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Oligochaete Distribution Patterns in Two German Hardwater Lakes of Different Trophic State

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With 7 Figures and 4 Tables

Key words: Oligochaeta, species composition, distribution patterns, lake trophic state, multivariate analysis

Abstract

We investigated the effect of contrasting trophic conditions on the distribution and dominance patterns of Oligochaeta species assemblages in lake sediments and their relation to the environmental variables depth, season, and substrate. The study was performed on the highly eutrophic Lake Haussee and the oligotrophic Lake Stechlin, both hardwater lakes in the Baltic Lake District of Northern Germany. Quantitative monthly and seasonal sampling took place over one year at 14 representative sites, covering littoral and profundal sediments of both lakes. Between-lake differences in the profundal were clearcut with an absence of any zoobenthos in Lake Haussee and a peculiar meiobenthic species assemblage in Lake Stechlin (COLLADO et al. 1999). Between-lake differences in the littoral, however, were small and mainly attributable to a small number of species exclusive to Lake Stechlin and an overall higher abundance of oligochaetes, especially naidids, in Lake Haussee. Species-richest family in both lakes were Naididae; Tubificidae were dominant in Lake Stechlin; in Lake Haussee Tubificidae and Naididae were equally abundant. Most striking were diversity of habitat types and species distribution patterns in the littoral. Multivariate analysis (CA, CCA) showed that the distribution patterns of oligochaete species assemblages are significantly correlated with depth, season and substrate. Depth is the major factor when the whole water body is considered. When confining to the littoral, species abundance and distribution are strongly related to seasonality and substrate type. Naididae show, in general, maximal abundances in autumn and summer and a preference for plants, plant debris and soft sediments; Tubificidae are more abundant in spring and prefer mineral substrate. The relation between seasonality, substrate and food availability is discussed.

Introduction

Lake Haussee („Feldberger Haussee“) and Lake Stechlin („Stechlinsee“) are well-characterized and intensely studied hardwater lakes located in the Baltic Lake District of Northern Germany (CASPER 1985; CASPER & KOSCHEL 1995; KOSCHEL et al. 1993; KASPRZAK et al. 1988, 1993; KRIENITZ et al. 1996; MEHNER et al. 2001). The former is classified as eutrophic (KOSCHEL et al. 1985; KRIENITZ et al. 1996), the latter is an example of an oligotrophic hardwater lake (CASPER & KOSCHEL 1995). The large amount of hydrological, limnological and sediment data available for the two lakes, and their similar size class, water chemistry and stratification patterns, make them especially suitable for a comparative study of species distribution in contrasting trophic conditions. We wanted to know, whether and in which way the species assemblages of aquatic annelids reflect this contrast in trophism. Another objective was to analyze the main patterns of annelid distribution in these types of lakes in relation to environmental variables.

For this purpose, a programme of qualitative and quantitative samples was carried out in both lakes covering all depth zones and as many habitat types as possible. As there was very little previous information about the zoobenthic species composition in both lakes (CASPER 1985), this study also contributed to the faunistic knowledge of Lake Haussee and Lake Stechlin. The species inventory of Oligochaeta and Aphanoneura yielded 59 taxa, 52 of them determined to species level (COLLADO et al. 1999). Surprisingly, Lake Stechlin was only slightly species-richer (53 species) than Lake Haussee (41 species). In both lakes, the littoral was species-richest and most diverse. Sublittoral and profundal of Lake Stechlin exhibited peculiar species assemblages mainly composed of meiobenthic naidids, whereas the profundal of Lake Haussee was nearly devoid of any kind of zoobenthos.

In this paper we present and analyze the dominance and distribution patterns of the studied oligochaete communities. We compare the species assemblages of both lakes in order to evaluate the influence of the general trophic conditions on the dominance and distribution patterns on the aquatic annelids. We further analyze, by means of multivariate analysis, the main patterns of oligochaete spatial and temporal distribution in relation to environmental variables in the littoral. Studies on oligochaetes in lakes often neglect the littoral and concentrate on the spatially and temporally more homogeneous profundal in order to detect trophic indicators (e.g. LANG 1989; SÄRKKÄ 1994). The focus here is on the littoral because of its species richness and habitat complexity.

Fig. 1. Location of Lake Stechlin and Lake Haussee in Germany.

Descriptions of studied sites

Lake Haussee and Lake Stechlin, both located in northeastern Germany (Fig. 1), belong to the Mecklenburg Lake District („Mecklenburgische Seenplatte“) which itself is part of the Baltic Lake District, formed by melting of dead ice blocks after the last glaciation, about 12,000 years ago. Both lakes are hardwater lakes. The climate of the area is characterized by maritime influence with moderately warm summer and relatively mild winter seasons. The macro-climate belongs to the humid-moderate climates of Europe.

Lake Stechlin (Fig. 2) lies on the northern border of State Brandenburg, 53°10' NL and 13°02' EL. The deepest point of the lake basin (68 m) lies at the intersection of two dead ice channels. They are the basis for the cross-like outline of the lake. The lake is divided into four basins or bays. 80% of the area is covered with forest. The lake shores are entirely surrounded by mixed forests, mainly consisting of beeches, pines, willows and alders; the fallen leaves are deposited on the bottom of the littoral and profundal region, giving the lake a limnological peculiarity designated by the high organic carbon content of the profundal sediments. Profundal sediments are a calcite-free, fine-grained gyttja rich in organic carbon, with a 100 cm thick layer of fluid/soft sediment (MOTHES & PROFT 1985; PROFT 1995). Lake Stechlin is a dimictic lake with complete circulation periods in spring and autumn. Mean summer oxygen saturation in 65 m depth is

