIGURE 3 The relationships of primary community variation (DCA 1 axis scores [SD units]) to mean depth (A) and depth of a sampling site (B) among the 55 REF sites.

The predictor groups 1, 2 and 3 together explained 29.4 % of the total inertia of partial CCA. Group 1 (mean depth, water colour and hypolimnetic temperature)

contributed 66.8 % of the total explained variance, of which 38.5 % was unique for this group. When these variables were each used in turn as the only constraining variable, 45.9 % of community variation was explained by mean depth, 25.7 % by water colour and 23.6 % by temperature. The contribution of the spatial variation was marginal (5.47 %), and the unique contribution of DO and TP was 20.9 %. The considerable (28.3 %) proportion of community variation shared by groups 1 and 3 indicated a strong redundancy between these groups.

All three community indices showed considerable variation among 55 REF sites. Variation of these indices was primarily attributed to lake mean and relative depth (Fig. 4) and water colour, which in various combinations accounted for 54.8 %, 38.4 % and 63.7 % of variation of the O/C index, Shannon H' and BQI, respectively.

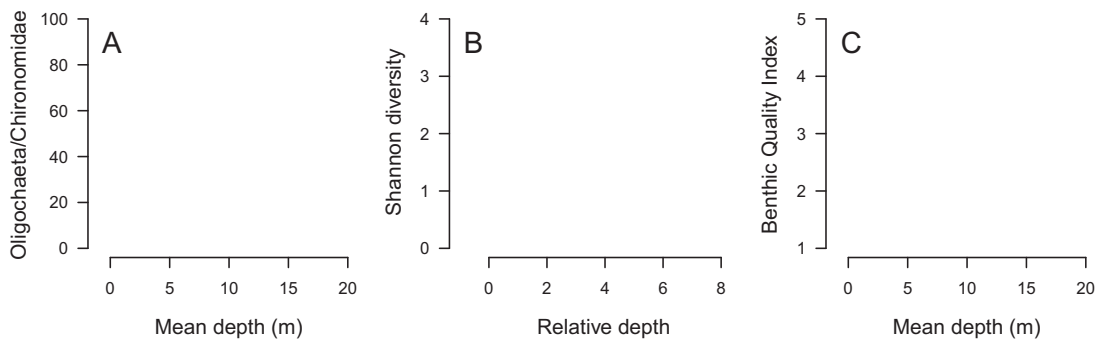


FIGURE 4 The relationships of Oligochaeta/Chironomidae index (A), Shannon diversity (B) and Benthic Quality Index (C) to lake morphometry (i.e. mean and relative depth).

The major contribution of lake morphometry in structuring the lake profundal fauna is not a particularly novel finding, as numerous studies based on both paleolimnological and contemporary data have observed a widespread and strong relationship between lake depth and community variation within (Hynynen et al. 1999, Heiri 2004, Eggermont et al. 2008, Kurek & Cwynar 2009, Engels & Cwynar 2011) and among lakes (Brundin 1949, Wiederholm 1980, Johnson & Wiederholm 1989, Korhola et al. 2000). It is generally well known that lake morphometry, and lake mean depth in particular, is a common denominator for numerous limnological characters (Wetzel 2001) and is also the main natural determinant of lake trophic status (Moss 1980, Jeppesen et al. 1997, Cardoso et al. 2007). This relationship was documented as early as the 1950s by Rawson (1955), who noted that lentic secondary production (plankton, benthic invertebrates, and fish) was strongly related to lake mean depth.

Lakes with naturally high dissolved organic carbon concentration seemed to have a characteristic profundal fauna. Highly coloured humic lakes are typical of the boreal coniferous region with a high percentage of peatland coverage (Kortelainen 1999). Due to dark colour and usually small size, humic lakes are prone to strong thermal stratification (Jones 1992) and consequential chronic oxygen depletion (Fulthorpe & Paloheimo 1985). Thus, the profundal

fauna in humic lakes is rather distinctive and normally restricted to a few taxa (e.g., *Chaoborus flavicans* and *Chironomus* spp. larvae) adapted to oxygen-poor conditions (Jäger & Walz 2002, Brodersen et al. 2004). The operative Finnish lake typology is largely based on lake surface area and water colour, the latter as a surrogate for catchment soil geology (Vuori et al. 2006). Despite the dependence of water colour on anthropogenic activity, it tends naturally to vary strongly among boreal lakes. Thus, considering the major influence of colour on profundal assemblages, it is apparently an important factor that should be taken into account when predicting benthic fauna in undisturbed lakes. To identify reference communities and make valid assessments for impacted lakes, the original water colour should be known from historical measurements or be estimated by palaeolimnological techniques (Miettinen et al. 2005) or hydrogeomorphological modelling.

This study was first to assess profundal macroinvertebrate community variation among minimally disturbed boreal lakes with extensive ranges of environmental gradients (size, depth, humidity). The results showed that the occurrence of profundal fauna generally considered indicative of disturbed status is actually natural in shallow lakes. Therefore, the comparison of profundal fauna among lakes with differing morphometries is unjustified without controlling for lake depth, for example by statistical modelling.

