Macroinvertebrate communities in Danish lakes
Classification and trophic reconstruction

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Ph.D. -thesis
1998

Freshwater Biological Laboratory, University of Copenhagen

Foreword

This thesis is the result of my Ph.D. study at the Freshwater Biological Laboratory, University of Copenhagen, in the period May 1995 to June 1998. The project was funded by a Ph.D. grant from the Faculty of Natural Science.

I wish to thank everyone at The Freshwater Biological Laboratory for the ever good atmosphere. Special thanks are due to my supervisor, Claus Lindegaard, not just for always being prepared for scientific discussions and inspiration, but also for his excellent company and friendship during our many sampling trips, conferences and travels. I hope our close collaboration will continue for many years. Also many thanks to Peter Dall, Dean Jacobsen, Ole Pedersen, Angelo Vermeulen and Mel Whiteside for their prompt help, technical and personal advice, and their bad humour when it was needed.

Many people outside the laboratory have also been of great help and inspiration to the project. I am very grateful to Bent Odgaard, John Anderson, Julie Wolin, Peter Rasmussen and Erik Jeppesen for their co-operation in the paleo-project. Thanks to my Chiro-paleo-colleagues Steve Brooks, Heiki Olander, Lars Eriksson and Ian Walker for discussions on taxonomy and identification. We proved the Chiro-team to be superior to other paleo-disciplines - at least in bowling! Also many thanks to all of the people and their great hospitality that I met on the tours in Germany (1996) and in Canada/USA (1997). Last but not least, many thanks to Liselotte for her good-will and flexibility when making arrangements with our girls. It has been a great help.

Klaus Peter Brodersen

Hillerød, June 1998

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[1] Presented at *The International conference on Trophic Cascades in Shallow Freshwater and Brackish Lakes*, August 21-26, 1995, Mikolajki, Poland.

[2] Preliminary data presented at the *20th International Congress of Entomology*, August 25-31, 1996, Florence, Italy.

[3] Results presented at the *North American Benthological Society 44th annual meeting*, June 3-7, 1996, Kalispell, Montana.

[4] Results presented at the *13th International Symposium on Chironomidae*, September 5-10, 1997, Freiburg, Germany.

[7] Data were collected in 1990 during the MSc study at FBL. Data were re-analyzed and the paper was written on an introductory grant from The Faculty of Natural Science in 1993.

Macroinvertebrate communities in Danish lakes - Classification and trophic reconstruction. Introduction, summary and perspectives

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The present thesis consists of eight papers, published in or submitted to international journals. Five of the presented papers deal with numerical analysis, lake classification, and trophic reconstruction based on recently deposited subfossil chironomid and chydorid assemblages (a paleolimnological approach). Two papers focus on distribution patterns and trophic relations in assemblages of living invertebrates from the upper stony littoral of Danish lakes. A single paper is a classification of Danish springs and springbrooks, using the same numerical methods as those from the lake studies. One article in Danish is enclosed for non-English readers. This introductory chapter provides a summary and a further discussion of methods, results, appliance and perspectives in numerical analysis of present and past macroinvertebrate communities in temperate freshwater lakes.

CONTENTS

INTRODUCTION

Denmark has a long tradition involving studies of macroinvertebrates in freshwater lakes. Within several studies, primarily from the *Freshwater Biological Laboratory*, the Furesø studies (Wesenberg-Lund, 1917), Gribsø studies (Berg & Petersen, 1956) and the Lake Esrom studies (Berg, 1938; Jónasson, 1972; Dall, 1987; Lindegaard *et al.*, 1997) should be mentioned. These studies have focused mainly on population ecology in terms of abundance parameters, behavioral and feeding ecology and nutrient- energy dynamics. Energy metabolism and energy budgets for selected profundal and littoral species have recently been investigated by Hamburger *et al.* (1994, 1995, 1996) and Lindegaard *et al.* (1994). A thorough description of the invertebrate populations in the upper littoral of Lake Esrom was done by Dall *et al.* (1984) and a study of the in-lake variations in this habitat was presented by Dall *et al.* (1990). However, only a few scientific studies have focused on the distribution patterns in species assemblages (communities), and until now, the study on Chydoridae by Whiteside (1970) was the only classification and among-lake study of invertebrate assemblages in Danish lakes.

Several reasons for this research area still being open after so many years of Danish limnology can be mentioned. *First*, the profundal fauna in most (stratified and eutrophic) Danish lakes is very weakly developed due to pronounced oxygen depletion during the summer stratification. If zoobenthos is present at all, the communities will be restricted to very few highly tolerant species with very low or unpredictable abundances. Comparisons of these communities are only interesting at population-level and therefore require many hours of field and laboratory work. *Second*, studies of zoobenthos distribution patterns in the heterogeneous lake littoral is difficult due to lack of standardized sampling procedures. *Third*, descriptive studies of community patterns have for many years been regarded (underrated) as a more or less subjective and non-scientific research strategy due to problems (and lack of tools) in generating and testing hypotheses. *Fourth*, documented patterns and variability in species assemblages have still not been adequately supported to warrant the appliance of macrozoobenthos in biomonitoring of Danish (eutrophic) lakes. A final applied aim for lake classification has therefore not been seriously considered.

However, since the 1980's, the development of computing power has resulted in new and robust multivariate numerical methods to objectively analyze biological community data and relate these to sets of environmental data (Hill, 1979; Gauch, 1982; Jongman *et al.*, 1987; ter Braak, 1986, 1992). The methods consist primarily of ordination techniques in which samples (sites), based on the species composition, are arranged in relation to one or more coordinate axes such that their relative position to the axes and to each other provides maximum information about their ecological similarities. In this way, massive data sets can be condensed and simplified, and the underlying gradients (factors, variables) that may be responsible for the observed patterns can be analyzed.

Throughout this thesis, it will be difficult not to notice the authors interests in the applied (monitoring) potential of combining the biological information with the robust numerical methods. A great part of this project was inspired by the concluding remarks of Johnson *et al.*, (1993):

> *The next generation of pollution or environmental monitoring studies should consists not only of qualitative and quantitative analyses of benthic macroinvertebrate communities, but also of hypothesis generation through classification, ordination, and model construction; the accuracy of model prediction also must be tested. ... This would be a major step toward the establishment of tolerance levels of macroinvertebrates and their ordination along environmental gradients.*

This approach and strategy was followed throughout the eight papers presented in this thesis. Numerical analyses were performed on both living and subfossil[1] assemblages of freshwater invertebrates and the results presented in the thesis thus cover the link between limnology and paleolimnology with focus on community classification and species-environmental relations. The many aspects of paleolimnology, such as hydrology, sedimentation processes, geochronology, geochemistry, physics, dating methods, climatology, archeology, history etc. are only peripherally discussed in this project.

In this chapter, the major results of the overall project will be summarized and some of the potentials of the obtained models will be emphasized. References to papers presented in the thesis are given as numbers in squared brackets referring to the table of contents.

SUMMARY AND RESULTS

Data material and study sites

Spatial variation in assemblages of living invertebrates was analyzed in two data sets from the upper stony littoral of Danish lakes, covering both the in-lake variation (21 sites in Lake Esrom; Brodersen, [7]) and the among-lake variation (39 lakes all over Denmark; Brodersen *et al.*, [8]). A classification of macroinvertebrates from springs and springbrooks was performed on data from 110 Danish localities (Lindegaard *et al.*, [9]). Assemblages of subfossil Chydoridae and Chironomidae were collected from surface sediments (uppermost one centimeter) of 32 and 54 Danish lakes, respectively (Brodersen *et al.*, [5]; Brodersen & Lindegaard, [2]). A data combination of chironomid subfossils, living larvae and adult midges from Lake Stigsholm was analyzed for differences and similarities in species composition (Brodersen & Lindegaard, [1]).

Variations in time were investigated from subfossil chironomid assemblages in sediment cores of the two shallow and eutrophic lakes, Lake Søbygaard (Brodersen, [3]) and Lake Stigsholm (Brodersen & Lindegaard, [4]). A reconstruction of past

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[1] The terms *"fossils* or *subfossils"* are frequently used in paleolimnology and refer to the biological remains deposited and stored in the lake sediments. In fact, they are not fossilized, and the term is simply meant to imply *"a remain from a paleoenvironment"* (Whiteside & Swindoll, 1988).

