Combined influence of river discharge and wind on littoral nematode communities of a river mouth area of Lake Constance

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Abstract The littoral nematode community adjacent to a river mouth (River Schussen) on Lake Constance (Germany) was studied from February 1999 to January 2000 in order to determine the influence of stress resulting from fluctuations in river discharge on local nematode assemblages. Additionally, the influence of wind as a second important stress factor was considered. Six sample sites were chosen, reflecting a gradient of river influence within the broader river mouth area. Nematode communities, varying in a mean range from 121 to 165 ind/10 cm², were found to differ significantly in terms of abundance, feeding type composition and species diversity. Deposit feeders were most abundant at all sites followed by chewers. Deposit feeders were affected mainly by wind events, while

species diversity and the occurrence of chewers were influenced mainly by river discharge. The impact of both these stress factors was modified by a third variable, water level. Moderate and high levels of combined habitat stress led to significant changes in community structure. Under conditions of calm weather and low discharge, reduced species diversity and an increased predominance of deposit feeders were observed. In most cases, species diversity was found to be higher under moderate stress conditions, an observation that offers support for Connell's Intermediate Disturbance Hypothesis.

Keywords Habitat stress · Feeding types · Diversity · Spatial pattern · Temporal pattern · Disturbance

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Introduction

Nematodes are one of the most abundant taxa in freshwater benthic communities (Traunspurger 2000). Four of five multicellular animals are nematodes with estimated 10⁵ species (Coomans 2000). Freshwater nematode densities can reach up to 3.5 × 10⁶ individuals per m² (Traunspurger 2002). They play a major role in ecosystem processes like grazing on periphyton assemblages (bacteria, protists, algae, Montagna 1995). Working in terrestrial environments, Bongers (1990)

developed an environmental monitoring system by classifying nematode communities into colonizers and persisters. Today this Maturity Index (MI) is also used as bioindicator in aquatic benthic assessments (Bongers and Ferris 1999). Summing up, due to their abundance, species richness, ecology, functional morphology (with regard to feeding type), and short life cycles they are able to respond quickly to environmental change, making them ideal subject organisms for ecological studies (Platt and Warwick 1980; Giere 1993; Hakenkamp et al. 2002).

Seasonal and spatial distribution patterns of nematodes are well described for several lakes (Biró 1973; Holopainen and Paasivirta 1977; Prejs 1977b; Bretschko 1984; Strayer 1985; Prejs and Prejs 1992; Raspopov et al. 1996; Traunspurger 1996; Bergtold and Traunspurger 2004; Wu et al. 2004; Michiels and Traunspurger 2005b). However, studies dealing with the nematode communities of river mouth areas are rare (Nalepa and Quigley 1983). The area used for the current study can be described as lenticular aquatic-terrestrial ecotone, *sensu* Pieczynska (1990), coupling a water body and adjacent riparian system. Ecotonal habitats exhibit great heterogeneity with respect to abiotic and biotic factors due to the import of organic and inorganic components into the transition zone and offer opportunities to test important ecological concepts. River mouth areas represent zones of transition between rivers and pelagic habitats and function as river-lake interfaces. Among external physical factors influencing the littoral benthic community, wind forces are considered to be of strong importance due to generation of waves and consequent resuspension of sediment. In river-lake ecotones, the river discharge is presumed to play a significant further role in shaping the benthic community. In a previous study, we showed that wind and river discharge have a combined impact on the meiofaunal community of a river mouth ecotone, however the strength of both components was highly variable (Witthöft-Mühlmann et al. 2005a). In addition to causing direct mortality and relocation of organisms, disturbance (*sensu* Connell 1978) by these factors can alter habitat stability, food supply and inter- and intra-specific competition, and thus ultimately affect community

composition and species diversity (Petraitis et al. 1989; Death and Winterbourn 1995; Taniguchi and Tokeshi 2004). In the present study, six sample sites were investigated on a monthly basis over a one year-period within a river-lake-ecotone, thus covering a broad potential range of disturbance stress. We investigated the functional diversity of the nematode community in relation to the pattern of local disturbance and distinguished differences in feeding type compositions and species diversity. The following objectives were addressed in detail: (1) Does disturbance caused by wind and/or river discharge alter nematode communities of the river mouth ecotone? (2) Do “unstable” habitat conditions favour colonizers or affect feeding type composition? (3) Is species diversity increased under moderate habitat stress as predicted by the Intermediate Disturbance Hypothesis (Connell 1978)?