3.2 Development and validation of BQI regression model (II)

Mean depth contributed most strongly to the variation of BQI among the 73 sites, and explained 61.2 % of the variation in BQI. The ratio of mean to maximum depth (i.e. depth ratio) nearly significantly explained part of the residual variation, being only weakly correlated with mean depth ($r = -0.28$, VIF = 1.1). Compared to the single variable (mean depth) model, inclusion of depth ratio for a secondary predictor variable provided more accurate estimation of site-specific reference BQI for multiple sub-basins within a single lake. The final two-order model explained 63.2 % of BQI variation in the calibration data and was formulated as follows:

$$\text{Reference BQI} = 0.572 + 0.994 \times \sqrt{\text{Mean depth (m)}} - 1.212 \times \text{Depth ratio}$$

The variation of BQI within each lake type was large (SD range = 0.40–0.99, mean SD = 0.71) and thus the estimated reference values were imprecise (internal cross-validation, $R^2 = 0.28$, RMSEP = 0.86). The regression modelling performed much better, as the estimated BQI correlated more strongly ($R^2 = 0.58$) with and were closer (RMSEP = 0.65) to the observed BQI. The regression model also produced considerably more accurate estimates of the historical reference BQI ($R^2 = 0.71$, RMSEP = 0.55) compared to the estimates obtained by typology ($R^2 = 0.10$, RMSEP = 0.97). Similarly, the O/E_{BQI} ratios based on

modelled reference values corresponded to the actual O/E_{BQI} ratios from the paleolimnological data much more closely ($R^2 = 0.79$, $RMSEP = 0.09$) than did the O/E_{BQI} ratios derived by the typology approach ($R^2 = 0.62$, $RMSEP = 0.23$).

The correlation between lake depth and BQI was first observed by the index developer himself (Wiederholm 1980), who represented a strong curvilinear relationship of BQI with lake nutrient status (chlorophyll *a*) divided by the mean depth. This relationship actually does not resolve the unique effects of depth and productivity (if any). Wiederholm (1980) admitted the crudity of this procedure and the need for alternative approaches to control for the effect of depth. However, this has been largely neglected by later studies and BQI has been widely applied in profundal bioassessment with some possible misleading interpretations.

The BQI is based on seven key chironomid taxa with highly differing preferences for temperature, oxygen and nutrient status (Brodersen & Anderson 2002, Brodersen & Quinlan 2006). Hence, BQI taxa exhibit strict ecological niches and this is manifested by their systematic positioning along primary community and environmental gradients of multivariate ordination planes in a variety of profundal studies (Fig. 5A, see also Johnson et al. 1990, Kansanen et al. 1990, Mousavi 2002). Consequently, BQI seems to integrate effectively the variation of the whole profundal macroinvertebrate community both in space (Fig. 5B, Kansanen et al. 1990) and time (Hynynen et al. 2004). BQI can thus be considered a representative metric for assessment of the status of the profundal macroinvertebrate community. Indeed, it has been provisionally used as a key macroinvertebrate metric in Finnish and Swedish lake bioassessment mandated by the WFD (Anon. 2000), as it corresponds to the 'taxonomic composition and abundance' and 'ratio of disturbance-sensitive taxa to insensitive taxa' included in the WFD's normative definitions of ecological status classification. The apparent response of BQI to human disturbance has been convincingly documented by paleolimnological case studies that reported consistent changes in BQI values with lake degradation by municipal and industrial wastewaters, and with recent recovery (e.g. Meriläinen et al. 2003, Hynynen et al. 2004).

The paleolimnological validation data showed that the model based on contemporary reference data provided accurate estimation of the historical BQI. Thus, the model reliably estimates the "true" reference values and, moreover, the results suggest that criteria and practices for selecting the reference lakes, at least for profundal fauna, has been successful. The paleolimnological literature data provided an exceptional opportunity to validate and compare the performance of lake typology and modelling in estimation reference values for an assessment metric, and even more importantly, to authenticate the performance of the approaches based on contemporary data and modelled reference values in estimation of actual site-specific change in metric values.