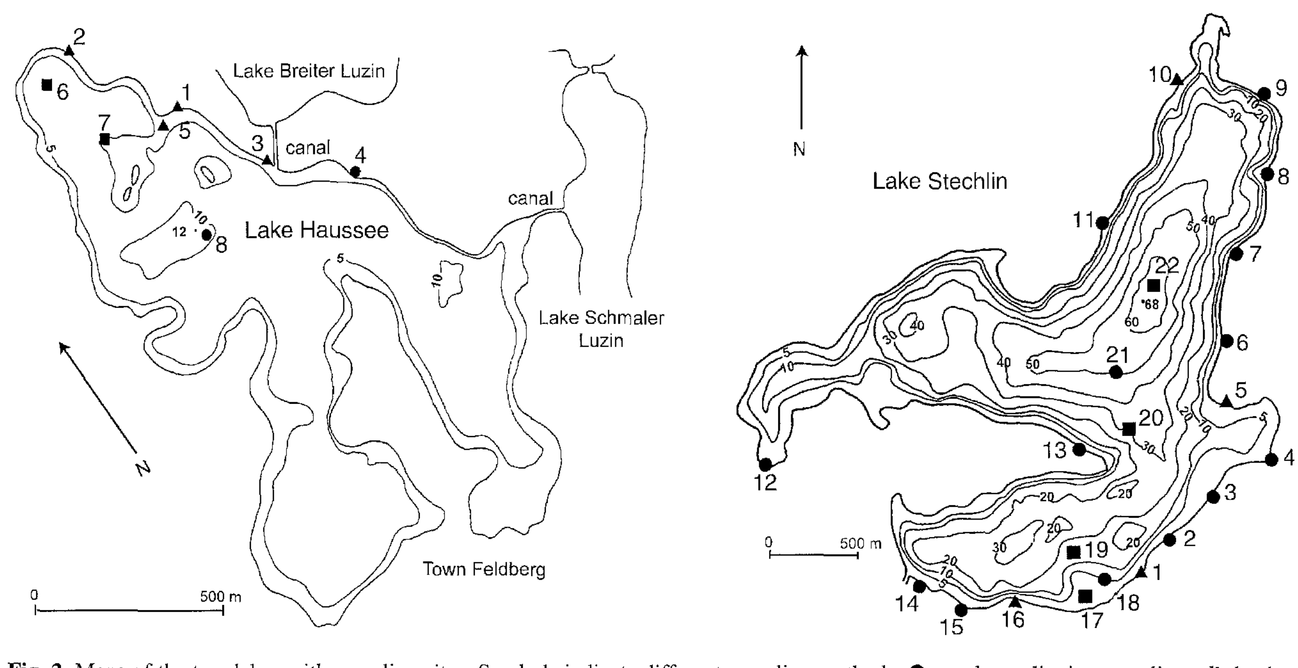

Fig. 2. Maps of the two lakes with sampling sites. Symbols indicate different sampling methods: ● = only qualitative sampling, all depths, species inventory; ■ = quantitative, sublittoral and profundal, seasonal; ▲ = quantitative, littoral, monthly.

well above 60% (Table 1). At present, the lake is characterized as oligotrophic (Table 1).

Lake Haussee (Fig. 2) is located about 100 km north of Berlin near the town of Feldberg (Mecklenburg-Vorpommern, Germany). It is much shallower than Lake Stechlin (average depth 6 m, max.12 m), but stratified as well. It consists of four basins, the two southernmost of them being surrounded by the town of Feldberg (4000 inhabitants). The catchment area of Lake Haussee is 400 ha (KOSCHEL et al. 1985), 40% of which is developed area (buildings, gardens, etc.), 30% forest, 30% grassland. The main lake water supply is by atmospheric precipitation. Lake Haussee is dimictic with complete circulation in spring and autumn. Summer stagnation period is from mid-May to mid-September. From mid-June to mid-September, the hypolimnion is anoxic (see Table 1), whereas the epilimnion is often oversaturated with oxygen. At present, Lake Haussee is characterized as eutrophic (e.g. KRIENITZ et al. 1996; MEHNER et al. 2001).

For more information see CASPER (1985), CASPER & KOSCHEL (1995), RICHTER & RICHTER (1986) and KOSCHEL et al. (1985). Actual limnological criteria are given in Table 1.

Methods

Sampling

First, a series of qualitative samples was realized in the littoral and profundal of both lakes for an oligochaete species inventory. Number and locations of sampling sites were chosen to maximise habitat diversity (Fig. 2). A total of 30 sites were sampled, 22 in Lake Stechlin and 8 in Lake Haussee. Sites and species occurrences are described in COLLADO et al. (1999). After qualitative sampling, 14 representative sites among the 30 previously sampled were selected for quantitative sampling at regular intervals, 8 sites in Lake Stechlin and 6 sites in Lake Haussee. These quantitative samples are analyzed in this paper. Table 2 gives an overview of the characteristics of these sites. Sampling took place from August 1995 to July 1996. The sublittoral and profundal zones were sampled seasonally, in Lake Stechlin at sites 18, 19, 20, and 22, and in Lake Haussee at sites 6 and 7. Site 5 in Lake Haussee, lying at the border between littoral and sublittoral at 2 m depth, was sampled monthly (except from December 1995 to March 1996, due to ice covering); it was assigned to the sublittoral for the data analysis because of its different substrate type. The littoral sites were sampled monthly, in Lake Stechlin at sites 1, 5, 10, and 16 and in Lake Haussee at sites 1, 2 and 3 (Fig. 2).

From January to March 1996 a 20 cm thick ice layer had to be broken to get ahold of the samples.

Sampling at the shore line was performed with a Surber sampler (surface area 784 cm^2, mesh size 100 µm), samples in the sublittoral and profundal were taken with an Ekman grab (surface area 196 cm^2) and a Jenkins corer (surface area 19.6 cm^2), respectively. The samples were fixed in formalin (4%). After washing the samples, oligochaete worms were sorted under a stereomicroscope and preserved in 70% ethanol. They were identified to species level with a compound photomicroscope with Nomarski (interference contrast) optics.

Table 1. Limnological characteristics of Lake Stechlin and Lake Haussee in 1996 (KOSCHEL, unpublished)

Criteria	Lake Stechlin		Lake Stechlin		Lake Haussee		Lake Haussee	
	0–10 m depth		65 m depth		0–2.5 m depth		7.5 m depth	
	yearly mean	summer mean (May–September)	yearly mean	summer mean (May–September)	yearly mean	summer mean (May–September)	yearly mean	summer mean (May–September)
Secchi depth (in m)	8.4	7.9			2.6	1.9		
O_2 (in mg l^{-1})	11.5	11.2	8.5	8.6	9.0	9.6	2.3	0.1
O^2 (in %)	100	108	66	67	83	101	18	1
pH	8.3	8.5	7.7	7.6	8.1	8.6	7.3	7.1
Dissolved N (NO_3-N, NH_4-N) (in µg l^{-1})	47	30	147	86	273	88	1,358	1,733
Total-P (in µg l^{-1})	17	16	32	26	126	75	279	384
$CaCO_3$ (in µg l^{-1})	111	125	–	–	323	603	163	186
Chl a (phytoplankton) (in µg l^{-1})	2	1	–	–	13	15	–	–
Primary production (in g m^{-2} $year^{-1}$ C (phytoplankton)	111[1]	64[1]	–	–	220[2]	127[2]	–	–

[1]Yearly primary production from 0 to 25 m depth; [2]summer primary production from 0 to 5 m depth, May - September.

Table 2. Description of sampling sites in Lake Stechlin and Lake Haussee. Site numbers as in COLLADO et al. (1999).

	Site number	Depth	Sediment	Tree litter layer	Macrophytes	Exposure
Lake Stechlin						
Littoral	1	20–25 cm	sand, few stones	abundant	no	wind-exposed
	5	20–24 cm	organic mud	abundant	abundant, mainly *Phragmites australis*	sheltered
	10	20–30 cm	sand, stones	present	submerged macrophytes	sheltered
	16	surf shore	sand, pebbles	sparse	no	wind-exposed
Sublittoral	18, 19	5 m, 15 m	organic mud, rich in calcite, abundant mollusc shell debris	no	abundant, mainly *Chara*-species	–
Profundal	20, 22	30 m, 68 m	planktogeneous fine-gyttja, coprogeneously transformed, black-brown, oxygenated	no	no	–
Lake Haussee						
Littoral	1	20 cm	sand	abundant	emerged macrophytes (e.g. *Nuphar* sp.)	wind-exposed
	2	25 cm	sand, stones	very abundant	emerged, sparse	sheltered
	3 *	20–25 cm	sand, small pebbles, coated with algae	no	*Fontinalis* spp.	sheltered
Sublittoral	5	2 m	fine mud, mollusc shell debris	very abundant	no	–
Profundal	6, 7	5 m, 8 m	sapropel; strong smell of H_2S	sparse	no	–

* At 25 m distance to the outlet of Lake Haussee (canal), connecting it with Lake Breiter Luzin; continuous low-velocity water flow.

For each sample we recorded the types of substrate, differentiating between pebbles [PE], gravel [GR], coarse sand [CSA], fine sand [FSA], macrophytes [MA], plant debris [DE], and mud [MU]. Further, depth and exposure were noted (Table 2).