Material and methods

Study area

Lake Constance is the second largest lake in Central Europe (surface area: 571.5 km²; mean depth: 91 m, max. depth: 254 m, catchment area: 11,487 km², IGKB 1994) and is located on the northern fringe of the Alps (47°39' N). This study covers the river mouth of the River Schussen and the adjacent littoral area. The Schussen (discharge: 15.5 ± 0.15 m³/s (mean ± SE; Hydrological Services Agency Baden Württemberg); catchment area: 790 km², IGKB 1994) enters the lake on the northern shore and the river mouth is characterized by an extended littoral area (width: 1.2 km, slope: <0.2%). The inflow pattern of the river depends largely on the wind direction, wind speed, and discharge rate. Since the mean wind direction is south-westerly (German Weather Agency DWD), the main inflow angle of the Schussen River is toward the south-east. Based on this prevailing pattern, six sample sites were chosen, representing the area directly in contact with river discharge, an intermediate zone, and a far distant zone (Fig. 1). Further details are given in Witthöft-Mühlmann et al. (2005a).

Fig. 1 The littoral zone influenced by the Schussen River at Lake Constance (Germany). Characteristic features, prevailing annual wind direction, and sample sites are shown. Different zones are represented schematically. Sample sites **E1** **E3** are located within the transition zone of the river mouth, which is adjacent to the littoral area containing samples site **C**, which presumably experiences low influence of the river. Sample site **LB** lies on the border of the littoral and pelagic zones and sample site **R** is at the river mouth. The aerial view shows the ripples generated by wind action (**1**), river borne ditches (**2**), and patches of river borne dissolved and particulate matter (**4**). Dynamics of wind and river can lead to resuspension of the upper sediment layer (**3**). Two further important aspects are interactions (e.g., sediment import/export) with the pelagic zone (**5**) and seasonally changing water level (**6**). For further details, see Table 1 and the text. The aerial picture was reproduced with kind permission of the German Aerospace Centre

Habitat stress was assumed to be dependent on the strength of the river discharge and wind conditions. Both forces were categorized into classes of low (1), moderate (2), and high stress (3) (Table 1). Low habitat stress is characterized by reduced wave action and/or low river discharge. Moderate conditions mean higher wind

Table 1 Definition of habitat stress resulting from wind strength and river discharge, classified for the month preceding each sampling day

Force	Habitat stress class		
	Low	Moderate	High
Wind speed ≥ 7 m/s and duration ≥ 8 h	≤ 5 events	5 10 events	>10 events
River discharge	≤ 10 m ³ /s	10 20 m ³ /s	>20 m ³ /s

speeds and consequent higher waves that can cause the resuspension of sediments, and/or enhanced discharge. High habitat stress is typical of storms and/or high river discharge is characterized by strong sediment erosion and high deposition of river-borne seston. Habitat stress was calculated and classified for the month preceding each sampling day.

Sampling and processing

Sediment cores (surface area: 26.4 cm²) were taken from the study sites using a hand-held corer at monthly intervals from February 1999 through January 2000. Sampling of site **LB** commenced one month later. At each site, four replicate samples were taken randomly within a rough circle of diameter 8 m. In the laboratory, water overlying the sediment cores was carefully siphoned off, leaving the sediment surface undisturbed. Subsequently, cores were sliced in half longitudinally and photographed in order to document the various sediment layers. One half-core was then used for meiobenthic processing, while the second half-core was set aside for microbial and chemical analyses. Each half-core was divided into four layers at: 0–13, 14–23, 24–53, and 54–103 mm depth. Prior to chemical and microbial analysis, corresponding depth layers of all four replicate half-cores were pooled.