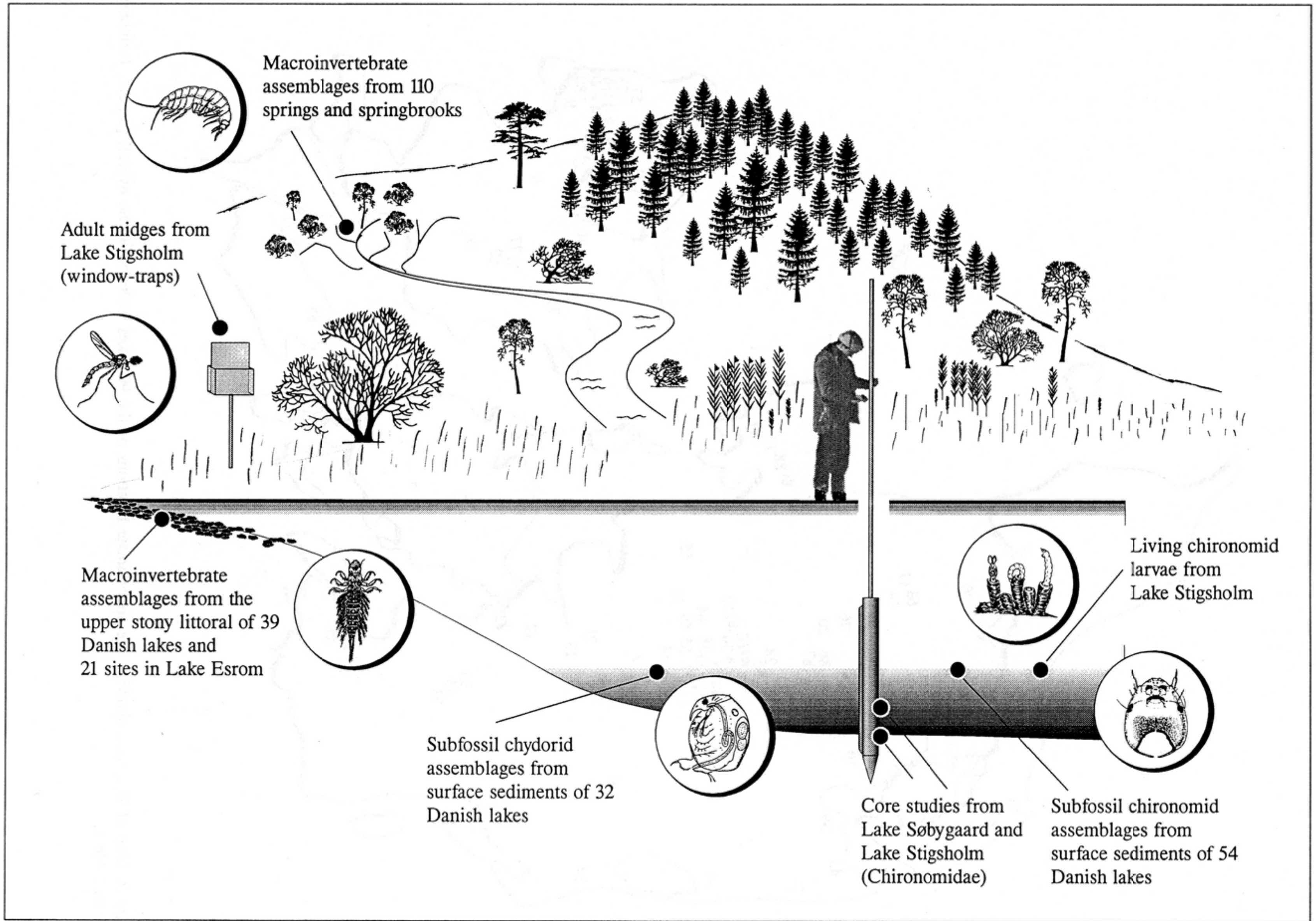

Figure 1. A summary of biological data sets included in the overall project

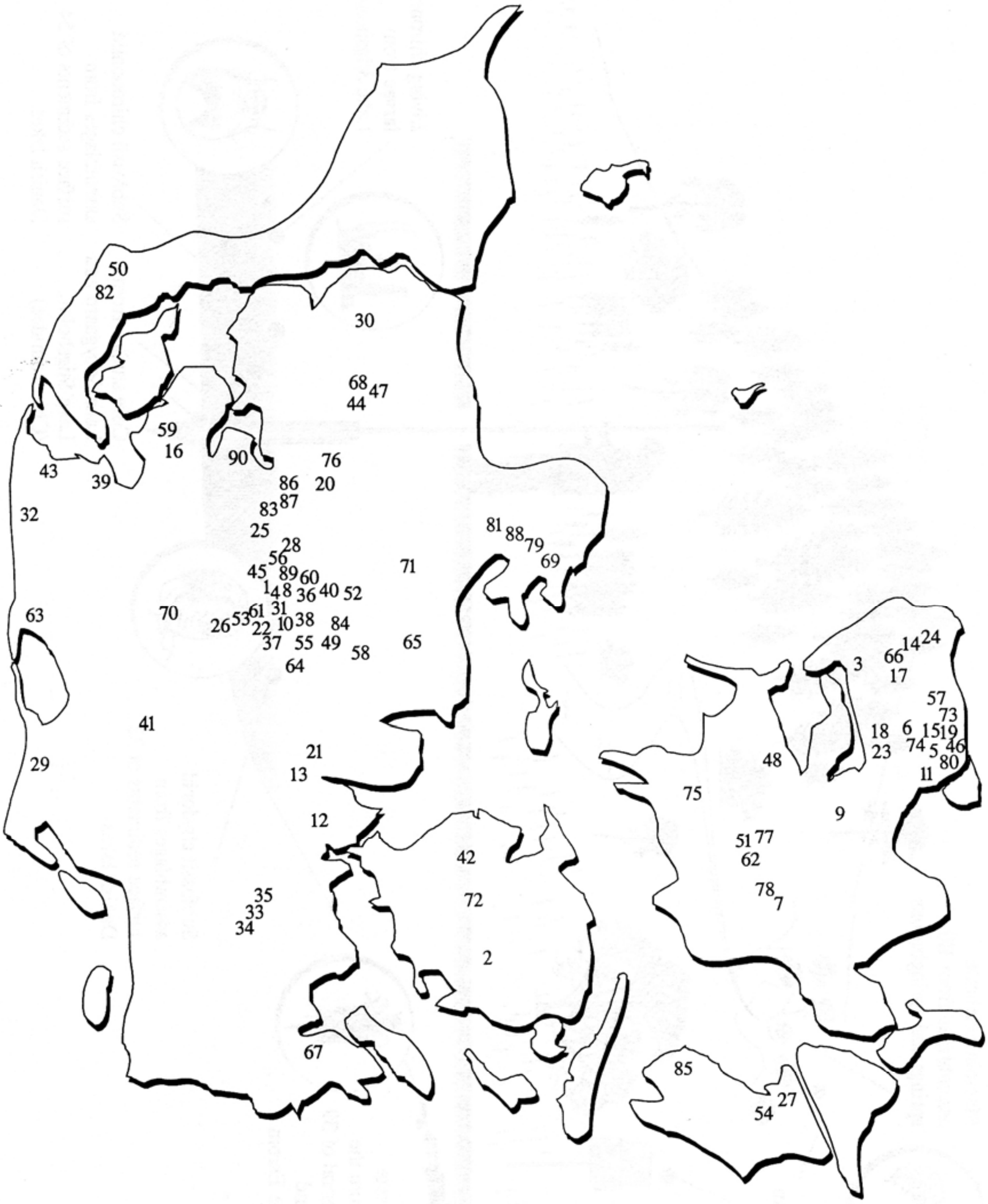

Figure 2. Map of Denmark showing the approximate locations of the 90 lakes included in the overall project. Numbers refer to Table 1.

Table 1. List of lakes investigated in the three classification studies. Chy: subfossil chydorid surface samples; chi: subfossil chironomid surface samples and lit: littoral stone samples. Numbers corresponds to map (Fig. 2). *) core studies; **) core study not presented. *Note*: numbers does *not* correspond to numbers in articles.

1)	*Almindsø*	chy, lit, chi
2)	*Arreskov sø*	chi
3)	*Arresø*	chy, lit
4)	*Avn sø*	chi
5)	*Bagsværd sø*	chy, chi
6)	*Bastrup sø*	lit, chi
7)	*Bavelse sø*	chy
8)	*Borre sø*	lit
9)	*Borup sø*	chi
10)	*Bryrup langsø*	lit, chi
11)	*Damhussøen*	chi
12)	*Dons Nørresø*	chi
13)	*Engelsholm sø*	chi
14)	*Esrum sø*	chy, lit, chi
15)	*Farum sø*	chy
16)	*Flyndersø*	lit
17)	*Frederiksborg Slotssø*	chy
18)	*Fugle sø*	lit, chi
19)	*Furesø*	chy, lit, chi
20)	*Fussing sø*	chy, lit
21)	*Fårup sø*	chi
22)	*Grane Langsø*	chy, chi
23)	*Gundsømagle sø*	chi
24)	*Gurre sø*	lit
25)	*Hald sø*	lit
26)	*Hampen sø*	chy, lit, chi
27)	*Hejrede sø*	chi
28)	*Hinge sø*	chy, chi
29)	*Holm sø*	chi
30)	*Hornum sø*	chi
31)	*Hund sø*	chy
32)	*Indfjorden*	lit
33)	*Jels Midtsø*	lit
34)	*Jels Nedersø*	lit
35)	*Jels Oversø*	lit, chi
36)	*Julsø*	lit
37)	*Kalgaard sø*	chi
38)	*Karl sø*	chi
39)	*Kilen*	chi
40)	*Knud sø*	chy, lit
41)	*Kvie sø*	chi
42)	*Lange sø***	chi
43)	*Lemvig sø*	chi
44)	*Lille Økssø*	chy
45)	*Lyngsø*	chi
46)	*Lyngby sø*	chy
47)	*Madum sø*	chy, lit, chi
48)	*Magle sø*	chi
49)	*Mossø*	lit, chi
50)	*Nors sø*	chy, lit, chi
51)	*Pedersborg sø*	chy
52)	*Ravn sø*	chy, lit, chi
53)	*Ræv sø*	chi
54)	*Røgbølle sø*	chi
55)	*Salten Langsø*	lit, chi
56)	*Silkeborg Langsø*	chy
57)	*Sjælsø*	lit
58)	*Skanderborg sø*	chy
59)	*Skån sø*	chi
60)	*Slåensø*	chy
61)	*Snabe-Igelsø*	chy
62)	*Sorø sø*	chy
63)	*Stadil Fjord*	lit
64)	*Stigsholm sø**	chi
65)	*Stilling-Solbjerg sø*	lit, chi
66)	*Store Gribsø*	chy
67)	*Store Søgaard sø*	chi
68)	*Store Økssø*	chy, lit
69)	*Stubbe sø*	chi
70)	*Søby sø*	chi
71)	*Søbygaard sø**	chi
72)	*Søholm sø*	chi
73)	*Søllerød sø*	chy
74)	*Søndersø*	chi
75)	*Tissø*	chy, chi
76)	*Tjele Langsø*	lit
77)	*Tuel sø*	chy
78)	*Tystrup sø*	chy, chi
79)	*Ulstrup Langsø*	lit
80)	*Utterslev mose*	chi
81)	*Vallum sø*	chi
82)	*Vandet sø*	lit
83)	*Vedsø*	lit
84)	*Vessø*	chi
85)	*Vesterborg sø*	chi
86)	*Viborg Nørresø*	lit
87)	*Viborg Søndersø*	lit
88)	*Øje sø*	chi
89)	*Ørn sø*	chy, lit, chi
90)	*Ørslev Klostersø*	lit