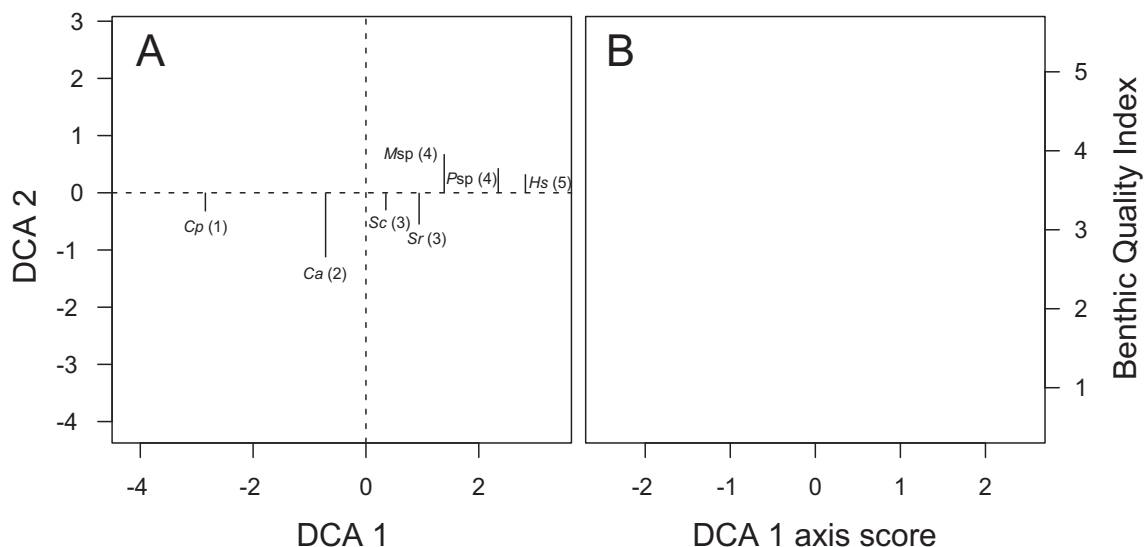


FIGURE 5 A) Two-dimensional DCA ordination based on the 73 REF sites (II). Abbreviations of only the chironomid taxa included in the Benthic Quality Index are displayed (together with their BQI scores) and their positioning along with the first DCA -dimension (DCA 1 axis [SD units]) is illustrated with solid vertical lines. B) The relationship between DCA 1 axis scores (i.e. community variation) and Benthic Quality Index.

3.3 Estimation of expected taxa (III)

All five evaluated approaches yielded reasonably accurate predictions of expected taxa (E) (Fig. 6). Mean O/E_{TAXA} among the 33 validation sites varied between 0.964 (MRT) and 1.029 (RIVPACS) when all 39 taxa were included ($P_t = 0+$) and between 0.966 (NPMR) and 1.053 (RIVPACS) after omission of the rare taxa ($P_t = 0.25$). When all taxa were included, MRT was most precise (SD of O/E_{TAXA} 0.298). Other models were markedly less precise, lake typology being even inferior to the null model. Exclusion of rare taxa ($P_t = 0.25$) improved the precision of all approaches and then NPMR was the most precise method (SD = 0.279) (Fig. 6). Typology was outperformed by the models, which produced an average 13.5 % (range 11.56 - 18.77 %) improvement of precision over the null model.

The average taxonomic completeness among the 72 IMP sites was lowest for typology (Mean $O/E_{TAXA} = 0.734$ for $P_t = 0.25$) and LED (0.759). MRT, NPMR and RIVPACS suggested much better status of macroinvertebrate fauna among the IMP sites (Mean O/E_{TAXA} range 0.817 - 0.842 for $P_t = 0.25$). The omission of rare taxa increased the sensitivity of all predictive approaches and all four models provided a relatively consistent suggestion of the faunal impairment in IMP sites (35-46 %), whereas typology was again more sensitive implying that 56 % of IMP sites were taxonomically incomplete (Fig. 6).

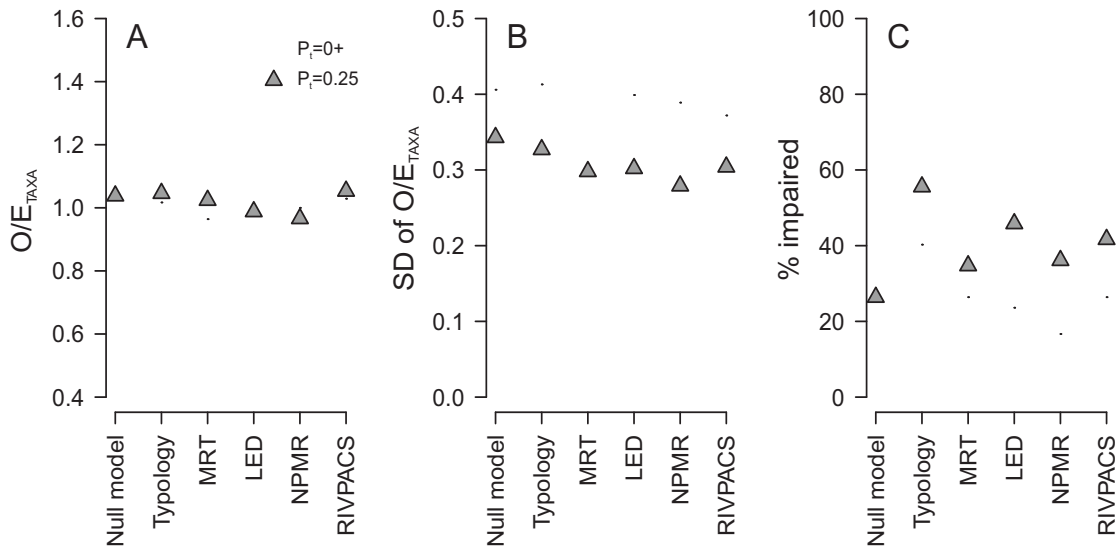


FIGURE 6 Approach-specific means (A) and standard deviations (B) of O/E_{TAXA} among 33 validation sites and percentage of 72 IMP sites interpreted as biologically impaired (C).

