

Eulittoral macroinvertebrate communities of lowland lakes: discrimination among trophic states

MARIO BRAUNS, XAVIER-FRANÇOIS GARCIA, MARTIN T. PUSCH AND NORBERT WALZ
Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm, Berlin, Germany

SUMMARY

1. Nutrient inputs from urban and agricultural land use often result in shifts in species composition of pelagic and profundal invertebrate communities. Here, we test if nutrient enrichment affects the composition of eulittoral macroinvertebrate communities, and, if so, if macroinvertebrate communities of five different habitat types reflect differences in trophic state.

2. Macroinvertebrate community composition of 36 lakes was significantly correlated with total phosphorus (TP) concentration, the proportion of coarse woody debris (CWD) and root habitats and the proportion of grassland.

3. However, macroinvertebrate communities of five major habitat types from eight lakes were more dissimilar among habitats than among trophic states. Community composition of reed and stone habitats was significantly correlated with wind exposure but not TP concentration, while macroinvertebrate composition of sand habitats was related to TP concentration and coarse sediments. In CWD and root habitats, both TP concentration and a predominance of invasive species covaried, which made it difficult to relate the observed compositional differences to either trophic state or to the effects of competition between native and invasive species.

4. Trophic state influenced the composition of eulittoral macroinvertebrate communities but to a lesser extent than has been previously reported for profundal habitats. Moreover, the effects of trophic state were nested within habitat type and were partially superseded by biotic interactions and small-scaled habitat complexity. Although eulittoral macroinvertebrate communities were not strong indicators of the trophic state of lowland lakes, they may be used to assess other anthropogenic impacts on lakeshores.

Keywords: eutrophication, habitat, invasive species, lakeshore, land use

Introduction

Anthropogenic eutrophication continues to be a major threat to lake ecosystems, despite efforts to reduce nutrient inputs into lakes. The construction of wastewater treatment plants greatly reduced the direct discharge of industrial and/or domestic wastewater, but many lakes still receive substantial inputs of phosphorus (P) and nitrogen from urban and agricultural land use (Behrendt, 1996; Carpenter *et al.*, 1998;

Sanyanga & Hlanga, 2004) and atmospheric deposition (Vitousek *et al.*, 1997). Regardless of the source, inputs of nutrients can substantially alter the ecological function of lake ecosystems. For example, increased nutrients, especially P, often result in increased pelagic primary production (Vollenweider, 1968) and algal blooms, which may inhibit the growth of submerged macrophytes (Egertson, Kopaska & Downing, 2004) and benthic primary production (Vadeboncoeur *et al.*, 2003; Chandra *et al.*, 2005). Moreover, decomposition of algal biomasses may result in anoxic conditions in profundal habitats, adversely affecting community composition. For example, pioneering work by Thienemann (1918,

Correspondence: Mario Brauns, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 301, D-12587 Berlin, Germany. E-mail: brauns@igb-berlin.de

1928) showed that the composition of profundal macroinvertebrate communities was strongly related to dissolved oxygen (DO) concentrations. This early work inspired the use of profundal macroinvertebrate communities to classify the trophic status of lakes (Thienemann, 1921; Saether, 1979; Brodersen & Lindegaard, 1999; Langdon *et al.*, 2006).

In contrast to a number of studies showing the efficacy of using profundal communities in monitoring the effects of eutrophication on lakes, only a few studies have focused on the use of macroinvertebrate communities of nearshore, stony habitats and fewer still have taken a multihabitat approach. For instance, Macan & Maudsley (1969) studied English lakes along a gradient from oligotrophic to eutrophic conditions and found that macroinvertebrate communities were only partially related to trophic state because wind exposure superseded the compositional differences among trophic states. In Danish lakes, only a few macroinvertebrate species colonising stony shores were significantly related to trophic state, while morphometric variables influenced the majority of species (Brodersen, Dall & Lindegaard, 1998). Similarly, Johnson & Goedkoop (2002) found that environmental factors other than nutrient concentration explained most of the variance of macroinvertebrate communities from wind exposed stony shores of Swedish lakes. However, the applicability of these results to other eulittoral habitats is unknown, and to our knowledge only one study has previously determined if littoral macroinvertebrate communities reflect lake trophic state across multiple habitat types (Tolonen *et al.*, 2001). In a study of a large Finish lake system, Tolonen *et al.* (2001) showed that macroinvertebrate communities of macrophyte, sand and stone habitats primarily differed among habitat types, while within each habitat type community composition differed among trophic states. However, total phosphorus (TP) concentrations (range 3–26 $\mu\text{g L}^{-1}$) did not exceed mesotrophic conditions (Vollenweider & Kerekes, 1982), and habitat types, such as coarse woody debris (CWD) and submerged tree roots were not studied.

In the present study, we use macroinvertebrate data from 36 lakes to test the hypothesis that eulittoral macroinvertebrate communities of North-German lowland lakes are related to differences in trophic state. Further, based on habitat-specific macroinvertebrate data from eight lakes, we test if macroinvertebrate communities of CWD, reed, root, sand and stone

habitats comparably reflect among-lake differences in trophic state.

Methods

Sampling

Lake-specific analysis. Macroinvertebrates were collected in autumn 2001 (September–December) and spring 2002 (April–July) from six equidistant sampling sites situated along the shoreline of 36 North-German lowland lakes (Table 1, Fig. 1). A composite macroinvertebrate sample was taken from each sampling site (water depth <1.2 m) using standardised kick-sampling (10 min. sampling effort, hand net: 250- μm mesh, width 24 cm). In the laboratory, samples were sorted and counted using a stereo-dissecting microscope, and individuals were identified to the lowest taxonomic level possible.

Electric conductivity, DO concentration, pH and water temperature were recorded at each sampling site using a multiparameter probe (HydroLab H20; HydroLab Corporation, Austin, TX, U.S.A.). Habitat availability at the sampling sites was expressed as the proportion of CWD, pebbles, reed (*Phragmites australis*, Cav. Trin. ex Steud.), sand, stones, submerged macrophytes and roots (e.g. if roots were present at three of the six sampling sites they accounted for 50% availability). Root habitats consisted of submerged roots of riparian alder trees (*Alnus glutinosa*, L.) and constitute an important habitat type in the eulittoral zone of North-German lowland lakes.