Data analysis

We analyzed the faunistic and environmental data by means of different multivariate techniques - Correspondence Analysis and Canonical Correspondence Analysis - using the CANOCO program Version 4.0 (TER BRAAK & SMILAUER 1998). Correspondence Analysis (CA) is an indirect gradient analysis, which only uses species data. It extracts from the species data the dominant pattern of variation in community composition, represented by one or more axes, assuming a unimodal response of the species data. These axes are interpreted with the help of external knowledge on environmental variables. Canonical Correspondence Analysis (CCA) (TER BRAAK 1986) is a multivariate analysis technique developed to relate community composition to known variation in the environment. It is a form of direct gradient analysis where a set of species is related directly to a set of environmental variables. The ordination axes are derived as linear combinations of environmental variables, and individual taxa are related to these axes assuming a unimodal response. The lengths of the arrows in the ordination diagram are proportional to the influence of these variables in species data variation.

The importance of the association between species and environment is expressed by the eigenvalues which measures how much variation in the species data is explained by the axes, and hence, by the environmental variables. The statistical significance of the canonical axes is assessed by the Monte Carlo permutation test (P value < 0.05).

Twelve out of the 14 quantitatively sampled sites were selected; sites 7 and 8 in the profundal of Lake Haussee were omitted because they were practically devoid of specimens. For the analyses carried out on quantitative species data at the site level, the numbers of individuals not identified to species level (i.e. immature tubificids with or without hair chaetae and immature lumbriculids) were proportionately assigned to the identified species with mature individuals. For the analyses carried out on quantitative species data at the sample level, the individuals not identified to species level were not considered. In all analyses the species abundance was log-transformed ($\ln(y+1)$).

The analyses that were included in this study are:

– A correspondence analysis (CA) applied to 12 sites and 34 species after omitting species present at only one or two sites. The analysis was carried out on qualitative data (presence/absence of species).

– Two correspondence analyses (CA) applied to the 7 littoral sites and 36 species after omitting the species only present in one station or with abundance lower than 8 in the second analysis. The first analysis was carried out on qualitative data (presence/absence of species), the second one included quantitative data (abundance of species).

– A canonical correspondence analysis (CCA) applied to 83 quantitative littoral samples and 30 species after omitting the species present in six samples or less. The parameters included as environmental variables were seasonality and substrate type, both as nominal variables.

– Two CCA analyses applied to the same 83 quantitative littoral samples, 30 species and environmental variables as above; but here seasonality and substrate type were treated separately from each other in two different analyses.

The species used in the data analysis are listed in Table 3.

Results

Species composition and dominance patterns

• **Lake Stechlin**

At the littoral sites, Naididae were the species richest family (22 species), but Tubificidae were dominant as to numbers of individuals; the 12 tubificid species found accounted for 71% of the collected specimens. The remaining 29% were distributed among 38 species. The six most abundant species were (in decreasing order): *Tubifex tubifex*, *Limnodrilus hoffmeisteri*, *Psammoryctides barbatus*, *Potamothrix hammoniensis*, *Bothrioneurum vejdovskyanum*, *Stylaria lacustris*. The sites differed considerably between each other: Sites 1 and 16, situated in the wind-exposed southwest basin of the lake, showed the highest species numbers of all littoral sites. At site 1 *Potamothrix hammoniensis* and *Limnodrilus hoffmeisteri* were most abundant; at site 16 Tubificidae and Naididae had about equal species numbers, but *Tubifex tubifex* accounted for about 50% of the specimens. It was fol-

Table 3. Overview of oligochaete species used in the data analysis. Ind.: total number of collected specimens; ST, HS: number of individuals collected in Lake Stechlin and Lake Haussee, respectively; Sites: number of sites where the species were present. +, *, ×: species included in the different analyses, +: CA, all 12 sites (Fig. 3); *: CA, littoral sites Fig. 4); x: CCAs, 83 littoral samples (Figs 5,6).

	Species	Codes	Ind.	ST	HS	Sites
	Lumbriculidae					
+ * ×	*Lumbriculus variegatus*	LUMVAR	80	28	52	7
+ * ×	*Stylodrilus heringianus*	STYHER	58	56	2	5
	Naididae					
+ * ×	*Chaetogaster diaphanus*	CHADPH	318	13	305	7
+ * ×	*Chaetogaster diastrophus*	CHADIA	110	52	58	11
+ * ×	*Dero digitata*	DERDIG	345	17	328	8
+ * ×	*Dero obtusa*	DEROBT	103	1	102	5
+ * ×	*Nais barbata*	NAIBAR	468	12	456	7
+ * ×	*Nais christinae*	NAICHR	25	5	20	5
+ * ×	*Nais communis*	NAICOM	24	6	18	7
+ * ×	*Nais pardalis*	NAIPAR	49	35	14	8
+ * ×	*Nais pseudobtusa*	NAIPSE	96	4	92	6
+ * ×	*Nais simplex*	NAISIM	28	1	27	4
+ * ×	*Nais variabilis*	NAIVAR	92	11	81	7
+ * ×	*Pristina aequiseta*	PRIAEQ	171	9	162	8
+ * ×	*Pristina longiseta*	PRILON	108	2	106	5
+ * ×	*Slavina appendiculata*	SLAAPP	11	5	6	4
+ * ×	*Stylaria lacustris*	STLLAC	858	140	718	10
+ * ×	*Uncinais uncinata*	UNCUNC	12	4	8	5
+	*Vejdovskyella intermedia*	VEJINT	52	52	0	4
	Tubificidae					
+ * ×	*Bothrioneurum vejdovskyanum*	BOTVEJ	536	149	387	8
*	*Limnodrilus claparedeanus*	LIMCLA	30	30	0	2
+ * ×	*Limnodrilus hoffmeisteri*	LIMHOF	743	292	451	8
+ * ×	*Limnodrilus udekemianus*	LIMUDE	56	21	35	6
+ *	*Potamothrix bavaricus*	POTBAV	110	67	43	4
+ * ×	*Potamothrix hammoniensis*	POTHAM	737	239	498	10
+ * ×	*Potamothrix heuscheri*	POTHEU	206	25	181	5
+ * ×	*Psammoryctides albicola*	PSAALB	75	2	73	3
+ * ×	*Psammoryctides barbatus*	PSABAR	174	155	19	5
* ×	*Psammoryctides deserticola*	PSADES	15	7	8	2
+ *	*Tubifex ignotus*	TUBIGN	9	9	0	3
+ * ×	*Tubifex tubifex*	TUBTUB	924	697	227	5
	Enchytraeidae					
+ * ×	*Cognettia cognettii*	COGCOG	18	11	7	4
+ * ×	*Cognettia glandulosa*	COGGLA	13	2	11	3
+ *	*Cognettia* sp.	COGSPE	16	12	4	4
*	*Lumbricillus fennicus*	LMBFEN	36	36	0	2
+ * ×	*Marionina riparia*	MARRIP	17	0	17	3
	Aeolosomatidae					
+ *	*Aeolosoma* spp.	AEOSPE	26	26	0	3