chlorophyll *a* concentrations in these two lakes using the models from Brodersen & Lindegaard [2]is presented in this chapter only, and not in the original papers.

A summary of data sets for the overall project are shown in Fig. 1, and a list of study lakes is found in Table 1 and Fig. 2. Unfortunately, there are only a few (seven) lakes in common among the three lake data sets, resulting in a total of 90 lakes. Lakes for the chydorid study were chosen among lakes investigated by Whiteside (1970) to allow for comparison and re-evaluation of lake typology and trophic state. Lakes for littoral communities were chosen among lakes having a well developed and well defined upper stony littoral. For all data sets, high quality monitoring data was a requisite, and this was the main requirement for lakes included in the chironomid analysis.

The paleoecological approach

The aim in pelaeolimnology is to reconstruct and interpret past environmental conditions from the information contained in the sediment profiles. The sedimentary record can be used as an archive of past environmental changes and events related to anthropogenic activities such as lake eutrophication and acidification (e.g., Warwick, 1980). The sclerotized chitinous head capsules of non-biting midge larvae (Chironomidae) are well preserved and often very abundant in freshwater sediments where they can be used as biological indicators. The Chironomidae are useful indicators because they are (1) widely distributed (ubiquitous), (2) identifiable to subfamily, genus or species (-group) level, (3) a diverse group adapted to particular ecological conditions and thus reflect the environmental conditions at the time of sedimentation, (4) good indicators of benthic and profundal conditions (contrary pelagic indicators e.g., diatoms).

The same arguments are valid for the exoskeleton remains of Chydoridae (Cladocera). This group, however, reflect both the pelagic environment and the shallow littoral lake habitats.

The subfossil chironomid assemblages

One of the first investigations in the project was a comparison of three different types of chironomid samples. From the shallow Lake Stigsholm (Brodersen & Lindegaard, [1]), a very small variation in subfossil chironomid assemblages along a five-point sampling transect was demonstrated. Samples of living chironomid larvae from the same transect showed considerable variation in species composition and a lower species richness than the subfossil samples. Adult midges collected in flight traps over the season made low-level taxon identification possible and helped to verify the subfossil identifications.

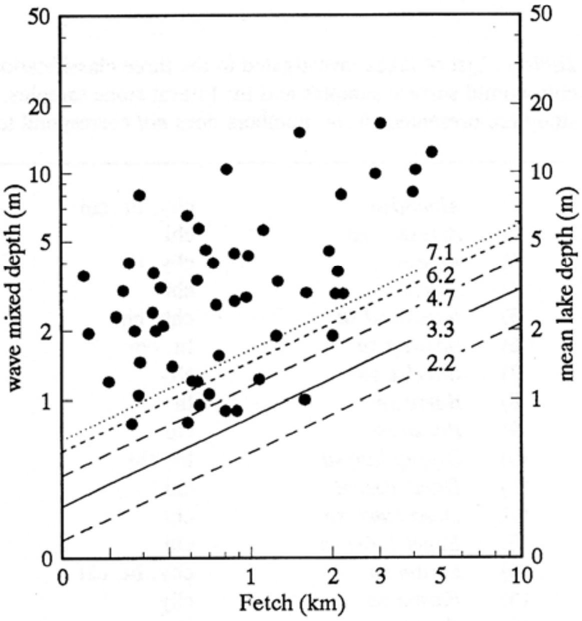

Figure 3. Diagram showing the calculated wave mixed depths in relation to wind fetch (km) at various wind speeds (m s^{-1}). Lines indicates wind speeds at the 25 percentile (2.2 m s^{-1}), median (3.3), 75 percentile (4.7), 90 percentile (6.2) and 95 percentile (7.1). Wind data from Brodersen [7], (n = 1095 days). Dots are the coordinates of (an approximate estimate of) wind fetch (km) and mean lake depth (m) for lakes in the chironomid surface data set (n = 54 lakes).

Wind-induced resuspension is probably the main reason for the low variation in the subfossil surface sediment samples. In very shallow lakes wave action is often effective over the entire lake bottom (Bengtsson & Hellström, 1992). The wave height and wave period are determined by fetch, wind speed and the depth where the waves are generated. When using the wind data from Brodersen [7] and the models of Smith & Sinclair (1972), the water mixed depth at a given speed and fetch can be calculated (Fig. 3). If the resuspension depth is considered as the depth at which the water mixed layers reach the lake bottom (Scheffer, 1998) it is seen that sediments in many of the shallow lakes included in the chironomid surface data set are potentially resuspended to the mean depth, up to 50% of the time (i.e.,. the median wind speed =3.3 m s^{-1}) (Fig. 3). However, this is calculated on maximum wind fetch in non-sheltered lakes. The small Lake Søbygaard is almost surrounded by mixed forest and Søndergaard (1986) found the critical wind speed for significant resuspension (for this lake) to be about 15 m s^{-1}, which occurs only infrequently. The very high correspondence in stratigraphic signals from the down-core study of Lake Søbygaard (Odgaard *et al.*, 1997; Brodersen, [3]; Brodersen, [6] Fig. 3) also indicates that resuspension is not invalidating the sediment record. Contrary, Anderson & Odgaard (1994) considered frequent sediment resuspension to be an essential problem in diatom inferred total phosphorus reconstruction in three shallow Danish lakes.

A reduced in-lake variation due to sediment mixing can be considered as an advantage when few (or a single) surface sediment samples are intended to reflect the recent (< decade) chironomid communities e.g. for classification or monitoring purposes. Pronounced sediment mixing, however, might be a serious problem in down-core studies in shallow lakes when time resolution should be well defined.

Subfossil Chironomidae as trophic indicators

The subfossil chironomid assemblages sampled at the deepest point in lakes were shown to have the highest resemblance to the littoral communities when compared to the bathymetric distribution of living larvae (Brodersen & Lindegaard, [2]). This is an advantage in classification and reconstruction of trophic state in nutrient rich eutrophic/hypertrophic lakes where the profundal fauna has become fully extinct (o-eutrophic, Sæther, 1979). On the other hand, it also stresses some problems to be expected in future chironomid-oxygen reconstruction models for lakes "above" the mesotrophic category. Nonetheless, the presence of the "true" profundal taxa, *Chironomus* type *anthracinus* and the littoral *Stictochironomus* sp., were important when separating the stratified lakes from the non-stratified lakes in the Danish surface data set. Figure 4 shows the results of canonical correspondence analysis (CCA), presented in Brodersen & Lindegaard ([2] Table 3). The analysis illustrates that mean lake depth clearly captures the variation along axis 2, but only in the mesotrophic end of the gradient. When the lakes becomes enriched with nutrients and increases in trophic state (horizontally to the left along axis 1), the differences between deep and shallow lakes are equalized due to loss primarily of *C. anthracinus* and *Stictochironomus* in the large and deep lakes and loss of *Psectrocladius*, *Pseudochironomus* and Pentaneurini in the shallow lakes.

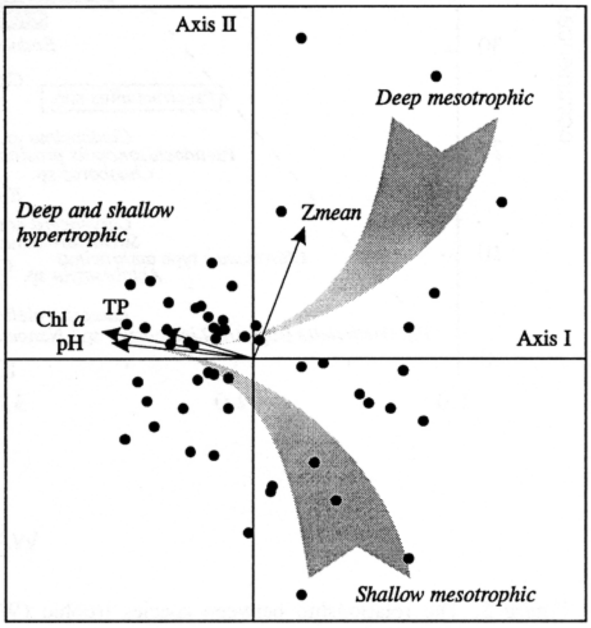

Figure 4. Results of CCA on subfossil chironomid assemblages from 54 Danish lakes (Table 3, Brodersen & Lindegaard, [2]). Shaded arrows illustrate the direction of change when large stratified and small shallow Danish lakes become eutrophied.