Land use within a buffer zone around each lake (from the shoreline to 500-m inland) was estimated by GIS (ArcView, version 3.2, Esri, Redlands, CA, U.S.A.). Data on the lake surface area, TP concentration (annual mean concentrations in 2001), water residence time and trophic state were provided by the Regional Environmental Agency (Landesumweltamt Brandenburg). The 36 lakes were assigned to trophic state classes by the Regional Environmental Agency in 2001 (Länderarbeitsgemeinschaft Wasser [LAWA], 1998) using TP concentration, chlorophyll *a*, and water transparency and the classification system of Vollenweider & Kerekes (1982).

Habitat-specific analysis. Eulittoral macroinvertebrate samples were collected from 33 sampling sites in eight lakes in October 2003 and April 2004 (Table 1).

| Code | Lake | Area (km ²) | RT (year) | Trophic state | TP (µg L ⁻¹) |
|------------|--------------------------------|-------------------------|-----------|---------------|--------------------------|
| Ba | Blankensee | 2.9 | 1.2 | Hypertrophic | 366 |
| Be1 | Beetzsee, southern basin | 4.0 | 1.5 | Hypertrophic | 97 |
| Be2 | Beetzsee, middle basin | 1.9 | 1.5 | Hypertrophic | 97 |
| Be3 | Beetzsee, northern basin | 2.6 | 1.5 | Hypertrophic | 97 |
| Br | Breitlingsee | 5.1 | 2.8 | Hypertrophic | 121 |
| Fa | Fährsee | 2.1 | 4.0 | Mesotrophic | 43 |
| <u>Gi</u> | Grienericksee | 0.7 | 4.2 | Eutrophic | 37 |
| Gl | Glienicker See | 0.7 | 6.8 | Eutrophic | 29 |
| Gr | Grimnitzsee | 7.8 | 4.6 | Eutrophic | 50 |
| Gu | Gülper See | 4.4 | 0.6 | Hypertrophic | 278 |
| Ho | Hohennauener See | 3.6 | 3.4 | Hypertrophic | 104 |
| <u>Ku</u> | Küstrinsee | 2.2 | 6.0 | Mesotrophic | 27 |
| <u>La</u> | Langer See | 2.5 | 0.1 | Hypertrophic | 168 |
| Lu1 | Lübbesee, southern basin | 2.1 | 5.0 | Mesotrophic | 22 |
| Lu2 | Lübbesee, northern basin | 0.9 | 5.0 | Mesotrophic | 22 |
| Me | Mellensee | 2.2 | 3.3 | Hypertrophic | 96 |
| <u>Mu</u> | Müggelsee | 7.3 | 4.8 | Eutrophic | 108 |
| Ne | Neuendorfer See | 3.0 | 2.4 | Hypertrophic | 86 |
| Pa | Parsteiner See | 8.9 | 7.7 | Mesotrophic | 31 |
| <u>Pl</u> | Plauer See | 6.7 | 2.8 | Hypertrophic | 121 |
| Ra | Rangsdorfer See | 2.4 | 1.5 | Hypertrophic | 113 |
| Ro | Röddelinsee | 1.8 | 9.0 | Eutrophic | 52 |
| Ru1 | Ruppiner See, northern basin | 1.7 | 8.2 | Eutrophic | 108 |
| <u>Ru2</u> | Ruppiner See, southern basin | 6.3 | 8.2 | Eutrophic | 108 |
| Sa | Sacrower See | 1.1 | 19.3 | Eutrophic | 122 |
| Sc | Schwielochsee | 11.5 | 2.0 | Hypertrophic | 159 |
| Sm1 | Scharmützelsee, southern basin | 10.7 | 9.9 | Eutrophic | 64 |
| Sm2 | Scharmützelsee, northern basin | 1.2 | 9.9 | Eutrophic | 64 |
| Sn | Schauener See | 1.5 | 3.1 | Hypertrophic | 222 |
| So | Stolpsee | 3.8 | 6.4 | Eutrophic | 27 |
| St | Stechlinsee | 4.2 | 22.8 | Oligotrophic | 13 |
| Sw | Schwielowsee | 7.9 | 2.8 | Hypertrophic | 157 |
| <u>Un</u> | Unteruckersee | 10.4 | 9.2 | Mesotrophic | 25 |
| <u>We</u> | Werbellinsee | 7.8 | 22.1 | Mesotrophic | 26 |
| Wi | Wittwese | 1.6 | 5.5 | Mesotrophic | 14 |
| Wo | Wolziger See | 5.6 | 5.7 | Eutrophic | 102 |
| Wu | Wummsee | 1.5 | 11.8 | Oligotrophic | 18 |
| Ze | Zechliner See | 1.8 | 11.3 | Mesotrophic | 26 |

Table 1 Lake area (Area), residence time (RT), trophic state and total phosphorus concentration (TP, mean annual concentration of 2001) of 38 lakes

Underlined codes represent lakes sampled for habitat-specific analysis.