The discrepancy in sensitivity between lake typology and predictive models was mainly confined to one abundant lake type (large, humic lakes). More detailed analyses revealed a strong correlation between depth of the sampling site and O/E_{TAXA} ratios for the IMP sites of this type; shallower basins had consistently lower taxonomic completeness but only when assessed by TYPO.

O/E_{TAXA} based on MRT and TYPO showed moderately poor correlation with the other approaches, whereas the outputs of LED, NPMR and RIVPACS were strongly correlated. The pair-wise comparisons revealed considerable discrepancy between the approaches in assigning sites as impaired. Typology indicated an impaired status of macroinvertebrate fauna at many sites (13 - 20 %) assessed to be in reference condition by the models. RIVPACS and NPMR provided most concordant assessment and uniquely classified only 8 and 5 % of sites as biologically impaired, respectively.

A plausible explanation for the observed less precise predictability of profundal fauna compared to stream or lake littoral macroinvertebrates (Ostermiller & Hawkins 2004, Van Sickle et al. 2005, Neale & Rippey 2007, Aroviita et al. 2009) is the typically small number of species persisting in the harsh environment in the profundal zone: poor nutritional conditions, cold water and possible oxygen deficiency (e.g. Jónasson 1996, 2003). The low number of species evidently leads to an even lower number of expected taxa and, in consequence, to unstable O/E_{TAXA} ratios; a single missing or extra taxon then contributes significantly to the O/E_{TAXA} (Marchant 2002). However, accurate and precise predictive models have been developed for equally species-poor fish assemblages (Oberdorff et al. 2001, Joy & Death 2002, Kennard et al. 2006, Chessman et al. 2008, Meador & Carlisle 2009). In contrast to fish communities, profundal communities are typically composed of only a few core taxa and numerous 'satellite' taxa (Hämäläinen et al. 2003) apparently visiting

from littoral and sublittoral areas and their occurrence may thus not be predictable from environmental attributes driving the actual profundal fauna.

The better sensitivity of lake typology seemed to be a bias and more specifically a result of a strong association between sampling depth and O/E_{TAXA} ratios derived by the typology approach. This result is consistent with the conclusion of study I, that taking lake morphometry into account merely by a categorical division into shallow and deeper lakes is insufficient and may lead to erroneous inferences of integrity of the profundal fauna.

Even though the predictive models tested here provided improved estimation of the native fauna compared to lake typology, the utilisation of taxonomic completeness in assessment of species-poor profundal assemblages is questionable. To reduce the major impact of having a missing or extra taxon on the variation of the presence/absence-based O/E_{TAXA} , the predictive approaches tested here could be similarly used to estimate the relative abundances of the native taxa, which could be furthermore summarised into a one-dimensional index of community similarity, such as Percent Model Affinity (Novak & Bode 1992).

3.4 Role of food in structuring profundal communities (IV)

Principal component analysis of sedimenting organic matter variables generated three latent principal components, which were used as proxies of food quality and quantity (hereafter food). The three evaluated community predictor 'groups' (food, temperature and oxygen) jointly explained 23.1 % of the total macroinvertebrate community variation (inertia) in CCA. Food contributed 45 % to the total explained community variance, whereas the temperature (23 %) and oxygen (13 %) seemed to be of minor importance in controlling community composition.

According to partial regression analysis (Legendre & Legendre 1998), food explained 28.4 % of the variation of total biomass. Dissolved oxygen was the best predictor of Shannon H' explaining 34.7 % of the variation and only minor part of variation (10.5 %) was attributed to food. The regression model developed for Benthic Quality Index included all three predictor variables which together accounted for 84.4 % of the index variation. Perhaps surprisingly, temperature contributed by far the most strongly to the variation of BQI, alone explaining 32.6 % of the total explained variance.

Profundal fauna in meso/eutrophic basins (Total phosphorus > 10 $\mu\text{g l}^{-1}$) and oligotrophic basins (< 10) showed markedly different response to the variation of food quantity. In oligotrophic lakes, the community composition was closely related to the organic content of sedimenting material and the inputs of OM, C and N, whereas macroinvertebrate assemblages of more nutrient rich sites showed no correlations with SOM. Community variation did not correlate with stoichiometric ratios of food. In contrast, community

variation showed strong correlation with the origin of food resources (inferred from $\delta^{13}\text{C}$), regardless of the nutrient status of a basin.

Chironomid indicator taxa with varying trophic preferences differed markedly in their body stoichiometry. A consistent pattern was observed between chironomid body stoichiometry and their indicator value (BQI score; see above); the taxa preferring oligotrophic conditions had higher C:N ratios and lower C:P and N:P ratios. The degree of deviation of chironomid larval body $\delta^{13}\text{C}$ signatures from those measured from SOM was also closely associated with their trophic preference; eutrophic taxa deviated more from SOM $\delta^{13}\text{C}$ whereas oligotrophic chironomids seemed to be more directly relying on sedimenting organic matter as a food source (Fig. 7).