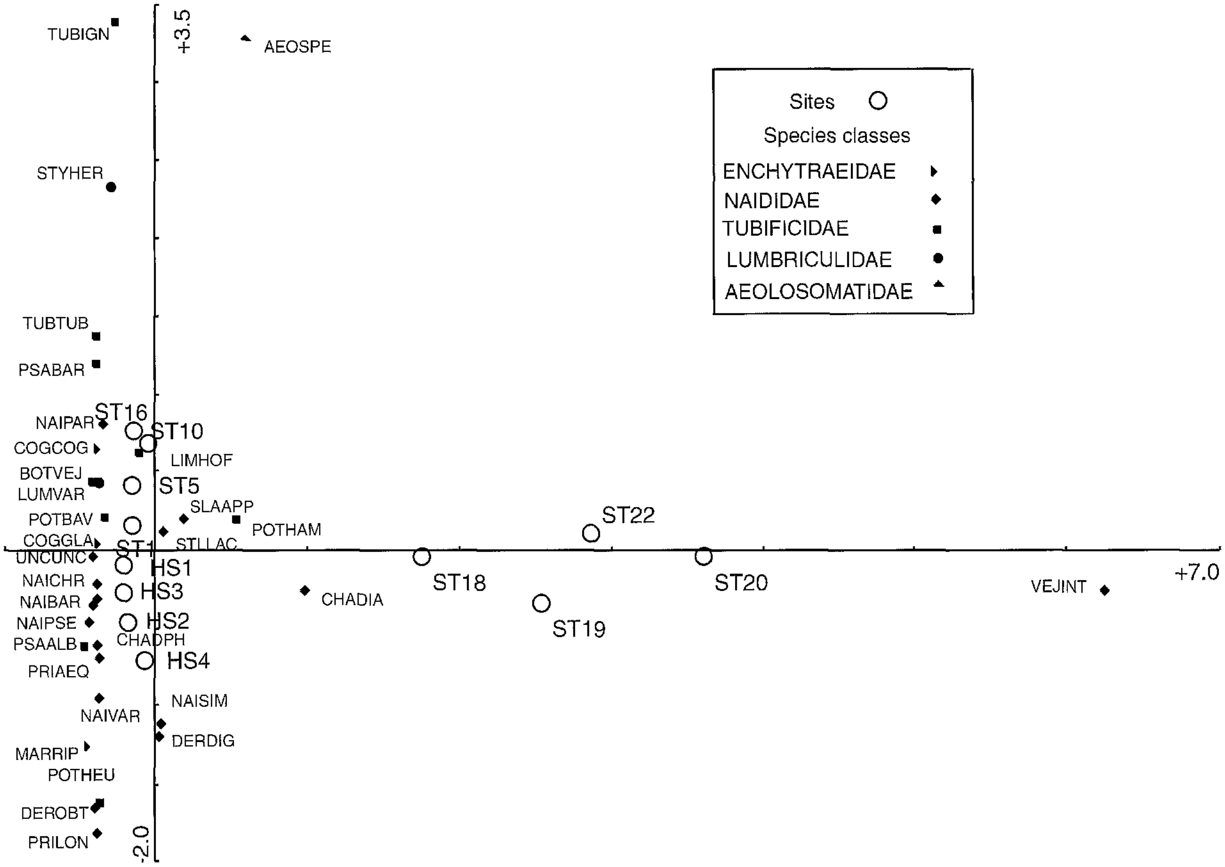

Fig. 3. CA diagram based on oligochaete species abundance at the 12 quantitatively sampled sites. For site locations see Fig. 2; HS: sites of Lake Haussee; ST: sites of Lake Stechlin; for species codes see Table 3.

lowed by *Psammoryctides barbatus*. At site 5 (*Phragmites*-mud, wind-sheltered) there were nearly exclusively Tubificidae. Most abundant species were *Bothrioneurum vejdovskyanum*, *Limnodrilus hoffmeisteri* and *Stylodrilus heringianus*. Station 10 (wind-sheltered, north basin) had lowest oligochaete densities and species numbers; here *Stylodrilus heringianus* was dominant, followed by *Bothrioneurum vejdovskyanum* and *Potamothrix bavaricus*.

In the sublittoral species numbers were low (9), Naididae were species-richest and clearly dominant. *Chaetogaster diastrophus*, *Vejdovskyella intermedia* and *Stylaria lacustris* were most abundant. There was little spatial and seasonal difference between sampling sites.

In the profundal, Naididae accounted for 72% of all collected specimens. Most abundant was *Vejdovskyella intermedia*, followed by *Amphichaeta leydigii* and *Potamothrix hammoniensis*. Again there was little spatial and seasonal difference between sampling sites.

• Lake Haussee

In the littoral, Naididae and Tubificidae had about the same percentage of individuals, representing 49% and 47%, respectively, of all annelids collected. Naididae were the species-richest family at all sites. The six most abundant species were (in decreasing order): *Stylaria lacustris*, *Potamothrix hammoniensis*, *Nais barbata*, *Limnodrilus hoffmeisteri*, *Bothrioneurum vejdovskyanum*, *Dero digitata*, *Chaetogaster diaphanus*. As in Lake Stechlin, the littoral sites differed considerably with respect to species dominance patterns. At the species-richest sampling point (site 3, 37 species), located at the mouth of a canal (Fig. 2) and with much submerged vegetation, Naididae were most abundant with *Stylaria lacustris*, *Nais barbata* and *Chaetogaster diaphanus* as dominating species (in decreasing order). There were also many tubificids, mainly *Bothrioneurum vejdovskyanum*, *Potamothrix hammoniensis* and *Limnodrilus hoffmeisteri*. At site 1 with sandy sediment, Tubificidae were dominant, especially *Tubifex tubifex* and *Potamothrix hammoniensis*, followed by the naidid species *Stylaria lacustris* and *Nais barbata*. At site 2, characterized by considerable accumulations of plant detritus, Naididae were dominant, with *Dero digitata* and *Pristina aequiseta* being most abundant. The sublittoral site (site 5), with muddy sediment, differed from the littoral sites in a lower species number (12) and a clear dominance of Tubificidae, especially *Potamothrix heuscheri* and *Potamothrix hammoniensis*. The profundal was practically devoid of species (see COLLADO et al. 1999).

Distribution patterns

• **General patterns of spatial distribution (CA analyses)**
The CA carried out with the quantitative data of the 12 sites shows a depth distribution of sites and species (Fig. 3). 60.6% of the species variance is explained by the first two axes. The first axis describes the depth gradient, from littoral (left, both lakes) over sublittoral (Lake Stechlin, sites 18, 19) to profundal (Lake Stechlin, sites 20, 22). *Vejdovskyella intermedia* (Fig. 3, right) is the only species that appears exclusively at sublittoral and profundal sites. The other species to the right of the vertical axis (*Chaetogaster diastrophus, Nais simplex, Dero digitata, Potamothrix hammoniensis, Stylaria lacustris, Slavina appendiculata*) occurred at all depths, all other species (to the left of axis 2) were restricted to the littoral. Note that the profundal sites of Lake Haussee were excluded from the analyses because almost no individuals had been found.