At each sampling site (water depth <1.2 m), the main habitat types (CWD, reed, roots, sand and stones) were sampled. Sampling effort differed among the different habitat types. Macroinvertebrates were brushed from three pieces of CWD (with bark) and sieved through a 250-µm mesh. The length and diameter of the CWD was measured to estimate surface area. For reed habitats, sampling consisted of five 1-m sweeps using a hand net (250-µm mesh, width 24 cm). The area of reed habitats sampled was estimated by multiplying hand net width by the length of the sampled area. In addition, reed stem density was determined by counting stems within a

0.25 m² area in each reed habitat. Five sub-samples from root habitats were collected with a hand net (250-µm mesh, width 24 cm), and the area sampled was estimated by multiplying hand net width by the water depth. Although the sampling techniques used for reed and root habitats did not permit the sampled area to be precisely quantified, they assured an efficient sampling of highly mobile species such as Dytiscidae (Coleoptera) that frequently colonise these structurally complex habitats. Sand habitats were sampled by taking 10 modified Surber samples (area 0.05 m², 250-µm mesh). At each site, sediment particle size (three size fractions: fine <0.03 mm; middle

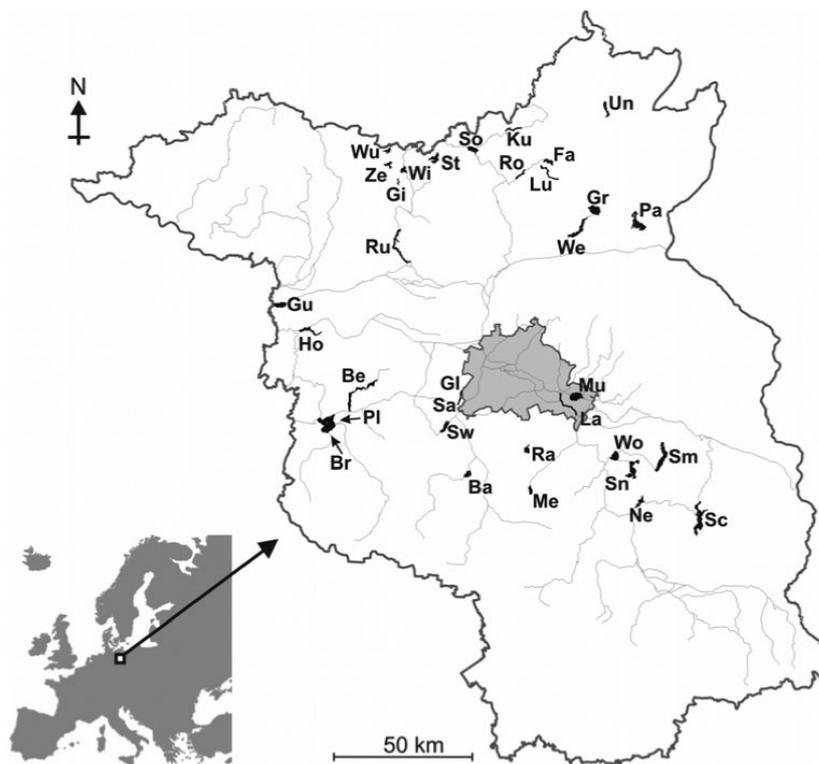


Fig. 1 Map of Europe (lower left), the federal states of Berlin (grey) and Brandenburg showing the location of the 38 study lakes. For lake codes see Table 1.

0.063–1.12 mm and coarse >2 mm, Analysette 3 Pro, Fritsch, Germany) was determined on the surficial sediment (top 5 cm) collected with a gravity corer (inner diameter 5 cm, UWITEC, Mondsee, Austria). Stone habitats were sampled by brushing macroinvertebrates from 10 arbitrarily selected stones. The length, height and width of the individual stones were used to calculate surface areas, assuming an ellipsoid shape. Surface areas estimated by ellipsoid surface calculation did not differ from estimations based on the more precise foil wrapping method (paired *t*-test, $P = 0.760$, $n = 20$). The multiple sub-samples for each habitat type were pooled in the field and processed as described above.

Wind exposure of each sampling station was calculated using the formula of Brodersen (1995) that combines data on frequency and velocity of the wind, fetch area and water depth at the sampling site. Wind data from nearby meteorological stations was provided by the German Weather Service.

Statistical analyses

Prior to statistical analyses, species that were recorded from only a single lake were removed from the lake- and habitat-specific datasets. Furthermore, we tested

if macroinvertebrate community composition differed between sampling dates using analysis of similarity (ANOSIM, PRIMER, version 5, Primer-E Ltd., Plymouth, U.K.). No differences were noted between seasons for the lake-specific community (R -statistic = 0.036, $P = 0.057$) or for the CWD (R -statistic = 0.047, $P = 0.146$), root (R -statistic = 0.017, $P = 0.325$) and stone (R -statistic = 0.017, $P = 0.579$) habitats. By contrast, communities of reed (R -statistic = 0.205, $P = 0.001$) and sand (R -statistic = 0.071, $P = 0.032$) habitats differed, but, albeit significant, the differences (as shown by the R -statistics) were small between sampling dates. Consequently, data from both sampling dates were pooled for further analyses.

Non-metric multidimensional scaling ordination (NMS) was used to examine relationships between macroinvertebrate community composition, TP concentration and other selected environmental variables. Non-metric multidimensional scaling was performed on square root-transformed relative abundances for lake-specific data and on square root-transformed densities (individuals m^{-2}) for habitat-specific data using the PC-ORD software (version 4.25, MjM Software, Gleneden Beach, OR, U.S.A.). Square root-transformation was used as it results in a medium down-weighting of common species and allows for a

good discrimination of sampling sites (Clarke & Warwick, 2001).

Bray–Curtis distance was used in NMS ordination with the stability criterion set at 0.0001, 100 iterations to evaluate stability and initial step length set at 0.2. The appropriate dimensionality was chosen based on results of a Monte Carlo test (100 runs, $P = 0.01$). The final run was carried out with the optimum dimensionality as the starting configuration and by applying varimax rotation (McCune & Grace, 2002). Pearson's correlation (SPSS version 9.0, SPSS, Chicago, IL, U.S.A.) between lake scores from the NMS axes and environmental variables was performed to determine the best predictors of the variability in community composition. For correlation analyses, environmental data were tested for deviation from normality and transformed when necessary using arcsine square root-transformation on proportional and Box–Cox transformation (Box & Cox, 1964) on continuous data.

In addition to the habitat-specific analyses, we tested if trophic state or habitat type was the more important driver of macroinvertebrate community composition in lowland lakes. Using pooled macroinvertebrate data for each lake and habitat type, we calculated Bray–Curtis dissimilarities for all combinations with habitat type nested within trophic state ($n = 30$) and with trophic state nested within habitat type ($n = 15$). Between-group differences were tested using a Mann–Whitney test (SPSS version 9.0, SPSS), assuming that if trophic state was the more important driver of macroinvertebrate community composition then compositional dissimilarities among trophic states within a habitat type would be higher than dissimilarities among habitat types within a given trophic state.