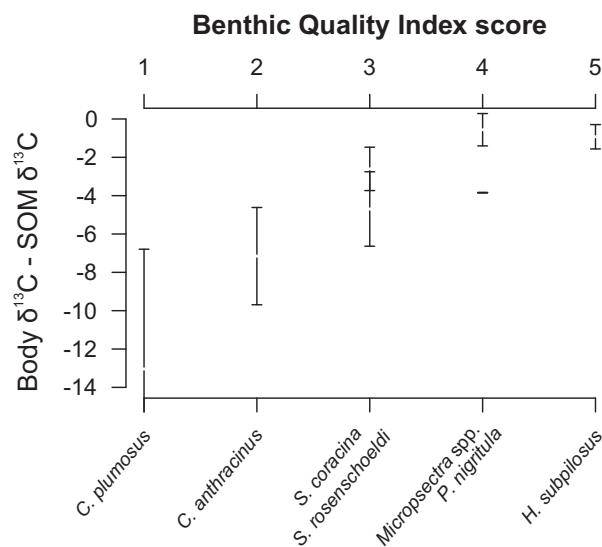


FIGURE 7 Relationship between the deviations (mean \pm SD) of larval body and SOM carbon isotope signatures ($\delta^{13}\text{C}$) and Benthic Quality Index scores of seven chironomid taxa with differing trophic preferences.

The direct qualitative and quantitative measurements of SOM enabled me to provide the first comprehensive evaluation of the relative importance of food, oxygen and temperature in controlling different aspects (composition, diversity, productivity, ecological status) of profundal communities. The results agreed with the general consensus that profundal macroinvertebrate communities are fuelled by sedimenting organic material (Graf 1989, Johnson & Wiederholm 1992, Goedkoop & Johnson 1996) and, furthermore, stressed that profundal assemblages are indeed controlled by food, oxygen and temperature in concert rather than any of these factors alone or even predominantly (Brodersen & Andersen 2002, Brodersen & Quinlan 2006).

The chironomid larval analyses suggested appealing relationships between chironomid stoichiometry and their ecological niches. Stoichiometric ratios differed markedly among the studied chironomid indicator taxa. The observed correlations between taxa-specific elemental ratios (C:N:P) and the BQI score (i.e. tolerance to environmental stress) were partly counterintuitive compared to the general theorem about consumer-resource coupling (Tilman

1980). The peculiar stoichiometric variation of chironomids suggest that chironomids with differing ecological niches varyingly assimilate the central macroelements, either due to differences in feeding habits (Johnson 1987, Goedkoop et al. 1998), selective feeding (Johnson et al. 1989) or stoichiometric requirements of available food.

Carbon stable isotopic signatures of chironomid larvae suggested among taxa differences in utilisation of SOM. The taxa preferring eutrophic conditions (*Chironomus anthracinus* and *C. plumosus*) presumably utilized methane-oxidising bacteria (Jones et al. 2009, Jones and Grey 2011), whereas the taxa inhabiting deep and oligotrophic lake basins (*Heterotrissocladius subpilosus* and *Micropsectra* spp.) were likely more directly dependent on freshly deposited organic material as their energy source.

The somewhat unexpected strong association between profundal assemblage turnover and carbon stable isotope signal ($\delta^{13}\text{C}$) of SOM suggested that the origin of carbon is of major importance in determining the species composition of profundal assemblages. The carbon isotopic signatures (see France 1995) as well as low carbon:nitrogen ratios (C:N; Håkanson & Jansson 1983, Meyers & Teranes 2001) suggested that SOM is primarily of autochthonous origin. The variation of carbon isotope signatures of SOM suggests differences in epilimnetic algal composition, which might in turn control the profundal invertebrate communities by the consequential alteration of e.g. fatty acid composition of SOM (Veefkind 2003). This could be a novel and important link between profundal macroinvertebrate assemblages and lake nutrient status and future studies are needed for validation of these relationships.

3.5 A note on depth preferences of profundal macroinvertebrates

A strong relationship between lake depth and profundal macroinvertebrate community structure is primarily an end-product of varying depth preferences of dominating profundal chironomid and oligochaete taxa (Fig. 8). These fairly strongly confined depth optima with small tolerances (abundance-weighted SD) are admittedly due to among taxa differences in preference of oxygen and thermal conditions, but as the study IV suggests, are also a consequence of divergences in utilisation and assimilation of organic matter deposited on the lake bottom.

Nonetheless, the correlation between depth preferences and 'trophic' indicator scores of profundal taxa has marked implications for interpretation of the occurrence of these indicator species and, thus, for community level bioassessment of boreal lakes. For instance, *C. plumosus* inhabits only the shallowest basins, *H. subpilosus* can be found exclusively in the deepest boreal lake basins and the coexistence of these two taxa is hardly ever possible. Moreover, community turnover from the fauna dominated by *H. subpilosus* to *C. plumosus*-communities requires an extensive nutrient loading and massive

deterioration of lake status (Meriläinen & Hamina 1993, Meriläinen et al. 2001, Hynynen et al. 2004).