The two CAs that confine to the littoral sites explain a similar percentage of variance for the first two axes (Table 4). In both analyses (Figs. 4, 5), the sites of Lake Haussee are more similar to each other with respect to their oligochaete distribution than the sites of Lake Stechlin, i.e. the diversity of Lake Stechlin littoral sites is higher. In the CA with qualitative data (presence/absence of species), the sites of Lake Haussee and Lake Stechlin are not clearly separated from each other (Fig. 5). The CA with quantitative data (species abundance), however, shows a clear separation of sites according to their lake affiliation along the first axis (Fig. 4). The distribution of species along the first axis (Fig. 4), explaining 37% of data variance, reflects between-lake differences in abundance patterns of oligochaetes. On the family level, Tubificidae have a broad distribution, but they are the dominating family (as regards number of specimens) in Lake Stechlin. Lumbriculidae and Aeolosomatidae are characteristic of Lake Stechlin, whereas Naididae are more abundant in Lake Haussee. Enchytraeidae show similar abundances (though with different species) in both lakes. As to the species level, on the rightmost side of axis 1 (Fig. 4) appear species found only in Lake Stechlin: the tubificids *Tubifex ignotus* and *Limnodrilus claparedeanus*, the enchytraeid *Lumbicillus fennicus*, and various species of the

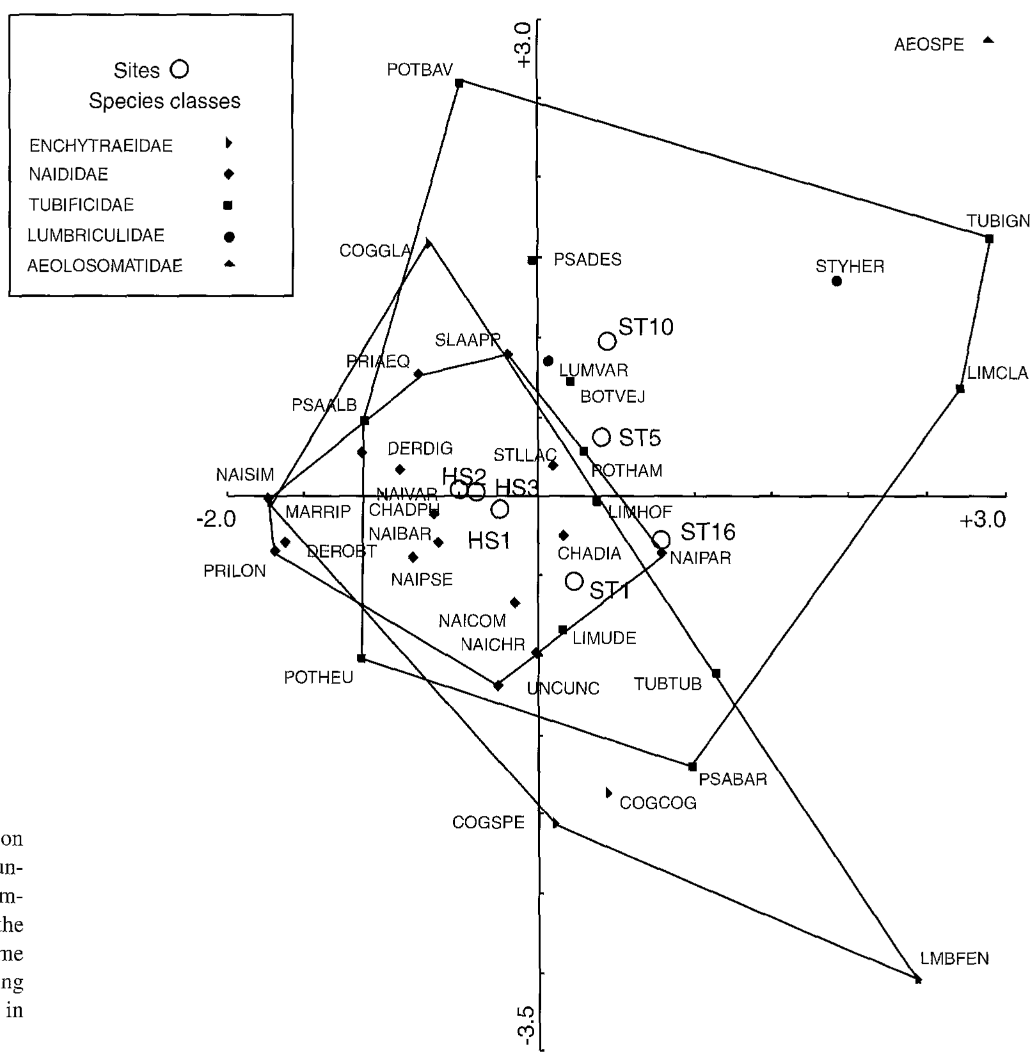

Fig. 4. CA diagram based on oligochaete species abundance at the 7 littoral sampling sites. Lines join the species showing the extreme values for each family, giving a picture of its distribution in the plot. Codes as in Fig. 3.

Table 4. Some statistical values from the correspondence (CA) and canonical correspondence (CCA) analyses carried out on species and environment data.

	CA quantitative all sites	CA quantitative littoral	CA qualitative littoral	CCA season + substrate	CCA season	CCA substrate
Eigenvalue (axis 1)	0.438	0.212	0.177	0.248	0.154	0.215
Eigenvalue (axis 2)	0.199	0.131	0.112	0.141	0.104	0.075
Species-environment correlations (axis 1)				0.819	0.726	0.765
Cumulative percentage variance						
of species data (first two axes)	60.6	59.9	60.7	11.6	7.7	8.6
of species-environment relation (axis 1)				32.2	49.0	42.7
of species-environment relation (axis 2)				50.6	83.4	57.6
Sum of all unconstrained eigenvalues	1.037	0.574	0.475	3.353	3.430	3.353
Sum of all canonical eigenvalues				0.770	0.308	0.503
P-value of Monte Carlo test				0.005	0.005	0.005

aphanoneuran genus *Aeolosoma*. Other characteristic species are *Stylodrilus heringianus* and *Psammoryctides barbatus*. Species situated on the left side of the plot, such as *Marionina riparia*, *Pristina longiseta*, *Nais simplex* and *Dero obtusa*, are most characteristic of Lake Haussee: *Marionina riparia* was only found in this lake; the others were also found in Lake Stechlin but in low numbers (Table 3).

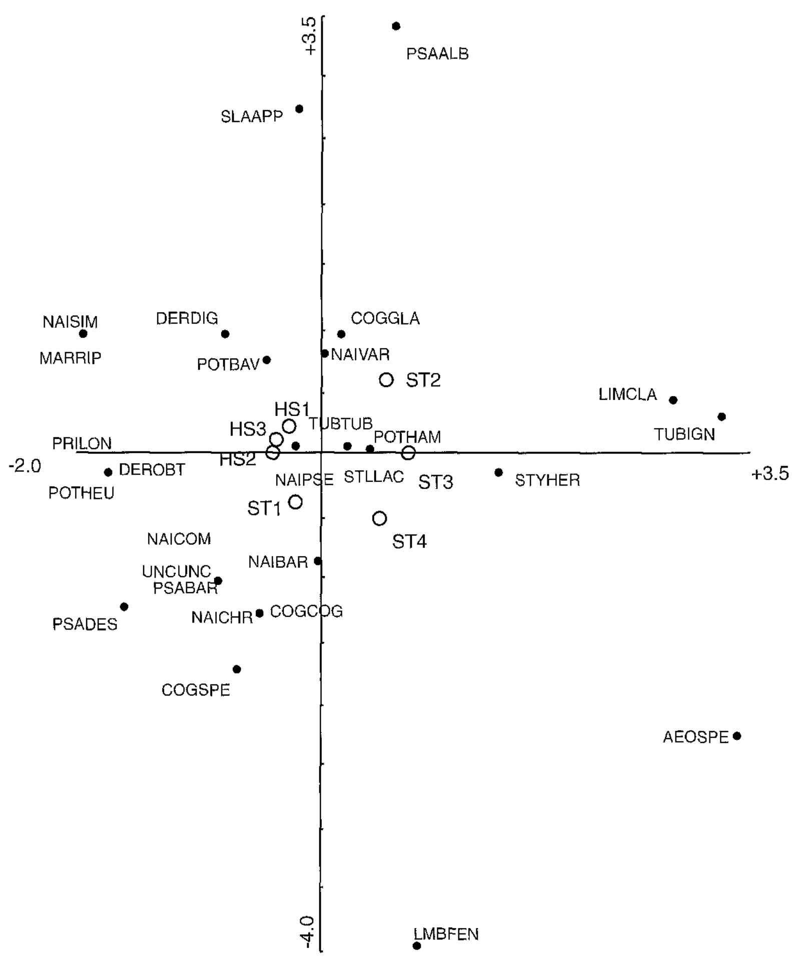

Fig. 5. CA diagram based on qualitative species data (presence/absence) at the 7 littoral sampling sites. Codes as in Fig. 3.