Results

Lake-specific analysis

Total phosphorus concentration was significantly correlated with NMS axis 1 and lakes were arranged by trophic state, with oligo- to mesotrophic lakes being grouped in the upper left and eu- to hypertrophic lakes in the lower right part of the NMS plot (Table 2, Fig. 2). However, oligotrophic Lake Wummssee as well as several eutrophic and hypertrophic lakes such as Mellensee and Neuendorfer See were positioned closer to the mesotrophic lakes, indicating similarities in community composition (Fig. 2). Only

Table 2 Environmental variables included in the lake-specific analysis and Pearson's correlation coefficients with non-metric multidimensional scaling (NMS) axes (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$)

| | | NMS | |
|---|-----------------|----------|----------|
| Number of axes | | 3 | |
| Stress | | 0.13 | |
| Cumulative variance (%) | | 86.0 | |
| Variable (unit) | Mean (min–max) | Axis 1 | Axis 2 |
| Land use (%) | | | |
| Agriculture | 17 (0–55) | | |
| Forest | 41 (0–93) | –0.46** | 0.54*** |
| Grassland | 7 (0–24) | 0.66*** | –0.43** |
| Impervious surface | 12 (0–60) | | –0.54*** |
| Water | 8 (0–20) | –0.41** | |
| Habitat type (%) | | | |
| Coarse woody debris | 39 (0–100) | | 0.56*** |
| Pebbles | 6 (0–83) | –0.44** | 0.41* |
| Reed | 60 (17–100) | | |
| Roots | 28 (0–100) | –0.51*** | 0.62*** |
| Sand | 50 (17–100) | –0.51** | |
| Stones | 12 (0–67) | –0.53*** | |
| Submerged macrophytes | 18 (0–50) | | 0.48** |
| Lake water | | | |
| Conductivity ($\mu\text{S cm}^{-1}$) | 510 (216–1001) | 0.45** | –0.61*** |
| Dissolved oxygen (mg L^{-1}) | 10.7 (8.6–12.7) | | |
| pH | 8.5 (7.7–8.9) | | |
| Temperature ($^{\circ}\text{C}$) | 13.0 (7.3–21.4) | | |
| Total phosphorus ($\mu\text{g L}^{-1}$) | 89 (13–366) | 0.76*** | –0.70*** |
| Hydrology | | | |
| Water residence time (year) | 8.6 (0.0–57.8) | –0.35* | 0.55*** |

23% of all species recorded were significantly correlated with NMS axis 1, among them *Dreissena polymorpha* (Pallas) (Bivalvia) and *Lype phaeopa* (McLachlan) (Trichoptera) that decreased in abundance along NMS axis 1 (Table 3). On NMS axis 2, lakes were arranged along a gradient of decreasing proportion of CWD and roots and increasing conductivity (Fig. 2, Table 2). Lakes with high proportions of CWD, roots and a low conductivity were characterised by high abundances of *Palpomyia* sp. (Diptera), *Oulimnius* sp. (Coleoptera) and *Gammarus pulex* (L.) (Crustacea), whereas the invasive crustaceans *Dikergammarus* sp. and *Pontogammarus robustoides* (Sars) were characteristic for the lakes with high conductivity and low proportions of allochthonous habitats (Table 3). Hence, these findings indicate that TP and habitat characteristics were the main factors influencing the composition of the eulittoral macroinvertebrate communities.

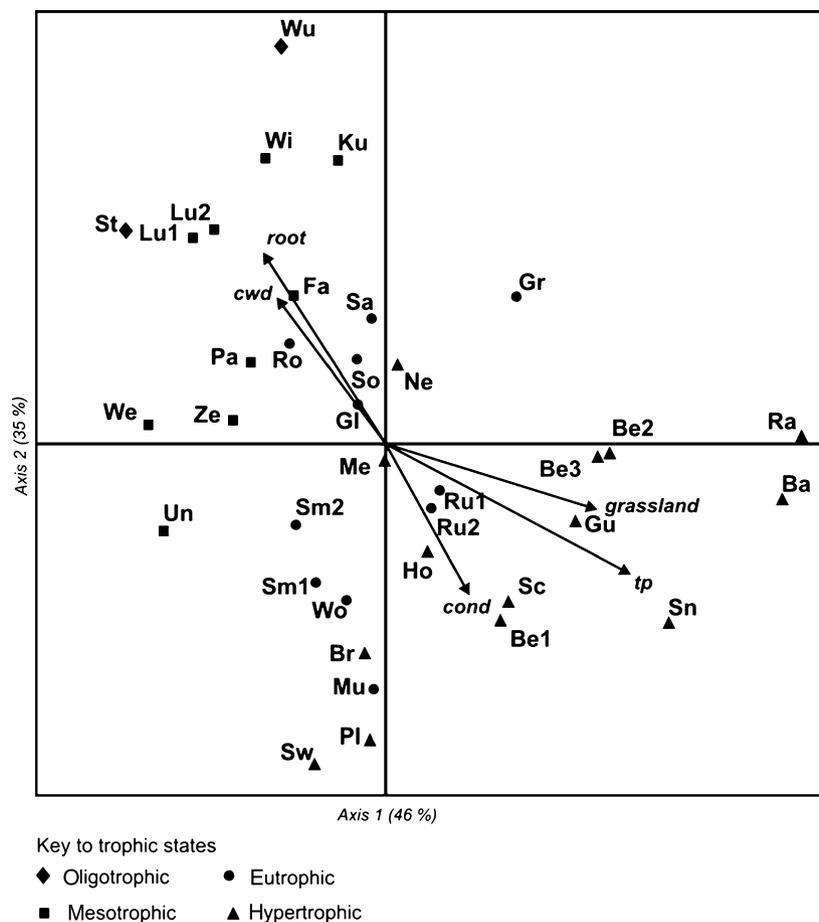


Fig. 2 Non-metric multidimensional scaling (NMS) ordination of 36 lakes of the lake-specific analysis. Only the first two NMS axes are shown as axis 3 explained only 5% of the variance. The trophic state of each lake is superimposed. The most important environmental variables (*italic*) (Pearson's r to NMS axes >0.55) are displayed as vectors (*cond*, conductivity; *cwd*, proportion of coarse woody debris habitats; *grassland*, proportion of grassland; *root*, proportion of root habitats; *tp*, total phosphorus). For lake codes see Table 1, for stress, number of axes and cumulative explained variance see Table 2.