Meiobenthic fauna were extracted by means of a modified gravity gradient centrifugation technique after Pfannkuche and Thiel (1988) using Ludox AM 40TM (DuPont, Inc., Sigma-Aldrich Chemical Co.; colloidal silica, specific density: 1.21 g/cm³) and preserved in formaldehyde (4% final concentration). For counting purposes, each

processed sample was stained with 1% Rose-Bengal. Nematodes were classified into four feeding types: epistrate feeder, deposit feeder, suction feeders and chewers (Yeates et al. 1993; Trautspurger 1997).

Microbial, chemical, and granulometric analyses

A detailed description of the methods applied is given in Witthöft-Mühlmann et al. (2005a). Briefly, algal pigment composition was analysed using a modified HPLC technique after Schmid and Stich (1995). One gram fresh sediment was suspended in 3 ml filtered lake-water (0.45 µm, Schleicher & Schuell OE 67), again diluted 1:100 and then aliquots used for analyses. Bacteria were fixed in 4% formaldehyde, stained with diamidinophenylindole (DAPI), and then counted directly using epifluorescence microscopy. Total carbon was determined with an infrared analyzer (Leco CS 125) using 200–300 mg dry sediment. Organic carbon was measured after acidification with HCl. Inorganic carbon was calculated as the difference between total and organic carbon. Granulometry of the <63-µm fraction was conducted via Laser-particle sizing (Galai CIS-01; 100–200 mg DW); the >63-µm fraction was obtained by sequential sieving of the sample (6–10 g DW) through mesh sizes of >500-, 250–500-, 126–250-, and 64–125-µm.

Data analysis

Univariate diversity indices were calculated with the DIVERSE routine: species number S , species richness d (Margalef's index (Clifford and Stephenson 1975)), Shannon-Wiener-Index H' ($\log_e$) and Evenness J' . The disturbance/enrichment related MI was calculated according to Bongers (Bongers 1990; Bongers and Ferris 1999). ANOVA was used to test for differences in diversity index values and feeding type abundance between locations and with habitat stress parameters (wind direction and river discharge). Details are given in Table 3. Water level was included as a factor affecting the strength of habitat stress. Season was considered as random effect using the restricted residual maximum likelihood method to fit the

present models (Smyth and Verbyla 1996). Whenever model results were significant, Tukey's HSD post hoc test was applied to identify differing means (overall p -level 0.05). To fit assumptions for ANOVA, data were $\log + 1$ transformed. DIVERSE is a routine of the PRIMER software package V5.2.9 (Primer-E Ltd.). All other procedures were computed with JMP V5.0.1 (SAS Institute Inc.).

Results

Study sites conditions

River discharge and lake levels fluctuated considerably over the study period, and the site experienced a series of storms with wind speeds >7 m/s (Fig. 2). Increased river discharges often coincided with stormy periods in spring and winter, but not during summer and autumn. The study year had a long period of calm conditions from mid-July to mid-November, whereas the remaining months were marked by alternating periods of moderate and high habitat stress. Lake levels followed a seasonal pattern with strong seasonal fluctuations in water level at the sample sites (maximal range: 2.30 m; Table 2). At the site

Fig. 2 Schussen River discharge, lake level, and wind events from February 1999 until January 2000. Black line = lake level, grey shading = discharge, open dot s = hours with wind speed >7 m/s, black triangles = sampling days. L = low, M = moderate, and H = high discharge and wind strength respectively. Sources wind, lake level, and discharge data: German Weather Agency (DWD) & Environmental Protection Agency Baden Württemberg (LUBW)