• Factors correlated with species abundance and distribution at the sample level (CCA analyses)

Fig. 6 shows the results of the CCA carried out on the 83 quantitative samples from the littoral sites, using as environmental variables seasonality and substrate, in order to evaluate their influence on the species distribution. The ordination diagram shows that the first two axes describe a seasonal gra-

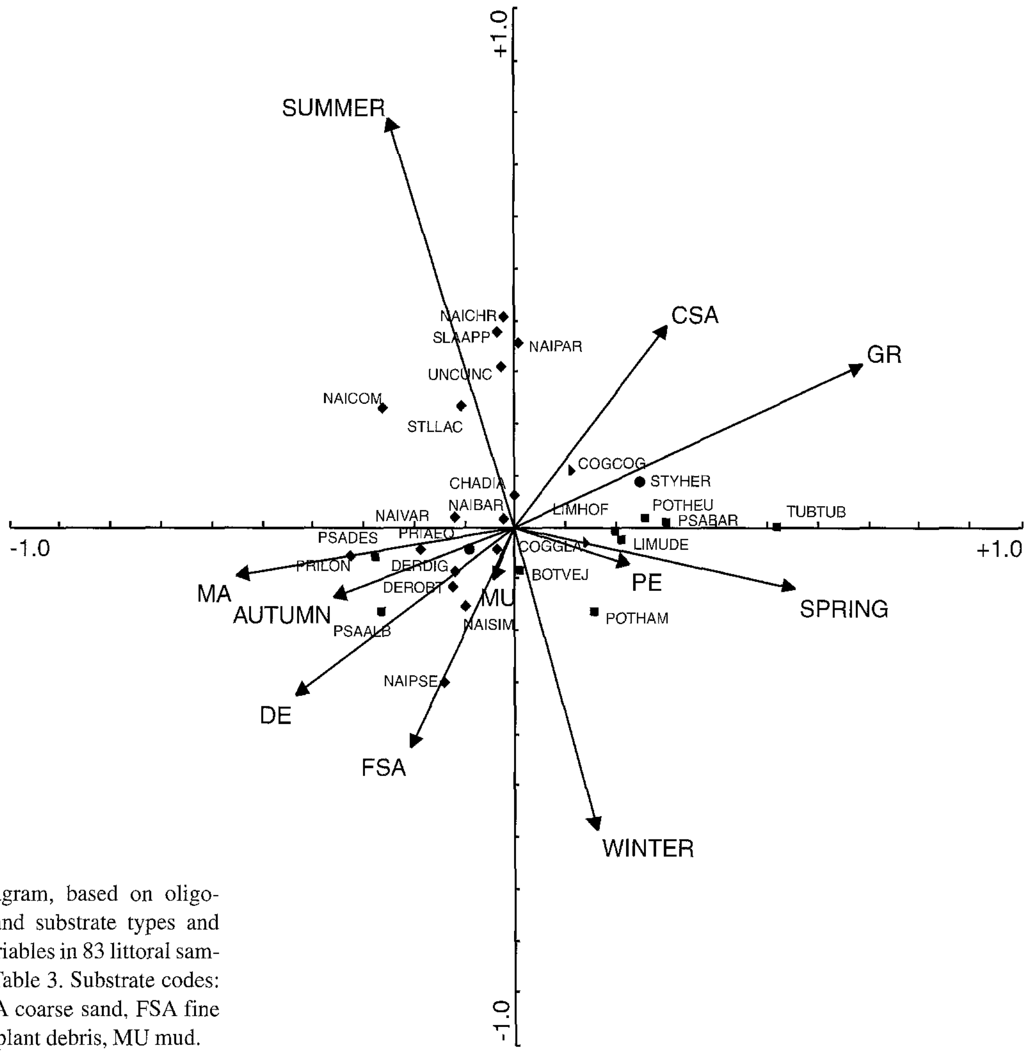

Fig. 6. CCA ordination diagram, based on oligochaete species abundance and substrate types and seasons as environmental variables in 83 littoral samples. For species codes see Table 3. Substrate codes: PE pebbles, GR gravel, CSA coarse sand, FSA fine sand, MA macrophytes, DE plant debris, MU mud.

dient and a juxtaposition of coarse-grained sediments (PE, GR, CSA) to plant material (DE, MA) plus fine-grained sediments with (MU) or without (FSA) organic material (50.6% of the variance in the species-environment relation). The parameters are significantly correlated with the distribution of the oligochaetes among the samples (Monte Carlo permutation test: $P = 0.005$). The dominant oligochaete families, Naididae and Tubificidae, show different seasonal patterns: Naidids are most abundant in summer and autumn while most of the tubificid species are more abundant in spring and some of them in winter.

To better distinguish between seasonal and substrate effects, both parameters were treated separately in two different CCA ordinations, using the same set of 83 littoral samples.

The CCA with seasonality as variable explains 83.6% of the variance in the species-environment relation for the first two axes, suggesting a close relation between season and species abundance. The results on the species distribution are similar to those of the first CCA (Fig. 6) and therefore not shown here.

The CCA with substrate as variable (Fig. 7) explains 57.6% of the variance in the species-environment relation for the first two axes. Along the first axis, large-grained mineral substrates are separated from the rest (fine-grained mineral substrate with or without organic material, plant material). Most clearly opposed are gravel (GR) and plant material (DE, MA). A further distinction appears along the second axis between fine sand (FSA) and mud, coarse sand and pebbles (MU, PE, CSA). Some species show clear correlations with specific substrate types: *Tubifex tubifex*, *Psammoryctides barbatus*, *Limnodrilus hoffmeisteri*, *Stylodrilus heringianus* and *Nais christinae* to coarse mineral substrates, *Lumbriculus variegatus*, *Marionina riparia*, *Cognettia glandulosa*, *Nais simplex* and *Nais communis* to vegetation and fine substrates with an organic component; *Slavina appendiculata* to mud. A faint correlation with fine sand devoid of organic particles appears for *Psammoryctides albicola*, *Nais pseudobtusa*, *Dero obtusa* and the interstitial species *Pristina longiseta* and *Uncinais uncinata*. *Bothrioneurum vejdovskyanum*, *Potamothrix hammoniensis*, *Dero digitata*, *Nais barbata*, *Chaetogaster diaphanus* and *Stylaria lacustris*