Habitat-specific analysis

The relative importance of TP and habitat type was further studied on the habitat-specific level with an initial comparison of dissimilarities. Dissimilarity among trophic states within a given habitat type (median = 77.6, range 68.8–89.6) was lower than dissimilarity among habitat types within a given trophic state (median = 84.8, range 51.8–93.0) (Mann–Whitney test, $P = 0.001$). Based on this result, we performed NMS analyses on habitat-specific macroinvertebrate communities to test whether discrimination of trophic state by macroinvertebrate communities differed between habitat types.

Coarse woody debris

Non-metric multidimensional scaling and correlation analyses showed that TP concentration was significantly correlated with community composition along

NMS axis 1 (Table 4). Furthermore, this axis was correlated with densities of the invasive crustaceans *Dikerogammarus villosus* (Sowinsky) ($r = -0.90$, $P = 0.000$) and *Chelicorophium curvispinum* (Sars) ($r = -0.83$, $P = 0.000$). For example, mean density (\pm SE) of *C. curvispinum* increased markedly from 5 ± 3 individuals m^{-2} in mesotrophic to 919 ± 667 individuals m^{-2} in hypertrophic lakes.

Reed

Community composition of reed habitats was significantly correlated with conductivity, wind exposure and water residence time but not TP concentration (Table 4). Furthermore, wind exposure was significantly correlated with stem density ($r = -0.73$, $P = 0.001$). Densities of Ephemeroptera *Cloeon dipterum* (L.) and *Caenis luctuosa* (Burmeister) were highly correlated with NMS axis 1 (both $r = -0.69$, $P = 0.002$).

Table 3. Pearson's correlation coefficients of macroinvertebrate species with non-metric multidimensional scaling axes of the lake-specific analysis

| Species | Axis 1 | Axis 2 |
|-------------------------------------|--------|--------|
| <i>Alboglossiphonia heteroclita</i> | 0.60 | |
| <i>Brachytron pratense</i> | | 0.67 |
| <i>Centroptilum luteolum</i> | | 0.67 |
| Chironomidae | 0.68 | |
| <i>Cyrrhus flavidus</i> | | 0.60 |
| <i>Dikerogammarus</i> sp. | | -0.60 |
| <i>Dreissena polymorpha</i> | -0.80 | |
| <i>Gammarus pulex</i> | | 0.78 |
| <i>Halesus radiatus</i> | | 0.58 |
| <i>Haliplus fulvus</i> | | 0.57 |
| <i>Hydroglyphus hamulatus</i> | | 0.60 |
| <i>Kageronia fuscogrisea</i> | | 0.59 |
| <i>Leptophlebia marginata</i> | | 0.65 |
| <i>Lype phaeopa</i> | -0.63 | |
| <i>Nemoura cinerea</i> | | 0.61 |
| <i>Oulimnius</i> sp. | | 0.79 |
| <i>Oxyethira</i> sp. | | 0.67 |
| <i>Palpomyia</i> sp. | | 0.80 |
| <i>Pontogammarus robustoides</i> | | -0.65 |
| <i>Potamopyrgus antipodarum</i> | -0.77 | |
| <i>Stagnicola</i> sp. | | 0.62 |

Only species with correlation coefficients >0.55 are shown ($P < 0.001$).

Roots

Community composition of root habitats was correlated with TP concentration, conductivity, pH, water

Table 4 Environmental variables included in the habitat-specific analysis and Pearson's correlation coefficients with the non-metric multidimensional scaling axes (** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$)

| | | Coarse woody debris | Reed | Roots | Sand | Stones | | |
|--|-----------------|---------------------|--------|----------|--------|----------|--------|---------|
| | Mean | | | | | | | |
| | (min-max) | Axis 1 | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Number of axes | | 2 | 3 | 2 | 2 | 2 | | |
| Stress | | 0.14 | 0.11 | 0.09 | 0.12 | 0.09 | | |
| Cumulative variance (%) | | 70.3 | 75.6 | 89.7 | 78.5 | 79.0 | | |
| <i>Habitat attributes</i> | | | | | | | | |
| <i>Sediment particle size (%)</i> | | | | | | | | |
| <0.03 mm | 0.7 (0.0–3.7) | | | | | -0.49* | | |
| 0.063–1.12 mm | 88 (13.6–100) | | | | 0.47* | | | |
| >2 mm | 12 (0.1–85) | | | | -0.45* | | | |
| Stem density (no. m ⁻²) | 129 (40–240) | | | | | | | |
| Wind exposure | 0.8 (0.0–2.6) | | 0.63** | | | | | 0.69*** |
| <i>Lake water</i> | | | | | | | | |
| Conductivity (µS cm ⁻¹) | 552 (371–791) | 0.59* | -0.53* | -0.72** | -0.49* | -0.88*** | | |
| Dissolved oxygen (mg L ⁻¹) | 11 (8.6–12.6) | | | 0.67** | | | | |
| pH | 8.0 (6.3–8.6) | 0.62* | | -0.80*** | 0.44* | -0.73*** | | |
| Temperature (°C) | 9.4 (6.4–11.6) | | | | | -0.66*** | | |
| Total phosphorus (µg L ⁻¹) | 77 (25–168) | 0.53* | | -0.83*** | | 0.52** | | |
| <i>Hydrology</i> | | | | | | | | |
| Water residence time (year) | 12.3 (0.0–54.8) | | | -0.48* | 0.73** | | 0.62** | -0.54* |

residence time and DO (Table 4). Similarly, the density of the native *G. pulex* was negatively ($r = -0.74$, $P = 0.002$) and the density of the invasive *P. robustoides* was positively ($r = 0.76$, $P = 0.002$) correlated with NMS axis 1.