Therefore, it is recommended that future studies based on either contemporary data or palaeolimnological records should take the role of lake depth in the occurrence of profundal macroinvertebrate taxa carefully into account. Indeed, the community metric candidates developed for the assessment of profundal fauna must recognise the depth dependence of profundal key taxa, and preferably disentangle the effect of lake depth by means of species or community level predictive modelling.

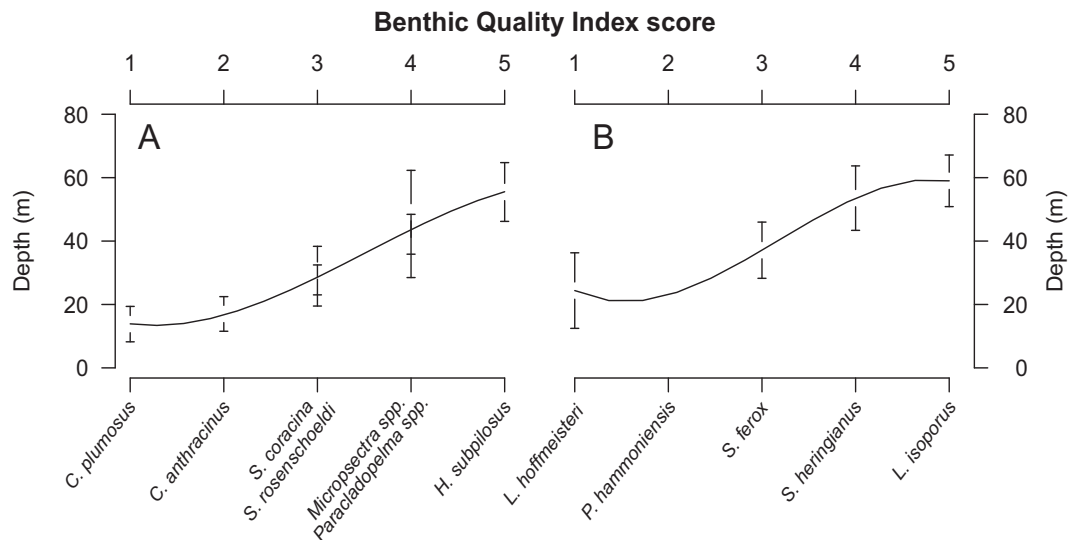


FIGURE 8 Weighted averaged (ter Braak & Prentice 1988) depth optima and tolerances of the seven chironomid (A) and four oligochaete (B) Benthic Quality Index indicator taxa. Optima calculations are based on 107 REF sites. Solid curves denote the third order polynomial regression lines. The original oligochaete BQI (Wiederholm 1980) is modified according to Kansanen et al. (1986) by adding *Lamprodrilus isoporus* as an indicator of highly oligotrophic conditions (cf. *Heterotrissocladius subpilosus*). Note also that the data for *Potamothenix hammoniensis* were not available due to taxonomic inconsistency of the data.

4 CONCLUSIONS

The results of this thesis indicated a major contribution of lake morphometry to structuring profundal macroinvertebrate assemblages among minimally disturbed boreal lakes. Parallel to community variation, the values of widely applied community indices were strongly related to lake morphometry; the fauna in shallow lakes indicated highly eutrophic conditions and poor ecological status. This result has considerable implications for modern bioassessment, in which the biological status of evaluated site is compared to the expected natural conditions. Due to strong dependence of profundal fauna on lake morphometry, the profundal fauna is not directly comparable among lakes with differing morphometries. This might result in erroneous interpretations of ecological status with significant economic or ecological implications, depending on the direction of bias.

Although the effect of lake depth on the prevailing conditions is most palpable at the bottom of lakes, depth has also been frequently reported to be a major regulatory factor for other biota, including zooplankton (O'Brian et al. 2004, Amsinck et al. 2006), and fish (Jackson and Harvey 1992, Olden 2003, Mehner et al. 2007). Considering this and the predominant role of lake morphometry in determining the general trophic status of lake (Moss 1980, Cardoso et al. 2007), it is possible, and is even supported by empirical data (Researcher J. Alahuhta, Finnish Environment Institute, unpublished data), that similarly strong relationships between lake morphometry and other groups of aquatic organisms might exist.

This study demonstrated that predictive modelling is an efficient approach to disentangle the effect of lake depth and other important environmental factors on profundal macroinvertebrate community variation. In comparison to categorical *a priori* typology, modelling provided more precise estimates of reference conditions, particularly for a univariate metric, the chironomid BQI, and, in consequence, more trustworthy judgment of the biological impairment. Further development of predictive modelling for lake bioassessment purposes not only for profundal macroinvertebrates, but also for other biological groups, is thus strongly recommended.

The general assumption that profundal communities are simultaneously driven by multiple environmental factors (oxygen, temperature and food) seems to be valid and these complex inter-relations should be considered in assessment and, in particular, protection and management of the profundal invertebrate communities as an integral constituent of functional lake ecosystems. This study provided the first comprehensive quantitative and qualitative evaluation of the role of actual food resources in among lake variation of profundal macroinvertebrate communities and concludes that food is of major importance, particularly in nutrient-poor lakes. The fact that the origin of food correlated most strongly with the community variation, implies that some additional, but yet poorly understood depth-dictated mechanisms might be driving the occurrence of profundal macroinvertebrate fauna, and hence the whole community structure.