Table 2 Main features of sample sites during the investigation period

Sites						
R	E1	E2	E3	LB	C	
River water contact	Continuous	Frequent	Flood event	Less frequent	Strong flood event	Scarce
Distance to river mouth (m)	100	930	865	1000	1120	2130
Depth (m)	0.88 ± 0.71	1.51 ± 0.65	1.47 ± 0.63	1.47 ± 0.65	2.40 ± 0.63	1.23 ± 0.61
Nematodes (Ind/10 cm ²)	128 ± 156	121 ± 81	133 ± 76	163 ± 68	138 ± 102	165 ± 141
Bacteria (cells/g DW)	4.60 × 10 ⁹ ± 4.28 × 10 ⁹	1.78 × 10 ⁹ ± 8.60 × 10 ⁸	1.64 × 10 ⁹ ± 1.14 × 10 ⁹	2.23 × 10 ⁹ ± 9.57 × 10 ⁸	1.66 × 10 ⁹ ± 7.75 × 10 ⁸	2.48 × 10 ⁹ ± 1.38 × 10 ⁹
Algal pigments (µg/g DW)	30.6 ± 26.6	19.2 ± 16.2	20.5 ± 8.4	30.8 ± 19.2	22.5 ± 9.9	43.1 ± 12.6
Organic carbon (%)	3.47 ± 2.88	0.62 ± 0.24	0.66 ± 0.30	0.92 ± 0.38	0.56 ± 0.14	0.88 ± 0.18
Grain size (µm)	170 ± 162	183 ± 106	166 ± 20	121 ± 13	163 ± 10	91 ± 8
Species number <i>S</i>	71	52	46	43	31	33
Species richness <i>d</i>	8.2 ± 6.1	8.1 ± 2.5	8.0 ± 2.8	7.9 ± 2.8	6.9 ± 2.1	7.4 ± 1.5
Shannon-Wiener <i>H'</i>	1.17 ± 0.82	1.51 ± 0.29	1.51 ± 0.35	1.52 ± 0.32	1.31 ± 0.41	1.53 ± 0.22
Evenness <i>J'</i>	0.56 ± 0.24	0.74 ± 0.08	0.75 ± 0.10	0.76 ± 0.09	0.70 ± 0.14	0.77 ± 0.06
Maturity Index, MI	2.20 ± 0.22	2.35 ± 0.20	2.40 ± 0.20	2.43 ± 0.23	2.25 ± 0.17	2.40 ± 0.17
Sample size (<i>n</i>)	35	43	43	43	39	41

Values are presented as mean ± standard deviation. For location of sample sites R, E1–E3, LB & C see Fig. 1.

nearest to the river mouth (site R) the mean organic carbon content was 3.8- to 7-fold (3.47%) and the mean bacteria concentration 1.9- to 2.7-fold higher (4.6×10^9 cells/g DW; $p < 0.0001$, Tukey's HSD) than those recorded at all other sites. Organic carbon levels varied significantly between sites (Table 3 a, b). Mean algal pigment concentration was 47–126% higher at the remote site C (43.1 µg/g DW). All sites are characterized as fine-sandy according to mean grain size. In general, the range and variability of all parameters was highest at site R (Table 2).

Nematode community pattern

Mean annual abundance of nematodes ranged from 121 ind/10 cm² (site E1) to 165 ind/10 cm² (site C; Table 2) and nematodes were the prevailing taxon of the meiobenthic community (49.2%, site C to 71.4%; site LB). Altogether 106 species were identified and recorded. Deposit feeders dominated at all sites in terms of abundance (58–81%) followed by chewers (12–35%) and epistrate feeders (3–11%). Suction feeders were rare (1–4%). The differences between sites were significant with respect to total nematode abundance and for abundance of epistrate feeders and chewers, but not for deposit feeders (Table 3). No site differed completely from the others. Table 4 summarizes the dominant species categorized according to feeding type.

Mean annual values for univariate diversity measures varied significantly between sites with exception of Margalef's species richness *d* (Table 3). The Shannon-Wiener diversity index *H'* was significantly lower at river mouth site R ($H' = 1.17$) than at sites E1–E3 and the remote site C ($H' = 1.51$ – 1.53). Species number *S* was highest at site R, but the community was characterized by just a few dominant species (Evenness $J' = 0.56$). Species richness and MI varied within a narrow range at all sites ($d = 6.8$ – 8.2 ; $MI = 2.2$ – 2.4). Seasonal variation in species diversity indices was strong with higher values in spring and lower values in autumn, with exception of site C where seasonality was less pronounced (Fig. 3). Margalef's species richness and the Shannon-Wiener-Index increased substantially in spring at the river mouth site R. No clear seasonality was

Table 3 ANOVA, model results; H' = Shannon Wiener Index, J' = Evenness, S = species number, d = species richness, MI = Maturity Index, C_{org} = organic carbon