Sand

Community composition of sand habitats was correlated with TP concentration and sediment particle size (Table 4). In particular, sediment particle size was a strong predictor of macroinvertebrate composition. Densities of almost 45% of all species recorded from sand habitats were significantly negatively correlated with NMS axis 1, which was explained by an increase in the middle particle fraction (0.063–1.12 mm) and a decrease in the coarse particle fraction (>2 mm). Ordination of sampling sites along NMS axis 2 followed a gradient of increasing TP concentration and decreasing proportion of the fine particle fraction (<0.03 mm) (Table 4). However, only 9% of all species recorded were significantly correlated with this axis.

Stones

Community composition of stone habitats was significantly correlated with wind exposure and water residence time but not TP concentration (Table 4);

hence, community composition responded in a complex pattern to these environmental factors. The density of invasive species was negatively correlated with NMS axis 1. For example, the strongest correlation was shown by *D. polymorpha* ($r = -0.97$, $P = 0.000$); this species increased more than 10-fold from lakes with high water residence times (groundwater supplied lakes) to lakes with low water residence times (riverine lakes). Conversely, densities of lotic species, such as *Oulimnius tuberculatus* (Müller) (Coleoptera) ($r = 0.56$, $P = 0.017$) and *Theodoxus fluviatilis* (L.) (Gastropoda) ($r = 0.64$, $P = 0.005$) increased along NMS axis 1.

Discussion

Lake-specific analysis

Distinct differences in composition of eulittoral macroinvertebrate communities were found between oligotrophic and hypertrophic lakes. However, similarities between oligotrophic and mesotrophic and between mesotrophic and eutrophic lakes indicated that community composition between these trophic states was less distinct. Even the compositional differences between oligotrophic and hypertrophic lakes were not unequivocally related to differences in TP concentration, as the proportion of grassland was also related to community composition. Grasslands are predominantly used as pasture, and hence it seems unlikely that they constitute a potential source of nutrient inputs. This conjecture was also supported by the lack of a significant relationship between grassland and TP concentration (Pearson's $r = 0.23$, $P = 0.174$). However, lakes with a high proportion of grassland in their buffer zones often lacked of riparian trees, as this type of land use usually extended to the lakeshore. Hence, we assume here that grassland may reflect the effects of human-generated shoreline modification and a decrease in the amount of CWD in the littoral zone (Christensen *et al.*, 1996). This is supported by the distribution of the wood-associated *L. phaeopa* (Hoffmann & Hering, 2000) which decreased in abundance as the proportion of grassland increased. Similarly, the low abundances of *D. polymorpha* in hypertrophic lakes may not be directly related to trophic state (Ludyanskiy, McDonald & MacNeil, 1993), but may rather indicate a lack of suitable habitat such as CWD. Indeed, macro-

invertebrate community composition was strongly related to the presence of CWD and root habitats, both of which contribute to habitat heterogeneity and are known to be good predictors of macroinvertebrate community composition (Nilsson, Elmberg & Sjöberg, 1994; Heino, 2000; Harrison & Hildrew, 2001).

Habitat-specific analysis

Macroinvertebrate communities were more dissimilar among habitat types than among trophic states, indicating the importance of intrinsic habitat properties in determining community composition. Trophic state was shown to be a good predictor of the community composition of CWD, root and sand habitats, while community composition of sand habitats was also determined by small-scale differences in the structural complexity of sediments. As more species were related to particle size than to TP concentration, we conclude that trophic state may not be the primary factor determining the shift in community composition observed in sand habitats. For CWD and root habitats, considerably higher densities of invasive crustaceans were related to high trophic state. However, the predominance of invasive species in hypertrophic lakes may not necessarily be related directly to increased TP concentration, but may rather be a result of the low water residence times in these hypertrophic lakes. In the lowland lakes studied here, low water residence times reflect a connection to a larger river system that also serves as a commercial navigation route. Furthermore, as commercial navigation is known to accelerate the dispersal of invasive species (de Vaate *et al.*, 2002; Grigorovich *et al.*, 2003; Duggan *et al.*, 2005), there is a higher probability for these lakes to be colonised by invasive species. As hypertrophic state and the predominance of invasive species coincided, the observed compositional differences among trophic states cannot be unambiguously related to differences in TP concentration, as mass occurrences of invasive species might similarly affect community composition (Hall & Mills, 2000; Rahel, 2002). Hence, two alternative explanations are possible for the observed differences in community composition of CWD and root habitats. Eutrophication might have caused an extinction of native species and a subsequent colonisation of the vacant ecological niches by invasive species. Alternatively, invasive species might have outcompeted native species, implying that biotic

interactions and not trophic state resulted in the observed differences. At least *D. villosus* might actively displace native species regardless of trophic state, because it exerts a strong predatory impact on native species (Dick, Platvoet & Kelly, 2002; Krisp & Maier, 2005; MacNeil & Platvoet, 2005). Thus, it remains unclear whether the predominance of invasive species in the hypertrophic lakes studied here was the cause or the consequence of the alteration of the macroinvertebrate communities of the CWD and root habitats and whether these communities discriminate among trophic states.

Wind exposure but not TP concentration was significantly correlated to macroinvertebrate community composition of the reed and stone habitats. Moreover, this result was unaffected by the smaller range of TP concentration in the habitat-specific dataset (no oligotrophic lakes), as the correlation coefficient between TP and lake-specific NMS axis 1 decreased only slightly (from $r = 0.76$, $P = 0.000$ to $r = 0.66$, $P = 0.000$) after omitting oligotrophic lakes ($TP < 27 \mu\text{g L}^{-1}$) from the lake-specific correlation analysis. Assuming that the effect of TP range on statistical results was similar in the habitat-specific dataset, we conclude that the lack of a significant relationship between trophic state and macroinvertebrate community composition of reed and stone habitats was not an artefact of the study design. This finding is also supported by earlier studies that have shown how eulittoral macroinvertebrate communities on stony shores reflect environmental variables other than trophic state (Barton & Carter, 1982; Dall *et al.*, 1984; Johnson & Goedkoop, 2002).