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Analogous to the dependence of the lake status to the integrity of the surrounding catchment area, our acts and achievements are largely dependent on people beside us. I have been privileged to be supervised by Heikki Hämäläinen and Roger Jones. Heikki's expertise in aquatic invertebrates and statistics provided me with the best available know-how to do this study. His extensive knowledge of aquatic ecology and his profound and often critical thinking yielded to not only interesting discussions but led to a scientific path to follow. I also deeply thank my second supervisor, Roger Jones, for the encouraging support and supervision and all the opportunities he has provided.

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- and me emphasizing the importance of genitals in identification of Oligochaeta worms. My dear parents Arja and Simo as well my parents-in-law Maija and Leo have provided safe home, encouraging, family company and delicious food always when needed.

I owe my greatest thanks to my wife Leila, whose endless love, understanding, and support encouraged me to finish this work. Finally, I want to dedicate this book to my three month old son Leevi. His innocent smile and laughter reminds me of the relevance of my work: the world is an incredible place and even the smallest attempt to protect and conserve it for the future generations should be considered valuable.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Järvisyvänteiden pohjaeläinyhteisöjä säätelevät ympäristötekijät ja niiden merkitys järvien biologisen tilan arvioinnissa

Vaativiin olosuhteisiin nähden runsaslukuinen ja monimuotoinen järvien syvännepohjaeläimistö reagoi voimakkaasti ravinnekuormituksen aiheuttamaan levätuotannon lisääntymiseen ja siitä seuraavaan pohjan happitilanteen heikentymiseen. Tämän vuoksi syvänteiden pohjaeläimiä on pitkään hyödynnetty järvien tilan seurannassa.

Euroopan Unionin vuonna 2000 asettaman vesipolitiikan puitedirektiivin (VPD) keskeisin tavoite on yhtenäistää eurooppalaista vesiensuojelua ja mahdollistaa vesistöjen hyvän ekologisen tilan saavuttaminen vuoteen 2015 mennessä sekä sen säilyttäminen tulevaisuudessa. Uusi lainsäädäntö muuttaa perinteistä veden käyttökelpoisuuteen perustuvaa tila-arviota asettamalla tavoitteet ensisijaisesti vesistön eliöyhteisöjen tilan perusteella. Muiden vesieliöiden ohella pohjaeläimillä on keskeinen rooli tilan määrittelyssä ja seurannassa.

Järvien ekologinen tila luokitellaan sen mukaan, kuinka paljon eliöyhteisöt poikkeavat luonnontilaisten järvien yhteisöistä. Yksittäisten järvien luonnontila ei kuitenkaan yleensä ole tiedossa puuttuvan historiallisen aineiston vuoksi. Siksi järvien luonnontilan arvioimiseen käytetään ensisijaisesti VPD:n ehdottamaa tyypittelyä, jossa vesimuodostumat ryhmitellään mahdollisimman samankaltaisiin tyyppisiin niiden luonnollisiin ominaisuuksiin perustuen ja kullekin tyyppille määritellään tyyppikohtaiset vertailuolot. Vaihtoehtoisesti vertailuolosten määrittämiseen voidaan käyttää tilastolliseen mallinnukseen perustuvia menetelmiä. Kategoriseen tyypittelyyn verrattuna ennustava mallinnus huomioi paremmin biologisen vaihtelun jatkuvuuden, tuottaen näin paikkakohtaisia ja ainakin teoriassa luotettavampia arvioita vertailuoloista. Vertailuolosten luotettavuus on edellytys sille että ekologinen luokka voidaan määrittää oikein. Virheellisillä tila-arvioinneilla voi olla huomattavia taloudellisia ja yhteiskunnallisia vaikutuksia, sillä vesistöön ja sitä ympäröivään valuma-alueeseen kohdistettavien hoitotoimenpiteiden tarve ja laajuus perustuvat arvioon vesistön ekologisesta tilasta. Siksi ekologisen tilan arvioinnissa käytettyjen eliöryhmien luonnollisen yhteisövaihtelun sekä sitä säätelevien ympäristötekijöiden perusteellinen tuntemus on avainasemassa arvioitaessa yhteisöjen tilan heikentymistä ihmisen toiminnan vuoksi.

Tässä väitöskirjassa tarkastelin järvisyvänteiden pohjaeläinyhteisörakenteen vaihtelua suhteessa eri ympäristötekijöihin pääasiassa laajaan, 179 järvisyvännettä käsittävään aineistoon perustuen. Osoitin, että luonnollinen yhteisövaihtelu on huomattavan suurta järvien välillä ja voimakkaasti yhteydessä ennen kaikkea järven syvyyteen. Myös yleisesti vesistöseurannoissa käytettyjen yhteisömuuttujien vaihtelu selittyi ensisijaisesti järvioltaan syvyyttä tai muotoa kuvaavilla ympäristömuuttujilla. Arviot syvännetyhteisöjen tilasta

voivat siten olla virheellisiä ilman syvyyden erityistä huomioimista esimerkiksi mallinnuksen keinoin.