Dependent variable	Global effect	Effect tests					
		Site	Water level	Wind	Discharge	Water level $\times$ wind	Water level $\times$ discharge
Nematodes	$r^2 = 0.33$; $F = 6.68$; $P < 0.0001$	$P = 0.0001$	$P = 0.059$	$P = 0.013$	$P = 0.59$	$P = 0.053$	$P = 0.011$
Epistrate feeders	$r^2 = 0.41$; $F = 9.29$; $P < 0.0001$	$P \leq 0.0001$	$P = 0.46$	$P = 0.28$	$P = 0.078$	$P = 0.88$	$P = 0.74$
Deposit feeders	$r^2 = 0.42$; $F = 9.69$; $P < 0.0001$	$P = 0.17$	$P = 0.09$	$P = 0.005$	$P = 0.055$	$P = 0.011$	$P = 0.009$
Chewers	$r^2 = 0.43$; $F = 10.04$; $P < 0.0001$	$P \leq 0.0001$	$P = 0.66$	$P = 0.39$	$P = 0.044$	$P = 0.38$	$P = 0.36$
H'	$r^2 = 0.50$; $F = 13.60$; $P < 0.0001$	$P \leq 0.0001$	$P = 0.40$	$P = 0.44$	$P = 0.03$	$P = 0.99$	$P = 0.66$
J'	$r^2 = 0.41$; $F = 9.21$; $P < 0.0001$	$P \leq 0.0001$	$P = 0.024$	$P = 0.41$	$P = 0.22$	$P = 0.33$	$P = 0.73$
S	$r^2 = 0.48$; $F = 12.22$; $P < 0.0001$	$P = 0.025$	$P = 0.11$	$P = 0.32$	$P = 0.028$	$P = 0.34$	$P = 0.84$
d	$r^2 = 0.42$; $F = 9.45$; $P < 0.0001$	$P = 0.09$	$P = 0.3$	$P = 0.5$	$P = 0.054$	$P = 0.04$	$P = 0.15$
MI	$r^2 = 0.55$; $F = 16.25$; $P < 0.0001$	$P \leq 0.0001$	$P = 0.98$	$P = 0.42$	$P \leq 0.0001$	$P = 0.032$	$P = 0.21$
C_{org}	$r^2 = 0.66$; $F = 27.16$; $P < 0.0001$	$P \leq 0.0001$	$P = 0.005$	$P \leq 0.0001$	$P = 0.011$	$P = 0.067$	$P = 0.06$

Italicized values indicate significant difference; $n = 243$ (number of samples)

Table 4 The relative abundance of the three most dominant species categorized according to feeding type, respectively

Feeding type	Dominant species	S	Relative density (% $\pm$ SD)
Epistrate feeders	<i>Ethmolaimus pratensis</i>	13	5.2 $\pm$ 7.7
	<i>Prodesmodora circulata</i>		0.35 $\pm$ 1.15
	<i>Chromadorita leuckarti</i>		0.16 $\pm$ 0.77
Deposit feeders	<i>Monhystera stagnalis/paludicola</i>	49	32.3 $\pm$ 21.8
	<i>Daptonema dubium</i>		28.4 $\pm$ 20.6
	<i>Eumonhystera filiformis</i>		1.17 $\pm$ 2.73
Chewers	<i>Tobrilus medius</i>	17	13.5 $\pm$ 12.0
	<i>Tobrilus gracilis</i>		5.1 $\pm$ 7.6
	<i>Tobrius stefanskii</i>		4.4 $\pm$ 5.0
Suction feeders	<i>Dorylaimus stagnalis</i>	27	0.55 $\pm$ 1.69
	<i>Mesodorylaimus spec.</i>		0.12 $\pm$ 0.57
	<i>Aporcelaimus spec.</i>		0.03 $\pm$ 0.23

S = number of found species, SD = standard deviation

evident in the MI, which decreased continuously at all sites until autumn, followed by a slight increase during winter.