While community composition in stone habitats was directly related to wind exposure, community composition in reed habitats reflected more the effect of wind exposure on stem density. Increasing the density of macrophyte stands has been shown to influence community composition by providing refuges against predation (Diehl, 1992; Tolonen *et al.*, 2003; Warfe & Barmuta, 2004; Rennie & Jackson, 2005). In our study, a high density of reed stands also seemed to favour the sedimentation of organic detritus, which was reflected in higher densities of the detritus collecting mayflies' *C. luctuosa* and *C. dipterum* (Schmedtje & Colling, 1996).

Macroinvertebrate community composition was related to conductivity, pH and DO in the habitat types. However, as these environmental variables

exhibited little variability and did not reach extreme values that would directly affect community composition, we conclude that there is no mechanistic relation between conductivity, pH, DO and macroinvertebrate community composition.

In conclusion, trophic state influenced the composition of the macroinvertebrate community of the eulittoral zone, but not as much as has been previously reported for profundal communities (Thienemann, 1921; Saether, 1979; Brodersen & Lindegaard, 1999; Langdon *et al.*, 2006). Furthermore, our study showed that the effects of trophic state were nested within habitat type, and were partially superseded by biotic interactions and small-scaled habitat complexity (Fig. 3). For example, the influence of trophic state on macroinvertebrate communities of stone habitats was seemingly counteracted by wind exposure (Fig. 3), lending support to a number of other studies (Macan & Maudsley, 1969; Brodersen *et al.*, 1998; Johnson & Goedkoop, 2002). Moreover, our results indicate that eulittoral macroinvertebrate communities of the lowland lakes are not a reliable indicator of trophic state, as they were influenced by a number of factors, such

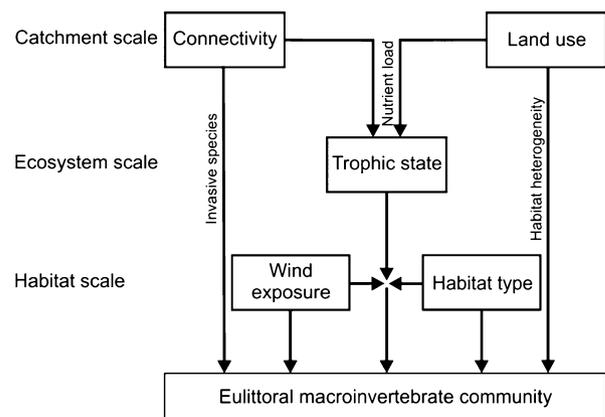


Fig. 3 Conceptual diagram representing the major environmental factors influencing the eulittoral macroinvertebrate communities of lowland lakes. Environmental variables act at different spatial scales, and connectivity of the lake to a larger river system influences macroinvertebrates either directly by accelerating the immigration of invasive species, or indirectly by increasing nutrient loads resulting in eutrophication. Land use influences macroinvertebrates directly through the alteration of littoral habitat structure, and indirectly via nutrient loading. Nutrient load determines the trophic state that in turn influences conditions in habitats in the lake ecosystem. Wind exposure and habitat type influence macroinvertebrates directly and substantially modify the effect of trophic state on the composition of the macroinvertebrate community.

as lake connectivity, habitat type, land use and wind exposure (Fig. 3). However, our results suggest that eulittoral macroinvertebrates may be useful for assessing other anthropogenic impacts such as human-generated effects on littoral habitats.

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References

- Barton D.R. & Carter J.C.H. (1982) Shallow-water epilithic invertebrate communities of eastern Georgian Bay, Ontario, in relation to exposure to wave action. *Canadian Journal of Zoology*, **60**, 984–993.
- Behrendt H. (1996) Inventories of point and diffuse sources and estimated nutrient loads – a comparison for different river basins in Central Europe. *Water Science and Technology*, **33**, 99–107.
- Box G.E.P. & Cox D.R. (1964) An analysis of transformations. *Journal of the Royal Statistical Society Series B*, **26**, 211–252.
- Brodersen K.P. (1995) The effect of wind exposure and filamentous algae on the distribution of surf zone macroinvertebrates in Lake Esrom, Denmark. *Hydrobiologia*, **597**, 131–148.
- Brodersen K.P. & Lindegaard C. (1999) Classification, assessment, and trophic reconstruction of Danish lakes using chironomids. *Freshwater Biology*, **42**, 143–157.
- Brodersen K.P., Dall P.C. & Lindegaard C. (1998) The fauna in the upper stony littoral of Danish lakes: macroinvertebrates as trophic indicators. *Freshwater Biology*, **39**, 577–592.
- Carpenter S.R., Caraco N.F., Correll D.L., Howarth R.W., Sharpley A.N. & Smith V.H. (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications*, **8**, 559–568.
- Chandra S., Vander Zanden M.J., Heyvaert A.C., Richards B.C., Allen B.C. & Goldman C.R. (2005) The effects of cultural eutrophication on the coupling between pelagic primary producers and benthic consumers. *Limnology and Oceanography*, **50**, 1368–1376.
- Christensen D.L., Herwig B.R., Schindler D.E. & Carpenter S.R. (1996) Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecological Applications*, **6**, 1143–1149.
- Clarke K.R. & Warwick R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd edn. PRIMER-E, Plymouth.
- Dall P.C., Lindegaard C., Jonsson E., Jonsson G. & Jonasson P.M. (1984) Invertebrate communities and their environment in the exposed littoral zone of Lake Esrom. *Archiv für Hydrobiologie*, **69**, 477–524.
- Dick J.T.A., Platvoet D. & Kelly D.W. (2002) Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1078–1084.
- Diehl S. 1992. Fish predation and benthic community structure – the role of omnivory and habitat complexity. *Ecology*, **73**, 1646–1661.
- Duggan I.C., van Overdijk C.D.A., Bailey S.A., Jenkins P.T., Limen H. & MacIsaac H.J. (2005) Invertebrates associated with residual ballast water and sediments of cargo-carrying ships entering the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2463–2474.
- Egertson C.J., Kopaska J.A. & Downing J.A. (2004) A century of change in macrophyte abundance and composition in response to agricultural eutrophication. *Hydrobiologia*, **524**, 145–156.
- Grigorovich I.A., Colautti R.I., Mills E.L., Holeck K., Ballert A.G. & MacIsaac H.J. (2003) Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 740–756.
- Hall S.R. & Mills E.L. (2000) Exotic species in large lakes of the world. *Aquatic Ecosystem Health and Management*, **3**, 105–135.
- Harrison S.S.C. & Hildrew A.G. (2001) Epilithic communities and habitat heterogeneity in a lake littoral. *Journal of Animal Ecology*, **70**, 692–707.
- Heino J. (2000) Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. *Hydrobiologia*, **418**, 229–242.
- Hoffmann A. & Hering D. (2000) Wood-associated macroinvertebrate fauna in Central European streams. *International Review of Hydrobiology*, **85**, 25–48.
- Johnson R.K. & Goedkoop W. (2002) Littoral macroinvertebrate communities: spatial scale and ecological relationships. *Freshwater Biology*, **47**, 1840–1854.
- Krisp H. & Maier G. (2005) Consumption of macroinvertebrates by invasive and native gammarids: a comparison. *Journal of Limnology*, **64**, 55–59.