The relatively short ecological (trophic) gradient from mesotrophic to eutrophic lakes makes it difficult to point out true chironomid indicator taxa from the Danish data sets. The characteristics for the ideal indicator species are a narrow and specific ecological tolerance, widespread distribution, high abundance and taxonomic soundness (Johnson *et al.*, 1993). Rare species can not be used because their absence in the habitat can be due to a number of factors other than the target variable in question (here trophic state, nutrient loading). On the contrary, very abundant taxa often display an opportunistic character and can be used as indicators only when

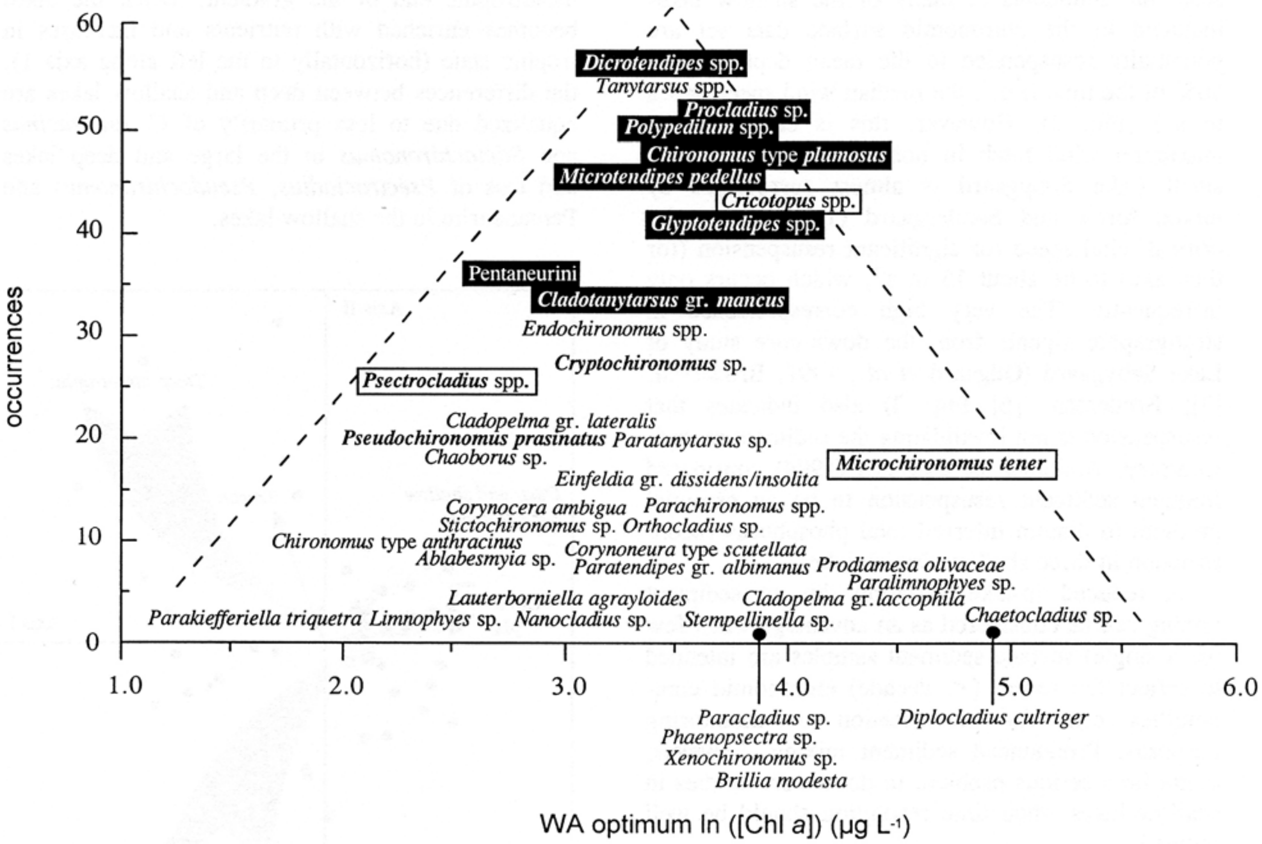

Figure 5. The relationship between species trophic (WA) optima (ln ([Chl *a*]) μg L^{-1}), occurrences (number of lakes present) and the TWINSPAN pseudospecies indicator cut-level for the subfossil chironomids in the Danish surface data set. Taxa in bold have an indicator cut-level at (0-1%), taxa in open boxes (2-4%), filled boxes (> 5%) (Brodersen & Lindegaard, [2] Fig. 3).

their quantitative dominance reflects specific habitat characteristics.

The relationship between taxa trophic optima (WA), occurrences (number of lakes with the taxa present) and the TWINSPAN pseudospecies indicator cut-level for the subfossil chironomids in the Danish surface data set (Brodersen & Lindegaard, [2]) is shown in Fig. 5. Most taxa have optima in the center of the diagram (~ 20 - 55 μg Chl *a* L^{-1}) and many are present in less than 15 lakes. Such taxa are weak trophic indicators. The good indicators are those located close to (or theoretically outside/above) the dotted line (e.g., *Psectrocladius*, *Microchironomus tener*, *Pseudochironomus*, Pentaneurini, *Cricotopus*). The indicator taxa in the top of the pyramid are all indicators only when their contribution to the assemblage exceeds 5 or 10% (Brodersen & Lindegaard, [2], Fig. 3).

It is therefore concluded that assessment of lake conditions should at least be based on total bioceonosis (community and associated environment) and semi-quantitative data. "Rapid assessment models" as proposed for profundal communities by Sæther (1979) and Wiederholm (1980) and a lucid classification scheme (Brundin, 1956) can not be established for Danish lakes.

Chironomid-chlorophyll transfer functions

The trophic variables and pH were highly correlated to the first CCA ordination axis (Fig. 4) and the ln-transformed chlorophyll *a* concentration captured most variation in the subfossil chironomid faunal data (DCA, Fig. 6). This strong correlation was used to create a weighted averaging regression and calibration model, or transfer function (Birks *et al.*, 1990; Line *et al.*, 1994). Transfer functions are generated by combining the modern surface samples of biological remains (here subfossil chironomid head capsules or chydorid remains, see below) with the corresponding contemporary water chemistry data from the lakes in the data set. It is assumed that the taxa have a unimodal or Gaussian distribution along the gradient of interest (here [Chl *a*]) and that the optimum of each taxa occurs at or close to its maximum abundance. The optimum is calculated by a simple abundance-weighted average (see formulas in Brodersen *et al.*, [8]). Once the WA optima and tolerances have been calculated, the WA model uses these in the quantitative inference (reconstruction) of past water chemistry from the subfossil assemblages in a sediment core (Birks *et al.*, 1990; Charles & Smol, 1994). Several models were compared (Brodersen & Lindegaard, [2], Table 5) and it was found that the best model was the simple WA using inverse deshrinking (root mean squared error of prediction = 0.65, $r^2 = 0.67$).

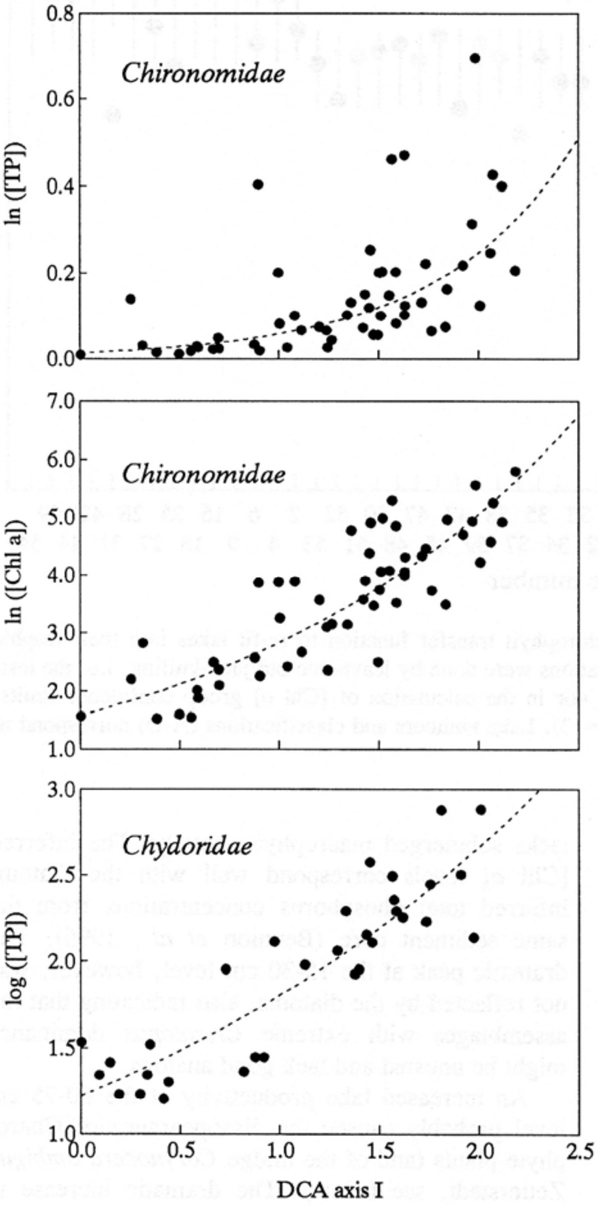

Figure 6. Correlations between species data (detrended correspondence analysis, axis 1 scores) and trophic parameters (epilimnetic summer mean concentrations of chlorophyll *a* and total phosphorus). Chironomidae n=54 lakes (Brodersen & Lindegaard, [2]). Chydoridae n=32 lakes (Brodersen *et al.*, [5]).