Influence of water level, wind field and river discharge on the nematode communities

Wind events and water level affected the abundance of nematodes in general and of deposit feeders in particular. Abundances of both groups were lowest when habitat stress caused by wind

events was high (nematodes: low = 144 ± 95.9 , moderate = 165.3 ± 123 , high = 114.7 ± 101.7 ind./10 cm² $\pm$ SD; deposit feeders: low = 109.9 ± 77.7 , moderate = 111.6 ± 115.1 , high = 67.3 ± 61.2 ind./10 cm² $\pm$ SD) and increased with rising water level. Furthermore, water level had a significant influence on wind and discharge effects (Table 3). Conversely increasing river discharge increased the abundance of chewers (low = 24.7 ± 22.8 , moderate = 36.9 ± 28.6 , high = 46.2 ± 48.8 ind./10 cm² $\pm$ SD) but water

Fig. 3 Site specific diversity patterns. Cumulative relative abundance curves in dependence of low (circles), moderate (triangles) and high discharge (squares; comp. Fig. 2). X axis = $\log_{10}$ scale. Embedded graphs illustrate seasonal

change in species richness (d), Shannon Wiener Index (H') and Maturity Index (MI). Numbers in parentheses refer to number of species with increasing discharge (L; M; H). Bars = standard error ($n = 4$)

level or its interaction with habitat stress was not significant. The abundance of both feeding types differed significantly between low and moderate stress. The relative abundance of deposit feeders was highest when sites were

exposed to low river discharge and calm wind conditions or high stress resulting from high discharge and strong wind effects. The relative abundance of chewers increased when river discharge was high and wind events were moderate.

Table 5 Mean values of relative abundance of feeding types and Shannon Wiener diversity index (H') differentiated according to increasing wind and discharge stress

		Epistrate feeders (%)			Deposit feeders (%)			Chewers (%)			H'		
		L	M	H	L	M	H	L	M	H	L	M	H
Wind stress	H	/	10.0	4.0	/	50.2	71.5	/	37.2	23.9	/	1.64	1.24
	M	3.3	7.3	6.2	78.9	60.4	57.4	17.8	29.1	33.5	1.12	1.70	1.82
	L	1.6	2.6	13.5	84.2	76.4	42.5	13.8	20.7	41.2	1.13	1.09	1.86

L = low, M = moderate, and H = high stress (comp. Table 1). Grey gradient: 0 5% (white), 5 10%, 10 15%, 15 25%, 25 35%, 35 45%, 45 65%, >65% relative abundance; / = combination did not occur

Epistrate feeders showed a similar pattern to chewers (Table 5).

Diversity indices and MI differed significantly between sites and were strongly affected by river discharge but not by wind events. Species diversity increased with increasing river discharge (H' : low = 1.13 ± 0.34 , moderate = 1.54 ± 0.37 , high = 1.63 ± 0.46 ; S : low = 5.9 ± 1.7 , moderate = 8.2 ± 2.8 , high = 9.0 ± 4.0 ; MI: low = 2.18 ± 0.11 , moderate = 2.41 ± 0.21 , high = 2.43 ± 0.20). Evenness was significantly reduced by rising water levels when discharge was low. Interaction between water level and habitat stress played a minor role. Annual variation of Shannon-Wiener species diversity differed between sites. H' altered greatly at site R and at the remote site C least (Fig. 3). Cumulative dominance plots differed in dependence of discharge stress and revealed three groups of sites. Dominance was strongest at site R, where under low stress only one species accounted for 88% of the entire assemblage. This dominance fell to 45–50% under conditions of moderate and high stress. Dominance was weakest at the remote site C, where the influence of habitat stress was marginal. The remaining sites E1–E3 and LB represent an intermediate group, in which a few species were dominant under low stress conditions, but less so under moderate and high stress (Fig. 3). In all cases, species number was lowest when discharge was low and highest under moderate discharge. A combination of intermediate wind and discharge stress yielded significantly higher species diversity (H') ($p < 0.0001$, Tukey's HSD; Table 5).

Discussion

The study revealed that (1) the abundance of nematodes in general and deposit feeders in particular were influenced by the strength of wind events, (2) the overall diversity and abundance of chewers are mainly affected by discharge stress, (3) the benthic organic matrix, represented by organic carbon content, was influenced by both forces and (4) changing water levels modified the impact of both wind events and river discharge on the community.