- Länderarbeitsgemeinschaft Wasser (LAWA) (1998) *Gewässerbewertung stehender Gewässer. Vorläufige Richtlinie für eine Erstbewertung von natürlich entstandenen Seen nach trophischen Kriterien*. LAWA, Berlin.
- Langdon P.G., Ruiz Z., Brodersen K.P. & Foster I.D.L. (2006) Assessing lake eutrophication using chironomids: understanding the nature of community response in different lake types. *Freshwater Biology*, **51**, 562–577.
- Ludyanskiy M.L., McDonald D. & MacNeil D. (1993) Impact of the zebra mussel, a bivalve invader – *Dreissena polymorpha* is rapidly colonizing hard surfaces throughout waterways of the United States and Canada. *BioScience*, **43**, 533–544.
- Macan T.T. & Maudsley R. (1969) Fauna of the stony substratum in lakes in the English Lake District. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **17**, 173–180.
- MacNeil C. & Platvoet D. (2005) The predatory impact of the freshwater invader *Dikerogammarus villosus* on native *Gammarus pulex* (Crustacea: Amphipoda); influences of differential microdistribution and food resources. *Journal of Zoology*, **267**, 31–38.
- McCune B. & Grace J.B. (2002) *Analysis of Ecological Communities. Version 4*. MjM Software Design, Glenden Beach, Oregon.
- Nilsson A.N., Elmberg J.K. & Sjöberg K. (1994) Abundance and species richness patterns of predaceous diving beetles (Coleoptera, Dytiscidae) in Swedish lakes. *Journal of Biogeography*, **21**, 197–206.
- Rahel F.J. (2002) Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics*, **33**, 291–315.
- Rennie M.D. & Jackson L.J. (2005) The influence of habitat complexity on littoral invertebrate distributions: patterns differ in shallow prairie lakes with and without fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2088–2099.
- Saether O.A. (1979) Chironomid communities as water quality indicators. *Holarctic Ecology*, **2**, 65–74.
- Sanyanga R.A. & Hlanga L. (2004) Limnology of Zimbabwe. In: *Limnology in Developing Countries* (Eds B. Gopal & R.G. Wetzel), pp. 117–170. International Scientific Publications, New Delhi.
- Schmedtje U. & Colling M. (1996) Ökologische Typisierung der aquatischen Makrofauna. *Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft*, **4**, 1–548.
- Thienemann A. (1918) Untersuchungen über die Beziehungen zwischen dem sauerstoffgehalt des wassers und der zusammensetzung der fauna norddeutscher seen. *Archiv für Hydrobiologie*, **12**, 1–65.
- Thienemann A. (1921) Seetypen. *Naturwissenschaften*, **18**, 1–3.
- Thienemann A. (1928) Der Sauerstoff im eutrophen und oligotrophen see. *Die Binnengewässer*, **4**, 1–175.
- Tolonen K.T., Hamalainen H., Holopainen I.J. & Karjalainen J. (2001) Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. *Archiv für Hydrobiologie*, **152**, 39–67.
- Tolonen K.T., Hamalainen H., Holopainen I.J., Mikkonen K. & Karjalainen J. (2003) Body size and substrate association of littoral insects in relation to vegetation structure. *Hydrobiologia*, **499**, 179–190.
- de Vaate A.B., Jazdzewski K., Ketelaars H.A.M., Gollasch S. & Van der Velde G. (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1159–1174.
- Vadeboncoeur Y., Jeppesen E., Vander Zanden M.J., Schierup H.H., Christoffersen K. & Lodge D.M. (2003) From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography*, **48**, 1408–1418.
- Vitousek P.M., Aber J.D., Howarth R.W., Likens G.E., Matson P.A., Schindler D.W., Schlesinger W.H. & Tilman D.G. (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737–750.
- Vollenweider R.A. (1968) Scientific fundamentals of the eutrophication of lakes and flowing waters with particular reference to nitrogen and phosphorus as factors in eutrophication. *OECD Report DAS/CJS*, **68**, 1–250.
- Vollenweider R.A. & Kerekes J. (1982) *Eutrophication of waters. Monitoring, assessment and control*. Organization for Economic Co-operation and Development (OECD) Paris, 1–154.
- Warfe D.M. & Barmuta L.A. (2004) Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia*, **141**, 171–178.

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