The observed changes in biological structure occurring in shallow lakes exposed to nutrient enrichment appears in intervals (thresholds) (Jeppesen *et al.*, 1990; Scheffer *et al.*, 1993). Therefore it should be considered whether a transfer function should aim for a continuous variable reconstruction or for a stepwise prediction of trophic intervals. The TWINSPAN ordination suggested a five-group-classification among which the trophic variables were significantly different (Brodersen & Lindegaard, [2], Fig. 3). The ability for the transfer functions to re-fit the lakes into their classification groups (trophic interval) were tested by leave-one-out jack-knifing, i.e. the test-lake was not included in the WA model, nor in the calculation of [Chl *a*] group confidence limits. The model mentioned above was the best model in this respect and the results are shown in Fig. 7. However, predicting a *trophic class* can probably be done more effectively using discriminant analysis. New results (not presented) using discriminant functions for only five "indicator taxa" (*Psectrocladius*, *Chironomus* type *plumosus*, *Microchironomus*, *Pseudochironomus* and *Corynocera*), correctly classified 93% of the study lakes (three lakes mis-classified), although it should be noted that cross validation tools were not available for this analysis (Brodersen *in prep.*).

Lake Søbygaard core study

The down-core study of chironomid remains from Lake Søbygaard clearly reflected the changes in lake productivity and closely followed the submerged macrophyte succession (Brodersen, [3]; Odgaard *et*

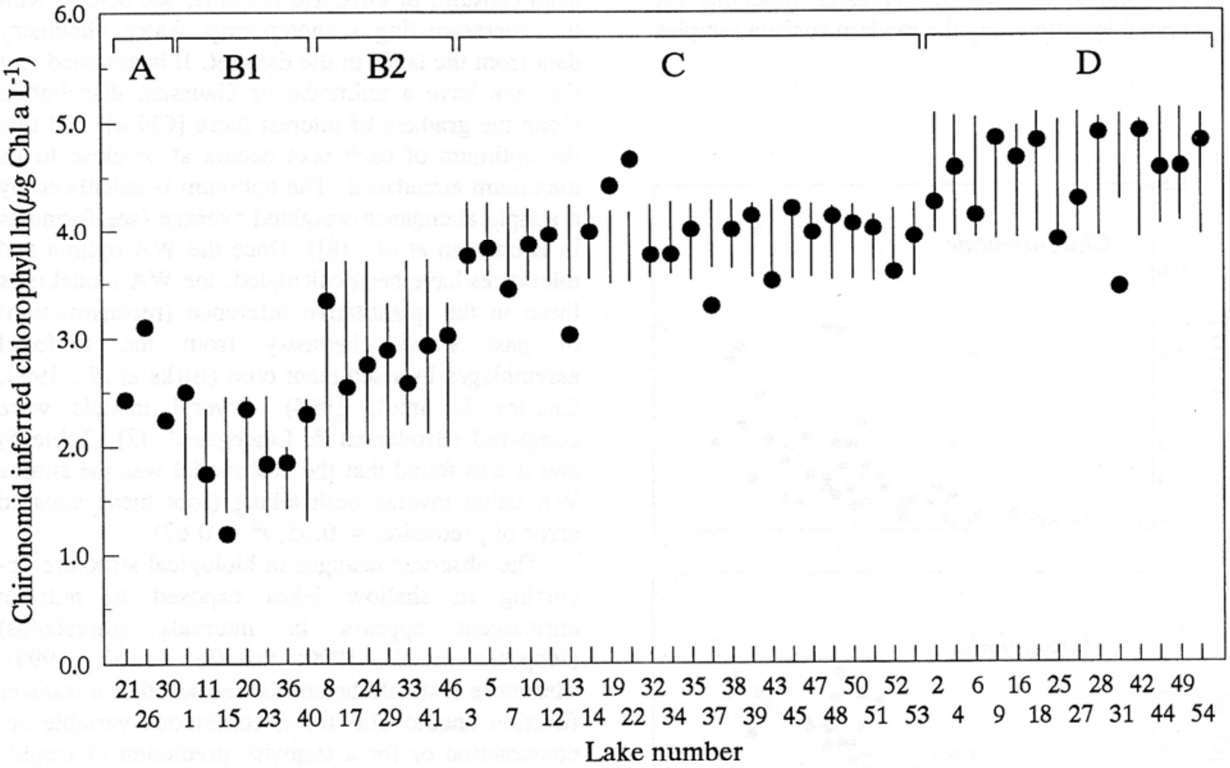

Figure 7. Diagram showing the ability for the chironomid-chlorophyll transfer function to re-fit lakes into their trophic intervals, defined by the TWINSPAN classification. All calculations were done by leave-one-out jack-knifing, i.e. the test-lake were not included in the calibration model when fitted, nor in the calculation of [Chl *a*] group confidence limits. Confidence intervals (95%) are shown except for group A (n = 3). Lake numbers and classifications (A-D) correspond to Brodersen & Lindegaard [2], Fig. 3.

al., 1997). In this summary, the reconstruction of lake chlorophyll *a* concentrations using the transfer functions discussed above is presented. Six different methods were used in the reconstruction and a very high agreement among these methods was found especially in the lower core sections (Fig. 8). However, at the 15-35 cm level, very large deviations in estimated [Chl *a*] were found. This was because the assemblages with extreme dominance of *Cricotopus* sp. (living at and on periphyton rich *Potamogeton*) had no good analogs in the training data set. The very high [Chl *a*] estimate at the 25 cm level (~260 μg Chl *a* L^{-1}) was from the WA model using classical deshrinking. The lowest model estimate at this level (~100 μg Chl *a* L^{-1}) was from the tolerance weighted WA using inverse deshrinking. No doubt, the lower estimate is the most probable since the lake with a present-day measured [Chl *a*] ~190 μg Chl *a* L^{-1} lacks submerged macrophytes totally. The inferred [Chl *a*] levels correspond well with the diatom-inferred total phosphorus concentrations from the same sediment core (Bennion *et al.*, 1996). The dramatic peak at the 15-30 cm level, however, was not reflected by the diatoms, also indicating that the assemblages with extreme *Cricotopus* dominance might be unusual and lack good analogs.

An increased lake productivity at the 60-75 cm level probably caused the disappearance of Charophyte plants (and of the midge *Corynocera ambigua* Zetterstedt, see below). The dramatic increase in chironomid inferred [Chl *a*] was captured by a high percentage of hypertrophic indicators (*Microchironomus tener* and *Chironomus* type *plumosus*). This response was not sufficiently reflected by multidimensional scaling (MDS), Shannon diversity or species richness (Brodersen [3]). The evenness index, however, did show changes at this core level.