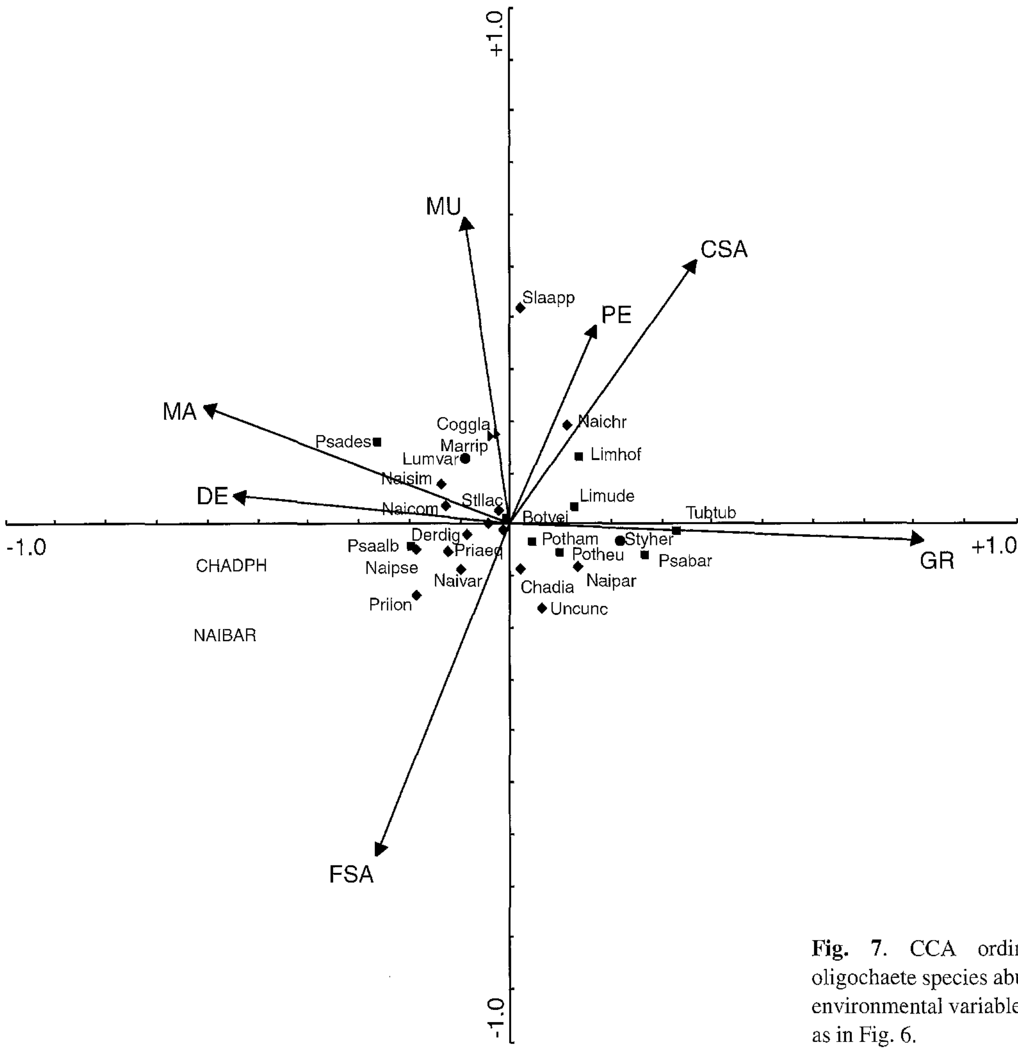

Fig. 7. CCA ordination diagram, based on oligochaete species abundance and substrate types as environmental variables in 83 littoral samples. Codes as in Fig. 6.

are at or near the center of the ordination and exhibit no clear correlation to a particular type of substrate.

The Monte Carlo permutation test ($P = 0.005$) indicated in both analyses a highly significant relationship between oligochaete communities and environmental factors.

Discussion

Regarding the profundal, the contrasting trophic degree of Lake Haussee and Lake Stechlin is evidently reflected by the assemblages of aquatic annelids, with a peculiar combination of species in the oligotrophic lake and an almost complete absence of oligochaetes (and any other kind of zoobenthos) in the eutrophic lake because of the long duration of summer anoxia.

In the littoral, however, there is only little reflection of the trophic degree. Species numbers of Oligochaeta, for example, are not much lower in the highly eutrophic Lake Haussee than in the oligotrophic Lake Stechlin. (Aphanoneura and a number of other species were not found in Lake Haussee; see Collado et al. (1999)). Furthermore, all species (with one exception, *Marionina riparia*) occurring in Lake Haussee were also found in Lake Stechlin. The CA carried out on presence/absence data of species at 7 littoral sites does not distinguish the sites of Lake Stechlin and Lake Haussee. The species-richest sites were found in the Lake Haussee littoral (32 species at site 1, 37 at site 3; the vicinity of site 3 to the outflow of the lake may account for parts of its diversity). The high species number found in Lake Haussee may be characteristic of Northern European eutrophic hardwater lakes in general. After a 10 years' study on the benthos of the eutrophic hardwater Lake Peipsi-Pikhva, Estonia, Timm et al. (1996) recorded 59 species of oligochaetes, most of them found in the littoral; regarding the high diversity they speak of a „mesotrophic“ expression. However, mere sampling effort may also play a role (Collado et al. 1999).

Only when abundance data are included in the CA does a lake-specific distinction of sites become evident. This may be the expression of a generally higher abundance of oligochaetes in the Lake Haussee littoral but also of differing dominance patterns on the species and family level. In Lake

Stechlin, Tubificidae are dominant even at sites with little accumulation of organic matter. This situation has already been described from other oligotrophic lakes. SÄRKKÄ (1982) reports a 40.5% dominance of *Limnodrilus hoffmeisteri* in the littoral of the oligotrophic Lake Könnevesi, Finland, and he concludes that the littoral is usually a more eutrophic environment than the profundal. The two most abundant tubificid species in Lake Stechlin littoral are *Tubifex tubifex* and *Psammoryctides barbatus*. The former (by far the dominant species, see Table 3) is known as a widespread colonizer of much different environments (MILBRINK 1980; LAFONT 1989), and the latter, according to MILBRINK (1980) and LANG & REYMOND (1989), inhabits non-contaminated sediments and indicates oligotrophy/mesotrophy. In Lake Haussee, the increase in abundance, compared to Lake Stechlin, is higher in the Naididae than in the Tubificidae. The most abundant species in the Lake Haussee littoral is phytophilous *Stylaria lacustris*. Still, the dominance patterns in the littoral of both lakes show some resemblance: *Limnodrilus hoffmeisteri*, *Potamothrix hammoniensis*, *Bothrioneurum vejdovskyanum* and *Stylaria lacustris* are in both lakes among the six most abundant species.

We conclude that the complex of factors determining the general trophic state of a lake is apparently of minor significance for the littoral oligochaete species assemblages. More striking than the between-lake differences are the between-site differences irrespective of their lake affiliation.

The analyses carried out to explain these differences by possible correlations with the environmental factors depth, season, and substrate, first show (Fig. 3) that depth-related differences override any heterogeneity existing in the littoral. Note that the sites in Fig. 3 were not coded for depth and that their arrangement along axis 1 is an expression of the oligochaete data. The following CCAs (Figs. 4, 5), confining to the littoral, demonstrate a strong correlation of spatial and temporal distribution patterns of oligochaetes with seasonality and substrate type.