General composition of nematode communities

With 106 species identified, the study area is one of the most species rich freshwater habitats studied thus far. Michiels and Traunspurger (2005a) described 152 species in the littoral area of Lake Obersee, but in most other studies of littoral habitats the number of species recorded is below 50 (Table 6). Species number was highest at the most heterogeneous site R, followed by sites E1–E3 and lower at the remote site C and the deeper site LB. Hence, species numbers decrease with decreasing influence of the river. Thus our sample sites are seen to provide an accurate representation the transition zone from the river to the lake. However, this pattern was not repeated by the pattern of Shannon-Wiener-species diversity, which indicated the greatest diversity in sites E1–E3 and the remote site C. The dominance of three species (*Daptonema*

Table 6 Compilation of diversity indices in shallow zones of lakes and estuaries with different trophy

Lake/Estuary	Trophy	Depth (m)	<i>S</i>	<i>H'</i>	MI	Authors
Char	Oligotrophic	<3	21	2.4 2.7		Prejs ^a
Zielony Gasienicowy	Oligotrophic	6 9	7 9	1.7 2.0		Prejs ^b
Konigssee	Oligotrophic	1 5	48 51	1.0 2.1		Traunspurger ^c
11 alpine lakes	Oligotrophic	<2	24 75	1.7 3.6		Michiels ^h
3 swedish lakes	Oligotrophic	<2	14 22	1.5 2.0		Peters ^j
Lake Constance	Oligo /mesotrophic	0.5 4.2	31 71, total: 106	1.2 1.5	2.2 2.4	This study
Zarnowieckie	Mesotrophic	<3	16	2.8		Prejs ^a
8 swedish lakes	Mesotrophic	<2	11 33	1.2 2.1		Peters ^j
Neusiedlersee	Thalassohyalin, meso/eutrophic	<3	26	0.1 2.0		Schiemer ^d
Obersee	Eutrophic	1	152			Michiels ⁱ
Czarna Kuta	Eutrophic	2.5 3.0	3	0.9 1.2		Prejs ^b
Donghu	Eutrophic	2.2	7 20	1.0 2.1	2.6 3.3	Wu ^e
Mikolajskie	Eutrophic	<3	52	2.3 2.4		Prejs ^a
Smolak	Eutrophic	4.5	2	0.30		Prejs ^b
6 swedish lakes	Eutrophic	<2	8 34	1.0 2.9		Peters ^j
Ems estuary	Eutrophic	Estuary			1.4 2.5	Essink ^f
Gironde Estuary	Eutrophic	Estuary			1.6	Soetart ^g

^a Prejs (1977a), ^b Prejs (1977b), ^c Traunspurger (1991), ^d Schiemer (1978), ^e Wu et al. (2004), ^f Essink and Keidel (1998), ^g Soetart et al. (1995), ^h Michiels and Traunspurger (2005a), ⁱ Michiels and Traunspurger (2004), ^j Peters (2005)

S, Species number; *H'*, Shannon Wiener Index, MI, Maturity Index. All *H'* values calculated as log base e. Values given in the studies of Schiemer and Peters have been transformed

dubium, *Monhystrera stagnalis/paludicola*, and *Tobrilus medius*) resulted in low evenness scores. The combination of high species numbers and dominance of only few species has previously been described as characteristic of lotic habitats (Beier and Traunspurger 2003). The MI, calculated as a measure of pollution was >2.0 at all sites, indicating comparatively low levels of pollution (Beier and Traunspurger 2003). The study revealed significant differences in feeding type composition between all sites with regard to epistrate feeders and chewers, but not to deposit feeders, which were well represented at all sites. This outcome may be indicative of the role of deposit feeders as colonizers, able to recover quickly after disturbance events in dynamic environments (Death and Winterbourn 1995).

Influence of wind effects and river discharge on nematode community structure

In a previous study at the same investigation site, we were able to show that deposition of river borne benthic particulate matter (rBPM) is a function of primary settlement of matter suspended in by river discharge, and subsequent

resuspension, resettlement and relocation of abiotic matter and organisms under the influence of wind events (Witthöft-Mühlmann et al. 2005a). The littoral area can switch within days or even hours from one set of more or less stable physical habitat conditions to another. The import of lotic species and relocation of littoral nematodes by the river may result in increased inter- and intra-specific competition between members of the *in situ* community and relocated organisms. The same mechanism can also influence resource allocation within the entire river mouth area, as observed in the case of organic carbon. However, we were unable to estimate the degree to which passive recruitment contributes to the species diversity observed.