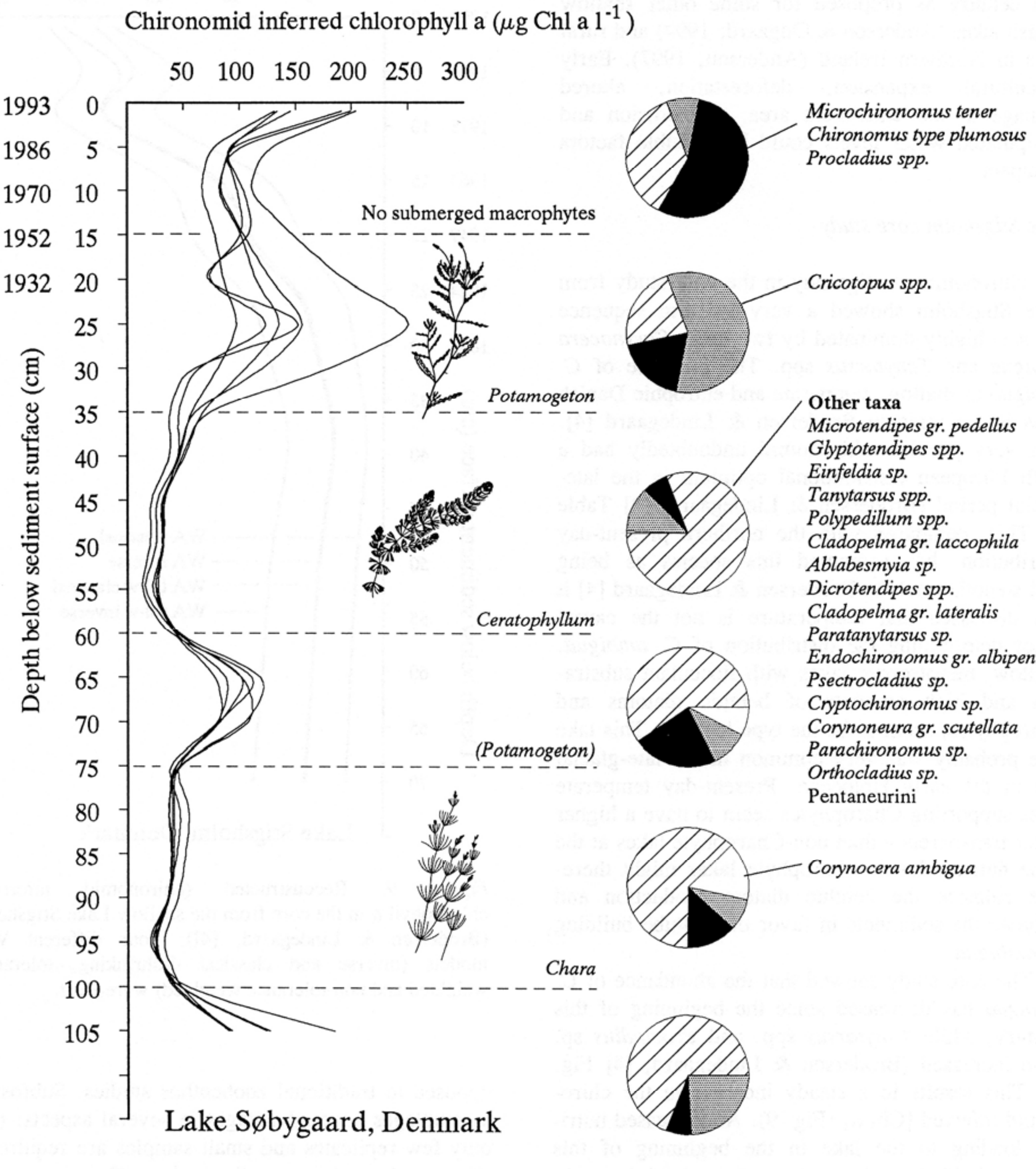

Figure 8. Reconstructed (chironomid inferred) chlorophyll *a* in the core from the shallow Lake Søbygaard (Brodersen, [3]). Four WA models (inverse and classical deshrinking, tolerance weighted and non-tolerance weighted) were used. Reconstructions by passive fits of test-samples in a DCA using external regressions (linear and exponential) are shown also. Largest fluctuations are WA-classical estimates. Lowest fluctuations are tolerance weighted WA-inverse estimates.

The results indicate that Lake Søbygaard has already suffered from nutrient loading in the 16th or 17th century as proposed for some other shallow Danish lakes (Anderson & Odgaard, 1994) and rural lakes in Northern Ireland (Anderson, 1997). Early agricultural expansion, deforestation, altered drainage in the catchment area, soil erosion and manipulated water levels could be possible factors of impact.

Lake Stigsholm core study

The chironomid stratigraphy in the core study from Lake Stigsholm showed a very uniform sequence and was highly dominated by two taxa: *Corynocera ambigua* and *Tanytarsus* spp. The presence of *C. ambigua* in shallow, temperate and eutrophic Danish lakes is the topic in Brodersen & Lindegaard [4]. This very peculiar chironomid undoubtedly had a north European distributional optimum in the late-glacial period (Brodersen & Lindegaard, [4] Table 2). This, compared with the northern present-day distribution, has promoted this species as being cold-stenothermal. In Brodersen & Lindegaard [4] it was discussed that temperature is not the causal factor determining the distribution of *C. ambigua*. Shallow, mesotrophic lakes with flocculant substratum and high amounts of benthic diatoms and Charophytes, seem to be the type locality. This lake type probably was very common in the late-glacial and in the early Holocene. Present-day temperate lakes supporting Charophytes seem to have a higher water transparency than non-Charophyte lakes at the same nutrient level. Charophyte lakes might therefore enhance the benthic diatom production and stabilize the sediments in favor of the tube building *C. ambigua*.

The core study showed that the abundance of *C. ambigua* has decreased since the beginning of this century, while *Tanytarsus* spp. and *Procladius* sp. have increased (Brodersen & Lindegaard, [4] Fig. 1). This results in a steady increase in the chironomid inferred [Chl *a*] (Fig. 9). An increased nutrient loading to the lake in the beginning of this century is likely to have changed productivity, substratum, macrophyte composition and food availability for the zoobenthic populations, causing the decline in *C. ambigua*.

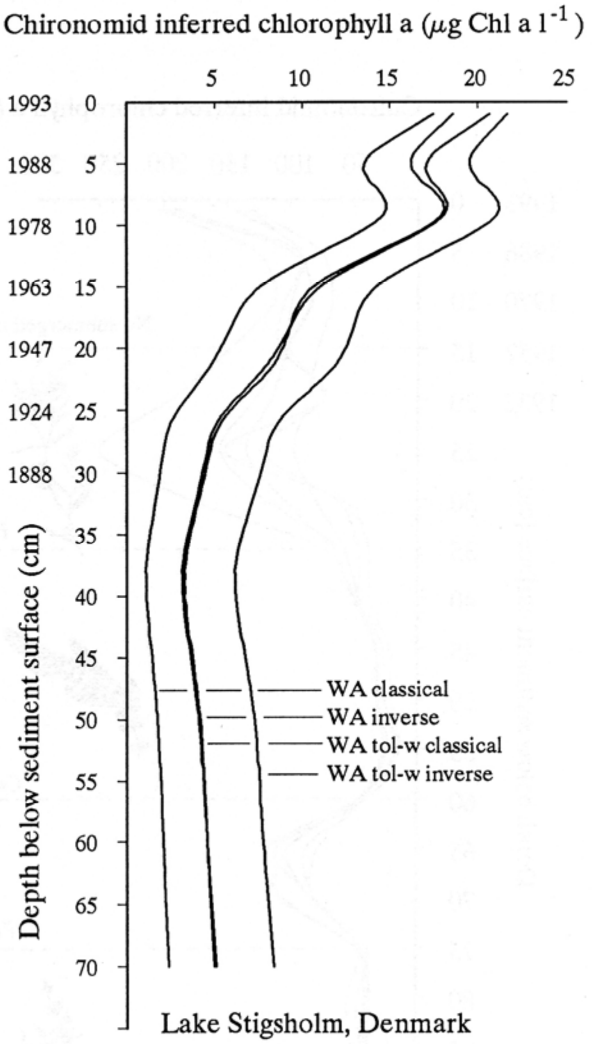

Figure 9. Reconstructed (chironomid inferred) chlorophyll *a* in the core from the shallow Lake Stigsholm (Brodersen & Lindegaard, [4]). Four different WA models (inverse and classical deshrinking, tolerance weighted and non-tolerance weighted) were used.

Chironomid analysis in general

Table 2, shows a comparison of results and possibilities in subfossil chironomid analysis as opposed to traditional zoobenthos studies. Subfossil assemblages have advantages in several aspects: (1) only few replicates and small samples are required, (2) a single or few sampling points, (3) no seasonal variation or dependence (4) low in-lake variation (5) a relatively high species richness (6) good time integration and (7) results are directly comparable to core studies. Quantitative paleo-reconstruction models for trophic variables (this study), salinity (Walker *et al.*, 1995), temperature (Walker *et al.*, 1991, 1997; Olander *et al.*, 1997) have already been developed. Chironomid transfer functions to

Table 2. Summary of possibilities and results of subfossil chironomid analysis compared to traditional zoobenthos studies. *) extensive sampling programs are prerequisite.

	Adult midges	Subfossil assemblages	Assemblages of living larvae
Identification level	high	low	moderate
Sample diversity/richness	high	moderate	low*
Seasonal variation	high	no	high
Sampling frequency	entire season	single	often (4-10 Y^{-1})
Sampling point	several	lake center	transects (several)
Sample replicates	-	few/single	many
Variation within lakes	-	low	high
Variation among lakes	-	high	high*
Short time monitoring (year to year)	-	poor	good*
Long term monitoring (years/decades)	-	good	good*
Population biology	-	no	good*
Modern (resent) samples comparable to core studies	-	yes	badly
Reconstructions			
Total phosphorus	-	(yes)	-
Chlorophyll	-	yes	-
Submerged plant communities	-	(yes)	-
Acidification (pH)	-	yes	-
Salinity	-	yes	-
Temperature	-	yes	-
Oxygen (hypolimnion)	-	probably	-
Fish communities	-	probably	-
Sediment characteristics	-	probably	-

acidification (Brodin *et al.*, 1990), to hypolimnetic oxygen concentration, to submerged macrophytes and to sediment characteristics are likely to be constructed as well. A Cladocera-fish transfer function for shallow lakes was created by Jeppesen *et al.* (1996). A corresponding model can probably also be constructed from chironomid remains.

The possibilities are numerous and it is suggested that subfossil samples are a superior tool for monitoring and classification of eutrophic and hypertrophic lakes compared to traditional zoobenthos sampling. However, if short term fluctuations/monitoring is essential (year-to-year), samples of living chironomid larvae are required, but in that case, extensive sampling programs are a prerequisite. Slightly better options for low-level taxa identification are possible with living chironomid larvae, but this is seldom used for monitoring purposes (Resh & McElravy, 1993).