Testasin työssäni kahden yhteisön tilaa kuvaavan muuttujan luonnontilaa vastaavien arvojen ennustamista tilastollisten mallinnusmenetelmien avulla. Syvänneseurannoissa yleisesti käytetyn, surviaissääskitoukkien runsaussuhteisiin perustuvan pohjalaatuindeksin (Benthic Quality Index; BQI) luonnontilaiset arvot kykenin ennustamaan lineaarisella monimuuttujaregressiomallilla, jossa pääasiallisena selittäjänä oli järvioltaan keskisyvyys. Esiteollista aikaa edustavan paleolimnologisen validointiaineiston avulla osoitin, että mallin tuottamat ennusteet BQ-indeksin luonnontilaa vastaavista arvoista (ns. vertailuarvot) ovat luotettavia ja että 1900-luvun aikana tapahtunut yhteisöjen tilan heikkeneminen kyetään luotettavasti arvioimaan mallinnettuihin vertailuarvoihin ja nykyhetkellä kerättyihin pohjaeläinaineistoihin perustuen.

Jokien pohjaeläimistön tila-arviointi perustuu usein arvioon alkuperäisen lajiston säilyneisyydestä. Vaikka tämä tilamittari on helposti yleistettävissä ja mielekkäästi tulkittavissa myös muissa elinympäristöissä ja eliöryhmissä, on sitä sovellettu järvissä vähän eikä lainkaan järvisyvänteiden pohjaeläimistön tilan arvioinnissa. Testasin voimassa olevan järvityypittelyn ohella neljää erityyppistä mallinnusmenetelmää alkuperäisen järvisyvänelajiston ennustamiseen ympäristötekijöiden perusteella. Mallit tuottivat järvityypittelyyn verrattuna hieman luotettavampia arvioita alkuperäisestä lajikoostumuksesta, mutta epätarkempia ennusteita vastaaviin jokieliöstölle kehitettyihin malleihin verrattuna. Järvisyväneyhteisöille tyypillinen vähäinen lajilukumäärä lienee keskeisin syy epätarkkuudelle ja siten esteenä tilamittarin soveltamiselle järvisyvänteiden ekologisen tilan arvioinnissa.

Järven syvyyden merkitys syväneyhteisöjen rakenteen säätelyssä liittyy syvyyden myötä tapahtuviin muutoksiin pohjan lämpötila-, happi- ja ravintoolosuhteissa. Näiden tekijöiden, erityisesti ravinnon määrän ja laadun rooli yhteisösäätelyssä on huonosti tunnettu. Tutkin ravinnon osuutta yhteisöjen säätelyssä suhteessa pohjan lämpötilaan ja happioloihin tekemällä suorita havaintoja sedimentoituvan orgaanisen aineksen määrästä ja laadusta (hiili-typpi-fosfori-stoikiometria) sekä arvioita aineksen alkuperästä (hiilen vakaat isotoopit). Osittaisordinaatio- ja -regressioanalyysillä osoitin ravinnon olevan keskeisin tekijä yhteisökoostumuksen ja biomassan säätelyssä, mutta lajiston monimuotoisuuden ja BQI:n vaihtelu liittyi voimakkaammin pohjan happipitoisuuteen ja lämpötilaan. Tulokseni kuitenkin tukivat yleistä oletusta, että syvänteiden pohjaeläinyhteisöjen rakenne ja toiminta ovat useiden ympäristötekijöiden yhtäaikaisesti säätelimiä. Syväneyhteisöjen koostumuksen ja sedimentoituvan aineksen alkuperää ilmentävän hiilen isotooppiarvon ($\delta^{13}\text{C}$) välillä oli voimakas yhteys, mikä viittaa kasviplanktoniyhteisökoostumuksen keskeiseen merkitykseen pohjaeläimistön yhteisörakenteen säätelyssä. Työ antaa aihetta jatkotutkimuksille, joiden kautta voidaan perusteellisemmin ymmärtää järvisyväneyhteisöjen rakenteen yhteys järven tuottavuuteen.

Väitöskirjani tulokset järvioltaan morfometrian keskeisestä merkityksestä syvänteiden pohjaeläinyhteisöjen rakenteen ja ekologisen tilan säätelyssä tulisi huomioida myös muiden eliöyhteisöjen tilan seurannassa. Järven syvyys on eräs keskeisimpiä järven toimintaa ja tuottavuutta sääteleviä ympäristötekijöitä, ja syvyyden vaikutus tulisi huomioida nykyistä paremmin niin veden kemiallisen kuin biologisenkin laadun seurannassa. Pääasiallisesti järvioltaan morfometriaan perustuva tilastollinen mallinnus osoittautui pohjaeläimistön osalta toimivaksi ratkaisuksi järven biologista luonnontilaa arvioitaessa, ja vastaavanlainen lähestymistapa voisi tuottaa nykyistä luotettavampia arvioita järvien ekologisesta tilasta myös muiden vesilainsäädännön edellyttämien biologisten elementtien osalta.

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