The results of this study have refined our understanding of river-lake interfaces. Wind events were important with regard to abundance of nematodes and in particular to deposit feeders, whereas species measures and the occurrence of chewers were influenced mainly by river discharge. Water level influenced the benthic assemblages generally. The littoral area undergoes large diurnal and seasonal changes in temperature. However, previous analyses indicated that this

parameter played only a minor role as stress factor (Witthöft-Mühlmann et al. 2005a).

Disturbance is known to alter species diversity in benthic communities (Peterson 1996; Schratzberger and Warwick 1999; Tolonen et al. 2001). Decreasing evenness resulting from rising water levels led to a shift in the nematode community towards few deposit feeders like *Monhystera stagnalis/paludicola* and *Daptonema dubium*, both of which have relatively short life cycles. Annual mean nematode abundances were relatively similar at all sites investigated. However, periods of low habitat stress, with calm wind conditions and low discharge, were linked with greater nematode abundance, a strong dominance of deposit feeders and low species diversity. Deposit feeders comprise both selective and non-selective species, feeding on bacteria and unicellular eucaryotes. In this group, reproduction rates are high. The importance of habitat stability and, indirectly, of water level, was demonstrated by the results from the littoral border site LB. This site is located 1 m deeper than all the others, and was thus less prone to resuspension of sediment by wave action. Here, deposit feeders remained very abundant under any stress condition. Stable conditions may enhance reproductive fitness of deposit feeders and inter-specific competition may be increased, reducing species diversity and evenness. Conversely, species diversity and the proportions of chewers and epistrate feeders all increased under conditions of moderate and high stress, with river discharge as the major driving factor. In a previous microcosm experiment using river-borne benthic particulate matter of the Schussen, we could show that increased rBPM can have a suppressive effect, especially on chewers (Witthöft-Mühlmann et al. 2005b). Concentration of rBPM is higher when discharge is low. These field results support our previous experimental findings.

According to Allan (1995) and Tokeshi (1993), abiotic factors and physical disturbance can weaken biological interactions. However, the four month-long calm period encountered during the investigation may have allowed the communities to equilibrate and given colonizers like deposit feeders an advantage over persisters such as chewers. Death and Winterbourn (1995) found

maximum species richness at sites of greatest stability, and maximum evenness at sites of intermediate stability. They stressed that high species diversity can be maintained by habitat patchiness. The results of mesocosm experiments of Austen et al. (1998) were consistent with Intermediate Disturbance Hypothesis (Connell 1978) and the authors suggested that dominance of few species, as it is the case in our study, is important in maintaining regional diversity. Our results agree with this study, in that species diversity (H') and species number (S) were reduced when wind stress and discharge stress were either both low and both high. Conversely, any other combination of stresses may enhance habitat patchiness. Urban (2004) showed in a freshwater-pond study that coping with local environmental heterogeneity requires trade offs between adaptations that increase environmental tolerance and those that promote fitness within intense biotic interactions. Such trade offs will often regulate metacommunity dynamics. Our results provided hints that these trade offs might vary along a disturbance gradient such as that within a river-lake interface.

Conclusion

The results obtained describe the broader river mouth area as a very dynamic, relatively unpolluted benthic habitat, representing a transition from riverine to fully littoral habitat with no river influence. Within this ecotone, the composition of nematode feeding types differed significantly between sample sites with the most pronounced differences recorded for the site closest to the river mouth. Consideration of habitat stress classes has improved understanding of the processes involved in regulating the composition of nematode communities. Disturbance or stress resulting from wind and river discharge regulated habitat patchiness and thereby led to changes in community composition. The impacts of wind and discharge are in turn regulated by water level. Low stress led to greater nematode abundance, reduced species diversity, and an increased dominance of deposit feeders, thus colonizers were in favour under more stable habitat conditions. The

results support the Intermediate Disturbance Hypothesis.

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