Subfossil Chydoridae

Chydoridae is the most diverse family of Cladocera and the majority of species which have been carefully investigated are quite habitat specific (Whiteside, 1988; Hann, 1989). Most chydorids are weak swimmers and they are found amongst submerged vegetation as well as on sandy, muddy and rocky substrata in the littoral regions.

The problem of defining (chironomid) indicator taxa, discussed above, was not as difficult in the analysis of chydorid data. The correlation between chydorid faunal data and total phosphorus was high (Fig. 6), and a very well defined species displacement occurred along the trophic gradient (Brodersen *et al.*, [5] Fig. 6). As in chironomid analysis, the faunal response to increased nutrient levels is not a direct response as e.g. for diatoms, but an indirect response to changed habitat structure and especially the composition and extension of the vegetated

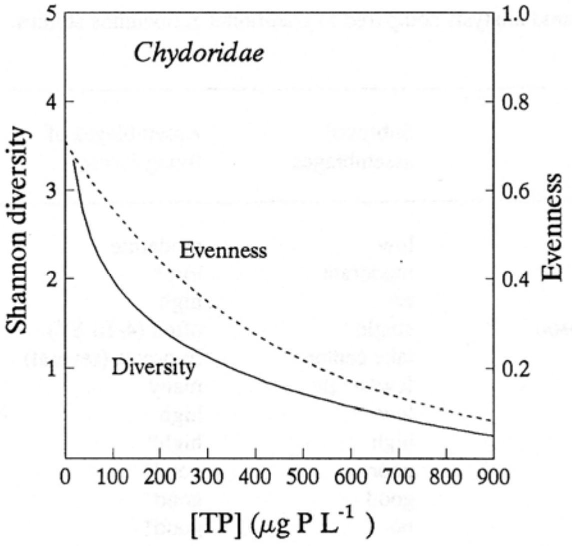

Figure 10. Shannon diversity and evenness in subfossil chydorid surface samples along a trophic (total phosphorus) gradient.

littoral regions. Species diversity and evenness declined rapidly from meso- to hypertrophic lakes (Fig. 10) with almost complete dominance of the limnetic (open water) species *Chydorus sphaericus* (O.F. Müller) and *Alona rectangula* Sars in the heavily polluted sites.

A very strong chydorid-[TP] WA reconstruction model was generated on the data set from 1992. The model was used to reconstruct [TP] from the data collected by Whiteside in the late 1960's (Whiteside, 1970) and the changes in lake trophic state could then be assessed. The lake changes fell into six different response groups and were in good agreement with the observed trends in lake quality.

The chydorid data were analyzed both by parametric and non-parametric methods. There was a fine concordance between the methods used, and it was clear that the same results could be obtained qualitatively using the non-parametric approach. However, the lack of regression and calibration functions in the non-parametric methods do not allow for quantitative reconstructions.

In summary, the chydorid study is a good example showing how successful subfossil assemblages from surface sediments can fill the gap between traditional biological monitoring and down-core paleolimnological studies of lake history (Smol, 1992; Anderson & Battarbee, 1994).

The fauna in the upper stony littoral

After intensive numerical and statistical analysis of the fauna in the upper stony littoral of thirty-nine lakes (Brodersen *et al.*, [8]), the statement of Wesenberg-Lund in his Furesø Studies (1917) is confirmed:

> *I have since (1908) had the opportunity to investigate this peculiar fauna in several other Danish lakes. It seem in general to consist of almost the same species. It can only be noted that the stony surf zone of Arresø in 1910 was inhabited by numerous* Hydropsyche-*larvae, spinning their nets just as they do in running waters.*

The faunal communities living on littoral stones in the meso- and eutrophic Danish lakes are indeed very similar and consist primarily of a few but very abundant taxa with a wide trophic tolerance range. Today, one line to the above statement of Wesenberg-Lund can be added: "...and some lakes support large populations of *Dreissena polymorpha..!*"

The factors responsible for the distribution of fauna in this habitat are highly complex, and it was not possible to present a clear lake classification based on the faunal assemblages. When comparing the among-lake study with the studies of in-lake variation (Brodersen, [7]; Dall *et al.*, 1990) it is easier to predict the composition of fauna within different sites of one lake rather than among several lakes. The extension, the character and the quality of the stony bottom habitat seem to be more important for defining the composition of epilithic fauna rather than the quality of the water surrounding it. The 78 individual stone samples from the study in Lake Esrom (Brodersen, [7]) could be clustered into six groups defined by their similarities in shore slope, wind exposure and the biomass of filamentous algae growing on the stones (Fig. 11, new analysis) using group-average clustering of euclidean distances. Using discriminant functions of thirteen invertebrate taxa, it was possible to correctly predict 83% (no cross validation) of the samples into these six groups (Fig. 11), clearly indicating the importance of habitat character when water quality parameters are held constant.

The characteristics of the upper littoral habitat and the lake trophic state, however, are to some extent coupled as hypothesized in the present papers [7, 8], and the calculation of taxa optima and

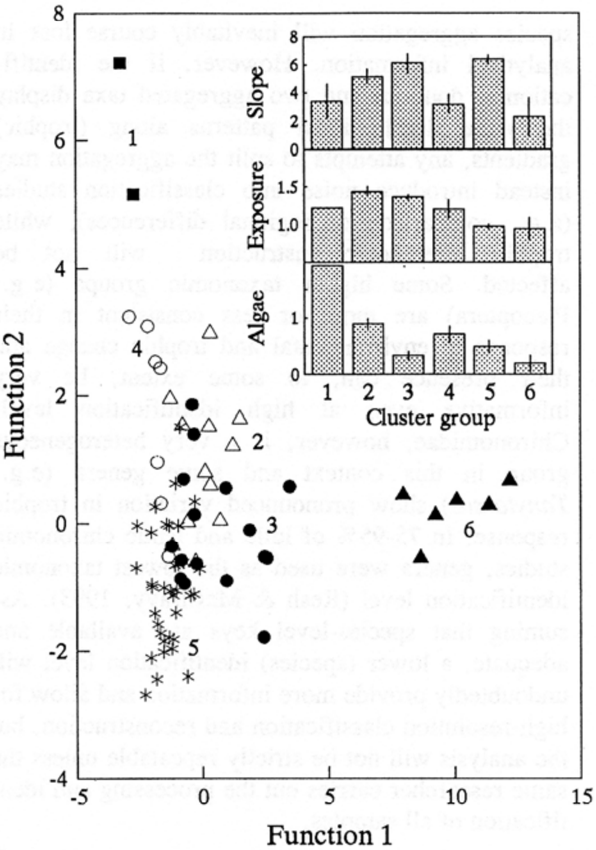

Figure 11. Discriminant analysis using 13 invertebrate taxa in 78 littoral stone samples from Lake Esrom (Brodersen, [7]). Six cluster groups (1-6) were defined by their similarities in shore slope, wind exposure and the biomass of filamentous algae growing on the stones (bars), using group-average clustering of euclidean distances. 83% of the samples were correctly predicted (no cross validation) into the six cluster groups.

tolerances across the thirty-nine lakes succeeded to predict the [Chl *a*] when applied in the WA transfer functions. Additional studies, including more nutrient poor lakes and a thorough description/definition of the physical and biological character of the stony habitat are required to identify the species distribution patterns and in order to build a well functioning trophic assessment model.

The fauna in springs and springbrooks

Data harmonization problems

The paper covering the fauna of Danish springs and springbrooks (Lindegaard *et al.*, [9]) is a fine example of the common and inevitable problems which arise when species data of different origin are combined and analyzed simultaneously in multivariate analysis.

The data material comprised fauna data, physico- chemical measures and habitat descriptions from 110 Danish springs and springbrooks originating from three different sampling programs. The study succeeded to describe the typical faunal composition of springs and springbrooks, and classify the faunal elements into seven groups of different (micro-) habitat preferences. A clear variation and significant difference among environmental variables in different geographical regions was shown (Lindegaard *et al*, [9], Fig. 2), however, a corresponding geographical variation in species data was not considered reliable due to obvious differences in sampling procedure and processing.

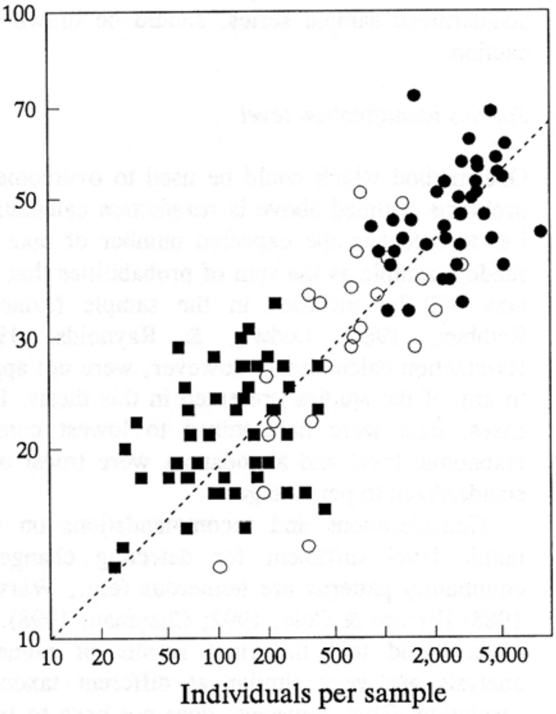

Figure 12. Number of individuals and recorded taxa in 110 samples from Danish springs and springbrooks (Lindegaard *et al.*, [9]). Data from the three data sets have different markers. Broken line is the fitted power equations for the two standardized data sets (kick-samples, open and filled circles); $y=5.30x^{0.27}$, $r^2=0.62$, n=63).