Seasonality implies a complex of factors and one of its major manifestations in lakes is the succesion of stagnation and water circulation periods. Different periods mean different temperature, oxygen content, mineral and organic matter content, etc. Lake Haussee and Lake Stechlin are both dimictic with complete water circulation in spring and autumn (CASPER 1985). These periods provide a renovation of mineral elements and nutrients in the whole water body, followed in spring by an increase in primary production, including epiphyte growth (CASPER 1985; KAIRESALO 1984; MÜLLER 1994), a very important source of food for phytophilous species (MOORE 1979; KAIRESALO 1984; MÜLLER 1994; LÖHLEIN 1996); in autumn, lake turnover coincides with the increase of leaves from littoral trees and decayed macrophytes that provide abundant plant debris and detritus for the rest of the year, also a good substrate for periphyton settlement as well as bacteria development (McMURTRY et al. 1983; LAZIM & LEARNER 1987; MÜLLER 1994). Therefore, seasonal changes also imply important changes in the composition of the substrate, especially in terms of content and quality of organic matter. The results of these processes imply an increase of food resources for oligochaetes, most of which are detritivore or/and phytophilous. The Naididae, a family with many phytophilous species, show an increase in abundance especially in summer (Fig. 6), probably soon after algal bloom, delayed in 1996 by late ice-cover break. Their phytophilous character explains also their strong correlation with macrophytes and substrate with organic components. The Tubificidae, in turn, are mostly correlated with mineral substrate, in agreement with their detritivore nature (e.g. McMURTRY et al. 1983; LAZIM & LEARNER 1987; VERDONSCHOT 1999). Their greater abundance in spring might be correlated with a high detritus and bacteria production.

Thus, seasonality and substrate are clearly related factors. Depth, when described as a succesion of different substrate types, may also be a part of this complex. The significance of these factors for the distribution of oligochaetes in lakes may be explained in terms of variations in the type and quantity of food available in each habitat during the different periods of the year. To confirm these results, future research should focus on the quantitative analysis of the organic matter content of the substrate along the year and its variations, as well as on food quality and substrate granulometry.

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References

CASPER, S.J. (1985): Lake Stechlin - a temperate oligotrophic lake. Monographiae Biologicae **58**, Dr. W. Junk Publishers, Dordrecht, 550 pp.

CASPER, P. & KOSCHEL, R. (1995): Description of Lake Stechlin. Limnologica **25**: 281–284.

COLLADO, R., KASPRZAK, P. & SCHMELZ, R.M. (1999): Oligochaeta and Aphanoneura in two Northern German hardwater lakes of different trophic state. Hydrobiologia **406**: 143–148.

KAIRESALO, T. (1984): The seasonal succession of epiphytic communities within an *Equisetum fluviatile* L. stand in Lake Pääjärvi, southern Finland. Int. Revue ges. Hydrobiol. **69**: 475–505.

KASPRZAK, P., BENNDORF, J., KOSCHEL, R. & RECKNAGEL, F. (1988): Applicability of the food-web manipulation in the restoration program of a hypertrophic stratified lake: Model studies for Lake Hausseesee (Feldberg, GDR). Limnologica **19**: 87–95.

– KRIENITZ, L. & KOSCHEL, R. (1993): Changes in the Lake Feldberger Haussee (Germany, Mecklenburg-Vorpommern) in response to biomanipulation. Arch. Hydrobiol. **128**: 149–168.

KOSCHEL, R., CASPER, S.J., DOLGNER, W., FESTERSEN, O., KASPRZAK, P., KRAUSCH, H.-D., KREY, L., PÄCHNATZ, M., PENZ, E., PROFT, G. & RONNEBERGER, D. (1985): Das Feldberger Seengebiet. Ein Beitrag zum Schutz und zur optimalen Nutzung der Feldberger Seen. Natur und Umwelt Bez. Neubrandenburg **3**: 1–96.

– KASPRZAK, P., KRIENITZ, L. & RONNEBERGER, D. (1993): Long-term effects of reduced nutrient loading and food-web manipulation on plankton in a stratified Baltic hardwater lake (Lake Hausee, Germany, Feldberg). Verh. Internat. Verein. Limnol. **25**: 647–651.

KRIENITZ, L., KASPRZAK, P. & KOSCHEL, R. (1996): Long-term study on the influence of eutrophication, restoration and biomanipulation on the structure and development of phytoplankton communities in Feldberger Haussee (Baltic Lake District, Germany). Hydrobiologia **330**: 89–110.

LAFONT, M. (1989): Contribution à la gestion des eaux continentales: Utilisation des Oligochètes comme descripteurs de l'état biologique et du degré de pollution des eaux et des sédiments. Thèse d'Etat. Université Claude Bernard, Lyon.

LANG, C. (1989): Eutrophication of Lake Neuchâtel indicated by the oligochaete communities. Hydrobiologia **174**: 57–65.

– & REYMOND, O. (1996): Reversal of eutrophication in four Swiss lakes: evidence from oligochaete communities. Hydrobiologia **334**: 157–161.

LAZIM, M.N. & LEARNER, M.A. (1987): The influence of sediment composition and leaf litter on the distribution of tubificid worms (Oligochaeta). Oecologia (Berlin) **72**:131–136.

LÖHLEIN, B. (1996): Seasonal dynamics of aufwuchs Naididae (Oligochaeta) on *Phragmites australis* in a eutrophic lake. Hydrobiologia **334**: 115–123.

MCMURTRY, M.J., RAPPORT, D.J. & CHUA, K.E. (1983): Substrate selection of tubificid oligochaetes. Can. J. Fish. Aquat. Sci. **40** (10): 1639–1646.

MEHNER, T., KASPRZAK, P., WYSUYACK, K., LAUDE, U. & KOSCHEL, R. (2001): Restoration of a stratified lake (Feldberger Haussee, Germany) by a combination of nutrient load reduction and long-term biomanipulation. Internat. Rev. Hydrobiol. **86**: 253–265.

MILBRINK, G. (1980): Oligochaete communities in pollution biology: the european situation with special reference to lakes in Scandinavia. In: R.O. BRINKHURST & D.G. COOK (eds.), Aquatic oligochaete biology, pp. 433–455. Plenum Press, New York.

MOORE, J.W. (1979): Influence of food availability and other factors on the composition, structure and density on a subarctic population of benthic invertebrates. Hydrobiologia **62** (3): 215–223.

MOTHES, G. & PROFT, G. (1985): Sediments and sedimentation. In: S.J. CASPER (ed.), Lake Stechlin – a temperate oligotrophic lake. Monographiae Biologicae **58**, pp. 375–397. Dr. W. Junk Publishers, Dordrecht.

MÜLLER, U. (1994): Seasonal development of epiphytic algae on *Phragmites australis* (CAV.) TRIN. ex STEIN. in a eutrophic lake. Arch. Hydrobiol. **129**: 273–292.

PROFT, G. (1995): Die Sedimente der Seen des Stechlinseegebietes (Deutschland): Seetyp, Verteilung im Seebecken, Trophie und Chemismus. Limnologica **25**: 333–351.

RICHTER, W.M. & RICHTER, I. (1986): Zeittafel zur Entwicklung der Feldberger Seenlandschaft. Natur und Naturschutz in Mecklenburg, Greifswald-Waren **23**: 12–26.

SÄRKKÄ, J. (1982): On the ecology of littoral Oligochaeta of an oligotrophic Finnish lake. Holarctic Ecology **5**: 396–404.

– (1994): Lacustrine, profundal meiobenthic oligochaetes as indicators of trophy and organic loading. Hydrobiologia **278**: 231–241.

TER BRAAK, C.J.F. (1986): Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **67** (5): 1167–1179.

– & SMILAUER, P. (1998): CANOCO reference manual and user´s guide to Canoco for Windows. Software for Canonical Community Ordination (version 4). Centre for Biometry, Wageningen.

TIMM, T., KANGUR, K. & TIMM, V. (1996): Macrozoobenthos of Lake Peipsi-Pikhva: taxonomical composition, abundance, and their relation to some ecological parameters. Hydrobiologia **338**: 139–154.

VERDONSCHOT, P.F.M. (1999): Micro-distribution of oligochaetes in a soft-bottomed lowland stream (Elsbeek; The Netherlands). Hydrobiologia **406**: 149–163.

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