The faunal samples from one data set (A) were taken exclusively from areas where water was seeping out, avoiding sampling in the proper spring-brook, whereas the other two sample series were taken by standardized kick-sampling, including all spring habitats. Analysis of data sets with such clear and known discrepancies can be controlled by proper data standardization and harmonization followed by a deliberate and careful interpretation. The difficulties lie in analysis of data, which in theory and practice should be of standardized origin, but apparently are not. Figure 12 clearly shows the large variation in sample size (number of individuals) and the corresponding species richness found within the three sampling programs. Both these parameters were significantly different ($P < 0.001$) between the two standardized kick-sample series. The good correlation between sample size and species richness (Fig. 12) emphasize that conclusions based on differences in richness, diversity and thus also community similarities, even among standardized sample series, should be drawn with caution.

Species identification level

One method which could be used to overcome the problems outlined above is *rarefaction* calculations, i.e. to calculate the expected number of taxa in a random sample as the sum of probabilities that each taxa will be included in the sample (James & Rathbun, 1981; Ludwig & Raynolds, 1988). Rarefaction calculations, however, were not applied to any of the studies presented in this thesis. In all cases, data were harmonized to lowest common taxonomic level and abundances were (most often) standardized to percentages.

Considerations and recommendations on taxonomic level sufficient for detecting changes in community patterns are numerous (e.g., Warwick, 1988; Ferraro & Cole, 1992; Chapman, 1998). It is often found that the final results of numerical analysis are very similar at different taxonomic resolution. This, however, does not have to be the rule. Decisions about identification levels should always depend on the purpose of the study, the level of sensitivity required, the type of analysis being used and the group of organisms of primary interest (Resh & McElravy, 1993).

Provided that the primary (species-) identification is reliable and that well defined distributional-/aut-ecological differences between two phenotypic closely related taxa really exist, such taxonomic species aggregation will inevitably course loss in analytical information. However, if the identification is doubtful and two aggregated taxa display the same distributional patterns along (trophic) gradients, any attempts to split the aggregation may instead introduce noise into classification studies (e.g., comparison of regional differences), while trophic inference/reconstruction will not be affected. Some higher taxonomic groups (e.g., Plecoptera) are more or less consistent in their response to environmental and trophic change and their presence can, to some extent, be very informative even at high identification level. Chironomidae, however, is a very heterogeneous group in this context and some genera (e.g., *Tanytarsus*) show pronounced variation in trophic response. In 75-95% of lotic and lentic chironomid studies, genera were used as the lowest taxonomic identification level (Resh & McElravy, 1993). Assuming that species-level keys are available and adequate, a lower (species) identification level will undoubtedly provide more information and allow for high-resolution classification and reconstruction, but the analysis will not be strictly repeatable unless the same researcher carries out the processing and identification of all samples.

Time series analysis of faunal data

A similar problem as discussed above (data harmonization), arises in multivariate analysis of time-series faunal data. Even small changes in sampling, sorting and identification procedures are effectively detected by the very sensitive numerical techniques. However, when sudden changes in faunal compositions can be related to documented events in the ecosystem, this high detection level can effectively be applied in time-series analysis and also for detecting signals in paleo-stratigraphies (Birks, 1986; Bennett, 1996). Figure 13 is an example of time-series analysis (multidimensional scaling) of macroinvertebrate assemblages from a small Danish stream (Ryds Å, Funen, Fyns Amt, 1997) for an eight year period. A dramatic change in faunal composition from 1991 to 1992 (springtime samples) was detected, primarily due to pronounced decline in *Gammarus*, *Baetis*, *Micropsectra* and *Polypedilum*. The regional monitoring program showed that the stream in the winter period had received insecticides from a commercial greenhouse, upstream of the sampling station. The fauna seemed to have recovered in the following years, but at a different similarity level. It is important to note that the same pattern could have been found if changes in sampling and analytical procedures had occurred. If so, similar abrupt changes would probably be discovered in several independent regional data sets at the same time.

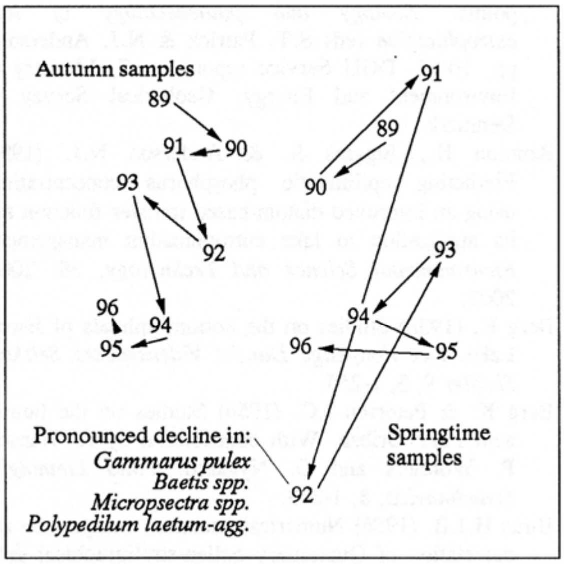

Figure 13. Non-metric multidimensional scaling (NMDS) of macroinvertebrate assemblages from a small Danish stream (Ryds Å, Funen) over an eight year period. A dramatic change in species composition from 1991 to 1992 (springtime samples) was detected, primarily due to pronounced decline in *Gammarus*, *Baetis*, *Micropsectra* and *Polypedilum* (Fyns Amt, 1997, numerical analysis by K.P. Brodersen).

The data harmonization problem is serious and requires far more attention in multivariate analysis of species data and for future database constructions. It is interesting to follow the discussions among statistically focused ecologists on the rationale in data processing and analytical strategies. Aspects such as optimal transformations, importance and down-weighting of rare taxa, qualitative versus quantitative conclusions, hypothesis generation and testing, validation, falsification, precision and accuracy etc., are all items discussed in a statistical context. This is without considering that the basic presumption for repeatable results is the ability to reproduce the primary tables of biological and environmental data.

Analytical quality control (AQC) and frequent inter-calibration workshops focusing on species identification are necessary in order to cope with this problem.

CONCLUSION AND PERSPECTIVES

This project has succeeded to prove the robustness of multivariate numerical methods in order to expand our understanding of macroinvertebrate communities and their distribution along (even very narrow) environmental trophic gradients in Danish lakes.

The null hypothesis that "there is no relation between macroinvertebrate assemblages and their environment in Danish lakes" was rejected by exploratory data analysis and the optimal variations in faunal data were described. The best subsets of *available* environmental variables in describing the organized faunal data were explored using direct and indirect ordination techniques as well as by non-parametric multivariate methods. Variables generally accepted to reflect lake trophic state: Secchi depth, epilimnetic concentrations of total phosphorus and chlorophyll *a*, were highly correlated to the faunal data, although not necessarily always reflecting a causal relationship in the very complex, interrelated and dynamic lentic ecosystems.

The subfossil assemblages showed very little within-lake variation and primarily reflected the upper littoral communities. This sample type proved to be an effective tool for simultaneous classification of both stratified and non-stratified nutrient rich lakes.

The strong relation between trophic variables and macroinvertebrate assemblages made it possible to create models and transfer functions to document the degree and directions in lake trophic changes. The trophic gradient within the Danish data set, including surface samples from 54 lakes, ranged from mesotrophy to hypertrophy and was too narrow to provide true chironomid indicator species. A "rapid assessment model" could not be achieved and a semiquantitative approach was necessary.

The presented examples of trophic reconstruction over centuries (Chironomidae in Lake Søbygaard and Lake Stigsholm) and over decades (Chydoridae from thirty-two lakes) came out successfully. The methods can be used to (1) predict "natural" conditions and trophic baseline levels, (2) show trophic trends and directions in lake history, (3) provide important background information for individual lakes prior to initiation of restoration projects (4) predict the outcome of manipulation and lake restoration.

Improvements and fine-tuning of the models should involve expansion of the training data set in both ends of the trophic gradient, cross validations through test-data-sets and comparison of down-core stratigraphies with other biological variables (diatoms, Cladocera, macro fossils etc.). Further studies of surface sample representativity (which assemblages reflects a lake stable state) and how the corresponding environmental variables should be summarized (year or summer, minimum, mean, median or maximum) are all important questions to be asked and resolved (Bennion, 1995). Finally, when using invertebrate communities as reconstruction parameters, studies of the interactions and impacts from higher invertebrates and vertebrates, especially fish communities, would be advantageous.

"There is a clear need for combining a variety of different approaches and including a longer temporal perspective to assist in the understanding of contemporary systems. Sometimes at least, the past can be the key to the present" (Anderson, 1995). Analyses of chironomid and chydorid remains are two components of the systems and their interpretive capacity can be enhanced in multi-disciplinary studies.

ACKNOWLEDGMENTS

Thanks to Claus Lindegaard and Peter Dall for comments to this summary. Many thanks to Fiona Curran for improving the English of the chapter.

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